

**THE USE OF CAMERA TRAPS AND SIGN SURVEYS TO INVESTIGATE A
PREDATOR ASSEMBLAGE AND ITS RESPONSE TO CARCASSES IN A
GRASSLAND BIOME ON TELPERION NATURE RESERVE, MPUMALANGA
PROVINCE, SOUTH AFRICA.**

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DECLARATION

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I declare that THE USE OF CAMERA TRAPS AND SIGN SURVEYS TO INVESTIGATE A PREDATOR ASSEMBLAGE AND ITS RESPONSE TO CARCASSES IN A GRASSLAND BIOME ON TELPERION NATURE RESERVE, MPUMALANGA PROVINCE, SOUTH AFRICA is my own work and that all the sources that I have used or quoted have been indicated and acknowledged by means of complete references, and that any use of Artificial Intelligence (AI) has been fully disclosed.

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DEDICATION

“Science can be a way of forming intimacy and respect with other species that is rivalled only by the observations of traditional knowledge holders. It can be a path to kinship.”

“Doing science with awe and humility is a powerful act of reciprocity with the more-than-human world.”

Robin Wall Kimmerer in Braiding Sweetgrass

This thesis is dedicated to our mother earth and all her myriad life forms, that we in our stupidity and apathy are driving to extinction, in the hope that in some small way, it may contribute to their conservation.

To Manana. The wild leopard I was privileged to know, who taught me everything.

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ABSTRACT

The effects of carrion on animal communities and ecological processes are poorly understood. Carcasses are valuable but short-lived resources and understanding how vertebrate scavengers interact with them and conversely, how carcass availability shapes predator communities, is essential for a deeper grasp of this ecosystem service. Such understanding is particularly important in transformed landscapes in the absence of apex predators. My study examines how decomposing adult male blue wildebeest (*Connochaetes taurinus*) carcasses affect predator and scavenger communities in the biodiverse but threatened Bankenveld grasslands of Telperion Nature Reserve, Mpumalanga, South Africa. Sign and camera trap surveys were implemented to study predator responses to three experimental treatments - open carcasses, caged carcasses and no carcasses (controls) - with five replicates each. Predator species diversity was reduced at both open and caged carcasses compared to controls. Occupancy models showed actively decaying carcasses lowered detection probability for most mesopredators, except for black-backed jackals (*Lupulella mesomelas*), whose detection increased. This suggests that many mesopredators who may be inclined to scavenge, exhibit a landscape of fear response proximate to carcasses, especially when jackal numbers are high. Carcass presence did not significantly affect jackal diel activity; however, jackals were significantly more active at open carcasses than caged carcasses or controls during periods when a low percentage of the lunar disc was visible. Their response (number of visits) to carcasses varied, influenced by proximity to dens, distance from human infrastructure and reserve boundaries, and local mammalian species richness. Furthermore, invertebrates attracted to the carcasses proved to be a valuable secondary resource that was heavily utilized by the jackals before they could access carrion. These findings demonstrate that the presence of carcasses significantly influenced the behaviour of predator assemblages within the surrounding landscape. Carcass ecology should therefore be carefully considered when managing and conserving predator assemblages, especially in small, protected areas and modified landscapes where predator assemblages are not intact.

Key Words: Predator assemblage, black-backed jackals, mesocarnivores, sign surveys, camera traps, resource pulses, carrion, species diversity, occupancy models, landscape of fear, diel activity, lunar phase.

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TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION.....	1
1.1. Overview of predator and scavenger conservation	1
1.2. Predator/Scavenger assemblage structure and function	4
1.3. Scavengers and scavenging within a predator assemblage	6
1.4. The landscape of fear	9
1.5. Carrion and its influence on predator behaviour.....	11
1.6. The ecology of carrion.....	13
1.7. Camera traps and sign surveys as research tools	15
1.8. Carnivore occupancy	18
1.9. Rationale	20
1.10. Study Aim and Objectives	21
1.11. Thesis Outline	22
 CHAPTER 2: STUDY AREA	 24
2.1. General	24
2.2. History	25
2.3. Vegetation.....	25
2.4. Hydrology.....	28
2.5. Climate	29
2.6. Geology and soils	29
2.7. Fauna	30
 CHAPTER 3: RESEARCH METHODOLOGY	 38
3.1. Research design	38
3.2. Data collection	38
3.2.1. <i>Camera trapping</i>	45
3.2.2. <i>Sign surveys</i>	47
 CHAPTER 4: DATA ANALYSIS.....	 56
4.1. A broad comparison of survey methods	56
4.1.1. <i>Species Detection</i>	56

4.1.2. Seasonality of species detections	56
4.1.3. Relative efficiency of each survey type.....	57
4.1.4. Latency to detection	57
4.1.5. Species accumulation curves.....	57
4.1.6. Cost-effort comparison of survey types	58
4.2. The effect of carrion on species diversity	58
4.2.1. Species Richness	58
4.2.2. Shannon-Weiner species diversity.....	59
4.2.3. Gini-Simpson Species Diversity	60
4.2.4. Rank abundance curves	61
4.3. The Impact of Fire.....	62
4.4. Carrion and the landscape of fear	62
4.4.1. Landscape of fear investigations from sign survey data	62
4.4.2. Landscape of fear investigations from camera traps	65
4.5. Carrion and predator occupancy.....	65
4.6. Predator presence and behaviour from camera traps	68
4.7. Jackal visitation frequency and duration.....	69
4.7.1. Jackal visitation frequency.....	69
4.7.2. Duration per visit at each treatment type.....	69
4.7.3. Seasonal variation in time spent per visit irrespective of treatment type.....	70
4.7.4. Seasonal variation in time spent per visit at each treatment type	70
4.7.5. Seasonal variation in time spent per visit at open carcasses.....	70
4.7.6. Jackal visits per day	70
4.7.7. Seasonal jackal visits per day for each treatment type.....	70
4.8. Carrion and jackal diel activity	71
4.9. Carrion, lunar phase and jackal activity	71
4.10. Carrion and jackal group size.....	72
4.11. Carrion and jackal vigilance behaviour	72
4.12. Jackal feeding behaviour	72
4.13. Variability in jackal response to available carrion.....	73
CHAPTER 5: RESULTS.....	78
5.1. A broad comparison of survey methods	78
5.1.1. Species detected.....	78
5.1.2. Seasonality of species detections	80

5.1.3. <i>Relative efficiency of each survey type</i>	82
5.1.4. <i>Latency to detection</i>	84
5.1.5. <i>Species accumulation curves</i>	86
5.1.6. <i>Cost comparison of survey types</i>	89
5.2. The effect of carrion on species diversity	89
5.2.1. <i>Species richness</i>	89
5.2.2. <i>Shannon-Weiner Species Diversity (H)</i>	91
5.2.3. <i>Gini-Simpson's Species Diversity (1 - D)</i>	92
5.2.4. <i>Rank Abundance Curves</i>	94
5.3. The impact of fire	96
5.3.1. <i>Shannon-Weiner species diversity</i>	96
5.3.2. <i>Gini-Simpson's Species Diversity</i>	97
5.4. Carrion and the landscape of fear	98
5.4.1. <i>landscape of fear investigations from sign survey data</i>	98
5.4.2. <i>Landscape of fear investigations from camera trap data</i>	103
5.5. Carrion and predator occupancy.....	106
5.6. Predator presence and behaviour from camera traps	109
5.7. Jackal visitation frequency and duration.....	110
5.7.1. <i>Jackal visitation frequency</i>	110
5.7.2. <i>Duration per visit at each treatment type</i>	112
5.7.3. <i>Seasonal variation in time spent per visit irrespective of treatment type</i>	113
5.7.5. <i>Seasonal variation in time spent per visit at open carcasses</i>	117
5.7.6. <i>Jackal visits per day</i>	118
5.7.7. <i>Seasonal jackal visits per day for each treatment type</i>	119
5.8. Carrion and jackal diel activity	122
5.9. Carrion, lunar phase and jackal activity	123
5.10. Carrion and jackal group size.....	126
5.10.1. <i>Jackal group size and lunar phase</i>	127
5.11. Carrion and jackal vigilance behaviour	128
5.12. Jackal feeding behaviour	130
5.13. Variability in jackal response to available carrion.....	131
 CHAPTER 6: DISCUSSION	 137
6.1. Overview	137
6.2. A broad comparison of survey methods	137

6.3. The effect of carcasses on species diversity	146
6.4. The impact of fire	147
6.5. Carrion and the landscape of fear	149
6.6. Carrion and predator occupancy.....	152
6.7. Jackal visitation duration and frequency.....	156
6.8. Carrion and jackal diel activity	157
6.9. Carrion, lunar phases and jackal activity	159
6.10. Carrion and jackal group size.....	160
6.11. Carrion and jackal vigilance behaviour	161
6.12. Jackal feeding behaviour	162
6.13. Variability in jackal response to available carrion.....	166
 CHAPTER 7: CONCLUSION AND RECOMMENDATIONS	170
7.1. Overview of study objectives and context	170
7.2. Summary of key findings.....	170
7.3. Methodological insights	171
7.4. Ecological and conservation implications	173
7.5. Future research directions.....	174
7.6. Recommendations for conservation management	177
7.7. Study limitations and final reflections.....	178
 REFERENCES.....	180
 APPENDIX	230

LIST OF FIGURES

CHAPTER 2

Figure 2.1: Location of Telperion Nature Reserve within the broader context of South Africa.....	24
Figure 2.2: Telperion Nature Reserve straddles the grassland and savanna biomes of Southern Africa.	26
Figure 2.3: Broad vegetation types of Telperion Nature Reserve. Adapted in QGIS from the South	26
Figure 2.4: Telperion Nature Reserve and Loskop Dam Nature Reserve to the Northeast are connected by the Wilge River, and its associated gorge which acts as an important wildlife corridor between the two protected areas.	28
Figure 2.5: The geological formations underlying Telperion Nature Reserve and surroundings, including adjoining Ezemvelo Nature Reserve. These formations are dominated by the Wilge River Formation with intrusions of Dwyka Group and Ecca Group formations. Adapted in QGIS from 1:250 000 Geological Map of 2528 Pretoria 1978. Council for Geoscience (2023).	30
Figure 2.6: Distribution of Cape Vulture (<i>Gyps coprotheres</i>) in Southern Africa with inset showing zoomed in perspective of Telperion Nature Reserve and closest pentads with confirmed observations (42 km away). Adapted in QGIS from SABAP 2 (2023a).	33
Figure 2.7: Distribution of Lappet-faced Vulture (<i>Torgos tracheliotos</i>) in Southern Africa with inset showing zoomed in perspective of Telperion Nature Reserve and closest pentads with confirmed observations (43 km away). Adapted in QGIS from SABAP 2 (2023b).....	34
Figure 2.8: Distribution of White-backed Vulture (<i>Gyps africanus</i>) in Southern Africa with inset showing zoomed in perspective of Telperion Nature Reserve and closest pentads with confirmed observations (62 km away). Adapted in QGIS from SABAP 2 (2023c).	35
Figure 2.9: Distribution of Hooded Vulture (<i>Necrosyrtes monachus</i>) in Southern Africa with inset showing zoomed in perspective of Telperion Nature Reserve and closest pentads with confirmed observations (186 km away). Adapted in QGIS from SABAP 2 (2023d).	36
Figure 2.10: Distribution of White-headed Vulture (<i>Trigonoceps occipitalis</i>) in Southern Africa with inset showing zoomed in perspective of Telperion Nature Reserve and closest pentads with confirmed observations (198 km away). Adapted in QGIS from SABAP 2 (2023e).	37

CHAPTER 3

- Figure 3.1:** Location of experimental sites and sign survey transects within Telperion Nature Reserve during the blue wildebeest (*Connochaetes taurinus*) decomposition study from January 2019 to February 2020.39
- Figure 3.2:** Control site used during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020. At control sites two camera traps were mounted on metal fence posts, but there were no blue wildebeest carcasses, grids or cages.40
- Figure 3.3:** Open site used during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020. At open sites two camera traps were mounted onto metal fence posts, and a blue wildebeest carcass was present and secured onto a metal grid for weighing purposes.....41
- Figure 3.4:** Caged site used during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion nature Reserve from January 2019 to February 2020. At caged sites two camera traps were mounted onto metal fence posts, and a blue wildebeest carcass was deployed inside an exclosure cage.....42
- Figure 3.5:** Weighing of open carcasses by attaching a weighing gantry to a metal grid of known weight (34.2 kg) on which the carcass was secured, during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020.44
- Figure 3.6:** Weighing of caged carcasses by attaching weighing gantry to cage of known weight (117 kg) during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020.45
- Figure 3.7:** A schematic representation of each road transect proximate to each of the 15 experimental sites on Telperion Nature Reserve during the blue wildebeest (*Chonochaetes taurinus*) decomposition project from January 2019 to January 2020)49
- Figure 3.8:** The roads, study sites, transects adjacent to experimental sites and low disturbance transects during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020.50

Figure 3.9: (a and b) Examples of 2 m x 2 m quadrats along a 1 km transect to assess black-backed jackal (*Lupulella mesomelas*) track density during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020.52

Figure 3.10: A 2 m x 2 m quadrat along a 1 km transect to assess black-backed jackal (*Lupulella mesomelas*) track density during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020. This quadrat clearly shows two sets of black-backed jackal tracks, one on either side of the road, likely indicating two animals moving straight through the quadrat without stopping.....53

Figure 3.11: A 2 m x 2 m quadrat along a 1 km transect to assess black-backed jackal (*Lupulella mesomelas*) track density during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature reserve from January 2019 to February 2020. This quadrat shows many sets of black-backed jackal tracks going in a number of different directions and also shows some indications of black-backed jackals lying down inside the quadrat (See Figure 3.12 for close up).54

Figure 3.12: A 2 m x 2 m quadrant along a 1 km transect to assess black-backed jackal (*Lupulella mesomelas*) track density during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020. This is a closer photo of the same quadrat in **Figure 3.11** and shows many sets of black-backed jackal tracks going in a number of different directions and also shows (red circles) some indications of black-backed jackals scratching the soil and lying down inside the quadrat.55

CHAPTER 5

Figure 5.1: Correlation matrices for the 17 carnivore species recorded during the study on Telperion Nature Reserve from January 2019 to January 2020. The plots depict relationships between transects with tracks of each species, number of camera trap images of each species, mean mass of each species and mean home range size of each species. Mean mass and home range size were as per Hunter (2020). X axes from left to right measure number of transects with tracks, number of images, and kilograms respectively. Y axes from bottom to top measure square kilometres, kilograms and number of images respectively.79

Figure 5.2: Number of species recorded per season for each survey type on Telperion Nature Reserve from January 2019 to January 2020. Pre-sampling represented sampling undertaken during summer immediately prior to the deployment of the blue wildebeest (*Connochaetes taurinus*) carcasses. “Summer of active decay” refers to the summer of 2019. “Summer” refers to summer of 2020.80

Figure 5.3: Number of species recorded each season per survey type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points (*grey dots*). Note: lack of whiskers in one direction on a box plot indicates that data is skewed in the opposite direction.81

Figure 5.4: Relative efficiency of camera trap surveys compared to sign surveys: means (*black squares*), medians (*dark horizontal lines*), individual data points (*grey dots*) and minimum and maximum range excluding outliers (*whiskers*) of the relative efficiency values for each of the sampling methods tested during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Missing whiskers indicate that data is skewed in the opposite direction to the missing whisker.....83

Figure 5.5: Latency to detection (LTD) per species for each of three survey types (camera traps of study sites 1 - 15, sign surveys of study sites 1 – 15, sign surveys of the entire reserve) during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020.....84

Figure 5.6: Mean latency to detection (LTD) in days of carnivore species for sign surveys and camera trap surveys during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020. Bars represent standard errors.85

Figure 5.7: Latency to Detection (LTD) (days) comparisons between sign surveys and camera trap surveys after carcass deployment for leopard (*Panthera pardus*), brown hyaena (*Parahyaena brunnea*), and black-backed jackal (*Lupulella mesomelas*) during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020. These results were from caged and open sites only. Bars are standard errors.86

Figure 5. 8: Species accumulation curves for all survey types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. **Panel a** contains collector’s curves for the different sampling methods. The dots are individual data points. The data were smoothed using the flexplot module in Jamovi (The Jamovi Project 2023) to create a locally estimated scatterplot smoothing (LOESS) curve. Lightly shaded areas around the lines represent standard errors. **Panel b** contains a rarefaction curve of sign survey data where the number of sampling units on the x axis refers to sampling days. Lightly shaded area around the line represents the standard error. **Panel c** contains a rarefaction curve of camera data where the number of sampling units on the x axis refers to sampling days. The lightly shaded area around the line represents the standard error. The curves in **panel b** and **panel c** were created using iNEXT online (Chao *et al.* 2016) software package.87

Figure 5.9: Seasonal species accumulation curves, comparing sign surveys to camera trap surveys during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Dots are individual data points. The data were smoothed using the flexplot module in Jamovi to create a locally estimated scatterplot smoothing (LOESS) curve. Shaded areas around the lines are standard errors.....88

Figure 5.10: Total species richness per treatment type from sign and camera surveys on during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 202090

Figure 5.11: Mean species richness per treatment type from sign and camera surveys during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside main box plot (*dots*). Note lack of whiskers in one direction on a box plot indicates that data is skewed in the opposite direction. The absence of a box for camera trap caged and control treatment types indicates that the middle 50% (Interquartile range) has zero spread, and most of the data points are clustered together.90

Figure 5.12: Shannon-Weiner predator species diversity (H) from sign surveys within 250m of experimental sites and camera trap surveys at experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*dots*). Absence of whiskers in one direction on a box plot means data is skewed in the opposite direction.91

Figure 5.13: Gini-Simpson's predator species diversity (D) from sign surveys within 250m of experimental sites and camera surveys of experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*dots*). Absence of whiskers in one direction on a box plot means data is skewed in the opposite direction.92

Figure 5.14: Mean species richness, Shannon-Weiner species diversity and Gini-Simpson's species diversity for all three treatment types for entire study period from 250m sign survey data during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.....93

Figure 5.15: Mean species richness, Shannon-Weiner species diversity and Gini-Simpson's species diversity for all three treatment types for entire study period from camera trap data during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.....94

Figure 5.16: Rank abundance curves of predator communities from sign surveys within 250m of experimental sites showing a shallow gradient for control sites and steeper gradients for open and caged carcass sites, indicating higher species evenness at controls during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.95

Figure 5.17: Rank abundance curves of predator communities from camera traps showing steep gradients for open and caged carcasses as well as control sites, indicating low species evenness at all sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.95

Figure 5.18: Shannon-Weiner predator species diversity (H) from sign surveys within 250 m of experimental sites as well as camera surveys, during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020 excluding fire affected site 6 as well as sites 5, and 9. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*dots*). Absence of whiskers from one side of a box plot indicates data is skewed in the opposite direction.....97

Figure 5.19: Gini-Simpson's predator species diversity ($1 - D$) from sign surveys within 250 m of experimental sites and camera trap surveys at experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020 excluding fire affected site 6 as well as sites 5, and 9. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*dots*). Box plot with missing whiskers in one direction indicate that data is skewed in the opposite direction.....98

Figure 5.20: Black-backed jackal (*Lupulella mesomelas*) track density between treatment types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*).99

Figure 5.21: Correlation matrix for the following variables mesopredator presence (Meso), number of mesopredator species' tracks present within 250 m (Meso250), number of mesopredator species' tracks present within 500 m (Meso500), black-backed jackal (*Lupulella mesomelas*) track density (JTD), leopard (*Panthera pardus*) tracks present (Leopard), brown hyaena (*Parahyaena brunnea*) tracks present (BHyaena) during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020..... 100

Figure 5.22: Estimated Marginal Means plots of mesocarnivore presence versus a) Black-backed jackal (*Lupulella mesomelas*) Track Density, b) Treatment Type and c) Season during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature reserve from January 2019 to January 2020. Line graph represents estimated marginal means for continuous data and grey polygon represents 95% confidence intervals. Dot plots represent estimated marginal means for nominal data with 95% confidence intervals. 102

Figure 5.23: Sensitivity vs specificity plot of most parsimonious model (model 2) to predict presence or absence of mesopredator tracks during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. The x axis represents the false positive rate (1 – specificity). The y axis represents the true positive rate (sensitivity). Note the cut off value was set at the intersection of the two lines at 0.41 as equal weight was given to sensitivity and to specificity as per (Habibzadeh *et al.* 2016)..... 103

Figure 5.24: Camera trap survey correlation plot of the number of black-backed jackal (*Lupulella mesomelas*) visits and the number of mesopredator visits at study sites for the entire study period from January 2019 to January 2020 during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve. 104

Figure 5.25: Seasonal associations between the number of black-backed jackal (*Lupulella mesomelas*) visits to all experimental sites and the number of mesopredator visits to all experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020 105

Figure 5.26: Predator visits to experimental sites during the period of active decay from camera trap data during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve. Black-backed jackal (*Lupulella mesomelas*) visits are presented on a separate axis to other predator visits were as black-backed jackal numbers far exceeded other predator numbers and thus a different scale was required. 106

Figure 5.27: Black-backed jackal (*Lupulella mesomelas*) visits to experimental sites associated with my blue wildebeest (*Connochaetes taurinus*) carcass decomposition study on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together. 110

Figure 5.28: Frequency of visits (0 – 233) by black-backed jackal (*Lupulella mesomelas*) to experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve presented as heatmaps, and relative to the broad vegetation types associated with each experimental site for the entire study period from January 2019 to January 2020. 111

Figure 5.29: Seasonal variation in the number of black-backed jackal (*Lupulella mesomelas*) visits to all experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together. 112

Figure 5.30: Black-backed jackal (*Lupulella mesomelas*) time spent per visit from camera trap videos for each treatment type for the entire study period during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together. 113

Figure 5.31: Black-backed jackal (*Lupulella mesomelas*) time spent per visit irrespective of treatment type from camera trap videos for each season for the entire study period during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together. 114

Figure 5.32: Seasonal variation in time spent per visit by black-backed jackals (*Lupulella mesomelas*) at each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together. 116

Figure 5.33: Time spent per visit by black-backed jackals (*Lupulella mesomelas*) at open carcasses for each season during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together. 117

Figure 5.34: Number of black-backed jackal (*Lupulella mesomelas*) visits per day for each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together. 119

Figure 5.35: Number of black-backed jackal (*Lupulella mesomelas*) visits per day at each treatment type for each season of sampling during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together. 121

Figure 5.36: Density plots created using kernel density estimation showing black-backed jackal (*Lupulella mesomelas*) diel activity over 24 hours for each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve for the entire study period from January 2019 to January 2020. Time was converted to decimal hours for these analyses. The X axis represents the time of day with zero being midnight. The Y axis represents number of visits and density plots were created using kernel density estimation in Jamovi..... 122

Figure 5.37: Density plots showing black-backed jackal (*Lupullela mesomelas*) visits to experimental treatments relative to the proportion (%) of the lunar disc visible during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve for the entire study period from January 2019 to January 2020. The Y axis represents number of visits and density plots were created using kernel density estimation in Jamovi. 123

Figure 5.38: Density plots showing black-backed jackal (*Lupullela mesomelas*) records from camera traps relative to the proportion (%) of the lunar disc visible for each season during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve for the entire study period from January 2019 to January 2020. The Y axis represents number of visits and density plots were created using kernel density estimation in Jamovi. 124

Figure 5.39: The number of black-backed jackals (*Lupullela mesomelas*) present per visit at each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve for the entire study period from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together. 126

Figure 5.40: Correlation of the number of black-backed jackals (*Lupullela mesomelas*) per visit and the proportion (%) of the lunar disc visible at the time of the visit for all visits to experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve during the entire study period from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). 127

Figure 5.41: Success of black-backed jackal (*Lupullela mesomelas*) accessing carrion from blue wildebeest (*Connochaetes taurinus*) carcasses as well as feeding on invertebrates associated with the carcasses during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Bars are standard errors. 130

Figure 5.42: Density plots of the time since deployment of blue wildebeest (*Connochaetes taurinus*) carcasses vs number of videos where black-backed jackals (*Lupulella mesomelas*) fed on invertebrates vs videos when they fed successfully on carrion from the blue wildebeest (*Connochaetes taurinus*) carcasses during my study on the influence of decomposing blue wildebeest carcasses on predators on Telperion Nature Reserve during the period of active decay. 131

Figure 5.43: Effect of season on number of black-backed jackal (*Lupullela mesomelas*) visits to blue wildebeest (*Connochaetes taurinus*) carcasses for the three different treatment types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Red dots represent the predicted number of jackal visits from the best supported model in Table 5.20. Vertical bars represent standard errors. 133

Figure 5.44: Effect of the presence of subadult jackals on number of black-backed jackal (*Lupullela mesomelas*) visits to blue wildebeest (*Connochaetes taurinus*) carcasses for the three different experimental treatment types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Red dots represent the predicted number of jackal visits from the best supported model in Table 5.20. Vertical bars represent standard errors. 134

Figure 5. 45: Effect of the total species richness (all mammals excluding jackals) on number of black-backed jackal (*Lupullela mesomelas*) visits to blue wildebeest (*Connochaetes taurinus*) carcasses for the three different experimental treatment types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. The blue lines represent the predicted change in jackal visits with increasing total species richness. Grey ribbons represent standard errors around the fixed effects. 135

Figure 5.46: Effect of the interaction between distance to nearest infrastructure (km) and distance to reserve boundary (km) on number of black-backed jackal (*Lupullela mesomelas*) visits to blue wildebeest (*Connochaetes taurinus*) carcasses for the three different treatment types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. The light grey lines are ghost lines indicating the effect on each treatment type separately. The top ghost line is treatment type ‘open carcasses’, the middle ghost line is treatment type ‘control’ and the lowest ghost line is treatment type ‘caged carcasses’. The grey ribbons represent standard errors. 136

LIST OF TABLES

CHAPTER 2

Table 2.1: Predator species recorded on Telperion Nature Reserve prior to my study (including the most recent (2025) IUCN Red List Status. Vulnerable and Near Threatened species are indicated in bold.....31

CHAPTER 5

Table 5.1: Carnivore species detected using sign surveys and camera traps on Telperion Nature Reserve from January 2019 to January 2020.78

Table 5.2: Species richness and relative efficiency (number of species detected at each site by a single method/total number of species recorded at each site by combining both methods) of the two methods at each experimental site sampled during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. The higher the relative efficiency value, the more efficient that survey type was at detecting species.....82

Table 5.3: Cost comparisons of camera trap and sign survey studies during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020.89

Table 5.7: Predictive measures classification for the most parsimonious model (model 2) to predict presence or absence of mesopredator tracks during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.103

Table 5.8: Kendall's TauB and Spearman's correlation coefficients for the relationship between number of black-backed jackal (*Lupulella mesomelas*) visits and number of mesopredator visits for each season at all experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.....105

Table 5.9: Outcomes of single season occupancy models for each species from sign surveys conducted during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators at Telperion Nature Reserve from January 2019 to January 2020. ψ is occupancy and ρ is detection probability. The covariates Habitat, Carcass Presence and Human Disturbance were used to construct various models for each species and the best models for each species are presented here. ΔAIC is the difference in Akaike Information Criterion between the best model and the null model [$\psi(.)\rho(.)$] for each species. Models with $\Delta AIC > 2$ are strongly supported. X^2 is the test statistic from a likelihood ratio test. The top ranked model was a significantly better fit than the null model except where $p > 0.05$, for civet (*Civettictis civetta*), caracal (*Caracal caracal*) and black-footed cat (*Felis nigripes*). For these species the sample numbers were < 30 and this would have affected statistical significance. Honey badger (*Mellivora capensis*) and Cape clawless otter (*Aonyx capensis*) have no p values as the null model was the best fit..... 108

Table 5.10: Behavioural summary for all predator species at experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators for the entire study period from January 2019 to January 2020 on Telperion Nature Reserve. 109

Table 5.11: Outcomes from Dwass-Steel-Critchlow-Fligner pairwise comparisons of time spent by black-backed jackals (*Lupulella mesomelas*) per visit per season at all treatment types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020..... 114

Table 5.12: Outcomes from Kruskal-Wallis ANOVA and Dwass-Steel-Critchlow-Fligner Pairwise Comparisons for the time spent per visit by black-backed jackals (*Lupulella mesomelas*) at each treatment type for each season during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020..... 115

Table 5.13: Outcomes from Dwass-Steel-Critchlow-Fligner pairwise comparisons for time (number of videos per visit multiplied by 15 seconds) spent per black-backed jackal (*Lupulella mesomelas*) visit at open carcasses for each season from January 2019 to January 2020 on Telperion Nature Reserve. 118

Table 5.14: Outcomes from Kruskal-Wallis ANOVA and Dwass-Steel-Critchlow-Fligner pairwise comparisons for the number of visits by black-backed jackals (*Lupulella mesomelas*) at each treatment type for each season during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020..... 120

Table 5.15: Outcomes of Dwass-Steel-Critchlow-Fligner pairwise comparisons for black-backed jackal (*Lupullela mesomelas*) activity relative to proportion of the lunar disc visible per season over the study period from January 2019 to January 2020 during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve..... 125

Table 5.16: Correlation of number of black-backed jackals (*Lupullela mesomelas*) at each visit and proportion of the lunar disc visible at the time of the visit for all visits during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve during the entire study period January 2019 to January 2020). 128

Table 5.17: Video clips with black-backed jackals (*Lupullela mesomelas*) visits to each treatment type, total number of videos where jackal exhibited vigilance behaviour for each treatment type and the percentage of videos with vigilance behaviour for each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature reserve from January 2019 to January 2020. 128

Table 5.18: Contingency table for *Chi-square* test of independence (X^2) to determine whether the observed instances of black-backed jackal (*Lupullela mesomelas*) vigilance behaviour was significantly different to expected vigilance behaviour for each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. 129

Table 5.19: Outcomes from Pearson’s residuals and Adjusted Standardised residuals *post-hoc* test for X^2 test of independence to determine whether the observed instances of black-backed jackal (*Lupullela mesomelas*) vigilance behaviour was significantly different to expected vigilance behaviour for each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020..... 129

Table 5.20: Outcomes from the Generalized Linear Mixed Models constructed to evaluate the variability of black-backed jackal (*Lupulella mesomelas*) visits to experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Null model was modelled first, with covariates added sequentially for comparison to the null model. ‘**JackVis**’ = Seasonal Jackal Visits, ‘**SubadJack**’ = Seasonal Site Subadult Jackal Presence, ‘**DistInfra**’ = Distance to Nearest Human Infrastructure, ‘**DistBound**’ = Distance to Nearest Reserve Boundary, ‘**SpRich**’ = Total Site Species Richness excluding Jackals, ‘Treatment Type’ = Treatment Type, ‘Season’ = Season 132

Table 5.21: Outcomes from the Fixed Effects Omnibus Tests for the top ranked model to explain variability of black-backed jackal (<i>Lupullela mesomelas</i>) visits to experimental sites on during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators Telperion Nature Reserve from January 2019 to January 2020.	136
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LIST OF APPENDICES

Appendix 1: Carcass mass and shoulder heights of the 10 Blue Wildebeest (<i>Connochaetes taurinus</i>) carcasses used in my study on the influence of decomposing blue wildebeest carcasses on predators on Telperion Nature Reserve from January 2019 to February 2020.	230
Appendix 2: The number of transects with tracks for each species, number of camera trap images of each species, mean mass of each species in kilograms and mean home range size of each species in km ² during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators on Telperion Nature Reserve from January 2019 to February 2020.....	230
Appendix 3: Global Positioning System (GPS) locations for the start and finish points of each site transect during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators on Telperion Nature Reserve from January 2019 to February 2020.....	231
Appendix 4: The Global positioning System (GPS) locations for the start and finish of the transects in low disturbance areas during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.....	232
Appendix 5: The Global Positioning System (GPS) locations of 2 x 2 m quadrats used to count black-backed jackal (<i>Lupulella mesomelas</i>) tracks at each study site as well as the distance in metres that the quadrats were away from the camera array at each site during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators...	232
Appendix 6: Outcomes from Shapiro Wilk tests for normality of data before choosing appropriate analyses based on whether data was parametric or non-parametric for all statistical analyses of data collected on Telperion nature Reserve during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020.	233
Appendix 7: The total number of jackal visits (from video and still cameras) per site, treatment type and season for the entire study period during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020 on Telperion Nature Reserve.....	234
Appendix 8: The total number of jackal visits (video cameras only) per site, treatment type and season during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators for the entire study period from January 2019 to January 2020 on Telperion Nature Reserve.....	234
Appendix 9: (a – ff) Photo records of tracks of all species recorded in the sign surveys during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.....	235
Appendix 10: (a – m) Photographic evidence of all predator species recorded on camera traps during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.	251

Appendix 11: Correlation Matrix for the 17 carnivore species recorded during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators, depicting relationships between: transects with tracks of each species, number of camera trap images of each species, mean mass of each species and mean home range sizes of each species on Telperion Nature Reserve from January 2019 to January 2020.....	264
Appendix 12: Total and seasonal records of all species from both sign and camera surveys conducted on Telperion during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020.	265
Appendix 13: Outcomes from Dwass-Steel-Critchlow-Fligner pairwise comparisons of days to detection results of the different survey types conducted on Telperion during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020.....	266
Appendix 14: Asymptotic analysis of rarefaction curves for species accumulation data collected during sign surveys on Telperion Nature Reserve from January 2019 to January 2020. Order.q refers to the mathematical order of Hill numbers with $q = 0$ representing species richness, $q = 1$ representing Shannon Diversity and $q = 2$, representing Simpson Diversity. Empirical refers to observed data collected, Estimate refers to extrapolated data. Comparing Empirical Species Richness to Extrapolated Species Richness ($q = 0$) allows one to determine if an asymptote has been reached and if sampling is sufficient.	267
Appendix 15: Asymptotic analysis of rarefaction curves for species accumulation data collected during camera surveys on Telperion Nature Reserve from January 2019 to January 2020. Order.q refers to the mathematical order of Hill numbers with $q = 0$ representing species richness, $q = 1$ representing Shannon Diversity and $q = 2$, representing Simpson Diversity. Empirical refers to observed data collected, Estimate refers to extrapolated data. Comparing Empirical Species Richness to Extrapolated Species Richness ($q = 0$) allows one to determine if an asymptote has been reached and if sampling is sufficient.	268
Appendix 16: Summary of all predator Visits (13 species) to experimental sites from camera trap surveys conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020.....	269
Appendix 17: Shannon-Weiner Species Diversity Indices for Sign Surveys conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020.	270
Appendix 18: Shannon-Wiener Species Diversity from Camera Trap Surveys conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020.	270
Appendix 19: Gini-Simpson's Species Diversity Indices for Sign Surveys conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020.	271
Appendix 20: Gini-Simpson Species Diversity for Camera Trap Surveys conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020.	271

Appendix 21: Fire affected calculations of Shannon-Weiner Species Diversity Indices for Sign Surveys conducted on Telperion Nature Reserve during the blue wildebeest (<i>Connochaetes taurinus</i>) decomposition study from January 2019 to January 2020.	272
Appendix 22: Shannon-Wiener Species Diversity from Camera Trap Surveys excluding fire affected sites conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020.	272
Appendix 23: Fire affected calculations of Gini-Simpson Species Diversity Indices for Sign Surveys conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020.	273
Appendix 24: Gini-Simpson Species Diversity from Camera Trap Surveys excluding fire affected sites conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020.	273
Appendix 25: Correlation matrix of variables believed to influence mesocarnivore presence at experimental sites during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators on Telperion nature Reserve from January 2019 to January 2020.	274
Appendix 26: Binomial logistic regression model comparisons assessing ‘Treatment’, ‘Jackal Track Density’ (JTD) and ‘Season’ as predictors of mesocarnivore presence/absence at experimental sites during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020.	275
Appendix 27: Pie charts showing detail of the number of predator visits to each experimental site during the period of active decay from camera trap data during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Pie charts show proportions of visits by different predator species.	275
Appendix 28: The total number of visits of all predator species (from video and still cameras) per site, treatment type and season during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators for the entire study period from January 2019 to January 2020 on Telperion Nature Reserve.	276
Appendix 29: Comparison of predator survey results during my study on the influence of decomposing blue wildebeest (<i>Connochaetes taurinus</i>) carcasses on predators from January 2019 to January 2020 and another recent camera trap study on Telperion Nature Reserve.	276

CHAPTER 1: INTRODUCTION

1.1. Overview of predator and scavenger conservation

Globally, predator populations (including scavengers) are experiencing ever increasing levels of threat and have suffered dramatic declines (Ray *et al.* 2005, Margalida *et al.* 2010, Fielding *et al.* 2014). These declines can be attributed to many factors including, habitat loss and fragmentation (Primack 2014), human-wildlife conflict (Ray *et al.* 2005) and in the case of scavenging species, a reduction in the availability of carrion, due partially to the loss of apex predators from many systems (Fielding *et al.* 2014). Global climate change may also affect predators by creating a mismatch in the timing of the life cycles of predator and prey species that disturbs long established patterns of synchrony (Durant *et al.* 2007).

Clarifying the distinction between carnivores, predators and scavengers is important at this point, as carnivores can be either predators or scavengers or both. The following definitions are used throughout this study. A predator kills and eats other animals whereas a scavenger feeds on carrion (Wilson and Wolkovich 2011). Scavengers may be obligate (consume carrion exclusively e.g., most vulture species) or facultative (consume carrion opportunistically e.g. hyaenas) (Wilson and Wolkovich 2011). Facultative scavengers are often predators and are more common than obligate scavengers (Wilson and Wolkovich 2011).

The conservation of predators presents many challenges to conservationists, not least because they tend to range extensively, and in so doing, are often found in fragmented landscapes, where protected areas are bordered and, in some cases, surrounded by human settlements or agricultural and livestock production (Romañach *et al.* 2011). In these areas, the perception that predators threaten livestock and/or human lives can result in pre-emptive killing of such species (Romañach *et al.* 2011). Even in areas dominated by game ranches, in southern Africa, predators like cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), wild dog (*Lycaon pictus*), spotted hyaena (*Crocuta crocuta*), brown hyaena (*Parahyaena brunnea*) and others are often eliminated, as they are perceived to be a threat to valuable antelope, in the game breeding and trophy hunting industries (Marker *et al.* 2003, Lindsey *et al.* 2005).

Predators can shape entire ecosystems (Ripple *et al.* 2001), and while the recognition of this is not new, the mechanisms by which this is achieved are not widely understood or appreciated, probably because the effects are difficult to observe or quantify, especially in the short term. However, the key roles that predators play in ecosystem function (such as triggering trophic

cascades and preventing overgrazing) have been demonstrated in many parts of the world (Estes *et al.* 2011, Ritchie *et al.* 2012): Yellowstone National Park in the USA (Ripple *et al.* 2001), Alaskan Kelp Forests (Estes and Duggins 1995), USA eastern seaboard (Myers *et al.* 2007), Asia, (Tossens *et al.* 2025), Serengeti National Park in Tanzania (Sinclair *et al.* 2010) and Hluhluwe-iMfolozi Park in South Africa (le Roux *et al.* 2018). Thus, it is widely accepted that predators shape ecosystems wherever they are components of such ecosystems (Finke and Snyder 2010, Tossens *et al.* 2025). Knowledge of the functional role of predators, in any ecosystem is critical (Ritchie *et al.* 2012), not only for their conservation, but because it allows predictions to be made of the likely implications of their absence in human modified landscapes.

As human populations increase and wilderness areas contract, the incorporation of human modified landscapes into conservation management plans is becoming increasingly necessary. However, much of the research on predators in Africa has focused on extensive conservation areas where relatively intact predator guilds persist (Hunter *et al.* 2007, Moleón *et al.* 2015). Historically this bias also applied to South Africa, but there has been a growing realisation that research effort needs to extend its focus beyond traditional protected areas (Ray *et al.* 2005, Balme *et al.* 2010). Predator populations persist beyond the borders of protected areas in shared landscapes where smaller protected areas are interspersed with a variety of other land uses including agriculture and livestock farming. Predators in these areas are not protected, and most large predators like lion (*Panthera leo*) and spotted hyaena have been completely extirpated while other predators such as cheetah and wild dog have either been exterminated or exist at very low densities (Ray *et al.* 2005, Bodasing 2022). More cryptic predators like leopard and brown hyaena, due to their solitary and elusive natures, often persist, but at low densities and under heavy threat of persecution (Balme *et al.* 2010, Thorn *et al.* 2011, Williams *et al.* 2017). In addition, the status of smaller members of the predator assemblage is often unknown and unstudied in these areas (Du Plessis *et al.* 2015, Pretorius 2019). Livestock farms, small private nature reserves and game farms are becoming increasingly important to the conservation of these species (Ray *et al.* 2005, Kent and Hill 2013, O'Bryan *et al.* 2018). However, the ecological function of predators in these areas is poorly understood and the implication of their continued persecution is unknown (O'Bryan *et al.* 2018). The extent of shared landscapes is increasing globally, and in most of these landscapes, predator guilds are not intact (O'Bryan *et al.* 2018), an important consideration when investigating these species and landscapes.

Predators regarded as scavengers are generally reviled by humans (De Vault *et al.* 2003). This attitude is often influenced by a person's level of education and socioeconomic status (Walkden 2019). Negative attitudes to scavengers are also often related to their association with death (particularly carcasses) and a revulsion for their feeding strategies (Walkden 2019). In South Africa's North-West and Gauteng provinces people's attitudes to scavengers (brown hyaenas, black-backed jackals (*Lupullela mesomelas*) hereafter jackal, vultures and Pied Crows, (*Corvus albus*)) were far less positive than to more predatory species such as lions, leopards and Fish Eagles (*Heliaeetus vocifer*) (Walkden 2019). Consequently, tolerance of scavenging species is often lower than for predators thought to predominantly catch live prey and the persecution of scavenging species like hyaenas is often more severe (Glickman 1995, Mills and Hofer 1998, Románach *et al.* 2011, Hugosson 2022) than for those species that are perceived to be more "noble" like leopard and cheetah (De Vault *et al.* 2003). Most tourists to Africa also place far less value in seeing scavengers like hyaena than they do for seeing other predators like lion and leopard. This attitude shifts as tourists become more experienced and educated but as many tourists to Africa are first time visitors, this attitude does influence perceived value of scavengers to ecotourism and may also affect funding for conservation initiatives for these species (Mills and Hofer 1998, Lindsey *et al.* 2007, Walkden 2019, Hugosson 2022, Mangachena and Pickering 2023). Consequently, the conservation of scavengers has historically been overlooked, and most studies have concentrated on individual species (Thorn *et al.* 2009, Thorn *et al.* 2011, James *et al.* 2017) rather than guilds or species assemblages (Ray *et al.* 2005).

Scavengers are relatively easy to persecute due to their propensity for consuming carrion. It is possible to treat carrion with poison and eliminate vast numbers of scavengers with minimal effort (Murn and Botha 2018). This method of controlling scavengers is used by many farmers (or even government departments and bodies), legally in countries like Australia and New Zealand to extirpate or control invasive predators (Glen *et al.* 2007, Riley 2019, Morris 2020). Although illegal in South Africa and many other countries, poison and other methods are frequently used to eliminate indigenous species perceived to be problem species (Allan 1989, Márquez *et al.* 2013, Drouilly *et al.* 2023). This stems, in part, from ignorance or generational belief systems, as many scavengers are blamed for livestock losses, that they may not have been responsible for (Maude and Mills 2005). Poisoning as well as other non-selective methods used to kill scavengers (e.g. gin traps and snares) are not only deadly and devastating to the target species, but they are also indiscriminate and are often responsible for the deaths of non-

target species such as lions, leopards and wild dogs (Memarian *et al.* 2018, Ogada *et al.* 2019, Becker *et al.* 2024).

Understanding how predators and scavengers contribute to ecosystem functioning, is essential for their conservation. Moreover, the effective conservation and management of wild animal populations (including scavengers), depends on comprehensive knowledge and understanding of animal behaviour (Sutherland 1998, Caro 1999). Disregarding animal behaviour may lead to the failure of conservation management programmes (Berger-Tal *et al.* 2011). Historically, animal behavioural studies have been underrepresented in the field of wildlife/nature conservation (Angeloni *et al.* 2008, Berger-Tal *et al.* 2016). However, recent consensus is that a focus on behaviour is required for a holistic picture of predator conservation to emerge (Macdonald 2016). Reduction in behavioural interactions, as species are lost or numbers decrease, has been linked to declines in populations of highly interactive species such as scavengers (Ives 2011). Scavenging networks are highly structured (Selva and Fortuna 2007, Cortéz-Avizanda *et al.* 2012, Mateo-Tomás *et al.* 2015) and ecosystem stability has been linked to the presence of scavengers and associated scavenging (DeVault *et al.* 2003, Wilson and Wolkovich 2011, Moleón *et al.* 2014). It is therefore important to understand scavenger behaviour, (at both an intraspecific and intraguild level) if scavengers and the ecosystems in which they occur, are to be adequately conserved.

1.2. Predator/Scavenger assemblage structure and function

Studies of predator assemblages and their interactions are underrepresented when compared to single species studies (Finke and Snyder 2010, Burton *et al.* 2011, Durant *et al.* 2011, Rich *et al.* 2016). Yet it is well known that ecological studies require a holistic approach (Estes *et al.* 2011), which includes an understanding of multiple species and how their interactions drive ecosystem functioning rather than focusing on individual species (Ripple *et al.* 2001). Predator assemblages are structured hierarchically with dominant species generally being larger than subordinate ones (Ritchie *et al.* 2009). This may however, be dependent on the number of individuals that form a cohesive unit in a specific context e.g. hyaenas (Höner *et al.* 2002) and lions (Périquet *et al.* 2015). The distribution of dominant species across the landscape is largely influenced by the availability and distribution patterns of suitable prey species (Spong 2002, Karanth *et al.* 2011, Balme *et al.* 2017, Balme *et al.* 2019) and less affected by other species within the predator assemblage (Balme *et al.* 2017). Subordinate species however, although

equally dependent on prey availability for survival, often exhibit distributions that are heavily influenced by the presence of more dominant competitors within the assemblage (Creel and Creel 1996, Durant 1998). Furthermore, larger members of the predator assemblage (e.g. leopards) appear to exhibit distributions that are more strongly influenced by anthropogenic disturbances (Loveridge *et al.* 2017), than are smaller predators (e.g. jackals) (Fritz *et al.* 2009, Burton *et al.* 2011, Torres-Romero *et al.* 2025).

In any predator assemblage, apex predators are those that occupy the top rung of the food chain and exert top-down control on the medium sized predators (mesopredators) that exist below them, who in turn suppress even smaller bodied mesopredators in a process known as an ecological or trophic cascade (Creel and Creel, 1996, Welch *et al.* 2022). Furthermore, when an apex predator is removed from an ecosystem, the position of top predator is assumed by the next most dominant species within the hierarchy. However, the mesopredator that becomes the new apex predator usually does not fulfil the same functional/ecological role as its predecessor (Creel and Creel 1996).

Such top-down pressure in a predator assemblage is prevalent in Africa (Creel and Creel 1996) and elsewhere (Ripple *et al.* 2001, Elmhagen *et al.* 2010, Letnic *et al.* 2012, Tossens *et al.* 2025). For example, in southern Africa, where apex predators like lion and spotted hyaena are removed and jackals become the dominant predator, they suppress numbers of smaller mesopredators like bat eared foxes (*Otocyon megalotis*) and Cape foxes (*Vulpes chama*), various mongoose species, black-footed cat (*Felis nigripes*) and Cape genets (*Genetta tigrina*) (Kamler *et al.* 2012b, Bagniewska and Kamler 2014). In Minnesota (USA), studies found that wolves (*Canis lupus*) suppressed coyote (*Canis latrans*) numbers, which in turn released foxes (*Vulpes vulpes*) from top-down control by coyotes (Levi and Wilmers 2012). Top-down pressure of this nature from predators has been shown to contribute to trophic cascades in the African context (Creel and Creel 1996, Sinclair *et al.* 2010).

In fact, changes in apex predator abundance can have disproportionate (up to four times) effects on mesopredator numbers (Ritchie and Johnson 2009). Conversely, under some circumstances, apex predators can provide benefits for mesopredators through the provision of scavenging opportunities (Wilson and Wolkovich 2011). Apex predators like lions have been shown to have both a positive and a negative influence on black-backed jackals and this may be site, context and time specific (Welch *et al.* 2022). Furthermore, apex predators influence diets of mesopredators and facultative scavengers. Sympatric populations of brown hyaena and black-

backed jackal show high dietary overlap where apex predator populations are low, but less dietary overlap where apex predator populations are higher (Ramnanan *et al.* 2016). The dietary overlap between black-backed jackal and brown hyaena demonstrates that the absence of a functional apex predator population, can restrict brown hyaena populations due to the resultant lack of carrion provisioning (Ramnanan *et al.* 2016). Thus, a better understanding of both positive and negative intraguild behaviour within different contexts is needed to guide conservation and management decision making (Tambling *et al.* 2018).

1.3. Scavengers and scavenging within a predator assemblage

Scavenging is a vital and widespread ecosystem service, the value of which is underestimated and understudied for most ecosystems (Moleón and Sanchez-Zapata 2015). Studies estimate that 2–15% of vertebrate species are scavengers (Mateo-Tomás *et al.* 2015), though this figure may be low due to underreported scavenging in dietary research, suggesting that vertebrate scavenging is more widespread than reported (Sebastián-González *et al.* 2023). Scavenger species play vital roles in ecosystems by supporting functions like food web dynamics, nutrient cycling, and disease control (Moleón and Sanchez-Zapata 2015). Species with traits such as dietary specialization, advanced olfaction, social behaviour, large home ranges, and nocturnal or crepuscular habits significantly influence scavenging processes (Inagaki *et al.* 2025). However, understanding of individual species' roles remains limited, as their effects are often specific to particular ecosystems. Furthermore, the functional importance of scavenging is increasingly being recognised as an important and undervalued aspect of ecology, impacting ecosystems, food web structure, nutrient cycling and population dynamics (De Vault *et al.* 2003, Wilson and Wolkovich 2011, Beasley *et al.* 2012, Barton *et al.* 2013, Pereira *et al.* 2014, Moleón *et al.* 2014, Sebastián-González *et al.* 2016).

Energy transferred via each scavenging link of a food chain is greater than the energy transferred via each predation link (Moleón and Sanchez-Zapata 2015). Scavengers use less energy searching for and handling carrion, than do predators having to hunt, capture, and kill prey. Consuming dead organisms is therefore a more efficient way for carnivores to gain energy, as it minimizes energy costs compared to hunting live prey. (Wilson and Wolkovich 2011, Moleón and Sanchez-Zapata 2015). Scavenging provides important top-down effects on prey populations due primarily to facultative scavenging by predators (Moleón *et al.* 2014). This is achieved by altering predator-prey relationships. Carrion availability, whatever the cause of death, may affect behaviour, kill rates and abundance of large carnivores, indirectly

shaping their effects on live prey and vultures (Moleón *et al.* 2014). High carrion availability has been linked to increased predation risk (Cortés-Avizanda *et al.* 2009), but it may also reduce predation on live prey by promoting scavenging. In European boreal systems, Eurasian lynx (*Lynx lynx*) can lower predation by opportunistic predators such as wolverines (*Gulo gulo*) by increasing scavenging opportunities for these animals (Mattison *et al.* 2011). However, because scavenging links in food webs are often ignored or misidentified as predation, the value of predation may be inflated (Wilson and Wolkovich 2011).

Historically, scavenging was attributed to specialist or obligate scavengers such as vultures, which are entirely dependent on carrion for their survival, and facultative scavengers, like hyaenas, that frequently scavenge (Moleón *et al.* 2014). It is becoming increasingly apparent, that the separation of a scavenging lifestyle from one of pure predation, is impossible, as many vertebrate predators will scavenge if an opportunity presents itself (De Vault *et al.* 2003, Moleón and Sanchez-Zapata 2015). Thus, for carnivores, predation and scavenging are the two ends of a continuum from exclusive hunting to obligate scavenging (Pereira *et al.* 2014). The realisation that facultative scavenging is far more prevalent in food webs than was previously thought, has led to the recognition that more research into scavenging as a process and the ecology of scavenger species is required (Moleón and Sanchez-Zapata 2015).

An understanding of the factors that influence carcass use by scavengers, is essential for effective predator and biodiversity conservation and management (DeVault *et al.* 2003). Various terrestrial predators scavenge opportunistically and there is a complex interspecific dynamic between species that comprise predator/scavenger guilds in ecosystems (Allen *et al.* 2015, Sebastián-González *et al.* 2016). For terrestrial (including avian) vertebrate predators, carrion is a valuable source of protein. Consequently, some species have evolved to depend entirely on carrion as a source of nutrition (Ruxton *et al.* 2004). Competitive interactions among scavengers influence the dynamics and the structure of species assemblages (Yarnell *et al.* 2013) and often take place at carcass sites (Hunter *et al.* 2006), providing opportunities to investigate interactions between species relative to this resource.

Many studies of African scavenger guild structures have focused on protected areas where vultures, lions and/or spotted hyaenas dominate carcasses leaving little opportunity for other scavengers: Serengeti National Park in Tanzania (Houston 1974, Hunter *et al.* 2007), Etosha National Park in Namibia (Gasaway *et al.* 1991) and Hluhluwe-Umfolozi Park in South Africa (Moleón *et al.* 2015). There is however a lack of information on scavenger guild functioning

in relation to human modified systems where top-level predators are absent (Ray *et al.* 2005, Du Plessis *et al.* 2015, Tambling *et al.* 2018).

Where present, vultures consume carrion quickly and where they are absent, carrion removal is slower (Samson and Ramakrishnan 2017), slower decomposition rates are likely (Samson and Ramakrishnan 2017, Grootaers *et al.* 2025) and consequently carcass persistence is extended. The absence of vultures may result in an increase in the total number of facultative mammalian scavengers and the duration and frequency of their visits at carcass sites (Samson and Ramakrishnan 2017). However, the presence of vultures often assists other scavengers to locate carrion, (Kane and Kendall 2017). Furthermore, the absence of vultures from some systems, especially as a result of deliberate human persecution (Nyirenda *et al.* 2024) or other anthropogenic activities like agriculture (Grande *et al.* 2018), non-targeted poisoning (Plaza *et al.* 2019) impacts with powerlines (Howes 2016) and wind turbines (Barrios and Rodriguez 2004), may influence the amount of time it takes for facultative scavengers to find carcasses. Vultures are also often able to open up carcasses and facilitate access for other scavengers, particularly in the absence of large apex predators like lion and spotted hyaena (Ogada *et al.* 2012, Santangeli *et al.* 2024).

The presence of carrion has important behavioural, ecological, conservation and management implications (Ogada *et al.* 2012, Sorensen *et al.* 2014) for any ecosystem. Large carcasses attract a greater variety and higher numbers of scavengers than smaller carcasses (Hunter *et al.* 2007, Moleón *et al.* 2015). This increases the potential for inter and intra-species interactions between scavengers at carcasses. Carcasses thus become social rendezvous points (Allen *et al.* 2015, Moleón *et al.* 2015) and contact points for both conspecifics and sympatric species. The presence of such carcasses leads to complex ecological relationships, especially relating to resource partitioning (Allen *et al.* 2015). However, close inter and intra specific contact between individuals, increases the likelihood of disease transmission (Cozzi *et al.* 2015).

Large scavengers like lions or groups of social scavengers like spotted hyaenas are capable of actively defending carcasses from other scavengers (Périquet *et al.* 2015) and there is often competition between scavengers for access to such high-value food resources (Hunter *et al.* 2007, Forsyth *et al.* 2014). In Africa, hierarchically subordinate species like cheetah and jackal or more solitary species like brown hyaena, avoid or abandon carcasses when dominant species like spotted hyaena or lions are present (Mills 1984, Hunter *et al.* 2007). The same applies in European and other ecosystems where, for example, Eurasian lynx prefer carcasses unattended

by brown bears (*Ursus arctos*) (Krofel *et al.* 2012). Interference competition and intraguild predation are known to result in spatial and temporal avoidance behaviour among scavenging species (Forsyth *et al.* 2014). Consequently, changes in the predator assemblage in the proximity of a carcass could be the result of interference competition between scavengers and/or predators (Samson and Ramakrishnan 2017).

1.4. The landscape of fear

The concept of the "landscape of fear" characterises how an animal's perception of predation risk shapes its behaviour and resource utilisation (Coleman and Hill 2014). This idea posits that animals, unable to continuously monitor potential threats, must balance their requirements for resources such as food and water with the risk of predation. As a consequence, animals may avoid particular areas or modify their behaviour, exerting marked influences on ecosystems, vegetation dynamics, and interspecies relationships. For certain species e.g. samango monkeys (*Cercopithecus albogularis*) (Coleman and Hill 2014) and vervet monkeys (*Chlorocebus pygerythrus*) (Willems and Hill 2009), the landscape of fear has been shown to be the primary determinant of space use, superseding resource availability in shaping ranging patterns (Brown and Kotler 2004, Coleman and Hill 2014). Furthermore, in ecosystems with multiple predator and prey species, guild-specific predation risk may vary among species occupying similar habitats (Coleman and Hill 2014).

Within a predator assemblage, the "landscape of fear" represents a dynamic spatial model illustrating how a predator's apprehension regarding other predators, alongside resource availability, directs its behaviour, movement, and hunting strategies (Cunningham *et al.* 2018). This includes both the recognition of conspecific and heterospecific predators, prey avoidance of high-risk sites, and the influence of social structure and apex predator presence on individual predators. Such perceived risk informs decisions related to hunting locations, tactics, and the trade-offs between the risk of other predators and the costs of avoiding resources (Forsyth *et al.* 2014). A predator's perceived "landscape of fear" is shaped by the distribution of other predators, resulting in zones of variable risk that are often unpredictable and fluid (Krofel *et al.* 2012, Forsyth *et al.* 2014). Accordingly, predators may adjust their movement and hunting activities to reduce encounters with more dominant predators; for example, mesopredators might refrain from utilising certain areas due to the presence of apex predators (Mills 1984, Hunter *et al.* 2007, Krofel *et al.* 2012, Forsyth *et al.* 2014).

Carrion also contributes to the “landscape of fear” by creating high-risk zones for both predator (Cunningham *et al.* 2018) and prey (Moleón and Sánchez-Zapata 2021) species, who may eschew these areas due to the likelihood of predator presence at carcasses (Cunningham *et al.* 2018). Nonetheless, carrion presents a valuable resource, compelling animals to weigh the potential risks against their nutritional needs, sometimes eliciting complex behavioural responses such as "fight-and-flight" reactions near carcasses (Redondo-Gómez *et al.* 2023). The existence of carrion can affect scavengers and other species influenced by scavenger presence, influencing individual animal behaviours, communities, populations and ecosystems via cascading effects (Moleón and Sánchez-Zapata 2021).

Investigations into vertebrate scavenging behaviour will lead to greater insight into the ecology of, and more accurate definitions of, the fundamental and the realised niche of terrestrial vertebrate predators (DeVault *et al.* 2003). The niche of any species in the absence of competition from other species is its fundamental niche and is defined by the combination of conditions and resources which allow the species to persist (Begon and Townsend 2020). Furthermore, the fundamental niche of any species can be described as an n dimensional hypervolume existing within a space defined by n independent axes (Hutchinson 1957, Blonder 2018). The axes correspond to the requirements of the species, for example food availability and temperature. The boundaries of the hypervolume or shape indicate the conditions that permit the species to grow and reproduce (Hutchinson 1957, Blonder 2018).

In the presence of competitors however, a species may be restricted to a realised niche, the precise nature of which is determined by which competing species are present and how resources are partitioned (Begon and Townsend 2020). Overlaps between sympatric species, along the food resource dimension of the realised niche, are likely to result in increased rates of interference competition between species with associated spatiotemporal avoidance, kleptoparasitism and direct killing of one another (Levi and Wilmers 2012). These interactions have the potential to cascade through the entire food chain including the predator guild in an area (Levi and Wilmers 2012). Mutualistic and commensal behaviour frequently occurs at carcasses, particularly when smaller carnivores require larger more powerful carnivores to open large carcasses before they can feed (Forsyth *et al.* 2014). Therefore, a hierarchy of access to carcasses is likely to exist within predator guilds and such a hierarchy will vary depending on the local composition of the predator assemblage (Forsyth *et al.* 2014).

Jackals are capable of exhibiting behavioural flexibility in their decision to hunt or scavenge, and their activity time based on whether apex predators are present or not (Welch *et al.* 2022). Where apex predators occur, jackals (black-backed and golden) and other small scavengers tend to avoid carcasses when these predators are present, as large predators often kill smaller scavengers (Hunter *et al.* 2007). Nevertheless, jackals and other small scavengers may still exploit carcasses under these conditions, although such feeding generally occurs when larger predators, are either absent from or have abandoned a carcass (Allen *et al.* 2015). For instance, where lion and spotted hyaena are absent, jackals are frequently observed scavenging (Fourie *et al.* 2015).

Scavenging by top-level predators, has complex effects on lower order scavengers and mesopredators. For example, pumas (*Puma concolor*) initiate a cascade of energy availability among scavengers by reducing the presence and total feeding time of avian scavengers and larger mesopredators that might prey on smaller carnivores. This allows smaller carnivores increased access to carrion (Allen *et al.* 2015). This influence over access and distribution of carrion could constitute a keystone effect, as it promotes biodiversity (Elbroch and Wittmer 2012).

1.5. Carrion and its influence on predator behaviour

Carcasses may fulfil needs unrelated to food acquisition for some predators. Species like brown hyaena are predominantly scavengers but they do occasionally hunt, albeit on smaller-bodied species (Maude and Mills 2005). Although carrion forms an important part of their diet, they have been observed visiting carcasses without feeding on them (Maude and Mills 2005). This was not necessarily related to competition at the carcasses as, on several occasions, no other scavengers were present (Maude and Mills 2005). Occasionally, brown hyaena defecate near and paste-mark on grasses near to carcasses (Maude and Mills 2005), suggesting that carcasses are not only important food sources for brown hyaena, but possibly also important places to communicate with conspecifics in the area. Scent marking and rubbing of glands on carcasses has also been observed in other species like serval (*Leptailurus serval*) (Keyes *et al.* 2021).

Carcasses have a role to play in the landscape beyond the obvious. For instance, they may be used by predators that are not usually associated with scavenging. Even leopards, despite being capable hunters, scavenge opportunistically (Du Preez *et al.* 2014). Carcasses may also provide

other sources of food besides the obvious carrion. Feeding on other organisms that are attracted to a carcass may be an understudied (but see Melville *et al.* 2023 and Mason *et al.* 2023) and little-known benefit provided by carcasses to some scavengers.

The circadian activity and habitat preferences of scavengers influence their behaviour patterns (Hunter *et al.* 2007) and consequently, their response to carcasses. If carcasses become available early in the morning, diurnal scavengers are likely to locate the carcass first, whereas if carcasses become available in the late afternoon/early evening, crepuscular and nocturnal scavengers are likely to discover them (Hunter *et al.* 2007).

Due to differential detectability, response times to new carcasses are likely to be shorter in open areas than in areas with thicker vegetation and closed canopies (Dominguez-Rodrigo, 2000, Hunter *et al.* 2007). For example, lions and spotted hyaena are more likely to respond to and have shorter response times to cheetah kills in short grass than in longer grass (Hunter *et al.* 2007).

Scavengers may also cue in on the behaviour of heterospecifics to aid in carcass location (Schaller 1972, Houston 1974, Creel *et al.* 2001). Although, in the Serengeti, only weak evidence was found of spotted hyaenas using vultures to locate food (Hunter *et al.* 2007), other studies found strong evidence for spotted hyaenas, lions and jackals using vultures to aid in carcass location (Cooper 1991, Cortés-Avizanda *et al.* 2014, Kane and Kendall 2017). Terrestrial scavengers (like lions and spotted hyaenas) respond more quickly to cheetah kills, than do vultures in the Serengeti (Hunter *et al.* 2007) and rely on all their senses to varying degrees when locating carrion. For example, spotted hyaenas are likely to arrive at kills before vultures, if they observe the kill taking place, or hear distress calls by prey, and see fleeing animals, but are likely to cue on the presence of vultures to detect carcasses from further away (Hunter *et al.* 2007).

Usually, carrion will attract scavengers from the immediate vicinity, and smaller carcasses are likely to be completely consumed relatively quickly by those scavengers. However, large carcasses may attract scavengers from further afield (Wilmers *et al.* 2003). The response of scavengers to a carcass is determined by a foraging radius: “*the distance over which an animal can locate and integrate a food resource in a given period of time*” (Wilmers *et al.* 2003). Scavengers with large foraging radii, like eagles and other large soaring raptors have a greater

number of potential scavenging opportunities (Wilmers *et al.* 2003). However, several terrestrial scavenging species are territorial, which may influence whether they respond to the presence of a carcass (Cozzi *et al.* 2015). Some authors (Egbert and Stokes 1976, Eriksson *et al.* 2022) have found that territoriality may break down when an abundant resource is present, while others have found that this is not the case and this may be species and context dependent (López-Bao *et al.* 2014). Detection time is also dependent on carcass size with detection times being three times longer for small (<10 kg) than for large (>100 kg) carcasses (Moleón *et al.* 2015). Variables including weather conditions, availability of alternative food resources, micro-habitat structure and cause of death, also influence scavenger responses to carrion (Selva *et al.* 2003, DeVault *et al.* 2004, Selva *et al.* 2005, Wilson and Wolkovich 2011, Olson *et al.* 2012 and Moleón *et al.* 2015).

The likelihood of finding scavengers at a carcass and the number of scavengers visiting a carcass, decreases over time (Cozzi *et al.* 2015). Additionally, the duration of carcass visits by scavengers' decreases over time, due to a decline in carrion quality and meat availability (Cozzi *et al.* 2015). Inter and intraspecific social hierarchy determines when individuals gain access to a carcass, with low-ranking species or individuals feeding at carcasses during the later stages of decay, although this may be species specific (Cozzi *et al.* 2015). Furthermore, the likelihood of finding scavengers at a carcass and the use of carrion by warier, heavily persecuted and cryptic carnivores e.g. wolves (*Canis lupus*), may be influenced by carcass proximity to human habitation (Forsyth *et al.* 2014, Ståhlberg and Apollonio 2023).

1.6. The ecology of carrion

Carrion is an ephemeral and pulsed resource, which appears with variable spatio-temporal predictability and therefore has several spatial and temporal effects on soil nutrients (Kullander *et al.* 2024), microbes (DeBruyn *et al.* 2025, Fouché *et al.* 2025), plants (Khumalo *et al.* 2025), arthropods (Kavazos and Wallman 2012) and vertebrates (Barton *et al.* 2013). Global climate change is linked to biodiversity loss. It is predicted to have multitrophic effects on the decomposer food web and is likely to have variable effects on carrion availability, decomposition rate and scavengers (Tylianakis *et al.* 2008). For instance, warmer winter months can reduce natural mortality that would have occurred due to harsh weather, reducing winter carrion pulses. However human-driven environmental shifts such as habitat

fragmentation and droughts can lead to concentrated mortality spikes at different times of the year than would have occurred naturally (Bartel *et al.* 2024). Apex predator declines lengthen the activity windows for smaller scavengers while climate-induced changes in rainfall can alter volatile organic compounds released by carcasses. Heavy rains dampen these olfactory cues, while higher temperatures can make them spread faster. This changes how quickly vertebrate and invertebrate scavengers detect the resource (Bartel *et al.* 2024). Ecosystem regime shifts linked to apex predator loss can favour smaller scavengers, which cascades into other indirect effects like elevated predation on ground-nesting birds or increased localised disease transmission (Bartel *et al.* 2024). Higher trophic levels are often affected disproportionately by habitat modification, and it is expected that their response to global climate change will also be disproportionately large in many cases (Tylianakis *et al.* 2008).

Globally, carrion availability is often seasonal (Pereira *et al.* 2014). In terrestrial systems in the high northern latitudes, an increase in carrion availability is associated with winter, when food scarcity leads directly to death or compromises the ability of some animals to withstand the cold (Pereira *et al.* 2014), making them vulnerable to predation. In more temperate regions, like much of Africa, and particularly southern Africa, winters are mild, but the mortality of terrestrial ungulates, often increases at the end of the dry season, when food and water are scarce (Pereira *et al.* 2013). Carrion pulses associated with disease outbreaks and drought are however often non-seasonal (Moleón *et al.* 2014). At a local scale, any animal carcass, can be considered a resource pulse (Moleón *et al.* 2014). In colder regions, decomposition may be relatively slow, and carcasses may persist as a food resource for an extended period (Moleón *et al.* 2014). In warmer regions, including southern Africa, carcasses undergo rapid decomposition and putrefaction in summer if not consumed by vertebrate scavengers (Moleón *et al.* 2014). In contrast, this process occurs at a slower rate in winter due to decreased invertebrate activity and reduced putrefaction (Parmenter and MacMahon 2009).

The impact of carrion on animal assemblages and ecological processes is poorly understood and understudied (Cortés-Avizanda *et al.* 2008, Sebastián-González *et al.* 2023, Fouché *et al.* 2025). A carcass has a low carbon to nitrogen ratio and a high water content and is therefore considered a high-quality resource (Carter *et al.* 2007). Although carrion constitutes a very small percentage of the total detritus pool in most ecosystems (Parmenter and MacMahon 2009), its role in nutrient cycling and food webs is disproportionately large compared to plant detritus (Barton *et al.* 2013). Unlike plant detritus, carrion is rich in key nutrients including nitrogen and phosphorous (Barton *et al.* 2013). Most carrion decomposes up to three orders of

magnitude faster than plant matter (Parmenter and MacMahon 2009). As a carcass decomposes, it releases a concentrated and localised pulse of nutrients and carbon into the soil, a process that is primarily regulated by microbial and invertebrate activity, scavengers and the mass of the carcass (Carter *et al.* 2007). Microbes, invertebrates and vertebrate scavengers compete for carcass resources (Carter *et al.* 2007). Sometimes, insects consume a carcass before vertebrate scavengers have utilised it at all (DeVault *et al.* 2004). Additionally, microbes can release toxins including botulin, which repel scavengers (Janzen 1977, Carter *et al.* 2007). Despite this, scavengers consume between 35% and 75% of the total number of carcasses in terrestrial ecosystems (DeVault *et al.* 2003). Larger carcasses are more likely to be predominantly removed by vertebrate scavengers than microbes and invertebrates. This is probably due to the increased detectability of larger carcasses, and the lower surface to volume ratio of large carcasses, which influences decomposers' ability to exploit the carrion (DeVault *et al.* 2003).

The process of microbial decomposition facilitates the transfer of nutrients from the carcass to the nearby soils and vegetation (Steinbeiser *et al.* 2017). Internal microorganisms are the first to exploit the resources in a carcass and the by-products of microbial decomposition attract invertebrate and vertebrate consumers to the carcass. Invertebrates transfer resources from carcasses, into the broader landscape and vertebrate scavengers distribute resources that result from their feeding on carcasses over an even larger area (Steinbeiser *et al.* 2017). For example, brown hyaena are known to carry pieces of a carcass distances of ≥ 2 km to den sites to feed their cubs (Owens and Owens 1978, Muller 2020). Understanding the role of scavenging in the process of carcass decomposition, and its associated ecosystem services, necessitates separation and quantification of the effects of vertebrate scavengers from the effects of invertebrates and microbes at a carcass.

1.7. Camera traps and sign surveys as research tools

Monitoring abundance, occupancy and behaviour of wildlife is critical to evaluate their conservation status and track population trends (Kendall *et al.* 1992). While direct observations and direct survey techniques (like aerial census') are considered the most accurate methods (but see Keeping *et al.* 2018), most predators are scarce, elusive, well camouflaged and often nocturnal. This obviates the use of direct methods to study predators in most ecosystems (Barea-Azcón *et al.* 2007) (but see Balme *et al.* 2017 and le Roux *et al.* 2023). Indirect methods

of studying carnivores are therefore often a necessity and a variety of techniques have emerged (Barea-Azcón 2007). Detection success of the available techniques can differ markedly, and it is therefore important to use the most appropriate detection method/s for a particular study or target species (Seidlitz *et al.* 2021). Inappropriate methods may result in inaccurate results, leading to incorrect inferences, which may result in incorrect management decisions and ultimately inefficient or inappropriate conservation practices (Seidlitz *et al.* 2021). Additionally, multi species approaches can increase field study productivity and provide insight into inter-specific relationships (Thorn *et al.* 2010). Thus, survey techniques that are applicable for a broad spectrum of species are particularly useful.

Camera trapping uses fixed cameras with passive infra-red and motion sensors to obtain still images and/or video clips of passing animals (Rowcliffe *et al.* 2008). Considered to be a relatively non-invasive and effective technique with minimal environmental disturbance, the use of camera traps (hereafter cameras) can allow for quantitative population analysis (Rowcliffe *et al.* 2008, Balme *et al.* 2009). Camera trapping is adaptable to many habitats and may be implemented under most climatic conditions by day and night. Most importantly it facilitates the recording of a variety of metrics associated with shy, cryptic and/or nocturnal animals (Rowcliffe *et al.* 2008). Cameras have been used successfully in many studies of carnivore occupancy and density (e.g. Balme *et al.* 2010; Harihar *et al.* 2011; Grey *et al.* 2013; Thapa *et al.* 2014). Additionally, they have been widely used to estimate abundance for species with pelage patterns (typically spots or stripes) that make identification of individuals possible (Karanth and Nichols 1998, Trolle and Kéry 2003, Silver *et al.* 2004, Balme *et al.* 2009). Furthermore, cameras have been successfully used to investigate carcass use by predators and predator guilds (Forsyth *et al.* 2014, Moleón *et al.* 2015). In addition to population, occupancy and density estimations, camera data, combined with advanced computer modelling, can be used in the study of spatiotemporal and avoidance behaviour in sympatric predators (Balme *et al.* 2010, Carter *et al.* 2015). Levels of interspecific competition can also be studied using cameras (Balme *et al.* 2010).

Baits are very effective in attracting predator species to cameras and as with un-baited cameras, detection probability can improve with increased trap density for a given area (Thorn *et al.* 2009). Moreover, baited cameras have the potential to accurately survey populations of some predators, particularly those that are individually recognisable and are attracted to carrion/baits like leopard (Du Preez *et al.* 2014) and brown hyaena (Yarnell *et al.* 2013). Placing baited

cameras in areas frequented by the target species, can further increase detection probability (Thorn *et al.* 2009). Baited camera traps may also be more cost effective and result in an increase in the number of predator species and individuals detected, when compared to un-baited cameras (Du Preez *et al.* 2014). Not only are detection rates improved, but more individuals of certain species, (particularly leopard) can often be detected using baited as opposed to un-baited cameras (Du Preez *et al.* 2014). Jackal and brown hyaena have been successfully recorded at baited cameras (Yarnell *et al.* 2013) and baited cameras have been used to estimate brown hyaena occupancy and density (Thorn *et al.* 2009, Satterfield *et al.* 2017).

Sign surveys (e.g. animal tracks and scat (faecal deposits)) are one of the oldest known ways to confirm an animal's presence in an area (Bider 1968) and they have been used extensively as a monitoring tool for carnivore species (Houser *et al.* 2009). While some authors (e.g., Balme *et al.* 2009) consider them inferior to cameras when investigating species richness, occupancy, behaviour and population ecology, others (e.g., Barea-Azcón *et al.* 2007, Thorn *et al.* 2010, Seidlitz *et al.* 2021) have found that sign surveys outperform cameras and other methods when surveying predators. Unlike cameras or telemetry tags, sign survey methods do not require expensive equipment, so they are cost effective (Keeping *et al.* 2018). Furthermore, they are reliable (Gusset and Burgener 2005) and allow large tracts of a landscape to be surveyed relatively easily (Rich *et al.* 2017b, Rich *et al.* 2017c). They do, however, require researchers to be proficient in the skills associated with locating and identifying tracks and other signs to species level which some feel may limit their utility (Stander 1998, Birks *et al.* 2005, Reid *et al.* 2013, Keeping *et al.* 2018). Van den Heever *et al.* (2017), however, demonstrated that the science of track identification and tracking is a highly trainable skill and not limited, in its application, to indigenous communities like the San Bushman of the Kalahari. Some authors (e.g., Birks *et al.* 2005, Balme *et al.* 2009, Roberts 2011) question the skill of researchers at track and sign recognition and identification whilst others (e.g., Lyra-Jorge *et al.* 2008, Findlay *et al.* 2023) favour cameras for the permanent, verifiable record of photographs that they produce. However, if animal signs are clearly photographed and photographic records include metadata tagged with location, date and species then there is little reason why cameras should have more evidentiary support than sign surveys. Furthermore, recent studies have combined AI with traditional tracker knowledge to identify wildlife, including carnivores, from tracks, for research. These programmes can successfully identify not only species, but individuals within species (Finerty *et al.* 2024).

Sign surveys on road transects have been successfully used as a monitoring technique for various carnivore species (Stander 1998, Funston *et al.* 2010, Karanth *et al.* 2011, Thorn *et al.* 2011), and guilds (Virgós 2001, Wang *et al.* 2014). Furthermore, sign surveys have been used to estimate species richness (Silveira *et al.* 2003) species occupancy (Hines *et al.* 2010) density (Houser *et al.* 2009), distribution and probability of patch use (Midlane *et al.* 2014) and abundance (Funston *et al.* 2010, Thorn *et al.* 2011).

The implementation of sign surveys may vary depending on the specific environmental conditions and constraints of individual study areas. Invariably a road, trail or game path is travelled by foot (Hines *et al.* 2010) or in a vehicle (Thorn *et al.* 2011, Midlane *et al.* 2014, Rich *et al.* 2017b) and any signs left by the target species are identified (Silveira *et al.* 2003). These signs may include footprints (Hines *et al.* 2010) feeding signs (Kshetry 2014), scent marks, scrape marks and scat (Hines *et al.* 2010, Thorn *et al.* 2011). The trail or road may be divided into several equal length transects whose length can vary depending on the study species. The transects serve as spatial replicates for data analyses (Thorn *et al.* 2011) and each transect may be sampled more than once over a specified timeframe thus resulting in temporal replicates (Stander 1998) for analysis.

Because the efficacy of different survey techniques varies across different habitats and species (Seidlitz *et al.* 2021), if time and resources allow, a combination of complementary survey methods allows for verification and validation of observed trends and increases confidence in results (Gompper *et al.* 2006, Lyra-Jorge 2008, Alexander *et al.* 2016, Li 2012, Rich *et al.* 2017b, Rich *et al.* 2017c). If investigating multiple carnivore species, then several independent techniques are recommended (Gompper *et al.* 2006). In addition, when studying scavengers at carcasses specifically, results from camera studies have demonstrated that scavenging species may visit carcasses without feeding on them and that reliance only on track surveys to estimate carcass use, may lead to an overestimation of carcass use by scavengers (Forsythe *et al.* 2014).

1.8. Carnivore occupancy

Species occupancy is defined as “the proportion of area, patches or sample units where the species is present.” (Mackenzie *et al.* 2017). Occupancy studies require collection of simple detection/non-detection data from cameras or sign surveys and normally require repeated observations at each study site (Mackenzie *et al.* 2017). The data are then used to build an

occupancy model, a type of Generalised Linear Mixed Model (GLMM), for each species observed in an area. Occupancy modelling has the potential to answer several different research questions from a simple sampling design. These models can be applied to single species (Thorn *et al.* 2011), multiple species (Van der Weyde *et al.* 2018) and to inter and intra-specific interactions (Rota *et al.* 2016, Rouse *et al.* 2021). Furthermore, occupancy models can be applied to data collected over a single season (Robinson *et al.* 2014) or from multiple seasons (Hines *et al.* 2014).

An overriding advantage of occupancy modelling is its ability to account for imperfect detection (Mackenzie *et al.* 2017). Imperfect detection often poses challenges in wildlife research, and models designed to address this issue present significant benefits compared to those that do not (Gopalaswamy *et al.* 2012). If a species is not observed at a sample site, it may be because it actually is absent from the site, or it is present but went undetected during sampling. The naive occupancy of a species would simply be the number of times a species was detected in a specific study divided by the number of survey sites. Naïve occupancy is often well below true occupancy because of the imperfect detection conundrum (Mackenzie *et al.* 2017). Occupancy models however take non-detection into account and produce, not just more realistic occupancy estimates but also detection probabilities at each sample site (Mackenzie *et al.* 2017). Additionally, occupancy models allow various site and survey specific environmental conditions to be built into a model as covariates. This allows the model to make predictions about which environmental factors are significant in their influence over occupancy and detectability for the study species (Mackenzie *et al.* 2017).

Occupancy models make several assumptions about the data and study site and these need to be considered for the models to have any relevance (Mackenzie *et al.* 2017). The main assumptions are:

- 1) Closure: The species of interest must be present at the site during the survey, and its occupancy status must not change for the duration of the survey. This means the species cannot go locally extinct or colonise a previously unoccupied site during the survey period.
- 2) Sampling sites must be independent. This means that the detection of a species at one site, must not be dependent on its detection at another site in the study area.
- 3) Detection probability must remain constant for a specific site, or if there is any variance in detection probability it should be explained by covariates.

- 4) Occupancy probability at each site must be constant or any variance must be explained by covariates.

There are however several modifications and additions to the basic occupancy model that allow for the relaxing of some of these assumptions (Kendall and White 2009, Kendall *et al.* 2013, Altwegg and Nichols 2019, Gould *et al.* 2019). Particularly valid for my study, is the assumption of sampling site independence often being violated in occupancy studies of large and wide-ranging carnivores (Hines *et al.* 2010). However, Markovian Occupancy Models (Charbonnel *et al.* 2014) obviate the need for independent spatial replicates and allow for spatial correlation of sign detections (Hines *et al.* 2010). These Markovian models have been successfully applied to leopards, tigers (*Panthera tigris*), brown hyaenas, lions (Hines *et al.* 2010, Thorn *et al.* 2011, Midlane *et al.* 2014, Thapa *et al.* 2021) and a variety of other species.

A broad range of concepts have been investigated using occupancy models: *Inter alia*, the geographic range of species (Midlane *et al.* 2014), anthropogenic effects on species (Strampelli *et al.* 2018, de Matos Dias *et al.* 2020), resource use (Mackenzie 2006), ecological niche partitioning (Kearney 2006, Schuette *et al.* 2013), and population abundance (Royle and Nichols 2003, Thorn *et al.* 2011). In addition, occupancy surveys can be applied at various spatial scales from small habitat patches to national (Karanth *et al.* 2009), regional and even global scale surveys (Rich *et al.* 2017a). Furthermore, the concurrent use of camera trapping and sign surveys, improves the accuracy of occupancy studies as they may complement each other when used together (Lyra-Jorge *et al.* 2008, Torrents-Ticó *et al.* 2017, Ponce-Martins *et al.* 2022).

1.9. Rationale

Inter and intraspecific predator interactions are increasingly being recognised as important drivers of ecosystem function (Ripple *et al.* 2001) and yet studies of entire predator assemblages are rare in comparison to those focusing on single species. This is even more applicable in mixed use landscapes outside of large, protected areas, where anthropogenic pressures impact heavily on guild structure and function.

In addition, despite carrion removal from the landscape by scavengers being a critical ecosystem service and being sensitive to perturbations within the scavenger assemblage, information on scavenging within predator guilds, particularly in areas where apex predators

and vultures have been extirpated, is also lacking. Given the anthropogenic pressures on natural ecosystems from increasing human populations and global climate change, advanced understanding of these mechanisms of ecosystem function is essential. Consequently, research into scavenger habitat requirements, adaptations to and tolerance of human encroachment, food habits and interactions with other guild members is crucial. Although it is well established that scavenging species compete for access to carrion (Morris *et al.* 2023, Honiball *et al.* 2024), the effect of carrion on the broader predator community proximate to a carcass is challenging to investigate and consequently not well understood.

Carcass decomposition is a complex process facilitated by a broad range of microbes, invertebrates and vertebrate scavengers (Carter *et al.* 2007). Separating the effects of invertebrates and microbial activity from the effects of vertebrate scavengers is necessary for a better understanding of the role that vertebrate scavengers play in this crucial ecosystem service, yet this has seldom been attempted.

While both cameras (Thorn *et al.* 2009, Chapman and Balme 2010, Tanwar *et al.* 2021, Arayanto *et al.* 2024) and sign surveys (Stander 1998, Funston *et al.* 2010, Thorn *et al.* 2010, Midlane *et al.* 2014, Lamichhane *et al.* 2021) have been used to monitor predators and scavengers, studies of carnivores that combine the two survey methods are far less common (but see Balme *et al.* 2009). Furthermore, to my knowledge, there is currently no published information combining the use of cameras to monitor predator activity at carcasses with sign surveys to study predator behaviour at increasing distances from carcasses into the broader landscape. Additionally, no information is available on using occupancy modelling on the occupancy and detection probability of predators with the effect of carcass presence as an environmental covariate.

1.10. Study Aim and Objectives

The aim of my study was to use both camera trapping and sign surveys to provide a better understanding of the predator guild on Telperion Nature Reserve (hereafter Telperion) and its response to carrion in the absence of apex predators like lion and spotted hyaena. Specifically, the implications of carrion in a human modified landscape to predator ecology, behaviour and diet, was examined, to aid in the conservation management of these species.

Following on from the aim, the objectives of my study were to:

- Investigate the mammalian predator assemblage and its inter and intraspecific behavioural responses to ungulate carcasses in a southern African grassland ecosystem.
- Compare the utility and cost of using camera traps versus sign surveys in determining responses of mammalian predators to carcasses.

The following research questions were derived from the above objectives:

1. Which species within the mammalian predator assemblage are present on Telperion?
2. Which mammalian predators approach carcasses and which species actively feed on carcasses?
3. Are there intra and interspecific interactions at carcasses and what is the nature of these interactions?
4. Do some mammalian predator species actively avoid carcasses and if so, can the reason for their avoidance be determined?
5. How do cameras and sign surveys compare in their utility and cost for investigating the response of mammalian predators to carcasses on Telperion?
6. Can occupancy models be used to determine which environmental factors (e.g., carrion, human disturbance, habitat and presence of other predator species) drive occupancy and detection probability for each mammalian predator species present on Telperion?
7. Using videos recorded with cameras what other aspects of predator behaviour around carcasses can be highlighted?

1.11. Thesis Outline

The outline and content of this thesis is described below:

- Chapter 1 is an introduction covering the predominant themes of the research and provides the rationale for my study.
- Chapter 2 describes the study area, Telperion, and provides details on climate, vegetation, and animals species present.
- Chapter 3 describes the materials and methods used to complete my study.

- Chapter 4 details the data analyses used during my study.
- Chapter 5 presents the results from my study.
- Chapter 6 provides a discussion of the results and the implications thereof.
- Chapter 7 comprises a general conclusion and recommendations for management and future research
- References provide a comprehensive list of the literature that was cited.
- Appendices provide additional information to support the arguments within my study.

CHAPTER 2: STUDY AREA

2.1. General

Telperion Nature Reserve – hereafter Telperion - (UTM: 35J 700893mE 7156779mN) is a ~7000 ha privately owned nature reserve located 25 km east of Bronkhorstspuit straddling the border between the Mpumalanga and Gauteng Provinces, South Africa (Figure 2.1). The elevation of the reserve extends from 1278 m to 1500 m above sea level. Approximately 45 km of boundary fences separate Telperion (to the North and South), from surrounding cattle and crop farms and the Renosterpoort Private Game Reserve to the southeast. The perennial Wilge River separates Telperion from eZemvelo Nature Reserve to the West creating a combined ~9000ha protected area. The Wilge River also forms the boundary of the reserve in the northeast. Open grassy plains, on undulating terrain, interspersed with wooded rocky ridges, dominate the landscape (Helm 2006, Gumbi *et al.* 2018).

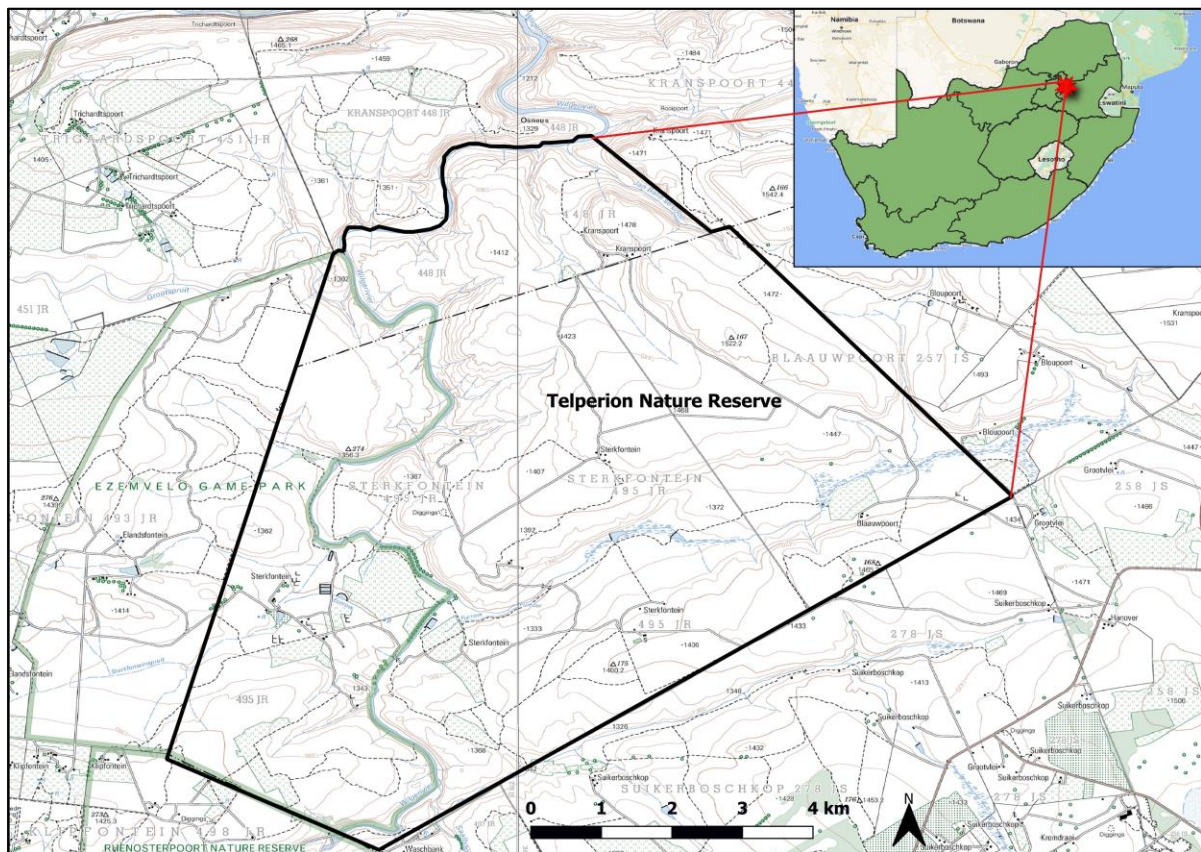


Figure 2.1: Location of Telperion Nature Reserve within the broader context of South Africa

2.2. History

Telperion bears evidence of occupation by humans dating back thousands of years, well before white settlers arrived in South Africa (Forssman and Louw 2018). However, the first farmers in the Telperion landscape probably settled in the area around the middle of the second millennium (Common Era) (Forssman and Louw 2018). Telperion is associated with several areas of historical interest and significance including iron smelting areas, circular rock structures believed to be dwellings, similar to those found in the Lydenberg area (although these have not been subject to archaeological scrutiny) (Forssman and Louw 2018), and a rock shelter with art by San bushman, Khoekhoe, Sotho-Tswana peoples and Boer War refugees who used the site to hide with their livestock from British soldiers (Forssman and Louw 2016).

Since 1974, the Oppenheimer family have purchased several former agricultural properties including Blaauwpoort, Kranspoort and Sterkfontein which were then amalgamated and subsequently named Telperion Nature Reserve (Helm 2006). Due to agriculture being the predominant, recent historical land use, old fields and infrastructure are still evident on the reserve. It has however been a protected area for approximately 50 years, is still owned and managed by the Oppenheimer family and has been developed to promote biodiversity conservation. Furthermore, Telperion serves as a research site for several universities (Gumbi *et al.* 2018).

2.3. Vegetation

Broadly, the vegetation on Telperion can be classified as Bankenveld, an ecotone between the grassland and savanna biomes, comprising a heterogenous landscape with a variety of habitats (Bredenkamp and Brown 2003, Swanepoel 2007, Brown *et al.* 2022) (Figure 2.2). Furthermore, Telperion is located within the endangered Rand Highveld Grassland vegetation type with intrusions of Loskop Mountain Bushveld on the mountain ridges (Mucina *et al.* 2006, Brown *et al.* 2022) (Figure 2.3).

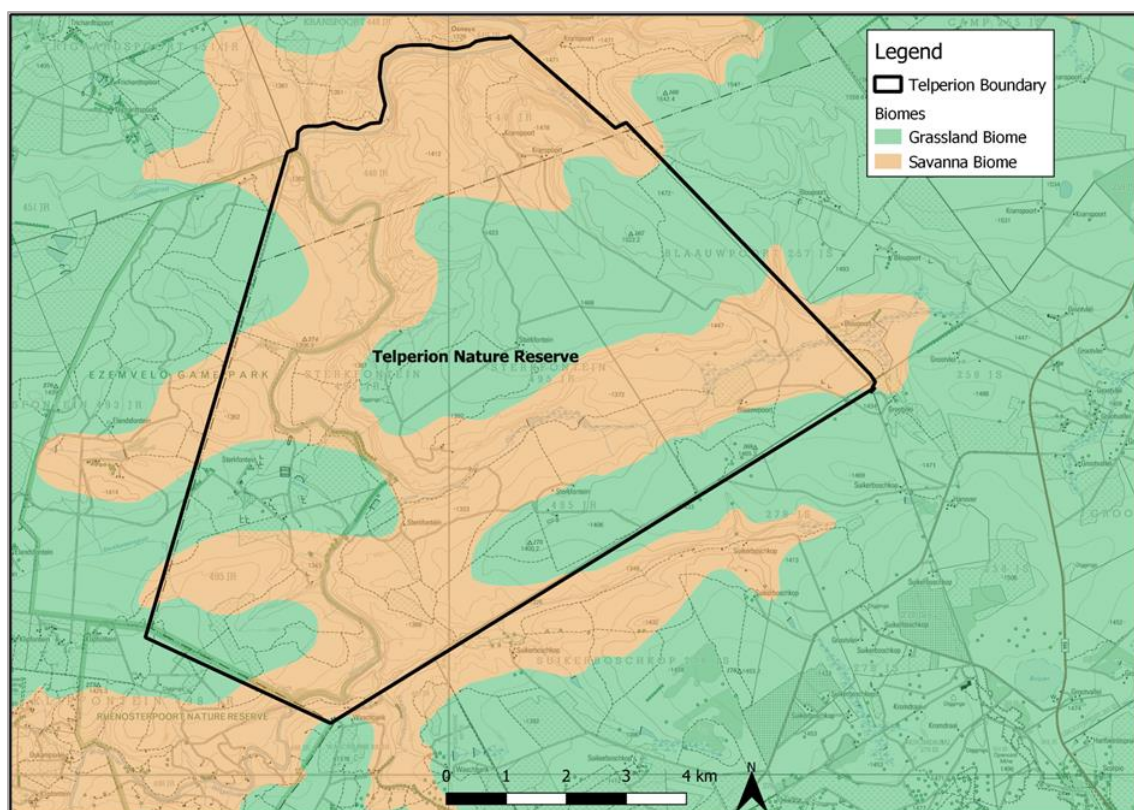


Figure 2.2: Telperion Nature Reserve straddles the grassland and savanna biomes of Southern Africa. Adapted in QGIS from Biomes data in SANBI (2006).

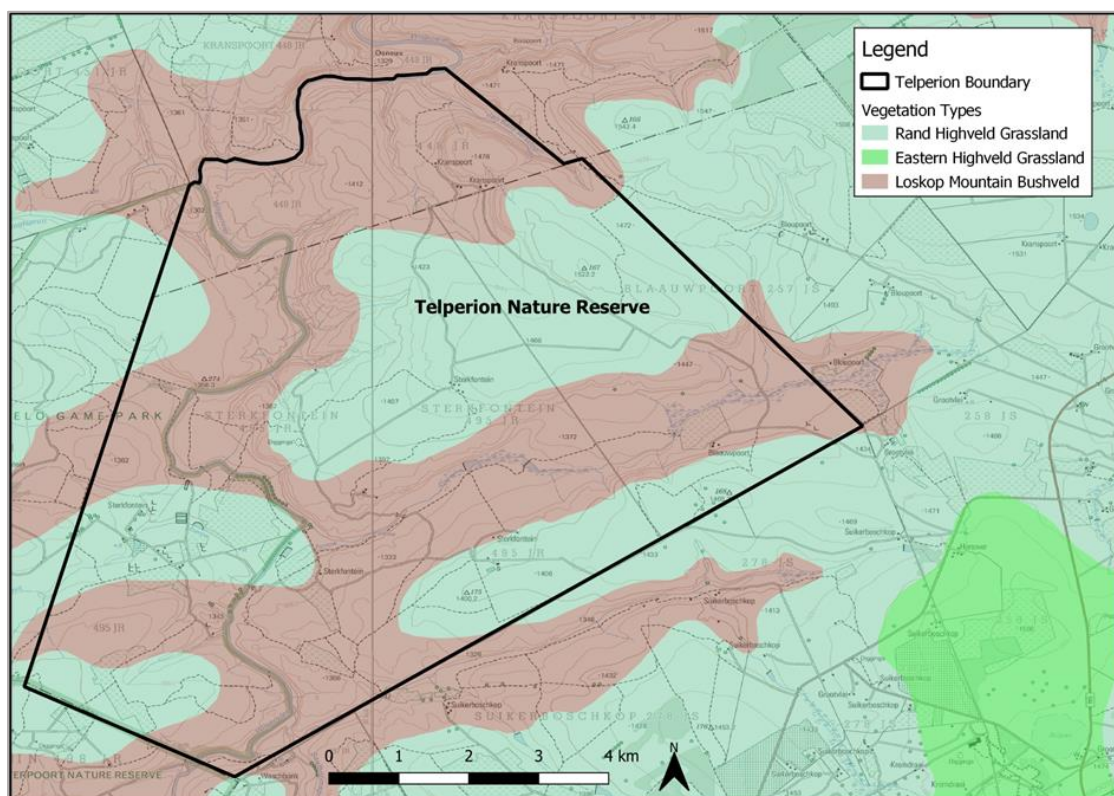


Figure 2.3: Broad vegetation types of Telperion Nature Reserve. Adapted in QGIS from the South African Vegetation Map SANBI (2018).

The grassland biome encompasses 28% of South Africa and is the second largest biome in the country. However, less than 3% of it is formally conserved and sixty-five percent of it is irreversibly transformed because its topography, geology, and soils, make it suitable and easy to exploit for mining, agriculture, and urbanisation (Birdlife 2020). This makes Telperion and the adjacent eZemvelo Nature Reserve critically important conservation areas as they occur in one of South Africa's most threatened biomes that urgently needs attention, and protection (Brown *et al.* 2022).

Grasslands are considered sensitive ecosystems, support a high level of biodiversity and are an important source of fresh water for many species, with water flow regulating capabilities (Brown *et al.* 2022). The grassland on Telperion is extensive, covering approximately 4688ha (Helm 2006) which is ~67% of the total area of the reserve and is characterised by open plains, encompassing wetlands, old agricultural fields and pockets of alien vegetation. They comprise predominantly *Erengrostis curvula*, *Eragrostis racemosa*, *Themeda triandra*, *Melinis repens*, *Setaria sphacelata* and *Tristachya rehmannii* species (Brown *et al.* 2022).

Rocky outcrops and longer rocky ridges are present in some parts of the reserve, and these are dominated by Loskop Mountain Bushveld vegetation (Mucina *et al.* 2006). On Telperion, Loskop Mountain Bushveld is characterised by shallow, rocky to loamy soils (Brown *et al.* 2022). The ridges have a high proportion of rock cover (~69%). This vegetation type on Telperion is dominated by the woody species *Combretum molle* and *Englerophytum magalismontanum* (Brown *et al.* 2022), while *Burkea africana* and *Protea caffra* are also common (Mucina *et al.* 2006, Brown *et al.* 2022).

There are five major plant communities on Telperion within the two broad vegetation types (Brown *et al.* 2022). These are linked to the topography of the reserve, and comprise 1) ravine woodlands, 2) valley bottom wetlands, 3) riparian woodlands, 4) plateau and mid-plateau grasslands and 5) rocky woodlands that supports a diverse plant assemblage, including two red listed species: *Frithia humilis* and *Encephalartos middelburgensis* (Swanepoel 2007). Consequently, suitable habitats exist for a wide variety of invertebrates, reptiles, amphibians, birds and mammals.

2.4. Hydrology

The Wilge River – a perennial tributary of the Olifants River – runs from south to north in the west of Telperion, for approximately 20 km. As the Wilge River enters Telperion in the south, it joins with the Sterkfonteinspruit and cuts a deep rocky gorge along much of its traverse through the reserve with shallower, wider sections in certain areas. The river forms an important wildlife corridor between Telperion and the ~22.9 km² Loskop Dam Nature Reserve, 25 km to the northeast (Figure 2.4), for leopard, brown hyaena and a variety of other species (Gerrie Camacho¹ personal communication 2019, Morris *et al.* 2022).

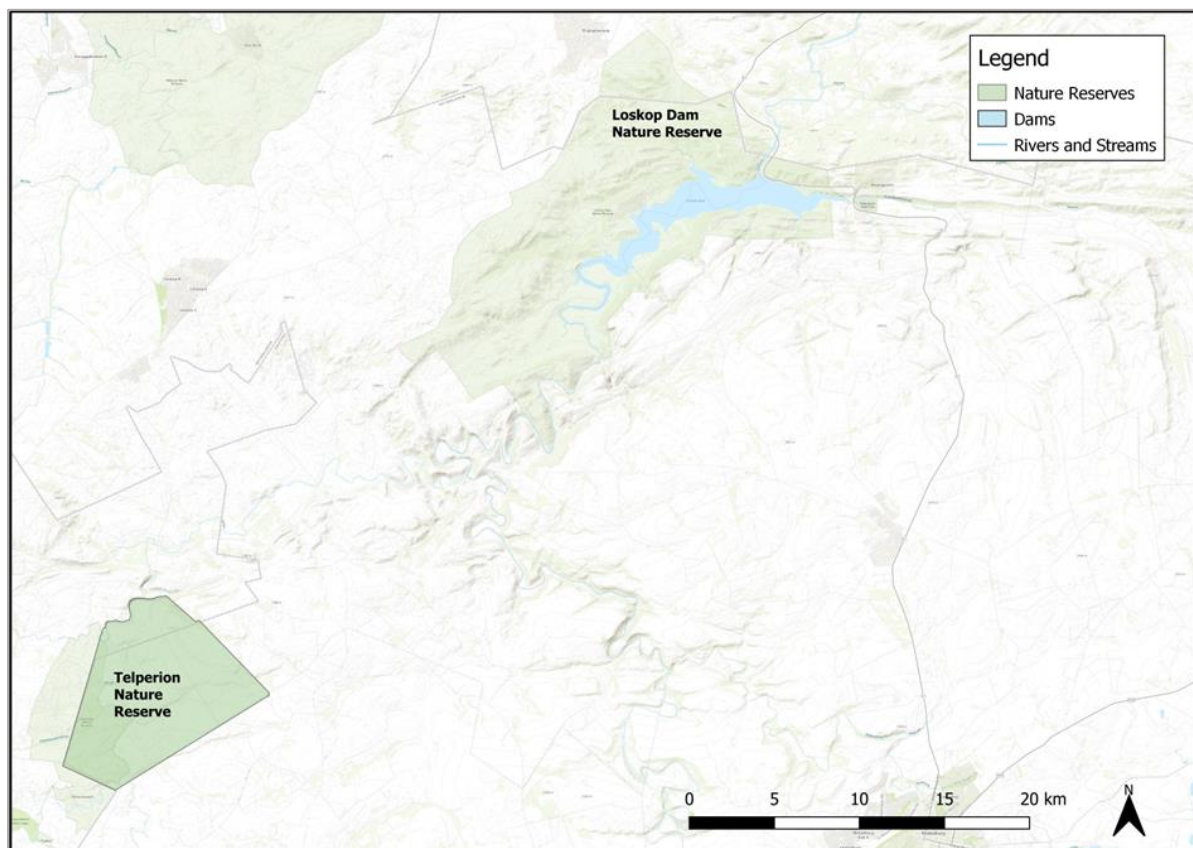


Figure 2.4: Telperion Nature Reserve and Loskop Dam Nature Reserve to the Northeast are connected by the Wilge River, and its associated gorge which acts as an important wildlife corridor between the two protected areas.

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Several perennial streams and springs originate in Telperion and feed into the Wilge River. These, along with the Wilge River itself, result in a network of wetlands and reedbeds providing water throughout the dry season on Telperion (Nkosi *et al.* 2018). Two historical man-made dams are also present on the reserve, but they are not maintained, are largely derelict, filled with reeds and hold little water (personal observation). Consequently, during my study, there were no artificial watering points of consequence on the reserve. Natural water sources like the Wilge River and its associated wetlands provide sufficient water for wildlife year-round (Mnendela *et al.* 2023).

2.5. Climate

Telperion is located in the summer rainfall region of southern Africa, and the grassland and savanna biomes are both characterised by summer rain and dry winters (Mucina *et al.* 2006). Frost is common in winter and frequent thunderstorms in summer result in a high incidence of lightening induced fires (Mucina *et al.* 2006). Rainfall for Telperion, varies between 570 and 730 mm per annum (Nkosi *et al.* 2018) and temperatures range from -3°C to 28°C. February is the hottest month of the year on Telperion, with the mean daily maxima and minima for this month being 26.4°C and 15.1°C respectively. The coldest month of the year on Telperion is July with mean daily maximum temperatures reaching 18.4°C, while average daily minimum temperatures drop to 4.2°C (Brown *et al.* 2022). For the purpose of my study, astronomical seasons were followed as closely as possible, with summer beginning on the 21st of December and ending on the 19th of March. Autumn beginning on the 20th of March and ending on the 20th of June. Winter Starts on the 21st of June and ends on the 21st of September and Spring starts on the 22nd of September and ends on the 20th of December (Trenberth 1983).

2.6. Geology and soils

The geology of Telperion and surrounds is dominated by the Wilge River Formation of the Waterberg Group and the Ecca and Dwyka formations of the Karoo group (Figure 2.5). The rocks of the Karoo Group weather to produce dystrophic (highly leached) and mesotrophic Arenite-Conglomerate soils (Grobler 1999). The Wilge River Formation of the Waterberg Group contains sandstone parent material rich in iron oxides that weather to produce deep, red soils. The soil texture is predominantly sandy, and is consequently vulnerable to water erosion, particularly in areas where vegetation cover is sparse (Helm 2006).

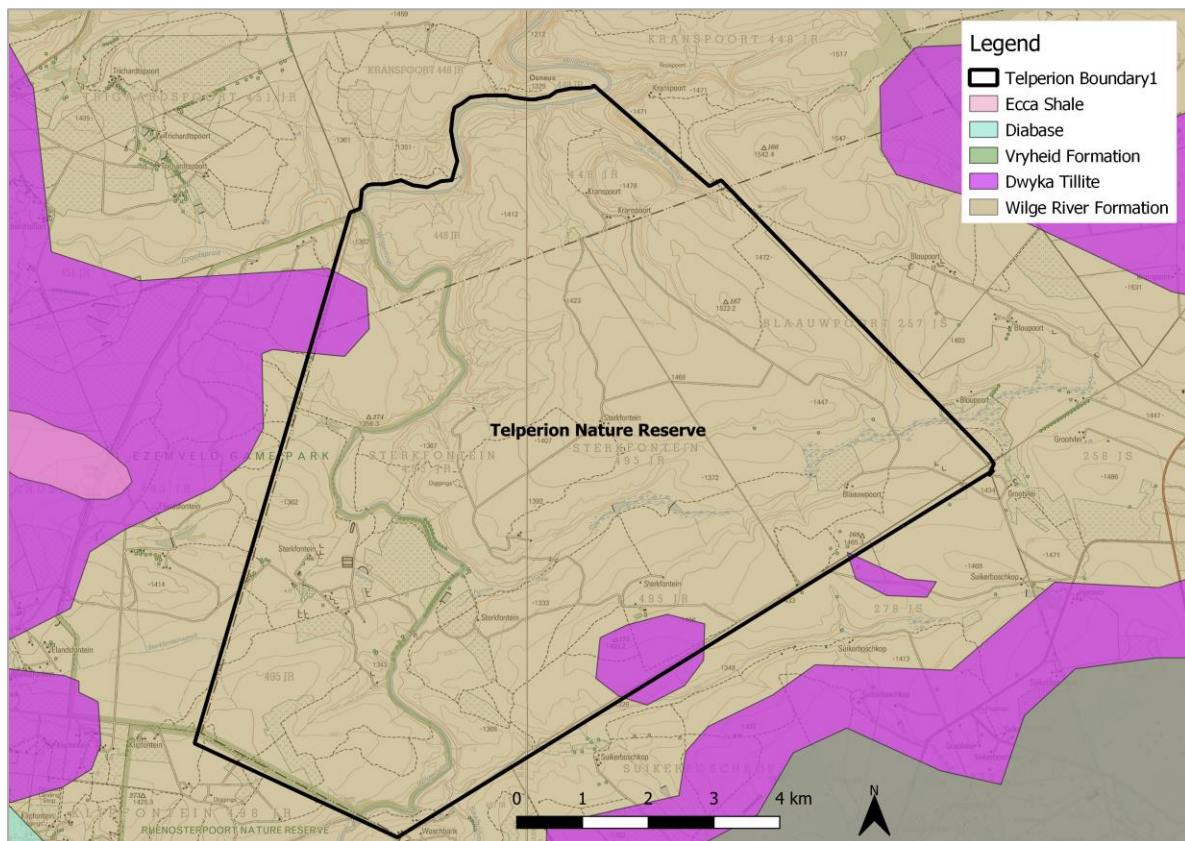


Figure 2.5: The geological formations underlying Telperion Nature Reserve and surroundings, including adjoining Ezemvelo Nature Reserve. These formations are dominated by the Wilge River Formation with intrusions of Dwyka Group and Ecce Group formations. Adapted in QGIS from 1:250 000 Geological Map of 2528 Pretoria 1978. Council for Geoscience (2023).

2.7. Fauna

Telperion is inhabited by a diversity of herbivores including South African giraffe (*Giraffa giraffa giraffa*), blue wildebeest (*Connochaetes taurinus*), black wildebeest (*Connochaetes gnou*), blesbok (*Damaliscus pygargus phillipsi*), red hartebeest (*Alcelaphus buselaphus*), eland (*Tragelaphus oryx*), kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazella*), waterbuck (*Kobus ellipsiprymnus*), plains zebra (*Equus quagga*), impala (*Aepyceros melampus*), springbok (*Antidorcas marsupialis*), warthog (*Phacochoerus africanus*) Bushpig (*Potamochoerus larvatus*) and Cape porcupine (*Hystrix africaeaustralis*) (Roux 2017).

A recent study recorded 16 mammalian predator species (Webster 2016) (Table 2.1). Six of these species have concerning red list status according to the Endangered Wildlife Trust: brown hyaena, serval (*Leptailurus serval*) and Cape clawless otter (*Aonyx capensis*) are listed as near threatened, while leopard, black-footed (*Felis nigripes*) cat, and spotted-necked otter (*Hydrictis*

maculicollis) are listed as vulnerable (International Union for Conservation of Nature (IUCN)) (Child *et al.* 2016) (Table 2.1).

Table 2.1: Predator species recorded on Telperion Nature Reserve prior to my study (including the most recent (2025) IUCN Red List Status. Vulnerable and Near Threatened species are indicated in bold.

	Common Name	Scientific Name	Red List Category
1	Aardwolf	<i>Proteles cristata</i>	Least Concern
2	Black-backed jackal	<i>Lupulella mesomelas</i>	Least Concern
3	Black-footed cat	<i>Felis nigripes</i>	Vulnerable
4	Brown Hyaena	<i>Parahyaena brunnea</i>	Near Threatened
5	Cape clawless otter	<i>Aonyx capensis</i>	Near Threatened
6	Caracal	<i>Caracal caracal</i>	Least Concern
7	Honey Badger	<i>Mellivora capensis</i>	Least Concern
8	Leopard	<i>Panthera pardus</i>	Vulnerable
9	Mongoose Slender	<i>Gallerella sanguinea</i>	Least Concern
10	Mongoose Water	<i>Atilax paludinosus</i>	Least Concern
11	Mongoose Yellow	<i>Cynictis penicillata</i>	Least Concern
12	Rusty-spotted genet	<i>Genetta maculata</i>	Least Concern
13	Serval	<i>Leptailurus serval</i>	Near Threatened
14	Spotted-necked otter	<i>Hydricetus maculicollis</i>	Vulnerable
15	Striped polecat	<i>Ictonyx striatus</i>	Least Concern
16	Suricate	<i>Suricata suricatta</i>	Least Concern

The protected status, varied habitats, and permanent water sources on Telperion along with dense vegetation along the Wilge River are thought to contribute to the carnivore diversity on the reserve (Webster 2016). Generally, carnivore occupancy is higher closer to permanent water (Webster 2016) and the dense riparian vegetation on Telperion provides concealment from prey as well as protection from humans and sympatric carnivore species (Webster 2016). Although predators are protected on the reserve, fences generally do not restrict their movements (Balme *et al.* 2010) and carnivores on Telperion do come into conflict with humans outside of the reserve. Brown hyaenas and leopards with snares around their necks (or related injuries) have been recorded on cameras on the reserve (Personal observation) and neighbouring landowners are known to set predator traps (pers. comm.^{1,2}).

1 Elsabe Bosch Reserve Manager Telperion Nature Reserve

2 Cassius M Mettle Employee Telperion Nature Reserve

More than 250 bird species have been recorded on Telperion (Helm 2006) including several vulnerable species. Birds of prey on the reserve include the vulnerable Black Eagle (*Aquila verreauxii*) (Taylor *et al.* 2015) which appears to breed on Telperion in the rocky gorge associated with the Wilge River (Personal observation). However large obligate scavengers like vultures are absent from the reserve and surrounding areas according to the most recent distribution maps of the Southern African Bird Atlas Project (Brooks *et al.* 2022) (Figures 2.6 – 2.10). Three species, Cape Vulture (*Gyps coprotheres*), Lappet-faced Vulture (*Torgos tracheliotos*) and White-backed Vulture (*Gyps africanus*) have been recorded within 62 km of Telperion (Figures 2.6, 2.7 and 2.8). All five species do travel extensive distances in the search for carrion, with recorded distances of over 200 km flown in less than a single day by some species (Monadjem *et al.* 2018). Nevertheless, no vulture species were observed on the reserve during my study (personal observation). Furthermore, discussions with Telperion staff revealed that no vultures have been seen on Telperion for several years.

In many instances where vultures are absent from a system, Corvid species fill that vacant niche (Buechley and Şekercioğlu 2016, Jenkins and van Zyl 2020). However, they do this imperfectly as they do not have the ability to open carcasses like vultures do and are not capable of consuming as much per unit time (Jenkins and van Zyl 2020). Pied Crows were recorded on Telperion during the study albeit in very low numbers.

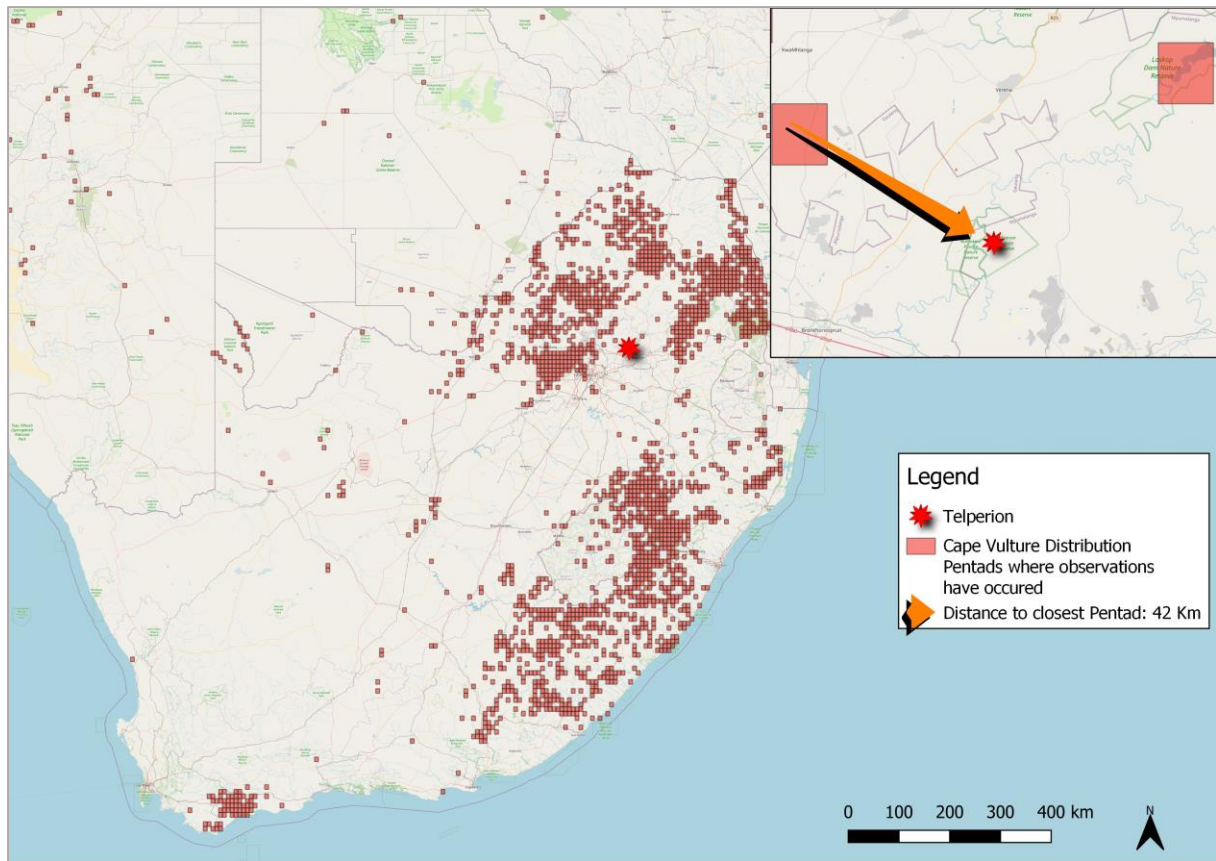


Figure 2.6: Distribution of Cape Vulture (*Gyps coprotheres*) in southern Africa with inset showing zoomed in perspective of Telperion Nature Reserve and closest pentads with confirmed observations (42 km away). Adapted in QGIS from SABAP 2 (2023a).

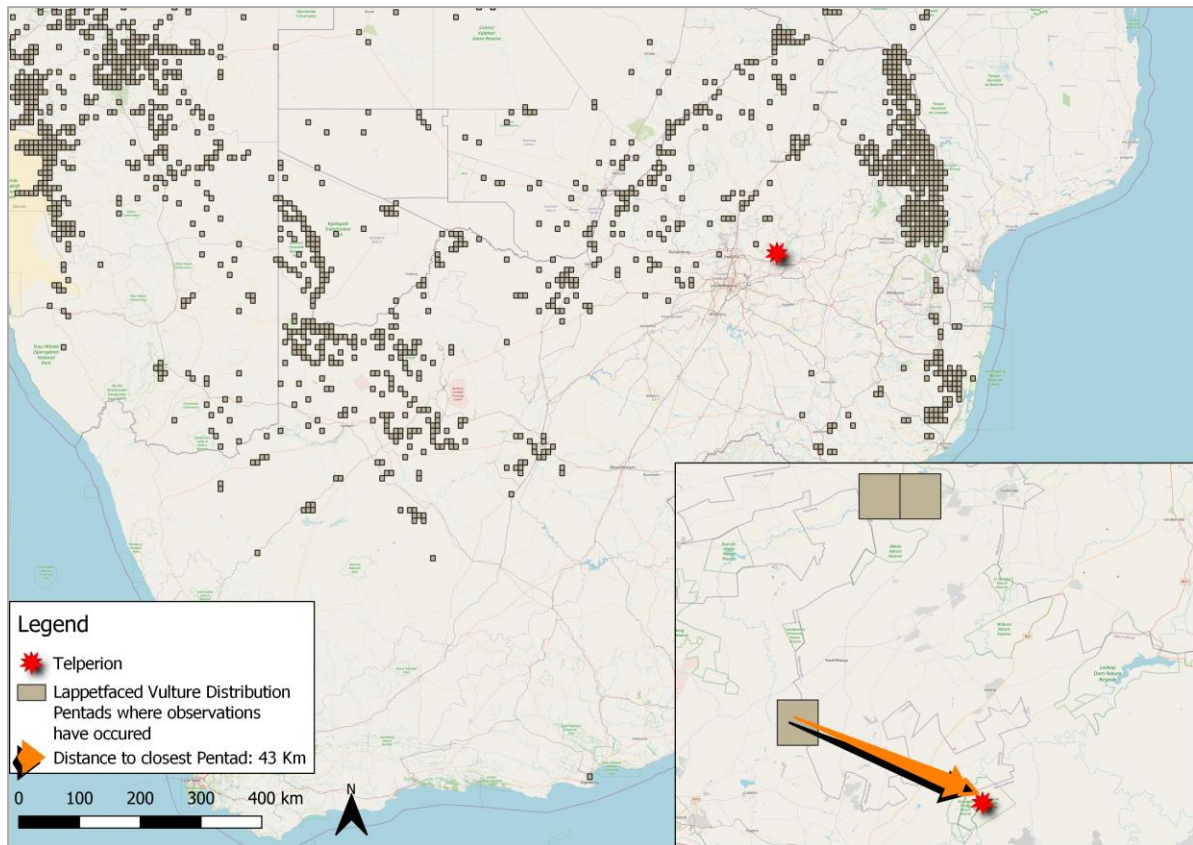


Figure 2.7: Distribution of Lappet-faced Vulture (*Torgos tracheliotos*) in southern Africa with inset showing zoomed in perspective of Telperion Nature Reserve and closest pentads with confirmed observations (43 km away). Adapted in QGIS from SABAP 2 (2023b).

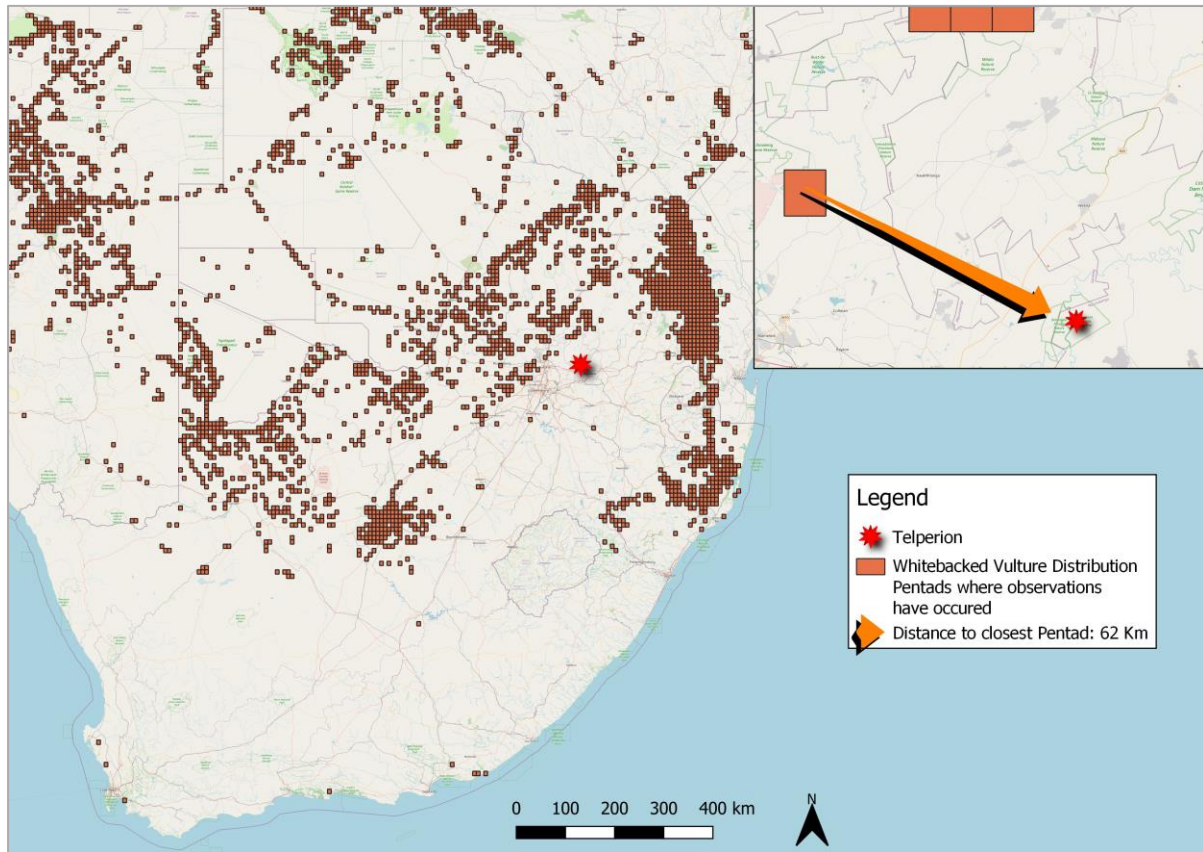


Figure 2.8: Distribution of White-backed Vulture (*Gyps africanus*) in southern Africa with inset showing zoomed in perspective of Telperion Nature Reserve and closest pentads with confirmed observations (62 km away). Adapted in QGIS from SABAP 2 (2023c).

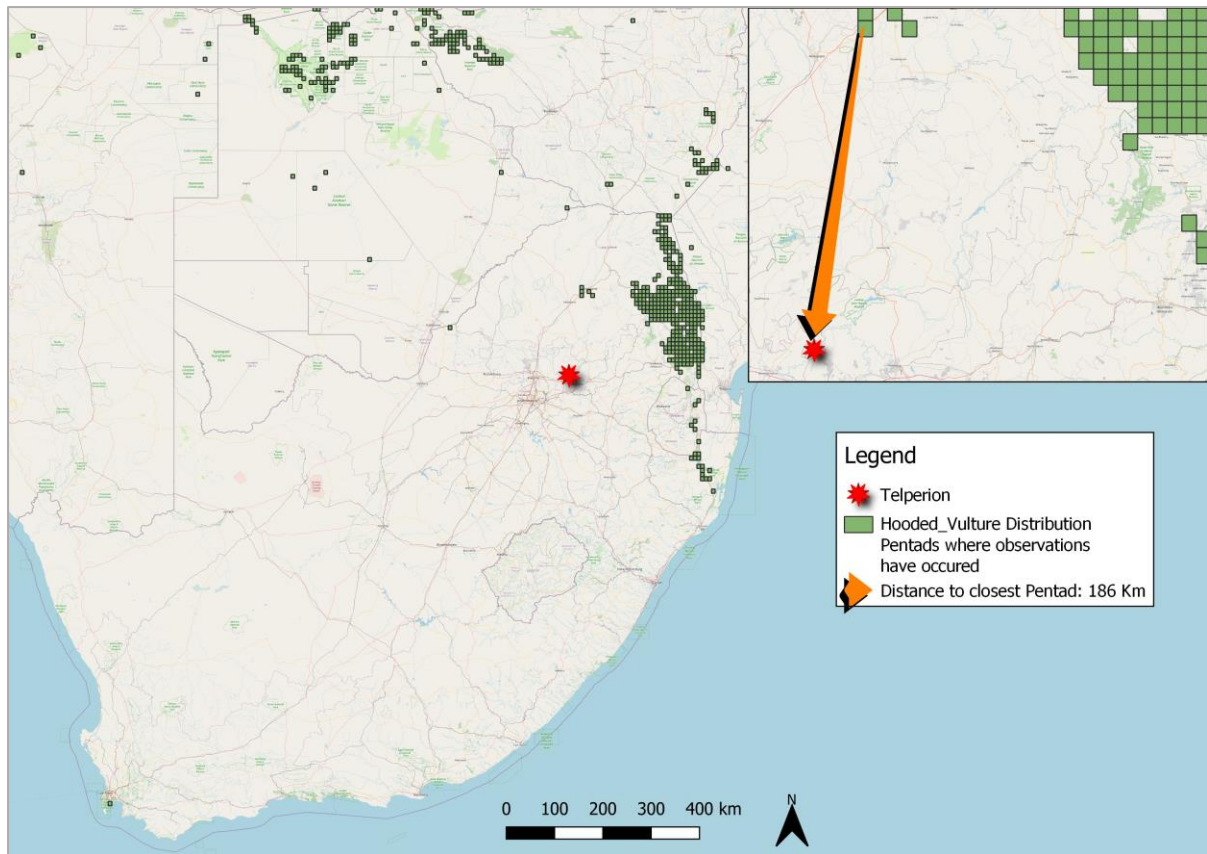


Figure 2.9: Distribution of Hooded Vulture (*Necrosyrtes monachus*) in southern Africa with inset showing zoomed in perspective of Telperion Nature Reserve and closest pentads with confirmed observations (186 km away). Adapted in QGIS from SABAP 2 (2023d).

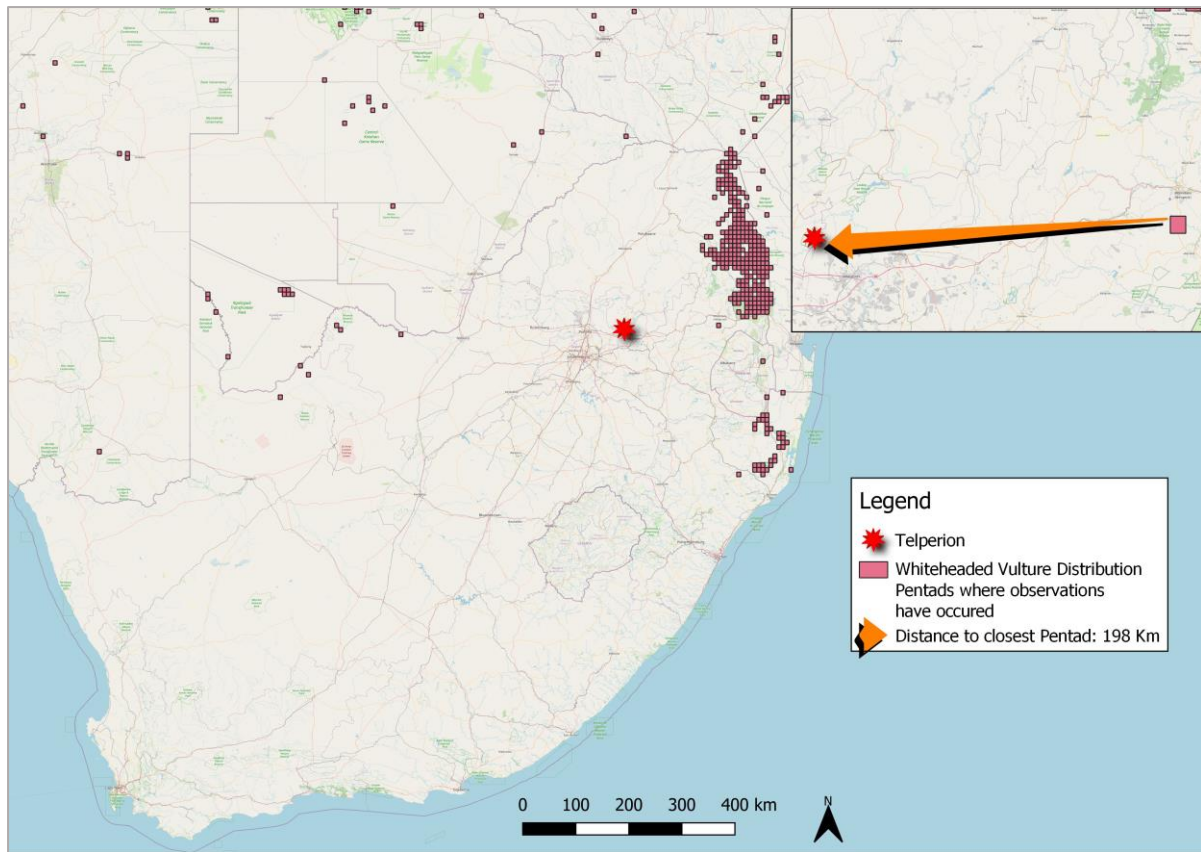


Figure 2.10: Distribution of White-headed Vulture (*Trigonoceps occipitalis*) in southern Africa with inset showing zoomed in perspective of Telperion Nature Reserve and closest pentads with confirmed observations (198 km away). Adapted in QGIS from SABAP 2 (2023e).

CHAPTER 3: RESEARCH METHODOLOGY

Disclaimer

This study formed part of a larger project on carcass decomposition and has ethical approval under the project application number CAES/2018/119 and was conducted in accordance with the American Society of Mammologists in relation to the use of animals in research (Sikes 2016) as well as adhering to the requirements for Research as stipulated by the South African Bureau of Standards (2021).

3.1. Research design

This study was an empirical study to investigate a predator guild's response to carcass decomposition, using primary data, collected during a field experiment and based on a modified "Before, After, Control, Impact (BACI)" design (Smith 2002). The study made use of sign surveys and cameras to investigate occupancy, species diversity and behaviour of predator species on Telperion Nature Reserve.

3.2. Data collection

Fifteen experimental sites were identified across Telperion prior to project initiation (coloured dots in Figure 3.1). The experimental sites were chosen to represent the widest possible coverage of the reserve while avoiding specific areas in the proximity of anthropogenic developments, (owner and guest housing, administrative buildings and staff accommodation). The 15 experimental sites were all located in grassland patches within the reserve. I randomly allocated five experimental sites to one of three treatment protocols (control, open and caged). Ten adult male blue wildebeest carcasses of mean shoulder height 1.27 m (± 0.07 m) and mean weight 223 kg (± 12.14) (Appendix 1) were used as representatives of a typical ungulate carcass for the purpose of my study.

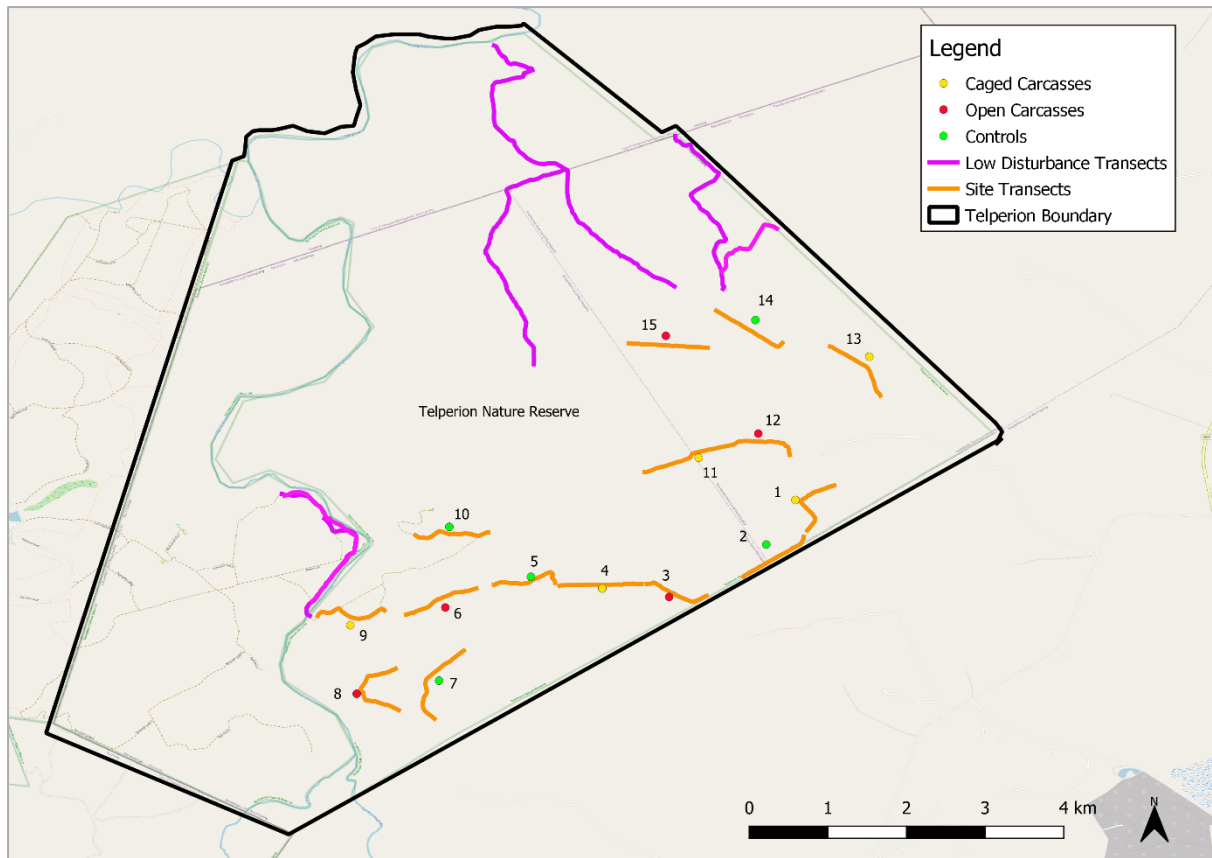


Figure 3.1: Location of experimental sites and sign survey transects within Telperion Nature Reserve during the blue wildebeest (*Connochaetes taurinus*) decomposition study from January 2019 to February 2020.

The carcasses of ten adult blue wildebeest bulls were sourced from a management culling operation on Telperion which was implemented to ensure that populations do not exceed the carrying capacity of the reserve. Monolithic brass bullets were used to cull the research animals to obviate the threat of lead poisoning to animals that might feed on the carcass and incidentally ingest bullet fragments (Hunt *et al.* 2006). Each carcass was transported directly from the location where it was culled, to one of the predetermined experimental sites where it was either fastened to a weighing platform (open sites) or enclosed within an exclosure cage (caged sites) by myself and other study participants.

To avoid flooding the system with fresh carrion, carcasses were supplied in two staggered batches. Five carcasses (three open and two caged) were supplied on the 21st of January, followed by a further five (two open and three caged), two weeks later on the 5th of February. I allocated five of the experimental sites as controls with no carcasses present (Figure 3.2), five as open sites with carcasses present, placed on a metal grid (2.5 m x 1.6 m) and pegged down but accessible to vertebrate scavengers (Figure 3.3) and a further five as caged sites with

carcasses present but enclosed within exclosure cages (2.5 m x 1.6 m x 0.7 m) to prevent vertebrate scavengers from gaining access to the carcasses (Figure 3.4). The exclosure cages were purposely designed for my study based on published morphometric values for adult blue wildebeest bulls (Skinner and Chimimba 2005).

The aperture size (10 mm x 25 mm) of the cage mesh allowed invertebrates such as insects and arthropods access to the carcasses but were small enough to prevent rodents and small reptiles from gaining access. This facilitated comparison between carcasses that were available to vertebrate scavengers and those that were not. The cages, the metal grids and the metal fencing poles for attaching the cameras were deployed by members of the study team at the respective sites on the 15th of December 2018, at least 6 weeks before the initiation of the decomposition component of the project to try and compensate for any potentially neophobic behaviour (Kimball and Lattin 2023) by allowing animals on the reserve a period of acclimation to the cages, grids and poles before the project started.



Figure 3.2: Control site used during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020. At control sites two camera traps were mounted on metal fence posts, but there were no blue wildebeest carcasses, grids or cages.



Figure 3.3: Open site used during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020. At open sites two camera traps were mounted onto metal fence posts, and a blue wildebeest carcass was present and secured onto a metal grid for weighing purposes.



Figure 3.4: Caged site used during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion nature Reserve from January 2019 to February 2020. At caged sites two camera traps were mounted onto metal fence posts, and a blue wildebeest carcass was deployed inside an exclosure cage.

Due to this study being a component of a larger research project, experimental sites were located at least one km apart. This distance was chosen to try to achieve spatial independence between sites for most experimental protocols. Although this assumption is unlikely to hold for vertebrate scavengers (Thorn *et al.* 2011), other predator studies have used similar distances between cameras (Wegge *et al.* 2004, Pettoirelli *et al.* 2010, Webster 2016, Rich *et al.* 2019) in studies of single small and large predator species and predator guilds. Additionally, spatial independence in biological data is not always essential as important biological information can be linked to the spatial dependence of biotic responses, and often spatial relationships need to be investigated directly to further our understanding of species and their relationships with one another (Liebhold and Gurevitch 2002).

Statistical methods that allow for meaningful analysis of spatially correlated or dependent data are available (Chao 2001, Liebhold and Gurevitch 2002, Hines *et al.* 2010, Thorn *et al.* 2011).

Therefore, once the data were collected, I assumed that in terms of the larger scavengers, (e.g., leopards, brown hyaenas and black backed jackal) the data were not spatially independent as typical home range sizes (Appendix 2) (Hunter 2020) far exceed the spatial separation of experimental sites from one another. For smaller scavengers (e.g., slender mongoose, yellow mongoose and rusty spotted genet), spatial independence was estimated on a species-by-species basis based on typical home range sizes (Appendix 2) (Hunter 2020) for each species. I implemented appropriate statistical methods for each species, that take spatial dependence or independence into account, to ensure meaningful data analysis. For example, the program PRESENCE (Hines 2006) includes the Markovian Occupancy Model that accounts for spatial correlation of animal sign detections (Hines *et al.* 2010).

To determine the proportional decline in mass for both open and caged carcasses over time, I (with the help of other project participants) weighed each carcass using a purpose-built weighing gantry and hanging scale (Figures 3.5 and 3.6). I weighed each open and caged carcass at the time of initial deployment and, subsequently once every seven days until it had either decomposed to the point where there was nothing but bone and skin remaining, or it had been completely removed from the site. To minimise disturbances at the carcasses, I timed weighing procedures to coincide with other activities at the carcass site (e.g., servicing of cameras).



Figure 3.5: Weighing of open carcasses by attaching a weighing gantry to a metal grid of known weight (34.2 kg) on which the carcass was secured, during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020.

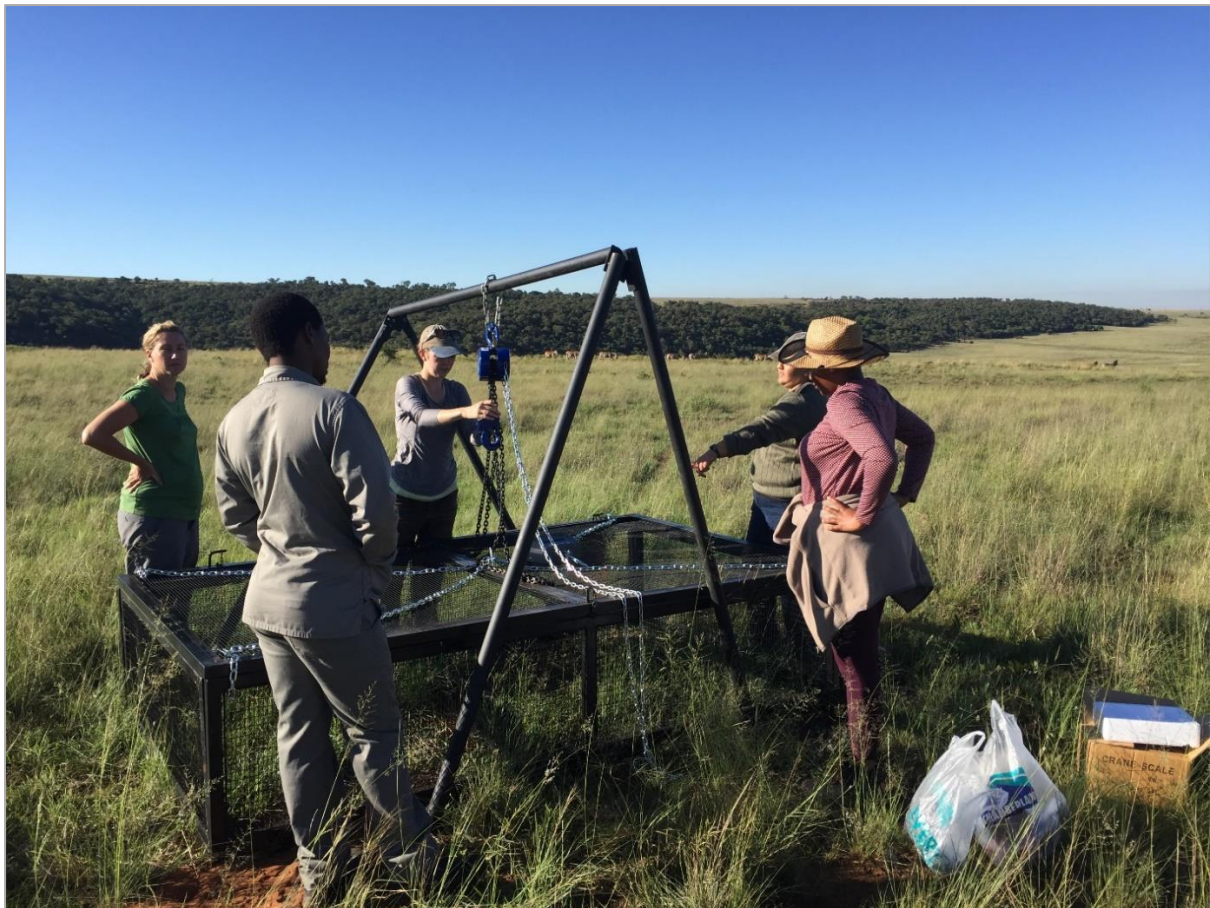


Figure 3.6: Weighing of caged carcasses by attaching weighing gantry to cage of known weight (117 kg) during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020.

3.2.1. Camera trapping

I deployed two Bushnell Trophy Cam HD E3[®] cameras with 0.3 second trigger response and low glow infrared LEDs at each of the 15 experimental sites (control, caged and open) for the duration of the carcass decomposition period of 45 days (pers. obs.). Cameras were active from one week before carcasses were deployed during a pre-sampling period which allowed for any minor issues with camera placement and operation to be resolved before carcass deployment. I drove two steel fence posts upon which to mount the cameras into the ground at each experimental site. One stake was 5m due east of the centre point of the site at which the carcass was positioned, and the second stake was placed 10 m due west of this centre point. I oriented the cameras east and west to avoid the glare of a north facing camera or the shadow of a south facing camera interfering with the view of the experimental sites. Placing the cameras at two different distances from the study sites allowed for both close up observations of animal behaviour at the sites as well as a wider field of view to capture animals that may have

approached the carcass but not come close enough for the 5 m camera to capture them. Furthermore, two cameras at each site allowed for both sides of an animal to be observed and also created a backup in case of camera failure. I positioned both cameras to include the carcass at the bottom of the frame. I standardised each camera's height at 1,5 m above the ground so that they were out of reach of brown hyaenas (Cozzi *et al.* 2015) and to ensure that a broad field of view was included in the frame of the cameras. As this was part of a larger study on carcass ecology, the vegetation monitoring protocol of other researchers meant that vegetation would not be cleared from in front of the cameras for the duration of the study. This was expected to increase the number of false triggers due to vegetation movement. Extra time was allocated to sorting through camera data accordingly.

I programmed the 10 m cameras to record three consecutive digital images upon activation with an interval of 30 seconds until further photos were taken (Rich *et al.* 2017a, Rich *et al.* 2019). I programmed the 5 m cameras to record one 15 second video clip upon each activation with an interval of two minutes between consecutive activations. Thus, I based behavioural analyses on 15 second discreet observation periods.

As photographic data accumulated rapidly, I monitored cameras closely for battery discharge and memory card use and replaced both and downloaded data weekly where necessary. Cameras were active 24 hours a day for the duration of their deployment throughout the period of active decay (45 days) and then seasonally for 30 days at a time for a year after the cessation of active decay. This was timed to coincide, as closely as logistically possible, with the middle of each astronomical season and each seasonal sampling period was buffered by at least 30 days. Astronomical seasons are defined by fixed celestial events, such as equinoxes and solstices, which create clear and widely recognised boundaries that remain consistent across years and regions (Trenberth 1983). By contrast ecological seasons vary with local climate, rainfall, vegetation and species activity, making them harder to define objectively and thus more difficult to compare across studies. Because astronomical seasons offer standardised, objective and reproducible boundaries linked to changes in photoperiod, they are often preferred in biological research (Morissette *et al.* 2009) hence I chose them for my monitoring protocol.

3.2.2. Sign surveys

I implemented sign surveys to obtain more information about carnivore activity around the carcasses, than was available from the camera images in the immediate vicinity of the carcasses. Sign surveys are a way of sampling the broader landscape around the experimental sites to gauge if predator behaviour was affected in this larger area. Other authors (e.g., Everatt *et al.* 2015 and Strampelli *et al.* 2018) have found that a distance of up to one km from each camera station is a meaningful distance to investigate the effect of various site covariates (in this case carcass presence) on site use by predators. Sign surveys are an additional way to determine carnivore presence, occupancy and behaviour (Silveira *et al.* 2003, Houser *et al.* 2009, Funston *et al.* 2010, Hines *et al.* 2010, Thorn *et al.* 2011 and Midlane *et al.* 2014) and form a useful point of comparison to camera results (Risch *et al.* 2020). I used the combination of cameras and sign surveys to provide a deeper insight into carnivore behaviour at the carcasses and in the broader landscape surrounding the carcasses.

I conducted sign surveys of the mammalian carnivore assemblage on Telperion prior to carcass placement to establish a baseline against which post carcass deployment metrics could be compared. I then repeated these surveys throughout the period of active decay of the carcasses which was deemed to be complete when all that was left was dry skin and bone (Lee Goff 2009) and took approximately 45 days (pers. obs.). I then conducted the surveys once per season for a year after the cessation of active carcass decomposition.

I questioned researchers involved in the greater project during early pre-sampling, as to their daily road use, and based on this, I assigned roads to two use categories: high disturbance or low disturbance. I assigned roads with five or more traverses by researchers per day to the high disturbance category, and roads where fewer than five traverses per day were anticipated, to the low disturbance category. This resulted in roads directly adjacent to the experimental sites and those linking one site to another, being assigned to the high disturbance category. These roads were relatively busy with a number of researchers, particularly during the period of active decay when most researchers were living on the reserve and conducting their sampling on a daily basis. Roads further away from the experimental sites were travelled less frequently and I assigned them to the category of low disturbance.

Other staff and researchers not linked to the carcass decomposition study also used the reserve and roads during the study period. However, their activity was not concentrated around the

carcass decomposition experimental sites and utilised both high and low disturbance areas, so for the purposes of this study, I ignored their activity.

The rationale behind sampling in both high disturbance and low disturbance areas, was based on predators' tendency to avoid anthropogenic disturbance (Strampelli *et al.* 2018, Ordiz *et al.* 2021). Separating roads into these two anthropogenic disturbance categories allowed me to compare predator activity in areas close to the experimental sites, with high human disturbance, to similar areas further away from the experimental sites with less human disturbance. Additionally, this allowed me to sample a larger area of the reserve than simply the portion near the experimental sites.

I undertook sign surveys by implementing sign identification and interpretation along 37 x 1 km transect sections traversed on foot (Figure 3.8). As the reserve is relatively small, with few roads, the number of transects was such that as much of the reserve was sampled as possible and sample size was as high as possible for adequate statistical analyses. Consequently, I sampled all roads except for areas around human habitation, administration offices and roads leading to the main entrance gate as these were areas of very high anthropogenic use. I also did not sample a few seldom used roads that were too overgrown with grass for tracks to be visible. Fifteen of these transects were located adjacent to the experimental sites (high disturbance category), and 22 transects were located away from the experimental sites (low disturbance category).

At each experimental site I identified the location closest to the carcass on the adjacent road using a Garmin GPSMap 64s™. This formed the centre point of the 1 km sign survey transect, which extended for 500m along the road in either direction from this centre point (Figure 3.7). I defined the start and end points of each transect as specific GPS locations (Appendix 3) using a Garmin GPSMap 64s™. Additionally, I divided the one-kilometre-long stretches at the experimental sites into smaller sample units of 250 m for more detailed analysis. While conducting the sign survey transects, I wore a Garmin Vivo Active™ GPS sports watch which can be set to vibrate on a wearers wrist when certain distances had been travelled, alleviating the need to keep checking the GPS and allowing me to maintain concentration on the interpretation of tracks and field signs. This also alerted me to when one 250 m segment was ending and the next one beginning.

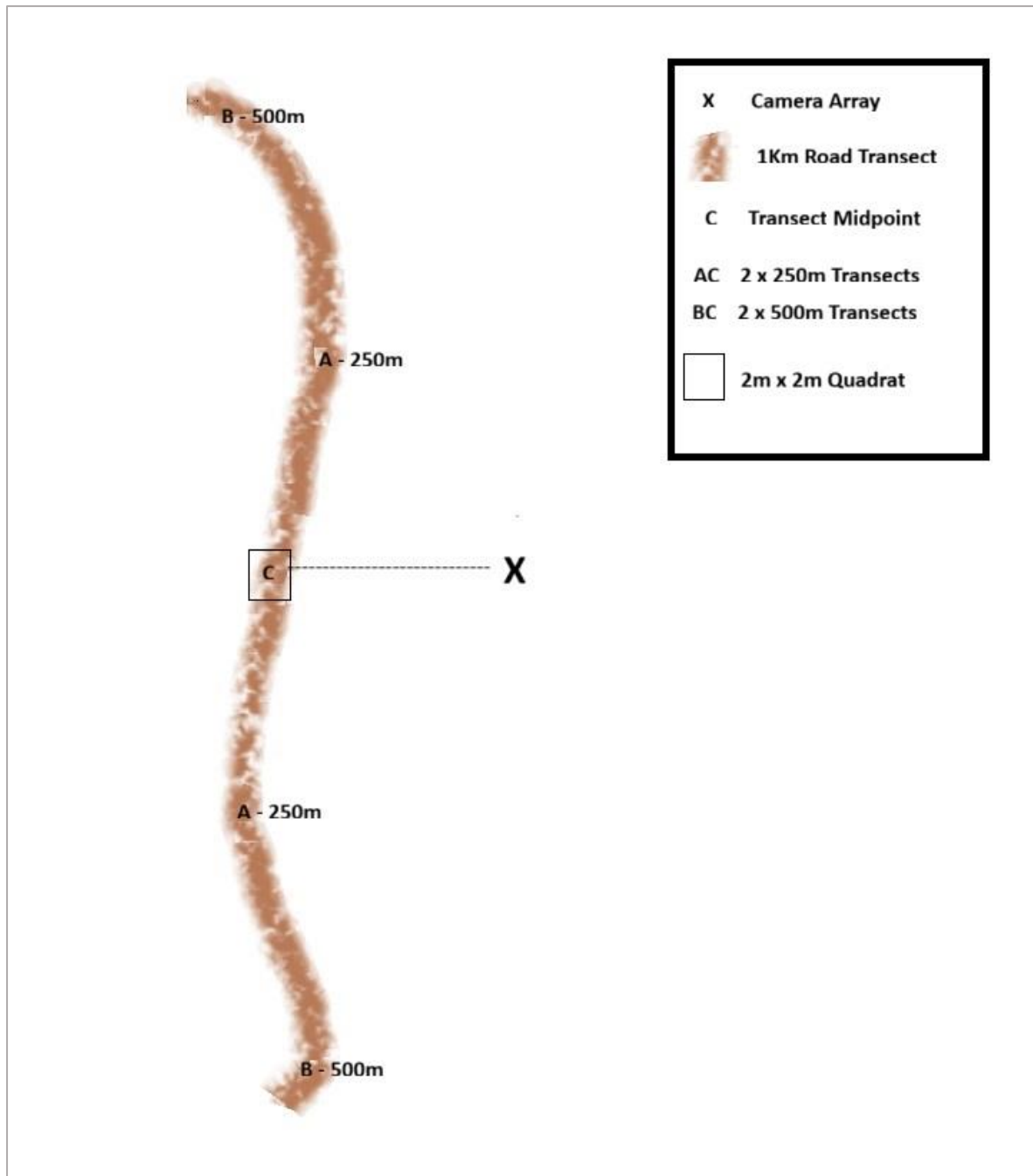


Figure 3.7: A schematic representation of each road transect proximate to each of the 15 experimental sites on Telperion Nature Reserve during the blue wildebeest (*Connochaetes taurinus*) decomposition project from January 2019 to January 2020)

I also marked the beginning and end of the transects in the low disturbance area with a Garmin GPSMap 64s™ (Appendix 4). Some of these ‘low disturbance’ transects were contiguous with one another and in such cases, I simply marked only the beginning and end of the entire set of transects and noted the end of one and the beginning of the next transect with my Garmin watch as I surveyed along the transect. Certain transects in the high disturbance areas were also very

close together and almost contiguous with one another. I implemented measurement and analysis protocols that took this into account and did not rely on spatial independence where necessary. By setting my Garmin Vivo Active™ GPS Sports Watch to vibrate after one km, I could keep track of where one kilometre segment ended and the next started on the contiguous segments.

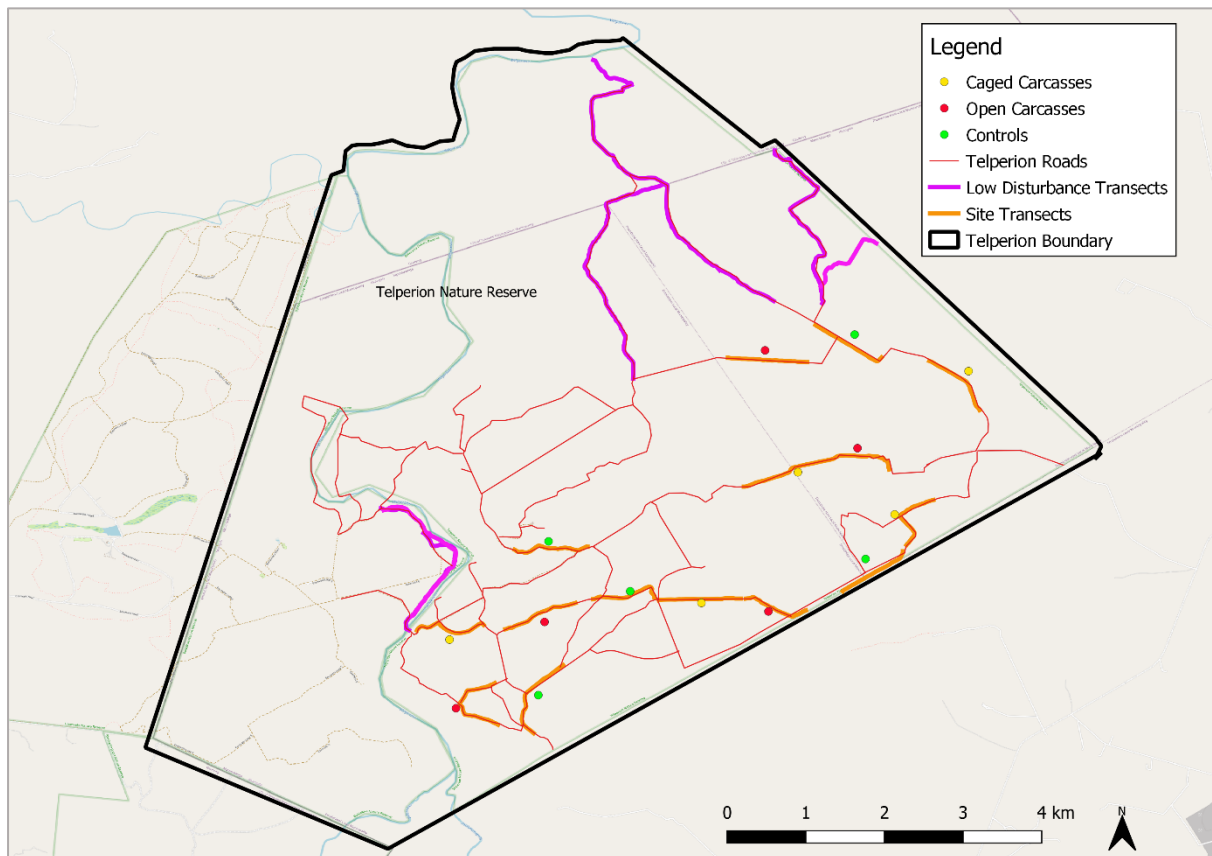


Figure 3.8: The roads, study sites, transects adjacent to experimental sites and low disturbance transects during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020.

A person walking at a moderate speed can walk one km in ~10 minutes (Bohannon 1997). Tracking, the process of finding and identifying the footprints and other signs left by animals on the road surface and adjacent surfaces and vegetation (Liebenberg 1990, Van Den Heever *et al.* 2017), requires more time. Thus, I allocated approximately 45-60 minutes to walk one km during sign survey sampling. I commenced all sign surveys early in the morning as soon as sufficient ambient light permitted unambiguous identification of tracks and field signs (Liebenberg 1990), and I ceased sign surveying by 11:30 as by midday the incident angle of the sunlight makes it difficult to discern tracks (Houser *et al.* 2009). Furthermore, vehicles driving along the roads later in the mornings, as other researchers started their work, would

obliterate the fresh tracks of nocturnal predators. It was thus necessary for me to conduct tracking surveys on all road transects as soon as the sun rose, before vehicles drove them.

I undertook four to seven hours of tracking, sampling between four and seven one km transects per day. I surveyed these transects iteratively as carcass decomposition proceeded (45 days of active decay) and then seasonally thereafter. I sampled each transect between five and 11 occasions over the course of a single year, including pre-sampling, active decay, and seasonal sampling. If the road surface had been disturbed by vehicles being driven along it, rendering tracks unidentifiable, before sampling could take place, I omitted the disturbed transect, and the closest transect was sampled in its place (Midlane *et al.* 2014). Unequal sampling across sites can be accounted for in statistical analyses (Mackenzie *et al.* 2002).

During active decay, I allowed at least three days to separate temporal replicates of the same transect. I deemed this sufficient to ensure that the same set of tracks were not counted during more than one sampling occasion, while still ensuring sufficient sampling to detect changes in predator activity close to experimental sites. After three days, older spoor that had previously been recorded would either have been obliterated by the weather or by vehicular and animal traffic or could clearly be confirmed as old by an experienced tracker.

I recorded all tracks and signs (e.g. scat and pastings) of predator presence. Both large and small predators often walk and mark (e.g. with scat, pastings or scrape marks) not only along roads, but also along game trails (Wilson and Delahay 2001, Hulsman *et al.* 2010, Mills *et al.* 2019), and therefore I also checked game trails at the locations where these intersected with roads. In addition, a two-metre strip on either side of the roads was also scanned for scats and tracks (Burgener and Gusset 2003).

I identified scats and tracks to species level, using a combination of personal field experience, various field guides (Murray 2011, Stuart and Stuart 2013, Gutteridge and Liebenberg, 2013, Van Den Heever *et al.* 2017), and the position and presence of accompanying confirmatory signs (Van Der Merwe *et al.* 2009) (for example fresh scats and pastings were often accompanied by tracks of the species that deposited them). I excluded from my analysis any signs/tracks for which identification could not be confirmed.

I subjected jackal tracks to additional sampling. This was deemed necessary as during pre-sampling it became evident that their tracks were widespread and common (present in 95% of total transects sampled) and simply recording their presence or absence within a transect was not sufficient to allow for behavioural analyses (e.g., landscape of fear and differences in jackal responses to caged, open and control sites). Therefore, I used track density within a 2 m x 2 m quadrat along each 1 km transect to further investigate their presence and the effects of their presence on other predators. I located the 2 m x 2 m jackal track density quadrats on the road adjacent to each experimental site at the centre point of each 1 km transect using the GPS location closest to the carcass and/or camera array (at control sites) (Figure 3.7, Figure 3.9 and Appendix 5).

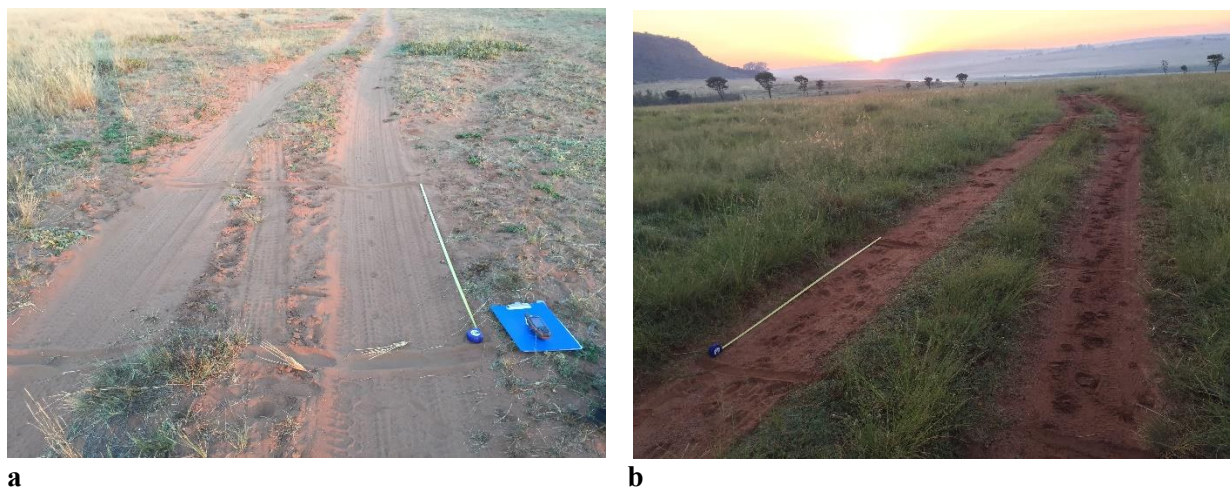


Figure 3.9: (a and b) Examples of 2 m x 2 m quadrats along a 1 km transect to assess black-backed jackal (*Lupulella mesomelas*) track density during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020.

I counted the total number of jackal footprints in each 2 m x 2 m quadrat. I did this, not to determine how many jackals were present, but rather to obtain a measure of jackal activity in the area. This activity could be a combination of, the number of individual jackals traversing the transect and/or the same individual traversing the transect numerous times and/or spending time within the transect (Figure 3.10, Figure 3.11 and Figure 3.12). For example, one jackal moving around within a transect may result in ~24 individual tracks within the transect. Four jackals simply moving through the transect may also result in ~24 tracks within the transect. Both these situations indicate higher jackal activity within the designated area than a transect with just one animal moving through and leaving the area in which case there are likely to be just six to eight individual tracks within the transect depending on how fast the animal was

moving. More tracks within the transect is therefore a sign of more jackal activity (either one animal spending time in the transect, multiple animals moving through the transect or both these scenarios combined).



Figure 3.10: A 2 m x 2 m quadrat along a 1 km transect to assess black-backed jackal (*Lupulella mesomelas*) track density during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020. This quadrat clearly shows two sets of black-backed jackal tracks, one on either side of the road, likely indicating two animals moving straight through the quadrat without stopping.



Figure 3.11: A 2 m x 2 m quadrat along a 1 km transect to assess black-backed jackal (*Lupulella mesomelas*) track density during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature reserve from January 2019 to February 2020. This quadrat shows many sets of black-backed jackal tracks going in a number of different directions and also shows some indications of black-backed jackals lying down inside the quadrat (See Figure 3.12 for close up).



Figure 3.12: A 2 m x 2 m quadrat along a 1 km transect to assess black-backed jackal (*Lupulella mesomelas*) track density during the blue wildebeest (*Connochaetes taurinus*) decomposition study on Telperion Nature Reserve from January 2019 to February 2020. This is a closer photo of the same quadrat in **Figure 3.11** and shows many sets of black-backed jackal tracks going in a number of different directions and also shows (red circles) some indications of black-backed jackals scratching the soil and lying down inside the quadrat.

CHAPTER 4: DATA ANALYSIS

Unless otherwise stated I conducted statistical analyses using Jamovi version 2.6.26 (The Jamovi Project 2023). Jamovi is a free open-source statistical program with a user-friendly interface, that functions as a graphical front end to Program R (R Core Team 2023). It executes analyses using R packages and links data acquisition with analytical tools. I conducted statistical analyses for occupancy modelling using the Programme PRESENCE (Hines 2006) (hereafter PRESENCE). I evaluated the outcomes from all inferential statistical tests at $\alpha = 0.05$.

I tested all data that were to be subjected to statistical analysis for normality using a Shapiro-Wilks test (Shapiro and Wilk 1965) (Appendix 6) and appropriate statistical analyses (parametric or non-parametric) were chosen depending on whether data were normally distributed or not. Furthermore, I also checked for equal vs unequal variances and chose appropriate statistical tests in Jamovi (The Jamovi Project 2023).

4.1. A broad comparison of survey methods

4.1.1. *Species Detection*

I recorded all species detected on Telperion during the year-long study period using both sign surveys and camera surveys. Furthermore, I recorded the number of detections of each species by each survey type and constructed a correlation matrix to determine if there were correlations between the number of camera images and the number of tracks recorded for each species. I added the mean mass and home range size of each species (Hunter 2020) to the correlation matrix to determine whether the mass and / or the home range size of each species influenced detection on cameras or sign surveys.

4.1.2. *Seasonality of species detections*

I compared the seasonal number of species detected by each survey type using an independent samples t-test (Fowler *et al.* 2013).

4.1.3. Relative efficiency of each survey type

Relative efficiency refers to how well a survey method detects species. It is calculated by dividing the number of species found by that survey type, by the total number of species identified by both methods combined (Barea-Azcon *et al.* 2007). I calculated the relative efficiency of each survey type by dividing the species richness of each survey type at each experimental site, by the total species richness at that site from both survey types as per Barea-Azcon *et al.* (2007):

$$\text{Relative efficiency of survey type} = \frac{\text{Species richness detected by survey type}}{\text{Total species richness detected by both survey types}}$$

I compared the relative efficiency of survey types using a paired samples t-test (Fowler *et al.* 2013). The paired samples t-test is appropriate here as each site was sampled in two ways (camera surveys and sign surveys). Therefore, each site presents a pair of results.

4.1.4. Latency to detection

Using sign survey and camera data, I determined the latency to detection (LTD) (time from the start of active monitoring until a species is first detected) for each species, for each survey type. I then conducted a Kruskal-Wallis ANOVA (Kruskal and Wallis 1952) to determine if there were differences in the LTD results between survey types. I conducted *post hoc* analyses using Dwass-Steel-Critchlow-Fligner pairwise comparisons (Hollander *et al.* 2013) to identify which specific groups differed following a significant outcome for the overall test.

4.1.5. Species accumulation curves

Species accumulation curves are a useful means to assess sampling efficiency and can be used to indicate the adequacy of a survey type in representing the species of a particular area. These curves provide the number of observed species as a function of sampling effort (Thompson and Withers 2003, Thompson *et al.* 2003). I constructed two types of species accumulation curves. Firstly, collector's curves, by placing days to detection (sampling effort) on the x-axis of the graph and the cumulative number of species detected by each survey type on the y-axis (Rovero *et al.* 2014). These curves show when the rate of detecting new species slows down (when the curve starts to flatten out). The flattening curve (asymptote) suggests that most species have likely been recorded and that sampling effort is sufficient. I smoothed the curves using the flexplot module in Jamovi (The Jamovi Project 2023) which uses locally estimated scatterplot

smoothing (Loess) (Jacoby 2000). Secondly, I constructed rarefaction curves for the sign survey and the camera survey data by using the iNEXT online software (Chao *et al.* 2014, Chao *et al.* 2016) and performed $B = 1000$ bootstrap resamples. I compared these rarefaction curves from sign and camera survey data over the entire study period by running asymptotic analyses in iNEXT online (Chao *et al.* 2014, Chao *et al.* 2016). I compared collector's curves for the entire study period and seasonally.

4.1.6. Cost-effort comparison of survey types

I compared costs associated with each survey type (equipment, petrol and the cost of employing an experienced tracker for the duration of the sign surveys) to ascertain which survey type was the most cost effective. Budgets included initial costs of equipment as well as monthly running costs for each survey type.

4.2. The effect of carrion on species diversity

I calculated three measures of species diversity: Species richness, a Shannon-Weiner species diversity index and a Gini-Simpson species diversity index. Species richness is simply the number of species in a community while species diversity consists of two components (species richness and species evenness). Species evenness considers that some species are common, and some are rare (Peet 1974). All diversity measures/indices depend on sampling effort and rare species require disproportionately larger sampling effort to be detected than common species. Different diversity measures or indices vary in terms of the weight they place on either species richness or evenness (Crupi 2019). Hence, I chose three different diversity measures to obtain a more complete understanding of species diversity for the experimental sites.

4.2.1. Species Richness

Species richness (denoted by S) is simply a count of the number of species present at a site (Crupi 2019). Although it is the most intuitive index of species diversity, it is also the most sensitive to differences in sampling effort, as it weights all species equally, regardless of their relative abundances (Chao and Chiu 2016, Crupi 2019). Rare species would therefore have equal weight to common species, even though they have a higher probability of going undetected and require greater sampling effort to detect (Chao and Chiu 2016).

I calculated total predator species richness for the reserve (from all transects sampled) and for each treatment type (control, open and caged), by simply adding up the number of species detected on the reserve and then separately for each treatment type. This was calculated for sign surveys and for camera surveys from all experimental sites. I used a one-way ANOVA (Scheiner and Gurevitch 2001, Fowler *et al.* 2013) to compare species richness between treatment types.

4.2.2. Shannon-Weiner species diversity

This is an uncertainty index derived from information theory (Crupi 2019). It considers both species richness and evenness but places more weight on richness than evenness (Jost 2019). The higher the index, the higher the species diversity. The minimum value possible for this index is zero, which would indicate that only one species is present (Crupi 2019). There is no upper limit to the index, but numbers are usually low, (e.g. for a community composed of 100 species using the natural logarithm as the base, the maximum possible value (H) for the index would be 4.605). Typical values for this index using real ecological data usually range from $H = 1.5 - 3.5$ (Rain 2020).

The Shannon-Weiner species diversity (Shannon 1948) index was calculated using the following equation:

$$H = - \sum \left(\frac{n}{N} \ln \frac{n}{N} \right)$$

Where: H = Shannon-Weiner Species Diversity
 n = Number of individuals of a specific species
 N = Total number of individuals
 $\ln$ = The Natural Log

In my study I calculated the Shannon-Weiner Index using the number of independent detections of a species as a proxy for the number of individuals of a species as most species detected were not individually identifiable. In order to ensure that detections were independent, a species was only counted once per 1km transect (Karanth *et al.* 2011) no matter how many tracks of that

species occurred in that transect unless the tracks were clearly different individuals e.g. male and female leopard tracks where the size difference is very obvious to an experienced tracker.

4.2.3. Gini-Simpson Species Diversity

To understand the Gini-Simpson index, an explanation of the Simpson's index (from which it is derived) is required. The Simpson index considers both species richness and species evenness, but compared to the Shannon's index, it places more emphasis on evenness than richness (Guiasu and Guiasu 2010). Simply put, it represents the probability that two randomly selected individuals will be of the same species. This probability decreases with increasing species richness; therefore, the Simpson's index also decreases with increasing species richness. This is counterintuitive and consequently I used the more meaningful Gini-Simpson Species Diversity index, which is simply 1-Simpson Index. Gini-Simpson's Index therefore increases with increasing species richness (Crupi 2019). Values for the Gini-Simpson diversity index range from 0 to 1 with 1 representing infinite diversity and 0 representing no diversity (Guiasu and Guiasu 2010).

The Gini-Simpson species diversity index (Simpson 1949, Guiasu and Guiasu 2010) was calculated using the following equation:

$$1 - D = 1 - \left(\frac{\sum n(n-1)}{N(N-1)} \right)$$

Where: $1 - D$ = Gini-Simpson Species Diversity
 n = Number of individuals of a specific species
 N = Total number of individuals

In my study I calculated the Gini-Simpson Index using the number of independent detections of a species as a proxy for the number of individuals of a species as most species detected were not individually identifiable. In order to ensure that detections were independent, a species was only counted once per 1km transect (Karanth *et al.* 2011) no matter how many tracks of that species occurred in that transect unless the tracks were clearly different individuals e.g. male and female leopard tracks where the size difference is very obvious to an experienced tracker.

Using the sign survey data I collected, I calculated Shannon-Wiener and Gini-Simpson species diversity for transects stretching 250 m in both directions from the centre point of each transect proximate to each experimental site (Figure 3.7). I used a One Way ANOVA (Fowler *et al.* 2013) to compare species diversity between treatment types. Where I found significant outcomes from the ANOVA, I used a Tukey *post hoc* test (Keselman and Rogan 1977) to identify where the significant differences were. The above process was repeated for distances of 500 m in both directions from the centre point of each transect proximate to each experimental site (Figure 3.7) to ascertain if increasing distance from each site influenced species diversity.

Following the same data analysis methodology, I calculated species richness, Shannon-Weiner species diversity and Gini-Simpson species diversity for camera surveys based on the species captured on still photographs and videos by the pairs of cameras at each experimental site. For camera traps, a detection was considered independent of a previous detection of the same species if the interval between detections was > 30 minutes (Thorn *et al.* 2009). If the time between successive videos was < 30 minutes, then I deemed all those detections to be the same individual.

4.2.4. Rank abundance curves

A rank abundance curve is useful for displaying relative species abundance. The rank abundance curve visually displays species richness and species evenness (Avolio *et al.* 2019). The x axis represents the species rank in order of decreasing abundance with the most abundant species being assigned a rank of 1. The y axis of the graph represents the relative abundance of each species. This is calculated by tallying the total number of detections of each species (n) and dividing this by the total number of detections of all species (N).

On a rank abundance curve, species richness is displayed as the number of different species on the graph, in other words the number of species that were ranked on the x axis. The slope of the graph depicts the species evenness. A steep gradient signifies low evenness as the high-ranking species have much higher abundance than the lower ranking species. A shallow gradient indicates high evenness as the abundances of different species are similar (Avolio *et al.* 2019). I created rank abundance curves using species data from both the 250 m sign survey transects and camera surveys and these curves were compared for control, caged and open experimental sites.

4.3. The Impact of Fire

Sometime between the autumn and winter sampling periods a fire passed through site 6 (an open carcass site). This fire removed all vegetation within range of the camera providing a much better field of view and potential for cameras to capture some of the smaller carnivore species that may have been overlooked at other sites and treatment types. Furthermore, the flush of fresh green grass likely attracted herbivores to the area the following spring (Archibald *et al.* 2005). This in turn had the potential to draw predatory species to the area, attracted to the herbivorous insects, rodents, birds and larger mammals. I was concerned that the fire could skew the results of species diversity analyses and thus where appropriate further analyses were undertaken and site 6 was excluded. To allow for meaningful comparisons with one less open site I excluded the closest control site (Site 5) and caged site (Site 9) to site 6 and the fire affected area from these analyses.

4.4. Carrion and the landscape of fear

4.4.1. Landscape of fear investigations from sign survey data

To investigate a possible mesopredator landscape of fear associated with the carcasses, I divided predators into two categories. Category one (referred to as dominant predators) included leopard, brown hyaena and jackal. Although these three species are not typical apex predators in Africa, in the absence of lion and spotted hyaena intraguild relationships can be altered (Palomares and Caro 1999, Allen *et al.* 2015, Curveira-Santos *et al.* 2021, Davis *et al.* 2021). In these altered ecosystems, these three species are likely to intimidate smaller or solitary predators at carcasses, due to their size and / or social structure (Caro and Stoner 2003, Williams *et al.* 2017, Selva *et al.* 2019, Kamler *et al.* 2020, Tobajas *et al.* 2021). They are also commonly known to scavenge and prey on smaller predators (Hayward *et al.* 2006, Williams *et al.* 2018, Kamler *et al.* 2020). The responses of other predators (referred to in this study as mesopredators) to large carcasses is seldom recorded and consequently not as well understood (Begg *et al.* 2003, Roberts *et al.* 2007, De Vries *et al.* 2011, Thiel 2011, Kamler *et al.* 2012, Bizani 2014, Klare *et al.* 2014, Amiard *et al.* 2015, Kamler *et al.* 2015, Pohl 2015, Shaw and Ryan 2015, Carter *et al.* 2017, Zemouche 2018, Rowe-Rowe 2019, Do Linh San *et al.* 2020) and may be influenced positively or negatively by the presence of species commonly associated with carcasses (Avenant and Nel 2002).

To understand mesopredator (all predators excluding jackal, leopard and brown hyaena) presence in relation to carcasses and the scavengers associated them I investigated a relationship between the following variables:

- a) Jackal track density (from 2 m x 2 m quadrat at the centre of each 1 km transect) associated with each experimental site.
- b) Leopard track presence in each 1 km transect associated with each experimental site
- c) Brown hyaena track presence in each 1 km transect associated with each experimental site
- d) Mesopredator track presence in each 1 km transect associated with each experimental site
- e) Species count from mesopredator tracks within 250 m of experimental sites
- f) Species count from mesopredator tracks within 500 m of experimental sites

I constructed a correlation matrix for these variables to evaluate correlations (positive or negative) between them. I then checked correlations for significance using Pearson's correlation coefficient (Fowler *et al.* 2013) for normally distributed data and Spearman's correlation coefficient (Fowler *et al.* 2013) for data that were not normally distributed (Fowler *et al.* 2013).

Based on the resultant correlations, I proposed three candidate models to explain the relationship between experimental treatments. I constructed these models to predict mesopredator presence in association with carcasses using binomial logistic regression. Covariates ("treatment type", "jackal track density" and "season") were added sequentially to create three different models.

- In model one I used "treatment type" as a predictor with "control" as the reference level.
- In model two I retained "treatment type" as a predictor with "control" as the reference level and added "jackal track density" as a second predictor.
- In model three I retained the previous two predictors and added "season" as a third predictor with "active decay" as the reference level.

Thereafter I used information theoretic approaches for model selection to identify the most parsimonious model that best supported the data. To assess overall model fit I considered the Akaike Information Criterion (AIC) score (Akaike 1998), the Bayesian Information Criteria (BIC) score (Aho *et al.* 2014), McFadden's Pseudo R^2 (McFadden 1972) and a likelihood ratio test (Moreira 2003) score, comparing the full model against an intercept only/null model. I considered the model with the lowest AIC score to be most parsimonious and models with ΔAIC values > 2 to have significantly less support than the previous model.

I carried out assumption checks for the model by investigating collinearity statistics for the various predictors and checking that Tolerance scores and Variance Inflation Factor (VIF) scores were within acceptable levels (Midi *et al.* 2010). Tolerance and VIF are key statistics used to diagnose high degrees of correlation among independent predictor variables in a regression model (Tay 2017, Fox 2019). They are reciprocals of one another. The tolerance score measures the percentage of variance in a given predictor variable that cannot be explained by all the other predictor variables in the model. Tolerance score values close to '1' indicate low multicollinearity as most of the variable's variance is unique and not shared with other variables in the model. The VIF quantifies how much of the variance of an estimated regression coefficient is inflated due to collinearity with the other independent variables (Tay 2017, Fox 2019). VIF scores close to '1' indicate a complete absence of multicollinearity. Values between '1' and '5' suggest moderate collinearity. Values above '5' are a cause for concern, indicating severe multicollinearity (Tay 2017, Fox 2019).

I then used the most parsimonious model to construct plots of estimated marginal means for the model. These are estimates of what the means would be if all covariates had the same sample size or the same mean value (Fieberg *et al.* 2009). Thus, the plots are a more accurate comparison of group means by accounting for other variables in the model and allowed me to visualise interactions among variables (Fieberg *et al.* 2009)

Next, I assessed the predictive power of the model using specificity and sensitivity measures (Coughlin *et al.* 1992) which are provided in the outputs for binomial logistic regression models. Sensitivity (true positive rate i.e. mesopredators are truly present when predicted to be present) and specificity (true negative rate i.e. mesopredators are truly absent when predicted to be absent) are key metrics that describe a model's predictive accuracy for each outcome class (in this case the presence or absence of mesopredators at treatment sites). As there is often

an inherent trade off, i.e., increasing sensitivity tends to decrease specificity and *vice versa*, the cut-off value is often adjusted (as I did in this analysis) to correspond with where the sensitivity and specificity coincide on a specificity vs sensitivity graph (Habibzadeh *et al.* 2016).

4.4.2. Landscape of fear investigations from camera traps

Using camera data, I investigated a correlation between the number of mesopredator visits and the number of jackal visits at each site. I then checked these correlations for significance using Pearson's correlation coefficient (Fowler *et al.* 2013) for normally distributed data and Spearman's correlation coefficient (Fowler *et al.* 2013) for data that were not normally distributed.

Furthermore, I investigated correlation of the above two variables seasonally using Spearman's (Fowler *et al.* 2013) and Kendall's Tau B (Fowler *et al.* 2013, Bishara and Hittner 2017) correlation coefficients. These coefficients are both robust for non-parametric data and Kendall's Tau B is not sensitive to small sample sizes (Bishara and Hittner 2017).

4.5. Carrion and predator occupancy

Using sign survey data and the programme PRESENCE (Hines 2013), I constructed occupancy models for mammalian predators on Telperion. Camera data for the purposes of developing occupancy models were too sparse for most predator species other than jackals to build occupancy models and therefore I only used sign survey data for this analysis.

Occupancy studies assume population closure for the duration of the study period, and my study limited it's sampling to one year to minimise the likelihood of species disappearing from or new species colonising the study area within the timeframe of the study. For occupancy modelling, closure is defined at a species level and not associated with individual animals as would be the case with population studies and thus longer timeframes for closure are acceptable (Mackenzie *et al.* 2017). Further, my study assumed an approach where estimates of occupancy were interpreted as the probability of site use rather than the proportion of area occupied (Mackenzie *et al.* 2006, Strampelli *et al.* 2018) and thus the closure assumption could be relaxed.

For inferences from occupancy models to be considered valid, species detections need to be independent of each other (Mackenzie *et al.* 2006). I avoided temporal dependence of sign

surveys by ensuring that at least three days passed between samplings of the same site. Spatial independence was not possible as experimental sites were relatively close together and transects were in many cases sequential segments of roads. However, many animals, including cryptic carnivores, travel along roads and trails and these are therefore logical places to survey such elusive species. A Markovian model for spatial dependence was developed by Hines *et al.* (2010) that accounts for the spatial correlation of animal sign along sequential segments of a trail, thus overcoming any violation of this assumption of occupancy models and can be used where appropriate.

Predator detection is imperfect and varies from site to site and among species. The modelling of relevant experimental site and sampling specific covariates (in this case habitat type, carcass presence, substrate type and human disturbance) in occupancy analysis ensured that this study did not violate the assumption that both occupancy and detection probabilities remain constant across survey sites (Midlane *et al.* 2014). I separated survey roads into 1 km transects and used these as replicates (Thorn *et al.* 2010). These were the same 1 km transects used for sign surveys. The 1 km transects were assigned a binary value of one to indicate detection of a species or zero to indicate non-detection of a species.

For site specific covariates I initially assigned each 1km transect a habitat type: grassland, riverine, woodland or rocky ridges. However, due to low sample sizes, I further condensed habitat type into two categories (Strampelli *et al.* 2018), Grassland and Other, for statistical analysis as other studies (Thorn *et al.* 2011) have found that for small sample sizes models with too many covariates may fail to converge.

I considered three survey specific covariates in the occupancy models:

a. Human disturbance.

I allocated the transects ($n = 15$) adjacent to the 15 experimental sites as high disturbance during active decay (because of high researcher activity) and low disturbance during seasonal sampling (when there was reduced researcher activity). The other transects ($n = 22$) were allocated as low disturbance for the entire duration of the study as they were in areas distant from the 15 experimental sites and were therefore subject to markedly less researcher traffic and disturbance.

b. Carcass presence.

Of the transects (n = 15) adjacent to the 15 experimental sites, I classified control sites (n = 5) as having no carcass present throughout the study. I classified sites with carcasses (caged and open) (n = 10) as having a carcass present during the period of active decay only. Thereafter I classified sites with carcasses as not having a carcass present. Thus, carcass presence refers to actively decaying carcasses only. The other 22 sites were classified as having no carcasses.

c. Substrate quality

I assessed substrate quality, the likelihood of tracks being visible on a given substrate, (Funston *et al.* 2010, Midlane *et al.* 2014) for each transect for each sampling session. Substrate was allocated a score of 1, 2 or 3 depending on the quality of the substrate:

- A score of 1 indicated transects where tracks were very hard to detect due to grass or rocks covering the tracking surface.
- A score of 2 indicated a surface where tracks were detectable but obscured by either vehicles or other tracks, or the presence of very thick sand that made species identification difficult.
- A score of 3 indicated a hard surface covered by fine soft sand, or a muddy surface, making track identification easy.

I carried out a Chi-square (χ^2) tests of independence (Fowler *et al.* 2013) to check for relationships between the presence of predator tracks and the various covariates (habitat, disturbance, carcass presence and substrate quality). I used the results of this test to guide the choice of covariates used for occupancy modelling in PRESENCE (Hines 2013). Covariates with significant results were those that resulted in the most parsimonious models in PRESENCE (Hines 2013).

I used the programme PRESENCE (Hines 2013) for all occupancy analyses and constructed standard detection histories for each species (Mackenzie *et al.* 2006). These were essentially a matrix of 0's and 1's recorded during repeated surveys at each site. Zero indicates non detection and 1 indicates detection. These were imported into PRESENCE (Hines 2013) along with corresponding covariate values.

Initially, processing detection histories in PRESENCE (Hines 2013) without covariates allowed me to choose between 'single season', 'multi season' and 'correlated detection' occupancy models for each species. I used the top ranked model with the lowest AIC score

from this process to create a null model for each species that was then used for further analyses with covariates (Hines *et al.* 2010, Thorn *et al.* 2011). In each case the null model with the lowest AIC score was the ‘single season’ null model and consequently this was used for further analyses.

I fitted this null model to each species detection history by holding both occupancy (ψ) and detection probability (ρ) constant [$\psi(.) \rho(.)$]. I fitted subsequent models by including various covariates that may affect ψ or ρ . I used AIC scores to rank the various models (Anderson and Burnham 2004). I did not use the small sample correction AICc (Burnham and Anderson 2002) as effective sample size could not be determined (Mackenzie *et al.* 2006, Hines *et al.* 2010, Thorn *et al.* 2011). The lowest AIC score indicated the top ranked model. The difference in AIC score between the null model and another model was denoted by ΔAIC . I considered models with $\Delta AIC > 2$ relative to the null model to be strongly supported (Mackenzie *et al.* 2017) compared to the null model [$\psi(.) \rho(.)$]. Covariate models with $\Delta AIC < 2$ between themselves and the top model also showed some support (Midlane *et al.* 2014).

To build candidate models, I considered survey specific covariates, affecting detection probability (p) first (carcass presence, disturbance and substrate quality). I carried out univariate analyses of each covariate as well as multivariate analysis of additive combinations of covariates in PRESENCE (Hines 2013), modelling the sum of their individual effects while holding occupancy constant. I excluded covariates with non-significant effects from the final model set.

The models with the lowest AIC scores were carried forward to a model with the site-specific covariate (habitat type) included. I then conducted univariate analyses in PRESENCE (Hines 2013). I considered the resulting models with the lowest AIC score for each species to be the model that best explained occupancy for that species.

4.6. Predator presence and behaviour from camera traps

I noted all predators recorded visiting the experimental sites and the behaviour of each species whilst at the experimental sites. If a species produced too few records (fewer than 30) for meaningful statistical analysis of behaviour, I then simply recorded basic behavioural data including number of visits, interspecific encounters (if any), records of feeding activity, number of animals present per visit, nocturnal or diurnal activity and scent marking activity for each

species. Where enough data were available for a species (only in the case of jackals) for meaningful behavioural analyses, I carried these out as below.

I only used camera video footage to analyse jackal behaviour as photographic results, being a snapshot in time, give less behavioural insight (Caravaggi *et al.* 2017, Tagg *et al.* 2018, Janisch *et al.* 2021, Green *et al.* 2023). For a comparison of the number of jackal visits from video footage only to stills and videos combined see Appendix: 7 and Appendix: 8.

4.7. Jackal visitation frequency and duration

4.7.1. Jackal visitation frequency

I recorded the number of Jackal visits to each site. I recorded a visit as a new visit if the time between successive videos was > 30 minutes (Thorn *et al.* 2009). If the time between successive videos was < 30 minutes, then I deemed all those videos to be the same visit. Using QGIS I created a heatmap to visualise any variation in frequency of jackal visits to different sites (Kulyk and Sossa 2018, Pawluczuk and Iskrzyński 2023).

To determine if the frequency of jackal visits differed significantly for all three treatment types combined and per treatment type over the entire study period and seasonally, I conducted a Kruskal-Wallis ANOVA (Kruskal and Wallis 1952) and used a Dwass-Steel-Critchlow-Fligner *post hoc* test to interrogate pairwise comparisons (Hollander *et al.* 2013).

4.7.2. Duration per visit at each treatment type

It was likely that several consecutive videos would represent a single visit. Where this occurred, I calculated time spent per visit by multiplying the number of videos recorded in each visit by 15 seconds as each video was 15 seconds long. This gave a proxy for actual time spent (in seconds) at each experimental site per visit. For example, 1 visit may have comprised 30 videos in this case I multiplied the number of videos (30) by the time of each video (15 s) to obtain a time proxy ($30 \times 15 \text{ s} = 450 \text{ s}$) for the duration of the visit. I then compared time spent per visit among treatments over the course of the entire study period using a Kruskal-Wallis ANOVA (Kruskal and Wallis 1952) and then conducted a Dwass-Steel-Critchlow-Fligner *post hoc* test to interrogate pairwise comparisons (Hollander *et al.* 2013).

4.7.3. Seasonal variation in time spent per visit irrespective of treatment type

I conducted seasonal analysis of time spent per visit to determine if time spent per jackal visit differed significantly per season irrespective of treatment type. I conducted a Kruskal-Wallis ANOVA (Kruskal and Wallis 1952) on these data and used a Dwass-Steel-Critchlow-Fligner *post hoc* test to interrogate pairwise comparisons (Hollander *et al.* 2013).

4.7.4. Seasonal variation in time spent per visit at each treatment type

I conducted further seasonal analysis of time spent per visit among treatments to determine if time spent per jackal visit differed significantly seasonally per treatment type. I conducted a Kruskal-Wallis ANOVA (Kruskal and Wallis 1952) on these data and used a Dwass-Steel-Critchlow-Fligner *post hoc* test to interrogate pairwise comparisons (Hollander *et al.* 2013).

4.7.5. Seasonal variation in time spent per visit at open carcasses

I anticipated that open carcasses would receive more attention from jackals and thus carried out further seasonal analysis specifically on this treatment type. I conducted a Kruskal-Wallis ANOVA (Kruskal and Wallis 1952) on these data and used a Dwass-Steel-Critchlow-Fligner *post hoc* test to interrogate pairwise comparisons (Hollander *et al.* 2013).

4.7.6. Jackal visits per day

I compared the daily jackal visitation rate among treatments to determine if jackal visits per day differed significantly per treatment type irrespective of season. I added together jackal visits per site for each day of sampling if they fell on the same day (a day was defined as beginning at 00:01 and ending at 00:00) and belonged to the same treatment type. This resulted in visit totals per day per treatment type. I conducted a Kruskal-Wallis ANOVA (Kruskal and Wallis 1952) on these data and used a Dwass-Steel-Critchlow-Fligner *post hoc* test to interrogate pairwise comparisons (Hollander *et al.* 2013).

4.7.7. Seasonal jackal visits per day for each treatment type

I analysed the number of visits per day for each treatment type separately for each season to determine if season influenced number of visits per treatment type. I then conducted a Kruskal-Wallis ANOVA (Kruskal and Wallis 1952) on these data and used a Dwass-Steel-Critchlow-Fligner *post hoc* test was used to interrogate pairwise comparisons (Hollander *et al.* 2013).

4.8. Carrion and jackal diel activity

To evaluate variation in jackal diel activity patterns at sample sites, I converted the time of each video to decimal hours in order for time to be treated as a continuous variable for statistical analyses. I then created density plots per treatment type using the time in decimal hours of each video. Jamovi creates density plots using kernel density estimation (KDE) (Wand and Jones 1994). A density plot estimates the probability density function of the variable (in this case number of visits at a specific time of day in decimal hours) and uses kernel smoothing to display the distribution of continuous data using a continuous curve, making it cleaner than a histogram (Węglarczyk 2018). These density plots represent the probability density function of the time of day (in decimal hours) of jackal visits to sample sites. I conducted a Kruskal-Wallis ANOVA (Kruskal and Wallis 1952) on the time of day (in decimal hours) data of every video for each treatment type and used a Dwass-Steel-Critchlow-Fligner *post hoc* test to interrogate pairwise comparisons (Hollander *et al.* 2013).

4.9. Carrion, lunar phase and jackal activity

I investigated jackal activity relative to lunar phase (proportion of the lunar disc visible), for each treatment type for the entire study period and seasonally. I attributed a proportion of lunar disc visible value (from 0 to 100%) to each jackal visit video by using the Heavens Above (Peat 2023) database. This database provides moon phase (proportion of the lunar disc visible) and illumination data for each date. Although cloud cover may affect nocturnal visibility, this was not considered as moonlight can penetrate total cloud cover (Ferguson *et al.* 1988). I used proportion of the lunar disc visible (%) rather than lunar phase so that I could treat it as a continuous variable for kernel density estimation (KDE) (Wand and Jones 1994). To evaluate jackal activity relative to proportion of the lunar disc visible, I created a density plot for each treatment type. These density plots represented the probability density function of the proportion of the lunar disc visible (%) during jackal visits to sample sites. I conducted a Kruskal-Wallis ANOVA (Kruskal and Wallis 1952) on overall and seasonal data and used Dwass-Steel-Critchlow-Fligner *post hoc* tests (Hollander *et al.* 2013) to interrogate pairwise comparisons of proportion of lunar disc visible data for each treatment type during each visit.

4.10. Carrion and jackal group size

For each jackal visit, I noted the number of jackals present. To determine if the number of jackals per visit differed significantly per treatment type, I conducted a Kruskal-Wallis ANOVA (Kruskal and Wallis 1952) on these data and used a Dwass-Steel-Critchlow-Fligner *post hoc* test (Hollander *et al.* 2013) to interrogate pairwise comparisons.

4.10.1. Jackal group size and lunar phase

To determine if proportion of the lunar disc visible (%) had any effect on jackal group size I constructed a correlation matrix (Pearson 1896). As the data were non-normally distributed, I evaluated correlations using Spearman's correlation coefficient (Spearman 1987, Fowler *et al.* 2013).

4.11. Carrion and jackal vigilance behaviour

To determine whether jackals displayed different levels of vigilance at different treatment types, I noted the presence or absence of overt vigilance (Le Saout *et al.* 2015, Haswell *et al.* 2018) for each video. I defined overt vigilance as when a jackal lifted their head above shoulder height, with ears pricked and ceased all other activity (e.g. chewing, feeding, grooming) for any length of time (Le Saout *et al.* 2015, Haswell *et al.* 2018). I used a Chi-square test of independence (McHugh 2013) to test significant differences between records of 'vigilance' vs 'no vigilance' between the treatment types and conducted *post-hoc* tests consisting of an analysis of Pearson's residuals and adjusted standardised residuals (Okwonu *et al.* 2023).

4.12. Jackal feeding behaviour

As jackals could only access carrion at open carcass sites, I could only record feeding behaviour at these experimental sites (Sites 3, 6, 8, 12 and 15). For each video, whether the jackal tried to feed on the carcass was assessed. When jackals attempted to feed, I recorded 'success' or 'failure' of such attempts. I identified 'success' as when the jackal removed, chewed and swallowed a piece of carrion from the carcass. I identified 'failure' as when the jackal tugged or scratched at the carcass but was unable to remove any material from it to eat. Additionally, I recorded any other behaviours related to feeding proximate to the carcass (for instance, feeding on other species that may also be attracted to the carcasses) and analysed accordingly.

I then created density plots of jackal feeding behaviour based on what they were eating at the carcass over time to see if this changed over time (Number of days after deployment) using KDE (Wand and Jones 1994). The density plots were used to estimate the probability density function of the number of videos of jackals feeding over time and used kernel smoothing to display the distribution of continuous data using a continuous curve (Węglarczyk 2018).

4.13. Variability in jackal response to available carrion

I anticipated that jackal visitation to sites (the number of times a jackal visited a specific site) might be variable and thus developed a model to understand the factors that may cause such variability. Several variables may have had an influence on which sites jackals preferred to visit. The candidate variables were:

Dependent variable – Seasonal Jackal Visits. The number of jackal visits per site per season. Jackal visits to each site were recorded. As jackals are not individually identifiable, a new visit was recorded if the time between successive videos was > 30 mins (Thorn *et al.* 2009). If the time between successive videos was < 30 mins, then all those videos were deemed to be the same visit.

Independent variables

A – Variables associated with the number of species at each site.

- **Total species richness:** This was calculated as the total number of mammal species (excluding jackals) recorded on cameras at a specific site.
- **Total Gini-Simpson species diversity:** This was calculated for each site using camera visits for all mammal species excluding jackals.
- **Total Shannon-Weiner species diversity:** This was calculated for each site using camera visits for all mammal species excluding jackals.
- **Total number of visits by all mammal species:** The total number of visits on cameras for all mammal species (excluding jackals) was recorded. For each species, distinguishing between individual animals was not possible, thus a new visit was recorded if it occurred > 30 mins after the previous detection.

As all of the above variables are associated with the number of species to visit each site, there were problems of collinearity when used together in the model, thus I included each of the

above candidate variables into the null model (detailed below) separately. I then used the candidate variable that produced the model with the lowest AIC score (Akaike 2003, Kuha 2004, Aho *et al.* 2014) for all models going forward.

B – Environmental variables.

- **Habitat type:** I determined the broad habitat type for each experimental site by superimposing the GPS location of each site onto a map of broad vegetation types (SANBI 2018) for Telperion. I allocated the vegetation type within which that GPS location fell as the habitat type for that location.

C - Anthropogenic disturbance variables.

- **Distance (km) to the nearest reserve boundary:** I calculated this distance using a straight line from the camera array at each experimental site to the nearest reserve boundary in QGIS (QGIS version 3.28.9 2024).
- **Distance (km) to nearest human infrastructure:** I calculated this distance using a straight line from the camera array at each experimental site to the nearest human infrastructure (including housing and offices) using QGIS (QGIS version 3.28.9 2024). I did not consider roads for these calculations as all sites were proximate to roads, so they were unlikely to account for variability in jackal visitation to sites.

D - Other variables.

- **Subadult jackal presence:** I noted subadult and/or juvenile jackals in close proximity to the camera array of four sites (6, 12, 14 and 15) on a number of occasions during active decay and to a lesser extent during summer sampling. It was thought that the proximity of these immature jackals to specific sites could be an indicator of a nearby den site (Ferguson *et al.* 1988). The proximity of food to a den site may influence the foraging behaviour of jackals in relation to that food (Loveridge and Macdonald 2001). Therefore, I recorded the presence or absence of subadult jackals at a site across the entire study period and seasonally. (Subadults and/or juveniles were in the presence of an adult in each sighting. Subadults and/or juveniles were visibly smaller in stature and had duller colouration without the well-defined black saddle marking that is typical of adult jackals).
- **Treatment Type:** (Control, Open or Caged) of each visit was noted.

- **Season:** (Active decay, Autumn, Winter, Spring, Summer) for each visit was noted.

I created a GLMM using the GAMLj3 package (GAMLj 2025). I chose this type of model as some variables were clustered into groups where independence may have been violated within the group. Such GLMM's are designed to deal with this issue and with iterative data from samples while being less confined to a normal distribution than other similar models (Bolker *et al.* 2009). I started with a Poisson distributed GLMM however, it was clear after running the model that there was overdispersion in the data. Consequently, I chose a Negative Binomial distributed GLMM for further analysis as it is capable of dealing with overdispersion in the data (Gardner *et al.* 1995). In the GLMM implementation in Jamovi (The Jamovi Project 2023) variables are classified as Factors (Categorical variables) or Covariates (Continuous variables).

The shortlist of variables used for the model was therefore divided into:

A - Categorical variables

- Habitat Type (Rand Highveld Grassland and Loskop Mountain Bushveld)
- Seasonal Subadult Jackal presence in close proximity to camera array (Yes, No)
- Treatment Type (Control, Caged and Open)
- Season (Active Decay, Autumn, Winter, Spring, Summer)

B – Continuous variables

- Total Species Richness per Site
- Distance (km) to the Nearest Reserve Boundary
- Distance (km) to Nearest Human Infrastructure

I added the above covariates and factors sequentially to the null model and I assessed each model's performance.

Model A: a random intercept or null model with no predictors where the intercept of the dependent variable (number of jackal visits) was allowed to fluctuate randomly between the groups (the group in this case is the cluster variable) I set the intercept to vary randomly across the clusters. I included no independent variables in this model as the purpose of the null model is to estimate the variance components without any predictors. In the null model I used Treatment Type as the Grouping or Cluster Variable (The variable that defines the random

effect structure). The reason treatment type was chosen as the grouping variable was to attempt to explain within treatment type variability in jackal visitation.

Model B: I added the categorical variable ‘Season’ as a fixed effect to the null model.

Model C: I added the categorical variable ‘Seasonal Subadult Jackal Presence’ as a fixed effect to model B.

Model D: I added the continuous variable ‘Total Species Richness’ as a fixed effect to model C.

Model E: I added the continuous variable ‘Distance to Nearest Human Infrastructure’ as a fixed effect to model D

Model F: I added the continuous variable ‘Distance to Nearest Reserve Boundary’ as a fixed effect to model E.

Model G: I added the interaction of the above two variables ‘Distance to Nearest Human Infrastructure and Distance to Nearest Reserve Boundary’ to model F

Model H: I included all of the above variables but included ‘Distance to Nearest Human Infrastructure’ and ‘Distance to Nearest Reserve Boundary’ as an interaction only, not as main effects

I deemed the best model to be the model with the lowest AIC score and correspondingly low BIC (Akaike 2003, Kuha 2004, Aho *et al.* 2014). As AIC and BIC values speak to the predictive and interpretive power of the model, I used these criteria primarily for model selection. I considered models with $\Delta AIC > 2$ from the top model to be inferior and considered models with $\Delta AIC \leq 2$ from the top model to show some support (Akaike 2003, Kuha 2004, Aho *et al.* 2014).

Additionally, I used Conditional and Marginal R-squared values to judge model fit as they assess the amount of variance explained by the model (Nakagawa and Schielzeth 2013). Marginal R-squared values represent the proportion of variance explained by the fixed effects only, while Conditional R-squared values represent the proportion of variance explained by the entire model (Nakagawa and Schielzeth 2013).

I performed a fixed effects omnibus test (Bolker *et al.* 2009) using the GAMLj3 package (GAMLj 2025) on the top ranked model to assess whether the covariates assigned as fixed effects had an effect on jackal visits to the experimental site.

I created regression plots (Figures 5.43 – 5.46) of the individual covariates in the GLMM, grouped by treatment type (the cluster variable) indicating their influence on ‘Seasonal Jackal Visits’ (the dependent variable) using the Flexplot module (Fife 2022). These plots display the effect of one predictor while holding the other predictors constant (Fox 2003, Fox and Weisberg 2018, Fife 2022).

CHAPTER 5: RESULTS

5.1. A broad comparison of survey methods

5.1.1. Species detected

During my study from January 2019 to January 2020, Cameras were active at 15 sites, seasonally over the course of a year for a total of 2893 trap nights. Sign surveys were also conducted seasonally over the course of a year. I conducted repeated sign surveys on 37 1 km transects over 59 sampling days totalling 266 transects. I recorded 17 carnivore species on Telperion (Table 5.1). Of these, 16 were recorded using sign surveys (Appendix 9: a - ff) and 13 using cameras (Appendix 10: a – m). Twelve of the species were detected by both cameras and sign surveys. Sign survey results indicated no difference in the species identified or the number of species recorded at the 15 experimental sites, compared to the areas of the reserve not associated with the experimental sites (Sign survey away) (Table 5.1).

Table 5.1: Carnivore species detected using sign surveys and camera traps on Telperion Nature Reserve from January 2019 to January 2020.

	Species	Common Name	Cameras Sites 1-15	Sign Survey Sites 1-15	Sign Survey Away
1	<i>Proteles cristatus</i>	Aardwolf	✓	✓	✓
2	<i>Parahyaena brunnea</i>	Brown Hyaena	✓	✓	✓
3	<i>Lupulella mesomelas</i>	Black-backed Jackal	✓	✓	✓
4	<i>Felis nigripes</i>	Black-footed Cat		✓	✓
5	<i>Aonyx capensis</i>	Cape Clawless Otter		✓	✓
6	<i>Vulpes chama</i>	Cape Fox	✓		
7	<i>Caracal caracal</i>	Caracal	✓	✓	✓
8	<i>Civettictis civetta</i>	Civet		✓	✓
9	<i>Mellivora capensis</i>	Honey Badger	✓	✓	✓
10	<i>Panthera pardus</i>	Leopard	✓	✓	✓
11	<i>Galerella sanguinea</i>	Mongoose Slender	✓	✓	✓
12	<i>Atilax paludinosus</i>	Mongoose Water	✓	✓	✓
13	<i>Cynictis penicillata</i>	Mongoose Yellow	✓	✓	✓
14	<i>Genetta maculata</i>	Rusty Spotted Genet		✓	✓
15	<i>Leptailurus serval</i>	Serval	✓	✓	✓
16	<i>Ictonyx striatus</i>	Striped Polecat	✓	✓	✓
17	<i>Suricata suricatta</i>	Suricate	✓	✓	✓

My correlation matrix (Figure 5.1 and Appendix 11) showed that there was a significant positive correlation between the number of camera images of each species and the number of transects containing tracks of each species ($r_{(15)} = 0.898, p < 0.001$).

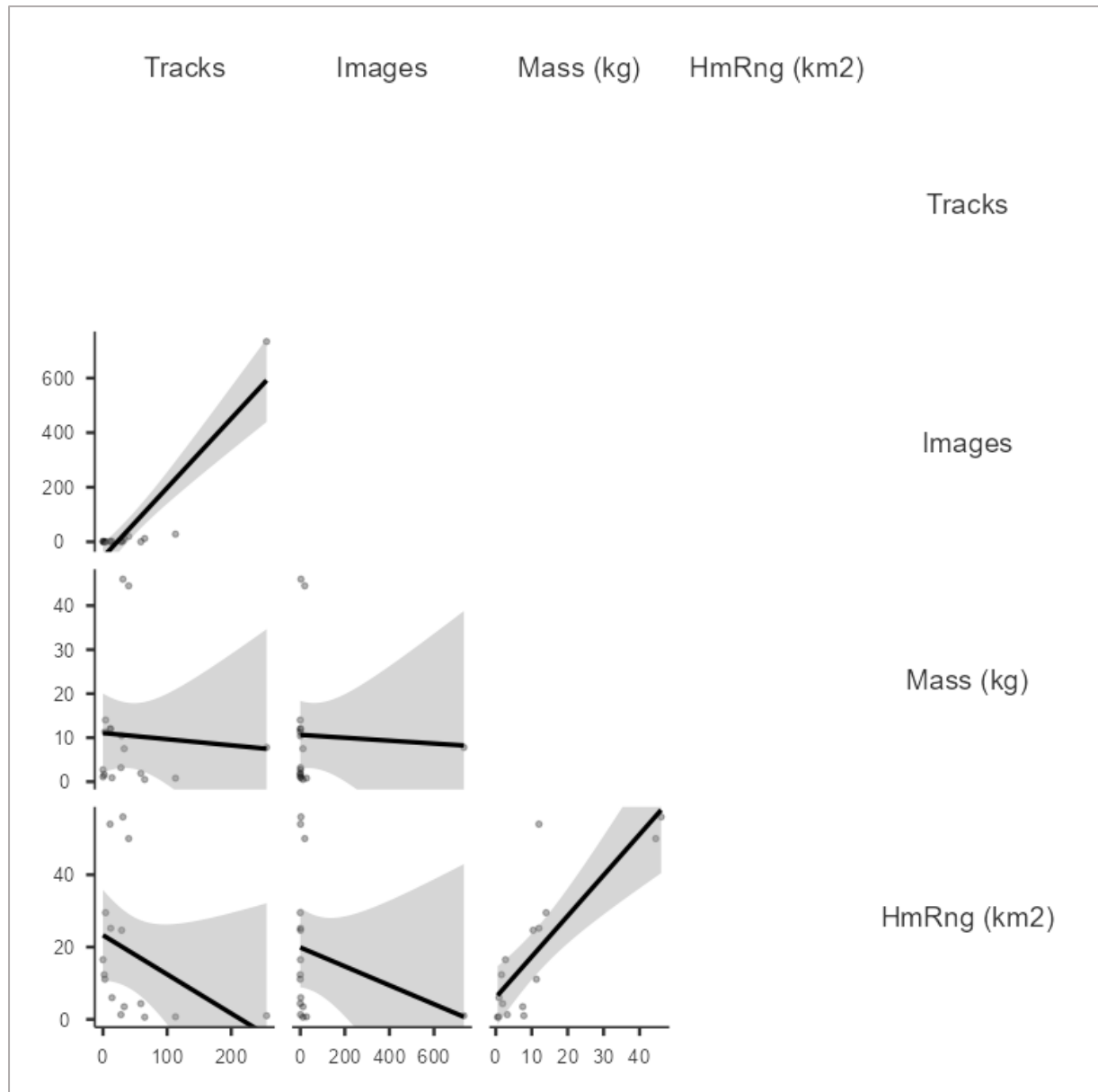


Figure 5.1: Correlation matrices for the 17 carnivore species recorded during the study on Telperion Nature Reserve from January 2019 to January 2020. The plots depict relationships between transects with tracks of each species, number of camera trap images of each species, mean mass of each species and mean home range size of each species. Mean mass and home range size were as per Hunter (2020). X axes from left to right measure number of transects with tracks, number of images, and kilograms respectively. Y axes from bottom to top measure square kilometres, kilograms and number of images respectively.

There was no significant correlation between the mean mass of each species and the number of camera images of each species ($r_{(15)} = -0.04, p = 0.873$). There was no significant correlation between the mean mass of each species and the number of transects containing tracks of each

species ($r_{(15)} = -0.063, p = 0.81$). Additionally, there was no significant correlation between the mean home range size of each species and the number of camera images of each species ($r_{(15)} = -0.243, p = 0.365$). There was no significant correlation between the mean home range size of each species and the number of transects containing tracks of each species ($r_{(15)} = -0.351, p = 0.183$). All home range sizes are average continental home range sizes (Hunter 2020).

5.1.2. Seasonality of species detections

I timed seasonal surveys to coincide as far as was logistically possible with the middle of each astronomical season to account for seasonal changes in scavenging behaviour. Each seasonal sampling period was buffered by at least 30 days to ensure temporal independence of seasonal data. On a seasonal basis, sign surveys resulted in significantly more predator detections (13.5 ± 0.85 , mean $\pm$ SE) than cameras (4.67 ± 0.92 , mean $\pm$ SE) ($t_{(10)} = 7.07, p < 0.001$) (Figure 5.2, Figure 5.3, and Appendix 12).

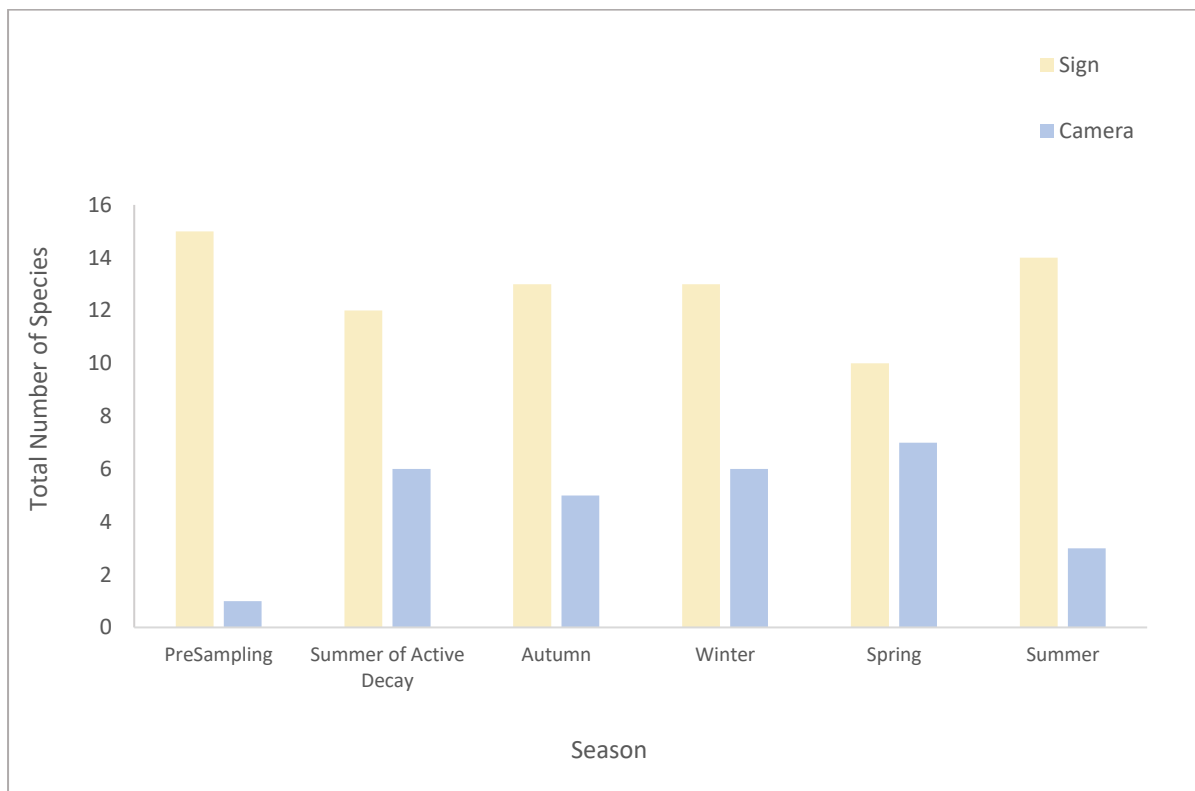


Figure 5.2: Number of species recorded per season for each survey type on Telperion Nature Reserve from January 2019 to January 2020. Pre-sampling represented sampling undertaken during summer immediately prior to the deployment of the blue wildebeest (*Connochaetes taurinus*) carcasses. “Summer of active decay” refers to the summer of 2019. “Summer” refers to summer of 2020.

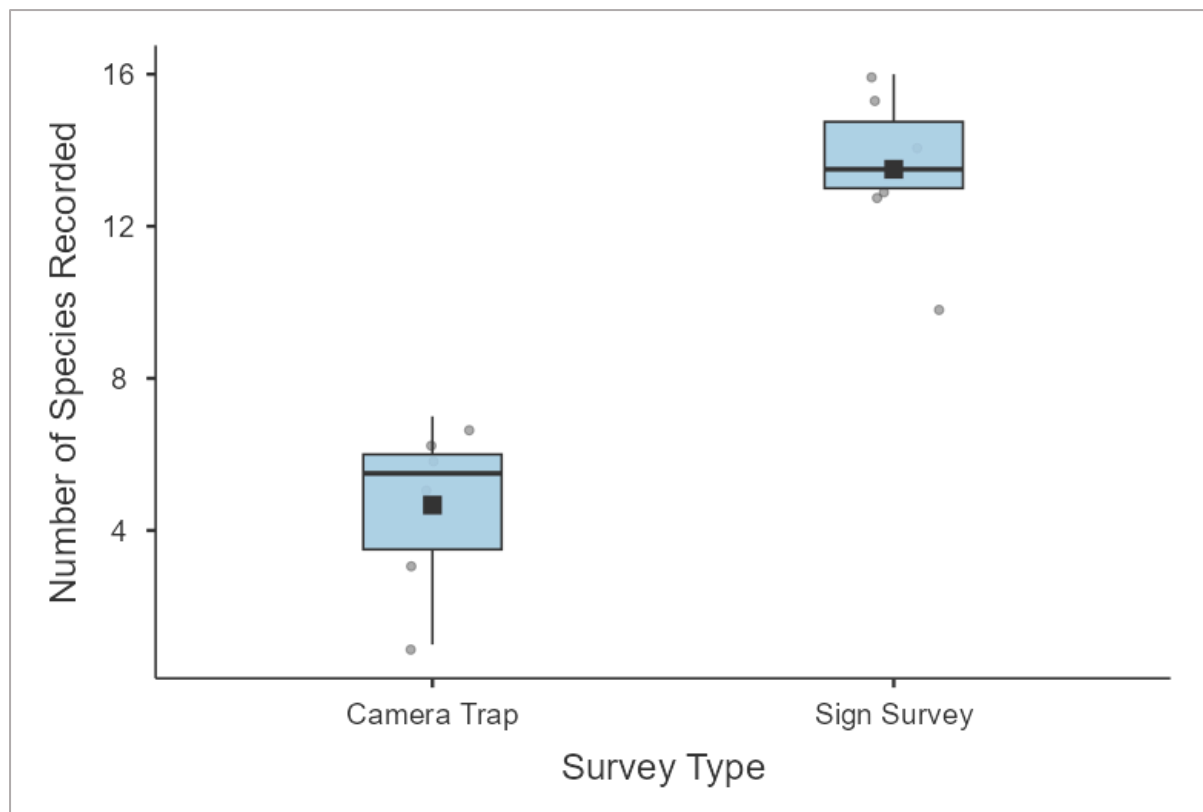


Figure 5.3: Number of species recorded each season per survey type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points (*grey dots*). Note: lack of whiskers in one direction on a box plot indicates that data is skewed in the opposite direction.

5.1.3. Relative efficiency of each survey type

Sign surveys (0.93 ± 0.02 , mean $\pm$ SE) were significantly ($t_{(28)} = 11.1$, $p < 0.001$) more efficient than camera surveys (0.34 ± 0.04 , mean $\pm$ SE) for the detection of carnivores (Table 5.2, Figure 5.4).

Table 5.2: Species richness and relative efficiency (number of species detected at each site by a single method/total number of species recorded at each site by combining both methods) of the two methods at each experimental site sampled during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. The higher the relative efficiency value, the more efficient that survey type was at detecting species.

Sites	Species richness Sign Surveys	Species richness Camera Trap Surveys	Total species richness Both Surveys	Relative efficiency Sign Surveys	Relative efficiency Camera Trap Surveys
1	7	2	8	0.88	0.25
2	6	2	8	0.75	0.25
3	6	2	7	0.86	0.29
4	7	3	7	1.00	0.43
5	8	1	8	1.00	0.13
6	6	4	7	0.86	0.57
7	10	3	11	0.91	0.27
8	7	5	8	0.88	0.63
9	5	2	5	1.00	0.40
10	11	2	11	1.00	0.18
11	5	1	5	1.00	0.20
12	8	3	8	1.00	0.38
13	8	2	8	1.00	0.25
14	7	2	7	1.00	0.29
15	4	3	5	0.80	0.60

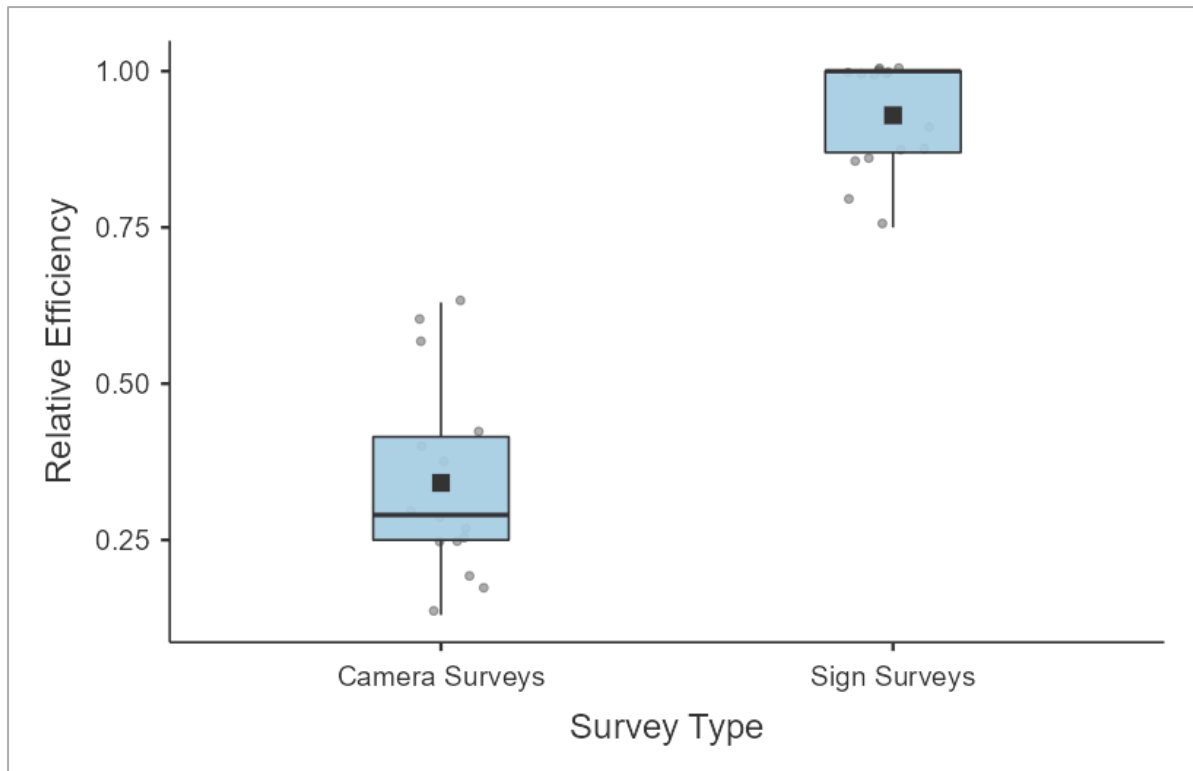


Figure 5.4: Relative efficiency of camera trap surveys compared to sign surveys: means (*black squares*), medians (*dark horizontal lines*), individual data points (*grey dots*) and minimum and maximum range excluding outliers (*whiskers*) of the relative efficiency values for each of the sampling methods tested during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Missing whiskers indicate that data is skewed in the opposite direction to the missing whisker.

5.1.4. Latency to detection

Latency to detection (LTD) was considerably shorter for sign surveys (1 – 15 days) than for camera surveys (1 – 156 days) for all species except jackal which was recorded on the first day of surveying by both survey techniques (Figure 5.5).

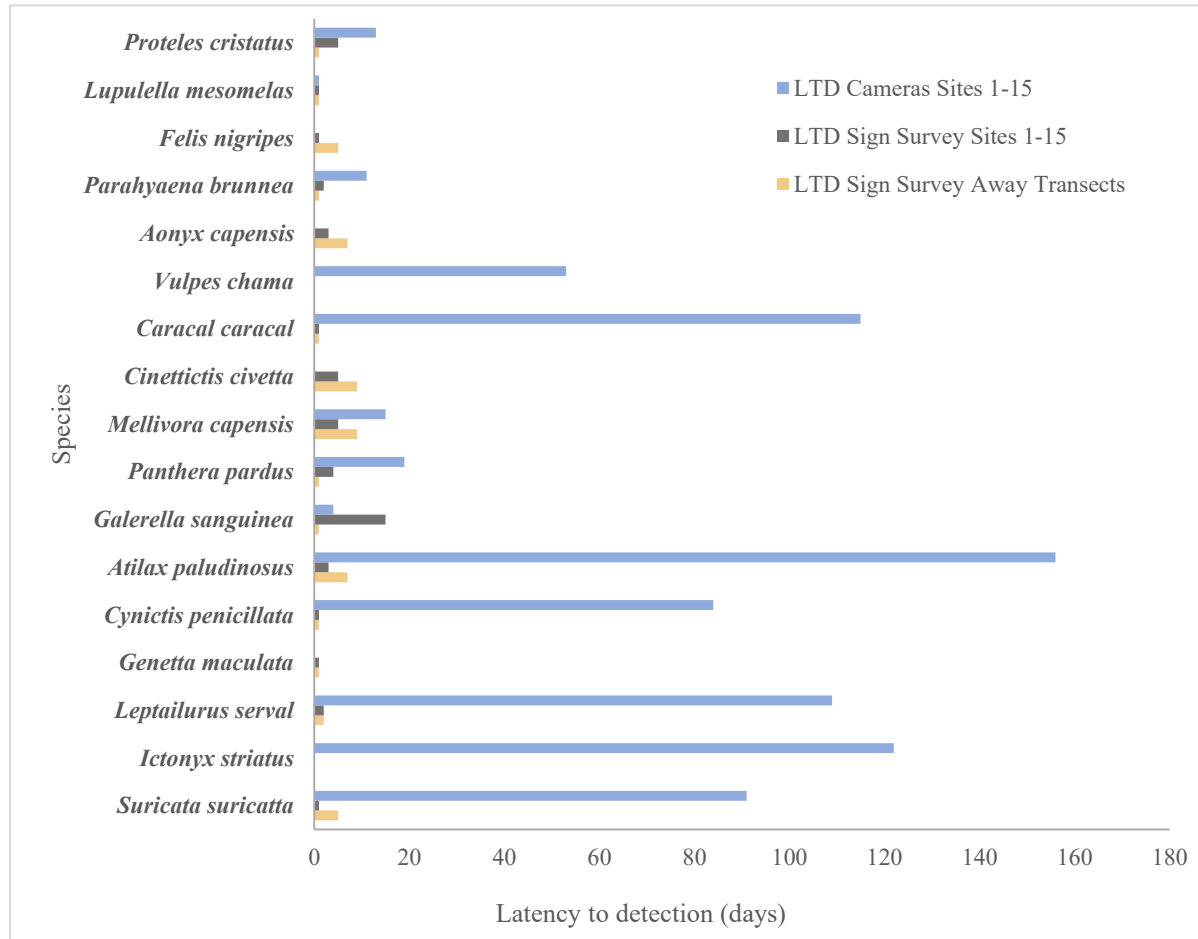


Figure 5.5: Latency to detection (LTD) per species for each of three survey types (camera traps of study sites 1 - 15, sign surveys of study sites 1 – 15, sign surveys of the entire reserve) during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020.

There were significant differences between LTD for sign surveys of the transects away from the experimental sites, sign surveys of the 15 experimental sites only and camera surveys ($H_{(2)} = 18.7, p < 0.001$). LTD was significantly shorter for sign surveys at experimental sites 1-15 ($W = 5.25, p < 0.001$) and sign surveys away from the experimental sites ($W = 5.35, p < 0.001$) than for camera surveys. There was no significant difference ($W = 0.3, p = 0.97$) when comparing the LTD's of sign surveys away from the experimental sites, to sign surveys of experimental sites only (Figure 5.6 and Appendix 13).

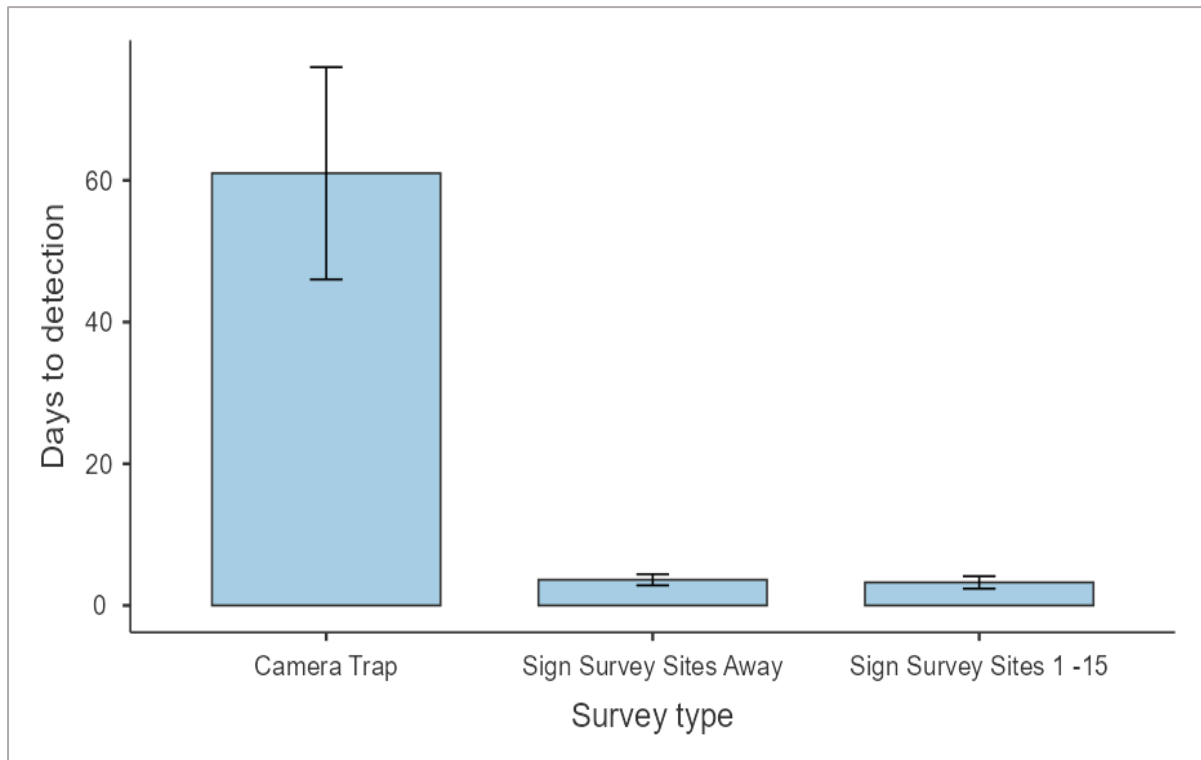


Figure 5.6: Mean latency to detection (LTD) in days of carnivore species for sign surveys and camera trap surveys during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020. Bars represent standard errors.

Specifically at open carcasses after carcass deployment, jackals were detected using both sign surveys and cameras on the first day after deployment (Figure 5.7). Brown hyaena were detected at the carcass sites on the first day after deployment using sign surveys, and after 10 days using cameras (Figure 5.7). Leopards were detected at the carcass sites, five days after carcass deployment when using sign surveys whereas cameras detected leopard 18 days after carcass deployment (Figure 5.7).

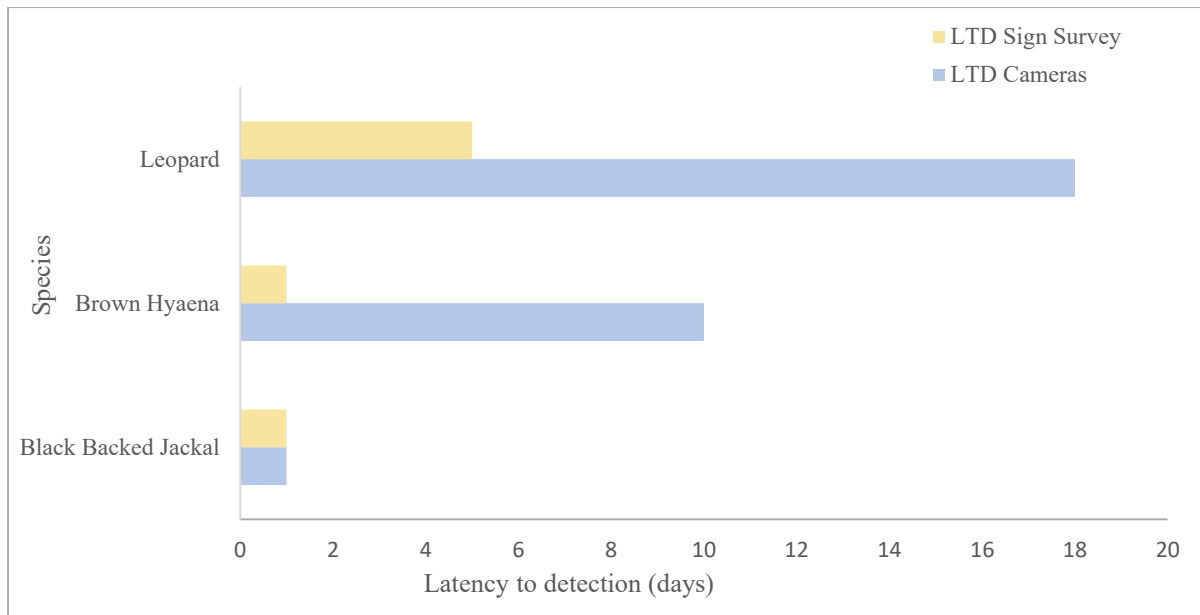


Figure 5.7: Latency to Detection (LTD) (days) comparisons between sign surveys and camera trap surveys after carcass deployment for leopard (*Panthera pardus*), brown hyaena (*Parahyaena brunnea*), and black-backed jackal (*Lupulella mesomelas*) during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020. These results were from caged and open sites only. Bars are standard errors.

5.1.5. Species accumulation curves

Species accumulation curves for the entire study period (Figure 5.8 Panel a) indicated that sign surveys for the transects away from the experimental sites took nine survey days to reach an asymptote, whereas sign surveys proximate to the experimental sites took 15 days to reach an asymptote. In contrast, after 185 days (2775 camera trap days) of camera surveys the associated species accumulation curve had not yet reached an asymptote.

Asymptotic analyses of the data used to create the rarefaction curves (Figure 5.8 panels b and c, Appendix 14, Appendix 15) indicate that for sign surveys observed predator species richness was 16 while asymptotic richness was estimated at 16 species (95% CI 13.97 – 17.93) suggesting that approximately 100% of the estimated species pool was sampled after 15 days and indicates that sampling is adequate. Sample coverage was 1 which further supports this finding (Chao and Jost 2012). For camera surveys observed predator species richness was 13 while asymptotic richness was estimated at 21 species (95% CI 11.35 – 47.20), indicating that approximately only 62% of the estimated species pool was sampled after 185 days. Sample coverage was still high at 0,97.

Thus, sufficient sampling has taken place for sign surveys as a clear asymptote has been reached, however further sampling is likely to discover more species for camera surveys.

Additionally, seasonal species accumulation curves (Figure 5.9) showed that for every season, sign surveys outperformed camera surveys in terms of the number of species recorded and LTD.

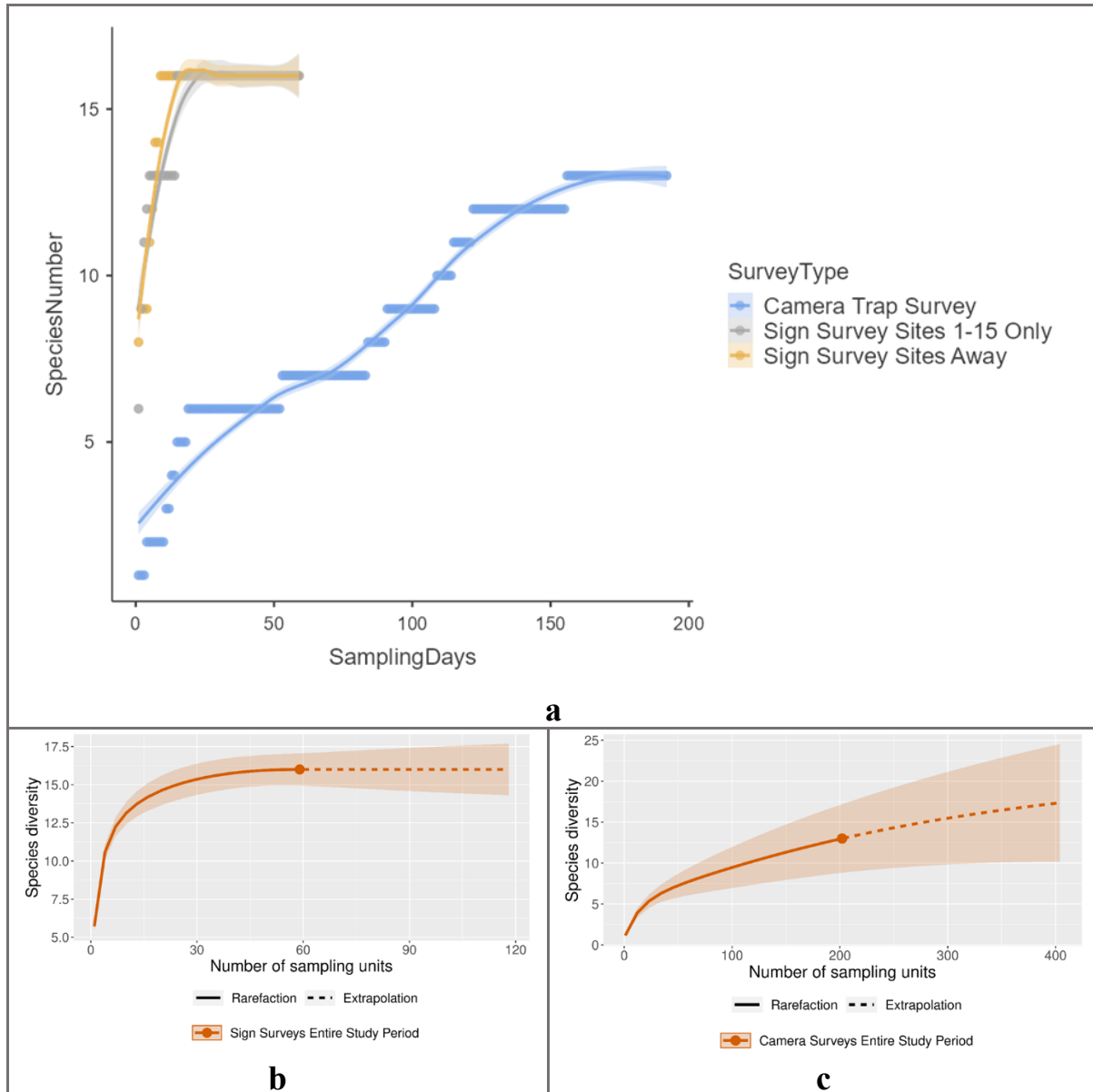


Figure 5. 8: Species accumulation curves for all survey types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. **Panel a** contains collector's curves for the different sampling methods. The dots are individual data points. The data were smoothed using the flexplot module in Jamovi (The Jamovi Project 2023) to create a locally estimated scatterplot smoothing (LOESS) curve. Lightly shaded areas around the lines represents the standard error. **Panel b** contains a rarefaction curve of sign survey data where the number of sampling units on the x axis refers to sampling days. Lightly shaded area around the line represents 95% confidence intervals. **Panel c** contains a rarefaction curve of camera data where the number of sampling units on the x axis refers to sampling days. The lightly shaded area around the line represents 95% confidence intervals. The curves in **panel b** and **panel c** were created using iNEXT online (Chao *et al.* 2016) software package.

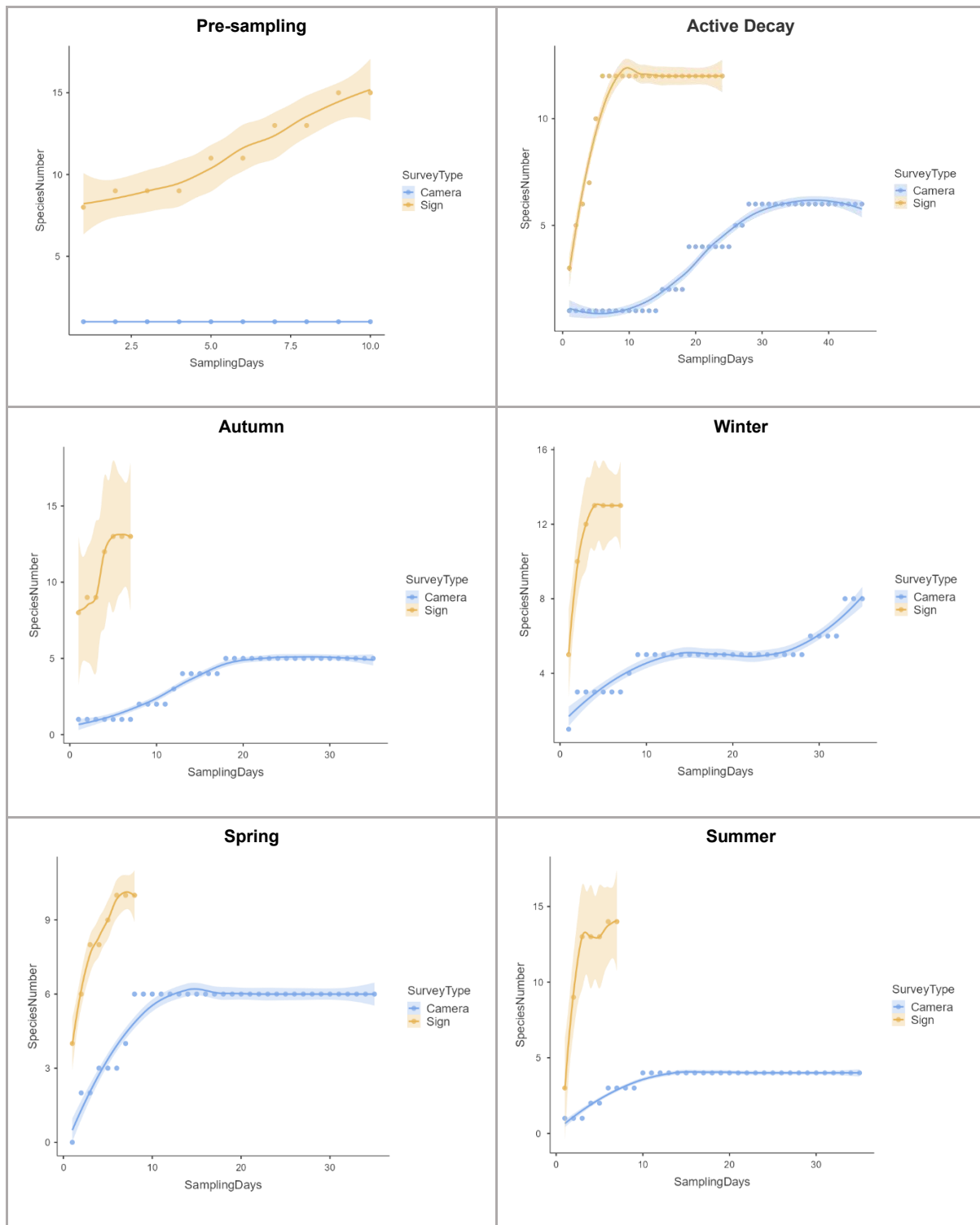


Figure 5.9: Seasonal species accumulation curves, comparing sign surveys to camera trap surveys during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Dots are individual data points. The data were smoothed using the flexplot module in Jamovi to create a locally estimated scatterplot smoothing (LOESS) curve. Shaded areas around the lines are standard errors.

5.1.6. Cost comparison of survey types

Comparative budgets (Table 5.3) show camera surveys were markedly more expensive than sign surveys during my study.

Table 5.3: Cost comparisons of camera trap and sign survey studies during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020.

Camera Trap Surveys				Sign Surveys			
Equipment or Cost Items	Number of Units	Price Per Unit	Total Costs Per Unit	Equipment or Cost Items	Number of Units	Price Per Unit	Total Costs Per Unit
Cameras*	30	4181	125430	Garmin GPS	1	8099	8099
128GB Sandisk Memory Cards*	60	630	37800	Memory Card*	1	630	630
Batteries pack of 16*	135	169	22815	Smartphone with camera	1	2500	2500
Labour to install and check	0	0	0	Monthly Wage Tracker**	3 months	6000	18000
Petrol to install and check cameras	300km	3.5	1050	Petrol to sampling sites	354km	3.5	1239
		4983.5	187095			17232.5	30468

* C Pearson. Founder and owner of Camera Traps cc. sales@cameratraps.co.za (personal communication Jan 2024)

** A van den Heever. Founder of the tracker academy alex@nns.co.za (personal communication Jan 2024)

Note: Currency in above calculations is in South African Rands. As of 25 February 2026 1 US \$ = 15.91 ZAR

5.2. The effect of carrion on species diversity

5.2.1. Species richness

Over the 12 months of my study the overall predator species richness on Telperion was 16 based on sign surveys and 13 based on camera surveys (Figure 5.10 and Appendix 16). For sign surveys at the experimental sites, controls had higher overall species richness ($n = 15$ species) compared to caged ($n = 13$ species) and open ($n = 13$ species) carcasses (Figure 5.10). Mean species richness was highest for controls ($\bar{x} = 9.6$, $SD = 2.07$) lower for caged carcasses ($\bar{x} = 6.4$, $SD = 1.34$) and lowest for open carcasses ($\bar{x} = 6.2$, $SD = 1.48$). (Figure 5.11 and Figure 5.14). However, these differences were not statistically significant ($F_{(2, 7.79)} = 2.31$, $p = 0.163$). Camera surveys recorded highest species richness at open sites (9 species), followed by controls ($n = 7$ species) and caged ($n = 3$ species) (Figure 5.10 and Figure 5.15). Mean species richness (Figure 5.11) was highest for open sites ($\bar{x} = 3.4$, $SD = 1.14$), followed by control ($\bar{x} = 2$, $SD = 0.71$) and caged ($\bar{x} = 2$, $SD = 0.71$) (Figure 5.11), however these results were not statistically significant ($F_{(2, 7.74)} = 2.91$, $p = 0.114$).

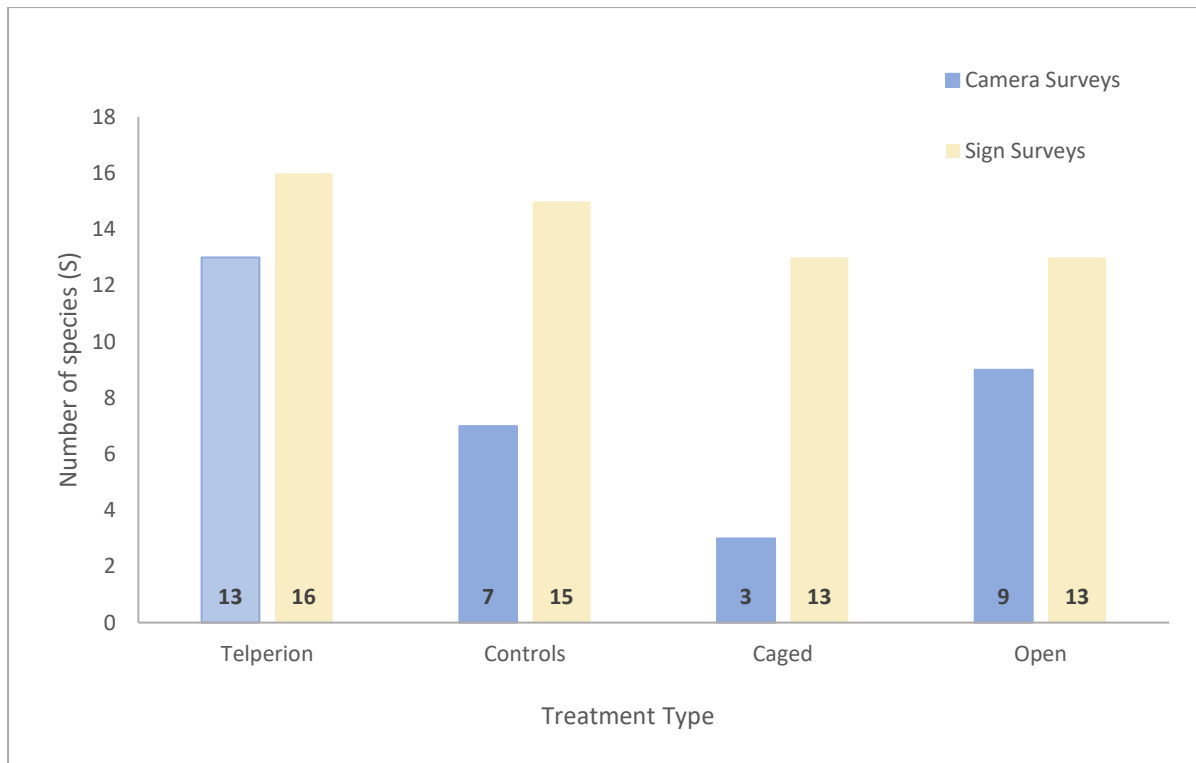


Figure 5.10: Total species richness per treatment type from sign and camera surveys on during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020

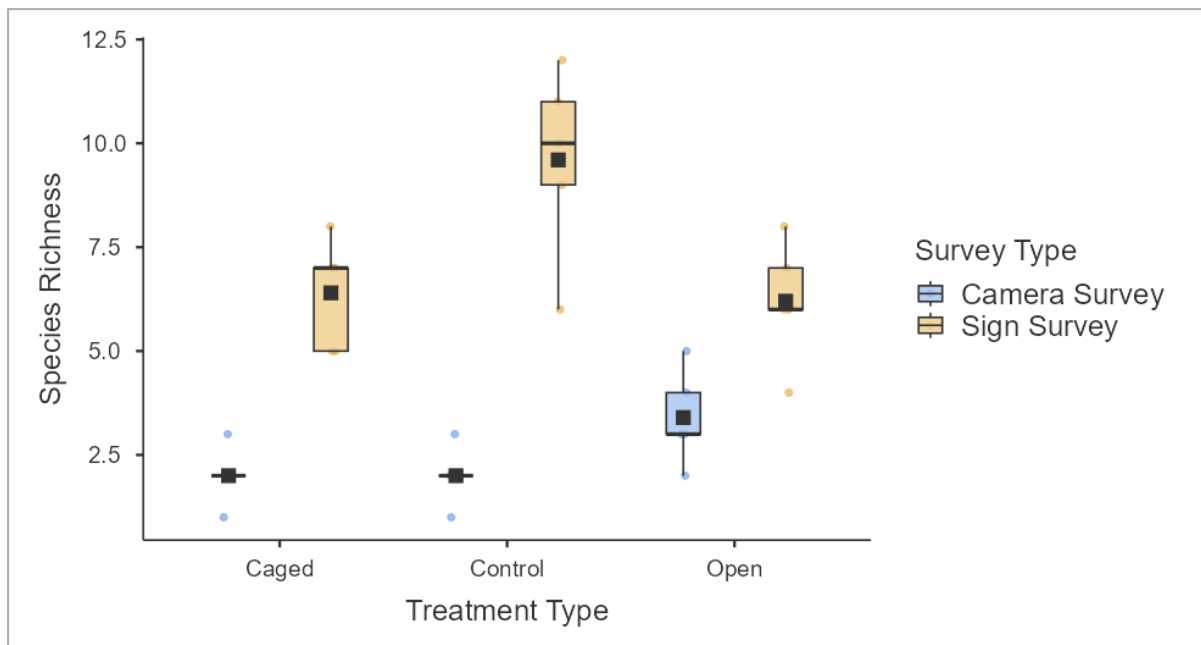


Figure 5.11: Mean species richness per treatment type from sign and camera surveys during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020. Means (black squares), medians (dark horizontal lines), minimum and maximum range excluding outliers (whiskers) and individual data points falling outside main box plot (dots). Note lack of whiskers in one direction on a box plot indicates that data is skewed in the opposite direction. The absence of a box for camera trap caged and control treatment types indicates that the middle 50% (Interquartile range) has zero spread, and most of the data points are clustered together.

5.2.2. Shannon-Weiner Species Diversity (*H*)

I calculated Shannon-Weiner predator species diversity from sign surveys within 250 m of each experimental site for the entire study period (Figure 5.12, Figure 5.14 and Appendix 17). Shannon-Weiner predator species diversity was significantly different among treatments ($F_{(2, 7.59)} = 9.96, p = 0.008$). A Tukey *Post hoc* test revealed that the predator species diversity was significantly lower at open sites (0.99 ± 0.08 , mean $\pm$ SE) than controls (1.52 ± 0.09 , mean $\pm$ SE) ($t_{(12)} = 3.25, p = 0.02$) and at caged sites (0.86 ± 0.15 , mean $\pm$ SE) than controls ($t_{(12)} = 4.09, p = 0.004$). There was no significant difference in the predator species diversity between open carcasses sites and caged carcass sites ($t_{(12)} = 0.84, p = 0.69$). As distance increased from experimental sites up to 500 m, Shannon-Wiener carnivore species diversity was still lower for open (1.45 ± 0.12 , mean $\pm$ SE) and caged (1.43 ± 0.08 , mean $\pm$ SE) sites than control (1.79 ± 0.13 , mean $\pm$ SE) sites (Appendix 12), but these differences were no longer significant ($F_{(2, 7.68)} = 2.75, p = 0.126$). I calculated Shannon-Weiner predator species diversity from camera data for the entire study period (Figure 5.12 Figure 5.15 and Appendix 18). Although open carcasses had a slightly higher mean predator species diversity (0.41 ± 0.19 , mean $\pm$ SE), than caged carcasses (0.38 ± 0.17 , mean $\pm$ SE) and controls (0.37 ± 0.14 , mean $\pm$ SE) (Figure 5.12), these differences were not statistically significant ($F_{(2, 7.8)} = 0.05, p = 0.95$).

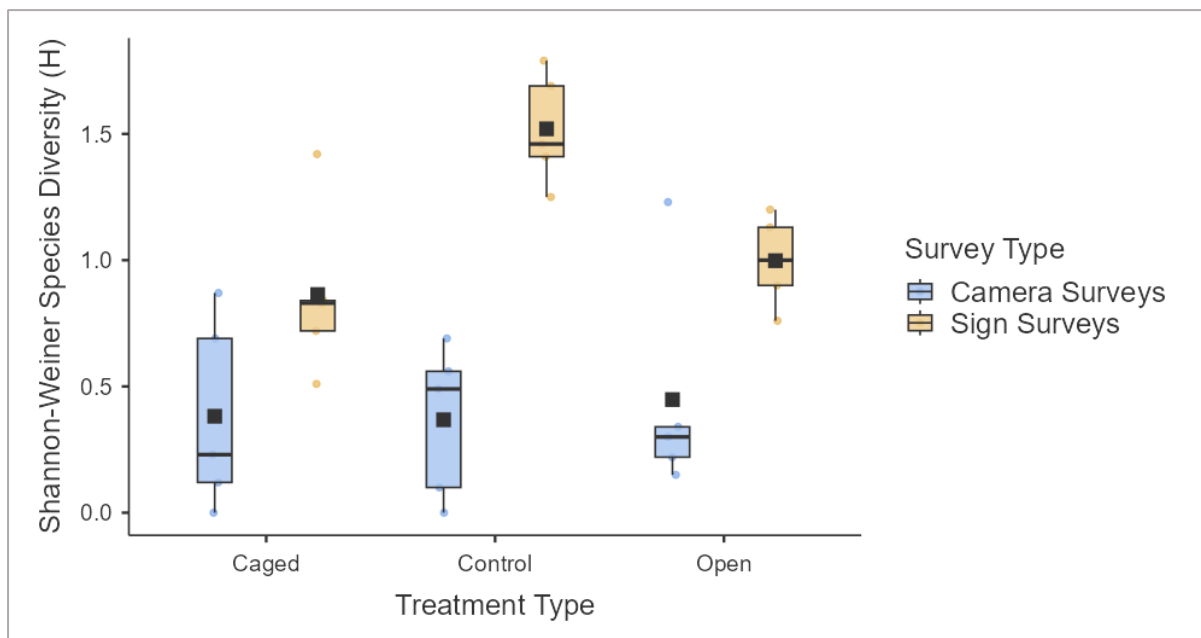


Figure 5.12: Shannon-Weiner predator species diversity (*H*) from sign surveys within 250m of experimental sites and camera trap surveys at experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (black squares), medians (dark horizontal lines), minimum and maximum range excluding outliers (whiskers) and individual data points falling outside the box plot (dots). Absence of whiskers in one direction on a box plot means data is skewed in the opposite direction.

5.2.3. Gini-Simpson's Species Diversity (1 - D)

I calculated Gini-Simpson's predator species diversity within 250 m of each site for the entire study period (Figure 5.13, Figure 5.14 and Appendix 19). Species diversity was significantly different among treatments ($F_{(12.9, 2)} = 12.9, p = 0.004$). A Tukey *Post Hoc* test revealed that the predator species diversity was significantly lower at open sites (0.54 ± 0.03 , mean $\pm$ SE) than controls (0.75 ± 0.03 , mean $\pm$ SE) ($t_{(12)} = 2.99, p = 0.03$) and caged sites (0.48 ± 0.07 , mean $\pm$ SE) than at control sites ($t_{(12)} = 3.82, p = 0.006$). There was no significant difference in the predator species diversity between open carcass sites and caged carcass sites ($t_{(12)} = 0.83, p = 0.69$). As distance increased from experimental sites up to 500 m, Gini-Simpson's predator species diversity was still lower for open (0.72 ± 0.04 , mean $\pm$ SE) and caged (0.71 ± 0.02 , mean $\pm$ SE) sites than control (0.82 ± 0.03 , mean $\pm$ SE) site species diversity, but these differences were no longer significant ($F_{(2, 7.81)} = 4.75, p = 0.05$).

I calculated Gini-Simpson's species diversity for predators from camera data for the entire study period (Figure 5.13 Figure 5.15 and Appendix 20). Although mean carnivore Gini-Simpson's species diversity was higher at controls (0.36 ± 0.18 , mean $\pm$ SE) than at open (0.22 ± 0.11 , mean $\pm$ SE) and caged (0.35 ± 0.19 , mean $\pm$ SE) sites (Figure 5.13), these differences were not significant ($H_{(2)} = 0.02, p = 0.99$).

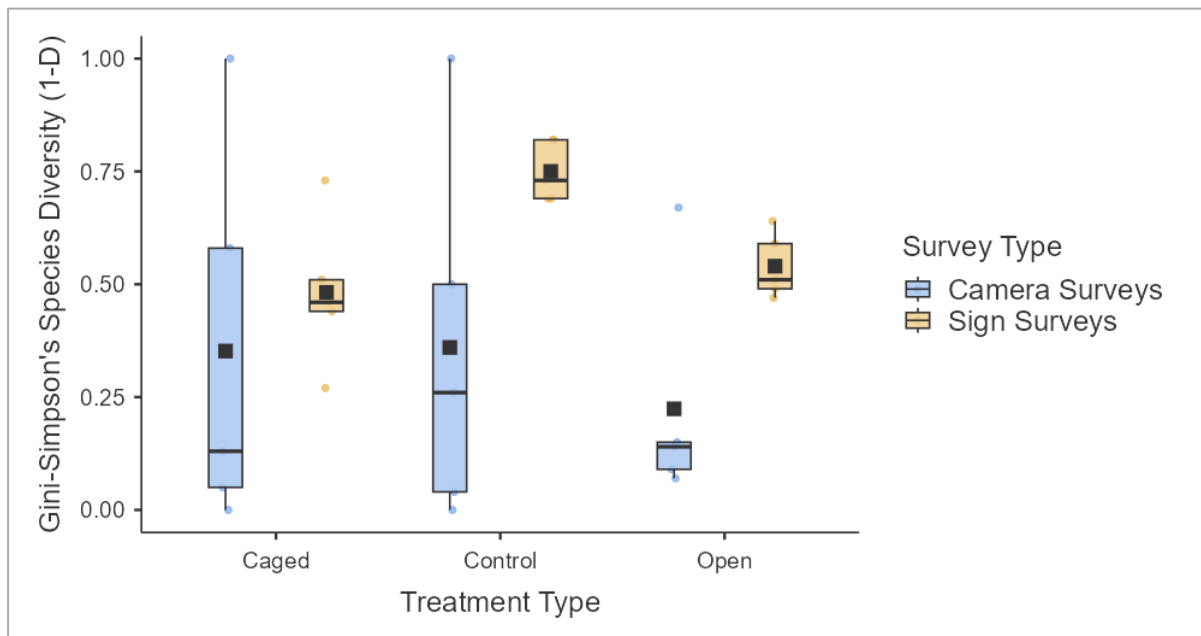


Figure 5.13: Gini-Simpson's predator species diversity (D) from sign surveys within 250m of experimental sites and camera surveys of experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (black squares), medians (dark horizontal lines), minimum and maximum range excluding outliers (whiskers) and individual data points falling outside the box plot (dots). Absence of whiskers in one direction on a box plot means data is skewed in the opposite direction.

All three species diversity measures (species richness, Shannon-Weiner species diversity and Gini-Simpson species diversity) are presented together but separately for each survey type in Figure 5.14 (sign surveys) and Figure 5.15 (camera trap surveys) below for ease of comparison per survey type.

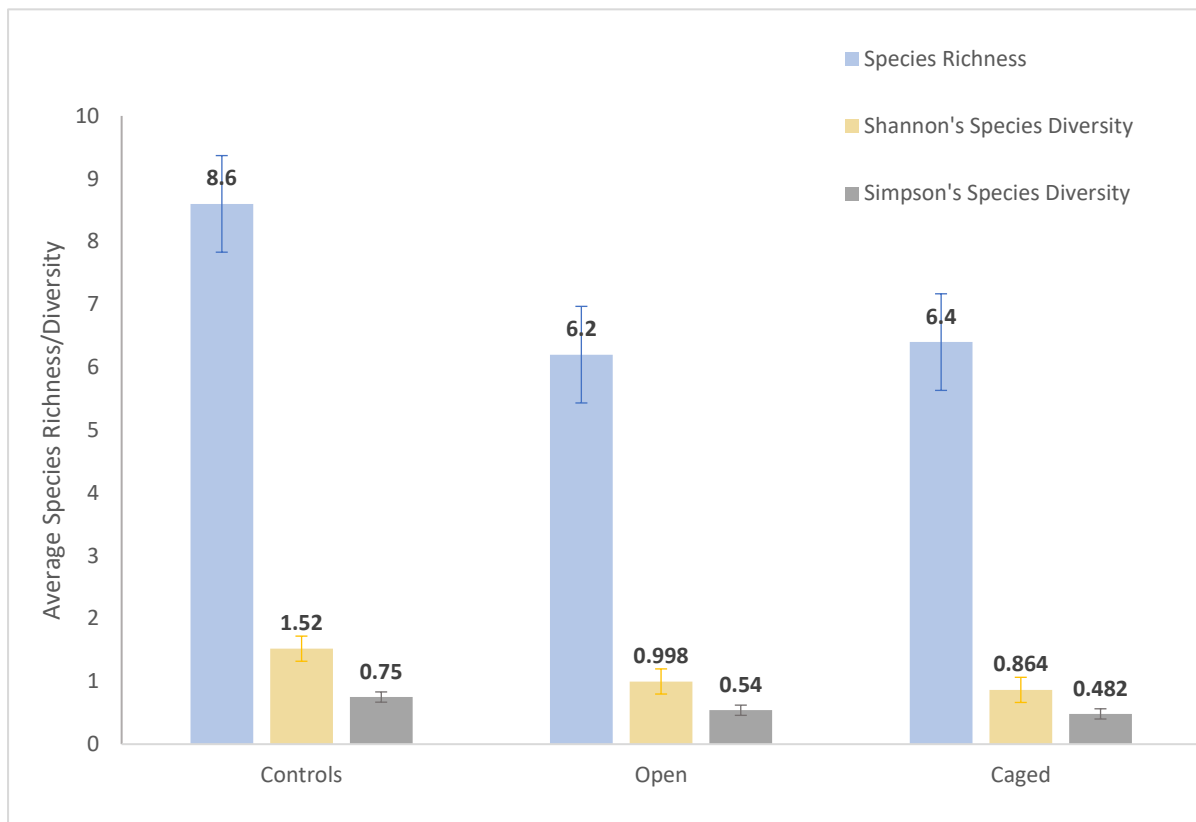


Figure 5.14: Mean species richness, Shannon-Weiner species diversity and Gini-Simpson's species diversity for all three treatment types for entire study period from 250 m sign survey data during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.

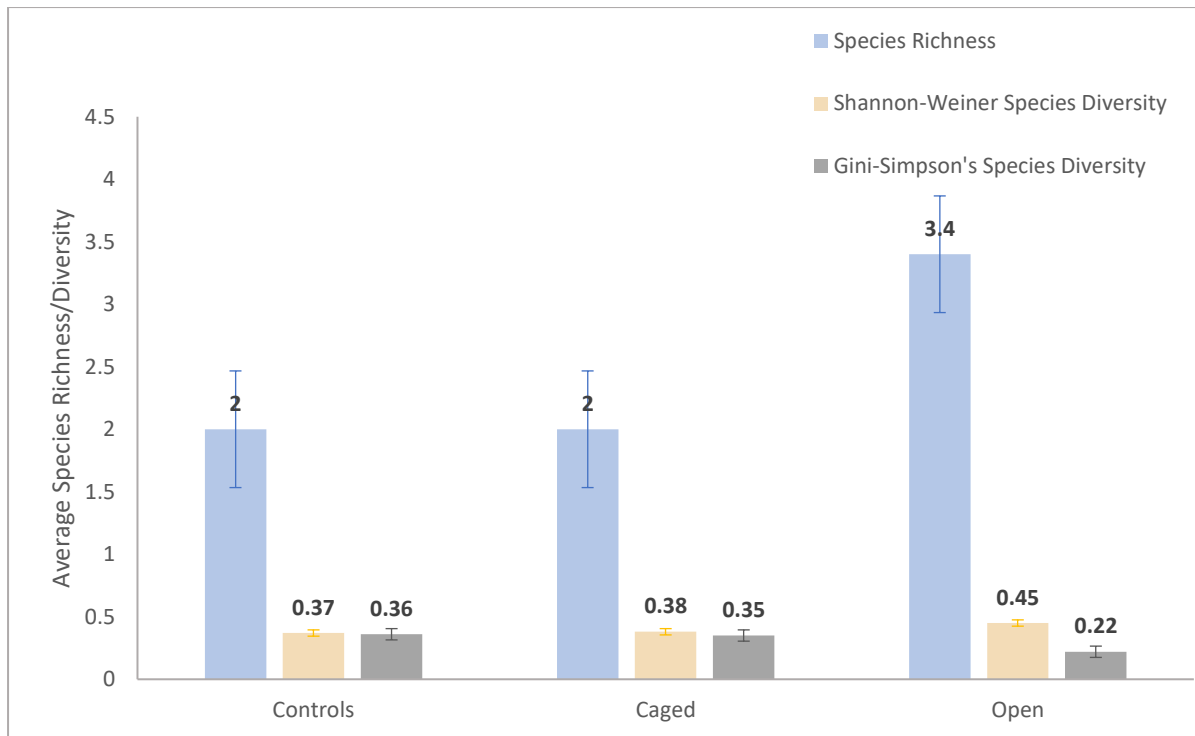


Figure 5.15: Mean species richness, Shannon-Weiner species diversity and Gini-Simpson's species diversity for all three treatment types for entire study period from camera trap data during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.

5.2.4. Rank Abundance Curves

Rank abundance curves from sign surveys (Figure 5.16) showed a shallow gradient for control sites and steeper gradients for open and caged sites. Thus, there was a higher degree of species evenness at control sites than at either caged or open sites. Rank abundance curves from camera surveys (Figure 5.17) showed very little difference in the gradient between the three treatment types with all three gradients being steep. Thus, cameras showed a low degree of evenness at all three treatment types.

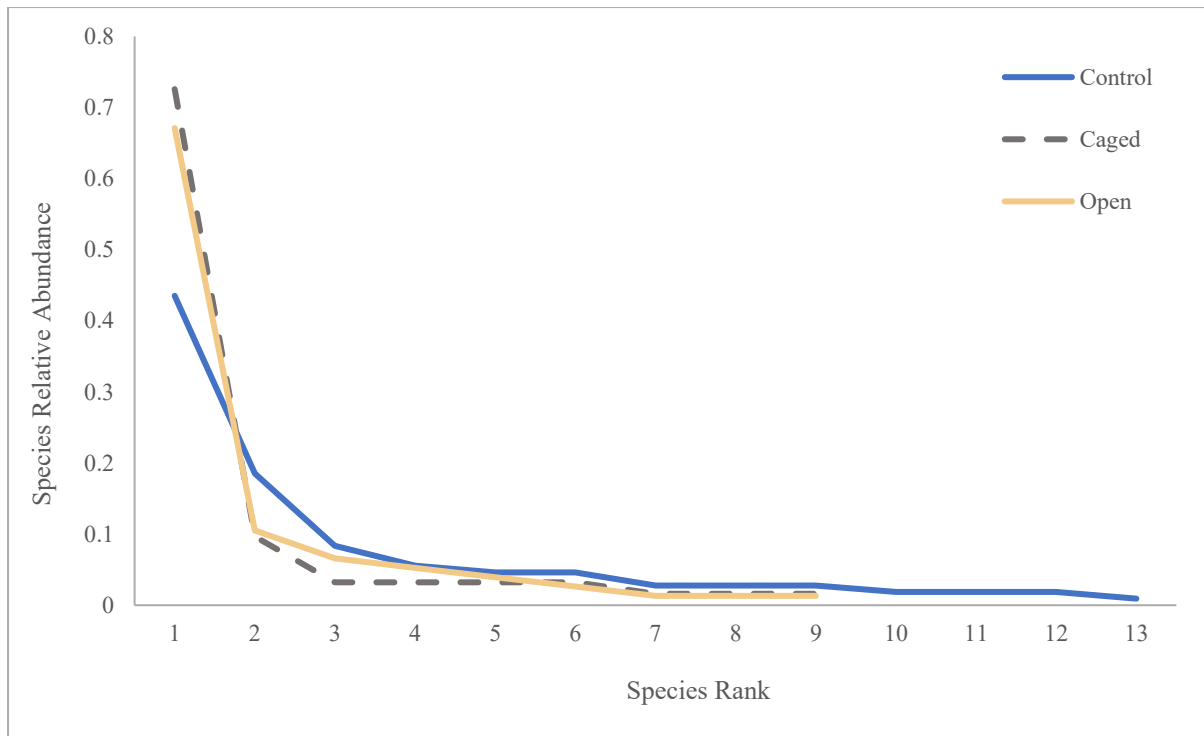


Figure 5.16: Rank abundance curves of predator communities from sign surveys within 250 m of experimental sites showing a shallow gradient for control sites and steeper gradients for open and caged carcass sites, indicating higher species evenness at controls during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.

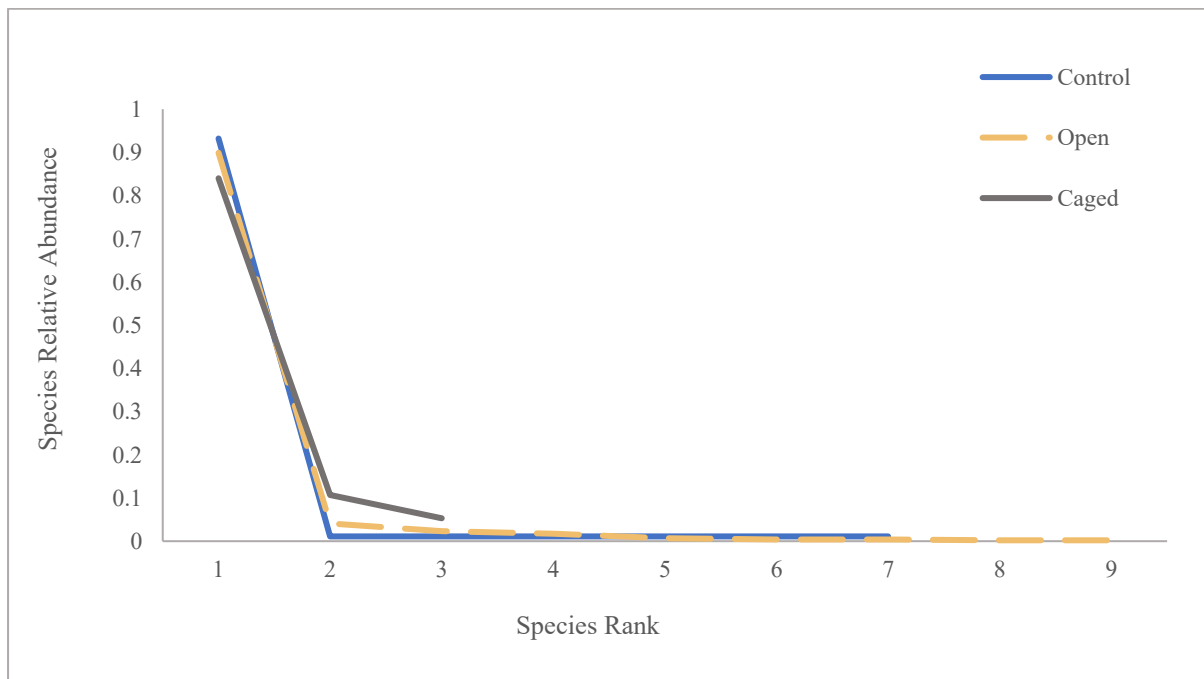


Figure 5.17: Rank abundance curves of predator communities from camera traps showing steep gradients for open and caged carcasses as well as control sites, indicating low species evenness at all sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.

5.3. The impact of fire

Without taking into account the impact of fire, Shannon-Weiner species diversity for sign surveys was significantly lower at open sites than caged or controls while camera surveys showed open sites to have the highest Shannon-Weiner species diversity although not significantly higher. In order to understand these seemingly conflicting Shannon-Weiner species diversity results produced by the camera and sign surveys above, I undertook further analyses whereby I excluded three sites – open site 6 (fire affected) as well as the nearest control site (site five) and the nearest caged site (site nine). I re-examined Shannon-Weiner and Gini-Simpson's species diversity for the remaining sites in the same manner as described above for these Indices.

5.3.1. *Shannon-Weiner species diversity*

Using sign survey data excluding fire affected sites, I calculated Shannon-Weiner predator species diversity within 250 m of each site for the entire study period (Figure 5.18 and Appendix 21). Shannon-Weiner species diversity was significantly different among treatments ($F_{(2, 5.6)} = 6.47, p = 0.035$). I found that the predator species diversity was significantly lower at open sites (0.99 ± 0.10 , mean $\pm$ SE) than controls (1.45 ± 0.09 , mean $\pm$ SE) ($t_{(5.92)} = 3.33, p = 0.037$). There was no significant difference in the predator species diversity between open carcass sites and caged carcass sites (0.87 ± 0.19 , mean $\pm$ SE) ($t_{(4.53)} = 0.569, p = 0.842$). There was also no significant difference in the predator species diversity between caged sites and control sites ($t_{(4.25)} = 2.7, p = 0.106$). As distance increased from experimental sites to 500 m both open carcass Shannon-Weiner predator species diversity (1.49 ± 0.15 , mean $\pm$ SE) and caged carcass Shannon-Weiner predator species diversity (1.46 ± 0.09 , mean $\pm$ SE) was still lower than control site Shannon-Weiner predator species diversity (1.77 ± 0.17 , mean $\pm$ SE) (Appendix 21), but these differences were no longer significant ($F_{(2, 5.69)} = 1.21, p = 0.365$).

Using camera traps, Shannon's predator species diversity was calculated for the entire study period (Figure 5.18 and Appendix 22). Mean predator species diversity went from being highest at open sites when the fire affected site was included to being lowest for open sites (0.43 ± 0.26 , mean $\pm$ SE), higher at caged carcasses (0.44 ± 0.20 , mean $\pm$ SE) and highest at controls (0.45 ± 0.13 , mean $\pm$ SE), (Figure 5.18), but these differences were not significant ($F_{(2, 5.49)} = 0.002, p = 0.998$).

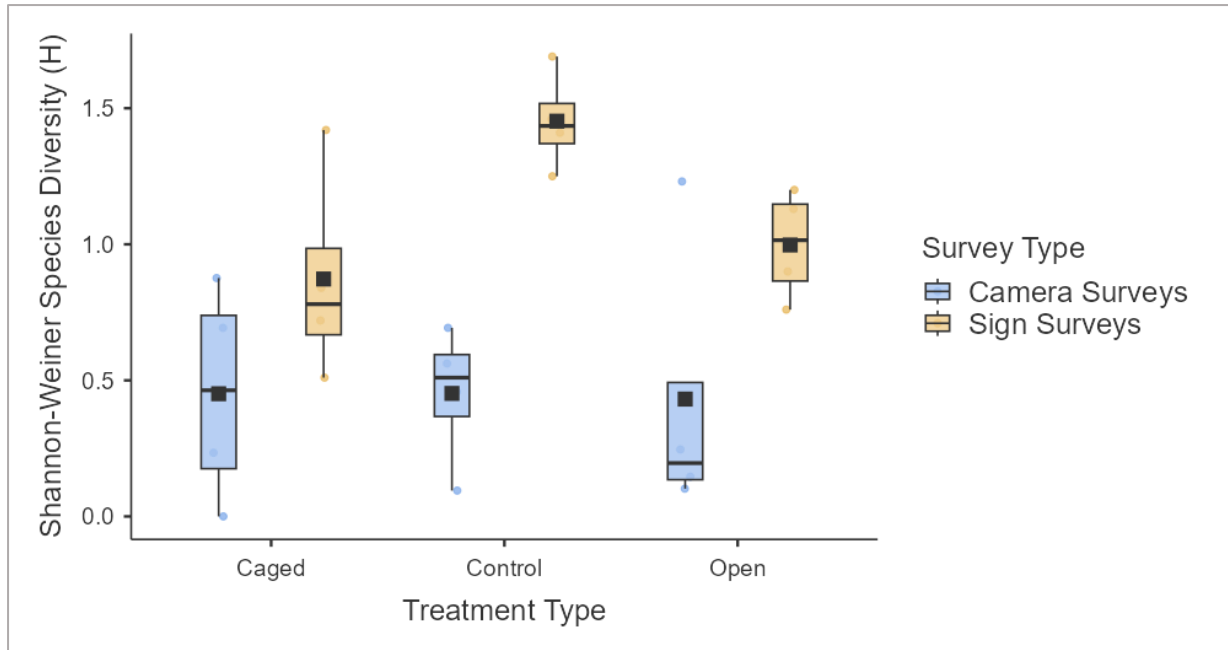


Figure 5.18: Shannon-Weiner predator species diversity (H) from sign surveys within 250 m of experimental sites as well as camera surveys, during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020 excluding fire affected site 6 as well as sites 5, and 9. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*dots*). Absence of whiskers from one side of a box plot indicates data is skewed in the opposite direction.

5.3.2. Gini-Simpson's Species Diversity

Using sign survey data and excluding fire affected sites, I calculated Gini-Simpson's predator species diversity within 250 m of each site for the entire study period excluding the fire effected sites and closest control and caged sites (Figure 5.19 and Appendix 23). Gini-Simpson's Species diversity was still significantly different among treatments ($F_{(2, 5.42)} = 7.58, p = 0.027$). The predator species diversity was significantly lower at open sites (0.55 ± 0.04 , mean $\pm$ SE) than controls (0.73 ± 0.03 , mean $\pm$ SE) ($t_{(5.59)} = 3.64, p = 0.028$). There was no significant difference in the predator species diversity between open carcass sites and caged carcass (0.48 ± 0.09 , mean $\pm$ SE) sites ($t_{(4.05)} = 0.7, p = 0.775$) or between caged sites and control sites ($t_{(3.62)} = 2.58, p = 0.136$). As distance increased from experimental sites, from 250m to 500 m both mean open carcass Gini-Simpson's predator species diversity (0.742 ± 0.04 , mean $\pm$ SE) and mean caged carcass Gini-Simpson's predator species diversity (0.715 ± 0.03 , mean $\pm$ SE) carcass predator species diversity was still lower than mean control sites Gini-Simpson's predator species diversity (0.815 ± 0.03 , mean $\pm$ SE) (Appendix 23), but these differences were no longer significant ($F_{(2, 5.93)} = 2.33, p = 0.179$).

Gini-Simpson's predator species diversity calculated from camera data for the entire study period (Figure 5.19 and Appendix 24) showed that mean species diversity was lowest for open carcasses (0.239 ± 0.15 , mean $\pm$ SE), higher at caged carcasses (0.427 ± 0.23 , mean $\pm$ SE) and highest at controls (0.449 ± 0.21 , mean $\pm$ SE), when excluding fire affected and nearest other sites (Figure 5.19), but these differences were still not significant ($H_{(2)} = 0.299$, $p = 0.861$).

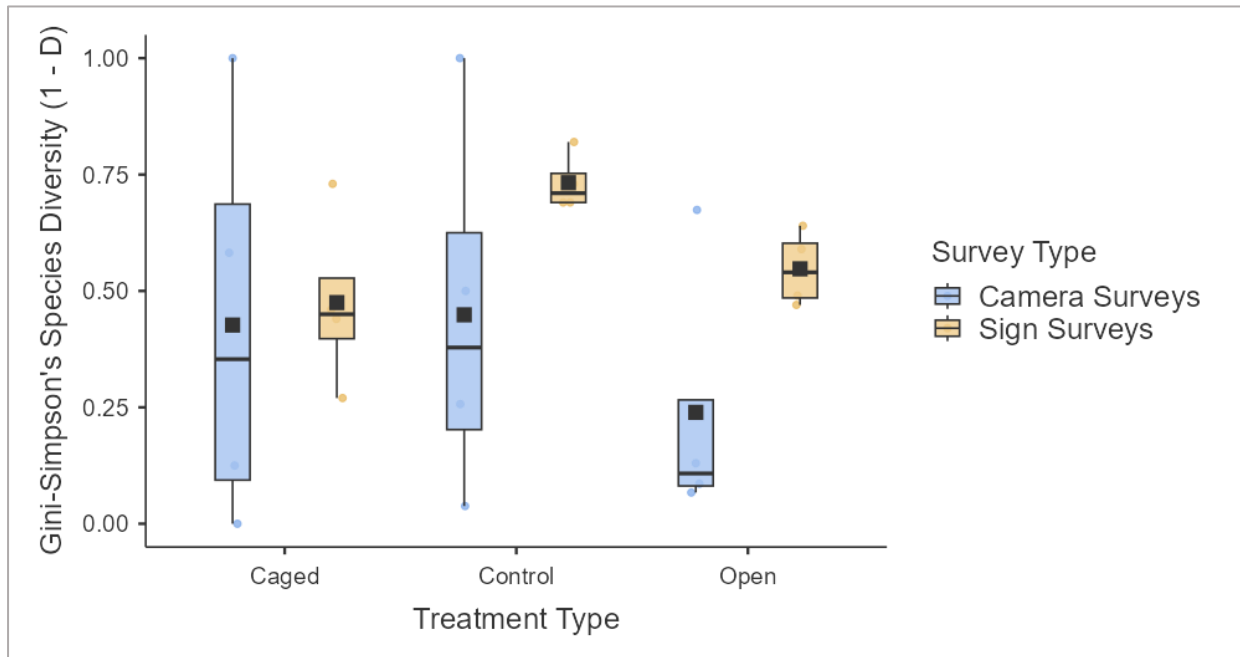


Figure 5.19: Gini-Simpson's predator species diversity ($1 - D$) from sign surveys within 250 m of experimental sites and camera trap surveys at experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020 excluding fire affected site 6 as well as sites 5, and 9. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*dots*). Box plot with missing whiskers in one direction indicate that data is skewed in the opposite direction.

5.4. Carrion and the landscape of fear

5.4.1. landscape of fear investigations from sign survey data

a) Jackal track density

Jackal track density differed significantly among treatment types ($H_{(2)} = 31.6$, $p < 0.001$) being significantly higher ($W_{(91)} = 7.4$, $p < 0.001$) at open sites than at control sites and at caged sites ($W_{(86)} = 6.22$, $p < 0.001$) than control sites. There was no significant difference ($W_{(89)} = 1.14$, $p = 0.7$) between jackal track densities at caged and open sites (Figure 5.20).

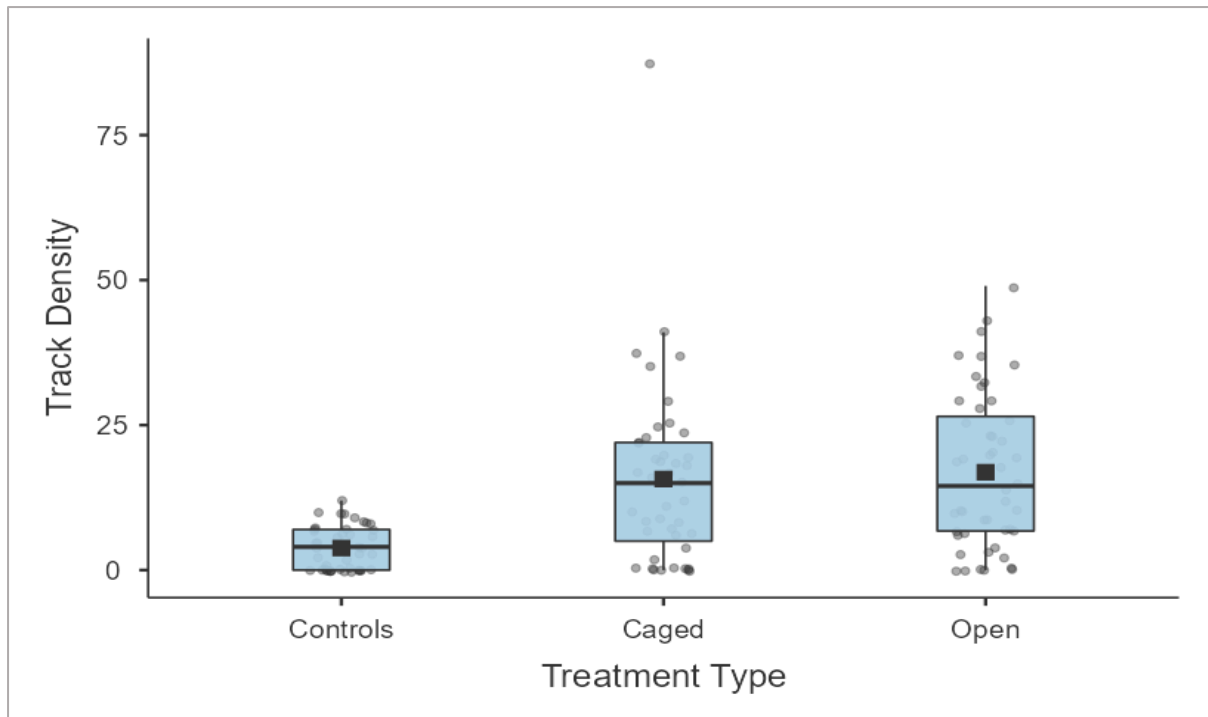


Figure 5.20: Black-backed jackal (*Lupulella mesomelas*) track density between treatment types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*).

b) Mesopredator presence at experimental sites

A correlation matrix (Figure 5.21 and Appendix 25) shows that mesopredator (excluding jackals) presence was significantly negatively correlated ($\rho_{(134)} = -0.49, p < 0.001$) with jackal track density (Figure 5.21). Furthermore, the mesopredator track species count along the 1 km transect within 250 m of experimental sites (Meso250) was significantly negatively correlated to jackal track density ($\rho_{(134)} = -0.48, p < 0.001$) (Figure 5.21). As distance increased along the transect to 500 m a significantly negative correlation between mesopredator track species count (Meso500) and jackal track density ($\rho_{(134)} = -0.64, p < 0.001$) persisted (Figure 5.21). There were no statistically significant correlations between any of the measures of mesopredator presence (Meso, Meso250, Meso500) and the presence of leopard or brown hyaena tracks (Figure 5.21 and Appendix 25).

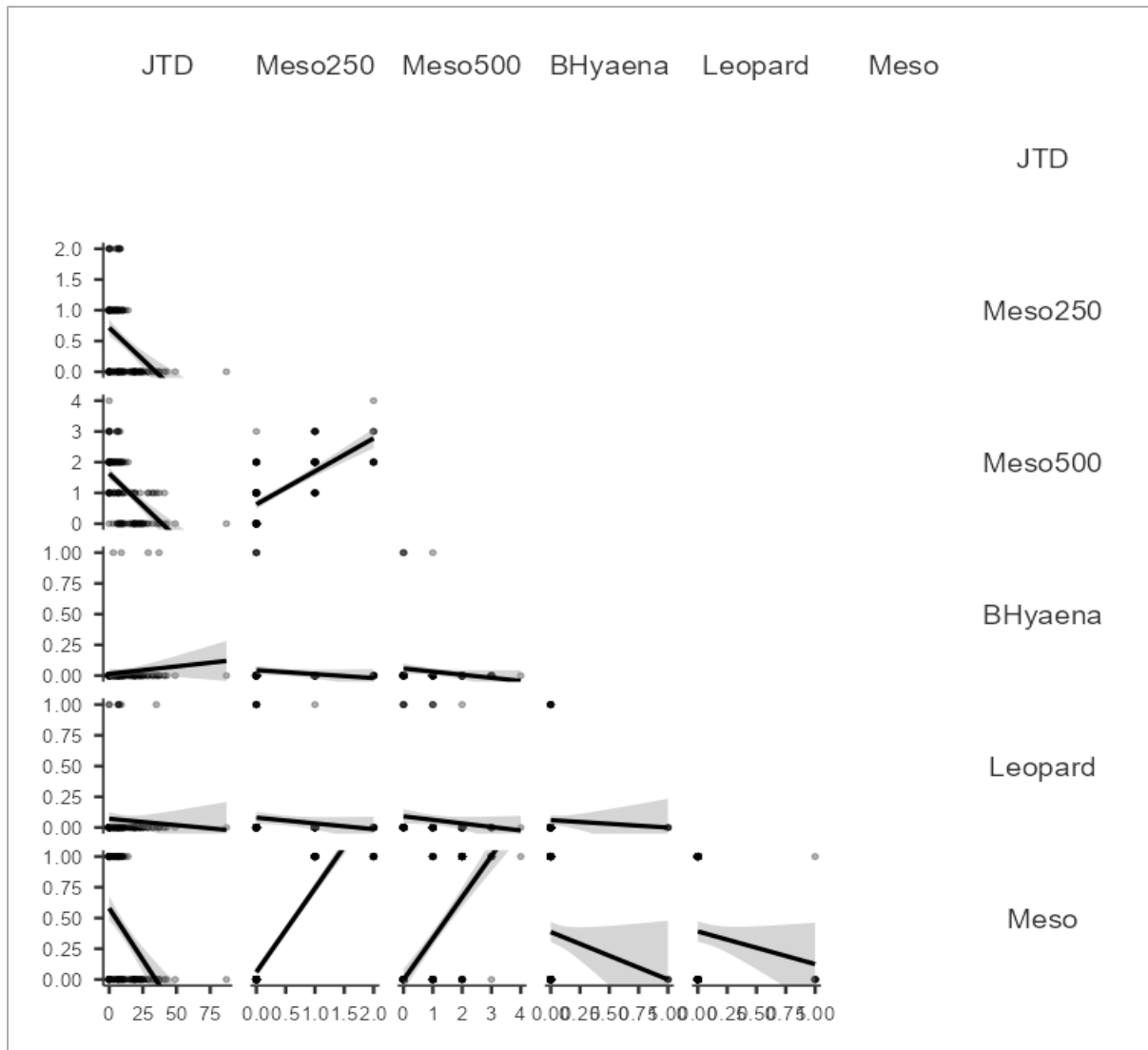


Figure 5.21: Correlation matrix for the following variables mesopredator presence (Meso), number of mesopredator species' tracks present within 250 m (Meso250), number of mesopredator species' tracks present within 500 m (Meso500), black-backed jackal (*Lupulella mesomelas*) track density (JTD), leopard (*Panthera pardus*) tracks present (Leopard), brown hyaena (*Parahyaena brunnea*) tracks present (BHyaena) during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020.

I proposed three candidate models to explain the relationship between experimental treatments (open carcasses, caged carcasses and controls) and mesopredator presence. Collinearity statistics (VIF scores > 5 and Tolerance scores of < 0.1) suggest multicollinearity was not a factor in the regression model I developed to predict mesopredator presence/absence (Table 5.4). The model I proposed (Table 5.5, Figure 5.22) showed that the combination of treatment type and jackal spoor density (Model 2) best predicted mesopredator track density (Table 5.6 and Appendix 26).

Table 5.4: Collinearity statistics for the three predictor variables included in the binomial logistical regression model to predict mesopredator presence/absence during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020

	VIF	Tolerance
Treatment	1.07	0.934
JTD	1.23	0.814
Season	1.06	0.939

Table 5.5: Summary of three different models developed using binomial logistic regression to investigate treatment type (open carcasses, caged carcasses and controls), black-backed jackal (*Lupulella mesomelas*) track density (JTD) and season as predictors for mesopredator presence during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020

Model	Predictor	Estimate	SE	Z	p	Odds Ratio	95% Confidence Intervals	
							Lower	Upper
1	Intercept	1.13	0.35	3.25	0.001	3.09	1.57	6.1
	Treatment:							
	Caged-Control	-2.77	0.54	-5.13	< 0.001	0.06	0.02	0.18
	Open-Control	-2.46	0.5	-4.96	< 0.001	0.09	0.03	0.23
2	Intercept	1.67	0.39	4.25	< 0.001	5.33	2.47	11.52
	Treatment:							
	Caged-Control	-2.07	0.58	-3.6	< 0.001	0.13	0.04	0.39
	Open-Control	-1.52	0.55	-2.77	0.006	0.22	0.08	0.64
	JTD	-0.13	0.04	-3.5	< 0.001	0.88	0.82	0.95
3	Intercept	1.69	0.52	3.27	0.001	5.44	1.97	15.01
	Treatment:							
	Caged-Control	-2.13	0.64	-3.33	< 0.001	0.12	0.03	0.42
	Open-Control	-1.5	0.6	-2.48	0.013	0.22	0.069	0.73
	JTD	-0.5	0.05	-3.09	0.002	0.86	0.78	0.95
	Season:							
	Autumn-Active decay	-0.03	0.74	-0.04	0.964	0.97	0.23	4.1
	Spring-Active Decay	0.36	0.8	0.45	0.654	1.43	0.3	6.9
	Summer-Active Decay	-0.69	0.79	-0.88	0.382	0.5	0.11	2.34
	Winter-Active Decay	1.4	0.8	1.75	0.08	4.05	0.85	19.33

Note: Estimates represent the log odds of "Meso = Present" vs "Meso = Absent"

Table 5.6: Model fit measures for the three candidate models used to predict mesopredator presence/absence at experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve between January 2019 and January 2020.

Model	Deviance	AIC	Δ AIC	BIC	Δ BIC	R^2_{MCF}	Overall Model Test		
							χ^2	df	p
2	118	126		137		0.35	62.3	3	< 0.001
3	112	128	2	151	14	0.38	67.9	7	< 0.001
1	137	143	15	152	1	0.24	42.6	2	< 0.001

Note: Model 1 only used treatment type as a predictor of mesopredator presence/absence

Model 2 included treatment type and jackal track density as predictors of mesopredator presence/absence

Model 3 included treatment type, jackal track density and season as predictors of mesopredator presence/absence

Estimated Marginal Means graphs for the most parsimonious model, show the means of each covariate adjusted for other variables in the model (Figure 5.22).

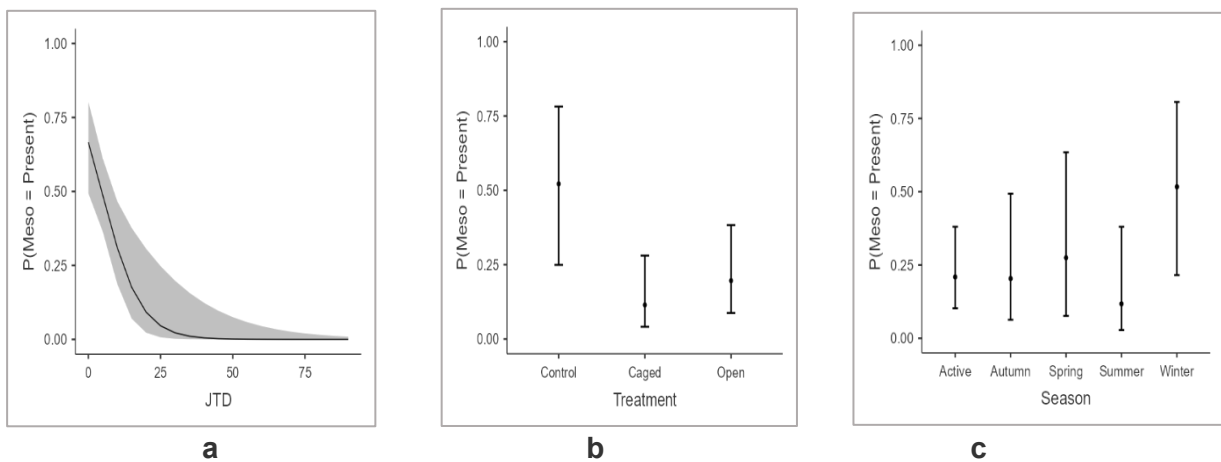


Figure 5.22: Estimated Marginal Means plots of mesocarnivore presence versus a) Black-backed jackal (*Lupulella mesomelas*) Track Density, b) Treatment Type and c) Season during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature reserve from January 2019 to January 2020. Line graph represents estimated marginal means for continuous data and grey polygon represents 95% confidence intervals. Dot plots represent estimated marginal means for nominal data with 95% confidence intervals.

The model predicted mesopredator absence correctly 82.4% of the time and it predicted mesopredator presence correctly 78.4% of the time (Table 5.7) based on a cut-off value of 0.41 i.e. where sensitivity and specificity intersected on a sensitivity vs specificity graph (Figure 5.23).

Table 5.4: Predictive measures classification for the most parsimonious model (model 2) to predict presence or absence of mesopredator tracks during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.

Observed	Predicted		% Correct
	Absent	Present	
Absent	70	15	82.4
Present	11	40	78.4

Note. The cut-off value is set to 0.41 (See below graph for explanation)

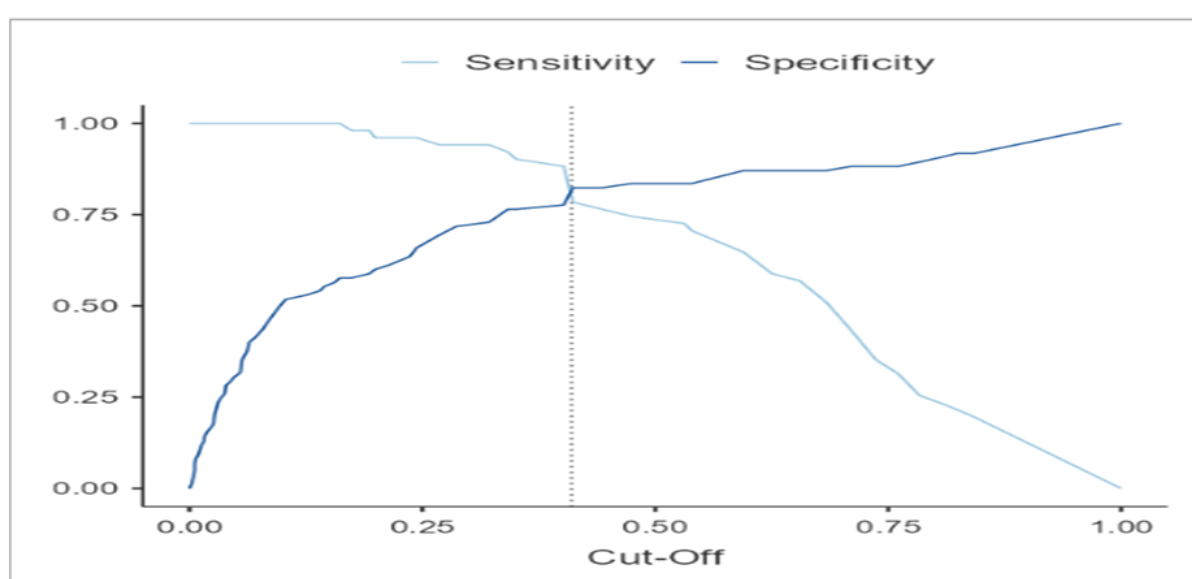


Figure 5.23: Sensitivity vs specificity plot of most parsimonious model (model 2) to predict presence or absence of mesopredator tracks during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. The x axis represents the false positive rate (1 – specificity). The y axis represents the true positive rate (sensitivity). Note the cut off value was set at the intersection of the two lines at 0.41 as equal weight was given to sensitivity and to specificity as per (Habibzadeh *et al.* 2016).

5.4.2. Landscape of fear investigations from camera trap data

Camera data indicated a slight positive, non-significant correlation ($r_{(73)} = 0.128$, $p = 0.273$) between the number of mesopredator visits at each experimental site and the number of jackal visits at each site (Figure 5.24).

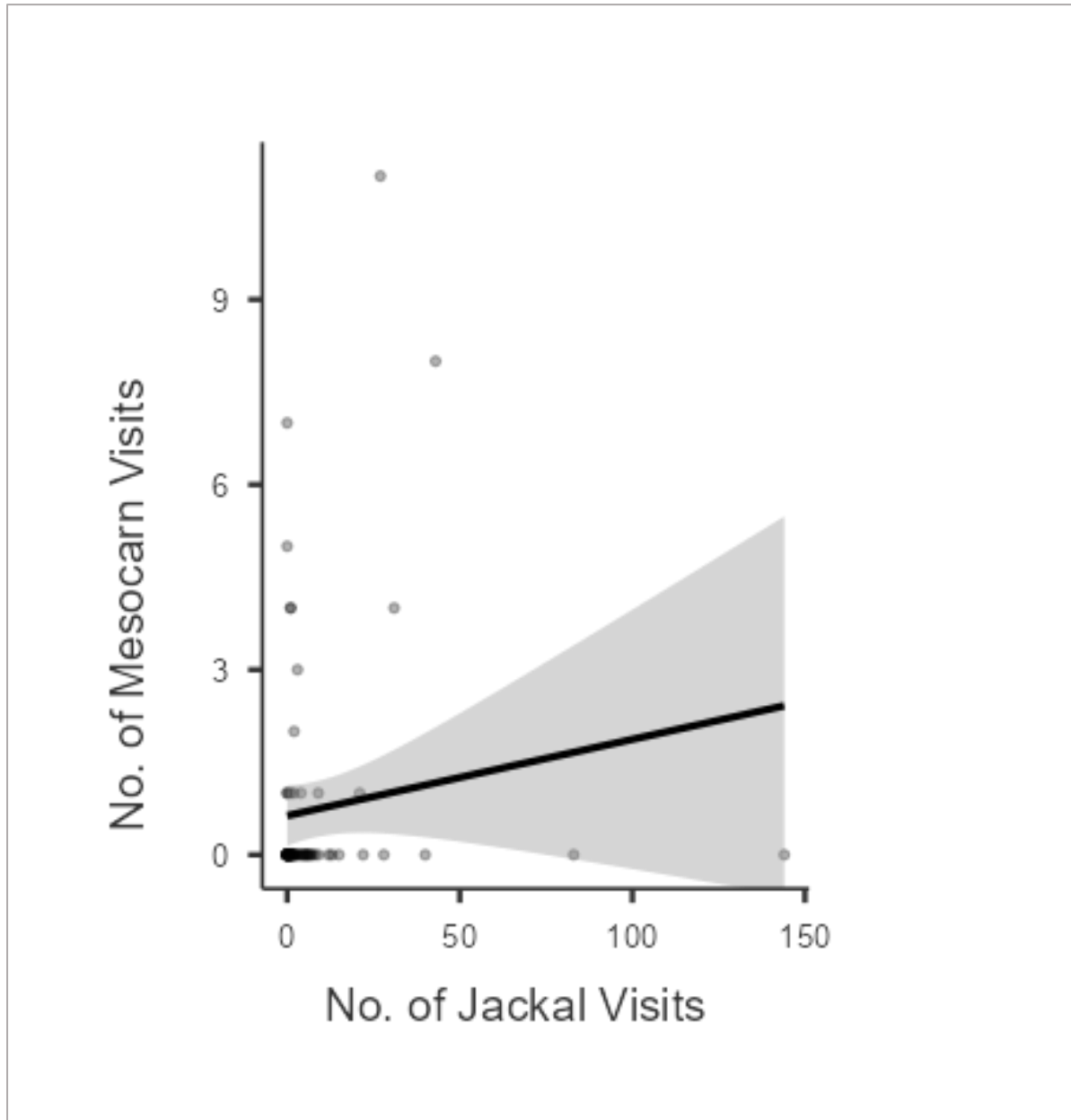


Figure 5.24: Camera trap survey correlation plot of the number of black-backed jackal (*Lupulella mesomelas*) visits and the number of mesopredator visits at study sites for the entire study period from January 2019 to January 2020 during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve.

However, seasonal evaluation of the data revealed contrasting relationships (Figure 5.25 and Table 5.8). During active decay, there was a significant negative correlation ($T_{b(13)} = -0.59, p = 0.009$) between jackal visits and mesopredator visits to experimental sites. Although I found evidence of positive correlations between jackal and mesopredator visitation to experimental sites during all seasons after the cessation of active decay, none of these were statistically significant (Autumn: $T_{b(13)} = 0.21, p = 0.374$; Winter: $T_{b(13)} = 0.32, p = 0.188$; Spring: $T_{b(13)} = 0.40, p = 0.07$; Summer: $T_{b(13)} = 0.47, p = 0.053$).

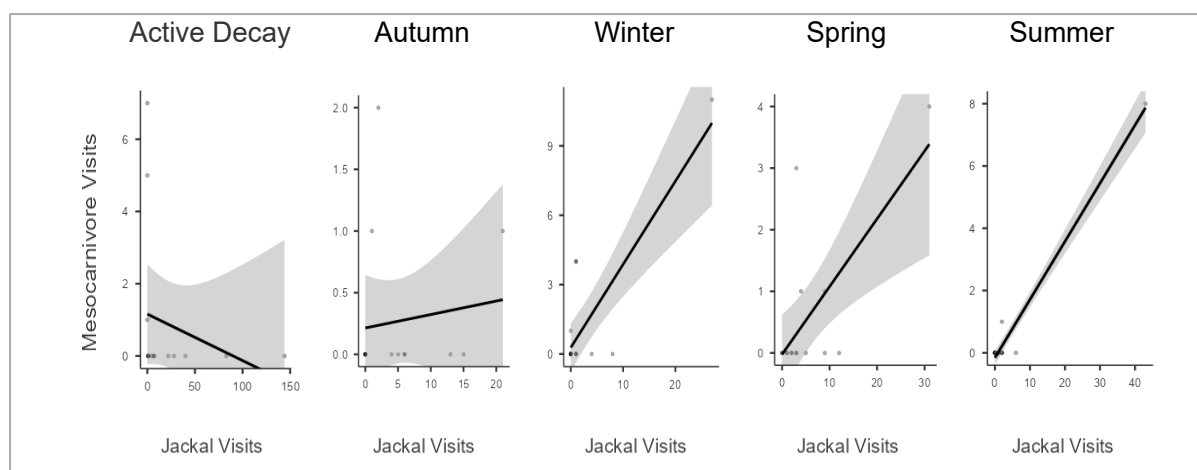


Figure 5.25: Seasonal associations between the number of black-backed jackal (*Lupulella mesomelas*) visits to all experimental sites and the number of mesopredator visits to all experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020

Table 5.5: Kendall's TauB and Spearman's correlation coefficients for the relationship between number of black-backed jackal (*Lupulella mesomelas*) visits and number of mesopredator visits for each season at all experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.

Season	Kendall's TauB Correlation Coefficient (τ_B)	Kendall's p-value	Spearman's Correlation Coefficient (ρ)	Spearman's p-value
Active Decay	-0.59	0.009*	-0.70	0.004*
Autumn	0.21	0.374	0.22	0.426
Winter	0.32	0.188	0.34	0.214
Spring	0.40	0.07	0.49	0.066
Summer	0.47	0.053	0.50	0.055

Note: * Denotes statistically significant outcomes evaluated at $\alpha = 0.05$

Investigating the camera results for the period of active decay in more detail, (Figure 5.26 and Appendix 27) showed that mesopredators were only present at three sites during active decay: one control (site two), one caged (site four) and one open (site eight). These were also the only sites at which jackals were never detected by cameras for the duration of the period of active decay. Brown hyaena and leopard were present at sites eight and 15.

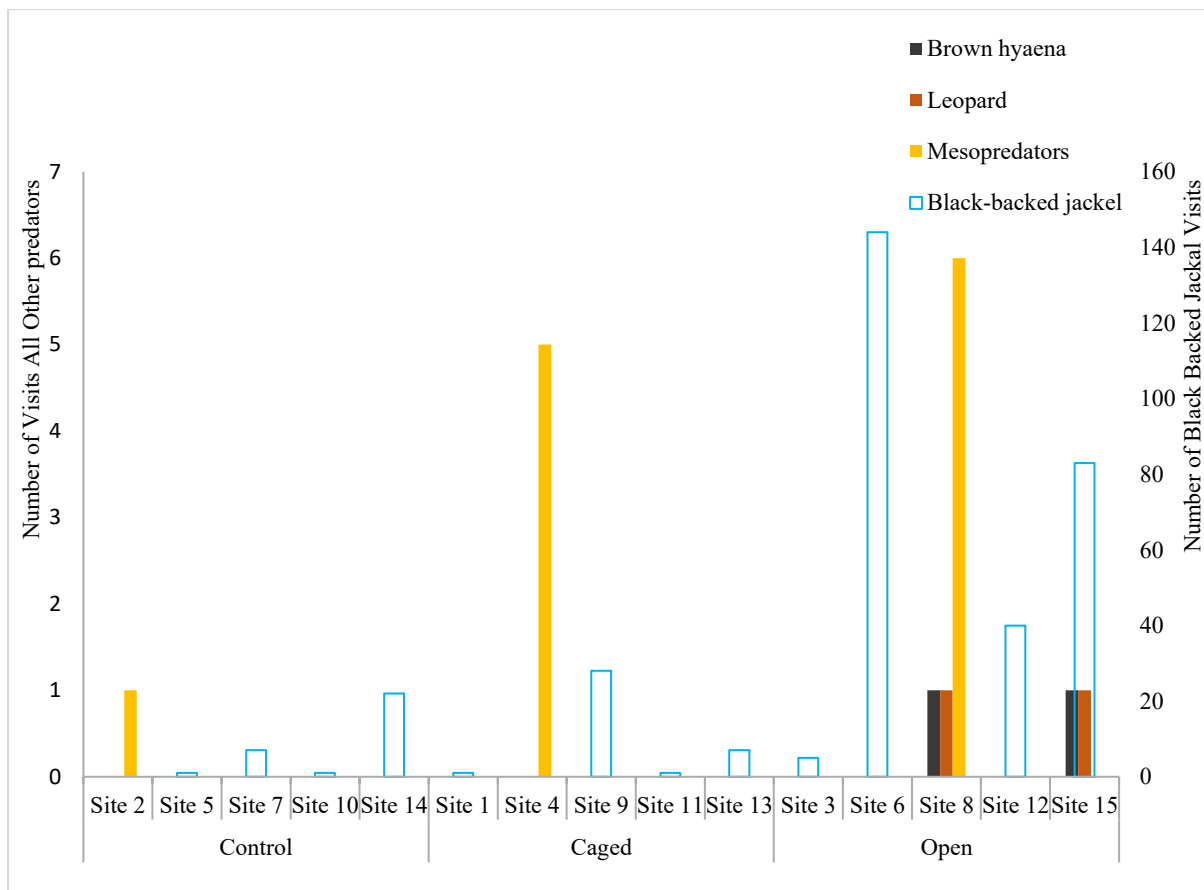


Figure 5.26: Predator visits to experimental sites during the period of active decay from camera trap data during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve. Black-backed jackal (*Lupulella mesomelas*) visits are presented on a separate axis to other predator visits were as black-backed jackal numbers far exceeded other predator numbers and thus a different scale was required.

5.5. Carrion and predator occupancy

My species-specific occupancy models from sign survey data that included various environmental factors (habitat type, substrate quality score, carcass presence and human disturbance) as covariates (Table 5.9) showed that occupancy for brown hyaena was negatively affected by human disturbance, while detection probability for leopard and serval was negatively affected by human disturbance.

Jackal were the only predators whose detection probability I found to be positively influenced by the presence of an actively decaying carcass (Table 5.9). The detection probability of aardwolf, caracal, slender mongoose, yellow mongoose, rusty spotted genet and suricate were all negatively affected by the presence of an actively decaying carcass (Table 5.9). Habitat was the predominant influencer of occupancy for water mongoose and civet, while none of the covariates included in the models seemed to influence the occupancy and detection probability

of Cape clawless otter and honey badger and thus the null model was the best predictor of occupancy and detection probability (Table 5.9).

Table 5.6: Outcomes of single season occupancy models for each species from sign surveys conducted during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators at Telperion Nature Reserve from January 2019 to January 2020. ψ is occupancy and ρ is detection probability. The covariates Habitat, Carcass Presence and Human Disturbance were used to construct various models for each species and the best models for each species are presented here. ΔAIC is the difference in Akaike Information Criterion between the best model and the null model [$\psi(.)\rho(.)$] for each species. Models with $\Delta AIC > 2$ are strongly supported. X^2 is the test statistic from a likelihood ratio test. The top ranked model was a significantly better fit than the null model except where $p > 0.05$, for civet (*Civettictis civetta*), caracal (*Caracal caracal*) and black-footed cat (*Felis nigripes*). For these species the sample numbers were < 30 and this would have affected statistical significance. Honey badger (*Mellivora capensis*) and Cape clawless otter (*Aonyx capensis*) have no p values as the null model was the best fit.

Description of Grouping	Species	Best Occupancy Model for Each Species	AIC	ΔAIC	AIC Weight	Model Likelihood	Number of Parameters	-2log Likelihood	-2 log Likelihood of Default Model	Degrees of Freedom	X^2	p-value
Species where Human Disturbance influenced Occupancy (ψ) or Detection Probability (ρ).	<i>Hyaena brunnea</i>	ψ (Disturbance) ρ (.)	193.23	7.11	0.2176	1	3	187.23	176.34	1	10.89	< 0.001
	<i>Panthera pardus</i>	ψ (Habitat) ρ (Disturbance)	151.73	9.24	0.9311	1	4	143.73	156.97	2	13.24	< 0.001
	<i>Leptailurus serval</i>	ψ (Habitat) ρ (Disturbance)	161.49	4.99	0.2937	1	4	153.49	162.48	2	8.99	$0.025 > p > 0.01$
	<i>Felis nigripes</i>	ψ (Habitat) ρ (Disturbance)	25.11	1.76	0.1327	1	4	17.11	22.87	2	5.76	$0.10 > p > 0.05$
Species where Carcass Presence influenced Detection probability positively** or negatively*	<i>Lupulella mesomelas**</i>	ψ (.) ρ (Carcass Presence)	88.03	3.82	0.4662	1	3	82.03	87.85	1	5.82	$0.025 > p > 0.01$
	<i>Proteles cristatus*</i>	ψ (.) ρ (Carcass Presence)	151.55	11.49	0.9536	1	3	145.55	159.04	1	13.49	< 0.001
	<i>Caracal caracal*</i>	ψ (.) ρ (Carcass Presence)	69	1.44	0.4488	1	3	63	66.44	1	3.44	$0.10 > p > 0.05$
	<i>Galerella sanguinea*</i>	ψ (Habitat) ρ (Carcass Presence)	212.26	20.36	0.9937	1	4	204.62	228.98	2	24.36	< 0.001
	<i>Cynictis penicillata*</i>	ψ (Habitat) ρ (Carcass Presence)	261.14	37.87	1	1	4	253.41	295.01	2	41.6	< 0.001
	<i>Genetta maculata*</i>	ψ (Habitat) ρ (Carcass Presence)	196.89	20.65	1	1	4	188.89	213.54	2	24.65	< 0.001
	<i>Suricata suricatta*</i>	ψ (.) ρ (Carcass Presence)	79.18	6.5	0.8979	1	3	73.18	81.68	1	8.5	$0.01 > p > 0.005$
Species whose Occupancy and/or Detection Probability are not influenced by Human Disturbance or Carcass presence	<i>Atilax paludinosus</i>	ψ (Habitat) ρ (.)	127.24	3.97	0.4486	1	3	121.24	127.21	1	5.97	$0.025 > p > 0.01$
	<i>Civettictis civetta</i>	ψ (Habitat) ρ (.)	26.48	0.39	0.3633	1	3	20.48	22.87	1	2.39	$0.9 > p > 0.1$
	<i>Mellivora capensis</i>	ψ (.) ρ (.)	79.57	10.88	0.2773	1	2	75.57	66.45	0	-9.12	-
	<i>Aonyx capensis</i>	ψ (.) ρ (.)	21.05	12.14	0.4105	1	2	21.05	9.19	0	-11.86	-

5.6. Predator presence and behaviour from camera traps

I recorded 13 predator species with cameras at the experimental sites. Of these, four species were only recorded at control sites, while nine species visited carcasses sites (caged and open). Of the nine species that visited carcass sites, I recorded none at caged sites only (Appendix 28). I only recorded three species of predator actively scavenging on the carcasses: jackal, brown hyaena and slender mongoose (Table 5.10). I recorded leopards at the carcasses on two occasions during my study and on neither occasion did they actively scavenge on the remains. On one occasion a leopard rubbed himself on the carcass (Table 5.10). I recorded aardwolf, water mongoose, yellow mongoose, serval and suricate at the carcasses but did not record any of these species scavenging on the carcasses (Table 5.10).

I recorded no interspecific interactions among predator species at any of my study sites; however, I did record multiple members of the same species visiting sites together on numerous occasions (Table 5.10).

Table 5.7: Behavioural summary for all predator species at experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators for the entire study period from January 2019 to January 2020 on Telperion Nature Reserve.

Species Common Name	Species Scientific Name	Maximum number of animals active at the same time at the same experimental site	Maximum number of animals active at the same time at the same carcass	Time of day active	Activity at carcass			
					Actively scavenging	Passing by	Sniffing Carcass Only	Scent Marking
Aardwolf	<i>Proteles cristatus</i>	2	2	Nocturnal		✓	✓	
Brown hyaena	<i>Parahyaena brunnea</i>	3	3	Nocturnal	✓	✓	✓	✓
Black-backed jackal	<i>Lupulella mesomelas</i>	5	5	Nocturnal, Diurnal	✓	✓	✓	✓
Cape fox	<i>Vulpes chama</i>	1	Only recorded at controls	Nocturnal	Not recorded at carcasses only controls			
Caracal	<i>Caracal caracal</i>	1	Only recorded at controls	Nocturnal	Not recorded at carcasses only controls			
Honey badger	<i>Mellivora capensis</i>	2	Only recorded at controls	Nocturnal	Not recorded at carcasses only controls			
Leopard	<i>Panthera pardus</i>	1	1	Nocturnal, Diurnal		✓		✓
Mongoose slender	<i>Galerella sanguinea</i>	1	1	Diurnal	✓	✓		
Mongoose water	<i>Atilax paludinosus</i>	1	1	Nocturnal		✓		
Mongoose yellow	<i>Cynictis penicillata</i>	2	2	Diurnal		✓	✓	
Serval	<i>Leptailurus serval</i>	1	1	Nocturnal		✓		
Striped polecat	<i>Ictonyx striatus</i>	1	Only recorded at controls	Nocturnal	Not recorded at carcasses only controls			
Suricate	<i>Suricata suricatta</i>	5	5	Diurnal		✓		

Jackals were the most active species at carcasses with multiple recorded visits throughout the study period. The number of visits for this species allowed for statistical analysis of various aspects of their behaviour. However, data relating to visits by other species were too few for detailed statistical analysis of their behaviour.

5.7. Jackal visitation frequency and duration

5.7.1. Jackal visitation frequency

I recorded jackals at the experimental sites on 489 separate occasions (1667 separate videos) during the study. There was marked variability in the frequency of jackal visitation to the experimental sites (controls $n = 49$, caged carcasses $n = 32$ and open carcasses $n = 408$) (Figure 5.27 and Figure 5.28 and Appendix 7). There were significant differences in the number of jackal visitations to the different treatment types ($H_{(2)} = 8.89$ $p = 0.012$). *Post-hoc* pairwise comparisons indicated that jackal visitation to open carcasses ($n = 408$) was significantly higher than to caged carcasses ($n = 32$) ($W = 3.52$, $p = 0.03$) and to control sites ($n = 49$) ($W = 3.58$, $p = 0.03$). There was no significant difference in jackal visitations between caged carcasses ($n = 32$) and control sites ($n = 49$) ($W = 0.43$, $p = 0.95$).

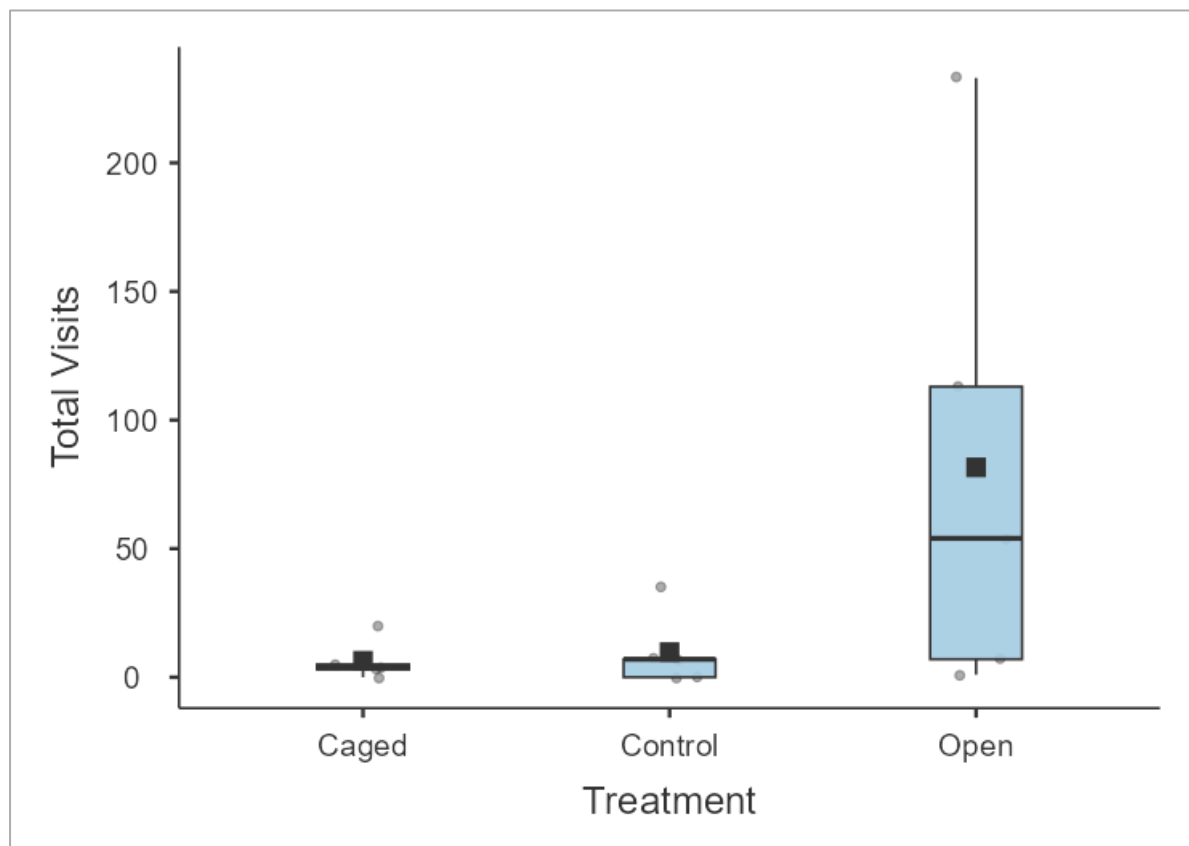


Figure 5.27: Black-backed jackal (*Lupulella mesomelas*) visits to experimental sites associated with my blue wildebeest (*Connochaetes taurinus*) carcass decomposition study on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together.

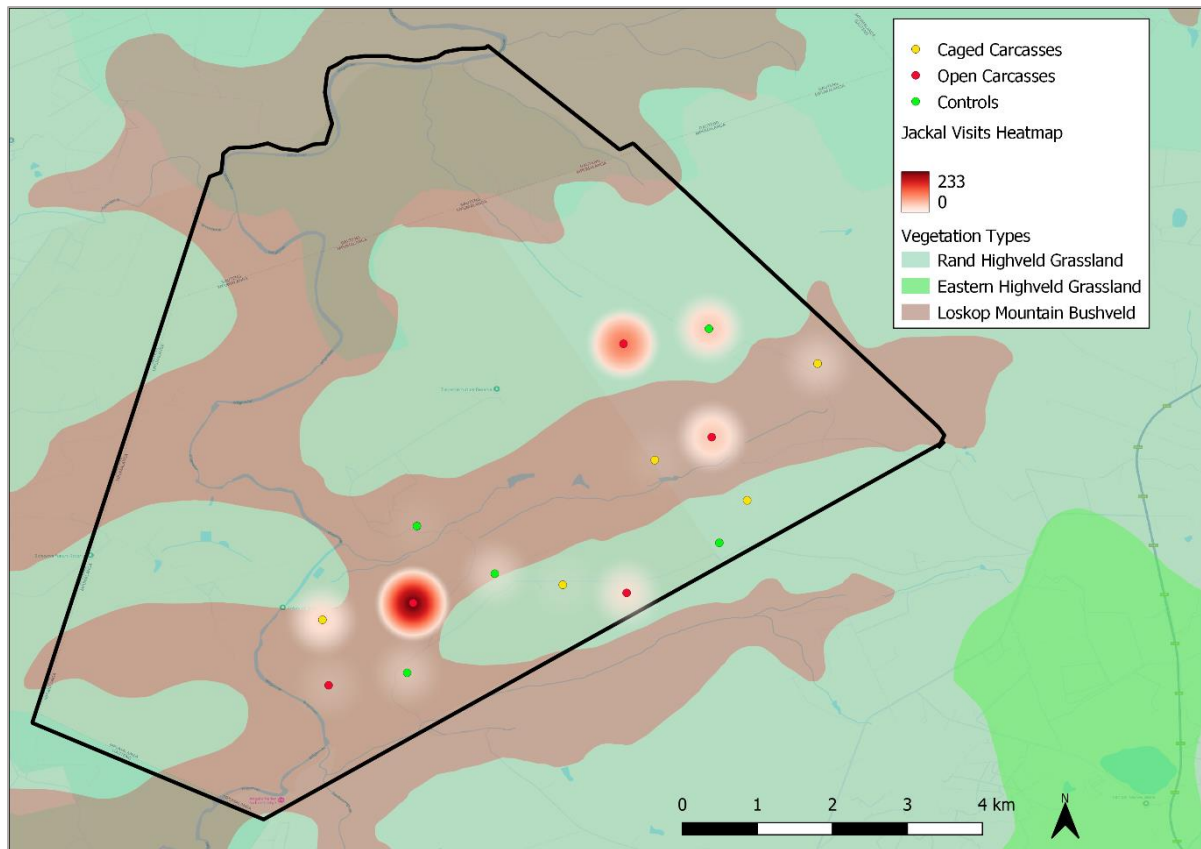


Figure 5.28: Frequency of visits (0 – 233) by black-backed jackal (*Lupulella mesomelas*) to experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve presented as heatmaps, and relative to the broad vegetation types associated with each experimental site for the entire study period from January 2019 to January 2020.

I found no significant differences ($H_{(4)} = 8.27$, $p = 0.082$) in the number of seasonal visits by jackals to the experimental sites when treatment type was not considered (Figure 5.29).

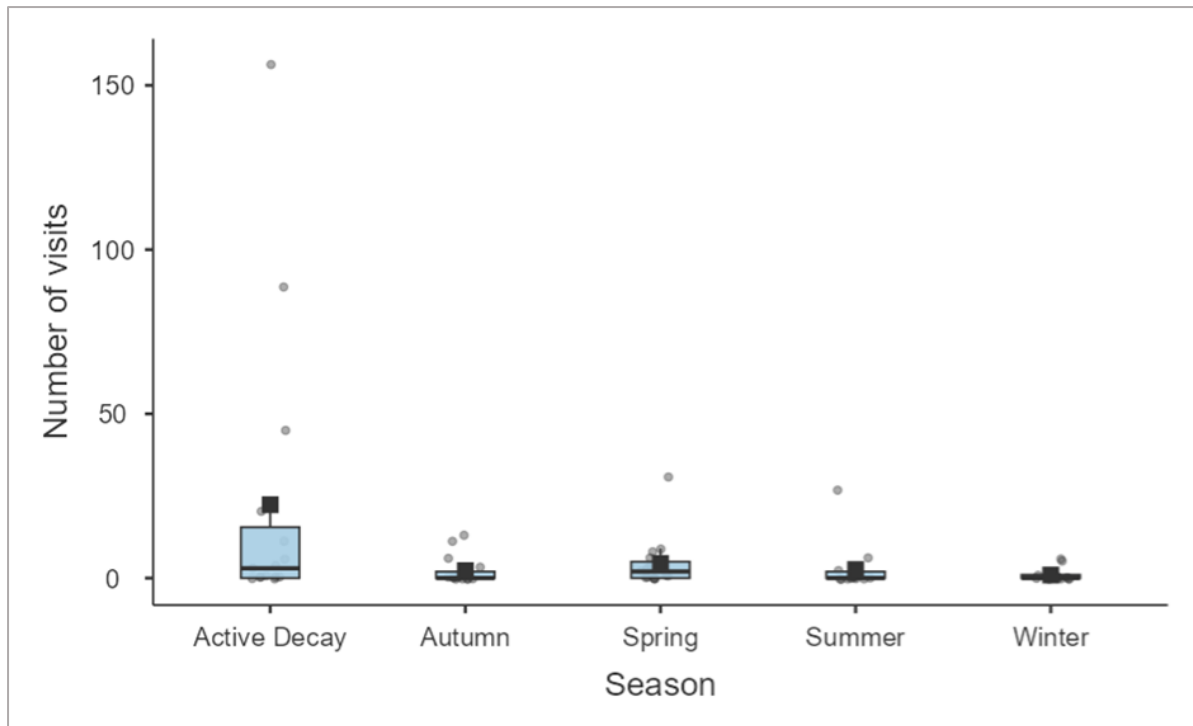


Figure 5.29: Seasonal variation in the number of black-backed jackal (*Lupulella mesomelas*) visits to all experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together.

5.7.2. Duration per visit at each treatment type

The duration that jackals spent per visit to experimental sites (Figure 5.30) differed significantly ($H_{(2)} = 67.5$, $p < 0.001$) among treatments. The time spent per visit by jackals at open carcasses was significantly higher than at caged carcasses ($W = 7.012$, $p < 0.001$) and control sites ($W = 9.65$, $p < 0.001$). However, there was no significant difference between the time spent per visit at caged carcasses and at control sites ($W = 2.05$, $p = 0.317$).

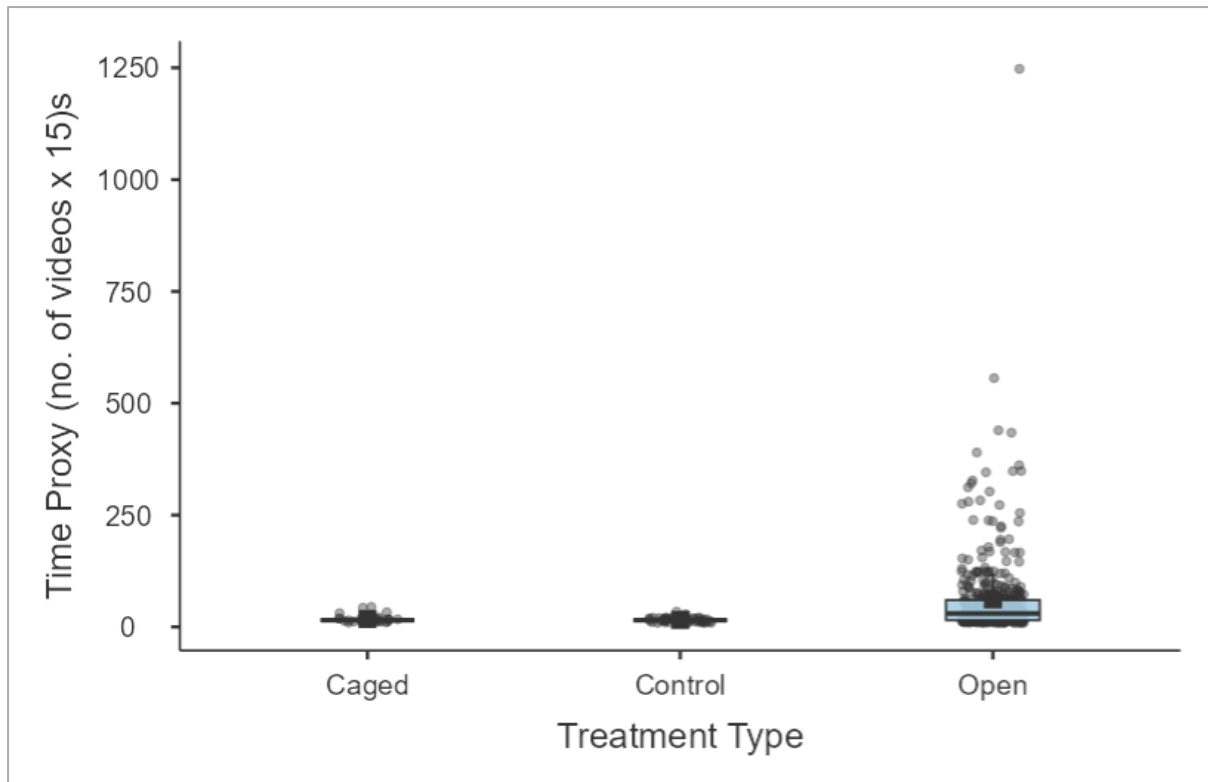


Figure 5.30: Black-backed jackal (*Lupulella mesomelas*) time spent per visit from camera trap videos for each treatment type for the entire study period during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together.

5.7.3. Seasonal variation in time spent per visit irrespective of treatment type

The duration of jackal visits to experimental sites showed significant ($H_{(4)} = 114, p < 0.001$) seasonal variation (Figure 5.31). *Post-hoc* comparisons (Table 5.11) indicated that time spent per visit by jackals to experimental sites was significantly higher during the period of active decay than in all other seasons. No other seasonal comparisons displayed significant differences in the time spent per visit.

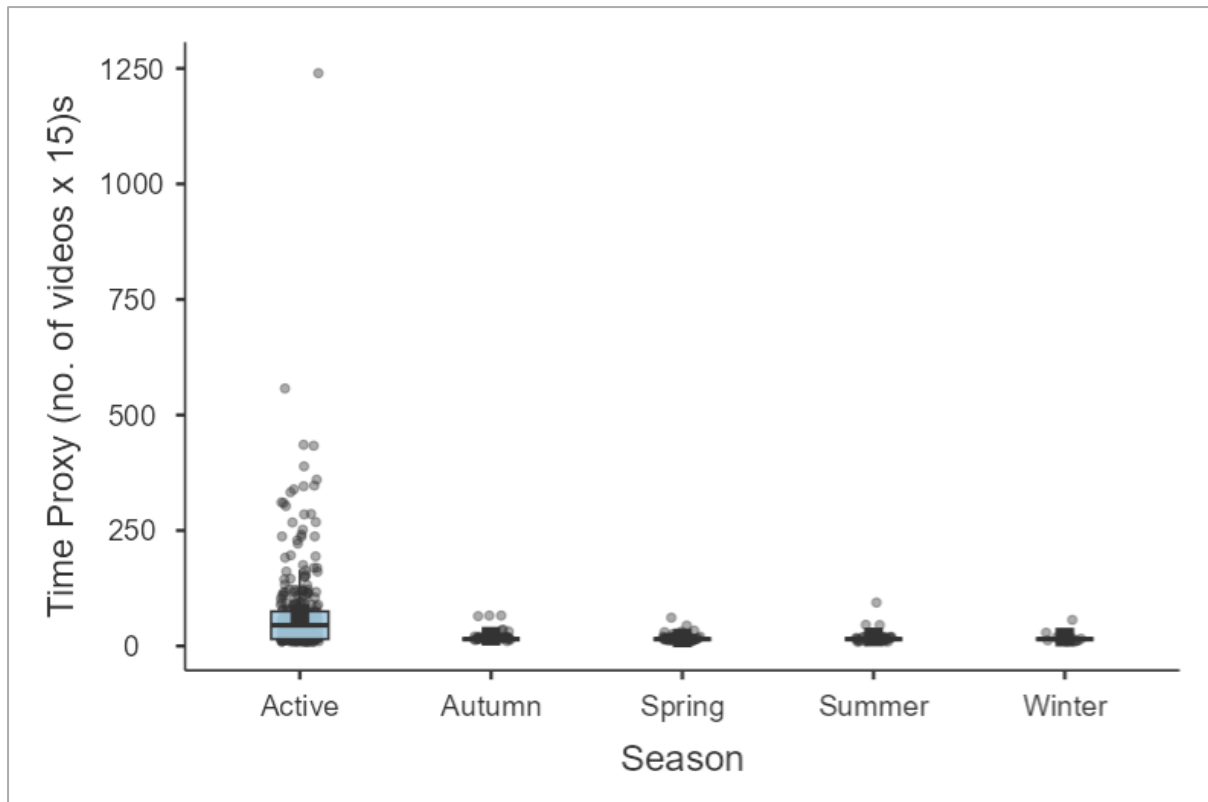


Figure 5.31: Black-backed jackal (*Lupulella mesomelas*) time spent per visit irrespective of treatment type from camera trap videos for each season for the entire study period during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together.

Table 5.8: Outcomes from Dwass-Steel-Critchlow-Fligner pairwise comparisons of time spent by black-backed jackals (*Lupulella mesomelas*) per visit per season at all treatment types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.

Season Comparison		W	p
Active	Autumn	-7.057	< 0.001*
Active	Spring	-11.284	< 0.001*
Active	Summer	-8.260	< 0.001*
Active	Winter	-5.125	0.003*
Autumn	Spring	-2.202	0.525
Autumn	Summer	-1.197	0.916
Autumn	Winter	-0.951	0.962
Spring	Summer	0.804	0.980
Spring	Winter	0.418	0.998
Summer	Winter	-0.115	1.000

Note: * Denotes statistically significant outcomes evaluated at $\alpha = 0.05$

5.7.4. Seasonal variation in time spent per visit at each treatment type

I found that jackals spent significantly more time per visit at open carcasses than at either caged carcasses or control sites, irrespective of season (Table 5.12 and Figure 5.32). There was no significant difference between the time spent per visit at caged carcasses and controls for any season (Table 5.12 and Figure 5.32).

Table 5.9: Outcomes from Kruskal-Wallis ANOVA and Dwass-Steel-Critchlow-Fligner Pairwise Comparisons for the time spent per visit by black-backed jackals (*Lupullela mesomelas*) at each treatment type for each season during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.

Season	Kruskal-Wallis Anova			Pairwise Comparisons			
	<i>H</i>	<i>df</i>	<i>p</i>	Treatment	Treatment	<i>W</i>	<i>p</i>
Active Decay	112	2	< 0.001	Caged	Control	2.85	0.108
				Caged	Open	12.65	< 0.001*
				Control	Open	12.19	< 0.001*
Autumn	13.3	2	0.001	Caged	Control	-2.80	0.118
				Caged	Open	2.92	0.097
				Control	Open	4.84	0.002*
Winter	12.9	2	0.002	Caged	Control	0.00	1.000
				Caged	Open	3.83	0.019*
				Control	Open	3.83	0.019*
Spring	23.5	2	< 0.001	Caged	Control	2.07	0.308
				Caged	Open	6.21	< 0.001*
				Control	Open	4.83	0.002*
Summer	29.8	2	< 0.001	Caged	Control	2.14	0.285
				Caged	Open	6.83	< 0.001*
				Control	Open	5.20	< 0.001*

Note: * Denotes statistically significant outcomes evaluated at $\alpha = 0.05$

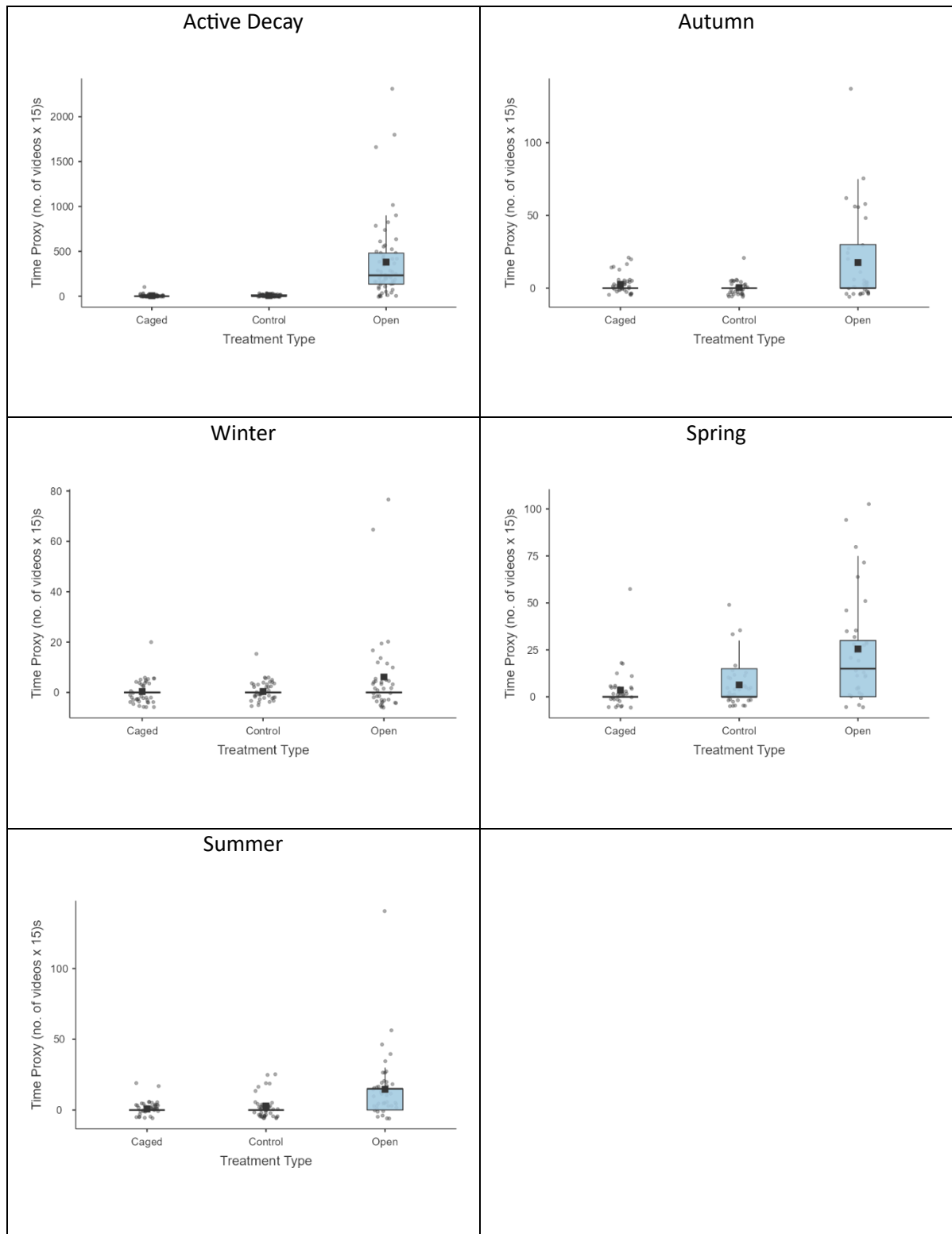


Figure 5.32: Seasonal variation in time spent per visit by black-backed jackals (*Lupullela mesomelas*) at each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together.

5.7.5. Seasonal variation in time spent per visit at open carcasses

Due to the variance in time spent per visit at open carcasses and the fact that open carcasses showed significant differences to both other treatment types for all seasons, I examined this treatment type in more detail, from a seasonal perspective (Figure 5.33). I found significant ($H_{(4)} = 101, p < 0.001$) seasonal variation in the duration of jackal visits to open carcasses. Jackal visits to open carcasses during the summer of active decay were significantly longer than all other seasons (Table 5.13). No other comparisons were significantly different.

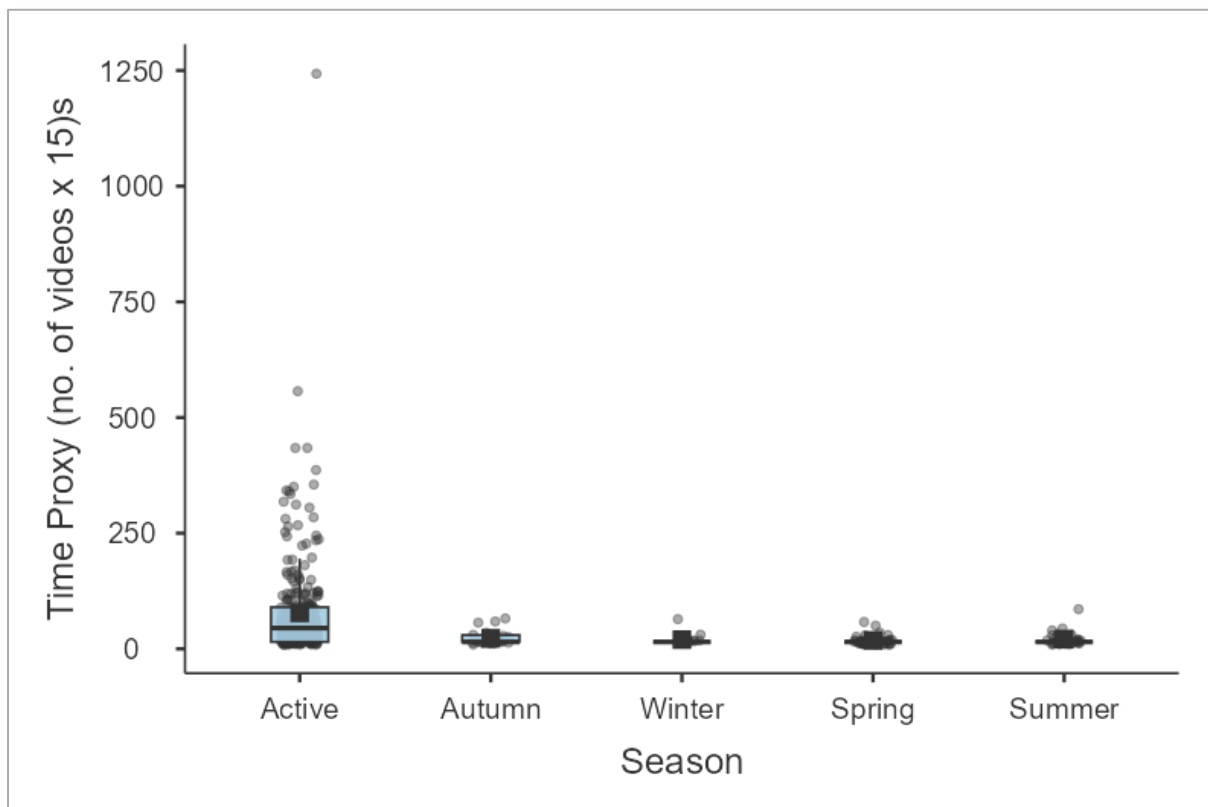


Figure 5.33: Time spent per visit by black-backed jackals (*Lupulella mesomelas*) at open carcasses for each season during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together.

Table 5.10: Outcomes from Dwass-Steel-Critchlow-Fligner pairwise comparisons for time (number of videos per visit multiplied by 15 seconds) spent per black-backed jackal (*Lupullela mesomelas*) visit at open carcasses for each season from January 2019 to January 2020 on Telperion Nature Reserve.

Season	Season	W	p
Active	Autumn	-6.839	<.001*
Active	Winter	-5.242	0.002*
Active	Spring	-10.325	<.001*
Active	Summer	-7.677	<.001*
Autumn	Winter	-1.126	0.932
Autumn	Spring	-2.146	0.551
Autumn	Summer	-1.024	0.951
Winter	Spring	-0.259	1.000
Winter	Summer	0.381	0.999
Spring	Summer	0.958	0.961

Note: * Denotes statistically significant outcomes evaluated at $\alpha = 0.05$

5.7.6. Jackal visits per day

Over the entire study period regardless of season, there was a significant difference ($H_{(2)} = 143$, $p < 0.001$) in the number of daily jackal visits among treatment types (Figure 5.34). *Post-hoc* analyses showed the number of jackal visits per day to open carcasses was significantly higher than visits to control sites ($W = 12.74$, $p < 0.001$) and visits to caged carcasses ($W = 14.55$, $p < 0.001$). There was no significant difference between the number of visits per day to caged carcasses and to control sites ($W = 2.86$, $p = 0.107$).

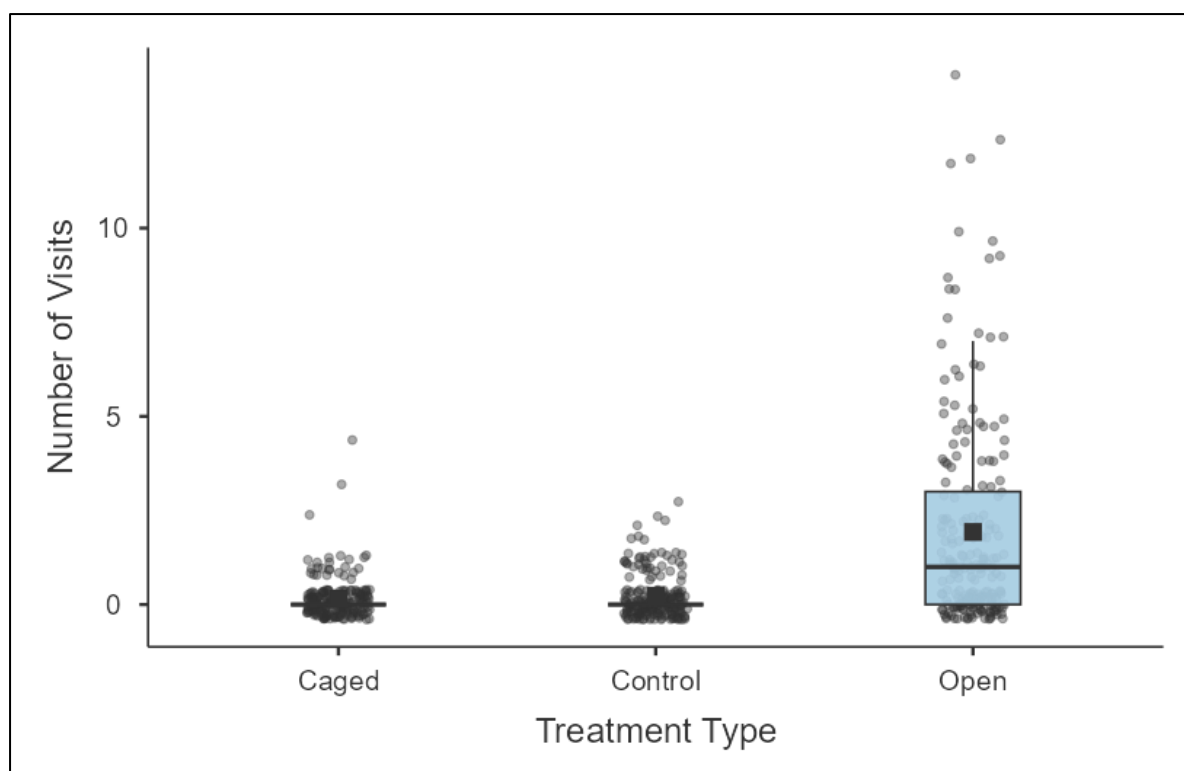


Figure 5.34: Number of black-backed jackal (*Lupullela mesomelas*) visits per day for each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together.

5.7.7. Seasonal jackal visits per day for each treatment type

The number of visits per day for each treatment type was analysed separately for each season. For every season, the number of visits by jackals to open carcasses was significantly higher than at controls. The number of visits by jackals to open carcasses was also significantly higher than at caged carcasses for every season except for autumn. There was no significant difference between the number of visits by jackals at caged carcasses and controls for any season (Table 5.14 and Figure 5.35).

Table 5.11: Outcomes from Kruskal-Wallis ANOVA and Dwass-Steel-Critchlow-Fligner pairwise comparisons for the number of visits by black-backed jackals (*Lupullela mesomelas*) at each treatment type for each season during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020

Season	Kruskal-Wallis ANOVA			Pairwise Comparisons			
	<i>H</i>	<i>df</i>	<i>p</i>	Treatment	Treatment	<i>W</i>	<i>p</i>
Active Decay	106	2	< 0.001*	Caged	Control	3.03	0.082
				Caged	Open	12.41	< 0.001*
				Control	Open	11.77	< 0.001*
Autumn	12.7	2	0.002*	Caged	Control	-2.80	0.118
				Caged	Open	2.73	0.129
				Control	Open	4.80	0.002*
Winter	12.8	2	0.002*	Caged	Control	0.00	1.000
				Caged	Open	3.82	0.019*
				Control	Open	3.82	0.019*
Spring	23.2	2	< 0.001*	Caged	Control	2.03	0.325
				Caged	Open	6.14	< 0.001*
				Control	Open	4.85	0.002*
Summer	29.3	2	< 0.001*	Caged	Control	2.14	0.285
				Caged	Open	6.82	< 0.001*
				Control	Open	5.10	< 0.001*

Note: * Denotes statistically significant outcomes evaluated at $\alpha = 0.05$

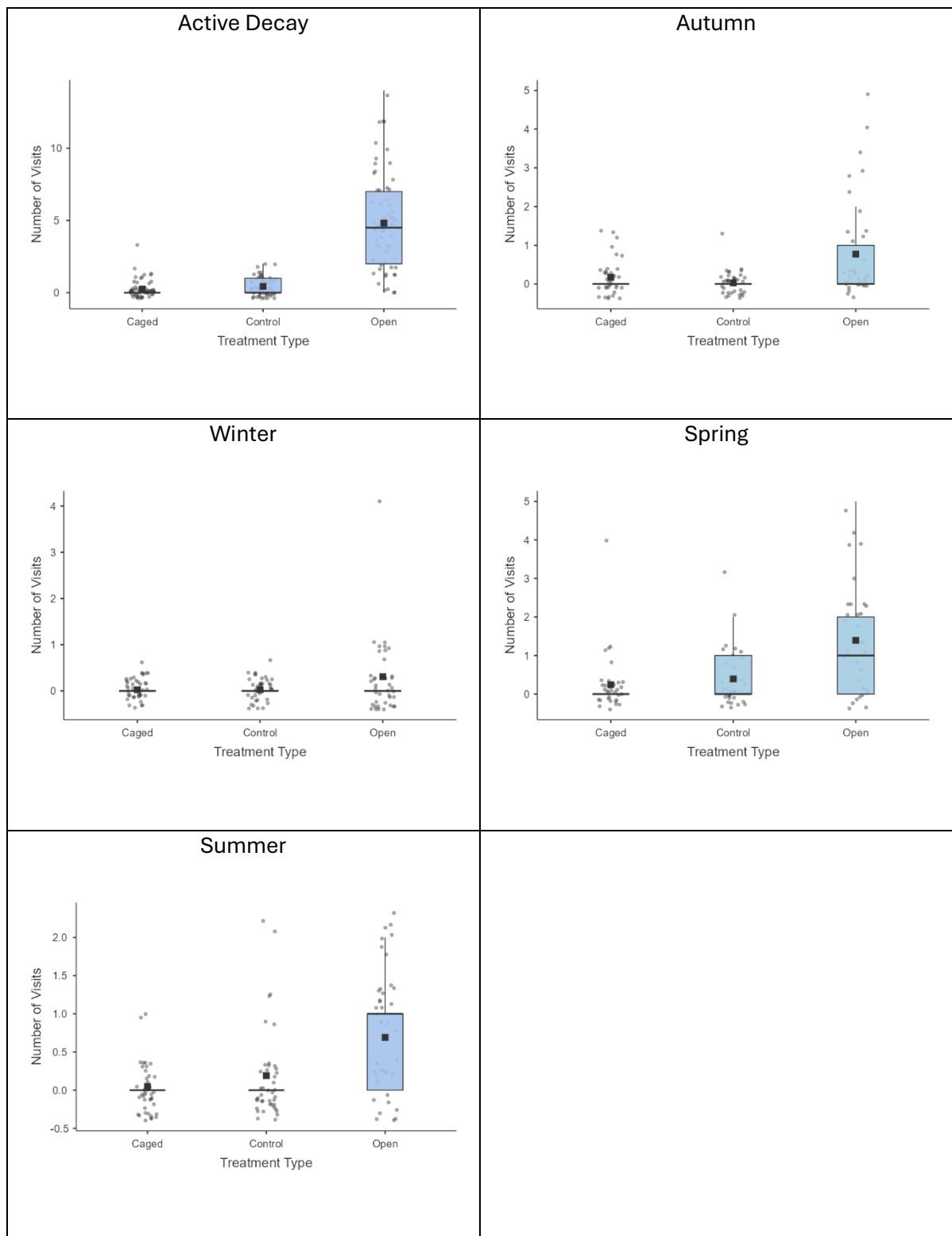


Figure 5.35: Number of black-backed jackal (*Lupulella mesomelas*) visits per day at each treatment type for each season of sampling during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together.

5.8. Carrion and jackal diel activity

Jackal diel activity at each treatment type (Figure 5.36) showed a decrease in activity during the middle of the day and peaks in activity around 05:00 and 20:00 was evident for all three treatment types. However, the highest peak in activity at caged carcasses was in the early hours of the morning while the highest peak in activity at open carcasses was in the early evening.

I found that jackal diel activity differed significantly ($H_{(2)} = 6.37, p = 0.041$) among treatment types. Jackal diel activity at control sites was not significantly different to jackal diel activity at open carcasses ($W = 1.26, p = 0.644$) Jackal diel activity was significantly different between control sites and caged carcasses ($W = 3.31, p = 0.049$) but only marginally so. Furthermore, jackal diel activity at open carcasses was marginally non-significantly different to jackal diel activity at caged carcasses ($W = 3.31, p = 0.051$) as the highest peak in activity at caged carcasses was in the early hours of the morning while the highest peak in activity at open carcasses was in the early hours of the night (Figure 5.36).

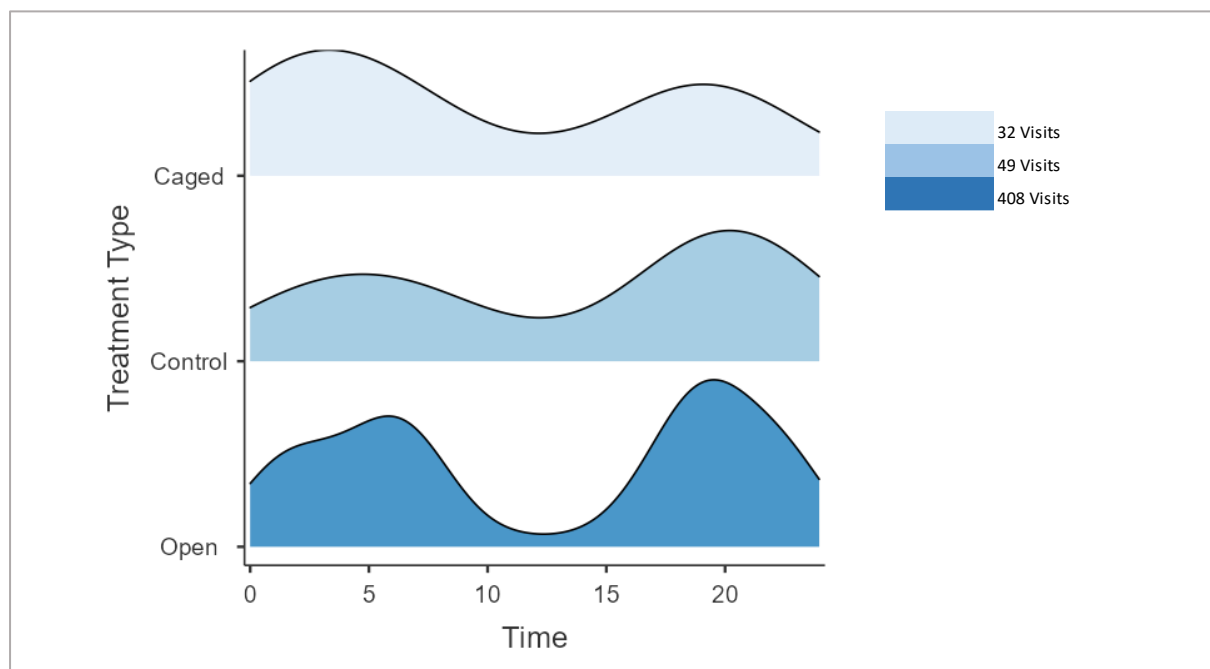


Figure 5.36: Density plots created using kernel density estimation showing black-backed jackal (*Lupulella mesomelas*) diel activity over 24 hours for each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve for the entire study period from January 2019 to January 2020. Time was converted to decimal hours for these analyses. The X axis represents the time of day with zero being midnight. The Y axis represents number of visits and density plots were created using kernel density estimation in Jamovi.

5.9. Carrion, lunar phase and jackal activity

I recorded jackal activity relative to lunar phase at each treatment type (Figure 5.37). Only at open carcasses did I find that there was a clear peak in jackal visits during periods when the proportion of lunar disc visible was low (between 0 and 25%). I found little variation in jackal visits relative to the proportion of the lunar disc that was visible at either caged carcasses or control sites. I found that the visible portion of the lunar disc visible during jackal visits varied significantly ($H_{(2)} = 16.6$, $p < 0.001$) among treatment types. Jackal visits relative to moon illumination at open carcasses was significantly different to jackal visits relative to proportion of the lunar disc visible at control sites ($W = 4.922$, $p = 0.001$) and at caged carcasses ($W = 3.121$, $p = 0.049$). Jackal visits relative to proportion of the lunar disc visible at caged carcasses was not significantly different to control sites ($W = 0.764$, $p = 0.852$).

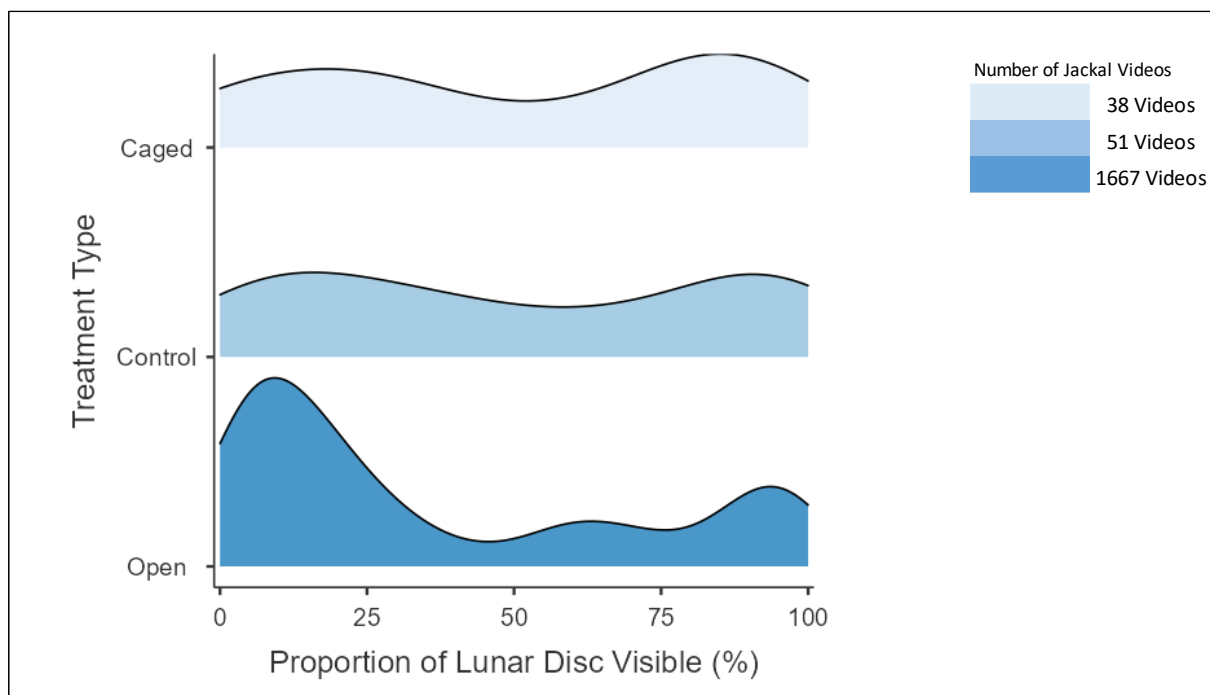


Figure 5.37: Density plots showing black-backed jackal (*Lupulella mesomelas*) visits to experimental treatments relative to the proportion (%) of the lunar disc visible during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve for the entire study period from January 2019 to January 2020. The Y axis represents number of visits and density plots were created using kernel density estimation in Jamovi.

I found that regardless of treatment type, jackal activity relative to proportion of the lunar disc visible during the summer of active decay was significantly different to autumn and spring but not to winter and the following summer (Figure 5.38 and Table 5.15). Despite the difference in jackal activity between the period of active decay and the following summer being marginally non-significant, there may still be biological significance to this phenomenon. During active decay and winter jackals were significantly more active during periods when the proportion of the lunar disc visible was low, whereas this was not the case in any other season (Figure 5.38 and Table 5.15). Autumn visitations were significantly different to those in any other season in that the peak of jackal activity happened during periods when there was a high proportion of the lunar disc visible (Figure 5.38 and Table 5.15).

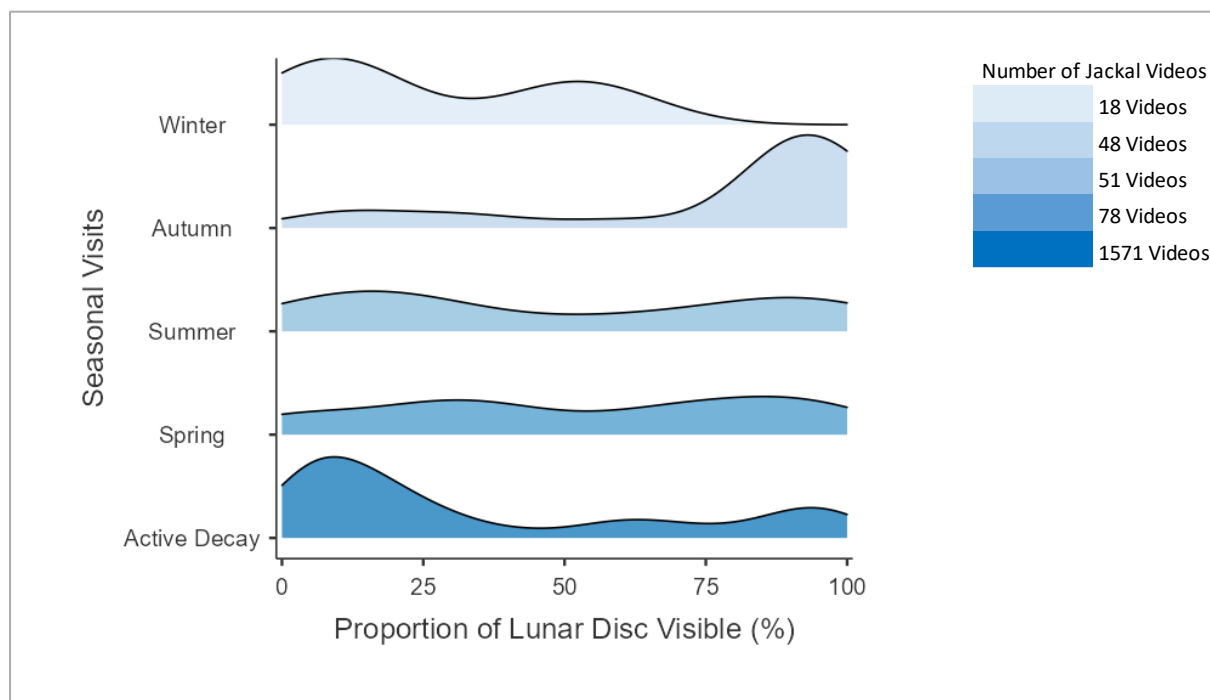


Figure 5.38: Density plots showing black-backed jackal (*Lupullela mesomelas*) records from camera traps relative to the proportion (%) of the lunar disc visible for each season during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve for the entire study period from January 2019 to January 2020. The Y axis represents number of visits and density plots were created using kernel density estimation in Jamovi.

Table 5.12: Outcomes of Dwass-Steel-Critchlow-Fligner pairwise comparisons for black-backed jackal (*Lupullela mesomelas*) activity relative to proportion of the lunar disc visible per season over the study period from January 2019 to January 2020 during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve.

Seasonal Comparisons		W	p
Active Decay	Spring	6.119	< 0.001*
Active Decay	Summer	3.824	0.053
Active Decay	Autumn	9.986	< 0.001*
Active Decay	Winter	-1.062	0.944
Spring	Summer	-0.914	0.967
Spring	Autumn	5.847	< 0.001*
Spring	Winter	-4.108	0.030*
Summer	Autumn	4.918	0.005*
Summer	Winter	-3.351	0.124
Autumn	Winter	-6.964	< 0.001*

Note: * Denotes statistically significant outcomes evaluated at $\alpha = 0.05$

5.10. Carrion and jackal group size

The number of jackals present per visit differed significantly ($H_{(2)} = 16.4$ $p < 0.001$) between treatment types. My *post-hoc* analyses revealed that the number of jackals present per visit at open carcasses was significantly higher than at control sites ($W = 4.11$, $p < 0.01$) and at caged carcasses ($W = 4.10$, $p < 0.011$). There was no significant difference between the number of jackals present per visit to caged carcasses and control sites ($W = 1.63$, $p = 0.484$)

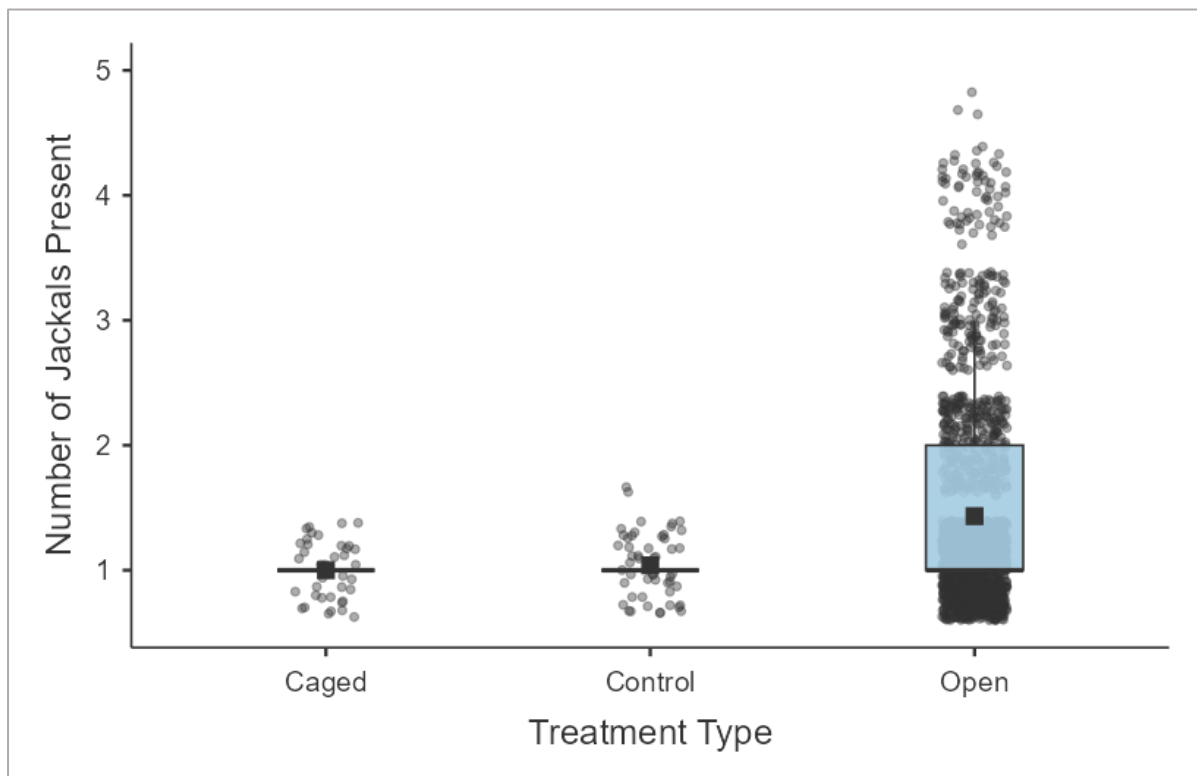


Figure 5.39: The number of black-backed jackals (*Lupulella mesomelas*) present per visit at each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve for the entire study period from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*). Missing whiskers indicate the data is skewed in the opposite direction to the missing whisker. The absence of a box indicates that the middle 50% (Interquartile range) has zero spread, and most data points are clustered together.

5.10.1. Jackal group size and lunar phase

There was a significant negative correlation ($\rho_{(487)} = 0.162$, $p < 0.001$) between number of jackals per visit and moon illumination (Figure 5.40 and Table 5.16).

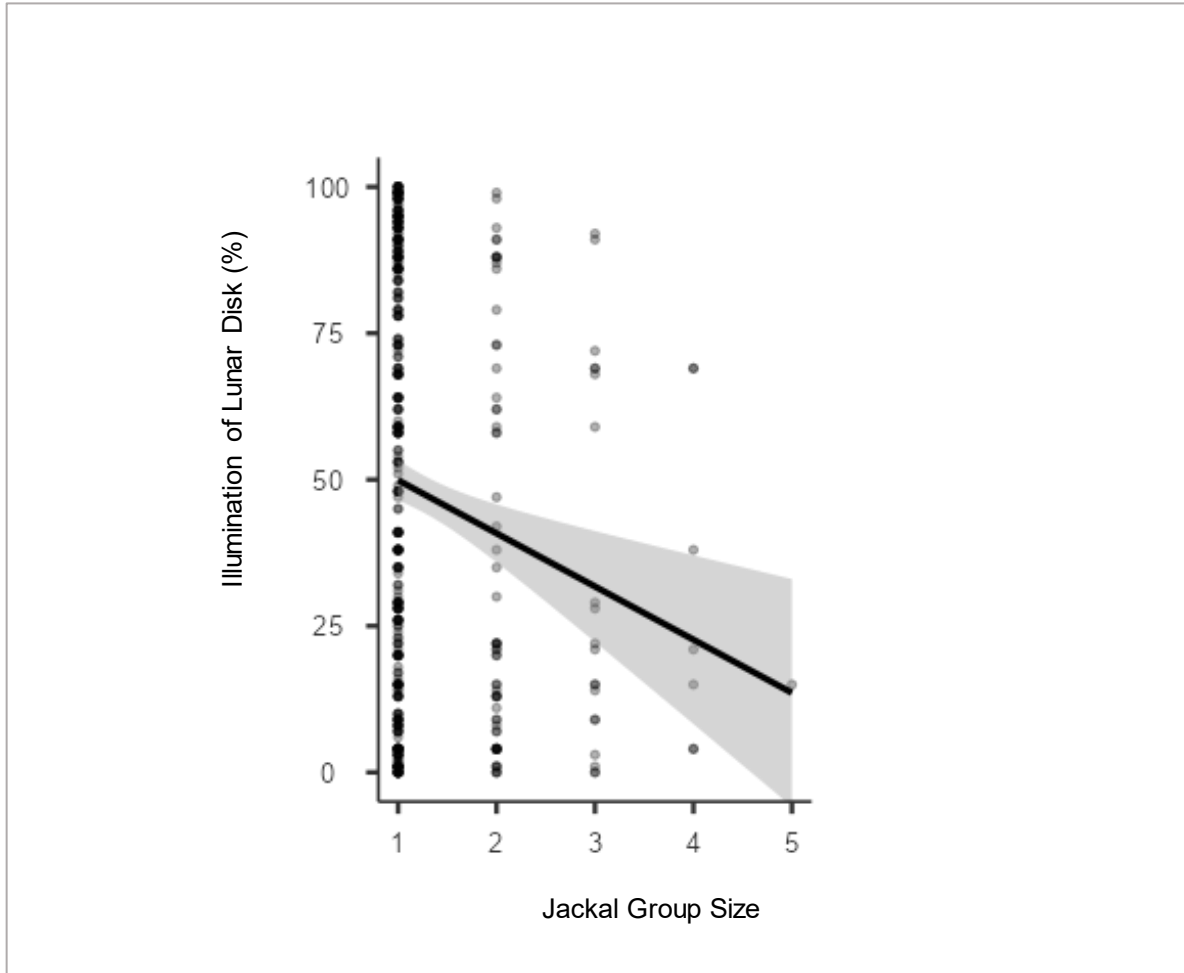


Figure 5.40: Correlation of the number of black-backed jackals (*Lupullela mesomelas*) per visit and the proportion (%) of the lunar disc visible at the time of the visit for all visits to experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve during the entire study period from January 2019 to January 2020. Means (*black squares*), medians (*dark horizontal lines*), minimum and maximum range excluding outliers (*whiskers*) and individual data points falling outside the box plot (*grey dots*).

Table 5.13: Correlation of number of black-backed jackals (*Lupullela mesomelas*) at each visit and proportion of the lunar disc visible at the time of the visit for all visits during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve during the entire study period January 2019 to January 2020).

Correlation statistics for Figure 5.40	
Pearson's r	-0.156
df	487
p-value	< 0.001*
Spearman's rho	-0.162
df	487
p-value	< 0.001*
N	489

Note: * Denotes statistically significant outcomes evaluated at $\alpha = 0.05$

5.11. Carrion and jackal vigilance behaviour

I recorded the highest percentage (74%) of jackal videos containing evidence of vigilance at caged sites. Jackal vigilance at other sites was lower (Table 5.17).

Table 5.14: Video clips with black-backed jackals (*Lupullela mesomelas*) visits to each treatment type, total number of videos where jackal exhibited vigilance behaviour for each treatment type and the percentage of videos with vigilance behaviour for each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature reserve from January 2019 to January 2020.

Treatment Type	Total Videos	Videos with Vigilance	Percent with Vigilance
Open	1677	687	41%
Caged	38	28	74%
Control	51	14	27%

There was a significant difference ($X^2_{(2)} = 20.6, p < 0.001, N = 1776$) between the number of records of vigilant behaviour vs no vigilant behaviour among the three treatment types (Table 5.18). *Post-hoc* analysis revealed that jackals at caged carcasses displayed significantly more vigilance behaviour than was expected. neither of the other treatment types showed significant results (Table 5.19).

Table 5.15: Contingency table for *Chi-square* test of independence (X^2) to determine whether the observed instances of black-backed jackal (*Lupullela mesomelas*) vigilance behaviour was significantly different to expected vigilance behaviour for each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.

Treatment Type		Vigilance Behaviour Observed		Total
		No	Yes	
Caged	Observed	10	28	38
	Expected	22.3	15.7	38.0
Control	Observed	37	14	51
	Expected	29.9	21.1	51.0
Open	Observed	990	687	1677
	Expected	984.7	692.3	1677.0
Total	Observed	1037	729	1766
	Expected	1037	729	1766

Table 5.16: Outcomes from Pearson's residuals and Adjusted Standardised residuals *post-hoc* test for X^2 test of independence to determine whether the observed instances of black-backed jackal (*Lupullela mesomelas*) vigilance behaviour was significantly different to expected vigilance behaviour for each treatment type during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.

Treatment Type		Residuals	Vigilance Behaviour Observed	
			No	Yes
Caged	Pearson		-2.607 ^s	3.109 ^s
	Adjusted		-2.928 ^s	2.796 ^s
Control	Pearson		1.289	-1.537
	Adjusted		1.243	-1.638
Open	Pearson		0.168	-0.200
	Adjusted		0.168	-0.200

Note: Residuals > 2.58 are considered significant and are denoted with an ^s

5.12. Jackal feeding behaviour

At open carcasses (Figure 5.41) I recorded 1667 videos of jackal visits. Of these 732 showed jackals feeding on invertebrates, 638 showed jackals attempting to feed on the carcass and of those 638 feeding attempts, only 470 videos showed jackals successfully feeding on carrion from the carcasses. Nineteen videos showed jackals successfully feeding on both carrion and invertebrates in the same 15 second video clip.

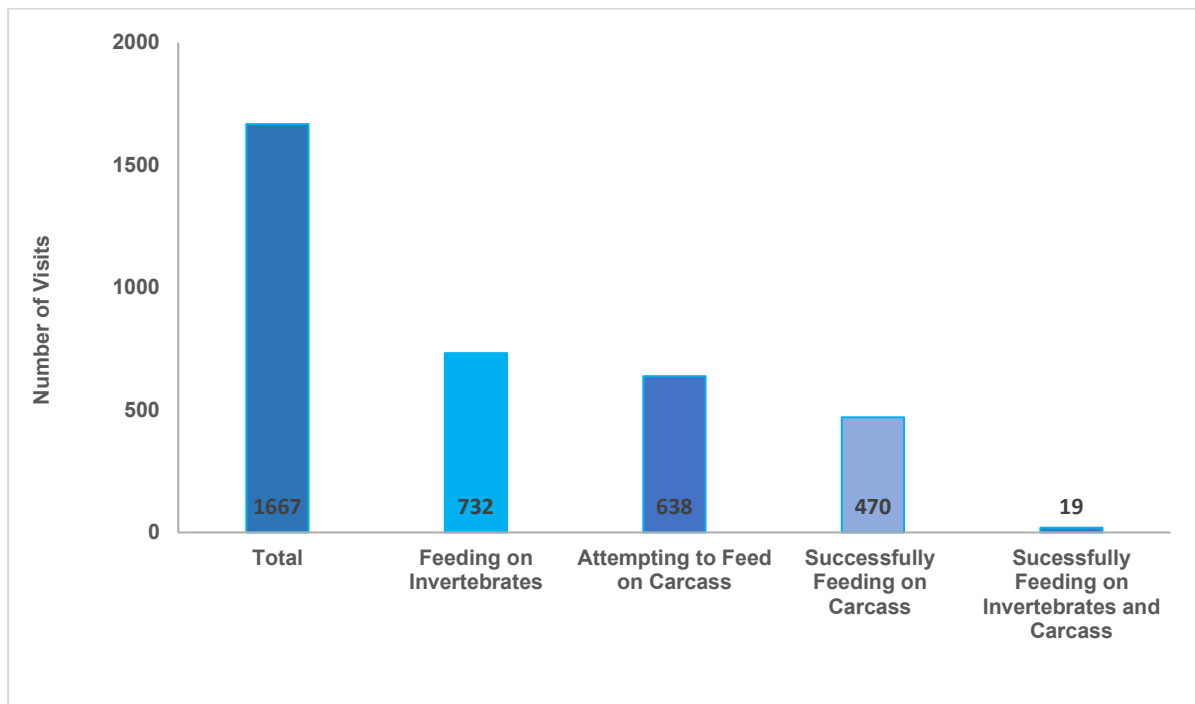


Figure 5.41: Success of black-backed jackal (*Lupulella mesomelas*) accessing carrion from blue wildebeest (*Connochaetes taurinus*) carcasses as well as feeding on invertebrates associated with the carcasses during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Bars are standard errors.

I found that the source of jackal food acquisition from carcasses during the period of active decay varied relative to the time since carcass deployment (Figure 5.42). Initially jackals fed primarily on invertebrates. The peak of invertebrate feeding happened earlier than successful feeding of carrion from the carcasses, and once successful feeding of carrion from the carcasses commenced, feeding on invertebrates tapered off rapidly.

I found that the timing of jackals feeding on invertebrates at the carcasses was significantly different to the timing of jackals successfully feeding on carrion from the carcass ($t_{(888)} = 50.5$, $p < 0.001$).

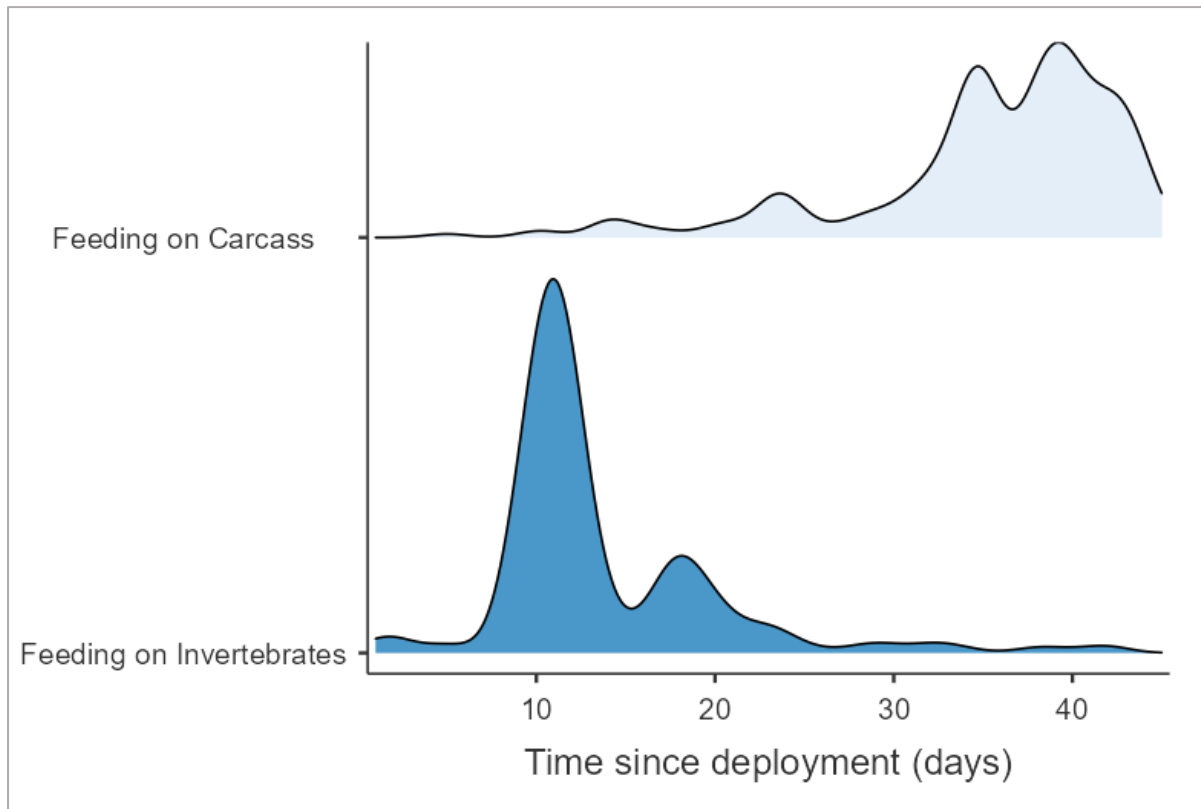


Figure 5.42: Density plots of the time since deployment of blue wildebeest (*Connochaetes taurinus*) carcasses vs number of videos where black-backed jackals (*Lupulella mesomelas*) fed on invertebrates vs videos when they fed successfully on carrion from the blue wildebeest (*Connochaetes taurinus*) carcasses during my study on the influence of decomposing blue wildebeest carcasses on predators on Telperion Nature Reserve during the period of active decay.

5.13. Variability in jackal response to available carrion

My most parsimonious GLMM model to explain the variability of jackal visitation rates to experimental sites was model H (Table 5.20) This model included ‘Season’, ‘Seasonal Site Subadult Jackal Presence’ and ‘Total Site Species Richness’ covariates as main effects and “distance to human infrastructure” and “distance to nearest reserve boundary” as an interaction term only.

Table 5.17: Outcomes from the Generalized Linear Mixed Models constructed to evaluate the variability of black-backed jackal (*Lupulella mesomelas*) visits to experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Null model was modelled first, with covariates added sequentially for comparison to the null model. ‘**JackVis**’ = Seasonal Jackal Visits, ‘**SubadJack**’ = Seasonal Site Subadult Jackal Presence, ‘**DistInfra**’ = Distance to Nearest Human Infrastructure, ‘**DistBound**’ = Distance to Nearest Reserve Boundary, ‘**SpRich**’ = Total Site Species Richness excluding Jackals, ‘Treatment Type’ = Treatment Type, ‘Season’ = Season

Model ID	Model Rank	Equation Representing Model	AIC	ΔAIC	BIC	ΔBIC	Conditional R ²	df	LRT X ²	p	Marginal R ²	df	LRT X ²	p
H	1	`JackVis` ~ 1 + Season + `SubadJack` + `SpRich` + `DistInfra`:`DistBound` + (1 Treatment Type)	289.16		312.91		0.76	9	132.25	< 0.001	0.73	7	84.07	< 0.001
G	2	`JackVis` ~ 1 + Season + `SubadJack` + `SpRich` + `DistInfra` + `DistBound` + `DistInfra`:`DistBound` + (1 Treatment Type)	289.73	0.57	316.97	4.06	0.76	11	151.64	< 0.001	0.75	9	96.86	< 0.001
D	3	`JackVis` ~ 1 + Season + `SubadJack` + `SpRich` + (1 Treatment Type)	294.35	5.19	315.20	-1.77	0.67	8	107.86	< 0.001	0.59	6	67.72	< 0.001
E	4	`JackVis` ~ 1 + Season + `SubadJack` + `SpRich` + `DistInfra` + (1 Treatment Type)	294.38	5.22	317.56	2.36	0.69	9	115.73	< 0.001	0.63	7	72.89	< 0.001
F	5	`JackVis` ~ 1 + Season + `SubadJack` + `SpRich` + `DistInfra` + `DistBound` + (1 Treatment Type)	294.54	5.38	320.04	2.48	0.70	10	125.14	< 0.001	0.64	8	78.89	< 0.001
C	6	`JackVis` ~ 1 + Season + `SubadJack` + (1 Treatment Type)	307.34	18.18	325.88	5.85	0.52	7	62.73	< 0.001	0.39	5	36.88	< 0.001
B	7	`JackVis` ~ 1 + Season + (1 Treatment Type)	315.34	26.18	331.56	5.68	0.56	6	39.11	< 0.001	0.31	4	20.52	< 0.001
A: Null Model	8	`JackVis` ~ 1 + (1 Treatment Type)	324.40	35.25	331.36	-0.20	0.37	2	10.67	0.005	0.00	0	0	< 0.001

I found strong support for season having an effect on the number of jackal visits to experimental sites (Table 5.20 and Figure 5.43). Open carcasses during active decay were predicted to have ~ 50 visits while other seasons for all treatment types were predicted to have very few jackal visits (Figure 5.43).

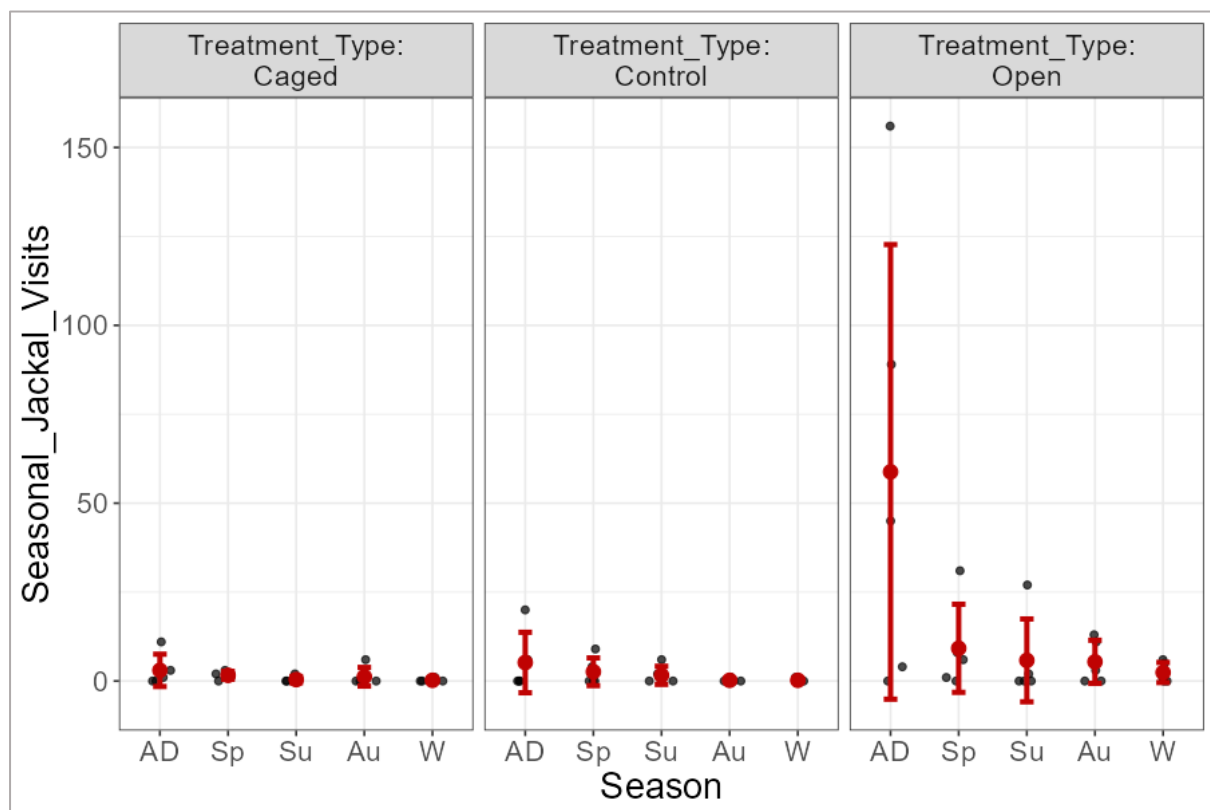


Figure 5.43: Effect of season on number of black-backed jackal (*Lupullela mesomelas*) visits to blue wildebeest (*Connochaetes taurinus*) carcasses for the three different treatment types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Red dots represent the predicted number of jackal visits from the best supported model in Table 5.20. Vertical bars represent standard errors.

Additionally, there was strong support for the presence of subadult jackals influencing the number of jackal visits (Table 5.20 and Figure 5.44). Open carcasses that also had sightings of subadult jackals in close proximity to the camera array had significantly more jackal visits than open carcasses that had no sightings of subadult jackals in close proximity to the camera array (Figure 5.44).

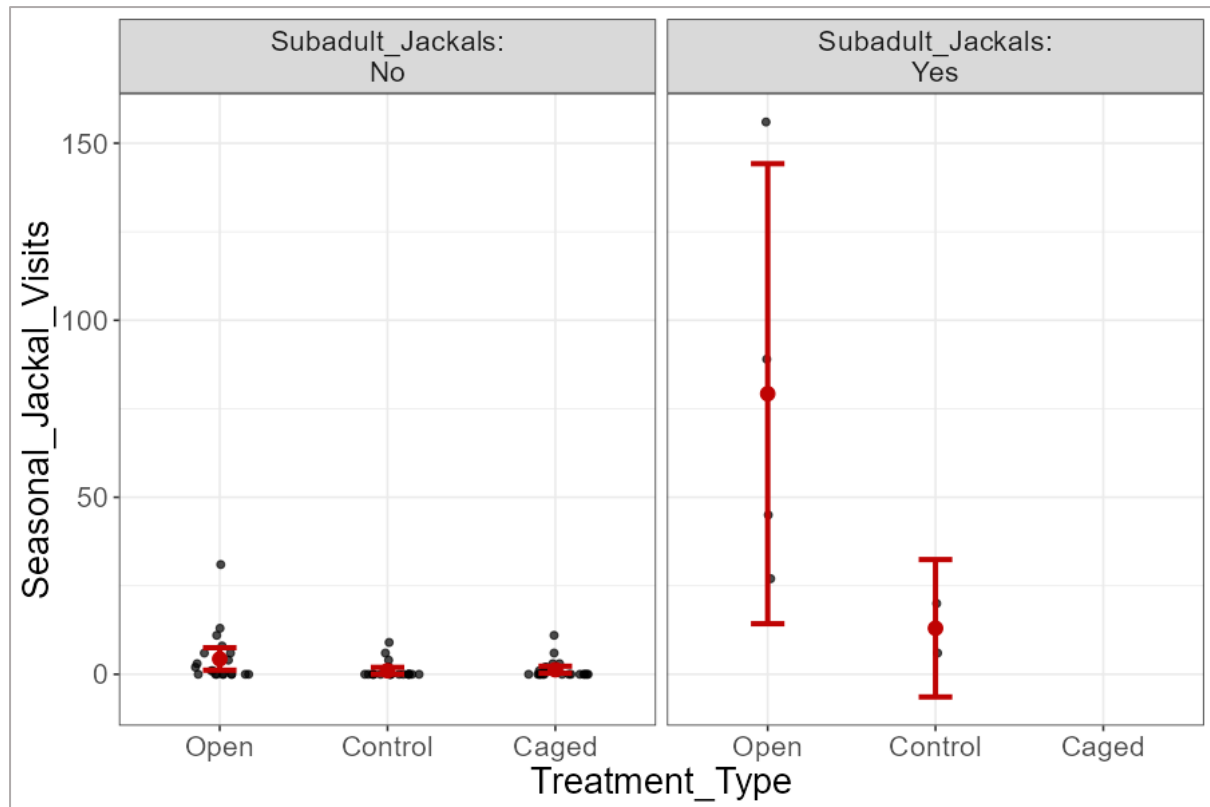


Figure 5.44: Effect of the presence of subadult jackals on number of black-backed jackal (*Lupullela mesomelas*) visits to blue wildebeest (*Connochaetes taurinus*) carcasses for the three different experimental treatment types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Red dots represent the predicted number of jackal visits from the best supported model in Table 5.20. Vertical bars represent standard errors.

Furthermore, there was strong support for total mammalian species richness (excluding jackals) at sites having an effect on jackal visits to the experimental sites (Table 5.20 and Figure 5.45). Increasing jackal visits at all treatment types was associated with increased species richness at all treatment types (Figure 5.45).

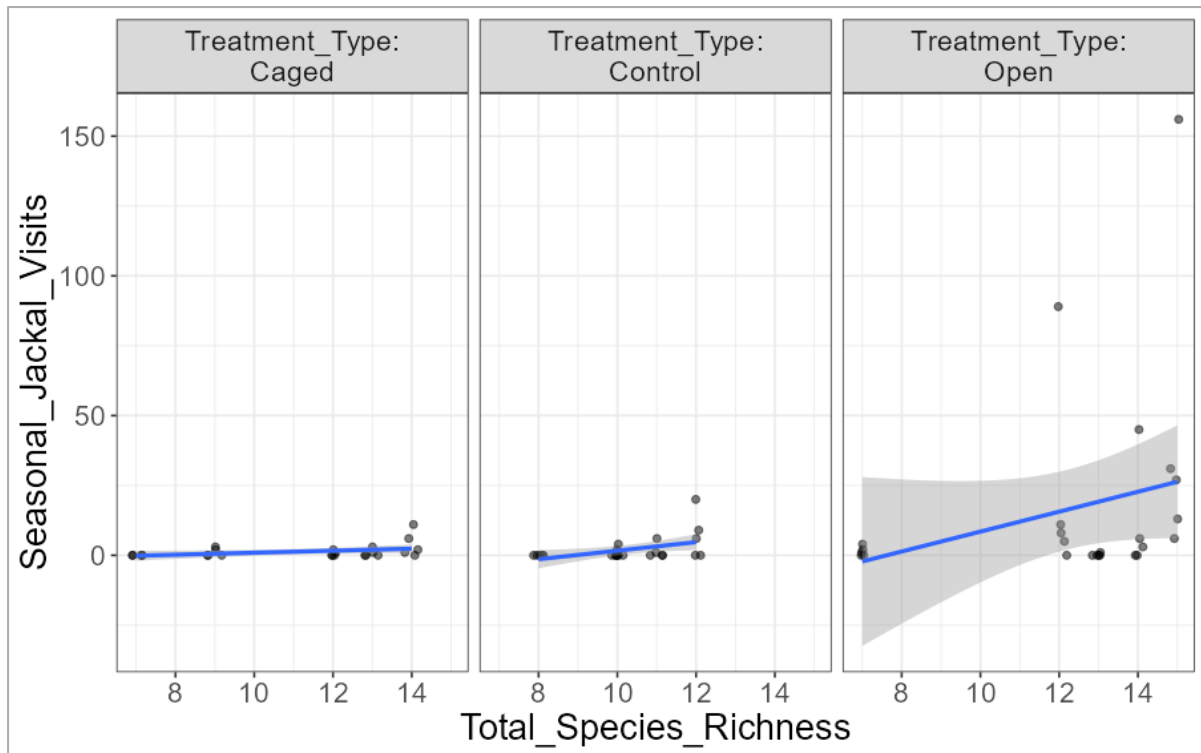


Figure 5. 45: Effect of the total species richness (all mammals excluding jackals) on number of black-backed jackal (*Lupullela mesomelas*) visits to blue wildebeest (*Connochaetes taurinus*) carcasses for the three different experimental treatment types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. The blue lines represent the predicted change in jackal visits with increasing total species richness. Grey ribbons represent standard errors around the fixed effects.

Additionally, the interaction between distance of site to nearest human infrastructure and distance of site to nearest reserve boundary also had a significant influence on the number of jackal visits to a site. Increased distance of an experimental site from these two variables was associated with more visits by jackals to the site (Table 5.20 and Figure 5.46).

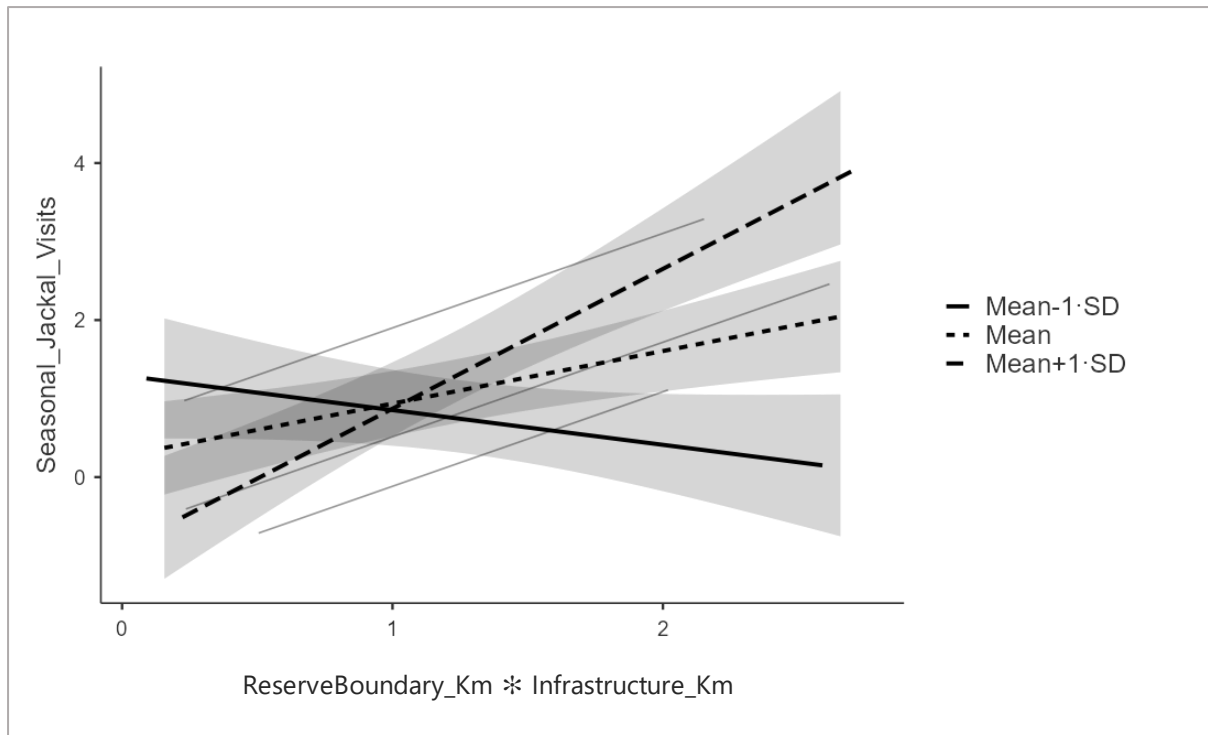


Figure 5.46: Effect of the interaction between distance to nearest infrastructure (km) and distance to reserve boundary (km) on number of black-backed jackal (*Lupullela mesomelas*) visits to blue wildebeest (*Connochaetes taurinus*) carcasses for the three different treatment types during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. The light grey lines are ghost lines indicating the effect on each treatment type separately. The top ghost line is treatment type ‘open carcasses’, the middle ghost line is treatment type ‘control’ and the lowest ghost line is treatment type ‘caged carcasses’. The grey ribbons represent standard errors.

I found that all covariates for my top ranked model had significant impact on the number of jackal visits to experimental sites (Table 5.21).

Table 5.18: Outcomes from the Fixed Effects Omnibus Tests for the top ranked model to explain variability of black-backed jackal (*Lupullela mesomelas*) visits to experimental sites on during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators Telperion Nature Reserve from January 2019 to January 2020.

Fixed Effect	X ²	df	p
Season	11.63	4.00	0.020*
Subadult Jackals Seen Nearby Seasonally	6.51	1.00	0.011*
Total Species Richness	16.72	1.00	< 0.001*
Distance to Nearest Human Infrastructure (Km) * Distance to Nearest Reserve Boundary (Km)	6.20	1.00	0.013*

Note: * Denotes statistically significant outcomes evaluated at $\alpha = 0.05$

CHAPTER 6: DISCUSSION

6.1. Overview

My study explored how decomposing blue wildebeest carcasses influence predator and scavenger communities in Telperion Nature Reserve, South Africa. I used a combination of open and caged carcasses alongside control sites, and a combination of sign and camera surveys. I found reduced predator diversity near experimental sites where carcasses were present compared to controls. Jackal presence increased at carcasses, and this was shown, by examining predator species diversity indices as well as with occupancy analyses, to negatively impact mesopredator diversity. These findings suggest that most mesopredators avoid carcasses, especially in the presence of more jackal activity, possibly reflecting a 'landscape of fear'. Jackal activity was markedly higher at open carcasses when percentage of the lunar disc visible was low but was not affected by lunar phase at caged carcasses or control sites. Invertebrates drawn to carcasses provided jackals with a supplementary food source before they could access the carrion with invertebrate consumption by jackals tapering off sharply once carrion was accessible. Factors such as subadult and/or juvenile jackal presence proximate to carcasses, human infrastructure as well as experimental site-specific mammalian species diversity influenced which carcasses received visits by jackals. The results highlight the importance of considering carcass ecology in managing predator communities, particularly in altered habitats lacking traditional apex predators.

6.2. A broad comparison of survey methods

Studies that use complementary methods to study species often find that the different techniques yield different results in terms of species numbers and composition (Gompper *et al.* 2006, Lyra-Jorge 2008, Alexander *et al.* 2016, Rich *et al.* 2017b, Seidlitz *et al.* 2021). However, the use of multiple survey types can complement each other (Garrote *et al.* 2014, Clare *et al.* 2017, Ponce-Martins *et al.* 2022) and strengthen inferences. Furthermore, the effectiveness of each method is often heavily dependent on the characteristics of the study species (Garden *et al.* 2007). Where a study's focus is on more than one species, a range of survey techniques that could include a combination of some of the following: live trapping, camera surveys, sign surveys, bioacoustics, hair snaring and visual observations is highly recommended (de Torrez *et al.* 2017, Garden *et al.* 2007, Hoefer *et al.* 2025).

Some studies have found cameras to outperform other survey types namely track counts (Balme *et al.* 2009, Espartosa *et al.* 2011) scat collection (Anile *et al.* 2014), hair catches, snow tracking (Clare *et al.* 2017) and live traps (Wearn and Glover-Kapfer *et al.* 2019) (but see Seidlitz *et al.* 2021, Ponce-Martins *et al.* 2022). However, my study found that sign surveys recorded more species than camera trapping, both overall and seasonally. The number and variety of species differed between the two techniques with some species being detected only by sign surveys and others exclusively by cameras. Therefore, the combined use of both methods yielded the most comprehensive results.

The study design parameters used in my study may have had some influence on the observed differences between the two survey techniques. Firstly, sign surveys were conducted along 1 km transects on roads near, but not directly adjacent to, the experimental sites. However, Torrents-Ticó *et al.* (2017) found that camera surveys conducted on the same road sections as concurrent sign surveys also yielded differing results. In my study, it was not feasible to conduct sign surveys immediately adjacent to the experimental sites (controls and carcasses) due to dense grass cover around these sites, which obscured tracks. Carnivores frequently use roads and trails to facilitate movement through the landscape and to and from resources (Karanth *et al.* 2011, Midlane *et al.* 2014). Furthermore, this behaviour has been effectively leveraged in many studies for monitoring carnivore presence and behaviour (Stander 1998, Virgós 2001, Houser *et al.* 2009, Funston *et al.* 2010, Karanth *et al.* 2011, Thorn *et al.* 2011, Midlane *et al.* 2014, Wang *et al.* 2014). Thus, surveying roads and intersecting game paths adjacent to carcass sites likely provided an accurate indication of which predators approached or moved past the experimental sites.

The differences that I observed are also likely attributable to the distinct detection zones of the two survey techniques. Cameras cover a relatively small area, which can result in missed detections, particularly for smaller species, which may pass close to the camera array but remain undetected (Seidlitz *et al.* 2021, Ebel and White 2024). Another study found similar constraints, in that small and medium-sized carnivore species were more reliably detected using track plates than cameras (Gompper *et al.* 2006). The use of track plates close to the carcasses may have been a consideration for this study where substrate was a limiting factor for sign surveys, however this may have led to increased neophobia (Gompper *et al.* 2006) and had a confounding effect. Furthermore, some studies have reported certain animals avoiding camera arrays, passing close-by but responding negatively to the sight of the cameras (Wegge *et al.* 2004, Meek *et al.* 2016). This may have been an issue in my study where a leopard reacted to

the camera at one site (whether to the noise or to the flash is uncertain) by rapidly turning to look towards the camera behind him and then speeding up his movement away from the camera array. Even jackals on numerous occasions reacted to the cameras, by looking at them or by jumping in alarm, seemingly in response to them.

While more species were identified more rapidly using sign surveys than camera surveys in my study, their effectiveness depends on the researcher's skill in detecting and identifying tracks (Stander 1998, Torrents-Ticó *et al.* 2017, Keeping *et al.* 2018, Gielen *et al.* 2024). This can make them more subjective than camera surveys, however, photographing tracks and including accompanying metadata (like GPS locations of photographs) and advances in AI track identification (Finerty *et al.* 2024) can help address this issue.

The detection zone of one sign survey transect versus one camera array, typically extends over a broader landscape (Rich *et al.* 2017b) than that within the detection zone of the cameras, and thus the combination of both techniques can provide a more holistic understanding of predator presence and response to carcasses. While cameras were only placed in grassland habitat, sign surveys were not restricted to this habitat type and surveyed a broader range of habitat types on Telperion (including woodland and riparian zones). The cameras were placed in grassland only as our sample size was restricted to 10 wildebeest carcasses (five open and five caged) and then five additional control (no carcasses present) sites. Thus, with a low sample size of 15, placing experimental sites in multiple habitat types would have reduced the inferential power of the study with a sample size that was already limited. This restriction to grasslands may have accounted for the absence of some species like rusty spotted genet from the camera survey results, as they are known to avoid grassland areas (Camps and Alldredge 2013, Roux 2017). Similarly, although African civets are known to consume carrion (Amiard *et al.* 2015), they too tend to avoid open grassy areas in preference for areas with better cover (Swanepoel *et al.* 2016). However, even though sign surveys encompassed more diverse habitat types than camera surveys, which were restricted to grasslands, there was no difference in species type or species richness when comparing the set of sign surveys restricted to the camera sites (grassland only) to the set of sign surveys away from the experimental sites (encompassing other habitats). This suggests that the broader habitat range covered by sign surveys in this study did not solely account for their higher detection rates. Accepted practice for monitoring predators using sign surveys is to survey one km transects along roads and trails (Stander 1998, Virgós 2001, Houser *et al.* 2009, Funston *et al.* 2010, Karanth *et al.* 2011, Thorn *et al.* 2011, Midlane *et al.* 2014, Wang *et al.* 2014) as has been done in my study. The reason they are so

attractive is their ability to cover large areas (Thorn *et al.* 2011). Cameras will always have a relatively small field of view in comparison to sign surveys, however they offer other advantages, such as the ability to record detailed behaviour of the study species. Consequently, the complementary strengths and limitations of both survey methods support using them together when studying cryptic carnivores, especially in multi-species studies.

A comparison of my study with a recent camera study conducted on Telperion (Webster *et al.* 2021) revealed similar results regarding total species richness. Webster *et al.* (2021) recorded 16 predator species, whereas my study identified 17 predator species when combining the camera and sign survey results (Appendix 29).

When comparing only camera results of the two studies, Webster *et al.* (2021) recorded three more species than my study, but employed more cameras at more sites (40 as opposed to 15). Furthermore, the minimum distance between traps was 800 m in grassland for Webster *et al.* (2021) and one kilometre in my study. Additionally, Webster *et al.* (2021) did not restrict their sites to grassland habitats.

The only species detected in the Webster *et al.* (2021) study but not in my study was the spotted-necked otter (*Lutra maculicollis*). This omission is likely due to Webster *et al.*'s (2021) study including river courses or deploying cameras in riparian habitats. Since the conservation status, land use, and habitat structure on Telperion remained relatively unchanged between 2016 (when the field work for the Webster *et al.* (2021) study took place and 2019 (my study's fieldwork), it is unlikely that the spotted-necked otter is no longer present on Telperion, but further research is required for confirmation.

Conversely, my study recorded the Cape fox and African civet, which were not detected by Webster *et al.* (2021), suggesting these species were possibly previously overlooked. The discrepancies between camera trapping and sign survey results in my study add further support to a growing number of studies suggesting that as standalone techniques they and other standalone techniques potentially underrepresent species that occur in a region (de Torez *et al.* 2017, Nuñez *et al.* 2019) and that multiple complementary survey methods are necessary to enhance predator community assessments (Gompper *et al.* 2006). Furthermore, the applicability of each technique is dependent on the specific aims of the intended research (Seidlitz *et al.* 2021), the nuances of how each data collection process is set up (Baird 2022) and the target species of the study (Funston *et al.* 2010). Additionally, the applicability of each technique may be habitat dependent (Wearn and Glover-Kapfer 2019, Seidlitz *et al.* 2021).

For species recorded by both survey types, my study found a strong positive correlation between the number of transects with tracks of a species and the number of camera images of that species. This suggests that despite some discrepancies in total counts of certain species and types of species detected, the results from both methods supported each other. Other studies have also found that despite discrepancies between sign and camera surveys, multiple survey types often complement one another, (Garrote *et al.* 2014) and many studies have found a strong linear relationship between track density and carnivore density (Van Dyke *et al.* 1986, Stander 1998, Gusset and Burgener 2005). Furthermore, co-detected species often had significantly higher occupancy than those species detected by one survey type alone (Torrents-Ticó *et al.* 2017), and thus more than one survey method is advisable.

When seasonality of data was considered, the sign surveys that I conducted, consistently identified significantly more species than cameras across all seasons. This suggests that factors beyond seasonal variation in vegetation cover - which is frequently responsible for low detection rates of both small and large species in camera studies (Glover-Kapfer *et al.* 2019, Moll *et al.* 2020, Palencia *et al.* 2022,) - influence detection rates. Trap shyness, as well as an increase in anthropogenic disturbance near the experimental sites, is likely a confounding factor for camera research in this and similar studies. In conservation areas, elusive carnivores may traverse fences into adjacent non-conservation zones, subsequently encountering elevated levels of human persecution. This exposure can heighten their wariness toward human activity in the protected area where they are not persecuted (Romañach *et al.* 2011, Loveridge *et al.* 2017). Consequently, certain predators may have been deterred from approaching the cameras at the sites where anthropogenic disturbance (particularly during active decay) was high, despite available food, resulting in irregular or absent detections.

This phenomenon highlights two distinct levels of human disturbance within the Telperion landscape during my study that are broadly applicable to other environments, especially those outside large, protected areas. At a broad scale, land-use transitions (e.g., from wilderness to agricultural, mining, and recreational uses) can substantially alter species' behaviour, often increasing nocturnal or cautious behaviour around humans compared to those in larger protected areas, who rarely if ever leave reserve boundaries and may become very habituated to human presence (Romañach *et al.* 2011, Balme *et al.* 2017, Loveridge *et al.* 2017, Le Roex *et al.* 2023). On a smaller scale, concentrated human activity at specific sites, such as the experimental sites in my study, can also influence wildlife presence and detection (Sytsma *et al.* 2022, Gaynor *et al.* 2025).

6.2.1. Relative efficiency of each survey type

The relative efficiency of a survey type is a measure of the effectiveness of each method in detecting species. It describes the number of species detected by that survey type divided by the total number of species recorded by both survey types (Barea-Azcon *et al.* 2007). Overall, sign surveys were more efficient than cameras at detecting species. This was true for all fifteen experimental sites and was likely due to limited camera detection zone (Siedlitz *et al.* 2021), some predators avoiding cameras (Wegge *et al.* 2004, Meek *et al.* 2016), animals not triggering the cameras even when moving through the detection zone (Lerone *et al.* 2015) and anthropogenic disturbance at study sites (Loveridge *et al.* 2017, Sytsma *et al.* 2022). These issues may be context and study specific.

Placing cameras overlooking survey roads at each experimental site might have improved coverage, but limitations like small detection areas and potential avoidance by some animals, due to anthropogenic disturbance or neophobia, would persist. Sign surveys covered greater distances (each transect being one km long with 37 transects surveyed repeatedly), whereas camera detection zones vary widely (Rovero *et al.* 2013). The 164 m² range of the Bushnell TrophyCam (Meek *et al.* 2012) used, while good in comparison to many other cameras, remained relatively restricted in comparison to sign survey coverage. This was particularly pertinent to small carnivores which need to move close to the cameras to set off the trigger. Despite this, cameras at several sites successfully detected small carnivores, demonstrating that the camera's motion/heat sensor was effective at detecting smaller animals within the camera's vicinity. However, long grass and other obstructive vegetation in the detection zones may have compromised this capability (Moll *et al.* 2020), as many detections of small predators occurred in spring following a fire, when the grass layer had been reduced. This again emphasises the necessity for multiple complimentary methodologies to augment results. Regarding clarity of images, my cameras produced images clear enough to identify animals to species level even for similar, smaller species such as yellow and slender mongooses. Although very few images ($n = 52$ out of 1315799 images = 0.004% of total images) had to be excluded due to image clarity issues that confounded species level identification, many images did not seem to have any animals present. It is unclear whether this was as a result of a trigger speed that was too slow to capture rapidly moving animals or whether moving vegetation resulted in false triggering of the cameras.

6.2.2. Latency to detection (LTD)

The time elapsed from the initiation of a survey until the first detection of a specific species (LTD), was significantly shorter for sign surveys than camera surveys for all species except jackal. Other studies on Telperion have found that while jackal density estimates may vary, depending on the estimation methods used (Melville and Strauss 2017), jackal are the most commonly accounted for predator species (Webster *et al.* 2021) on the reserve. The LTD results from my study therefore align with reports that common species have shorter LTD periods while rarer ones take longer to detect (Bennet *et al.* 2024). Although adding more cameras along roads and trails in my study might have improved LTD for camera surveys, sign surveys appear well suited to detect uncommon species relatively quickly.

While some studies have found cameras had lower LTDs than tracking surveys for larger species (Gompper *et al.* 2006,) this may have been linked to the use of tracking plates and a consequent neophobia (Gompper *et al.* 2006), which can be considered similar to trap shyness (Wegge *et al.* 2004). Sign surveys on roads and game trails do not suffer from this bias and my study produced lower LTD's using sign surveys for both brown hyaena and leopard, the two largest carnivore species in the study area. Gompper *et al.* (2006) found that sign surveys using artificial tracking surfaces like track plates were better than cameras at detecting small and medium sized carnivores. My study found the same but without the use of artificial tracking surfaces. Neophobia experienced by some animals to novel stimuli (Crane and Ferrari 2017, Natrass *et al.* 2017, Ryan-Schofield *et al.* 2024) may have influenced the LTD for camera surveys in my study as opposed to the sign surveys which did not introduce any foreign instruments or stimuli into the environment.

Baited cameras (like the 10 carcass sites in my study) are often used to increase the likelihood of detection and improve the LTD of camera surveys by attracting target animals (Thorn *et al.* 2009, Du Preez *et al.* 2014, Randler *et al.* 2020, Ebel and White 2024). However, in my study sign surveys still produced a lower LTD than baited cameras for all species except for jackal where the LTD was one day in both survey methods. Species accumulation curves (both collector's curves and rarefaction curves) from my study further emphasised how much more efficient sign surveys were in this study at detecting species rapidly.

Conservation decisions are often linked to confirmed occurrences of a species of interest, however, the ability to detect species using a particular survey method is never guaranteed (Benoit *et al.* 2018). Designing exhaustive surveys to confirm presence of species is crucial to

conservation (Bennet *et al.* 2024). Consequently, it makes sense to ensure that sampling to detect cryptic species is as rigorous as possible. Combining two or more different and complementary survey methods may achieve this. However, choosing the single most effective method for a quick survey may be all that is necessary to convince authorities that further study and funding is worthwhile. In my study, sign surveys were the quickest and most effective at confirming presence of most of the species detected.

Rapid species detection is vital for effective conservation, especially for threatened populations. Using survey methods with minimal LTD enables adaptive management and rapid response to threats, especially for protected or vulnerable species (Benoit *et al.* 2018). Detection delays can skew population estimates, limit intervention opportunities, and increase extinction risks if interventions are slow to be implemented due to slow detection rates for some vulnerable species. Slow detection may mean declines go unnoticed, particularly for rapidly declining species, making timely action impossible. Poor detectability can lead to mismanagement (Benoit *et al.* 2018), biased decisions, and possibly local extinction. Early detection enables prompt conservation responses and better resource allocation, while slow processes waste time and money without delivering the necessary up-to-date data for informed management. The results of my study highlight that, particularly where surveys of communities of species are concerned, combining more than one survey technique within a given timeframe will maximise efficiency, improve accuracy and facilitate better conservation decisions.

6.2.3 Species Accumulation Curves

For sign surveys, rarefied species accumulation curves indicated that empirical and asymptotic diversity estimates were identical for species richness, implying that the observed inventory was effectively complete and that little additional diversity was predicted to remain undetected. This conclusion was supported by the high sample coverage estimate of 100% obtained (Chao and Jost 2012, Chao *et al.* 2020). For cameras although sample coverage exceeded 90%, observed species richness represented only 62% of the estimated asymptotic richness. This apparent discrepancy can be explained because sample coverage quantifies the proportion of incidences belonging to detected species, whereas richness completeness measures the proportion of the total species pool that has been detected. Consequently, a survey may adequately characterise common species (high coverage) while missing a substantial number of rare species (lower richness completeness) (Chao and Jost 2012, Chao *et al.* 2020). These

results indicate that for cameras, further sampling would likely detect more species, while for sign surveys the surveying was sufficient. Differences in asymptotic species richness estimates are likely due to variation in species detectability and the incidence-frequency distributions generated by each survey method (Boulinier *et al.* 1998). Methods that detect a greater proportion of rare species typically produce higher asymptotic richness estimates because iNEXT (Chao *et al.* 2016) infers a larger pool of undetected data. As surveys rarely detect all species present and because estimates of species richness and community composition are affected by imperfect detection (Nichols *et al.* 1998) it would be prudent if time and resources allow, to implement more than one survey type when surveying cryptic carnivores as was done in my study.

6.2.4. Budget and Funding

Securing adequate funding for conservation initiatives is frequently challenging, making study designs with lower financial requirements particularly appealing. Sign surveys, for instance, demand significantly less capital investment compared to camera surveys (Seidlitz *et al.* 2021). My study's budget comparison revealed that sign surveys were considerably more cost-effective to implement. Furthermore, during my research, one camera was stolen—an issue that has not only previously occurred on Telperion (Webster *et al.* 2021) but remains a persistent concern in many protected and non-protected areas (Meek *et al.* 2019). Despite these challenges, conducting conservation research within mixed-use landscapes beyond formal protection zones remains essential. Safeguarding equipment against theft or vandalism in such contexts can be difficult, and insuring field equipment for these studies is often unfeasible. Sign surveys, which do not necessitate leaving equipment in the field, are therefore particularly well-suited for work in these environments.

Although my thesis focused mainly on start-up and short-term cost comparisons between the two survey methods, the cost of camera surveys will likely decline over time because the initial equipment investment is a once-off expense, aside from theft or damage. Tracker wages, by contrast, are an ongoing cost. However, the time required to install and remove cameras for repeated surveys must also be budgeted for, along with staff time to review the photographs and videos. Both these activities are ongoing, time consuming and likely costly and in my opinion, underestimated in many camera trap studies.

Man-hours were not included in the budgetary comparisons for my study due to the absence of recorded data during sampling; estimating these retrospectively would compromise accuracy. However, when accounting for set-up time and actual sampling duration, it is evident that the process of sorting through approximately 1.5 million camera trap images and videos produced from the cameras used in my study, prior to analysis, required significantly more time — by an order of magnitude — than any sign survey sampling or data sorting. Therefore, even if man hours were considered, I am of the view that overall budgets would still favour sign surveys over camera trap surveys.

The accumulation of large volumes of data is typical for camera trap research (Green *et al.* 2020, Leorna and Brinkman 2022, Bohnett *et al.* 2023, Velez *et al.* 2023, Huebner *et al.* 2024). While artificial intelligence and machine learning are increasingly utilized to alleviate the burden on researchers, multiple studies have demonstrated that human identification of species remains more accurate and reliable, or at minimum, requires human verification of AI outputs (Green *et al.* 2020, Leorna and Brinkman 2022, Bohnett *et al.* 2023, Velez *et al.* 2023, Huebner *et al.* 2024). Although future advancements in AI models may improve their performance, the accurate sorting of such datasets currently remains a time-intensive task.

Sign surveys therefore are especially appropriate for pilot studies to determine the necessity of further research or conservation measures. They deliver prompt, cost-effective results (Seidlitz *et al.* 2021) and enable conservationists to assess whether additional, more detailed investigations involving advanced equipment are justified.

6.3. The effect of carcasses on species diversity

When comparing species diversity at the three treatment types (open carcasses, caged carcasses and controls/no carcasses) throughout my study period, conflicting results emerged between the two survey methods (camera and sign surveys) in relation to the Shannon-Weiner diversity index. Sign surveys indicated that Shannon-Weiner species diversity was significantly lower at both open and caged carcass sites than control sites. By contrast, camera surveys, while not yielding statistically significant differences, showed the highest Shannon-Weiner species diversity at open carcass sites.

Results for Gini-Simpson's species diversity index were more closely aligned between the two survey approaches. Sign survey data revealed that Gini-Simpson's species diversity was significantly lower at open and caged carcass sites than at control sites. Similarly, camera data

indicated that open sites exhibited the lowest Gini-Simpson's species diversity, although—again—these findings were not statistically significant.

Several factors may have contributed to the discrepancies observed between sign and camera surveys regarding the Shannon-Weiner diversity index. Smaller species may have been underrepresented in camera data due to obscuring vegetation, such as long grass, which could block camera sensors and reduce their detection (Moll *et al.* 2020). The height of the cameras in my study was a trade-off between minimising false triggers and vegetation obscuring the view. Because my study was part of a greater carcass decomposition study the vegetation monitoring protocol of other researchers prevented me from clearing vegetation in front of the cameras. This potentially resulted in fewer detections of small carnivores than might have been the case if the area had been trimmed. Nevertheless, this limitation would likely have affected open, caged, and control sites equally, and so does not fully account for the difference in Shannon's diversity results between survey types. It is also possible that clearing of vegetation proximate to experimental sites might induce unexpected behavioural changes for some predator species resulting in attraction or avoidance and biasing the results.

6.4. The impact of fire

Another contributing factor was a fire at one open carcass (experimental site six) (Figure 3.1), which took place after autumn sampling but before the winter sampling period. While the fire did not damage the camera equipment, it created a much more open landscape around this camera array, potentially facilitating an increased detectability of smaller carnivore species. This could potentially have skewed camera results for open carcass sites during this period. The improved visibility and shorter grass persisted into the spring sampling period, and the post-fire flush of green vegetation attracted herbivores to the area as has been found in other studies (Wilsey 1996, Archibald *et al.* 2005). This, in turn, could have positively influenced carnivore presence, with small carnivores attracted by new prey opportunities like insects, rodents and birds also attracted to the lush new vegetation (Swengel 2001, Engstrom 2010, Lopes and Vasconcelos 2011). These factors may have contributed to higher apparent species diversity in camera data at open carcass sites.

I attempted to evaluate whether the fire had a confounding effect by further analyses excluding open carcass site six. The nearest control site (site five) and the nearest caged site (site nine) to the fire-affected site were also omitted from these analyses, even though they were not directly

impacted by the fire. Excluding these three sites did not substantially alter the sign survey results: both Shannon-Weiner and Gini-Simpson species diversity indices remained significantly lower at open sites compared to control sites. However, the camera survey results shifted, aligning more closely with the sign survey data. With these sites omitted, Shannon's species diversity was now lowest (albeit not significantly so) at open carcass sites, rather than highest as previously recorded. Similarly, Gini-Simpson's species diversity from camera data continued to indicate the lowest diversity at open sites, but the difference still lacked statistical significance.

The control sites were therefore associated with higher Gini-Simpson and Shannon-Weiner mesopredator species diversity than both open and caged carcasses, reflecting greater species richness and evenness at the controls. The Gini-Simpson diversity index, which considers dominance, was lower at carcass sites, suggesting that a single species (jackals) predominated among predators at these locations. The Shannon-Wiener index, less affected by dominant species and more responsive to rare species, showed that there were also fewer uncommon or rare predator species at carcass sites than at control sites.

The observed patterns of species diversity may initially seem counterintuitive as carcasses are important resources for several carnivorous species and short-term resource pulses are generally thought to increase species diversity (Chesson *et al.* 2004, Lancaster and Downes 2021) but see Miller *et al.* (2019). However, resource pulses such as carcasses generate feeding opportunities that must be weighed against the increased risk of predation at these sites (Howe 1979). Predators like coyotes and jackals are known to respond quickly to resource pulses (Hunter *et al.* 2007, Jensen *et al.* 2024). Smaller predators therefore quickly encounter heightened predation risk in areas where larger predators are concentrated (Hayward *et al.* 2006, Williams *et al.* 2018, Kamler *et al.* 2020), such as around carcasses. The interaction between risk, reward, and behavioural response is often nonlinear, varying by species and habitat (Avenant and Nel 2002, Gaynor *et al.* 2019). One study (Cortés-Avizanda *et al.* 2012) demonstrated that predictable carcasses, such as those at vulture restaurants, exhibited lower Shannon-Weiner scavenger species diversity compared to unpredictable carcasses distributed randomly across the landscape. Although our carcasses may have initially been classified as unpredictable, their sustained presence—due to an absence of large scavengers to facilitate feeding and removal—likely led to a reduced overall scavenger response characteristic of predictably provisioned sites. This pattern may suggest behavioural avoidance of the area by smaller scavengers. In addition, numerous studies have demonstrated that animals possess the

ability to assess and behaviourally manage their risk of predation within ecological timescales, beyond mere evolutionary adaptation (Lima and Dill 1990, Thaker *et al.* 2011).

6.5. Carrion and the landscape of fear

The "landscape of fear" describes how animals adjust their behaviour and resource use, based on perceived predation risk, balancing their needs with potential threats (Coleman and Hill 2014). The species diversity results discussed above suggest a landscape of fear response to carrion by some mesopredators. Furthermore, sign surveys revealed that jackal track density was significantly higher at both open and caged sites compared to control sites. In contrast, the number of other mesopredator tracks within 250 m of experimental sites demonstrated a significant negative correlation with jackal track density. This negative association persisted up to 500 m from experimental sites, though it ceased to be statistically significant at this distance. When this relationship was investigated from a seasonal perspective the season of active decay showed a significant negative correlation between jackal track density and the number of mesopredator tracks while other seasons did not.

Notably, no statistically significant correlation was observed between the presence of mesopredator tracks and either leopard or brown hyaena track presence, possibly because leopard and brown hyaena are not regarded as a significant threat to certain mesopredators compared to jackals (Kamler *et al.* 2012b), or they are uncommon enough that there is no perceived threat. This is supported by findings from other studies suggesting that when apex predators like leopards are removed or occur in low numbers, jackals become the dominant predator and suppress smaller mesopredators (Kamler *et al.* 2012b, Bagniewska and Kamler 2014). This suppression may be direct (jackals killing smaller mesopredators and reducing their numbers) or more of a behaviourally mediated effect causing spatiotemporal avoidance of jackals by smaller predators (Kamler *et al.* 2013).

Overall camera data indicated a different trend, revealing a slightly positive yet non-significant relationship between the frequency of jackal visits and mesopredator visits. However, as with my discussion on species diversity, these results may have been affected by the fire at site 6, which influenced camera coverage, as well as the subsequent green flush in burned areas following the rainy season. However, when analyses were restricted to the active decay period (prior to the fire, when jackal activity around carcasses peaked), a significant negative correlation emerged between jackal visits and mesopredator visits—consistent with sign survey

results given that during the active decay phase, mesopredators were recorded on cameras only at sites that had zero records of jackals.

It remains unclear whether smaller predators avoided carcasses themselves—potentially due to olfactory cues from the carcass—or instead, were responding to the presence of jackals in these areas. Nonetheless, my data demonstrate that sites with more jackal activity (higher track density and camera detections) were associated with fewer detections (from both camera and sign surveys) of small predators compared to sites with lower (or zero) jackal detections. These findings differed from initial expectations; I expected carcasses to attract a larger diversity of predators than controls, due to their role as a potential food source. Human activity did not account for the observed results, since all site treatment types had similar visitation rates by researchers. It is possible that visits by larger carnivores such as leopard and brown hyaena would have increased with reduced human presence. However, the species diversity data, along with jackal track density negatively correlating with mesopredator track presence, indicate that under certain conditions, some predator species may associate carcass sites with increased risk.

The mechanism underlying the reduced detection of small predators at carcasses in relation to jackal presence is unclear; it may result from spatial avoidance by small predators due to the threat of predation by jackals, or possibly even increased predation of small predators by jackals frequenting these sites, resulting in lower mesopredator populations in the areas close to the carcass sites. Further investigation is required to elucidate this dynamic. However, supporting evidence for jackal impacts on other small predator populations is available from prior research. For example, jackals in South Africa have been found to kill both bat-eared and Cape foxes during interference competition, but the smaller canids managed to coexist with jackals through a combination of spatial temporal avoidance and habitat and dietary partitioning (Kamler *et al.* 2012b). Another study in South Africa found that in the absence of jackals, Cape fox population density increased by 64% in areas with similar habitat and resources (Kamler *et al.* 2013). Furthermore, jackal presence had a sublethal effect on the interspecific relationships between bat-eared foxes and Cape foxes who became more spatiotemporally separated in the absence of jackals (Kamler *et al.* 2013). Numbers of jackals have been shown to be inversely related to numbers of bat-eared foxes, Cape foxes and small-spotted genets (*Genetta genetta*) (Blaum, Tietjen and Rossmanith, 2009). Studies also report negative relationships between the abundance of jackals and mongooses (Bagniewska and Kamler 2014). Additionally, there are previous records from Telperion Nature Reserve of incidents of jackal predation on smaller carnivores (Doh Linh San, personal communication).

Despite this evidence for mesopredator suppression, an Australian study cautions against concluding that it is a pervasive mechanism in all systems. The study found that dingoes (*Canis familiaris*) did not suppress feral cats (*Felis catus*) in a national park, suggesting that mesopredator suppression and release are context- and species-dependent (Fancourt *et al.* 2019). Furthermore, although sympatric predators may interact negatively at smaller spatiotemporal scales, these effects do not always appear at the population level and may be too weak to cause mesopredator suppression or release in certain contexts (Castle *et al.* 2021).

The concept of a landscape of fear, wherein prey animals alter their behaviour in response to the presence of predators, is however well documented in ecological research (Creel *et al.* 2008, Gaynor *et al.* 2019, Palmer *et al.* 2022). Traditionally, much of this work has focused on the impact of predators on their prey, demonstrating how the threat of predation can shape prey movements, habitat use, and even feeding patterns (Brown *et al.* 1999, Laundré *et al.* 2001). However, there is also growing evidence for landscapes of fear existing within predator guilds themselves. Most available research in this area has concentrated on large predators, such as lions and spotted hyaenas, and the ways in which these and other dominant species influence the behaviour and spatial distribution of other predators within the same ecosystem (Hunter *et al.* 2007, Krofel *et al.* 2012, Forsyth *et al.* 2014, Périquet *et al.* 2015, Swanson *et al.* 2016). However, there is evidence of the landscape of fear contributing to trophic structuring in North America between grey wolves, pumas, bears and various mesocarnivores (Wilmers *et al.* 2025), between dingoes (*Canis lupus dingo*) and red foxes in Australia (Wooster *et al.* 2022) and even in the marine setting for example between Cape gannets (*Morus capensis*) and their predator the Cape fur seal (*Arctocephalus pusillus*) (Courbin *et al.* 2022).

Despite these advances, there remains a relative dearth of research addressing the role of mesopredators—such as jackals and other similarly sized carnivores—in shaping the landscape of fear within predator communities. Work on the landscape of fear around carcasses is equally scarce but Frank *et al.* (2020) found ravens (*Corvus corax*) shaped a landscape of fear around carrion for scavenging rodents (Arvicolinae species), and that scavenging foxes (*Vulpes vulpes* and *Vulpes lagopus*) had less of a negative effect on the rodents, highlighting complex interactions between scavenging species attending carcasses. Understanding how these species interact, and whether they induce fear-driven responses in other predators, is essential for a more complete picture of predator guild dynamics, particularly outside of traditional protected areas where predator guilds are not intact.

6.6. Carrion and predator occupancy

6.6.1. The effect of human disturbance

Occupancy probability reflects the true underlying presence of a species at a site, even if it is not directly observed during a survey. Site-specific factors, such as persistent human disturbance, influence occupancy probability, whereas survey-specific variables like weather while not influencing occupancy, will have an impact on detection probability (MacKenzie *et al.* 2002).

Occupancy models revealed that the occupancy of brown hyaena and the detection probabilities for leopard and serval were all negatively affected by human disturbance. The presence of carcasses had no impact on the occupancy and detection probability of these three species. This finding indicates that human disturbance around the carcass and control sites during the period of active decay when many researchers were coming and going between the 15 experimental sites may account for the infrequent recordings of brown hyaena and leopard at the carcass sites, despite both species being present on the reserve and being known to feed on carrion and blue wildebeest. For the leopard in particular, recent research (Mann *et al.* 2018, Morris *et al.* 2022) has shown that the nearby (20 km away) Loskop dam nature reserve has a relatively high population density of leopard. Furthermore, the Wilge river drainage system forms a natural and relatively safe corridor between the two reserves (Morris *et al.* 2022). Therefore, the low occupancy of leopard found in my study was not believed to be the reason that so few of this species visited the carcasses although a population density study of leopard on Telperion would be needed to confirm this. However, given the data to hand, it is far more likely that leopard stayed away due to their shy nature. The occupancy model confirmed that more tracks of leopard were likely to be detected in areas of low disturbance on the reserve during the period of active decay when disturbance around the carcasses was high.

My results suggest that brown hyaenas moved away from the area close to the experimental sites during periods of active decay, when human presence was greatest, and spent time elsewhere in the reserve. Although researchers mainly worked during the day this was not always the case. Furthermore, although brown hyaena are primarily nocturnal, a wariness of the equipment used during the study as well as the residual scent of humans in the vicinity of the experimental sites may have deterred them, certainly initially. My occupancy model showed that leopard occupancy was primarily affected by habitat, with tracks less commonly

found in grassland areas and more commonly in the proximity of rocky ridges, woodland, and riverine habitats. However, leopard detection probability was also reduced in the presence of human disturbance, indicating that leopards may have remained on the reserve but avoided transects adjacent to the experimental sites while human disturbance there was high.

Serval were not expected to respond to the carcasses, as they are not commonly recorded feeding on carrion. Nevertheless, Keyes *et al.* (2021) documented servals rubbing and scent marking on carcasses, though not actively scavenging. During my study, servals were only recorded once on one of the cameras (site 12) throughout the survey period. Occupancy analyses based on sign survey data indicated that this limited detection may be attributed to an aversion to human activity, as detection probability was negatively affected by anthropogenic disturbance. Servals typically display diurnal and crepuscular behaviour in protected areas but become predominantly nocturnal in regions with greater human disturbance (Ramesh and Downes 2013; Bohm and Hofer 2018). Thus, as Telperion is a protected site, serval activity is likely diurnal and crepuscular, coinciding with peak human activity around the study sites, although further research on serval diel activity on Telperion would be necessary to confirm this. Numerous studies provide evidence that predators either avoid areas of human activity entirely, like bobcats (*Lynx rufus*) in urban spaces (Young *et al.* 2019) or adapt by temporally shifting their activity patterns (Ramesh and Downes 2013; Kittle and Watson 2025). Serval occupancy in this study was also influenced by habitat, with their tracks being most frequently encountered in grassland areas rather than woodland and rocky ridges.

6.6.2. The effect of carcasses on occupancy and detection probability

The occupancy models that I developed for this study, indicated that jackals were the sole carnivore whose detection probability increased in the presence of actively decaying carcasses. In contrast, the detection probabilities for aardwolf, caracal, slender mongoose, yellow mongoose, rusty spotted genet, and suricate were all negatively affected by actively decaying carcass presence. However, further research is required to clarify whether it is the carcass itself or the presence of jackals at carcasses that influences detection probabilities for these species. Data from my cameras seem to suggest it may be the presence of jackals that had an influence on some of the smaller predators as aardwolf were recorded by cameras at one of the caged carcass sites (site four) during the active decay period, but jackals were not observed at this carcass at all during this phase. Based on evidence that aardwolf diet is restricted to

invertebrates (De Vries *et al.* 2011), I suggest that perhaps the attraction for the aardwolf was the invertebrates present at the carcass rather than the carcass itself.

Scavenging by rusty spotted genets is considered to be rare, with documented cases restricted to very small carcasses such as bats (Zemouche 2018, Labadie *et al.* 2024). During my study period, rusty spotted genets were notably absent from areas surrounding the carcasses, even where the sign survey transects passed close to woodland or riverine vegetation proximate to the carcass sites. This suggests that their avoidance may be linked to the presence and activity of jackals in these locations as their tracks were frequently found on roads traversing woodland and riparian vegetation away from carcass sites.

Similarly, I could find no evidence to suggest that suricates engage in scavenging behaviour but see Doolan and MacDonald (1996) for details of typical suricate diet. However, the absence of suricate tracks on road transects proximate to carcass sites during the active decay phase, compared to their occurrence in other areas, suggests that increased jackal activity in the vicinity of carcasses may deter suricates from passing through or spending time in these areas.

Occupancy modelling indicated that caracals tended to avoid actively decaying carcasses. Caracals are known to scavenge only occasionally (Pohl 2015; Avenant and Nel 2002), predominantly in arid environments where natural prey is scarce (Avenant and Nel 2002). Telperion supports abundant natural prey for caracal, likely reducing the need for scavenging. However, in my study, I only recorded one image of a caracal at one of my experimental sites (a control site - site two). Even open carcasses with very low jackal numbers (site three), or none at all during active decay (site eight), produced no caracal records from cameras. This suggests that caracals may be present in low numbers, or that they avoid carcasses on Telperion, or both. Other research (Ferreira 1988; Avenant and Du Plessis 2008; Pohl 2015) indicates that where jackals are abundant, caracal numbers tend to be low, and vice versa. Jackals are likely abundant on Telperion based on sightings and detections during both my study and a previous study that estimated the jackal population to be ~ 50 animals (Melville and Strauss 2021). Additionally, several studies have documented reciprocal predation between jackals and caracals, suggesting these two species actively limit each other's populations (Ferreira 1988; Melville 2004; Pohl 2015).

Occupancy results showed that slender mongoose were negatively affected by the presence of actively decaying carcasses, which is counterintuitive given published records of their scavenging behaviour (Skinner and Chimimba 2005, Keyes *et al.* 2020, Keyes *et al.* 2021).

Furthermore, I have personally observed slender mongoose feeding on leopard kills in the Sabi Sand Game Reserve, on one specific occasion on an impala carcass that had been hoisted into a tree while the leopard responsible for the kill rested below. In my present study, camera footage recorded slender mongoose scavenging on an open carcass at experimental site eight on several occasions during active decay. Notably, this was the only open carcass experimental site where jackals were not recorded by cameras during the entire active decay period, suggesting that slender mongoose in Telperion may avoid jackals rather than carcasses themselves.

Occupancy modelling resulting from my study also indicated that yellow mongooses avoided actively decaying carcasses. One study (Keyes *et al.* 2021) has shown yellow mongooses visiting large carcasses without actively scavenging, while Herzig-Straschil (1977) and Shaw and Ryan (2015) recorded them scavenging on smaller carcasses and Avenant and Nel (1992) recorded springbok hair in yellow mongoose scat indicating that they are opportunistic and may scavenge on larger carcasses in certain circumstances. During my study, yellow mongooses were recorded visiting two of the five open carcasses, but not during the active decay period, and no scavenging behaviour was evident. Further research would be required to ascertain if the yellow mongoose avoided the carcasses or the jackals visiting the carcasses, but evidence from my study seems to suggest that jackals may play a role in limiting this and other species visits to carcasses.

Water mongoose and civet occupancy and detection probability were not influenced by carcasses but rather by habitat. Perhaps, if carcasses had been placed in woodland and riparian habitats, more data of these species would have been available enabling me to report on how carcasses influence their behaviour. Cameras were set only in grassland due to a small sample size—ten wildebeest carcasses (five open, five caged) and five control sites. With just 15 sites, including multiple habitats would have weakened the study's statistical power. Limiting the survey to grassland likely explains why species such as the African civet, who avoid open grassy areas (Camps and Alldredge 2013) and water mongoose who prefer riparian habitat (Webster *et al.* 2021), were not detected at carcasses. This is a consideration for further study.

The above findings prompt consideration of why jackals are so prevalent at Telperion and why they alone responded to carcasses in significant numbers. Evidence from other studies suggests that jackals may leverage human transformed landscapes to their advantage: they are more common than other predators in human-transformed landscapes, such as those surrounding

Telperion, because of their broad diet, high adaptability, and effective utilisation of human resources (Reasoner *et al.* 2024). Their omnivorous diet and behavioural plasticity enable them to coexist near humans and avoid larger predators (Natrass *et al.* 2017). Their medium size allows them to thrive undetected where larger predators are persecuted and displaced, yet they are sufficiently large to outcompete many smaller predators for food (Natrass *et al.* 2017). Despite the protection afforded to predators within Telperion, the reserve's relatively small size and the surrounding human-transformed environment may create a source-sink dynamic for certain predators (Fleming and Bateman 2018, Nisi *et al.* 2023) with the reserve acting as a source (perhaps providing safe habitat/refuge/breeding sites) while the surrounding countryside acts as a population sink for leopard and brown hyaena. However perhaps this does not apply as strongly to jackals. Jackals may even benefit from the landscapes surrounding the reserve (Minnie *et al.* 2016a, Minnie, *et al.* 2016b). These transformed landscapes may act as sources for new individuals entering the reserve as their smaller size, high reproductive rate and adaptable nature may allow them to thrive undetected in these areas (Kamler *et al.* 2020). Furthermore, Minnie *et al.* (2016b) found that jackals may compensate for ongoing persecution with higher breeding rates at a younger age as well as larger litter sizes. This strategy may be at play on Telperion and in surrounding landscapes and further research into this dynamic would be very enlightening.

6.7. Jackal visitation duration and frequency

Open carcasses were the focal point for jackal activity during the study. The seemingly minimal interest in caged carcasses may be attributable to jackals quickly learning that food was inaccessible. However, it is possible that the jackals were initially hesitant to approach the cages, perceiving them as unfamiliar and unnatural structures within their environment. The observation that control sites were visited more frequently than caged carcasses, lends further support to this suggestion; however, confirmation would require additional research. Despite deploying the cages at the experimental sites six weeks prior to the commencement of the study, in the hope that this would mitigate neophobia, it appears that jackals remained wary of these installations. This aligns with studies of other wild canids: wolves (Koch 2017) and coyotes (Mettler and Shivik 2007) in north America, two fox species in Patagonia (Travaini 2013) and jackals in Botswana (Kaunda 2001), which point to a high degree of neophobic behaviour in these species.

Jackals spent significantly more time per visit at open carcass sites compared to either caged or control sites. This increased duration is likely a direct consequence of food availability at open sites, making it energetically advantageous for jackals to linger. Furthermore, seasonal variation was evident in the time spent at open sites, with significantly longer visits at open carcasses during the summer of active decay than in other seasons, including the subsequent summer when no actively decaying carcass was present. This makes sense, as the amount of consumable biomass declines as the carcass decays and consequently the reward for visiting the carcass is less as time progresses (Parsons and Young 2024). Furthermore, Botha *et al.* (2022) also found distinct seasonal differences in jackal space and resource use. In my study, not only was the duration of visits longer at actively decaying open carcasses, but the frequency of visits within a 24-hour period significantly surpassed that of caged carcasses and control sites.

Although the number of jackal visits to open carcasses declined sharply following the active decay period, these sites continued to attract jackals for up to a year after deployment. This sustained interest is reflected in the significantly higher number of visits to open carcass sites compared to control sites across all seasons and not only during the summer of active decay. A similar trend was observed when comparing open sites with caged sites; the frequency of visits to open sites was significantly greater than to caged carcasses during all seasons except autumn, where no significant difference was detected. During autumn, visits to caged carcasses increased, potentially as a result of diminished food resources at open carcasses. This can be explained by optimal foraging theory (Kie 1999) which reasons that when food is limited, the benefit of feeding in riskier areas can outweigh the dangers. When food is abundant, predators choose safer, more efficient places to forage (Křivan 1996). Furthermore, a gradual acclimatisation of jackals to the cages present in their environment may also explain this behaviour. This extended interest in the carcasses is not unexpected, as jackals are often drawn by the scent of old carcasses and will frequently gnaw on old bones to satisfy nutritional requirements (Keyes *et al.* 2020).

6.8. Carrion and jackal diel activity

Analysis of jackal activity across the three treatment types (open carcasses, caged carcasses, and control sites) revealed distinct patterns in daily behaviour. All treatments exhibited pronounced peaks in jackal activity between 05:00 and 06:00, and again at approximately

20:00, with a noticeable decrease in activity during the middle of the day. This bimodal pattern is consistent with findings from previous studies on jackal species (Ferguson *et al.* 1988, Kaunda 1998, Botha *et al.* 2022), suggesting a general tendency for heightened activity during crepuscular hours. Wilkins (2021) found that despite heightened anthropogenic disturbance, jackals still displayed crepuscular activity similar to that in undisturbed environments, while Botha *et al.* (2022) found that jackals were active during crepuscular and nocturnal periods even in protected environments. Thus, crepuscular activity is likely a result of synchronising their activity to times when prey is active, when temperature is suitable for foraging and during times of day when anthropogenic activity decreases as other studies have also suggested (Kaunda 1998, Botha *et al.* 2022). This consistent diel activity contrasts with activity patterns in coyotes in Canada where anthropogenic disturbance caused a marked shift in coyote diel activity (Barrueto *et al.* 2014). My observed bimodal activity cycle for jackals also mirrors patterns recorded in related species such as coyotes (Andelt and Gibson 1979, Hidalgo-Mihart *et al.* 2009). This similarity can likely be attributed to comparable traits between the species, including social structure, dietary flexibility, opportunistic foraging behaviour, responses to anthropogenic pressures, and energetic demands (Andelt and Gibson 1979, Hidalgo-Mihart *et al.* 2009).

Conversely, some studies have found that in human transformed landscapes, coyotes' activity became more nocturnal than crepuscular, probably in response to anthropogenic disturbance in areas where they are heavily persecuted (Melville *et al.* 2020).

Jackal activity at open and control carcass sites demonstrated a more prominent evening peak compared to the early morning, a trend supported by earlier research on this species (Ferguson *et al.* 1988). In contrast, at caged carcass sites, jackals displayed a higher peak in the mornings. However, this result may be anomalous due to the relatively low sample size ($n = 32$) recorded at caged carcass sites.

Despite the provision of carcasses as a food resource, the overall diel activity of jackals appeared largely unchanged. Jackals utilised available carcasses when present, yet the timing of their activity around these food sources closely reflected their typical daily activity periods. Thus, rather than altering when jackals were active, the presence of a carcass seemed primarily to influence where jackals chose to spend their time. This finding is corroborated by other studies, which indicate that time of day consistently exerts the greatest influence on jackal activity patterns (Ferguson *et al.* 1988, Kaunda 1998, Wilkins 2021, Botha *et al.* 2022), and

that jackals maintain clear daily cycles of activity and rest regardless of season, region, or local environmental factors.

6.9. Carrion, lunar phases and jackal activity

The phase of the moon at the initiation of the experiment was full moon (100% lunar disc visible) for the first round of carcasses that were made available (Sites one, three, six, 13 and 15) and 1% lunar disc visible for the second round of carcasses that were made available (Sites four, eight, nine, 11 and 12). Active decay spanned more than one complete lunar cycle. Jackals demonstrated a clear preference for visiting open carcass sites during periods when the proportion of the moon disc that was visible was relatively low (less than 25%). In contrast, activity at caged and control experimental sites exhibited minimal variation with respect to proportion of the lunar disc that was visible. The pronounced increase in jackal activity at open carcasses during darker nights may stem from an avoidance strategy, whereby jackals seek to reduce the likelihood of detection by larger predators when visibility is higher. This is supported by evidence from Botha *et al.* (2022) who observed that jackals travel greater distances during new moon phases compared to full moon. Other studies have identified a negative relationship between moon phase, moon illumination and moon brightness and the activity of small predators and mammals, attributed to elevated predation risk under brighter conditions (Prugh and Golden 2014, Bhatt *et al.* 2021, Marneweck *et al.* 2022, Taylor *et al.* 2023). Although further investigation is needed to fully understand these mechanisms, the evidence from Telperion indicates that the presence of carcasses distinctly influences jackal behaviour in relation to lunar cycles.

Jackal activity in response to the percentage of the lunar disc visible varied seasonally. During the summer of active decay, there was a marked increase in activity at carcasses during periods when the proportion of the lunar disc visible was low, likely reflecting heightened caution due to the possibility of encounters with larger predators as discussed above. Melville *et al.* (2020) found that coyotes moved more during high moonlight intensity (measured as the percentage of the moon face visible), probably as the better visibility increased their chances of finding prey. While this may apply to jackals that are hunting, if a known carcass is available in the environment, then light to find prey becomes less important, while the cover of darkness as a protection against potential encounters with other predators at the carcass likely becomes more important. In other seasons, this pattern was not observed, except in winter, where a similar

peak occurred. The increased winter activity during darker nights may be further explained by reduced food availability, prompting jackals to take greater risks to locate resources, behaviour in line with optimal foraging theory (Křivan 1996, Kie 1999). In autumn, activity at the study sites increased during periods of high lunar illumination, a pattern not seen in other seasons. This may reflect declining food availability at the end of summer, which could have forced jackals to extend their foraging despite the risk of discovery by other predators (Brunet *et al.* 2023). Their increased activity under brighter moonlight may also indicate that carcasses were perceived (Moleón and Sánchez-Zapata 2021) as less risky once active decay had ended and the associated threat from larger predators had subsided.

Jackal group size during visits to experimental sites was negatively correlated with the proportion of the lunar disc visible. Higher levels of moonlight may deter larger group movements, as increased visibility could make larger groups of jackals more conspicuous to predators. Thus, jackals may opt to travel in smaller groups during bright nights to avoid detection however further research is required to confirm this but see Beauchamp (2014) where larger group size is linked to greater visibility and increased predation for both traditional prey species and smaller predators vulnerable to predation themselves.

Overall, the relationship between jackal activity and the percentage of the lunar face visible appears complex. While numerous studies highlight increased predator activity during darker phases, others report the opposite (Fergusson *et al.* 1988, Melville *et al.* 2020), suggesting that prey availability (since small mammals may be more active during brighter nights) also plays a role. The findings from my study reveal that the effect of moonlight on jackal behaviour is more nuanced than a straightforward inverse relationship and is likely shaped by the interplay of carcass availability, possible prey presence, predator presence, and changing environmental conditions (for instance nocturnal illumination). Nevertheless, open carcasses at Telperion altered jackal behaviour relative to the percentage of the lunar face visible, differentiating it from patterns observed at sites without carcasses or with caged carcasses.

6.10. Carrion and jackal group size

Jackals were observed visiting open carcass sites in notably larger groups compared to those seen at caged or control sites. This behaviour aligns with the social nature of jackals, as young individuals from previous litters often assist adult pairs in raising subsequent generations of puppies (Ferguson *et al.* 1988, Natrass *et al.* 2017). Consequently, it is reasonable to infer that

entire jackal families may gather at carcasses, taking advantage of the available resources. Similar results of jackals gathering in larger groups at resource nodes as opposed to where resources were scarce have been reported by Nel *et al.* (2013).

Additionally, territorial jackals have been documented tolerating the presence of neighbouring jackals at carcass sites when food is abundant (Natrass *et al.* 2017). This suggests that carcasses function as important focal points within the landscape, facilitating gatherings and interactions among jackal groups. In fact, Nel *et al.* (2013) found a complete lack of territoriality at seal rookeries which are a highly clumped and superabundant resource in some areas. A similar pattern has also been observed at a vulture supplementary site that is regularly supplied with carrion (Slater unpublished data¹). While it is doubtful that the duration of availability of food at a resource like a wildebeest carcass will influence the social structuring of jackal communities in my study area to the same degree as was found by Nel *et al.* (2013), it is still interesting to understand the social plasticity within the species and localised break downs in territoriality may have occurred at the carcass sites.

6.11. Carrion and jackal vigilance behaviour

Jackals exhibited a noticeably elevated level of vigilance at both open and caged carcass sites when compared to control sites. This is likely due to the increased chance of encounter with other predators at these sites as has been recorded in another study of jackals (Desterecke *et al.* 2025) and for cheetah (Hilborn *et al.* 2018). Among all experimental site types, jackals at caged sites showed the highest percentage of vigilance behaviour. Furthermore, statistically, vigilance was only significantly elevated at caged sites, distinguishing them from both open carcass and control sites.

This pattern is consistent with other findings from my study, which demonstrated that caged carcasses had the fewest jackal visits overall, even fewer than the control sites and seemed to have some sort of repulsive influence over jackals despite the presence of carcasses at these sites. When jackals visited caged carcasses, it was apparent that they were more vigilant and cautious than at sites associated with other treatments. This might be explained in part by neophobia (Kaunda 2001, Mettler and Shivik 2007, Travaini 2013, Koch 2017) as they perceive the cages as unfamiliar or threatening.

¹ Dr. K. Slater. Senior lecturer, Department of Environmental Sciences. University of South Africa.

As a result, jackals showed greater reluctance to approach and spent more time being alert when present at these sites. It is possible that allowing the cages to remain in place for a longer period before the study commenced might have reduced the jackals' wary response. However, further research would be necessary to determine whether prolonged exposure to the cages would mitigate this heightened vigilance behaviour.

6.12. Jackal feeding behaviour

The process by which jackals accessed and fed upon open carcasses in this study was unexpectedly protracted. Although jackals were recorded at three out of the five open carcass sites within the first 24 hours after deployment, they did not immediately begin feeding. The primary reason for this delay appeared to be their inability to penetrate the thick hide of the blue wildebeest carcasses (Melville *et al.* 2023). It was only after approximately ten days (by which time decomposition, facilitated by invertebrates and microbes, had progressed sufficiently to create openings in the skin) that jackals were able to gain access to the remaining flesh inside.

Other carnivores were observed at the carcass sites, but their feeding activity was limited. Leopards, which possess the strength and dentition necessary to open a wildebeest carcass, visited two carcasses (carcass eight and carcass 15) during the phase of active decay; however, in neither case did the leopards open the carcasses or feed on the carcasses. Brown hyaenas, also known for their powerful jaws and ability to open large carcasses and facilitate access for other scavengers, were similarly recorded only twice at open carcasses during the summer of active decay (once at carcass eight and once at carcass 15). Of these, only one individual was observed feeding, during active decay and this occurred just before the end of active decay monitoring, 45 days after the carcass was deployed, just before active decay monitoring ceased, which was well after the jackals had accessed it through openings produced by invertebrates.

The absence of higher order predators such as brown hyaenas and leopards that are able to open larger carcasses and facilitate access to carrion for smaller scavengers is more than likely attributable to their avoidance of anthropogenic disturbance surrounding the study sites as my occupancy model seemed to indicate. Both these species are commonly recorded with cameras, feeding on carrion (Thorn *et al.* 2009, Yarnell *et al.* 2013, Du Preez *et al.* 2014) and thus it is likely to be human disturbance that kept them away in this situation. It is also possible that low population densities of both leopards and brown hyaenas contributed to their infrequent

presence and lack of feeding behaviour observed. Confirming these factors would require further research in the area as I am unaware of any population density estimates for these two species on Telperion. However, the nearby Loskop Dam Nature Reserve had a relatively healthy leopard population density of 5.5 adult leopards per 100 km² (Mann *et al.* 2018). Whether this translates to similar population densities on Telperion or not was beyond the scope of this study but would be an interesting avenue for further investigation.

Vultures, which are obligate scavengers and possess powerful, sharp beaks capable of opening carcasses, were notably absent from the study area throughout the duration of my research. According to the South African Bird Atlas Project SABAP 2 (2023 a-c), three vulture species have been documented within pentads located 62 km from Telperion, with an additional two species recorded in pentads less than 200 km away SABAP 2 (2023 e-f). Given that many vulture species are capable of covering these distances in under a day (Monadjem *et al.* 2018), proximity alone does not account for their absence from available carrion in the study area. The landscape surrounding Telperion has been substantially transformed due to agriculture, livestock farming, mining, electricity generation, and the proximity of urban areas in Gauteng. These factors have rendered the region largely unsuitable for vulture populations, as natural food sources are scarce and risks such as powerline collisions, human interference, poisoning, illegal wildlife trade, and a lack of appropriate breeding habitats likely contribute to their absence from the area (Ogada *et al.* 2016).

Although the underlying causes of their absence remain uncertain and warrant further investigation, it is probable that the lack of vultures further restricted the rate at which carrion from carcasses could be accessed by small mesopredators (Ogada *et al.* 2012, Santangeli *et al.* 2024). Furthermore, Hill *et al.* (2018) found that vertebrate scavengers scavenged more from carcasses that vultures had access to than from carcasses where they had no access, and higher rates of carcass consumption by a scavenger community was linked to the presence of *Gyps* vultures in a study by Gutiérrez-Cánovas *et al.* (2020). The absence of vultures in my study also likely impacted negatively on the decomposition rate of the carcasses (Grootaers *et al.* 2025), extending the duration of their presence in the landscape (Samson and Ramakrishnan 2017) along with associated microbes and disease spreading invertebrates (Hill *et al.* 2018).

6.12.1. Implications of an incomplete predator and scavenger assemblage

Scavenging is an important but often overlooked ecosystem service (Moleón and Sanchez-Zapata 2015). Scavengers regulate food webs, nutrient cycling, and disease control. Key traits like dietary specialisation, strong olfaction, sociality, large ranges, and nocturnal activity influence scavenging processes (Inagaki *et al.* 2025). Large or social scavengers, such as lions and spotted hyaenas, defend carcasses from other scavengers but conversely facilitate smaller mesocarnivores access to food by opening carcasses (Hunter *et al.* 2007, Périquet *et al.* 2015). They also help prevent disease spread by rapidly removing carcasses (Sonawane *et al.* 2025).

My study's findings emphasise the ecological consequences of a reduced or incomplete assemblage of predators and scavengers. In landscapes where large predators are absent, animals in the landscape are more likely to succumb to disease and their carcasses more likely to persist for longer periods (Inger *et al.* 2016). This in turn increases the likelihood of disease spread (Sonowane *et al.* 2025). In contrast, protected areas with healthy populations of large predators benefit from the rapid removal of sick or diseased individuals, thereby limiting the potential for disease transmission within the environment (Le Sage *et al.* 2019).

Extended persistence of carcasses in areas lacking a complete predator and scavenger guild may have important consequences regarding disease transmission (Hill *et al.* 2018) by allowing disease-causing organisms to remain viable for longer periods (Le Sage *et al.* 2019). Invertebrates such as flies can exacerbate this problem (Grootaers *et al.* 2025) by spreading pathogens from carcasses to surrounding vegetation or directly to other animals (Basson *et al.* 2018). In large, protected areas, swift consumption of carcasses by predators and scavengers mitigates these risks. In systems without a complete predator assemblage, smaller mesopredators like jackals may fill the role of these larger predators in terms of removing carrion and associated disease from the system. They do this imperfectly as they lack the ability to open large thick-skinned carcasses, but records of them consuming quantities of flies and maggots at carcasses in my study (Melville *et al.* 2023) likely plays a role in mitigating the risk of disease spread. This is supported by evidence from other studies, that flies and other arthropods can spread diseases such as anthrax (Turell and Knudson 1987) and foot-and-mouth disease (Lendzele *et al.* 2019). If jackals consume large numbers of flies and maggots, they may reduce the movement of disease-carrying invertebrates across the landscape and thereby lower disease transmission. Further research is needed to test this, however.

These results highlight the importance of conserving larger predators and maintaining intact predator guilds (Haswell *et al.* 2017), even in mixed-use landscapes where there may be resistance to their presence. Effective predator conservation and the preservation of ecological functions provided by scavengers are crucial for disease control and ecosystem health outside of protected reserves (Kent and Hill 2013, Ćirović *et al.* 2016, Verschueren *et al.* 2024).

6.12.2. The relationship between jackals and invertebrates at carcasses

Camera footage revealed a notable dynamic between jackals and invertebrates at wildebeest carcasses in my study (Melville *et al.* 2023). Initially, jackals were unable to access nutritional resources from the carcasses directly due to the intact, thick hide (Jarman 1989), which prevented immediate feeding. This circumstance led to an unexpected behavioural adaptation observed throughout the study period. While unable to access the carcasses jackals spent much of their time at the carcasses feeding on invertebrates. Jackals were recorded feeding on maggots and flies directly from the carcass and, to a large extent, also consuming flies that congregated in numbers on surrounding vegetation. Similar feeding behaviours while rarely reported, have been documented in other carnivores. For example, Mason *et al.* (2023) reported coyotes eating flies at carrion, while Finaughty *et al.* (2025) noted grey mongoose (*Galerella pulverulenta*) consuming maggots associated with small carcasses.

My study along with these observations highlight the understudied but biologically significant role invertebrates play within carcass ecology—not only by facilitating decomposition, but also by providing an alternative food resource for smaller predators when access to carrion is restricted. This suggests that invertebrates can serve as an important and previously under recognized food source for predators when access to carrion from carcass is limited.

Once decomposition by invertebrates and microbes provided openings into the carcasses, jackal feeding patterns shifted. The availability of carrion after ~ 10 days of active decay resulted in a sharp decrease in jackals feeding on invertebrates at the carcasses and a near exponential increase in feeding directly on carcass tissue. Although it remains unclear whether this transition was due to reduced invertebrate numbers and decreased efficiency in searching for them, or whether jackals favoured the nutritional value of carrion over invertebrates. It is likely to be a combination of these factors. However, some studies on blowflies (*Chrysomia marginalis*) (Braack 1984b) do suggest that the entire larval stage from egg to maggots pupating on a large carcass takes anywhere between three and 10 days depending on climate conditions and is shorter in summer and longer in winter, (Braack 1984a). Thus, if my study

followed a typical summer pattern, the maggots would pupate after ~ three days. The pupation stage to the emergence of adult flies can take four to six days in warm weather (Braack 1984a). Thus, jackals feeding on flies may initially be feeding on flies that arrived at the carcass and later on flies that hatched on the carcass. There did appear to be a second wave of fly infestation while monitoring the carcasses (personal observation). However, after approximately ten days of active decay, jackals rapidly transitioned from feeding on invertebrates to consuming the remains of the wildebeest carcasses.

6.13. Variability in jackal response to available carrion

Analysis of the camera video data revealed significant variability in the number of jackal visits to experimental sites. Open carcasses received substantially more visits compared to control and caged carcasses; however, the variability within each treatment type was also considerable. For example, the highest number of visits at an open site was recorded at site six with 233 visits, whereas site eight, also an open site, had only one visit, and this single visit did not occur during the summer of active decay when the carcass would have represented a valuable food source. This variation highlights that the mere presence of carcasses in the landscape does not guarantee that predators will locate or utilise them. Other studies have found that where in the environment a carcass is located can influence how and which scavengers interact with them (Smith *et al.* 2017, Walker *et al.* 2021). The size of a carcass also influences if and how quickly it is discovered (Moleón *et al.* 2015). Furthermore, the presence or absence of vultures can also influence whether scavengers find a carcass or not (Kane and Kendall 2017). Thus, several factors appear to contribute to a predator's likelihood of visiting and feeding at a carcass and may explain the observed variability across experimental sites. However, unlike the examples cited above, the carcasses in my study were all approximately the same size, were all placed on the ground in the same type of habitat (i.e. grassland), with no obscuring vegetation and were all in an area where vultures are largely absent. Thus, the variability in visitation of jackals to the carcasses needed further investigation. The GLMM that I developed for my study explained 76% of the variability in visits by jackals. Season, subadult jackal presence, total species richness of the site and distance to nearest infrastructure and reserve boundaries had significant influence.

Season emerged as a significant factor influencing jackal visits. Specifically at open carcasses, where visitation rates increased notably during the summer of active decay when food

availability peaked. Since all experimental sites experienced the same seasonal changes simultaneously, one would expect a consistent seasonal effect across treatment types. However, substantial variation in jackal responses was evident even within a single season and treatment type. For instance, site eight recorded no jackal visits during the summer of active decay, while site six had 156 visits during the same season. This suggests that, although seasonality is a key driver, other factors must also be considered to fully explain the variability in jackal responses to sites of the same treatment type.

The presence of subadult/juvenile jackals in close proximity to a treatment site also influenced jackal visitation. Sites where subadult and/or juvenile jackals were regularly observed by field researchers within 250 m of the camera array had significantly higher numbers of adult jackal visits compared to sites without regular subadult/juvenile sightings proximate to the camera array. Regular observations of subadults and/or juveniles in an area are a strong indication of an active den site nearby, as subadult jackals typically remain close to their dens and are less mobile than adults (Ferguson *et al.* 1988). Adult jackals are also more likely to visit carcasses that are within easy reach of dens containing dependent young as their home range shrinks during the whelping season (Loveridge and Macdonald 2001) around October and for approximately three months afterwards as adults care for den bound pups (Skinner and Chimimba 2005). Consequently, sites with higher numbers of visits were likely closer to active jackal den sites, although this was not intentionally controlled for in the study and warrants further investigation.

Total species richness of all mammals at an experimental site, including herbivores (but excluding jackals) also appeared to significantly influence jackal visits to experimental sites. There was a clear positive relationship between total species richness of a site and the number of jackal visits at that site. This suggests that jackals may tend to spend more time in areas where a diverse assemblage of potential prey concentrate their activity, as has been found in some studies for other predator species (Kittle *et al.* 2016, Balme *et al.* 2019, Vinitpornsawan and Fuller 2020, Ariyanto *et al.* 2024) regardless of carcass presence, possibly even denning near to these areas. While larger herbivores are particularly vulnerable to jackals during the lambing season (Klare *et al.* 2010, Kamler *et al.* 2012, Hayward *et al.* 2017), jackals have been known to prey on medium sized adult herbivores (Mckenzie 2007, Natrass *et al.* 2017). The spatial distribution of prey on a reserve changes seasonally but can remain consistent from one year to the next and is likely linked to factors such as water availability, soil type, and nutritive

value of vegetation (Bailey and Provenza 2008). In small, protected areas like Telperion, herbivores usually move locally instead of migrating long distances. Their movements are mainly influenced by the search for food and water, and the restricted space means they gather in certain areas as resource changes result in concentrated use of certain habitat patches (Novellie and Gaylard 2013). Areas utilised seasonally by prey species may also influence where predators choose to establish den sites (Feizabadi *et al.* 2024). Therefore, carcasses located in these seasonal herbivore gathering areas may have received more jackal visits. Additional research is required to understand the seasonal movements of prey species in the Telperion landscape and their impact on predator behaviour. It is also worth noting that jackals prey on small mammals like rodents. Although I did not record rodent activity in this study, a concurrent study (Melville and Strauss 2026) found greater small mammal activity at carcass sites than at control sites. Whether this pattern relates to variation in jackal responses to carcasses warrants further investigation.

Distance to nearest infrastructure and distance to reserve boundaries had a combined effect on jackal visits to experimental sites with jackal visits being higher where distance to infrastructure and reserve boundaries was greatest. Disturbances outside of a protected area may have marked effects on the population and behaviour of species within the protected area and the closer to the boundary one gets, the more pronounced these effects can be (Woodroffe and Ginsberg 1998). This effect may be species specific and is related to the existence of fences and their permeability to certain species (Balme *et al.* 2010). In smaller reserves the distinction between edge and interior may be less marked as all animals are relatively close to the boundaries (Woodroffe and Ginsberg 1998). However, my model suggested that in the case of jackals on Telperion, there was a negative effect of proximity to reserve boundary on the number of jackal visits to experimental sites. Furthermore, even within protected areas, predators are known to avoid certain areas of heightened human activity, either by spatial avoidance or temporal avoidance of these areas and that this is context and often species specific (Smith *et al.* 2022, Zannette *et al.* 2023). The proximity of human infrastructure in Telperion certainly had a negative effect on jackal visitation to experimental sites.

While I expected habitat type to play a role in visits to carcasses the broad habitat types of Loskop Mountain Bushveld and Rand Highveld Grassland (Mucina *et al.* 2006) used in the model returned no significant results. Within these broad habitat categories, jackal responses remained highly variable. For example, within the Loskop Mountain Bushveld habitat, open carcass site six had 233 visits, while open carcass site eight recorded only one. Similarly, in the

Rand Highveld Grassland, open carcass site 15 had 113 visits compared to just seven at open carcass site three. This variation indicated that the influence of habitat type is nuanced and probably affected by smaller scale habitat variation not accounted for in my study. For example, site three was located in an area dominated by the invasive *Seriphium plumosum* (Bankrupt bush), which may have negatively impacted jackal and other species' use of the site. Supporting this, sites one, two, and four, which were also situated in areas with high prevalence of bankrupt bush, recorded low jackal visitation numbers when compared with other sites of the same treatment type. This is consistent with findings from previous studies (Blaum *et al.* 2007, Oosthuysen *et al.* 2023), which have demonstrated that the presence of bankrupt bush and other encroaching shrub species reduced the abundance of burrowing mammals and the number of sightings of jackals and other medium-sized carnivores reliant on burrows for den sites (Reyneke 2023). Other small scale habitat variations are likely to also have contributed to the variability in jackal visits to certain treatment types. I suggest that by taking finer scale habitat variations into account, different effects of habitat may be revealed that went undetected by only including broad habitat types. This may improve the predictability of the model but would need to be carried out in further research.

Although distance to closest water could possibly have influenced jackal visitation to certain sites, either directly if they were dependent on water themselves, or indirectly as it influences prey movements on the reserve, I did not record this distance for each site during initial sampling. Using GIS sources, a straight-line estimate to the river from each site could have been calculated retrospectively, however, there are smaller streams as well as ephemeral water sources that vary seasonally that are not apparent using GIS and thus this variable was not included in the model. Taking water availability into consideration may improve the predictability of a model such as this and would warrant further investigation.

CHAPTER 7: CONCLUSION AND RECOMMENDATIONS

7.1. Overview of study objectives and context

My research aimed to investigate the ecological consequences of carcass decomposition on predator community dynamics in the Telperion Nature Reserve and to evaluate the application of two different predator survey methods to do so. Telperion is an island of conservation in a mixed-use landscape with pronounced anthropogenic influences. My study's objectives centred on comparing complementary survey techniques—sign surveys and cameras—for their effectiveness in detecting predator species, elucidating predator occupancy patterns, and understanding predator behavioural responses to carrion in a grassland habitat. By deploying carcasses under various experimental conditions and systematically evaluating predator responses, my research sought to inform best practices for conservation monitoring and management in small reserves embedded in human-transformed environments, particularly in areas where traditional predator assemblages are incomplete.

7.2. Summary of key findings

Sign surveys consistently identified a greater number and diversity of species, detected them more rapidly, and provided broader landscape coverage than cameras. However, each method demonstrated unique strengths and weaknesses: cameras offered objective, verifiable records and detailed behavioural insights for some species, but were potentially limited by their smaller detection zone, potential animal avoidance, and in my study, habitat specificity. On the other hand, sign surveys leveraged researcher expertise and landscape connectivity but can be potentially susceptible to observer bias. The combined use of both approaches attempted to yield a complete assessment of predator presence and activity.

I documented clear landscape of fear effects associated with carcasses. These resource pulses exerted an influence on predator behaviour and community structure, particularly influencing mesopredator dynamics. Jackals were the most responsive species, dominating carcass sites both in visitation frequency and duration, while smaller carnivores and other mesopredators exhibited avoidance behaviours, likely mediated by the presence, abundance and activity of jackals. The presence of carcasses, unexpectedly, did not increase overall predator diversity at the experimental site level. Instead, sites with carcasses showed reduced species richness and

evenness compared to control sites, challenging assumptions about the uniformly positive ecological impact of resource pulses.

Occupancy modelling further indicated jackals in this system were the only predator whose presence was positively influenced by carcasses, with the occupancy of many small and medium-sized predators being negatively influenced by carcass presence. Furthermore, occupancy modelling suggested that human disturbance negatively impacted the presence and detectability of larger predators such as brown hyaena, leopard, and the medium sized but elusive serval.

The findings of my research have implications for predator guild dynamics, disease ecology, and conservation management. The dominance of jackals at carcass sites, coupled with the avoidance behaviours of smaller carnivores, suggests the presence of a mesopredator-driven "landscape of fear," where subordinate species modify their spatial use in response to dominant competitors or cues of dominant competitors.

Detailed behavioural analyses highlighted pronounced spatial and temporal patterns in jackal activity at carcass sites. Jackals visiting carrion, demonstrated a preference for periods when the proportion of the lunar disc visible was low. Jackals gathered in larger groups at open carcasses and displayed elevated vigilance in the presence of unfamiliar objects (cages) or inaccessible resources (i.e., caged carcasses). Their feeding behaviour was shaped by carcass accessibility, with initial feeding on invertebrate prey associated with the carcasses, until decomposition enabled access to carrion. Overall, jackals revealed nuanced patterns in site fidelity, vigilance, feeding strategies, diel activity, and lunar phase responses, underscoring their adaptability and behavioural plasticity in a landscape shaped by resource availability and anthropogenic pressures.

7.3. Methodological insights

My study highlights that, including many researchers in broad studies may yield cost-effective results across various fields, but is less suitable for researching elusive, cryptic predators. During the broader carcass decomposition project, daily visits by researchers studying effects on soil, plants, and animals, likely discouraged some carnivores from approaching, even at night. Evidence from my study indicates that some predators avoided sites due to human disturbance, and this may be more prevalent especially in areas where they are not habituated to people and/or face risks like persecution as is the case on Telperion and in the surrounding

landscape respectively. Although this limited observations of large scavengers, it revealed challenges posed by their absence or low density—such as reduced carcass access for smaller predators when no large predators or vultures are present to open remains.

A rigorous evaluation of survey techniques demonstrated that both sign surveys and cameras offered distinct advantages and limitations. Sign surveys proved to be more efficient, cost-effective, and rapid in detecting a wide range of species, especially smaller and more cryptic carnivores. Their broader spatial coverage and lower susceptibility to equipment loss or theft make them well-suited for pilot studies and work in landscapes with elevated anthropogenic disturbance. However, sign surveys may be limited by observer expertise and environmental conditions affecting track visibility, and potential bias in species identification. However, the subjectivity inherent in sign surveys can be mitigated through standardized protocols, digital documentation (track photography, GPS metadata), and emerging AI-assisted identification tools.

Cameras, while more expensive, resource-intensive and potentially vulnerable to theft or vandalism, provide objective, time-stamped records and enable valuable behavioural analyses. They facilitate temporal activity analyses and offer photographic evidence of rare or elusive species. Their detection range, however, is inherently limited, particularly for small carnivores and in habitats with dense vegetation. Their use may also be constrained by avoidance behaviour in certain landscapes and with certain species. My study demonstrates that integrating both methods maximises detection probabilities and yields a more holistic understanding of predator communities and their responses to ecological drivers.

Furthermore, different survey methods may yield complementary or conflicting results, especially for elusive species like cryptic carnivores. Using multiple survey types is beneficial when studying hard-to-detect animals, as techniques effective in one area or with certain individuals may not work elsewhere. For instance, camera trapping may be particularly suitable with habituated leopards in protected areas but underperform with unhabituated animals in mixed-use regions, potentially leading to population underestimates and inadequate conservation focus. Standardised, large-scale studies often use identical methods across regions for consistency, but integrating additional approaches like sign surveys can improve accuracy and provide more comprehensive insights.

Budgetary considerations favour sign surveys for pilot studies and rapid assessments, especially in resource-limited contexts. However, cameras remain indispensable for long-term

monitoring, behavioural studies, and research requiring photographic validation. Methodological rigor demands careful site selection, stratified habitat sampling, and adaptive survey designs that account for local species traits and landscape features.

7.4. Ecological and conservation implications

My study has demonstrated that carcass ecology is shaped by, and in turn shapes, numerous environmental factors. The presence or absence of apex predators and an intact predator guild contributes substantially to these dynamics—not solely because their absence limits access for mesopredators, but also due to their regulatory influence on small to medium-sized predator populations. Without this top-down regulation, species such as jackals may dominate carcass resources, entirely excluding smaller predators such as slender mongooses and civets. While these smaller predators may not be regular scavengers, carrion may be an important addition to their diet during lean times when arthropods are not readily available. Such mesopredator dominance not only restricts access for smaller carnivores but also generates a landscape of fear around the carcass, potentially altering movement and behaviour patterns within the local predator community. For small carnivores, the prolonged presence of a carcass and the scavengers it attracts may have negative consequences because it can turn a small territory into a focal point for competitors and potential predators. Carcasses often draw larger, dominant scavengers, increasing the risk of interference competition, kleptoparasitism, injury, or direct mortality for subordinate species that attempt to feed. Even when direct encounters are avoided, small carnivores may incur costs through heightened vigilance, disrupted movement, and reduced use of parts of their territory while the carcass remains present. This can limit access to other food resources, increase energetic expenditure, and reduce foraging efficiency. In this way, a carcass may represent not only a food opportunity but also a localized source of risk that lowers the net benefit of remaining in or using that area.

My study has contributed valuable insights into this topic, particularly with regard to carcasses and their influence on the landscape of fear, highlighting the need for further research to fully explain the influence of mesopredators on the landscape of fear within predator assemblages and more importantly, the consequences of this influence. Continued investigation into these dynamics is recommended to advance our understanding of the complex interactions that structure predator communities.

The absence of vultures further intensifies these effects, as vultures facilitate carcass access for mesopredators. In the absence of both apex predators and vultures, mesopredators must rely on arthropod and microbial activity to breach the carcass hide before feeding can commence.

An increased proliferation of arthropods and microbes in environments lacking apex predators may raise concerns regarding disease transmission and control. Prolonged carcass persistence in the absence of efficient scavenger assemblages elevates the risk of disease transmission, not only among carnivores but also to herbivores and, potentially, livestock. My study highlights the critical ecological roles fulfilled by large predators and scavengers in carrion removal from the landscape. Their absence could in some circumstances (like mass die offs due to drought or disease) impact nutrient cycling, disease control and broader ecosystem health. Nevertheless, the attending arthropods serve as an additional food source for mesopredators, such as jackals, during the interval preceding carcass accessibility. Facilitating mesopredator access to carcasses in areas where apex predators are absent could aid in decreasing the abundance of arthropods like blowflies, thereby potentially lowering rates of disease spread. In some areas, especially outside of large, protected reserves, carcasses are routinely removed to reduce the risk of disease transmission. In certain parts of the world, this removal is legislated. However, land managers and policy makers may need to reconsider this practice, as mesopredators such as jackals can remove carrion quickly when given the opportunity. Where apex predators are absent, managers could support mesopredator communities by opening carcasses, to give vertebrate scavengers access before invertebrates consume most of the nutrient-rich tissue. This could speed up carrion removal, support local scavenger communities and reduce the risk of disease spread.

These results therefore illustrate the complex interplay between predator occupancy, predator assemblage complexity, anthropogenic disturbance, seasonality and habitat heterogeneity, underscoring the need for landscape-scale approaches to predator management.

7.5. Future research directions

Several knowledge gaps and avenues for further investigation emerged from my study:

- **Mesopredator Interactions:** Further research is needed to disentangle the mechanisms underlying mesopredator avoidance at carcass sites—specifically, whether avoidance is driven by the presence of dominant competitors (e.g., jackals) or by the carcasses themselves.

- **Role of Habitat Complexity:** Investigate how small-scale habitat features, invasive plant species, and landscape structure influence predator movements, carcass discovery, and utilization rates.
- **Carcass Placement in Diverse Habitats:** Conduct studies deploying carcasses across a broader range of habitats, including woodland and riparian zones, to assess species-specific as well as predator assemblage responses in these habitats and refine recommendations for landscape, predator and carrion management. Comparing these results with a similar study on Telperion but in a different habitat, such as a riverine area, would offer insight into habitat specific influence on differences in predator assemblages at carcasses.
- To better understand carcass ecology without jackal as the dominant mesopredator, similar studies should be carried out in altered environments where jackal populations are lower. This will provide insight into carcass ecology in increasingly transformed landscapes where predator assemblages continue to disintegrate.
- Research designed to distinguish the effects of jackal presence on mesopredator behaviour, as compared to the influence exerted solely by the existence of carcasses in the environment, would provide valuable insights.
- Conducting studies that quantify the proportion of invertebrates to carrion in jackal and other scavenger diets, particularly when immediate access to carcasses is not available, would be valuable. Utilizing scat analysis for this purpose could provide significant insight into the role invertebrates play in the diets of jackals and similar predators in the presence of a carcass, while also enhancing understanding of jackals' contributions to the removal of potential disease-causing organisms from the environment.
- Conducting a similar study in the Telperion landscape, with less human disturbance around carcasses, could provide insight into whether the low presence of leopards and brown hyaenas in my study was due to naturally low occupancy or if human activity is a significant factor in deterring them from carcass sites.
- Adding a procedural control of an empty cage with no carcass in it may have provided additional insight into the potential effects of the cages in the environment and should be considered if similar studies are to be undertaken.
- It was noted during my study that there was a significant change in the remains of the carcasses between when active decay monitoring ceased and autumn monitoring started. It would be interesting to leave cameras in place for longer following carcass

deployment to better understand predator visitation after the initial active decay period concluded.

- **Restoration of Scavenger Guilds:** Evaluate the ecological and epidemiological outcomes of restoring large scavengers and apex predators, particularly with respect to carcass persistence and disease transmission dynamics.
- **Behavioural Responses to Anthropogenic Pressures:** Examine how varying levels and types of human disturbance alter predator behaviour, occupancy, and interspecific interactions, with a focus on developing mitigation strategies.
- **Ambient Light and its Effect on Predator Behaviour:** Further studies investigating the influence on lunar phases on nocturnal activity of black-backed jackals and other predators/scavengers should consider incorporating moonrise and moonset times, cloud cover and light from anthropogenic sources into their analyses to get a clearer picture on the influence of ambient light on nocturnal activity. Relying solely on lunar phase may provide an incomplete representation of the actual light conditions experienced by study animals. By accounting for temporal variation in moonlight availability, atmospheric conditions and anthropogenic light sources, researchers can obtain a more accurate measure of nocturnal illumination and better understand the mechanisms underlying responses to lunar cycles and light availability in black-backed jackals, as well as the potential impact of increasing light pollution on nocturnal predators.
- **Technological Innovations:** Explore emerging technologies (e.g., drone-based surveys, environmental DNA, AI assisted photograph and track identification) to complement traditional monitoring and improve detection of elusive species and the study of species responses to carrion in the landscape.
- **With regard to the predator assemblage at Telperion,** a study that examines the connectivity of Telperion to other nearby protected areas like Loskop Dam Nature Reserve and whether large predators do in fact move between the two areas would be worthwhile and would contribute to the conservation of these species in this landscape. This study should include the Wilge River corridor that connects the two areas to understand the extent to which it is used as a corridor. Sign surveys would be suitable for this undertaking as cameras in this area will likely be vulnerable to equipment theft.

7.6. Recommendations for conservation management

Based on the evidence that I have presented, the following actionable recommendations are proposed for wildlife researchers, conservationists, land managers, and policy makers:

- **Adopt Integrated Monitoring Approaches:** Employ both sign surveys and cameras in tandem to maximize efficiency, accuracy, detection probabilities and species coverage, especially when assessing diverse predator communities or targeting cryptic and rare species.
- **Prioritize Cost-Effective Survey Methods for Baseline Assessments:** Use sign surveys for initial, rapid, and cost-effective assessments to inform the need for more intensive, equipment-based studies. This is pertinent in resource limited, mixed use and or high-theft risk environments
- **Implement protocols to document and validate sign survey data,** incorporating GPS, photography and available AI tools
- **Mitigate Human Disturbance:** Particularly with regard to cryptic carnivores in areas where they may not be well protected, minimize anthropogenic activities during periods of monitoring and around sensitive sites to reduce negative impacts on large carnivore occupancy and detection.
- **Support Predator Assemblage Integrity:** Promote the conservation and, where feasible, restoration of complete predator and scavenger guilds to ensure ecosystem resilience, efficient carcass removal, and disease mitigation.
- **Design Studies for Habitat and Seasonal Variation:** Ensure that survey designs incorporate multiple habitat types and account for seasonal shifts in prey distribution, predator activity, and resource availability.
- **Foster community engagement and education** to reduce equipment theft, support conservation efforts and enhance data collection reliability.
- **Enhance Equipment Security:** Implement strategies to safeguard monitoring equipment, particularly in mixed-use or unprotected landscapes, to reduce data loss and financial risk.
- **Facilitate Knowledge Exchange:** Encourage collaboration and information-sharing between researchers, land managers, community members, traditional knowledge holders and policy makers to develop adaptive management strategies informed by current research findings.

- **Harnessing Sign Surveys for Community Employment and Skills Development:** My study demonstrated that sign surveys offer effective, efficient, and cost-effective methods for wildlife monitoring when compared to alternative survey approaches (i.e., camera traps) in certain regions. Therefore, there is significant potential to engage skilled professionals in conducting these surveys. The conservation sector is increasingly required to generate employment opportunities for local communities and contribute positively to the broader economy in addition to conservation goals. Sign surveys present substantial potential not only to create meaningful jobs for residents living near conservation areas but also to enhance the skills of those capable of tracking. These skills will enable them to broaden their expertise and employment prospects while contributing to scientific research. Incorporating the science of sign surveys into the curriculum of tracking schools could open a viable career path for skilled trackers and support the development of new professionals in this field beyond the traditional ecotourism sector.

7.7. Study limitations and final reflections

While my study provides robust insights into scavenger and predator ecology, survey methodology, and conservation practice, several limitations warrant acknowledgment. Restricted sample size, habitat specificity (grassland focus), and unmeasured fine-scale habitat variables may limit generalizability. Equipment loss and/or damage, observer bias, and variable anthropogenic disturbance represent inherent challenges in field research. The absence of population density data for key predators and scavengers constrained interpretations of guild completeness and ecosystem health.

Nevertheless, I believe that my research has contributed to advancing the understanding of predator community dynamics, survey method efficiency, and the ecological ramifications of resource pulses like carrion in small to medium-sized reserves. My findings reinforce the necessity of multi-method approaches, adaptive management, and integrated conservation strategies to safeguard biodiversity and ecosystem function in increasingly fragmented landscapes.

In closing, my study underscores the importance of methodological rigor, ecological synthesis, and evidence-based management in predator conservation. By leveraging complementary survey techniques, prioritising rapid detection, and fostering intact predator guilds,

conservation practitioners can enhance ecosystem resilience, mitigate disease risk, and support sustainable wildlife populations. Continued research, innovation, and collaboration are essential to address emerging challenges and ensure the long-term health of predator communities and the landscapes they inhabit.

REFERENCES

- Aho, K., Derryberry, D. and Peterson, T. (2014). Model selection for ecologists: the worldviews of AIC and BIC. *Ecology*, 95(3), 631-636.
- Akaike, H. (1998). Information theory and an extension of the maximum likelihood principle. In *Selected Papers of Hirotugu Akaike* (pp. 199-213). Springer New York.
- Akaike, H. (2003). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19(6), 716-723.
- Allan, D. G. (1989). Strychnine poison and the conservation of avian scavengers in the Karoo, South Africa. *South African Journal of Wildlife Research*, 19(3), 102-106.
- Alexander, J.S., Cusack, J.J., Pengju, C., Kun, S. and Riordan, P. (2016). Conservation of snow leopards: spill-over benefits for other carnivores? *Oryx*, 50(2), 239-243.
- Allen, L. M., Elbroch, L. M., Wilmers, C. C. and Wittmer, H. U. (2015). The comparative effects of large carnivores on the acquisition of carrion by scavengers. *The American Naturalist*, 185(6), 822-833.
- Altwegg, R. and Nichols, J.D. (2019). Occupancy models for citizen-science data. *Methods in Ecology and Evolution*, 10(1), 8-21.
- Amiard, P.J., Kruger, C.V., Mullers, R.H. and Schipper, J. (2015). The diet of African Civet *Civettictis civetta* in two vegetation types of the Savanna biome in South Africa. *Small Carnivore Conservation*, 52, 4-12.
- Andelt, W. F. and Gipson, P. S. (1979). Home range, activity, and daily movements of coyotes. *The Journal of Wildlife Management*, 43(4), 944-951.
- Anderson, D. and Burnham, K. (2004). Model selection and multi-model inference. *Second*. NY: Springer-Verlag, 63(2020), 10.
- Angeloni, L., Schlaepfer, M. A., Lawler, J. J. and Crooks, K. R. (2008). A reassessment of the interface between conservation and behaviour. *Animal Behaviour*, 75(2), 731-737.

- Anile, S., Ragni, B., Randi, E., Mattucci, F. and Rovero, F. (2014). Wildcat population density on the Etna volcano, Italy: a comparison of density estimation methods. *Journal of Zoology*, 293(4), 252-261.
- Archibald, S., Bond, W. J., Stock, W. D. and Fairbanks, D. H. K. (2005). Shaping the landscape: fire–grazer interactions in an African savanna. *Ecological Applications*, 15(1), 96-109.
- Ariyanto, A.C., Wang, T., Skidmore, A.K., Wibisono, H.T., Widodo, F.A., Firdaus, A.Y., Wiharismo, Y., Koliq, N. and Murdyatmaka, W. (2024). Range-wide camera traps reveal potential prey species for Javan leopards. *Global Ecology and Conservation*, 53, Article e03020.
- Avenant, N. L. and du Plessis, J. J. (2008). Sustainable small stock farming and ecosystem conservation in southern Africa: a role for small mammals? *Mammalia*, 72, 258-263.
- Avenant, N. L. and Nel, J. A. J. (1992). Comparison of the diet of the yellow mongoose in a coastal and a Karoo area. *South African Journal of Wildlife Research*, 22(4), 89-93.
- Avenant, N.L. and Nel, J.A.J. (2002). Among habitat variation in prey availability and use by caracal *Felis caracal*. *Mammalian Biology*, 67(1), 18-33.
- Avolio, M.L., Carroll, I.T., Collins, S.L., Houseman, G.R., Hallett, L.M., Isbell, F., Koerner, S.E., Komatsu, K.J., Smith, M.D. and Wilcox, K.R. (2019). A comprehensive approach to analyzing community dynamics using rank abundance curves. *Ecosphere*, 10(10), Article e02881.
- Bagniewska, J.M. and Kamler, J.F. (2014). Do black-backed jackals affect numbers of smaller carnivores and prey? *African Journal of Ecology*, 52(4), 564-567.
- Bailey, D. W. and Provenza, F. D. (2008). Mechanisms determining large-herbivore distribution. In HHT Prins, F Van Langevelde (Eds.), *Resource Ecology* (pp. 7-28). Springer.
- Baird, T. D. (2022). *Implications of camera trap survey design and analytical methods for large carnivores estimates* [Doctoral dissertation, University of Pretoria] Pretoria, South Africa. UP Repository. <https://repository.up.ac.za/bitstreams/26f10a93-e78e-4ec9-b909-9e002af25b6e/download>
- Balme, G. A., Hunter, L. T. and Slotow, R. O. B. (2009). Evaluating methods for counting cryptic carnivores. *The Journal of Wildlife Management*, 73(3), 433-441.

- Balme, G.A., Robinson, H.S., Pitman, R.T. and Hunter, L.T. (2017). Flexibility in the duration of parental care: Female leopards prioritise cub survival over reproductive output. *Journal of Animal Ecology*, 86(5), 1224-1234.
- Balme, G.A., Rogan, M., Thomas, L., Pitman, R., Mann, G., Whittington-Jones, G., Midlane, N., Broodryk, M., Broodryk, K., Campbell, M. and Alkema, M. (2019). Big cats at large: Density, structure, and spatio-temporal patterns of a leopard population free of anthropogenic mortality. *Population Ecology*, 61(3), 256-267.
- Balme, G. A., Slotow, R. O. B. and Hunter, L. T. (2010). Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda–Mkhuze Complex, South Africa. *Animal Conservation*, 13(3), 315-323.
- Barea-Azcón, J. M., Virgós, E., Ballesteros-Duperon, E., Moleón, M. and Chiroso, M. (2007). Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. *Biodiversity and Conservation*, 16, 1213-1230
- Barrios, L. and Rodriguez, A. (2004). Behavioural and environmental correlates of soaring-bird mortality at on-shore wind turbines. *Journal of Applied Ecology*, 41(1), 72-81.
- Barrueto, M., Ford, A. T. and Clevenger, A. P. (2014). Anthropogenic effects on activity patterns of wildlife at crossing structures. *Ecosphere*, 5(3), 1-19.
- Bartel, S. L., Stephenson, T., Crowder, D. W., Jones, M. E., Storfer, A., Strickland, M. S. and Lynch, L. (2024). Global change influences scavenging and carrion decomposition. *Trends in Ecology and Evolution*, 39(2), 152-164.
- Barton, P. S., Cunningham, S. A., Lindenmayer, D. B. and Manning, A. D. (2013). The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia*, 171(4), 761-772.
- Basson, L., Hassim, A., Dekker, A., Gilbert, A., Beyer, W., Rossouw, J. and Van Heerden, H. (2018). Blowflies as vectors of *Bacillus anthracis* in the Kruger National Park. *Koedoe: African Protected Area Conservation and Science*, 60(1), 1-6.
- Beasley, J. C., Olson, Z. H. and DeVault, T. L. (2012). Carrion cycling in food webs: comparisons among terrestrial and marine ecosystems. *Oikos*, 121(7), 1021-1026.
- Beauchamp, G. (2014). *Social predation: how group living benefits predators and prey*. Elsevier, UK.

- Becker, M.S., Creel, S., Sichande, M., de Merkle, J.R., Goodheart, B., Mweetwa, T., Mwape, H., Smit, D., Kusler, A., Banda, K. and Musalo, B. (2024). Wire-snare bushmeat poaching and the large African carnivore guild: Impacts, knowledge gaps, and field-based mitigation. *Biological Conservation*, 289, 110376.
- Begg, C. M., Begg, K. S., Du Toit, J. T. and Mills, M. G. L. (2003). Sexual and seasonal variation in the diet and foraging behaviour of a sexually dimorphic carnivore, the honey badger (*Mellivora capensis*). *Journal of Zoology*, 260(3), 301-316.
- Begon, M. and Townsend, C. R. (2020). *Ecology: from individuals to ecosystems*. John Wiley and Sons.
- Bennett, J.R., Edwards, B.P., Bergman, J.N., Binley, A.D., Buxton, R.T., Hanna, D.E., Hanson, J.O., Hudgins, E.J., Karimi, S., Raymond, C.V. and Robichaud, C.D. (2024). How ignoring detection probability hurts biodiversity conservation. *Frontiers in Ecology and the Environment*, 22(8), Article e2782.
- Benoit, D., Jackson, D.A. and Ridgway, M.S. (2018). Assessing the impacts of imperfect detection on estimates of diversity and community structure through multispecies occupancy modeling. *Ecology and Evolution*, 8(9), 4676-4684.
- Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B. P. and Saltz, D. (2011). Integrating animal behaviour and conservation biology: a conceptual framework. *Behavioral Ecology*, 22(2), 236-239.
- Berger-Tal, O., Blumstein, D.T., Carroll, S., Fisher, R.N., Mesnick, S.L., Owen, M.A., Saltz, D., St Claire, C.C. and Swaisgood, R.R. (2016). A systematic survey of the integration of animal behavior into conservation. *Conservation Biology*, 30(4), 744-753.
- Bhatt, U., Singh Adhikari, B., Habib, B. and Lyngdoh, S. (2021). Temporal interactions and moon illumination effect on mammals in a tropical semievergreen forest of Manas National Park, Assam, India. *Biotropica*, 53(3), 831-845.
- Bider, J.R. (1968). Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. *Ecological Monographs*, 38(4), 269-308.
- Birdlife South Africa (2020, August 15). *Conservation: terrestrial bird conservation: the grassland biome*. <https://www.birdlife.org.za/conservation/terrestrial-bird-conservation/the-grassland-biome>

- Birks, J., Messenger, J., Braithwaite, T., Davison, A., Brookes, R. and Strachan, C. (2005). Are scat surveys a reliable method for assessing distribution and population status of pine martens? In D.J. Harrison, A.K. Fuller, and G. Proux (Eds.), *Marten and fishers in human-altered environments: an international perspective* (pp. 235-252). Springer US.
- Bishara, A. J. and Hittner, J. B. (2017). Confidence intervals for correlations when data are not normal. *Behavior Research Methods*, 49(1), 294-309.
- Bizani, M. (2014). *Diet of the yellow mongoose (Cynictis penicillata) in the Albany Thicket Biome of South Africa* [Unpublished Doctoral dissertation, University of Fort Hare]. Alice, South Africa.
- Blaum, N., Rossmanith, E., Popp, A. and Jeltsch, F. (2007). Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. *Acta Oecologica*, 31(1), 86-92.
- Blaum, N., Tietjen, B. and Rossmanith, E. (2009). Impact of livestock husbandry on small-and medium-sized carnivores in Kalahari savanna rangelands. *The Journal of Wildlife Management*, 73(1), 60-67.
- Blonder, B. (2018). Hypervolume concepts in niche-and trait-based ecology. *Ecography*, 41(9), 1441-1455.
- Bodasing, T. (2022). The decline of large carnivores in Africa and opportunities for change. *Biological Conservation*, 274, 109724.
- Bohannon, R. W. (1997). Comfortable and maximum walking speed of adults aged 20—79 years: reference values and determinants. *Age and Ageing*, 26(1), 15-19.
- Bohm, T. and Hofer, H. (2018). Population numbers, density and activity patterns of servals in savanna patches of Odzala-Kokoua National Park, Republic of Congo. *African Journal of Ecology*, 56(4), 841-849.
- Bohnett, E., Faryabi, S.P., Lewison, R., An, L., Bian, X., Rajabi, A.M., Jahed, N., Rooyesh, H., Mills, E., Ramos, S. and Mesnildrey, N., (2023). Human expertise combined with artificial intelligence improves performance of snow leopard camera trap studies. *Global Ecology and Conservation*, 41, Article e02350.

- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. and White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in ecology and Evolution*, 24(3), 127-135.
- Botha, A. E., Bruns, A. C. and le Roux, A. (2022). The spatial ecology of black-backed jackals (*Canis mesomelas*) in a protected mountainous grassland area. *African Zoology*, 57(1), 43-55.
- Bothma, J. D. P. (1971). Food of *Canis mesomelas* in South Africa. *African Zoology*, 6(2), 195-203.
- Boulinier, T., Nichols, J. D., Sauer, J. R., Hines, J. E. and Pollock, K. H. (1998). Estimating species richness: the importance of heterogeneity in species detectability. *Ecology*, 79(3), 1018-1028.
- Braack, L. E. O. (1984a). *An ecological investigation of the arthropods associated with large animal carcasses in the northern Kruger National Park, with emphasis on the blow-flies Chrysomya albiceps (Wd.) and C. marginalis (Wd.) (Diptera: Calliphoridae)* [Doctoral dissertation, University of Natal] Pietermaritzburg, South Africa.
- Braack, L. E. O. (1984b). " Epidermal Streaming" and associated phenomena displayed by Larvae of *Chrysomya marginalis* (Wd.) (Diptera: CALLIPHORIDAE) at carcasses. *Koedoe*, 27(1), 9-12.
- Braack L. E.O. (1986). Arthropods associated with carcasses in the northern Kruger National Park. *South African Journal of Wildlife Research*, 16(3), 91-98
- Bredenkamp, G.J. and Brown, L.R. (2003). A reappraisal of Acocks' Bankenveld: origin and diversity of vegetation types. *South African Journal of Botany*, 69(1), 7-26.
- Brooks, M., Rose, S., Altwegg, R., Lee, A.T., Nel, H., Ottosson, U., Retief, E., Reynolds, C., Ryan, P.G., Shema, S. and Tende, T. (2022). The African Bird Atlas Project: a description of the project and BirdMap data-collection protocol. *Ostrich*, 93(4), 223-232.
- Brown, J. S., Laundré, J. W., and Gurung, M. (1999). The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, 80(2), 385-399.
- Brown, J. S. and Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, 7(10), 999-1014.

- Brown, L.R., Magagula, I.P. and Barrett, A.S. (2022). A vegetation classification and description of Telperion Nature Reserve, Mpumalanga, South Africa. *Vegetation Classification and Survey*, 3, 199-219.
- Brunet, M.J., Monteith, K.L., Huggler, K.S., Thompson, D.J., Burke, P.W., Zornes, M., Lionberger, P., Valdez, M. and Holbrook, J.D. (2023). Spatiotemporal predictions of the alternative prey hypothesis: Predator habitat use during decreasing prey abundance. *Ecosphere*, 14(1), p.e4370.
- Buechley, E.R. and Şekercioğlu, Ç.H. (2016). The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions. *Biological Conservation*, 198, 220-228.
- Burgener, N. and Gusset, M. (2003). The feeding habits of brown hyaenas (*Hyaena brunnea*) on a game ranch in Limpopo Province, South Africa. *African Zoology*, 38(1), 181-184.
- Burnham, K. P. and Anderson, D. R. (Eds.). (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer New York.
- Burton, A.C., Sam, M.K., Kpelle, D.G., Balangtaa, C., Buedi, E.B. and Brashares, J.S. (2011). Evaluating persistence and its predictors in a West African carnivore community. *Biological Conservation*, 144(9), 2344-2353.
- Camps, D. and Alldredge, J.R. (2013). Multi-scale habitat use and selection of common genet *Genetta genetta* (Viverridae, Carnivora) in a Mediterranean environment. *Mammalia*, 77(3), 285-295.
- Caravaggi, A., Banks, P.B., Burton, A.C., Finlay, C.M., Haswell, P.M., Hayward, M.W., Rowcliffe, M.J. and Wood, M.D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, 3(3), 109-122.
- Caro, T. (1999). The behaviour–conservation interface. *Trends in Ecology and Evolution*, 14(9), 366-369.
- Caro, T.M. and Stoner, C.J. (2003). The potential for interspecific competition among African carnivores. *Biological Conservation*, 110(1), 67-75.
- Carter, D. O., Yellowlees, D. and Tibbett, M. (2007). Cadaver decomposition in terrestrial ecosystems. *Naturwissenschaften*, 94(1), 12-24.

- Carter, N., Jasny, M., Gurung, B. and Liu, J. (2015). Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. *Global Ecology and Conservation*, 3, 149-162.
- Carter, S., Du Plessis, T., Chwalibog, A. and Sawosz, E. (2017). The honey badger in South Africa: biology and conservation. *International Journal of Avian Wildlife Biology*, 2(2), 00091.
- Castle, G., Smith, D., Allen, L. R. and Allen, B. L. (2021). Terrestrial mesopredators did not increase after top-predator removal in a large-scale experimental test of mesopredator release theory. *Scientific Reports*, 11(1), 18205.
- Chao, A. (2001). An overview of closed capture-recapture models. *Journal of Agricultural, Biological, and Environmental Statistics*, 6(2), 158-175.
- Chao, A. and Chiu, C.H. (2016). Species richness: estimation and comparison. *Wiley StatsRef: statistics reference online*, 1, 26.
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. and Ellison, A.M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84(1), 45-67.
- Chao, A. and Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, 93(12), 2533-2547.
- Chao, A., Kubota, Y., Zelený, D., Chiu, C.H., Li, C.F., Kusumoto, B., Yasuhara, M., Thorn, S., Wei, C.L., Costello, M.J. and Colwell, R.K. (2020). Quantifying sample completeness and comparing diversities among assemblages. *Ecological Research*, 35(2), 292-314.
- Chao, A., Ma, K. H., and Hsieh, T.C. (2016) iNEXT (iNterpolation and EXTrapolation) Online: Software for Interpolation and Extrapolation of Species Diversity. Program and User's Guide published at http://chao.stat.nthu.edu.tw/wordpress/software_download/inext-online/.
- Chapman, S. and Balme, G. (2010). An estimate of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture-recapture models. *South African Journal of Wildlife Research*, 40(2), 114-120.

- Charbonnel, A., d'Amico, F., Besnard, A., Blanc, F., Buisson, L., Némot, M. and Laffaille, P. (2014). Spatial replicates as an alternative to temporal replicates for occupancy modelling when surveys are based on linear features of the landscape. *Journal of Applied Ecology*, 51(5), 1425-1433.
- Chesson, P., Gebauer, R.L., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S., Sher, A., Novoplansky, A. and Weltzin, J.F. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141(2), 236-253.
- Child MF, Roxburgh L, Do Linh San E, Raimondo D, and Davies-Mostert HT, editors. (2016). The 2016 Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Child MF, Roxburgh L, Do Linh San E, Raimondo D, and Davies-Mostert HT. (2017). Mammal Red List 2016: Introduction and Methodology. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa
- Ćirović, D., Penezić, A. and Krofel, M. (2016). Jackals as cleaners: Ecosystem services provided by a mesocarnivore in human-dominated landscapes. *Biological Conservation*, 199, 51-55.
- Clare, J., McKinney, S. T., DePue, J. E. and Loftin, C. S. (2017). Pairing field methods to improve inference in wildlife surveys while accommodating detection covariance. *Ecological Applications*, 27(7), 2031-2047.
- Coleman, B. T. and Hill, R. A. (2014). Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour*, 88, 165-173.
- Cooper, S. M. (1991). Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. *African Journal of Ecology*, 29(2), 130-136.
- Cortés-Avizanda, A., Carrete, M., Serrano, D. and Donázar, J. A. (2009). Carcasses increase the probability of predation of ground-nesting birds: a caveat regarding the conservation value of vulture restaurants. *Animal Conservation*, 12(1), 85-88.
- Cortés-Avizanda, A., Jovani, R., Carrete, M. and Donázar, J. A. (2012). Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology*, 93(12), 2570-2579.

- Cortés-Avizanda, A., Jovani, R., Donázar, J. A. and Grimm, V. (2014). Bird sky networks: How do avian scavengers use social information to find carrion? *Ecology*, 95(7), 1799-1808.
- Cortés-Avizanda, A., Selva, N., Carrete, M. and Donázar, J. A. (2008). Effects of carrion resources on herbivore spatial distribution are mediated by facultative scavengers. *Basic and Applied Ecology*, 10, 265-272.
- Coughlin, S. S., Trock, B., Criqui, M. H., Pickle, L. W., Browner, D. and Tefft, M. C. (1992). The logistic modeling of sensitivity, specificity, and predictive value of a diagnostic test. *Journal of clinical epidemiology*, 45(1), 1-7.
- Council for Geoscience (2023 July 10). *Council for Geoscience Interactive Web Portal*. [Geology of South Africa | Council for Geoscience Interactive Web Map](#)
- Courbin, N., Pichegru, L., Seakamela, M., Makhado, A., Meýer, M., Kotze, P.G., Mc Cue, S.A., Péron, C. and Grémillet, D. (2022). Seascapes of fear and competition shape regional seabird movement ecology. *Communications Biology*, 5(1), 208.
- Cozzi, G., Borger, L., Hutter, P., Abegg, D., Beran, C., Weldon McNutt, J. and Ozgul, A. (2015). Effects of trophy hunting leftovers on the ranging behaviour of large carnivores: a case study on spotted hyaenas. *PLoS one*, 10(3), Article e0121471. <https://doi.org/10.1371/journal.pone.0121471>
- Crane, A. L. and Ferrari, M. C. (2017). Patterns of predator neophobia: a meta-analytic review. *Proceedings of the Royal Society B: Biological Sciences*, 284(1861), 20170583.
- Creel, S. and Creel, N.M. (1996). Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, 10(2), 526-538.
- Creel, S., Spong, G. and Creel, N. (2001). Interspecific competition and the population biology of extinction-prone carnivores. In J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, (Eds.), *Carnivore Conservation* (pp. 35-60). Cambridge University Press.
- Creel, S., Winnie Jr, J. A., Christianson, D. and Liley, S. (2008). Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour*, 76(4), 1139-1146.

- Crupi, V. (2019). Measures of biological diversity: Overview and unified framework. In E. Casetta, J. Marquez da Silva and D. Vecchi (Eds.), *From Assessing to Conserving Biodiversity: Conceptual and Practical Challenges*, 123-136. (Cham: Springer International Publishing) doi:10.1007/978-3-030-10991-2_6
- Cunningham, C. X., Johnson, C. N., Barmuta, L. A., Hollings, T., Woehler, E. J. and Jones, M. E. (2018). Top carnivore decline has cascading effects on scavengers and carrion persistence. *Proceedings of the Royal Society B*, 285(1892), 20181582.
- Curveira-Santos, G., Sutherland, C., Tenan, S., Fernández-Chacón, A., Mann, G.K., Pitman, R.T. and Swanepoel, L.H. (2021). Mesocarnivore community structuring in the presence of Africa's apex predator. *Proceedings of the Royal Society B*, 288(1946), 20202379.
- Davis, R.S., Yarnell, R.W., Gentle, L.K., Uzal, A., Mgoola, W.O. and Stone, E.L. (2021). Prey availability and intraguild competition regulate the spatiotemporal dynamics of a modified large carnivore guild. *Ecology and Evolution*, 11(12), 7890-7904.
- DeBruyn, J. M., Keenan, S. W. and Taylor, L. S. (2025). From carrion to soil: microbial recycling of animal carcasses. *Trends in Microbiology*, 33(2), 194-207.
- de Matos Dias, D., Ferreguetti, Á.C. and Rodrigues, F.H.G. (2020). Using an occupancy approach to identify poaching hotspots in protected areas in a seasonally dry tropical forest. *Biological Conservation*, 251, 108796.
- Destercke, A., Jansen van Vuuren, A. and Venter, J. A. (2025). Dominance at the Dinner Table: Interspecific Competition Between Hyaenas and Jackals at Scavenging Sites. *African Journal of Ecology*, 63(5), e70080.
- de Torrez, E. C. B., Wallrichs, M. A., Ober, H. K. and McCleery, R. A. (2017). Mobile acoustic transects miss rare bat species: implications of survey method and spatio-temporal sampling for monitoring bats. *PeerJ*, 5, Article e3940.
- DeVault, T. L., Brisbin, Jr, I. L. and Rhodes, Jr, O. E. (2004). Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. *Canadian Journal of Zoology*, 82(3), 502-509.
- DeVault, T. L., Rhodes, Jr, O. E. and Shivik, J. A. (2003). Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos*, 102(2), 225-234.

- De Vries, J.L., Pirk, C.W.W., Bateman, P.W., Cameron, E.Z. and Dalerum, F. (2011). Extension of the diet of an extreme foraging specialist, the aardwolf (*Proteles cristata*). *African Zoology*, 46(1), 194-196.
- Do Linh San, E., Ngqinana, A., Madikiza, Z.J. and Somers, M.J. (2020). Diet of the marsh mongoose around a non-permanent reservoir: response of a generalist opportunist forager to the absence of crabs. *African Zoology*, 55(3), 240-244.
- Dominguez-Rodrigo, M. (2000). A study of carnivore competition in riparian and open habitats of modern savannas and its implications for hominid behavioural modelling. *Journal of Human Evolution*, 40(2), 77-98.
- Doolan, S. P. and MacDonald, D. W. (1996). Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. *Journal of Zoology*, 239(4), 697-716.
- Drouilly, M., Natrass, N. and O’Riain, M. J. (2023). Small-livestock farmers’ perceived effectiveness of predation control methods and the correlates of reported illegal poison use in the South African Karoo. *Ambio*, 52(10), 1635-1649.
- Du Plessis, J.J., Avenant, N.L. and De Waal, H.O. (2015). Quality and quantity of the scientific information available on black-backed jackals and caracals: contributing to human-predator conflict management? *African Journal of Wildlife Research*, 45(2), 138-157.
- Du Preez, B. D., Loveridge, A. J. and Macdonald, D. W. (2014). To bait or not to bait: a comparison of camera-trapping methods for estimating leopard *Panthera pardus* density. *Biological Conservation*, 176 (2014), 153-161.
- Durant, J. M., Hjermann, D., Ø., Otterson, G. and Stenseth N., C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33(3), 271-283.
- Durant, S. M. (1998). Competition refuges and coexistence: an example from Serengeti carnivores. *Journal of Animal ecology*, 67(3), 370-386.
- Durant, S. M., Craft, M. E., Hilborn, R., Bashir, S., Hando, J. and Thomas, L. (2011). Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania. *Journal of Applied Ecology*, 48(6), 1490-1500.

- Ebel, K. and White, P.J. (2024). Scent lures and baits at camera traps improve time to first detection and detection probability of two typically elusive species of weasel. *Mammal Research*, 69(4), 461-478.
- Egbert, A. L. and Stokes, A. W. (1976). The social behaviour of brown bears on an Alaskan salmon stream. *Bears: their biology and management*, 3, 41-56.
- Elbroch, L. M. and Wittmer, H. U. (2012). Table scraps: inter-trophic provisioning by pumas in Patagonia. *Biology Letters* 8, 776-779.
- Engstrom, R. T. (2010). First-order fire effects on animals: review and recommendations. *Fire Ecology* 6: 115–130.
- Eriksson, C.E., Kantek, D.L., Miyazaki, S.S., Morato, R.G., dos Santos-Filho, M., Ruprecht, J.S., Peres, C.A. and Levi, T. (2022). Extensive aquatic subsidies lead to territorial breakdown and high density of an apex predator. *Ecology* 103 (1), e03543
- Espartosa, K. D., Pinotti, B. T. and Pardini, R. (2011). Performance of camera trapping and track counts for surveying large mammals in rainforest remnants. *Biodiversity and Conservation*, 20(12), 2815-2829.
- Estes, J. A. and Duggins, D. O. (1995). Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs*, 65(1), 75-100.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B. and Marquis, R.J. (2011). Trophic downgrading of planet Earth. *Science*, 333(6040), 301-306.
- Everatt, K.T., Andresen, L. and Somers, M.J. (2015). The influence of prey, pastoralism and poaching on the hierarchical use of habitat by an apex predator. *African Journal of Wildlife Research*, 45(2), 187-196.
- Fancourt, B. A., Cremasco, P., Wilson, C. and Gentle, M. N. (2019). Do introduced apex predators suppress introduced mesopredators? A multiscale spatiotemporal study of dingoes and feral cats in Australia suggests not. *Journal of Applied Ecology*, 56(12), 2584-2595.
- Ferguson, J. W. H., Galpin, J. S. and Wet, M. D. (1988). Factors affecting the activity patterns of black-backed jackals *Canis mesomelas*. *Journal of Zoology*, 214(1), 55-69.

- Feizabadi, H. A., Ashrafi, S., Hemami, M. R., Ahmadi, M. and Naderi, M. (2024). Mesocarnivores den site selection in arid ecosystems; A case study of Rüppell's fox and sand cat in central Iran. *Global Ecology and Conservation*, 49, Article e02793.
- Ferreira, N. A. (1988). Sekere aspekte van die ekologie en die beheer van die rooikat (*Felis caracal*) in die Oranje-Vrystaat. *Unpublished report, Orange Free State Provincial Administration, Directorate Environmental and Nature Conservation, Bloemfontein. (In Afrikaans.)*
- Fieberg, J., Rieger, R.H., Zicus, M.C. and Schildcrout, J.S. (2009). Regression modelling of correlated data in ecology: subject-specific and population averaged response patterns. *Journal of Applied Ecology*, 46(5), 1018-1025.
- Fielding, D., Newey, S., van der Wal, R. and Irvine, R. J. (2014). Carcass provisioning to support scavengers: Evaluating a controversial nature conservation practice. *Ambio*, 43(6), 810-819.
- Fife, D. (2022). Flexplot: Graphically-based data analysis. *Psychological Methods*, 27(4), 477.
- Finaughty, D. A., French, G. M., Adams, K. S., Spies, M. J. and Gibbon, V. E. (2025). Quantifying forensically relevant vertebrate scavenging: a pilot study to develop a methodological framework using Cape grey mongoose (*Galerella pulverulenta*) as an illustrative model. *Forensic Sciences Research*, 10(2), owa069.
- Findlay, M.A., Briers, R.A., Ingledew, R.P. and White, P.J. (2023). An evidence-based approach to identifying resting sites of Eurasian otter (*Lutra lutra*) from camera-trap and field-sign data. *Wildlife Biology*, 2023(1), Article e01036.
- Finerty, G.E., Borrego, N., Alibhai, S.K., Jewell, Z.C., Tschanz, P., Balone, T., Gabaikanye, T., Gana, M., Monnaanoka, S., Mamou, M. and Pudidaroma, S. (2024). The crossroads of tradition and modern technology: integrative approaches to studying carnivores in low density ecosystems. *Frontiers in Conservation Science*, 5, 1402500.
- Finke, D. L. and Snyder, W. E. (2010). Conserving the benefits of predator biodiversity. *Biological Conservation*, 143(10), 2260-2269.
- Fleming, P. A. and Bateman, P. W. (2018). Novel predation opportunities in anthropogenic landscapes. *Animal Behaviour*, 138, 145-155.

- Forssman, T. and Louw, C. (2016). Leaving a Mark: South African war-period (1899-1902) refuge graffiti at Telperion shelter in Western Mpumalanga, South Africa. *South African Archaeological Bulletin*, 71(203), 4-13.
- Forssman, T. and Louw, C. (2018). The space of flow at Telperion Shelter: the rock art of a recycled, reused and reimagined place. *Time and Mind*, 11(2), 185-208.
- Forsyth, D. M., Woodford, L., Moloney, P. D., Hampton, J. O., Woolnough, A. P. and Tucker, M. (2014). How does a carnivore guild utilise a substantial but unpredictable anthropogenic food source? Scavenging on hunter-shot ungulate carcasses by wild dogs/dingoes, red foxes and feral cats in south-eastern Australia revealed by camera traps. *PLoS One*, 9(6), Article e97937.
- Fouché, J., Lebre, P. H., Melville, H. A., and Cowan, D. A. (2025). The Functional and Structural Succession of Mesic-Grassland Soil Microbiomes Beneath Decomposing Large Herbivore Carcasses. *Environmental Microbiology*, 27(1), e70022.
- Fourie, R. M., Tambling, C. J., Gaylard, A. and Kerley, G. I. H. (2015). Short-term foraging responses of a generalist predator to management driven resource pulses. *African Journal of Ecology*, 53(4), 521-530.
- Fowler, J., Cohen, L. and Jarvis, P. (2013). *Practical Statistics for Field Biology*. John Wiley and Sons.
- Fox, J. (2003). Effect displays in R for generalised linear models. *Journal of statistical software*, 8, 1-27.
- Fox, J. (2019). Regression diagnostics: An introduction. In M.S. Lewis-Beck (Ed.), *Quantitative Applications in the Social Sciences* (pp. 07-079). Sage Publications.
- Fox, J. and Weisberg, S. (2018). Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. *Journal of statistical software*, 87, 1-27.
- Frank, S. C., Blaallid, R., Mayer, M., Zedrosser, A. and Steyaert, S. M. J. G. (2020). Fear the reaper: ungulate carcasses may generate an ephemeral landscape of fear for rodents. *Royal Society Open Science*, 7(6), 191644.
- Fritz, S. A., Bininda-Emonds, O. R. and Purvis, A. (2009). Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology letters*, 12(6), 538-549.

- Funston, P. J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D. M., Durant, S., Packer, C., Mosser, A. and Ferreira, S. M. (2010). Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, 281(1), 56-65.
- GAMLj Development Team (2025). *GAMLj: General Analyses for the Linear Model in jamovi* [Computer Software]. Retrieved on 10 March 2021 from <https://gamlj.github.io/>
- Garden, J. G., McAlpine, C. A., Possingham, H. P. and Jones, D. N. (2007). Using multiple survey methods to detect terrestrial reptiles and mammals: what are the most successful and cost-efficient combinations? *Wildlife Research*, 34(3), 218-227.
- Gardner, W., Mulvey, E. P. and Shaw, E. C. (1995). Regression analyses of counts and rates: Poisson, overdispersed Poisson, and negative binomial models. *Psychological Bulletin*, 118(3), 392.
- Garrote, G., de Ayala, R. P., and Tellería, J. L. (2014). A comparison of scat counts and camera-trapping as means of assessing Iberian lynx abundance. *European Journal of Wildlife Research*, 60(6), 885-889.
- Gasaway, W. C., Mossestad, K. T. and Standers, P. E. (1991). Food acquisition by spotted hyaenas in Etosha National Park, Namibia: predation versus scavenging. *African Journal of Ecology*, 29(1), 64-75.
- Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E. and Brashares, J. S. (2019). Landscapes of fear: spatial patterns of risk perception and response. *Trends in Ecology and Evolution*, 34(4), 355-368.
- Gaynor, K.M., Hayes, F.P., Manlove, K., Galloway, N., Benson, J.F., Cherry, M.J., Epps, C.W., Fletcher Jr, R.J., Orrock, J., Smith, J.A. and Aiello, C. (2025). The influence of human presence and footprint on animal space use in US national parks. *Proceedings of the Royal Society B: Biological Sciences*, 292(2051).
- Gielen, M. C., Johannes, X., Kashe, N., Khumo, G., Zoronxhogo, Z. and Schtickzelle, N. (2024). Monitoring wildlife abundance through track surveys: A capture-mark-recapture inspired approach to assess track detection by certified trackers in the Kalahari, Botswana. *Global Ecology and Conservation*, 51, Article e02924.
- Glen, A.S., Gentle, M.N. and Dickman, C.R. (2007). Non-target impacts of poison baiting for predator control in Australia. *Mammal Review*, 37(3), 191-205.

- Glickman, S.E. (1995). The spotted hyena from Aristotle to the Lion King: reputation is everything. *Social Research*, 501-537.
- Glover-Kapfer, P., Soto-Navarro, C.A. and Wearn, O.R. (2019). Camera-trapping version 3.0: current constraints and future priorities for development. *Remote Sensing in Ecology and Conservation*, 5(3), 209-223.
- Gompper, M.E., Kays, R.W., Ray, J.C., Lapoint, S.D., Bogan, D.A. and Cryan, J.R. (2006). A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. *Wildlife Society Bulletin*, 34(4), 1142-1151.
- Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N. S. and Karanth, K. U. (2012). Program SPACECAP: software for estimating animal density using spatially explicit capture–recapture models. *Methods in Ecology and Evolution*, 3(6), 1067-1072.
- Gould, M.J., Gould, W.R., Cain III, J.W. and Roemer, G.W. (2019). Validating the performance of occupancy models for estimating habitat use and predicting the distribution of highly mobile species: A case study using the American black bear. *Biological Conservation*, 234, 28-36.
- Grande, J.M., Orozco-Valor, P.M., Liébana, M.S. and Sarasola, J.H. (2018). Birds of prey in agricultural landscapes: The role of agriculture expansion and intensification. *Birds of prey: biology and conservation in the XXI century*, 197-228.
- Green, S. E., Rees, J. P., Stephens, P. A., Hill, R. A. and Giordano, A. J. (2020). Innovations in camera trapping technology and approaches: The integration of citizen science and artificial intelligence. *Animals*, 10(1), 132.
- Green, S. E., Stephens, P. A., Whittingham, M. J. and Hill, R. A. (2023). Camera trapping with photos and videos: implications for ecology and citizen science. *Remote Sensing in Ecology and Conservation*, 9(2), 268-283.
- Grey, J. N. C., Kent, V. T. and Hill, R. A. (2013). Evidence of a high-density population of harvested leopards in a montane environment. *PloS One*, 8(12), Article e82832.
- Grobler, A. (1999). *Phytosociology and veld condition assessment of eZemvelo Nature Reserve*. [Unpublished BSc Honours thesis]. Pretoria, South Africa: University of Pretoria.

- Grootaers, J., Hernández Campos, G., Marie Montenegro, V., Vega Quispe, R., Wicks, S., Campos Landázuri, S., Tubelli, E.F., Vega-Reyes, F., Basso, E., Whitworth, A. and Young, A. (2025). Vulture Exclusion Halves Large Carcass Decomposition Rates and Doubles Fly Abundance. *Ecology and Evolution*, 15(5), Article e71408.
- Guiasu, R.C. and Guiasu, S. (2010). The Rich-Gini-Simpson quadratic index of biodiversity. *Natural Science*, 2(10), 1130.
- Gumbi, B. C., Shapiro, J. T., Mahlaba, T., McCleery, R., MacFadyen, D. and Monadjem, A. (2018). Assessing the impacts of domesticated versus wild ungulates on terrestrial small mammal assemblages at Telperion Nature Reserve, South Africa. *African Zoology*, 53(1), 23-29.
- Gusset, M. and Burgener, N. (2005). Estimating larger carnivore numbers from track counts and measurements. *African Journal of Ecology*, 43, 320-324.
- Gutiérrez-Cánovas, C., Moleón, M., Mateo-Tomás, P., Olea, P.P., Sebastián-González, E. and Sánchez-Zapata, J.A. (2020). Large home range scavengers support higher rates of carcass removal. *Functional Ecology*, 34(9), 1921-1932.
- Gutteridge, L. and Liebenberg, L. (2013). *Mammals of Southern Africa and their Tracks and Signs*. Jacana Media.
- Habibzadeh, F., Habibzadeh, P. and Yadollahie, M. (2016). On determining the most appropriate test cut-off value: the case of tests with continuous results. *Biochemia Medica*, 26(3), 297-307.
- Harihar, A., Pandav, B. and Goyal, S. P. (2011). Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. *Journal of Applied Ecology*, 48(3), 806-814.
- Haswell, P.M., Jones, K.A., Kusak, J. and Hayward, M.W. (2018). Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. *Oecologia*, 187(3), 573-583.
- Haswell, P. M., Kusak, J. and Hayward, M. W. (2017). Large carnivore impacts are context-dependent. *Food Webs* 12(2017), 3–13.
- Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. and Kerley, G.I. (2006). Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology*, 270(2), 298-313.

- Hayward, M.W., Porter, L., Lanszki, J., Kamler, J.F., Beck, J.M., Kerley, G.I., Macdonald, D.W., Montgomery, R.A., Parker, D.M., Scott, D.M. and O'Brien, J. (2017). Factors affecting the prey preferences of jackals (Canidae). *Mammalian Biology*, 85(1), 70-82.
- Helm, C.V. (2006). *Ecological separation of the black and blue wildebeest on Ezemvelo Nature Reserve in the highveld grasslands of South Africa*. [Master's Thesis, University of Pretoria]. Pretoria, South Africa. <https://repository.up.ac.za/server/api/core/bitstreams/456280ef-c982-4e48-8a7d-32a6643a8f08/content>
- Herzig-Straschil, B. (1977). Notes on the feeding habits of the yellow mongoose *Cynictis penicillata*. *Zoologica Africana*, 12(1), 225-229.
- Hidalgo-Mihart, M. G., Cantú-Salazar, L., Carrillo-Percegué, S. E. and López-González, C. A. (2009). Daily activity patterns of coyotes (*Canis latrans*) in a tropical deciduous forest of western Mexico. *Studies on Neotropical Fauna and Environment*, 44(2), 77-82.
- Hilborn, A., Pettolelli, N., Caro, T., Kelly, M. J., Laurenson, M. K. and Durant, S. M. (2018). Cheetahs modify their prey handling behavior depending on risks from top predators. *Behavioral Ecology and Sociobiology*, 72(4), 74.
- Hill, J. E., DeVault, T. L., Beasley, J. C., Rhodes Jr, O. E. and Belant, J. L. (2018). Effects of vulture exclusion on carrion consumption by facultative scavengers. *Ecology and Evolution*, 8(5), 2518-2526.
- Hines, J. E. (2006). Presence – Software to estimate patch occupancy and related parameters. Retrieved on 10 March 2021, from USGS-PWRC. <http://www.mbr-pwrc.usgs.gov/software/presence/html>,
- Hines, J.E., Nichols, J.D. and Collazo, J.A. (2014). Multiseason occupancy models for correlated replicate surveys. *Methods in Ecology and Evolution*, 5(6), 583-591.
- Hines, J.E., Nichols, J.D., Royle, J.A., MacKenzie, D.I., Gopalaswamy, A.M., Kumar, N.S. and Karanth, K.U. (2010). Tigers on trails: occupancy modeling for cluster sampling. *Ecological Applications*, 20(5), 1456-1466.
- Hoefler, S., Allen-Ankins, S., McKnight, D. T., Nordberg, E. J. and Schwarzkopf, L. (2025). Sensors versus surveyors: Comparing passive acoustic monitoring, camera trapping and observer-based monitoring for terrestrial mammals. *Methods in Ecology and Evolution*, 16(11), 2603-2621.

- Hollander, M., Wolfe, D.A. and Chicken, E. (2013). *Nonparametric statistical methods*. John Wiley and Sons.
- Höner, O.P., Wachter, B., East, M.L. and Hofer, H. (2002). The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *Journal of Animal Ecology*, 71(2), 236-246.
- Honiball, T.L., Davis, R.S., Ntlokwana, L. and Venter, J.A. (2024). Lion lords and sharing hyaenas: Carnivore guild dynamics around elephant carcasses. *Ecology and Evolution*, 14(5), Article e11373.
- Houser, A. M., Somers, M. J. and Boast, L. K. (2009). Spoor density as a measure of true density of a known population of free-ranging wild cheetah in Botswana. *Journal of Zoology*, 278(2), 108-115.
- Houston, D. C. (1974). Food searching in griffon vultures. *African Journal of Ecology*, 12(1), 63-77.
- Howe, H. F. (1979). Fear and frugivory. *The American Naturalist*, 114(6), 925-931.
- Howes, C.G. (2016). *Power line risk to Cape (Gyps coprotheres) and White-backed (G. africanus) Vultures in Southern Africa*. [Master's Thesis, University of the Witwatersrand]. Johannesburg, South Africa. ProQuest Dissertations and Theses Global.
- Huebner, S. E., Palmer, M. S. and Packer, C. (2024). Human supervision is key to achieving accurate AI-assisted wildlife identifications in camera trap images. *Citizen Science: Theory and Practice*, 9(1).
- Hugosson, A. (2022). The spotted hyena in popular media and the biopolitical implications for conservation strategy. *Animal Studies Journal*, 11(1), 173-199.
- Hulsman, A., Dalerum, F., Swanepoel, L., Ganswindt, A., Sutherland, C. and Paris, M. (2010). Patterns of scat deposition by brown hyaenas *Hyaena brunnea* in a mountain savanna region of South Africa. *Wildlife Biology*, 16(4), 445-451.
- Hunt, W.G., Burnham, W., Parish, C.N., Burnham, K.K., Mutch, B.R.I.A.N. and Oaks, J.L. (2006). Bullet fragments in deer remains: implications for lead exposure in avian scavengers. *Wildlife Society Bulletin*, 34(1), 167-170.

- Hunter, J. S., Durant, S. M. and Caro, T. M. (2007). Patterns of scavenger arrival at cheetah kills in Serengeti National Park Tanzania. *African Journal of Ecology*, 45(3), 275-281.
- Hunter, L. (2020). *Field guide to carnivores of the world*. Bloomsbury Publishing.
- Hutchinson, G. E. (1957). A Treatise on Population Ecology. In C. L. Prosser (Ed.), *Symposia of the Society for Experimental Biology: Volume 11, Marine Biology* (pp. 294–302). University of Chicago Press.
- Inagaki, A., Allen, M. L., Sebastián-González, E. and Koike, S. (2025). Species roles and key interactions in vertebrate scavenger communities. *Trends in Ecology and Evolution*, 40(11), 1090-1100.
- Inger, R., Cox, D. T., Per, E., Norton, B. A. and Gaston, K. J. (2016). Ecological role of vertebrate scavengers in urban ecosystems in the UK. *Ecology and Evolution*, 6(19), 7015-7023.
- IUCN. (2012). IUCN Red List Categories and Criteria: Version 3.1. Second edition. Gland, Switzerland and Cambridge, UK, iv
- Ives, K. (2011). *Predicting conservation status of North American avian and mammalian scavengers: Implications of geography, life history, behaviour and human disturbance* [Doctoral dissertation, University of Alberta]. Edmonton, Canada. <https://ualberta.scholaris.ca/bitstreams/8e664326-077e-476f-831d-1d4e7b88bba8/download>
- Jacoby, W. G. (2000). Loess: a nonparametric, graphical tool for depicting relationships between variables. *Electoral Studies*, 19(4), 577-613.
- James, R. S., Robert, S., Scott, D. M., Yarnell, R. W. and Overall, A. D. J. (2017). Food availability and population structure: How do clumped and abundant sources of carrion affect the genetic diversity of the black backed jackal? *Journal of Zoology*, 301(3), 184-192.
- Janisch, J., Mitoyen, C., Perinot, E., Spezie, G., Fusani, L. and Quigley, C. (2021). Video recording and analysis of avian movements and behavior: insights from courtship case studies. *Integrative and Comparative Biology*, 61(4), 1378-1393.
- Janzen, D.H. (1977). Why fruits rot, seeds mold, and meat spoils. *The American Naturalist*, 111(980), 691-713.

- Jarman, P. J. (1989). On being thick-skinned: dermal shields in large mammalian herbivores. *Biological Journal of the Linnean Society*, 36(1-2), 169-191.
- Jenkins, A. and van Zyl, A. (2020). *Successful Citizen or Voracious Vermin?* in Howes-Whitcross, M., Walker, K., Smit-Robinson, H. and Anderson, M. (Eds.) <https://www.birdlife.org.za/wp-content/uploads/2021/06/Pied-Crows-Biodiversity.pdf>
- Jensen, A.J., Muthersbaugh, M., Ruth, C.R., Butfiloski, J.W., Cantrell, J., Adams, J., Waits, L., Kilgo, J.C. and Jachowski, D.S. (2024). Resource pulses shape seasonal and individual variation in the diet of an omnivorous carnivore. *Ecology and Evolution*, 14(7), Article e11632.
- Jost, L. (2019). What do we mean by diversity? The path towards quantification. *Mètode Science Studies Journal*, 2019(9), 55-61.
- Kamler, J. F., Klare, U. and Macdonald, D. W. (2012b). Seasonal diet and prey selection of black-backed jackals on a small-livestock farm in South Africa. *African Journal of Ecology*, 50(3), 299-307.
- Kamler, J. F., Loveridge, A., O'Donnell, H. and Macdonald, D. (2020). Effects of humans and large carnivores on the survival of black-backed jackals. *African Journal of Ecology*, 58(3), 557-562.
- Kamler, J.F., Stenkewitz, U., Klare, U., Jacobsen, N.F. and Macdonald, D.W. (2012). Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. *The Journal of Wildlife Management*, 76(6), 1241-1253.
- Kamler, J.F., Stenkewitz, U. and Macdonald, D.W., (2013). Lethal and sublethal effects of black-backed jackals on cape foxes and bat-eared foxes. *Journal of Mammalogy*, 94(2), 295-306.
- Kamler, J.F., Stenkewitz, U., Sliwa, A., Wilson, B., Lamberski, N., Herrick, J.R. and Macdonald, D.W., (2015). Ecological relationships of black-footed cats (*Felis nigripes*) and sympatric canids in South Africa. *Mammalian Biology*, 80, 122-127.
- Kane, A. and Kendall, C. J. (2017). Understanding how mammalian scavengers use information from avian scavengers: cue from above. *Journal of Animal Ecology*, 86(4), 837-846.
- Karanth, K. U. and Nichols, J. D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, 79(8), 2852-2862.

- Karanth, K.K., Nichols, J.D., Hines, J.E., Karanth, K.U. and Christensen, N.L. (2009). Patterns and determinants of mammal species occurrence in India. *Journal of Applied Ecology*, 46(6), 1189-1200.
- Karanth, K.U., Gopalaswamy, A.M., Kumar, N.S., Vaidyanathan, S., Nichols, J.D. and MacKenzie, D.I. (2011). Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. *Journal of Applied Ecology*, 48(4), 1048-1056.
- Kaunda, S. K. K. (2001). Capture and chemical immobilization of black-backed jackals at Mokolodi Nature Reserve, Botswana. *South African Journal of Wildlife Research*, 31(1), 43-47.
- Kaunda, S. K. K. (2010). *Black backed jackal (Canis mesomelas) predation on impala (Aepyceros melampus) at Mokolodi nature reserve Botswana* [Doctoral dissertation, University of Pretoria]. Pretoria, South Africa.
<https://repository.up.ac.za/bitstream/handle/2263/27975/04back.pdf?sequence=5>
- Kavazos, C. R. and Wallman, J. F. (2012). Community composition of carrion-breeding blowflies (Diptera: Calliphoridae) along an urban gradient in south-eastern Australia. *Landscape and Urban Planning*, 106(2), 183-190.
- Kearney, M. (2006). Habitat, environment and niche: what are we modelling? *Oikos*, 115(1), 186-191.
- Keeping, D., Burger, J.H., Keitsile, A.O., Gielen, M.C., Mudongo, E., Wallgren, M., Skarpe, C. and Foote, A.L. (2018). Can trackers count free-ranging wildlife as effectively and efficiently as conventional aerial survey and distance sampling? Implications for citizen science in the Kalahari, Botswana. *Biological Conservation*, 223, 156-169.
- Kendall, K. C., Metzgar, L. H., Patterson, D. A. and Steele, B. M. (1992). Power of sign surveys to monitor population trends. *Ecological Applications*, 2(4), 422-430.
- Kendall, W.L. and White, G.C. (2009). A cautionary note on substituting spatial subunits for repeated temporal sampling in studies of site occupancy. *Journal of Applied Ecology*, 46(6), 1182-1188.
- Kendall, W.L., Hines, J.E., Nichols, J.D. and Grant, E.H.C. (2013). Relaxing the closure assumption in occupancy models: staggered arrival and departure times. *Ecology*, 94(3), 610-617.
- Kent, V.T. and Hill, R.A. (2013). The importance of farmland for the conservation of the brown hyaena *Parahyaena brunnea*. *Oryx*, 47(3), 431-440.

- Keselman, H.J. and Rogan, J.C. (1977). The Tukey multiple comparison test: 1953–1976. *Psychological Bulletin*, 84(5), 1050.
- Keyes, C. A., Myburgh, J. and Brits, D. (2020). Taphonomic bone trauma caused by Southern African scavengers. *International Journal of Legal Medicine*, 134(3), 1227-1238.
- Keyes, C.A., Myburgh, J. and Brits, D. (2021). Scavenger activity in a peri-urban agricultural setting in the Highveld of South Africa. *International Journal of Legal Medicine*, 135(3), 979-991.
- Khumalo, R. C., Barrett, A. and Brown, L. R. (2025). Effects of carcass decomposition on vegetation dynamics in Bankenveld grasslands of South Africa. *Royal Society Open Science*, 12(10), 250509.
- Kie, J. G. (1999). Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *Journal of Mammalogy*, 80(4), 1114-1129.
- Kimball, M. G. and Lattin, C. R. (2023). The “seven deadly sins” of neophobia experimental design. *Integrative and Comparative Biology*, 64(1), 38-54.
- Kittle, A. M., Bukombe, J. K., Sinclair, A. R., Mduma, S. A. and Fryxell, J. M. (2016). Landscape-level movement patterns by lions in western Serengeti: comparing the influence of inter-specific competitors, habitat attributes and prey availability. *Movement Ecology*, 4(1), 1-18.
- Kittle, A.M. and Watson, A.C. (2025). Same place, different time: Leopards employ temporal partitioning as a co-existence mechanism in a human-dominated, unprotected agricultural landscape in Sri Lanka. *bioRxiv*, 2025(10), Article e10.681667.
- Klare, U., Kamler, J.F. and Macdonald, D.W. (2014). Seasonal diet and numbers of prey consumed by Cape foxes *Vulpes chama* in South Africa. *Wildlife Biology*, 20(3), 190-195.
- Klare, U. N. N., Kamler, J. F., Stenkewitz, U. T. E. and Macdonald, D. W. (2010). Diet, prey selection, and predation impact of black-backed jackals in South Africa. *The Journal of Wildlife Management*, 74(5), 1030-1041.
- Koch, P. M. (2017). *The influence of genetics on neophobia: responses of wolves, wolfdogs and dogs to visual stimuli* [Doctoral dissertation University of Northern British Columbia]. Prince George, British Columbia, Canada. <https://www.unbc.ca/sites/default/files/sections/ken-otter/paulkoch-finalthesis.pdf>

- Křivan, V. (1996). Optimal foraging and predator–prey dynamics. *Theoretical Population Biology*, 49(3), 265-290.
- Krofel, M., Kos, I. and Jerina, K. (2012). The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology*, 66(9), 1297-1304.
- Kruskal, W.H. and Wallis, W.A. (1952). Use of ranks in one-criterion variance analysis. *Journal of the American Statistical Association*, 47(260), 583-621.
- Kshetry, A. (2014). *Resource selection by leopards (Panthera pardus) in a landscape mosaic in northern West Bengal* [Master's Thesis, Tata Institute of Fundamental Research]. Mumbai, India. https://www.researchgate.net/profile/Aritra-Kshetry/publication/309194616_Resource_selection_by_leopards_Panthera_pardus_in_a_landscape_mosaic_in_northern_West_Bengal/links/580495f808ae310e0d9f5906/Resource-selection-by-leopards-Panthera-pardus-in-a-landscape-mosaic-in-northern-West-Bengal.pdf
- Kuha, J. (2004). AIC and BIC: Comparisons of assumptions and performance. *Sociological Methods and Research*, 33(2), 188-229.
- Kullander, E. A. Deutschländer, M. S., Ngole-Jeme, V. M., and Melville, H. I. (2024). The influence of *Connochaetes taurinus* carcass decomposition on soil nutrient composition in grasslands. *South African Journal of Plant and Soil*, 41(4-5), 72-82.
- Kulyk, V. and Sossa, R. (2018). Determining the tourist attractive regions by GIS analysis using heatmaps. *Geodesy and Cartography*, 44(1), 22-27.
- Labadie, M., Do Linh San, E., Morand, S., Caron, A., Niama, F.R., Nguilili, G.F., Tobi, N.K., De Nys, H.M. and Bourgarel, M. (2024). Video of rusty-spotted genets consuming bats and other prey: Behaviors observed and eco-epidemiological considerations. *Ecosphere*, 15(11), Article e70011.
- Lamichhane, B.R., Lamichhane, S., Regmi, R., Dhungana, M., Thapa, S.K., Prasai, A., Gurung, A., Bhattarai, S., Paudel, R.P. and Subedi, N. (2021). Leopard (*Panthera pardus*) occupancy in the Chure range of Nepal. *Ecology and Evolution*, 11(20), 13641-13660.
- Lancaster, J. and Downes, B. J. (2021). Multiyear resource enrichment creates persistently higher species diversity in a landscape-scale field experiment. *Ecology*, 102(9), Article e03451.

- Laundré, J. W., Hernández, L. and Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology*, 79(8), 1401-1409.
- Lee Goff, M. (2009). Early post-mortem changes and stages of decomposition in exposed cadavers. *Experimental and Applied Acarology*, 49, 21-36.
- Lendzele, S. S., Abdoulmoumini, M., Dickmu, S., Renz, A., Lydie, G., Mavoungou, J. F. and Garabed, R. (2019). Risk Factors for the Contamination of Wild *Stomoxys niger niger* Macquart 1851 (Diptera: Muscidae) with the Foot-and-Mouth Disease Virus. *Current Research in Agricultural Sciences*, 6(2), 95-108.
- Leorna, S. and Brinkman, T. (2022). Human vs. machine: Detecting wildlife in camera trap images. *Ecological Informatics*, 72, 101876.
- Lerone, L., Carpaneto, G. M. and Loy, A. (2015). Why camera traps fail to detect a semi-aquatic mammal: Activation devices as possible cause. *Wildlife Society Bulletin*, 39(1), 193-196.
- Le Roex, N., Bartlet, A., Hunter, L. T. and Balme, G. A. (2023). Just a cat fight or something more sinister? Infanticide is rare among female leopards. *Ecology*, 104(10), Article e4146.
- Le Roux, E., Kerley, G.I. and Cromsigt, J.P. (2018). Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. *Current Biology*, 28(15), 2493-2499.
- Le Sage, M. J., Towey, B. D. and Brunner, J. L. (2019). Do scavengers prevent or promote disease transmission? The effect of invertebrate scavenging on Ranavirus transmission. *Functional Ecology*, 33(7), 1342-1350.
- Le Saout, S., Martin, J.L., Blanchard, P., Cebe, N., Mark Hewison, A.J., Rames, J.L. and Chamaillé-Jammes, S. (2015). Seeing a ghost? Vigilance and its drivers in a predator-free world. *Ethology*, 121(7), 651-660.
- Levi, T. and Wilmers, C. C. (2012). Wolves–coyotes–foxes: a cascade among carnivores. *Ecology*, 93(4), 921-929.
- Li, S., McShea, W.J., Wang, D., Huang, J. and Shao, L. (2012). A direct comparison of camera-trapping and sign transects for monitoring wildlife in the Wanglang National Nature Reserve, China. *Wildlife Society Bulletin*, 36(3), 538-545.

- Li, X.Y., Bleisch, W.V., Liu, X.W., Hu, W.Q. and Jiang, X.L. (2021). Human disturbance and prey occupancy as predictors of carnivore richness and biomass in a Himalayan hotspot. *Animal Conservation*, 24(1), 64-72.
- Liebenberg, L. (1990). The Art of Tracking: The Origin of Science. *David Philip: Claremont, South Africa*.
- Liebhold, A. M. and Gurevitch, J. (2002). Integrating the statistical analysis of spatial data in ecology. *Ecography*, 25(5), 553-557.
- Lima, S. L. and Dill, L. M. (1990). Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68(4), 619-640.
- Lindsey, P. A., Du Toit, J. T. and Mills, M. G. L. (2005). Attitudes of ranchers towards African wild dogs *Lycaon pictus*: conservation implications on private land. *Biological Conservation*, 125(1), 113-121.
- Lindsey, P.A., Alexander, R., Mills, M.G., Romañach, S. and Woodroffe, R. (2007). Wildlife viewing preferences of visitors to protected areas in South Africa: implications for the role of ecotourism in conservation. *Journal of Ecotourism*, 6(1), 19-33.
- Lopes, C. T. and Vasconcelos, H. L. (2011). Fire increases insect herbivory in a Neotropical savanna. *Biotropica*, 43(5), 612-618.
- López-Bao, J. V., Rodríguez, A., Delibes, M., Fedriani, J. M., Calzada, J., Ferreras, P. and Palomares, F. (2014). Revisiting food-based models of territoriality in solitary predators. *Journal of Animal Ecology*, 83(4), 934-942.
- Loveridge, A. J. and Macdonald, D. W. (2001). Seasonality in spatial organization and dispersal of sympatric jackals (*Canis mesomelas* and *C. adustus*): implications for rabies management. *Journal of Zoology*, 253(1), 101-111.
- Loveridge, A. J., and Macdonald, D. W. (2003). Niche separation in sympatric jackals (*Canis mesomelas* and *Canis adustus*). *Journal of Zoology*, 259(2), 143-153.
- Loveridge, A. J., Valeix, M., Elliot, N. B. and Macdonald, D. W. (2017). The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *Journal of Applied Ecology*, 54(3), 815-825.

- Lyra-Jorge, M.C., Ciocheti, G., Pivello, V.R. and Meirelles, S.T. (2008). Comparing methods for sampling large-and medium-sized mammals: camera traps and track plots. *European Journal of Wildlife Research*, 54, 739-744.
- Macdonald, D.W. (2016). Animal behaviour and its role in carnivore conservation: examples of seven deadly threats. *Animal behaviour*, 120, 197-209.
- Mackenzie, D.I. (2006). Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. *Journal of Wildlife Management*, 70(2), 367-374.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. and Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8), 2248-2255.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L. and Hines, J.E. (2017). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier.
- Mangachena, J.R. and Pickering, C.M. (2023). Why are some animals popular with wildlife tourists: Insights from South Africa. *Journal of Ecotourism*, 22(2), 312-328.
- Mann, G., Pitman, R., Broadfield, J., Taylor, J., Whittington-Jones, G., Rogan, M., Dubay, S. and Balme, G. (2018). South African leopard monitoring project: annual report for the South African National Biodiversity Institute. Cape Town: Panthera and SANBI.
- Margalida, A., Donazar, J.A., Carette, M. and Sanchez-Zapata, J.A. (2010). Sanitary versus environmental policies: Fitting together two pieces of the puzzle of European vulture conservation. *Journal of Applied Ecology* 47, 931-935.
- Marker, L. L., Dickman, A. J., Mills, M. G. L. and Macdonald, D. W. (2003). Aspects of the management of cheetahs, *Acinonyx jubatus jubatus*, trapped on Namibian farmlands. *Biological Conservation*, 114(3), 401-412.
- Marneweck, C. J., Forehand, C. R., Waggy, C. D., Harris, S. N., Katzner, T. E., and Jachowski, D. S. (2022). Nocturnal light-specific temporal partitioning facilitates coexistence for a small mesopredator, the eastern spotted skunk. *Journal of Ethology*, 40(2), 193-198.
- Márquez, C., Vargas, J. M., Villafuerte, R. and Fa, J. E. (2013). Understanding the propensity of wild predators to illegal poison baiting. *Animal Conservation*, 16(1), 118-129.

- Mason, D.S., Jones, A.K., Barton, B.T., Proctor, M., Webb, S.L. and Lashley, M.A. (2023). Coyotes eat flies at carrion. *Food Webs*, 37, Article e00309.
- Mateo-Tomás, P., Olea, P. P., Moleón, M., Vicente, J., Botella, F., Selva, N., Vinuela, J. and Sánchez-Zapata, J. A. (2015). From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. *Diversity and Distributions*, 21(8), 913-924.
- Mattisson, J., Andrén, H., Persson, J. and Segerström, P. (2011). Influence of intraguild interactions on resource use by wolverines and Eurasian lynx. *Journal of Mammalogy*, 92(6), 1321-1330.
- Maude, G. and Mills, M. G. L. (2005). The comparative feeding ecology of the brown hyaena in a cattle area and a national park in Botswana. *South African Journal of Wildlife Research*, 35(2), 201-214.
- McFadden, D. (1972). Conditional logit analysis of qualitative choice behavior. In P. Zarembka (Ed) *Frontiers in Econometrics*. (pp 105-142) New York Academic press.
- McHugh, M. L. (2013). The chi-square test of independence. *Biochemia medica*, 23(2), 143-149.
- McKenzie, A. A. (2007). *Co-operative hunting in the black-backed jackal Canis mesomelas Schreber* [Doctoral dissertation, University of Pretoria]. Pretoria, South Africa. <https://repository.up.ac.za/bitstream/handle/2263/24492/08summary.pdf?sequence=10>
- Meek, P. D., Ballard, G., Fleming, P. and Falzon, G. (2016). Are we getting the full picture? Animal responses to camera traps and implications for predator studies. *Ecology and Evolution*, 6(10), 3216-3225.
- Meek, P.D., Ballard, G.A., Sparkes, J., Robinson, M., Nesbitt, B. and Fleming, P.J. (2019). Camera trap theft and vandalism: occurrence, cost, prevention and implications for wildlife research and management. *Remote Sensing in Ecology and Conservation*, 5(2), 160-168.
- Meek, P. D., Fleming, P. and Ballard, G. (2012). *An introduction to camera trapping for wildlife surveys in Australia* (pp. 1-94). Canberra, Australia: Invasive Animals Cooperative Research Centre.
- Melville, H. I. A. S., Bothma, J. D. P. and Mills, M. G. L. (2004). Prey selection by caracal in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, 34(1), 67-75.

- Melville, H. I., Conway, W. C., Hardin, J. B., Comer, C. E. and Morrison, M. L. (2020). Abiotic variables influencing the nocturnal movements of bobcats and coyotes. *Wildlife Biology*, 2020(3), 1-12.
- Melville, H., Gaines, M., Slater, K. and Strauss, W. M. (2023). Ecological gatekeeping: black-backed jackals are left to crave carrion in absence of large facultative scavengers. *Food Webs*, 37, Article e00310.
- Melville, H. I. and Strauss, W. M. (2021). Trialling a simple camera-trap based method to estimate Black-backed jackal population density. *Indago*, 37, 77-87.
- Melville, H. I. and Strauss, W. M. (2026). Fear or feast: small mammal activity increases in the presence of carcasses despite increased threat of predation by black-backed jackals. *Wildlife Biology*, e01620.
- Memarian, I., Ostrowski, S., Kordestani, H., Khakpour, F. and Pouyanshad, N. (2018). The illegal use of snares and gin traps threatens endangered leopards in Iran. *Cat News*, 67, 10-14.
- Mettler, A. E. and Shivik, J. A. (2007). Dominance and neophobia in coyote (*Canis latrans*) breeding pairs. *Applied Animal Behaviour Science*, 102(1-2), 85-94.
- Midi, H., Sarkar, S.K. and Rana, S. (2010). Collinearity diagnostics of binary logistic regression model. *Journal of Interdisciplinary Mathematics*, 13(3), 253-267.
- Midlane, N., O'Riain, M. J., Balme, G. A., Robinson, H. S. and Hunter, L. T. B. (2014). On tracks: A spoor-based occupancy survey of lion *Panthera leo* distribution in Kafue National Park, Zambia. *Biological Conservation*, 172, 101-108.
- Miller, T. E., Buhler, M. L. and Cuellar-Gempeler, C. (2019). Species-specific differences determine responses to a resource pulse and predation. *Oecologia*, 190(1), 169-178.
- Mills, D., Fattebert, J., Hunter, L. and Slotow, R. (2019). Maximising camera trap data: Using attractants to improve detection of elusive species in multi-species surveys. *PloS one*, 14(5), Article e0216447.
- Mills, G. and Hofer, H. (1998). *Hyaenas: status survey and conservation action plan* (No. 333.959 H992). IUCN, Gland (Suiza). SSC Hyaena Specialist Group.

- Mills, M. L. (1984). The comparative behavioural ecology of the brown hyaena (*Hyaena brunnea*) and the spotted hyaena (*Crocuta Crocuta*) in the southern Kalahari. *Koedoe*, 27(2), 237-247.
- Minnie, L., Avenant, N.L., Kamler, J., Butler, H., Parker, D., Drouilly, M., Du Plessis, J., Do Linh San, E., Do Linh San, E., Raimondo, D. and Davies-Mostert, H.T. (2016a). A conservation assessment of *Canis mesomelas*. *The red list of mammals of South Africa, Swaziland and Lesotho*, 1-14.
- Minnie, L., Gaylard, A. and Kerley, G. I. (2016b). Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. *Journal of Applied Ecology*, 53(2), 379-387.
- Mndela, M., Barrett, A.S. and Brown, L.R. (2023). Wild ungulates and shrub control interact to restore herbaceous vegetation in shrub-encroached mesic grassland of South Africa. *Frontiers in Ecology and Evolution*, 11, 1280157.
- Moleón, M., Sánchez-Zapata, J. A., Selva, N., Donázar, J. A. and Owen-Smith, N. (2014). Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews*, 89(4), 1042-1054.
- Moleón, M. and Sánchez-Zapata, J. A. (2015). The living dead: Time to integrate scavenging into ecological teaching. *BioScience*, 65(10), 1003-1010.
- Moleón, M. and Sánchez-Zapata, J. A. (2021). The Role of Carrion in the Landscapes of Fear and Disgust: A Review and Prospects. *Diversity* 2021, 13, 28. *Ecology of Predation and Scavenging and the Interface*, 75.
- Moleón, M., Sánchez-Zapata, J. A., Sebastián-González, E. and Owen-Smith, N. (2015). Carcass size shapes the structure and functioning of an African scavenging assemblage. *Oikos*, 124(10), 1391-1403.
- Moll, R.J., Ortiz-Calo, W., Cepek, J.D., Lorch, P.D., Dennis, P.M., Robison, T. and Montgomery, R.A. (2020). The effect of camera-trap viewshed obstruction on wildlife detection: implications for inference. *Wildlife Research*, 47(2), 158-165.
- Monadjem, A., Kane, A., Botha, A., Kelly, C. and Murn, C. (2018). Spatially explicit poisoning risk affects survival rates of an obligate scavenger. *Scientific Reports*, 8(1), 4364.

- Moreira, M.J. (2003). A conditional likelihood ratio test for structural models. *Econometrica*, 71(4), 1027-1048.
- Morisette, J.T., Richardson, A.D., Knapp, A.K., Fisher, J.I., Graham, E.A., Abatzoglou, J., Wilson, B.E., Breshears, D.D., Henebry, G.M., Hanes, J.M. and Liang, L. (2009). Tracking the rhythm of the seasons in the face of global change: phenological research in the 21st century. *Frontiers in Ecology and the Environment*, 7(5), 253-260.
- Morris, A.W., Smith, I., Chakrabarti, S., Lala, F., Nyaga, S. and Bump, J.K. (2023). Eating an elephant, one bite at a time: Predator interactions at carrion bonanzas. *Food Webs*, 37, Article e00304.
- Morris, D.R., Boardman, W.S., Swanepoel, L.H., Simpson, G., Coetzee, J., Camacho, G.J. and McWhorter, T.J. (2022). Population density estimate of leopards (*Panthera pardus*) in north-western Mpumalanga, South Africa, determined using spatially explicit capture–recapture methods. *Mammalian Biology*, 102(4), 1173-1183.
- Morris, M. C. (2020). Predator free New Zealand and the ‘War’ on pests: Is it a just war? *Journal of Agricultural and Environmental Ethics*, 33(1), 93-110.
- Mucina, L., Hoare, D. B., Marvyn, C., Lötter, P., du Preez, J., Rutherford, M. C., Scott-Shaw, R. C., Bredenkamp, G. J., Powrie, L. W., Scott, L., Camp, G.T. K., Cilliers, S. S., Bezuidenhout, H., Mostert, T. H., Siebert, S. J., Winter, P. J. D., Burrows, J. E., Dobson, L., Ward, R. A., Stalmans, M., Oliver, E. G. H., Siebert, F., Schmidt, E., Kobisi, K. and Kose, L. (2006). The grassland biome (Chapter 8) in Mucina, L. and Rutherford, M. C. (eds). *The vegetation of South Africa, Lesotho and Swaziland* (pp.350-431). Pretoria, South Africa: Strelitzia 19, South African National Biodiversity Institute.
- Muller, K. (2020). *Behavioural Ecology of brown hyaena on Shamwari Game Reserve, Eastern Cape*. [Masters’ Thesis, Department of Environmental Sciences, University of South Africa], Pretoria, South Africa. ProQuest Dissertations and Theses Global.
- Murn, C. and Botha, A. (2018). A clear and present danger: impacts of poisoning on a vulture population and the effect of poison response activities. *Oryx*, 52(3), 552-558.
- Murray, K. (2011). *Scatalog: quick ID guide to southern African animal droppings*. Random House Struik.

- Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P. and Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, 315(5820), 1846-1850.
- Nakagawa, S. and Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133-142.
- Nattrass, N., Conradie, B., Drouilly, M. and O'Riain, M.J. (2017). Understanding the black-backed jackal. CSSR Working Paper no. 399. University of Cape Town Press.
- Nel, J. A., Loutit, R. J., Braby, R. and Somers, M. J. (2013). Resource dispersion, territory size and group size of black-backed jackals on a desert coast. *Acta Theriologica*, 58(2), 189-197.
- Nichols, J. D., Boulinier, T., Hines, J. E., Pollock, K. H. and Sauer, J. R. (1998). Inference methods for spatial variation in species richness and community composition when not all species are detected. *Conservation biology*, 12(6), 1390-1398.
- Nisi, A. C., Benson, J. F., King, R. and Wilmers, C. C. (2023). Habitat fragmentation reduces survival and drives source–sink dynamics for a large carnivore. *Ecological Applications*, 33(4), Article e2822.
- Nkosi, S. E., Brown, L. R. and Barrett, A. S. (2018). A baseline study for controlling the indigenous encroacher *Stoebe vulgaris* in the natural grasslands of Southern Africa. *Agriculture, Ecosystems and Environment*, 265, 209-216.
- Novellie, P. and Gaylard, A. (2013). Long-term stability of grazing lawns in a small protected area, the Mountain Zebra National Park. *Koedoe: African Protected Area Conservation and Science*, 55(1), 1-7.
- Núñez, C.L., Froese, G., Meier, A.C., Beirne, C., Depenthal, J., Kim, S., Mbélé, A.E., Nordseth, A. and Poulsen, J.R. (2019). Stronger together: comparing and integrating camera trap, visual, and dung survey data in tropical forest communities. *Ecosphere*, 10(12), Article e02965.
- Nyirenda, V.R., Nkhata, B.A., Phiri, D., Nyirenda, W., Phiri, D.N., Malasa, M., Becker, M.S., Tembo, E.M., Nyirenda, M.A., Simpamba, T. and Mwitwa, J. (2024). Vulture poisoning in Sub-Saharan Africa and its implications for conservation planning: A systematic review. *Heliyon*, 10(3), Article e25126.

- O'Bryan, C. J., Brackowski, A. R., Beyer, H. L., Carter, N. H., Watson, J. E. and McDonald-Madden, E. (2018). The contribution of predators and scavengers to human well-being. *Nature Ecology and Evolution*, 2(2018), 229-236.
- Ogada, D., Richards, N. and Behmke, S. (2019). What makes carrion unsafe for scavengers? Considerations for appropriate regulatory policies and sound management practices. In *Carrion Ecology and Management* (pp. 213-240). Cham: Springer International Publishing.
- Ogada, D., Shaw, P., Beyers, R.L., Buij, R., Murn, C., Thiollay, J.M., Beale, C.M., Holdo, R.M., Pomeroy, D., Baker, N. and Krüger, S.C. (2016). Another continental vulture crisis: Africa's vultures collapsing toward extinction. *Conservation Letters*, 9(2), 89-97.
- Ogada, D. L., Torchin, M. E., Kinnaird, M. F. and Ezenwa, W. O. (2012). Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conservation Biology*, 26(3), 453-460.
- Okwonu, F. Z., Ahad, N. A., Apanapudor, J. S. and Arunaye, F. I. (2023). Chi-square and adjusted standardised residual analysis. *ASM Science Journal*, 18, 1-11.
- Olson, Z. H., Beasley, J. C., DeVault, T. L. and Rhodes Jr, O. E. (2012). Scavenger community response to the removal of a dominant scavenger. *Oikos*, 121(1), 77-84.
- Oosthuysen, M., Strauss, W.M. and Somers, M.J. (2023). The relationship between mammalian burrow abundance and bankrupt bush (*Seriphium plumosum*) encroachment. *Bothalia-African Biodiversity and Conservation*, 53(1), 1-8.
- Ordiz, A., Aronsson, M., Persson, J., Støen, O.G., Swenson, J.E. and Kindberg, J. (2021). Effects of human disturbance on terrestrial apex predators. *Diversity*, 13(2), 68.
- Owens, M. J. and Owens, D. D. (1978). Feeding ecology and its influence on social organization in brown hyenas (*Hyaena brunnea*, Thunberg) of the central Kalahari Desert. *African Journal of Ecology*, 16(2), 113-135.
- Palencia, P., Vicente, J., Soriguer, R.C. and Acevedo, P. (2022). Towards a best-practices guide for camera trapping: assessing differences among camera trap models and settings under field conditions. *Journal of Zoology*, 316(3), 197-208.

- Palmer, M. S., Gaynor, K. M., Becker, J. A., Abraham, J. O., Mumma, M. A. and Pringle, R. M. (2022). Dynamic landscapes of fear: understanding spatiotemporal risk. *Trends in Ecology and Evolution*, 37(10), 911-925.
- Palomares, F. and Caro, T.M. (1999). Interspecific killing among mammalian carnivores. *The American Naturalist*, 153(5), 492-508.
- Parmenter, R. R. and MacMahon, J. A. (2009). Carrion decomposition and nutrient cycling in a semiarid shrub–steppe ecosystem. *Ecological Monographs*, 79(4), 637-661.
- Parsons, M. A. and Young, J. K. (2024). Coyotes display minimal response to Cougar scent at experimental carcass sites. *Journal of Mammalogy*, 105(4), 729-739.
- Pawluczuk, Ł. and Iskrzyński, M. (2023). Food web visualisation: Heat map, interactive graph and animated flow network. *Methods in Ecology and Evolution*, 14(1), 57-64.
- Pearson, K. (1896). VII. Mathematical contributions to the theory of evolution. —III. Regression, heredity, and panmixia. *Philosophical Transactions of the Royal Society of London. Series A, containing papers of a mathematical or physical character*, (187), 253-318.
- Peat, C. (2023, January 9). *Heavens Above*. <https://heavens-above.com/moon.aspx?lat=-25.691&lng=28.9897&loc=Unnamed&alt=0&tz=SAST>
- Peet, R.K. (1974). The measurement of species diversity. *Annual Review of Ecology and Systematics*, 5(1), 285-307.
- Pereira, L. M., Owen-Smith, N. and Moleón, M. (2014). Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Review*, 44(1), 44-55.
- Périquet, S., Fritz, H. and Revilla, E. (2015). The Lion King and the Hyaena Queen: large carnivore interactions and coexistence. *Biological Reviews*, 90(4), 1197-1214.
- Pettorelli, N., Lobora, A.L., Msuha, M.J., Foley, C. and Durant, S.M. (2010). Carnivore biodiversity in Tanzania: revealing the distribution patterns of secretive mammals using camera traps. *Animal Conservation*, 13(2), 131-139.

- Plaza, P.I., Martínez-López, E. and Lambertucci, S.A. (2019). The perfect threat: Pesticides and vultures. *Science of the Total Environment*, 687, 1207-1218.
- Pohl, C.F. (2015). *The diet of caracal (Caracal caracal) in the southern Free State* [Doctoral Dissertation, University of the Free State]. Bloemfontein, South Africa. <https://scholar.ufs.ac.za/bitstream/handle/11660/2272/PohlCF.pdf?sequence=1&isAllowed=y>
- Ponce-Martins, M., Lopes, C.K.M., de Carvalho-Jr, E.A.R., dos Reis Castro, F.M., de Paula, M.J. and Pezzuti, J.C.B. (2022). Assessing the contribution of local experts in monitoring Neotropical vertebrates with camera traps, linear transects and track and sign surveys in the Amazon. *Perspectives in Ecology and Conservation*, 20(4), 303-313.
- Pretorius, M. (2019). *Mesocarnivores in Protected Areas: ecological and anthropogenic determinants of habitat use in northern Kwa-Zulu Natal, South Africa* [Master's Dissertation University of Cape Town], Cape Town, South Africa. https://open.uct.ac.za/bitstream/handle/11427/31789/thesis_sci_2019_pretorius_michelle.pdf?sequence=1
- Primack, R.B. (2014). *Essentials of Conservation Biology*, 6th ed. Sinauer Associates, Inc.
- Prugh, L. R. and Golden, C. D. (2014). Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology*, 83(2), 504-514.
- QGIS [Computer software]. (2024). Retrieved March 15, 2020, from <http://qgis.org>
- R Core Team (2023). *R: A Language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. (Version 4.3) [Computer software]. Retrieved June 11, 2023, from <https://cran.r-project.org>.
- Rain, R. (2020). Retrieved January 31, 2024, from <https://www.omnicalculator.com/ecology/shannon-index>
- Ramesh, T. and Downs, C.T. (2013). Impact of farmland use on population density and activity patterns of serval in South Africa. *Journal of Mammalogy*, 94(6), 1460-1470.
- Ramnanan, R., Thorn, M., Tambling, C. J. and Somers, M. J. (2016). Resource partitioning between black-backed jackal and brown hyaena in Waterberg Biosphere Reserve, South Africa. *Canid Biology and Conservation*, 19, 8-13.

- Randler, C., Katzmaier, T., Kalb, J., Kalb, N. and Gottschalk, T.K. (2020). Baiting/luring improves detection probability and species identification—a case study of mustelids with camera traps. *Animals*, 10(11), 2178.
- Ray, J. C., Hunter, L. and Zigouris, J. (2005). *Setting conservation and research priorities for larger african carnivores*. WCS Working Paper (Vol. 24). New York, U.S.A.: Wildlife Conservation Society.
- Reasoner, E., Marker, L., Verschueren, S., Briers-Louw, W.D., Mbidzo, M. and Cristescu, B. (2024). Relative abundance of a mesocarnivore in a human-dominated, semi-arid rangeland in Namibia. *Frontiers in Ecology and Evolution*, 12, 1333162.
- Redondo-Gómez, D., Rossi, L., Cardello, M., De Pasquale, S., Martínez-Carrasco, C., Sánchez-Zapata, J. A. and Moleón, M. (2023). Top-predator carrion is scary: Fight-and-flight responses of wild boars to wolf carcasses. *Ecology and Evolution*, 13(4), Article e9911.
- Reid, N., Lundy, M.G., Hayden, B., Lynn, D., Marnell, F., McDonald, R.A. and Montgomery, W.I. (2013). Detecting detectability: identifying and correcting bias in binary wildlife surveys demonstrates their potential impact on conservation assessments. *European Journal of Wildlife Research*, 59, 869-879.
- Reyneke, S.E.B. (2023). *The relationship between wildlife and livestock associated with aardvark (Orycteropus afer) burrows in pasturelands* [Doctoral Dissertation, University of Pretoria]. Pretoria, South Africa. <https://repository.up.ac.za/bitstreams/69259102-15cc-4f5f-a424-91f344aa51da/download>
- Rich, L.N., Davis, C.L., Farris, Z.J., Miller, D.A., Tucker, J.M., Hamel, S., Farhadinia, M.S., Steenweg, R., Di Bitetti, M.S., Thapa, K. and Kane, M.D. (2017a). Assessing global patterns in mammalian carnivore occupancy and richness by integrating local camera trap surveys. *Global Ecology and Biogeography*, 26(8), 918-929.
- Rich, L.N., Miller, D.A., Robinson, H.S., McNutt, J.W. and Kelly, M.J. (2016). Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. *Journal of Applied Ecology*, 53(4), 1225-1235.
- Rich, L., Weldon McNutt, J., Nthomiwa, M., Torrents-Ticó, M., Mothala, M., Motsamai, G. and Jordan, N.R. (2017b). On the right track? Comparing concurrent spoor and camera-trap surveys in Botswana. *African Journal of Wildlife Research*, 47(2), 128-137.

- Rich, L.N., Winterbach, C.W., Maude, G., Klein, R., Mahupeleng, G.N., Boast, L. and Somers, M.J. (2017c). Conservation implications of brown hyaena (*Parahyaena brunnea*) population densities and distribution across landscapes in Botswana. *Koedoe: African Protected Area Conservation and Science*, 59(2), 1-16.
- Rich, L.N., Miller, D.A., Muñoz, D.J., Robinson, H.S., McNutt, J.W. and Kelly, M.J. (2019). Sampling design and analytical advances allow for simultaneous density estimation of seven sympatric carnivore species from camera trap data. *Biological Conservation*, 233, 12-20.
- Riley, S. (2019). The changing legal status of cats in Australia: from friend of the settlers, to enemy of the rabbit, and now a threat to biodiversity and biosecurity risk. *Frontiers in Veterinary Science*, 5, 342.
- Ripple, W. J., Larsen, E. J., Renkin, R. A. and Smith, D. W. (2001). Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation*, 102(3), 227-234.
- Risch, D.R., Ringma, J., Honarvar, S. and Price, M.R. (2020). A comparison of abundance and distribution model outputs using camera traps and sign surveys for feral pigs. *Pacific Conservation Biology*, 27(2), 186-194.
- Ritchie, E.G. and Johnson, C.N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12(9), 982-998.
- Ritchie, E. G., Elmhagen, B., Glen, A. S., Letnic, M., Ludwig, G. and McDonald, R. A. (2012). Ecosystem restoration with teeth: what role for predators? *Trends in Ecology and Evolution*, 27(5), 265-271.
- Roberts, N.J. (2011). Investigation into survey techniques of large mammals: surveyor competence and camera-trapping vs. transect-sampling. *Bioscience Horizons*, 4(1), 40-49.
- Roberts, P.D., Somers, M.J., White, R.M. and Nel, J.A. (2007). Diet of the South African large-spotted genet *Genetta tigrina* (Carnivora, Viverridae) in a coastal dune forest. *Acta Theriologica*, 52, 45-53.
- Robinson, Q.H., Bustos, D. and Roemer, G.W. (2014). The application of occupancy modeling to evaluate intraguild predation in a model carnivore system. *Ecology*, 95(11), 3112-3123.

- Romañach, S. S., Lindsey, P. A. and Woodroffe, R. (2011). Attitudes toward predators and options for their conservation in the Ewaso Ecosystem. In *Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem*. Washington DC: Smithsonian Institution Scholarly Press. *Smithsonian Contributions to Zoology*. 85-93. Retrieved August 1, 2019, from <http://dx.doi.org/10.5479/si.00810282.632.85>.
- Rota, C.T., Ferreira, M.A., Kays, R.W., Forrester, T.D., Kalies, E.L., McShea, W.J., Parsons, A.W. and Millsaugh, J.J. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, 7(10), 1164-1173.
- Rouse, S., Behnoud, P., Hobeali, K., Moghadas, P., Salahshour, Z., Eslahi, H., Ommatmohammadi, M., Khani, A., Shabani, A., Macdonald, D.W. and Farhadinia, M.S. (2021). Intraspecific interactions in a high-density leopard population. *Ecology and Evolution*, 11(23), 16572-16584.
- Roux, R. (2017). *Spatio-temporal ecology of the rusty-spotted genet, Genetta maculata, in Telperion Nature Reserve (Mpumalanga, South Africa)*. [Masters' Thesis, Departmental of Environmental Sciences, University of South Africa]. Pretoria, South Africa. ProQuest Dissertations and Theses Global.
- Rovero, F., Zimmermann, F., Berzi, D. and Meek, P. (2013). " Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix*, 24, 148-156.
- Rovero, F., Martin, E., Rosa, M., Ahumada, J.A. and Spitale, D. (2014). Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. *PloS one*, 9(7), Article e103300.
- Rowcliffe, J. M., Field, J., Turvey, S. T. and Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 45(4), 1228-1236.
- Rowe-Rowe, D.T. (2019). Does the African (cape) clawless otter eat mammals?. *IUCN Otter Spec. Group Bull*, 36(1), 3-6.
- Royle, J. A. and Nichols, J. D. (2003). Estimating abundance from repeated presence-absence data or point counts. *Ecology*, 84(3), 777-790.

- Ruxton, G. D. and Houston, D. C. (2004). Obligate vertebrate scavengers must be large soaring fliers. *Journal of Theoretical Biology*, 228(3), 431-436.
- Ryan-Schofield, N. L., Read, J. L., McGregor, H. W., McWhorter, T. J. and Moseby, K. E. (2024). Evasive invasives? Implications of neophobia for feral cat (*Felis catus*) control. *Wildlife Society Bulletin*, 48(3), Article e1536.
- SABAP 2 (2023a). Southern African Bird Atlasing Project 2. Cape Vulture Distribution Map. Retrieved May 23, 2023, from <https://sabap2.birdmap.africa/species/106>
- SABAP 2 (2023b). Southern African Bird Atlasing Project 2. Lappetfaced Vulture Distribution Map. Retrieved May 23, 2023, from <https://sabap2.birdmap.africa/species/108>
- SABAP 2 (2023c). Southern African Bird Atlasing Project 2. White-backed Vulture Distribution Map. Retrieved May 23, 2023, from <https://sabap2.birdmap.africa/species/107>
- SABAP 2 (2023d). Southern African Bird Atlasing Project 2. Hooded Vulture Distribution Map. Retrieved May 23, 2023, from <https://sabap2.birdmap.africa/species/110>
- SABAP 2 (2023e). Southern African Bird Atlasing Project 2. Whiteheaded Vulture Distribution Map. Retrieved May 23, 2023, from <https://sabap2.birdmap.africa/species/109>
- Samson, A. and Ramakrishnan, B. (2017). Scavenging mode of vertebrate scavengers on domestic buffalos *Bubalus bubalis* (Linnaeus, 1785) killed by tiger *Panthera tigris* and natural deaths in southern India. *Podoces*, 12(1), 22-26
- SANBI (2006). South African Biodiversity Institute. Biomes of Southern Africa [vector geospatial dataset] 2006. Available from the Biodiversity GIS website Retrieved July 5, 2023, from <https://bgis.sanbi.org/SpatialDataset/Detail/329>
- SANBI (2018). South African Biodiversity Institute. Final Vegetation Map of South Africa, Lesotho and Swaziland [Vector] Available from the Biodiversity GIS website. Retrieved July 5, 2023, from <https://bgis.sanbi.org/SpatialDataset/Detail/1674>
- Santangeli, A., Lambertucci, S. A., Margalida, A., Carucci, T., Botha, A., Whitehouse-Tedd, K. and Cancellario, T. (2024). The global contribution of vultures towards ecosystem services and sustainability—an experts’ perspective. *IScience* 27(6), Article e109925.

- Satterfield, L. C., Thompson, J. J., Snyman, A., Candelario, L., Rode, B. and Carroll, J. P. (2017). Estimating occurrence and detectability of a carnivore community in eastern Botswana using baited camera traps. *African Journal of Wildlife Research*, 47(1), 32-46.
- Schaller, G. (1972). *The Serengeti Lion: A study of predator-prey relations*. University of Chicago Press.
- Scheiner, S. M. and Gurevitch, J. (Eds.). (2001). *Design and analysis of ecological experiments*. Oxford University Press.
- Sebastián-González, E., Moleón, M., Gibert, J.P., Botella, F., Mateo-Tomás, P., Olea, P.P., Guimaraes Jr, P.R. and Sánchez-Zapata, J.A. (2016). Nested species-rich networks of scavenging vertebrates support high levels of interspecific competition. *Ecology*, 97(1), 95-105.
- Sebastián-González, E., Morant, J., Moleón, M., Redondo-Gómez, D., Morales-Reyes, Z., Pascual-Rico, R., Pérez-García, J.M. and Arrondo, E. (2023). The underestimated role of carrion in vertebrates' diet studies. *Global Ecology and Biogeography*, 32(8), 1302-1310.
- Seidlitz, A., Bryant, K.A., Armstrong, N.J., Calver, M.C. and Wayne, A.F. (2021). Sign surveys can be more efficient and cost effective than driven transects and camera trapping: a comparison of detection methods for a small elusive mammal, the numbat (*Myrmecobius fasciatus*). *Wildlife Research*, 46, 491-500.
- Selva, N. and Fortuna, M. A. (2007). The nested structure of a scavenger community. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1613), 1101-1108.
- Selva, N., Jedrzejewska, B., Jedrzejewski, W. and Wajrak, A. (2003). Scavenging on European bison carcasses in Białowieża primeval forest (eastern Poland). *Ecoscience*, 10(3), 303-311.
- Selva, N., Jędrzejewska, B., Jędrzejewski, W. and Wajrak, A. (2005). Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology*, 83(12), 1590-1601.
- Selva, N., Moleón, M., Sebastián-González, E., DeVault, T.L., Quaggiotto, M.M., Bailey, D.M., Lambertucci, S.A. and Margalida, A. (2019). Vertebrate scavenging communities. *Carrion Ecology and Management*, 71-99.
- Shannon, C.E. (1948). A mathematical theory of communication. *The Bell System Technical Journal*, 27(3), 379-423.

- Shapiro, S.S. and Wilk, M.B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, 52(3-4), 591-611.
- Shaw, J.M. and Ryan, P.G. (2015). Winter scavenging rates under power lines in the Karoo, South Africa. *African Journal of Wildlife Research*, 45(1), 122-126.
- Sikes, R.S. and Animal Care and Use Committee of the American Society of Mammalogists, (2016). Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97(3), 663-688.
- Silveira, L., Jácomo, A.T. and Diniz-Filho, J.A.F. (2003). Camera trap, line transect census and track surveys: a comparative evaluation. *Biological Conservation*, 114(3), 351-355.
- Silver, S. C., Ostro, L. E., Marsh, L. K., Maffei, L., Noss, A. J., Kelly, M. J., Wallace, R. B., Gomez, H. and Ayala, G. (2004). The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx*, 38(2), 148-154.
- Simpson, E.H. (1949). Measurement of diversity. *nature*, 163(4148), 688-688.
- Sinclair, A. R. E., Metzger, K., Brashares, J. S., Nkwabi, A., Sharam, G. and Fryxell, J. M. (2010). Trophic cascades in African savanna: Serengeti as a case study. In Terborgh, J., and Estes, J. A. (Eds.), *Trophic cascades: predators, prey and the changing dynamics of nature* (pp. 255-274). Island Press.
- Skinner, J. D. and Chimimba, C. T. (2005). *The Mammals of the Southern African Sub-region*. Cambridge University Press.
- Smith, A. F., Ciuti, S., Shamovich, D., Fenchuk, V., Zimmermann, B. and Heurich, M. (2022). Quiet islands in a world of fear: Wolves seek core zones of protected areas to escape human disturbance. *Biological Conservation*, 276, 109811.
- Smith, E. P. (2002). BACI Design. In El-Shaarawi, A. H. and Piegorsch, W. W. (Ed.) *Encyclopedia of Environmetrics* (pp. 141 – 148). John Wiley and Sons Ltd.
- Smith, J. B., Laatsch, L. J. and Beasley, J. C. (2017). Spatial complexity of carcass location influences vertebrate scavenger efficiency and species composition. *Scientific Reports*, 7(1), 10250.

- Sonawane, C., Xu, M., Ward, N., Chichilnisky du Lac, A., Kamets, B. and Dirzo, R. (2025). Global decline of apex scavengers threatens human health. *Proceedings of the National Academy of Sciences*, 122(25), Article e2417328122.
- Sorensen, A., van Beest, F. M. and Brooke, R. K. (2014). Impacts of wildlife baiting and supplemental feeding on infectious disease transmission risk: A synthesis of knowledge. *Preventive Veterinary Medicine*, 113, 356-363.
- South African Bureau of Standards, (2021). *The care and use of animals for scientific purposes*. South African Bureau of Standards.
- Spearman, C. (1987). The proof and measurement of association between two things. *The American Journal of Psychology*, 100(3/4), 441-471.
- Ståhlberg, S. and Apollonio, M. (2023). Scavenger activity and anti-predator behaviour in an Apennine wolf area. *Sustainability*, 15(14), 11056.
- Stander, P. E. (1998). Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. *Journal of Applied Ecology*, 35(3), 378-385.
- Steinbeiser, C. M., Wawrzynowski, C. A., Ramos, X. and Olson, Z. H. (2017). Scavenging and the ecology of fear: do animal carcasses create islands of risk on the landscape? *Canadian Journal of Zoology*, 96(3), 229-236.
- Strampelli, P., Andresen, L., Everatt, K.T., Somers, M.J. and Rowcliffe, J.M. (2018). Habitat use responses of the African leopard in a human-disturbed region of rural Mozambique. *Mammalian Biology*, 89, 14-20.
- Stuart, C. and Stuart, T. (2013). *A field guide to the tracks and signs of Southern and East African wildlife*. Struick Nature.
- Sutherland, W. J. (1998). The importance of behavioural studies in conservation biology. *Animal Behaviour*, 56(4), 801-809.
- Swanepoel, B.A. (2007). *Vegetation ecology of Ezemvelo Nature Reserve, Bronkhorstspuit, South Africa* [Doctoral dissertation, University of Pretoria]. Pretoria, South Africa. <https://repository.up.ac.za/bitstream/handle/2263/27935/dissertation.pdf?sequence=1>

- Swanepoel, L., Camacho G., Power, J., Amiard, P., Child, M. and Do Linh San, E. *Civetticus civetta* (2016). In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, (Eds.). The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Swanson, A., Arnold, T., Kosmala, M., Forester, J. and Packer, C. (2016). In the absence of a “landscape of fear”: How lions, hyenas, and cheetahs coexist. *Ecology and Evolution*, 6(23), 8534-8545.
- Swengel, A. B. (2001). A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity and Conservation*, 10(7), 1141-1169.
- Sytsma, M. L., Lewis, T., Gardner, B. and Prugh, L. R. (2022). Low levels of outdoor recreation alter wildlife behaviour. *People and Nature*, 4(6), 1547-1559.
- Tagg, N., McCarthy, M., Dieguez, P., Bocksberger, G., Willie, J., Mundry, R., Stewart, F., Arandjelovic, M., Widness, J., Landsmann, A. and Agbor, A. (2018). Nocturnal activity in wild chimpanzees (*Pan troglodytes*): Evidence for flexible sleeping patterns and insights into human evolution. *American Journal of Physical Anthropology*, 166(3), 510-529.
- Tambling, C.J., Avenant, N.L., Drouilly, M. and Melville, H.I.A.S. (2018). The role of mesopredators in ecosystems: potential effects of managing their populations on ecosystem processes and biodiversity. In: *Livestock Predation and its Management in South Africa: A Scientific Assessment*, 205-277. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, South Africa.
- Tanwar, K.S., Sadhu, A. and Jhala, Y.V. (2021). Camera trap placement for evaluating species richness, abundance, and activity. *Scientific Reports*, 11(1), 23050.
- Tay, R. (2017). Correlation, variance inflation and multicollinearity in regression model. *Journal of the Eastern Asia Society for Transportation Studies*, 12, 2006-2015.
- Taylor, M. (2015). Verreaux's Eagle in Taylor, M.R. Peakock, F. Wanless, R.W. (Eds). *The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland*. BirdLife South Africa, Johannesburg.
- Taylor, P., Swan, M., Sitters, H., Smith, A. and Di Stefano, J. (2023). Small mammals reduce activity during high moon illumination under risk of predation by introduced predators. *Scientific Reports*, 13(1), 10532.

- Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Niemann, S. M. and Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, 92(2), 398-407.
- Thapa, K., Malla, S., Subba, S.A., Thapa, G.J., Lamichhane, B.R., Subedi, N., Dhakal, M., Acharya, K.P., Thapa, M.K., Neupane, P. and Poudel, S. (2021). On the tiger trails: Leopard occupancy decline and leopard interaction with tigers in the forested habitat across the Terai Arc Landscape of Nepal. *Global Ecology and Conservation*, 25, Article e01412.
- Thapa, K., Shrestha, R., Karki, J., Thapa, G.J., Subedi, N., Pradhan, N.M.B., Dhakal, M., Khanal, P. and Kelly, M.J. (2014). Leopard *Panthera pardus fusca* density in the seasonally dry, subtropical forest in the Bhabhar of Terai Arc, Nepal. *Advances in Ecology*. Retrieved August 5, 2019 from: <http://dx.doi.org/10.1155/2014/286949>
- The Jamovi Project (2023). *jamovi*. (Version 2.3) [Computer Software]. Retrieved March 5, 2023, from <https://www.jamovi.org>
- Thiel, C. (2011). *Ecology and population status of the Serval Leptailurus serval (Schreber, 1776) in Zambia* [Doctoral dissertation, Universitäts-und Landesbibliothek] Bonn, Germany. https://www.researchgate.net/profile/Christine-Thiel-Bender/publication/314838829_Ecology_and_population_status_of_the_Serval_Leptailurus_serval_SCHREBER_1776_in_Zambia/links/58c6671845851538eb8e0dd7/Ecology-and-population-status-of-the-Serval-Leptailurus-serval-SCHREBER-1776-in-Zambia.pdf
- Thompson, G.G. and Withers, P.C. (2003). Effect of species richness and relative abundance on the shape of the species accumulation curve. *Austral Ecology*, 28(4), 355-360.
- Thompson, G.G., Withers, P.C., Pianka, E.R. and Thompson, S.A. (2003). Assessing biodiversity with species accumulation curves; inventories of small reptiles by pit-trapping in Western Australia. *Austral Ecology*, 28(4), 361-383.
- Thorn, M., Green, M., Bateman, P. W., Cameron, E. Z., Yarnell, R. W. and Scott, D. M. (2010). Comparative efficacy of sign surveys, spotlighting and audio playbacks in a landscape-scale carnivore survey. *South African Journal of Wildlife Research*, 40(1), 77-86.
- Thorn, M., Green, M., Bateman, P. W., Waite, S. and Scott, D. M. (2011). Brown hyaenas on roads: estimating carnivore occupancy and abundance using spatially auto-correlated sign survey replicates. *Biological Conservation*, 144(6), 1799-1807.

- Thorn, M., Scott, D. M., Green, M., Bateman, P. W. and Cameron, E. Z. (2009). Estimating brown hyaena occupancy using baited camera traps. *South African Journal of Wildlife Research*, 39(1), 1-10.
- Tobajas, J., Descalzo, E., Ferreras, P., Mateo, R. and Margalida, A. (2021). Effects on carrion consumption in a mammalian scavenger community when dominant species are excluded. *Mammalian Biology*, 101(6), 851-859.
- Torrents-Ticó, M, Rich, L., McNutt, J. W., Nthomiwa, M., Mothala, M., Motsamai, G. and Jordan, N. R. (2017). On the right track? Comparing concurrent spoor and camera-trap surveys in Botswana. *South African Journal of Wildlife Research*, 47(2), 128-137.
- Torres-Romero, E.J., Eppley, T.M., Ripple, W.J., Newsome, T.M., Krofel, M., Carter, N.H., Ordiz, A., de Oliveira, T.G., Selva, N. and Penteriani, V. (2025). Global scale assessment of the human-induced extinction crisis of terrestrial carnivores. *Science advances*, 11(29), eadq2853.
- Tossens, S., Drouilly, M., Lhoest, S., Vermeulen, C. and Doucet, J.L. (2025). Wild felids in trophic cascades: a global review. *Mammal Review*, 55(1), Article e12358.
- Travaini, A., Vassallo, A. I., García, G. O., Echeverría, A. I., Zapata, S. C. and Nielsen, S. (2013). Evaluation of neophobia and its potential impact upon predator control techniques: A study on two sympatric foxes in southern Patagonia. *Behavioural Processes*, 92, 79-87.
- Trenberth, K. E. (1983). What are the seasons? *Bulletin of the American Meteorological Society*, 64(11), 1276-1282.
- Trolle, M. and Kéry, M. (2003). Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. *Journal of Mammalogy*, 84(2), 607-614.
- Turell, M. J. and Knudson, G. B. (1987). Mechanical transmission of *Bacillus anthracis* by stable flies (*Stomoxys calcitrans*) and mosquitoes (*Aedes aegypti* and *Aedes taeniorhynchus*). *Infection and immunity*, 55(8), 1859-1861.
- Tylianakis, J. M., Didham, R. K., Bascompte, J. and Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11(12), 1351 – 1363.
- Van den Heever, A., Mhlongo, R. and Benadie, K. (2017). *Tracker Manual*. Penguin Random House.

- Van Der Merwe, I., Tambling, C.J., Thorn, M., Scott, D.M., Yarnell, R.W., Green, M., Cameron, E.Z. and Bateman, P.W. (2009). An assessment of diet overlap of two mesocarnivores in the North West Province, South Africa. *African Zoology*, 44(2), 288-291.
- Van der Weyde, L.K., Mbisana, C. and Klein, R. (2018). Multi-species occupancy modelling of a carnivore guild in wildlife management areas in the Kalahari. *Biological Conservation*, 220, 21-28.
- Van Dyke, F.G., Brocke, R.H. and Shaw, H.G. (1986). Use of road track counts as indices of mountain lion presence. *Journal of Wildlife Management*, 50, 102-109.
- Vélez, J., McShea, W., Shamon, H., Castiblanco-Camacho, P.J., Tabak, M.A., Chalmers, C., Fergus, P. and Fieberg, J. (2023). An evaluation of platforms for processing camera-trap data using artificial intelligence. *Methods in Ecology and Evolution*, 14(2), 459-477.
- Verschueren, S., Hofmann, T., Briers-Louw, W.D., Kakove, M., Leirs, H., Bauer, H., Marker, L. and Cristescu, B. (2024). A diminished large carnivore guild with contrasting species-habitat associations persists outside national parks in Namibia's central-eastern landscape. *Biological Conservation*, 297, 110741.
- Vinitpornsawan, S. and Fuller, T. K. (2020). Spatio-temporal correlations of large predators and their prey in western Thailand. *Raffles Bulletin of Zoology*. 68, 118–131.
- Virgós, E. (2001). Relative value of riparian woodlands in landscapes with different forest cover for medium-sized Iberian carnivores. *Biodiversity and Conservation*, 10, 1039-1049.
- Walkden, N. (2019). *Attitudes Toward Vertebrate Scavengers in South Africa's North-West and Gauteng Provinces* [Doctoral dissertation, University of Brighton]. Brighton, United Kingdom. https://cris.brighton.ac.uk/ws/portalfiles/portal/10401126/Attitudes_towards_vertebrate_scavengers_in_South_Africa_s_North_West_and_Gauteng_provinces_August_2019_.pdf
- Walker, M. A., Uribasterra, M., Asher, V., Getz, W. M., Ryan, S. J. and Ponciano, J. M. (2021). *Factors influencing scavenger guilds and scavenging efficiency in southwestern Montana*. *Scientific Reports*, 11 (1): 4254.
- Wand, M. P. and Jones, M. C. (1994). *Kernel smoothing*. CRC press.

- Wang, J., Laguardia, A., Damerell, P.J., Riordan, P. and Shi, K. (2014). Dietary overlap of snow leopard and other carnivores in the Pamirs of Northwestern China. *Chinese Science Bulletin*, 59, 3162-3168.
- Wearn, O. R. and Glover-Kapfer, P. (2019). Snap happy: camera traps are an effective sampling tool when compared with alternative methods. *Royal Society Open Science*, 6(3), 181748.
- Webster, A. (2016). *Zooming in on mesocarnivores*. Africa Geographic. Retrieved June 12, 2019, from <https://africageographic.com/blog/zooming-in-on-mesocarnivores/>
- Webster, A.B., Pretorius, M.E. and Somers, M.J. (2021). The determinants of mesocarnivore activity patterns in highveld grassland and riparian habitats. *African Journal of Wildlife Research*, 51(1), 178-192.
- Wegge, P., Pokheral, C.P. and Jnawali, S.R. (2004). August. Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. In *Animal Conservation Forum*, 7(3), 251-256. Cambridge University Press.
- Węglarczyk, S. (2018). Kernel density estimation and its application. *ITM web of conferences* 23, 00037. EDP Sciences.
- Welch, R.J., Comley, J., Kok, A.D., Taylor, J.M. and Parker, D.M. (2022). Who's afraid of the big, bad predator? Contrasting effects of apex predator presence on the behaviour of a mesopredator. *Wildlife Research*, 50(3), 169-181.
- Wilkins, C. (2021). *Ecology of black-backed jackal (Canis mesomelas) in a small urban estate* [Masters' Thesis, University of the Witwatersrand]. Johannesburg, South Africa. <https://wiredspace.wits.ac.za/server/api/core/bitstreams/4e3a98bf-359d-4ef1b8f5-43341bb63c23/content>
- Willems, E. P. and Hill, R. A. (2009). Predator-specific landscapes of fear and resource distribution: effects on spatial range use. *Ecology*, 90(2), 546-555.
- Williams, K.S., Williams, S.T., Fitzgerald, L.E., Sheppard, E.C. and Hill, R.A. (2018). Brown hyaena and leopard diets on private land in the Soutpansberg Mountains, South Africa. *African Journal of Ecology*, 56(4), 1021-1027.

- Williams, S.T., Williams, K.S., Lewis, B.P. and Hill, R.A. (2017). Population dynamics and threats to an apex predator outside protected areas: implications for carnivore management. *Royal Society Open Science*, 4(4), 161090.
- Wilmers, C. C., Levi, T., Prugh, L. R., Ruprecht, J. and Stahler, D. R. (2025). The Ecological Impacts of Large-Carnivore Recovery in North America. *Annual Review of Ecology, Evolution, and Systematics*, 56(1), 337-363
- Wilmers, C. C., Stahler, D. R., Crabtree, R. L., Smith, D. W. and Getz, W.M. (2003). Resource dispersion and consumer dominance: scavenging at wolf - and hunter – killed carcasses in Greater Yellowstone, USA. *Ecology Letters*, 6, 996-1003.
- Wilsey, B. J. (1996). Variation in use of green flushes following burns among African ungulate species: the importance of body size. *African Journal of Ecology*, 34(1), 32-38.
- Wilson, E. E. and Wolkovich, E. M. (2011). Scavenging: how carnivores and carrion structure communities. *Trends in Ecology and Evolution*, 26(3), 129-135.
- Wilson, G. J. and Delahay, R. J. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research*, 28(2), 151-164.
- Woodroffe, R., and Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, 280(5372), 2126-2128.
- Wooster, E. I., Ramp, D., Lundgren, E. J., O'Neill, A. J., Yanco, E., Bonsen, G. T. and Wallach, A. D. (2022). Predator protection dampens the landscape of fear. *Oikos*, 2022(11), Article e09059.
- Yarnell, R. W., Phipps, W. L., Burgess, L. P., Ellis, J. A., Harrison, S. W., Dell, S., MacTavish, D., MacTavish, L.M. and Scott, D. M. (2013). The influence of large predators on the feeding ecology of two African mesocarnivores: the black-backed jackal and the brown hyaena. *South African Journal of Wildlife Research*, 43(2), 155-166.
- Young, J. K., Golla, J., Draper, J. P., Broman, D., Blankenship, T. and Heilbrun, R. (2019). Space use and movement of urban bobcats. *Animals*, 9(5), 275.
- Zanette, L. Y., Frizzelle, N. R., Clinchy, M., Peel, M. J., Keller, C. B., Huebner, S. E. and Packer, C. (2023). Fear of the human “super predator” pervades the South African savanna. *Current Biology*, 33(21), 4689-4696.

Zemouche, J.A.O. (2018). *Trophic ecology of rusty-spotted genet Genetta maculata and slender mongoose Herpestes sanguineus in Telperion Nature Reserve, with a focus on dietary segregation as a possible mechanism of coexistence* [Master's Thesis, University of the Witwatersrand]. Johannesburg, South Africa. ProQuest Dissertations and Theses Global.

APPENDIX

Appendix 1: Carcass mass and shoulder heights of the 10 Blue Wildebeest (*Connochaetes taurinus*) carcasses used in my study on the influence of decomposing blue wildebeest carcasses on predators on Telperion Nature Reserve from January 2019 to February 2020.

Site Number	Carcass mass (Kg)	Shoulder Height (m)
1	225	1.3
3	208.8	1.4
4	240	1.2
6	220.6	1.2
8	247.4	1.3
9	224.2	1.3
11	212.6	1.2
12	216.6	1.3
13	214	1.2
15	222.8	1.3
Mean	223.2	1.3
Std. Dev	12.1	0.07

Appendix 2: The number of transects with tracks for each species, number of camera trap images of each species, mean mass of each species in kilograms and mean home range size of each species in km² during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to February 2020.

Species		Number of transects with tracks	Number of Cam Trap Images	Mean* Mass (kg)	Mean* Home Range (km ²)
1 Aardwolf	<i>Proteles cristatus</i>	33	12	7.5	3.5
2 Brown Hyaena	<i>Parahyaena brunnea</i>	40	20	44.5	50
3 Black-backed Jackal	<i>Lupulella mesomelas</i>	255	734	7.8	1
4 Black-footed Cat	<i>Felis nigripes</i>	2	0	1.6	12.35
5 Cape Clawless Otter	<i>Aonyx capensis</i>	4	0	14	29.5
6 Cape Fox	<i>Vulpes chama</i>	0	1	2.7	16.5
7 Caracal	<i>Caracal caracal</i>	12	1	12	25.2
8 Civet	<i>Civettictis Civetta</i>	3	0	11.3	11.1
9 Honey Badger	<i>Mellivora capensis</i>	11	1	12	54
10 Leopard	<i>Panthera pardus</i>	31	3	46	56
11 Mongoose Slender	<i>Galerella sanguinea</i>	65	12	0.5	0.6
12 Mongoose Water	<i>Atilax paludinosus</i>	28	1	3.2	1.29
13 Mongoose Yellow	<i>Cynictis penicillata</i>	113	28	0.8	0.7
14 Rusty Spotted Genet	<i>Genetta maculata</i>	59	0	1.9	4.35
15 Serval	<i>Leptailurus serval</i>	29	1	10.4	24.65
16 Striped Polecat	<i>Ictonyx striatus</i>	3	1	1.1	no data
17 Suricate	<i>Suricata suricatta</i>	14	2	0.9	6

* Hunter (2020)

Appendix 3: Global Positioning System (GPS) locations for the start and finish points of each site transect during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to February 2020.

Site	Start/Finish	Latitude	Longitude
Site 1	Start	-25.70	29.05
	Finish	-25.70	29.05
Site 2	Start	-25.71	29.04
	Finish	-25.70	29.05
Site 3	Start	-25.71	29.03
	Finish	-25.71	29.03
Site 4	Start	-25.71	29.03
	Finish	-25.71	29.01
Site 5	Start	-25.71	29.01
	Finish	-25.71	29.01
Site 6	Start	-25.71	29.00
	Finish	-25.71	29.00
Site 7	Start	-25.72	29.00
	Finish	-25.72	29.00
Site 8	Start	-25.73	28.99
	Finish	-25.72	28.99
Site 9	Start	-25.71	28.98
	Finish	-25.71	28.99
Site 10	Start	-25.70	29.00
	Finish	-25.70	29.01
Site 11	Start	-25.69	29.03
	Finish	-25.70	29.03
Site 12	Start	-25.69	29.04
	Finish	25.69	29.04
Site 13	Start	-25.68	29.05
	Finish	-25.69	29.06
Site 14	Start	-25.68	29.03
	Finish	-25.68	29.04
Site 15	Start	-25.68	29.02
	Finish	-25.68	29.03

Appendix 4: The Global positioning System (GPS) locations for the start and finish of the transects in low disturbance areas during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.

Low Disturbance Transects	Start/Finish	Latitude	Longitude
Transects 1 - 4	Start	-25.67	-25.04
	Finish	-25.65	29.03
Transects 5 - 7	Start	-25.67	29.04
	Finish	-25.67	29.04
Transects 8 - 11	Start	-25.67	29.03
	Finish	-25.66	29.02
Transects 12 - 15	Start	-25.66	29.02
	Finish	-25.68	29.01
Transects 16 - 18	Start	-25.71	28.98
	Finish	-25.70	28.98
Transects 19 - 22	Start	-25.66	29.01
	Finish	-25.64	29.01

Appendix 5: The Global Positioning System (GPS) locations of 2 x 2 m quadrats used to count black-backed jackal (*Lupulella mesomelas*) tracks at each study site as well as the distance in metres that the quadrats were away from the camera array at each site during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators.

Site	Latitude	Longitude	Distance from Camera Array (m)
1	-25.70	29.05	72
2	-25.71	29.04	224
3	-25.71	29.03	64
4	-25.71	29.02	56
5	-25.71	29.01	53
6	-25.71	29.00	142
7	-25.72	29.00	125
8	-25.72	28.99	108
9	-25.71	28.99	107
10	-25.70	29.00	99
11	-25.69	29.03	77
12	-25.69	29.04	110
13	-25.68	29.05	145
14	-25.68	29.04	162
15	-25.68	29.03	137

Appendix 6: Outcomes from Shapiro Wilk tests for normality of data before choosing appropriate analyses based on whether data was parametric or non-parametric for all statistical analyses of data collected on Telperion nature Reserve during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.

Section	Shapiro Wilk Test Statistic	p value	Parametric or Non-Parametric	Subsequent Test Used	Test Statistic	p value
5.1.2	W = 0.93	p = 0.392	Parametric	Independent samples	T = 7.07	p < 0.001
5.1.3	W = 0.93	p = 0.06	Parametric	Paired Samples t-test	t = 11.1	p < 0.001
5.1.4	W = 0.55	p < 0.001	Non-Parametric	Kruskal Wallis ANOVA	H = 18.7	p < 0.001
5.2.2	W = 0.96	p = 0.63	Parametric	One Way ANOVA	F = 9.96	p = 0.008
5.2.2	W = 0.913	p = 0.15	Parametric	One Way ANOVA	F = 0.05	p = 0.95
5.2.3	W = 0.93	p = 0.25	Parametric	One Way ANOVA	F = 12.9	p = 0.004
5.2.3	W = 0.805	p = 0.004	Non-Parametric	Kruskal Wallis ANOVA	H = 0.02	p = 0.99
5.3.1	W = 0.964	p = 0.839	Parametric	One Way ANOVA	F = 6.47	p = 0.035
5.3.1	W = 0.921	p = 0.298	Parametric	One Way ANOVA	F = 0.002	p = 0.998
5.3.2	W = 0.95	p = 0.616	Parametric	One Way ANOVA	F = 7.58	p = 0.027
5.3.2	W = 0.848	p = 0.035	Non-Parametric	Kruskal Wallis ANOVA	H = 0.299	p = 0.861
5.4.1a	W = 0.81	p < 0.001	Non-Parametric	Kruskal Wallis ANOVA	H = 31.6	p < 0.001
5.7.1	W = 0.324	p < 0.001	Non-Parametric	Kruskal Wallis ANOVA	H = 8.89	p = 0.012
5.7.1b	W = 0.324	p < 0.001	Non-Parametric	Kruskal Wallis ANOVA	H = 8.27	p = 0.082
5.7.2	W = 0.453	p < 0.001	Non-Parametric	Kruskal Wallis ANOVA	H = 67.5	p < 0.001
5.7.3	W = 0.453	p < 0.001	Non-Parametric	Kruskal Wallis ANOVA	H = 114	p < 0.001
5.7.5	W = 0.488	p < 0.001	Non-Parametric	Kruskal Wallis ANOVA	H = 101	p < 0.001
5.7.6	W = 0.483	p < 0.001	Non-Parametric	Kruskal Wallis ANOVA	H = 143	p < 0.001
5.8	W = 0.872	p < 0.001	Non-Parametric	Kruskal Wallis ANOVA	H = 6.37	p = 0.041
5.9a	W = 0.837	p < 0.001	Non-Parametric	Kruskal Wallis ANOVA	H = 16.6	p < 0.001
5.9b	W = 0.838	p < 0.002	Non-Parametric	Kruskal Wallis ANOVA	H = 73.8	p < 0.001
5.1	W = 0.474	p < 0.001	Non-Parametric	Kruskal Wallis ANOVA	H = 16.4	p < 0.001

Appendix 7: The total number of jackal (*Lupulella mesomelas*) visits (from video and still cameras) per site, treatment type and season for the entire study period during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020 on Telperion Nature Reserve.

Season	Controls					Caged					Open					Total per Season
	Site 2	Site 5	Site 7	Site 10	Site 14	Site 1	Site 4	Site 9	Site 11	Site 13	Site 3	Site 6	Site 8	Site 12	Site 15	
Active Decay	0	1	7	1	22	1	0	28	1	7	5	144	0	40	83	340
Autumn	0	0	1	0	6	0	0	6	0	4	21	13	2	5	15	73
Winter	0	1	0	1	4	0	0	1	0	0	0	27	1	1	8	44
Spring	0	12	4	1	9	0	3	3	3	2	1	31	2	5	9	85
Summer	0	2	1	0	6	0	2	0	0	1	2	43	2	1	1	61
Total per site	0	16	13	3	47	1	5	38	4	14	29	258	7	52	116	603
Total per treatment type	79					62					462					

Appendix 8: The total number of jackal (*Lupulella mesomelas*) visits (video cameras only) per site, treatment type and season during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators for the entire study period from January 2019 to January 2020 on Telperion Nature Reserve.

Season	Controls					Caged					Open					Total per Season
	Site 2	Site 5	Site 7	Site 10	Site 14	Site 1	Site 4	Site 9	Site 11	Site 13	Site 3	Site 6	Site 8	Site 12	Site 15	
Active Decay	0	0	6	0	20	0	0	11	1	3	4	156	0	45	89	335
Autumn	0	0	1	0	0	0	0	6	0	0	0	13	0	3	11	34
Winter	0	1	0	0	0	0	0	1	0	0	0	6	1	0	5	14
Spring	0	4	0	0	9	0	1	2	3	2	1	31	0	6	8	67
Summer	0	2	0	0	6	0	2	0	0	0	2	27	0	0	0	39
Total per site	0	7	7	0	35	0	3	20	4	5	7	233	1	54	113	489
Total per treatment type	49					32					408					

Appendix 9: (a – ff) Photo records of tracks of all species recorded in the sign surveys during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020



a



b

Appendix 9 (a and b): Aardwolf (*Protelus cristatus*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020



c

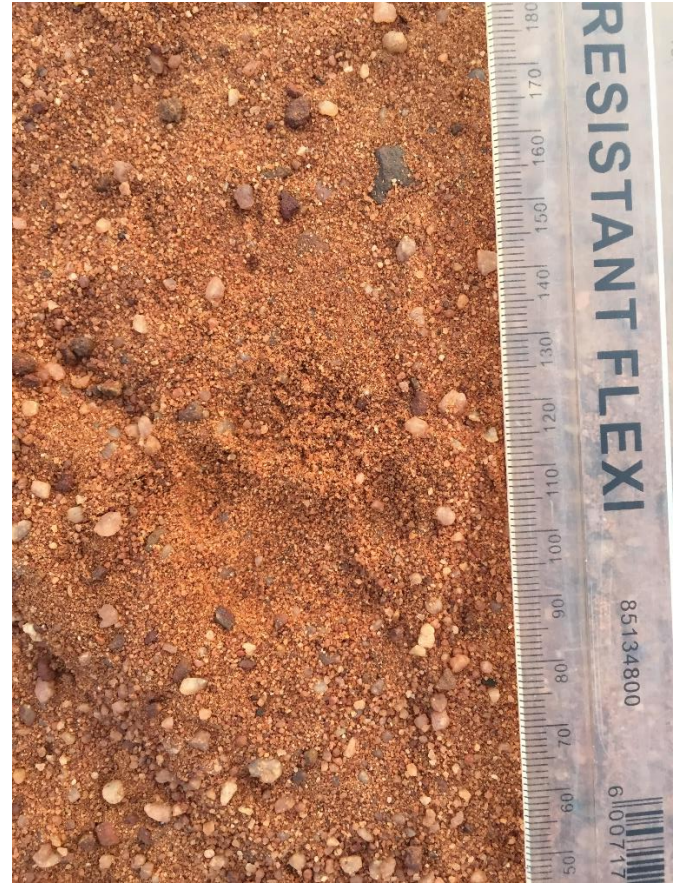


d

Appendix 9 (c and d): Black-backed jackal (*Lupulella mesomelas*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



e



f

Appendix 9 (e and f): Black-footed cat (*Felis nigripes*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



g



h

Appendix 9 (g and h): Brown hyaena (*Parahyaena brunnea*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



i



j

Appendix 9 (i and j): Cape clawless otter (*Aonyx capensis*) scat photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



k



l

Appendix 9 (k and l): Caracal (*Caracal caracal*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



m



n

Appendix 9 (m and n): Civet (*Civettictis civetta*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



o



p

Appendix 9 (o and p): Honey badger (*Mellivora capensis*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



q



r

Appendix 9 (q and r): Leopard (*Panthera pardus*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



s



t

Appendix 9 (s and t): Slender Mongoose (*Galerella sanguinea*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



u



v

Appendix 9 (u and v): Water Mongoose (*Atilax paludinosus*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



W



X

Appendix 9 (w and x): Yellow Mongoose (*Cynictis penicilata*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



y



z

Appendix 9 (y and z): Rusty spotted genet (*Genetta maculata*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



aa



bb

Appendix 9 (aa and bb): Serval (*Leptailurus serval*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



cc



dd

Appendix 9 (cc and dd): Striped polecat (*Ictonyx striatus*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.



ee



ff

Appendix 9 (ee and ff): Suricate (*Suricata suricatta*) tracks photographed on Telperion Nature Reserve during sign surveys undertaken during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.

Appendix 10: (a – m) Photographic evidence of all predator species recorded on camera traps during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 a: Aardwolf (*Proteles cristatus*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 b: Black-backed jackal (*Lupulella mesomelas*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 c: Brown hyaena (*Parahyaena brunnea*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 d: Cape fox (*Vulpes chama*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 e: Caracal (*Caracal caracal*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 f: Honey badger (*Mellivora capensis*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 g: Leopard (*Panthera pardus*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 h: Slender mongoose (*Galerella sanguinea*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 i: Water mongoose (*Atilax paludinosus*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 j: Yellow mongoose (*Cynictis penicillata*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 k: Serval (*Leptailurus serval*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 I: Striped polecat (*Ictonyx striatus*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.



Appendix 10 m: Suricate (*Suricata suricatta*) captured on camera trap during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020.

Appendix 11: Correlation Matrix for the 17 carnivore species recorded during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators, depicting relationships between: transects with tracks of each species, number of camera trap images of each species, mean mass of each species and mean home range sizes of each species on Telperion Nature Reserve from January 2019 to January 2020.

Tracks	Images	Mass	Home Range
0.898 ***	—		
< 0.001	—		
-0.063	-0.042	—	
0.810	0.873	—	
-0.351	-0.243	0.812 ***	—
0.183	0.365	< 0.001	—

Note. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Appendix 12: Total and seasonal records of all species from both sign and camera surveys conducted on Telperion during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.

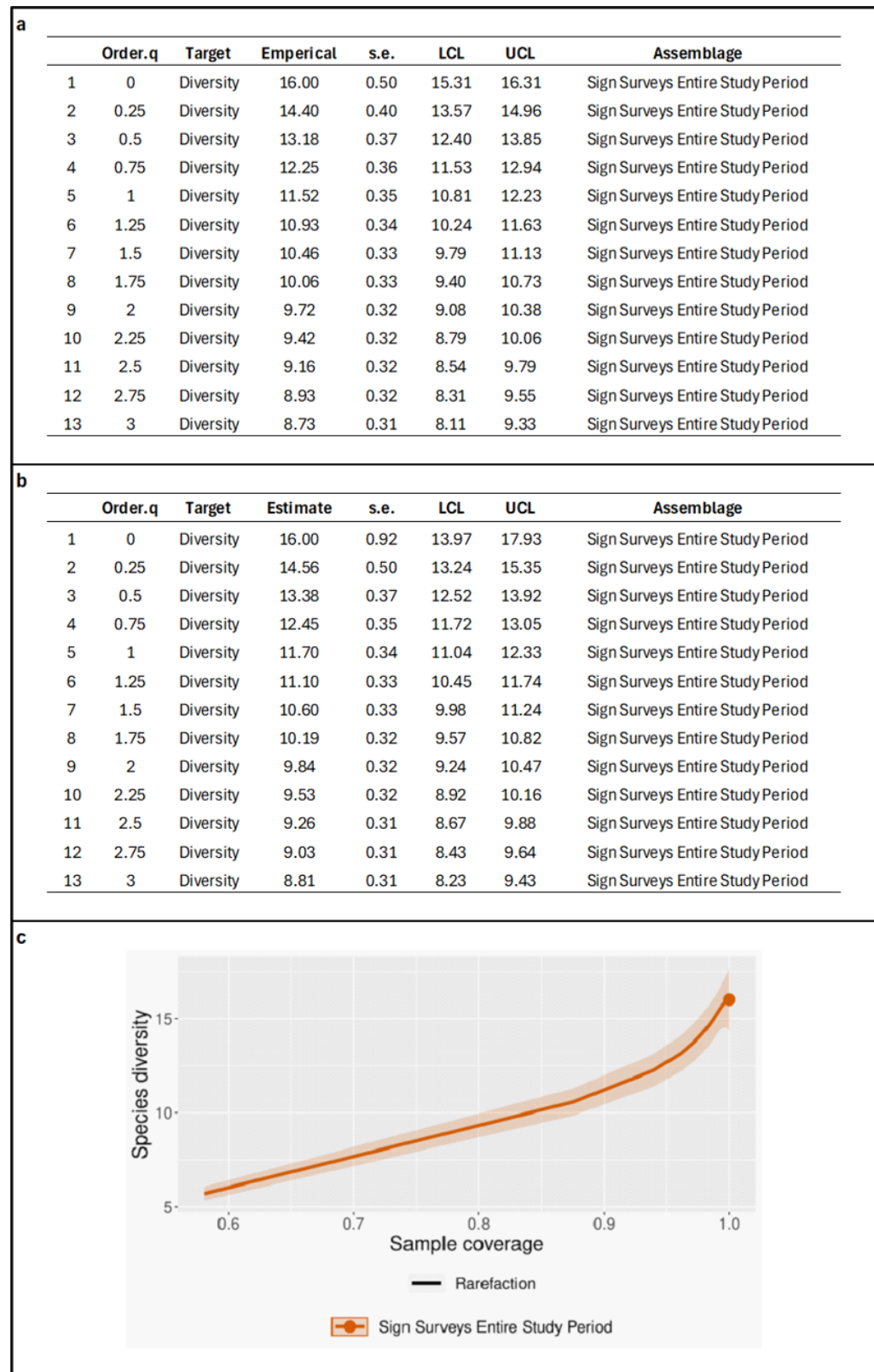
Species Scientific name	Species Common Name	Cameras Sites 1-15 Only	Sign Survey Sites 1-15 Only	Sign Survey Entire Reserve	Pre-sampling Camera	Pre-sampling Sign	Active Decay Camera	Active Decay Sign	Autumn Camera	Autumn Sign	Winter Camera	Winter Sign	Spring Camera	Spring Sign	Summer Camera	Summer Sign
1 <i>Proteles cristatus</i>	Aardwolf	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓		✓
2 <i>Parahyaena brunnea</i>	Brown Hyaena	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓		✓
3 <i>Lupulella mesomelas</i>	Black Backed Jackal	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
4 <i>Felis nigripes</i>	Black Footed Cat		✓	✓		✓		✓								
5 <i>Aonyx capensis</i>	Cape Clawless Otter		✓	✓		✓						✓				✓
6 <i>Vulpes chama</i>	Cape Fox	✓							✓							
7 <i>Caracal caracal</i>	Caracal	✓	✓	✓		✓		✓		✓	✓	✓				✓
8 <i>Civettictis civetta</i>	Civet		✓	✓		✓				✓						✓
9 <i>Mellivora capensis</i>	Honey Badger	✓	✓	✓		✓	✓	✓		✓		✓				✓
10 <i>Panthera pardus</i>	Leopard	✓	✓	✓		✓	✓	✓		✓		✓		✓		✓
11 <i>Galerella sanguinea</i>	Mongoose Slender	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓		✓		✓
12 <i>Atilax paludinosus</i>	Mongoose Water	✓	✓	✓		✓		✓		✓	✓	✓		✓	✓	✓
13 <i>Cynictis penicillata</i>	Mongoose Yellow	✓	✓	✓		✓		✓		✓	✓	✓	✓	✓	✓	✓
14 <i>Genetta maculata</i>	Rusty Spotted Genet		✓	✓		✓		✓		✓	✓	✓	✓	✓		✓
15 <i>Leptailurus serval</i>	Serval	✓	✓			✓		✓		✓		✓	✓	✓		✓
16 <i>Ictonyx striatus</i>	Striped Polecat	✓	✓	✓		✓		✓					✓			✓
17 <i>Suricata suricatta</i>	Suricate	✓	✓	✓		✓		✓		✓	✓	✓	✓	✓		✓
		13	16	16	1	16	6	14	5	13	7	13	7	10	3	15

Appendix 13: Outcomes from Dwass-Steel-Critchlow-Fligner pairwise comparisons of days to detection results of the different survey types conducted on Telperion during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020

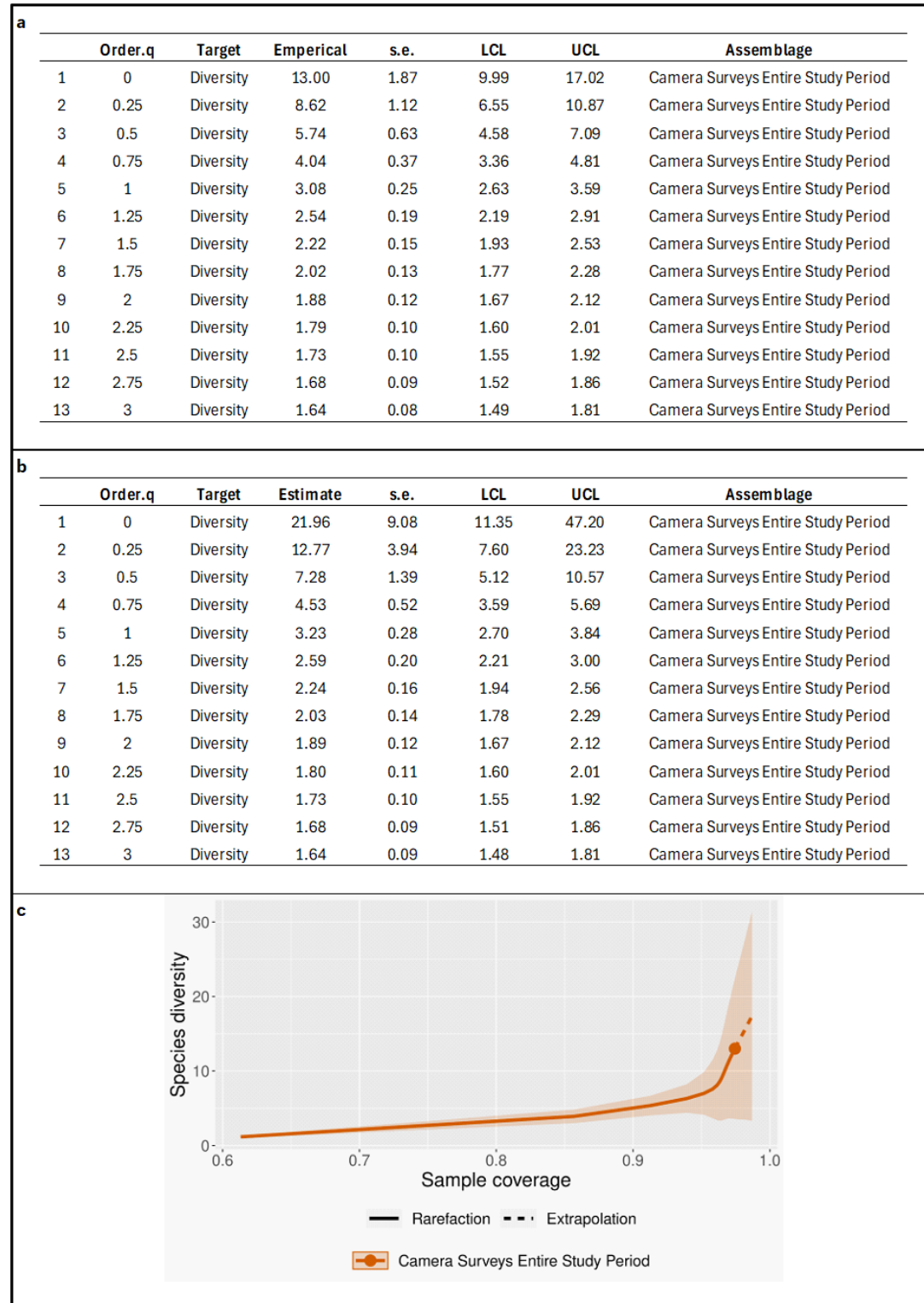
Pairwise comparisons - Days to detection		W	p
Camera Trap	Sign Survey All Transects	-5.353	< 0.001*
Camera Trap	Sign Survey Sites 1 -15	-5.253	< 0.001*
Sign Survey All Transects	Sign Survey Sites 1 -15	-0.307	0.974

Note: * Denotes statistically significant outcomes evaluated at $\alpha = 0.05$

Appendix 14: Asymptotic analysis of rarefaction curves for species accumulation data collected during sign surveys on Telperion Nature Reserve from January 2019 to January 2020. Order.q refers to the mathematical order of Hill numbers with $q = 0$ representing species richness, $q = 1$ representing Shannon Diversity and $q = 2$, representing Simpson Diversity. Empirical refers to observed data collected, Estimate refers to extrapolated data. Comparing Empirical Species Richness to Extrapolated Species Richness ($q = 0$) allows one to determine if an asymptote has been reached and if sampling is sufficient.



Appendix 15: Asymptotic analysis of rarefaction curves for species accumulation data collected during camera surveys on Telperion Nature Reserve from January 2019 to January 2020. Order.q refers to the mathematical order of Hill numbers with $q = 0$ representing species richness, $q = 1$ representing Shannon Diversity and $q = 2$, representing Simpson Diversity. Empirical refers to observed data collected, Estimate refers to extrapolated data. Comparing Empirical Species Richness to Extrapolated Species Richness ($q = 0$) allows one to determine if an asymptote has been reached and if sampling is sufficient.



Appendix 16: Summary of all predator Visits (13 species) to experimental sites from camera trap surveys conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.

	Controls																															
	2						5						7						10						14							
Species	Pre	AD	Aut	Win	Spr	Sum	Pre	AD	Aut	Win	Spr	Sum	Pre	AD	Aut	Win	Spr	Sum	Pre	AD	Aut	Win	Spr	Sum	Pre	AD	Aut	Win	Spr	Sum	Totals	
Aardwolf	0	0	0	0	0	0								0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Brown Hyaena	0	0	0	0	0	0															1					0	0	0	0	0	1	
Black Backed Jackal	0	0	0	0	0	0			1		12	2		7	1			4	1		1		1			4	22	6	4	9	6	
Cape Fox	0	0	0	0	0	0			0	0	0	0		0	1			0	0		0		0	0		0	0	0	0	0	1	
Caracal	0	0	0	1	0	0			0	0	0	0		0	0			0	0		0		0	0		0	0	0	0	0	1	
Honey Badger	0	1	0	0	0	0			0	0	0	0		0	0			0	0		0		0	0		0	0	0	0	0	1	
Leopard	0	0	0	0	0	0			0	0	0	0		0	0			0	0		0		0	0		0	0	0	0	0	0	
Mongoose Slender	0	0	0	0	0	0			0	0	0	0		0	0			0	0		0		0	0		0	0	0	0	0	0	
Mongoose Water	0	0	0	0	0	0			0	0	0	0		0	0			0	0		0		0	0		0	0	0	0	0	0	
Mongoose Yellow	0	0	0	0	0	0			0	0	0	0		0	0			0	0		0		0	0		0	0	0	1	0	1	
Serval	0	0	0	0	0	0			0	0	0	0		0	0			0	0		0		0	0		0	0	0	0	0	0	
Striped Polecat	0	0	0	0	0	0			0	0	0	0		0	0			1	0		0		0	0		0	0	0	0	0	1	
Suricate	0	0	0	0	0	0			0	0	0	0		0	0			0	0		0		0	0		0	0	0	0	0	0	
	Site 3						Site 6						Open Site 8						Site 12						Site 15							
Species	Pre	AD	Aut	Win	Spr	Sum	Pre	AD	Aut	Win	Spr	Sum	Pre	AD	Aut	Win	Spr	Sum	Pre	AD	Aut	Win	Spr	Sum	Pre	AD	Aut	Win	Spr	Sum	Totals	
Aardwolf	0	0	1	0	0	0	0	0	0	1	1	1		0	0	0	0	0			0	0	0	0			0	0	0	0	4	
Brown Hyaena	0	0	0	0	0	0	0	0	0	0	0	0		1	2	0		1	0		0	0	0	0		1	3	1	0	0	9	
Black Backed Jackal	0	5	21	0	1	2	1	144	13	27	31	43		0	2	1	2	2			40	5	1	5	1		83	15	8	9	1	463
Cape Fox	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Caracal	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Honey Badger	0	0	0	0	0	0	0	0	0	0	0	0									0	0	0	0			0	0	0	0	0	
Leopard	0	0	0	0	0	0	0	0	0	0	0	0		1	0	0	0	0			0	0	0	0			0	0	0	0	2	
Mongoose Slender	0	0	0	0	0	0	0	0	0	0	0	0		6	2	4		0			0	0	0	0		0	0	0	0	0	12	
Mongoose Water	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	1			0	0	0	0		0	0	0	0	0	1	
Mongoose Yellow	0	0	0	0	0	0	0	0	0	9	2	7		0	0	0	0	0			0	0	3	0		0	0	0	0	0	21	
Serval	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0			0	0	1	0		0	0	0	0	0	1	
Striped Polecat	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Suricate	0	0	0	0	0	0	0	0	0	1	1	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	2	
	Site 1						Site 4						Caged Site 9						Site 11						Site 13							
Species	Pre	AD	Aut	Win	Spr	Sum	Pre	AD	Aut	Win	Spr	Sum	Pre	AD	Aut	Win	Spr	Sum	Pre	AD	Aut	Win	Spr	Sum	Pre	AD	Aut	Win	Spr	Sum	Totals	
Aardwolf	0	0	0	0	0	0		5	0	0	3	0						0			0	0	0	0		0	0	0	0	0	8	
Brown Hyaena	0	0	0	1	0	0		0	0	1	0	0		0	0	1	0	0			0	0	0	0		0	0	0	1	0	4	
Black Backed Jackal	0	1	0	0	0	0		0	0	0	3	2		28	6	1	3	0			1	0	0	3	0		1	7	4	0	2	63
Cape Fox	0	0	0	0	0	0		0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Caracal	0	0	0	0	0	0		0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Honey Badger	0	0	0	0	0	0		0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Leopard	0	0	0	0	0	0		0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Mongoose Slender	0	0	0	0	0	0		0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Mongoose Water	0	0	0	0	0	0		0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Mongoose Yellow	0	0	0	0	0	0		0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Serval	0	0	0	0	0	0		0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Striped Polecat	0	0	0	0	0	0		0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	
Suricate	0	0	0	0	0	0		0	0	0	0	0		0	0	0	0	0			0	0	0	0		0	0	0	0	0	0	

Appendix 17: Shannon-Weiner Species Diversity Indices for Sign Surveys conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.

Shannon-Weiner Species Diversity							
Within 250 m of Site				Within 500 m of Site			
	Controls	Caged	Open		Controls	Caged	Open
	1.41	0.84	0.9		1.41	1.5	1.27
	1.79	1.42	1		1.88	1.58	1.29
	1.46	0.83	1.2		1.95	1.29	1.69
	1.69	0.72	1.13		2.14	1.17	1.79
	1.25	0.51	0.76		1.59	1.59	1.22
Mean	1.52	0.864	0.998		1.794	1.426	1.452

Appendix 18: Shannon-Wiener Species Diversity from Camera Trap Surveys conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.

Shannon Wiener Species Diversity			
	Controls	Caged	Open
	0.693	0.693	0.146
	0	0.876	0.337
	0.485	0.119	1.231
	0.562	0	0.246
	0.095	0.234	0.102
Mean	0.367	0.3844	0.4124

Appendix 19: Gini-Simpson's Species Diversity Indices for Sign Surveys conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.

Gini-Simpson's Species Diversity						
	Simpsons Species Diversity Within 250 m of Site			Simpsons Species Diversity Within 500 m of Site		
	Controls	Caged	Open	Controls	Caged	Open
	0.73	0.46	0.49	0.75	0.73	0.66
	0.82	0.73	0.51	0.83	0.77	0.65
	0.69	0.51	0.64	0.85	0.69	0.8
	0.82	0.44	0.59	0.89	0.63	0.82
	0.69	0.27	0.47	0.77	0.73	0.69
Mean	0.75	0.482	0.54	0.818	0.71	0.724

Appendix 20: Gini-Simpson Species Diversity for Camera Trap Surveys conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.

Gini-Simpson's Species Diversity			
	Controls	Caged	Open
	1.00	1.00	0.07
	0.00	0.58	0.15
	0.26	0.05	0.67
	0.50	0.00	0.13
	0.04	0.13	0.09
Mean	0.36	0.35	0.22

Appendix 21: Fire affected calculations of Shannon-Weiner Species Diversity Indices for Sign Surveys conducted on Telperion Nature Reserve during the blue wildebeest (*Connochaetes taurinus*) decomposition study from January 2019 to January 2020.

Shannon Weiner Species Diversity Excluding Sites 5,6,9						
Within 250 m of Site			Within 500 m of Site			
Controls	Caged	Open	Controls	Caged	Open	
1.41	0.84	0.9	1.41	1.5	1.27	
1.46	1.42	1.2	1.95	1.58	1.69	
1.69	0.72	1.13	2.14	1.17	1.79	
1.25	0.51	0.76	1.59	1.59	1.22	
Mean	1.45	0.87	1.77	1.46	1.49	

Appendix 22: Shannon-Wiener Species Diversity from Camera Trap Surveys excluding fire affected sites conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.

Shannon Weiner Species Diversity			
Excluding Sites 5,6,9			
	Controls	Caged	Open
	0.69	0.69	0.15
	0.49	0.88	1.23
	0.56	0.00	0.25
	0.10	0.23	0.10
Mean	0.46	0.45	0.43

Appendix 23: Fire affected calculations of Gini-Simpson Species Diversity Indices for Sign Surveys conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.

Gini-Simpson's Species Diversity Excluding Sites 5,6,9						
	Within 250 m of Site			Within 500 m of Site		
	Controls	Caged	Open	Controls	Caged	Open
	0.73	0.46	0.49	0.75	0.73	0.66
	0.69	0.73	0.64	0.85	0.77	0.80
	0.82	0.44	0.59	0.89	0.63	0.82
	0.69	0.27	0.47	0.77	0.73	0.69
Mean	0.73	0.48	0.55	0.82	0.72	0.74

Appendix 24: Gini-Simpson Species Diversity from Camera Trap Surveys excluding fire affected sites conducted on Telperion Nature Reserve during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.

Gini-Simpson's Species Diversity			
	Excluding Sites 5,6,9		
	Controls	Caged	Open
	1.00	1.00	0.07
	0.26	0.58	0.67
	0.50	0.00	0.13
	0.04	0.13	0.09
Mean	0.45	0.43	0.24

Appendix 25: Correlation matrix of variables believed to influence mesocarnivore presence at experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion nature Reserve from January 2019 to January 2020.

Correlation Matrix		JTD	Meso250	Meso500	BHyaena	Leopard	Meso
JTD	Pearson's r	—					
	p-value	—					
	95% CI Upper	—					
	95% CI Lower	—					
	Spearman's rho	—					
	p-value	—					
Meso250	Pearson's r	-0.426 ***	—				
	p-value	< .001	—				
	95% CI Upper	-0.278	—				
	95% CI Lower	-0.555	—				
	Spearman's rho	-0.478 ***	—				
	p-value	< .001	—				
Meso500	Pearson's r	-0.550 ***	0.693 ***	—			
	p-value	< .001	< .001	—			
	95% CI Upper	-0.420	0.772	—			
	95% CI Lower	-0.657	0.594	—			
	Spearman's rho	-0.639 ***	0.712 ***	—			
	p-value	< .001	< .001	—			
BHyaena	Pearson's r	0.095	-0.124	-0.151	—		
	p-value	0.270	0.151	0.080	—		
	95% CI Upper	0.259	0.046	0.018	—		
	95% CI Lower	-0.074	-0.286	-0.311	—		
	Spearman's rho	0.102	-0.132	-0.156	—		
	p-value	0.237	0.125	0.071	—		
Leopard	Pearson's r	-0.059	-0.130	-0.124	-0.044	—	
	p-value	0.493	0.132	0.151	0.615	—	
	95% CI Upper	0.110	0.040	0.046	0.126	—	
	95% CI Lower	-0.225	-0.292	-0.286	-0.210	—	
	Spearman's rho	-0.049	-0.132	-0.122	-0.044	—	
	p-value	0.572	0.125	0.158	0.615	—	
Meso	Pearson's r	-0.465 ***	0.917 ***	0.701 ***	-0.135	-0.129	—
	p-value	< .001	< .001	< .001	0.118	0.134	—
	95% CI Upper	-0.322	0.940	0.777	0.034	0.040	—
	95% CI Lower	-0.587	0.886	0.604	-0.296	-0.291	—
	Spearman's rho	-0.490 ***	0.980 ***	0.706 ***	-0.135	-0.129	—
	p-value	< .001	< .001	< .001	0.118	0.134	—

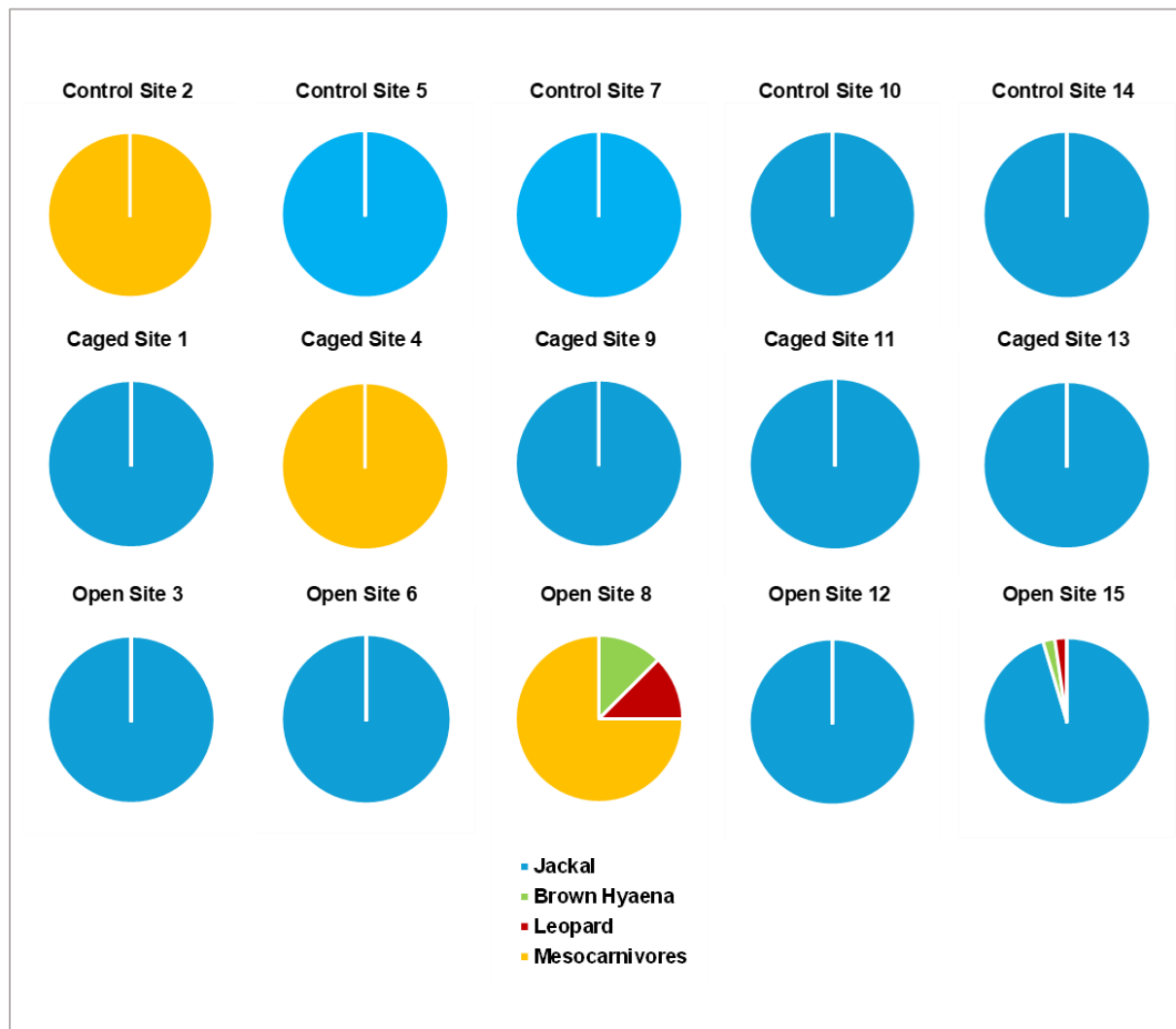
Note. * p < .05, ** p < .01, *** p < .001

Note: JTD = Jackal track density; Meso250 = Mesopredator tracks within 250m; Meso500 = Mesopredator tracks within 500m; BHyaena = Brown Hyaena; Meso = Mesopredator presence

Appendix 26: Binomial logistic regression model comparisons assessing ‘Treatment’, ‘Jackal Track Density’ (JTD) and ‘Season’ as predictors of mesocarnivore presence/absence at experimental sites during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020.

Comparison			χ^2	df	p
Model	-	Model			
1	-	2	19.75	1	< 0.001
2	-	3	5.62	4	0.229

Appendix 27: Pie charts showing detail of the number of predator visits to each experimental site during the period of active decay from camera trap data during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators on Telperion Nature Reserve from January 2019 to January 2020. Pie charts show proportions of visits by different predator species.



Appendix 28: The total number of visits of all predator species (from video and still cameras) per site, treatment type and season during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators for the entire study period from January 2019 to January 2020 on Telperion Nature Reserve.

Species Scientific Name	Species Common Name	Total Visits All Treatments	Total Visits Controls	Total Visits Caged	Total Visits Open	Total Visits Summer of Active Decay	Total Visits Autumn	Total Visits Winter	Total Visits Spring	Total Visits Summer	Total Visits All Seasons
<i>Proteles cristatus</i>	Aardwolf	12	0	8	4	5	1	1	4	1	12
<i>Parahyaena brunnea</i>	Brown Hyena	14	1	4	9	2	6	5	1	0	14
<i>Lupulella mesomelas</i>	Black Backed Jackal	603	79	62	462	340	73	44	85	61	603
<i>Felis nigripes</i>	Black Footed Cat	0	0	0	0	0	0	0	0	0	0
<i>Aonyx capensis</i>	Cape Clawless Otter	0	0	0	0	0	0	0	0	0	0
<i>Vulpes chama</i>	Cape Fox	1	1	0	0	0	1	0	0	0	1
<i>Caracal caracal</i>	Caracal	1	1	0	0	0	0	1	0	0	1
<i>Cinettictis civetta</i>	Civet	0	0	0	0	0	0	0	0	0	0
<i>Mellivora capensis</i>	Honey Badger	1	1	0	0	1	0	0	0	0	1
<i>Panthera pardus</i>	Leopard	2	0	0	2	2	0	0	0	0	2
<i>Galerella sanguinea</i>	Mongoose Slender	12	0	0	12	6	2	4	0	0	12
<i>Atilax paludinosus</i>	Mongoose Water	1	0	0	1	0	0	0	0	1	1
<i>Cynictis penicillata</i>	Mongoose Yellow	22	1	0	21	0	0	12	3	7	22
<i>Genetta maculata</i>	Rusty Spotted Genet	0	0	0	0	0	0	0	0	0	0
<i>Leptailurus serval</i>	Serval	1	0	0	1	0	0	1	0	0	1
<i>Ictonyx striatus</i>	Striped Polecat	1	1	0	0	0	0	0	1	0	1
<i>Suricata suricatta</i>	Suricate	2	0	0	2	0	0	1	1	0	2
Totals		673	85	74	514	356	83	69	95	70	673

Appendix 29: Comparison of predator survey results during my study on the influence of decomposing blue wildebeest (*Connochaetes taurinus*) carcasses on predators from January 2019 to January 2020 and another recent camera trap study on Telperion Nature Reserve.

Family	Scientific Name	Common Name	Cameras Sites 1-15	Sign Survey Entire Reserve	Combined Sign and Camera Survey results	Webster et al. (2021) Camera Study
1 Felidae	<i>Caracal caracal</i>	Caracal	✓	✓	✓	✓
2	<i>Felis nigripes</i>	Black Footed Cat		✓	✓	✓
3	<i>Leptailurus serval</i>	Serval	✓	✓	✓	✓
4	<i>Panthera pardus</i>	Leopard	✓	✓	✓	✓
5 Canidae	<i>Lupulella mesomelas</i>	Black Backed Jackal	✓	✓	✓	✓
6	<i>Vulpes chama</i>	Cape Fox	✓		✓	
7 Hyaenidae	<i>Parahyaena brunnea</i>	Brown Hyena	✓	✓	✓	✓
8	<i>Proteles cristatus</i>	Aardwolf	✓	✓	✓	✓
9 Viverridae	<i>Civettictis civetta</i>	Civet		✓	✓	
10	<i>Genetta maculata</i>	Rusty Spotted Genet		✓	✓	✓
11 Herpestidae	<i>Atilax paludinosus</i>	Mongoose Water	✓	✓	✓	✓
12	<i>Cynictis penicillata</i>	Mongoose Yellow	✓	✓	✓	✓
13	<i>Galerella sanguinea</i>	Mongoose Slender	✓	✓	✓	✓
14	<i>Suricata suricatta</i>	Suricate	✓	✓	✓	✓
15 Mustelidae	<i>Aonyx capensis</i>	Cape Clawless Otter		✓	✓	✓
16	<i>Lutra maculicollis</i>	Spotted-necked otter				✓
17	<i>Mellivora capensis</i>	Honey Badger	✓	✓	✓	✓
18	<i>Ictonyx striatus</i>	Striped Polecat	✓	✓	✓	✓
		Total	13	16	17	16