Determinants of predator abundance in northern KwaZulu-Natal: top-down or bottom-up?

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PLAGIARISM DECLARATION

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This work is being submitted for the degree of Bachelor of Science Honours in the Department of Biological Sciences, in the Faculty of Science, of the University of Cape Town, South Africa. It has not been submitted to any other university or institution for any other degree or examination.

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ABSTRACT

As protected areas ultimately aim to successfully conserve natural predator populations, an understanding of the non-anthropogenic drivers of their population change is critical. Both bottom-up (e.g. food limitation, competition) and top-down (e.g. predation, interference) processes play an important role in structuring predator guilds, yet there is a poor understanding of their relative importance. Here, I investigated whether the relative abundance of mesopredators, facultative scavengers, and an apex predator were affected primarily by bottom-up processes (prey abundance) or by top-down processes (predator abundance), or a combination of the two. Central to this study was elucidating the complex relationship between mesopredators and apex predators. Caracal (*Caracal caracal*), blackbacked jackal (*Canis mesomelas*), sidestriped jackal (*Canis adustus*), honey badger (*Mellivora capensis*) and serval (*Leptailurus serval*) were classed together as Mesopredators. Facultative scavengers included two hyaena species (spotted *Crocuta crocuta* and brown hyaena *Hyaena brunnea*). Leopards (*Panthera pardus)* were included as an example of an apex predator. Data was obtained from camera-trap surveys conducted in four protected areas located in northern KwaZulu-Natal (South Africa). Results of both a nested analysis of variance and generalised linear mixed models revealed that there was no mesopredator suppression present in protected areas with complete predator guild. In addition, prey and similarly sized predator relative abundance indices (RAIs) had a significant positive effect on mesopredator, hyaena and leopard RAI. The findings suggest that bottom-up drivers are more important than top-down processes in determining the relative abundance of mammalian predators in these protected areas. My study highlights the importance of monitoring prey populations in a protected area when attempting to successfully manage mammalian predator trophic guilds.

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INTRODUCTION

Mammalian predators are some of the world's most iconic species and feature prominently in human history and contemporary culture (Ripple et al. 2014). They also include some of the world's most threatened species and many have suffered marked reductions in both numbers and range (Winterbach et al. 2013; Ripple et al. 2014). This downward trend has significant ecological consequences as mammalian predators play a key role in maintaining ecosystem health, by influencing both community structure and functional strength (Prugh et al. 2009; Letnic et al. 2011; Sutherland et al. 2011; Ripple et al. 2014). Fluctuations in predator numbers may result in ecosystems becoming degraded. Consequently, knowledge of predator abundance is of great importance for reserve management and conservation in general.

There are few rigorous estimates for mammalian predator populations in Africa, and even less information exists on the drivers affecting population change (Winterbach et al. 2013; Edwards et al. 2014). Previous research has shown that predator populations are typically regulated by both bottom-up and top-down processes (Crooks & Soulé 1999; Kissui & Packer 2004; Ripple & Beschta 2012). Bottom-up processes are typically density-dependent and influenced by factors affecting resource availability (e.g. food limitation, competition). In contrast, top-down processes are usually density independent and involve interactions with natural enemies (e.g. predation; Kissui & Packer 2004, Hayward & Slotow 2009). Despite their apparent importance, surprisingly few studies have quantified the relative impacts of bottom-up and top-down processes in shaping predator populations (Elmhagen & Ludwig 2010; Ripple & Beschta 2012).

Research to date suggests that large predators are predominately regulated by bottom-up processes and, under certain environmental conditions, a combination of both bottom-up and top-down processes (Owen-Smith & Mills 2008). For example, the reproductive success of female leopards (*Panthera pardus)* in kwaZulu-Natal was shown to be primarily regulated by top-down processes such as infanticide (Balme et al. 2013). In contrast, smaller predators are primarily regulated by top-down processes, such as predation or persecution. "Mesopredator release", a term coined by Soulé et. al (1988), is a complex interaction of bottom-up and top-down control affecting subordinate predator abundance. It refers to a phenomenon in which extirpation of apex predators allows populations of smaller or less selective predators to increase, due to relaxed competition and/or predation (Prugh et al.

2009). Mesopredator release is frequently recorded in marine systems yet only a few terrestrial examples exist in the scientific literature (Ray et al. 2005). For example, the dingos (*Canis lupus dingo*) of mainland Australia suppress populations of the invasive red fox (*Vulpes vulpes*), a mesopredator, over large geographical scales (Letnic et al. 2011).

The distinction and subsequent relationship between mesopredators and apex predators is not always so clear-cut. Many carnivores scavenge; indeed for some species, such as the spotted hyaena (*Crocuta crocuta)* and brown hyaena (*Hyaena brunnea),* a significant portion of their diet may comprise scavenged food (East et al. 2013). For such species, the presence of apex predators may provide additional scavenging opportunities, thus facilitating increased, rather than decreased, population size. For example, Yarnell et al. (2013) showed that the population density of brown hyaenas was higher in a reserve which had lions (*Panthera leo),* an apex predator, than in a reserve without lions, even though the latter had more suitable prey populations.

Both bottom-up and top-down controls ensure that predators occupy large home ranges and occur at low densities (Balme et al. 2009; Ferreira & Hofmeyr 2014; Midlane et al. 2014; Ripple et al. 2014). These attributes make them some of the most difficult species to monitor. Determining baseline population figures is not only time consuming but also expensive (O'Connell et al. 2011). Remotely-triggered camera traps have helped to overcome many of these challenges. Since 1990, the use of camera traps in wildlife research has grown exponentially and they are currently the favoured method for monitoring rare, cryptic predators (Carbone et al. 2001; Wallace et al. 2003; O'Connell et al. 2011). As camera traps are both non-invasive and have nominal operation cost, they are ideal for both short and long term surveys of predator populations (Carbone et al. 2001). Camera traps could thus be extremely useful in answering many questions that ecologists, conservationists and reserve managers have about predator populations today.

Complex capture and recapture models have been developed to accurately estimate the density of individually distinguishable species, such as leopards or tigers, from independent photographic captures (O'Connell et al. 2011). However, in cases where the target species cannot be individually identifiable (for example, caracal), relative abundance indices (RAIs) are often used to make inferences about changes in abundance spatially or temporally (Sollmann et al. 2013). This makes them ideal for routine surveys of protected areas by reserve management. As RAIs fail to incorporate variability in the detection probabilities of different cryptic species they typically underestimate population size (Carbone et al. 2001; Sollmann et al. 2013). Consequently, RAI is only utilised in population monitoring over space and/or time if there is an already established monotonic relationship between actual density and RAI (Balme et al. 2010; O'Connell et al. 2011). Such calibrations are both site and species specific (Pearce & Ferrier 2001; Carbone et al. 2001; Treves et al. 2010; Sollmann et al. 2013).

The non-profit organisation Panthera, in cooperation with Ezemvelo KwaZulu-Natal Wildlife, Wildlife ACT and iSimangaliso Wetland Authority, perform yearly camera trap surveys in northern KwaZulu-Natal's protected areas, with the aim of monitoring changes in local leopard populations. However, such camera-trap surveys provide useful data on a wide range of animals, not only the target species (O'Connell et al. 2011). This is particularly true in this local context as the spacing between cameras was conservative relative to the ranging behaviour of leopards (Balme et al. 2009). This study utilised camera-trap data from four protected areas in northern KwaZulu Natal, South Africa. Although these protected areas are located in similar habitats, their predator communities are considerably different. The central aim of this study was to elucidate the complex relationship between mesopredators and apex predators.

To achieve this we investigated whether the relative abundance of mesopredators, facultative scavengers, and an apex predator are affected primarily by bottom-up processes (i.e. prey abundance and competition) or by top-down processes (i.e. predator), or a combination of the two. Mesopredators were classed as species that were smaller than 18 kg, and primarily hunt for themselves (caracal *Caracal caracal*; blackbacked jackal *Canis mesomelas*; sidestriped jackal *Canis adustus*; honey badger *Mellivora capensis*; serval *Leptailurus* serval). Facultative scavengers included two hyaena species (spotted *Crocuta crocuta*; brown hyaena *Hyaena brunnea*) as both obtain a significant portion of the daily food intake from scavenging (East et al. 2013). Leopards (*Panthera pardus*) were included as an example of an apex predator, as they were found at all sites and primarily hunt to obtain food (Hunter et al. 2013).

The importance of bottom-up processes in regulating species abundance was investigated based on the hypothesis that the relative abundance of prey would be a significant determinant of mesopredator, hyaena and leopard relative abundance. Additionally, the importance of competition (a bottom-up process) was investigated based on the hypothesis that the relative abundance of similarly sized predators would be a significant determinant of mesopredator, hyaena, and leopard relative abundance. In contrast, the importance of top-down controls (with particular reference to mesopredator release), were investigated based on the hypothesis that the relative abundance of larger predators would be the best determinant of mesopredator, hyaena, and leopard relative abundance.

METHODS

For this study, data was used from camera-trap surveys conducted in 2013/14 within four protected areas in northern KwaZulu-Natal, South Africa; namely, Hluhluwe-iMfolozi Game Reserve (hereafter HiP), iSimangaliso Wetland Park - uMkhuze section (uMkhuze), Somkhanda Community Reserve (Somkhanda) and Ithala Game Reserve (Ithala; Fig. 1; Appendix I). Cameras were placed to maximise the probability of capturing a leopard. Panthera$^{©}$ digital camera-traps, which use passive infrared sensors and emit a white flash, were strapped to trees (or metal stakes if no suitable tree was available) alongside roads or well-used animal paths. Each station comprised two camera traps set opposite one another to photograph both flanks of animal simultaneously. This facilitated identification of individual leopards for Panthera objectives (separate to this study) and also helped overcome instances of camera failure. Camera-trap stations were placed 2-3 km apart, ensuring a minimum of two stations per potential leopard home range (Balme et al. 2009). A conservative survey design was chosen to enable the analysis of photographic rates of species which range less widely than leopards (e.g. mesopredators; Sollmann et al. 2013).

Surveys were limited to 45 days to meet the assumption of population closure required for the generalised linear mixed models (GLMMs). All stations were visited weekly to download images, replace batteries and reposition cameras that had been dislodged. In cases where cameras failed or were lost, the missing days were removed in calculations of trap effort (see below).

All images were captured in Camera Base v1.6 (Tobler 2013). Independent captures were defined as successive photographs of different species, or different individuals of the same species. A 30 minute interval between photographs was used in cases where it was impossible to distinguish individuals (O’Brien et al. 2013). For the purposes of this study, I assigned independent captures of predators to one of three trophic classes; mesopredators, facultative scavengers, and an apex predator. Caracal (*Caracal caracal*), blackbacked jackal (*Canis mesomelas*), sidestriped jackal (*Canis adustus*), honey badger (*Mellivora capensis*) and serval (*Leptailurus serval*) were classed together as Mesopredators. Facultative scavengers included two hyaena species (spotted *Crocuta crocuta*; brown hyaena *Hyaena brunnea*). Leopards (*Panthera pardus)* were included as an example of an apex predator.

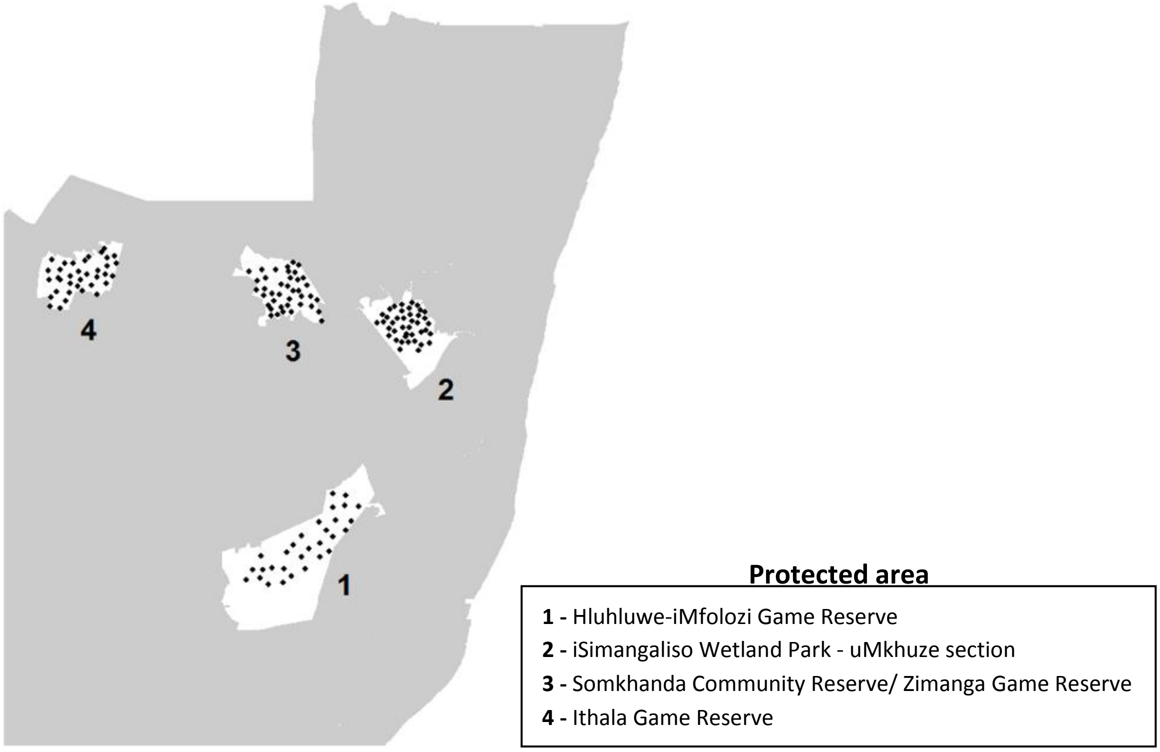

Figure 1: Map of northern KwaZulu-Natal showing the location of camera trap stations (dots) utilised in camera-trap surveys within the four conservation areas.

To estimate the relative abundance of prey, I extracted all independent captures of species fitting in the preferred prey weight range of the predator species mentioned above from the data (Mills & Mills 1978; Mills et al. 2004; Hayward 2006). Prey species were divided into three size classes based on the weight of adult females (Table 2), taken from Skinner & Chimimba (2005); small (<10 kg), medium (10 – 30 kg) or large (>30kg) (Mills et al. 2004; Mills & Mills 1978).

Similarly, to estimate the relative abundance of predators other than the trophic classes identified above, all independent captures of predator species from the order *Carnivora* were extracted from the data. Predator species were divided into three size classes based on the weight of adult females (Table 2), taken from Skinner & Chimimba (2005); small (<8 kg), medium (8 – 18 kg) or large (>18kg).

Table 2: Summary of study species and their size classification.

Species	Average female Weight Range (kg)	Category
Aardwolf	5.2 – 8.3	Small predator
Banded Mongoose	1 - 1.6	Small predator
Black-backed Jackal	7.4 - 10	Medium predator
Brown Hyaena	42	Large predator
Bushbuck	24 - 34	Medium prey
Bushpig	48 - 66	Large prey
Cane Rat	3.4 - 3.8	Small prey
Caracal	16	Medium predator
Chacma Baboon	14 - 17	Medium prey
Cheetah	43	Large predator
Common Reedbuck	31 - 52	Large prey
Grey Duiker	17 - 25.4	Medium prey
Honey Badger	8 - 14.5	Medium predator
Impala	32 - 52	Large prey
Klipspringer	10.5 - 16	Medium prey
Kudu	120 - 210	Large prey
Large-spotted Genet	1.8	Small predator
Leopard	32 - 35	Large predator
Lion	100 - 175	Large predator
Meller's Mongoose	2.5	Small predator
Mountain Reedbuck	28	Medium prey
Nyala	55 - 68	Large prey
Porcupine	18 - Oct	Medium prey
Red Duiker	13 - Oct	Medium prey
Scrub Hare	2.7 - 3.7	Small prey
Serval	8.6 - 11.8	Medium predator
Slender Mongoose	0.43	Small predator
Spotted Hyaena	70	Large predator
Side-striped Jackal	7.2 - 10	Medium predator
Steenbok	9.6 - 13.2	Small prey
Striped Polecat	0.420 – 1.3	Small predator
Suni	5.1 - 5.9	Small prey
Tsessebe	126	Large prey
Vervet Monkey	3.4 - 5.2	Small prey
Warthog	44 - 69	Large prey
Water Mongoose	05 -	Small predator
Waterbuck	180	Large prey
White-Tailed Mongoose	3.2 - 5.5	Small predator
Wild Dog	24 - 30	Large predator
Wildebeest	180 - 215	Large prey
Zebra	260	Large prey

All independent captures for predator and prey categories were converted into RAIs, to account for variable sampling effort between sites and stations. RAI is calculated as the number of independent captures per 100 active trap days (O’Brien et al. 2013). Balme et. al. (2010) demonstrated that in at least one site (uMkhuze) RAIs for both predator and prey species generated from camera-trap data shared a strong monotonic relationship with independent estimates of absolute abundance (Fig. 2). Given that there is no marked variation in habitat or species composition between survey sites (with the exception of medium and large predators), the photographic rates that are used in this study are likely reflective of real differences in abundance (Appendix I).

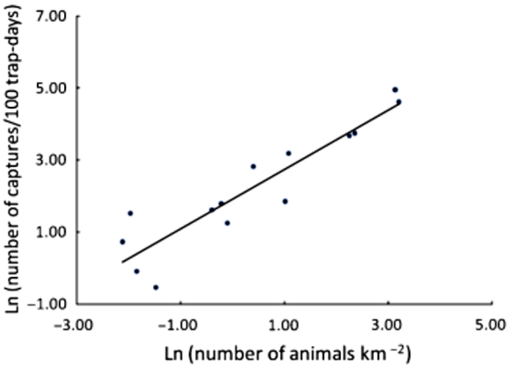

Figure 2: Relationship between independent density estimates and the corresponding relative abundance indices (r2=0.850) (Balme et al. 2010).

All statistical analyses were undertaken in R (studio version 3.1.0, R Core Development Team 2010). A hierarchical (nested) analysis of variance (nested ANOVA) was used to investigate differences in RAI of the different trophic classes, namely mesopredators, hyaenas and leopards, between protected areas (Appendix III). Normality in the data was assessed visually (Appendix IV) and with the Shapiro–Wilk test of normality (w = 0.62, p <0.001). If the data deviated from normality an optimal transformation of the response variable was chosen via the box-cox procedure (trophic classes: λ = -0.25; for trophic classes). Model diagnostics were then graphed to ensure that all assumptions had been met (Appendix V). Post-hoc analysis of the nested ANOVA was done with a Tukey's honest significant difference (Tukey's HSD) test in order to further understand patterns of significance in the model comparisons.

Generalized linear mixed models (GLMM) were used to investigate how variation in mesopredator, hyaena and leopard RAI's was driven by variation in either prey or predator RAI's (Bolker et al. 2009). The response variables were assumed to fit a Poisson distribution (Appendix VI). GLMM models were fitted with the "glmer" function in R studio 3.1.0 and ranked according to Akaike information criterion (AIC) and Bayesian information criterion (BIC) as protected area was defined as being a random variable (Appendix VII, VIII & IX). In the case that the AIC and BIC values are in conflict an ANOVA was performed to rank the models with a chi-squared test. This was to identify the most suitable model by assessing whether a reduction in the residual sum of squares was significant enough to justify dropping a predictor variable. Model diagnostics were then graphed to ensure that all assumptions had been met for the final model (Appendix X). Verification of the independence of fixed effects was assessed by analysis of the approximate correlations between them. For both the investigation of differences across the four protected areas and identifying the most important drivers of relative predator abundance, additional packages were utilised (Appendix II).

RESULTS

The four protected areas investigated in this study differed significantly based on the RAI of the trophic classes ($p < 0.001$, Table 3). A Tukey's HSD test revealed that most comparisons between the four protected areas were significantly different (Fig. 3). However Ithala was not significantly different to HiP ($M = 0.008$, $P = 0.958$). Somkhanda and Ithala were the most different according to the Tukey's HSD test ($M= 0.136$, $P < 0.000$).

Table 3: Summary of the nested ANOVA results for of protected area in relation to the RAI of mesopredator, hyaena and leopard (trophic classes).

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Among protected areas	3	0.82	0.27	20.09	<0.001
Among trophic classes within protected areas	8	1.10	0.14	10.08	<0.001
Residuals	315	4.29	0.01		

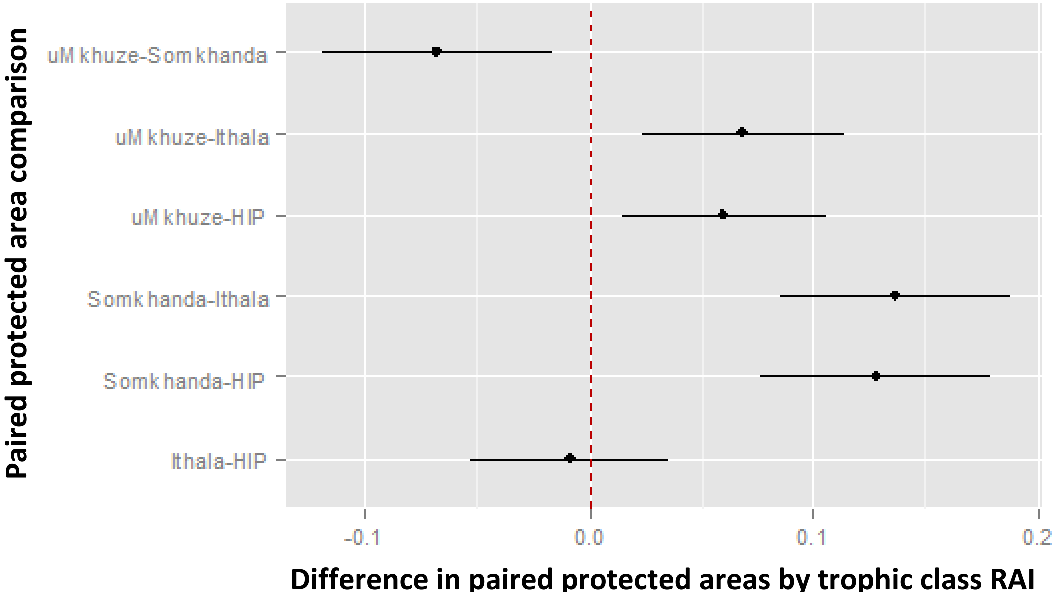

Figure 3: Tukey's HSD tests comparing between paired protected area means for a) nested ANOVA based on the trophic classes RAI's.

There was considerable variation amongst the protected areas with regards to the relative abundance of mesopredators (Appendix III). The GLMM results showed that the RAI of mesopredators increased with the RAI of large prey, yet decreased with the RAI of medium prey (Fig. 4; Table 5). The RAI of large predators was dropped from the model as it did not contribute significantly to variation in the RAI of mesopredators (Appendix VII). The relative abundance of medium prey had the greatest effect on the relative abundance of mesopredators (estimate = -0.039, p = 0.0068).

Table 5: Summary of the GLMM results for results for factors determining mesopredator RAI

Independent Variable	Estimate	Standard Error	Z Value	Pr(>|z|)
Intercept	-3.4712	0.4223	-8.2200	0.0000
Small prey	0.0011	0.0035	0.3000	0.7638
Medium prey	-0.0039	0.0014	-2.7050	0.0068
Large prey	0.0008	0.0004	2.0170	0.0437
Small predator	-0.0119	0.0062	-1.9190	0.0550

RANDOM EFFECTS: Protected area estimated variance ± SD=0.65±0.80

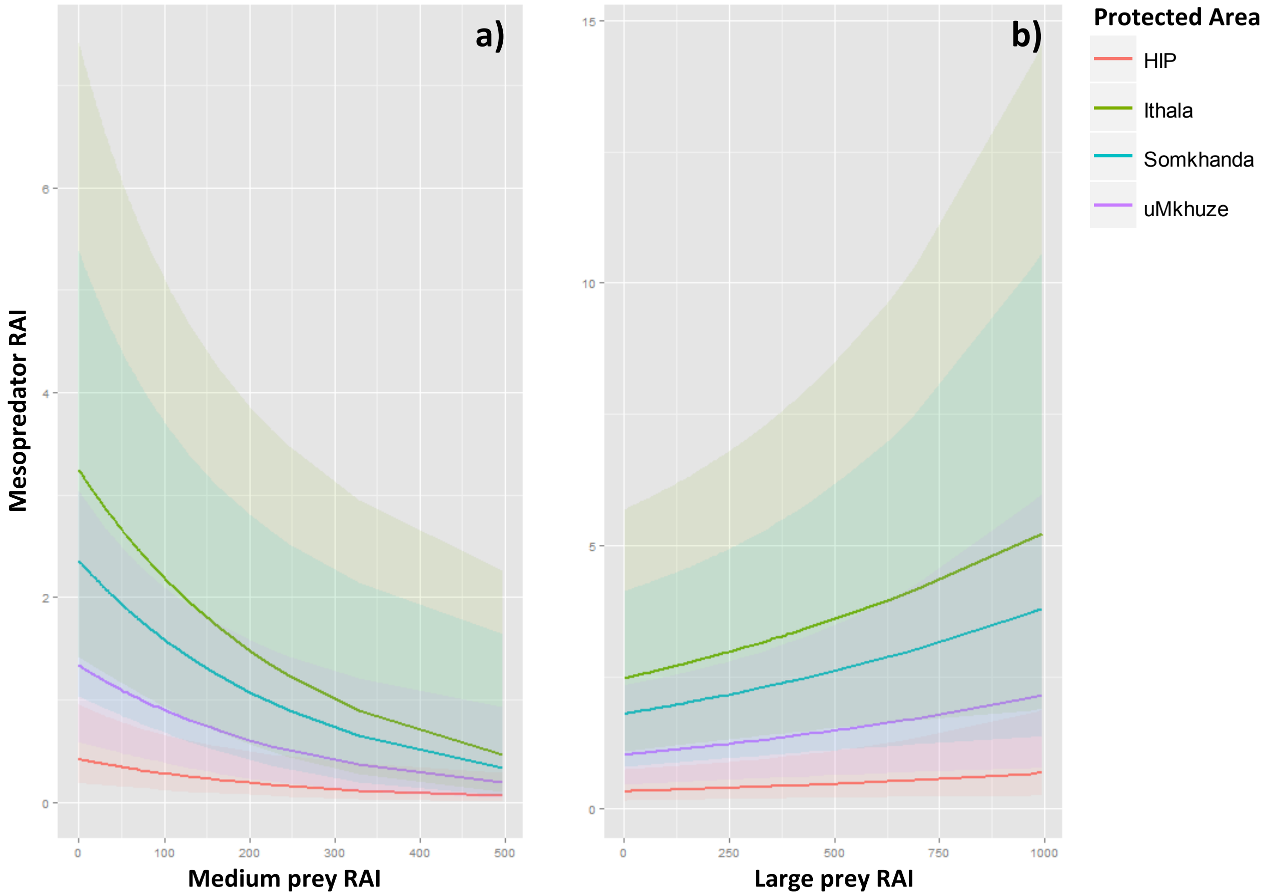

Figure 4: Probability of mesopredator RAI across a range of prey size categories RAI of a) medium and b) large for all four protected areas. Shaded ribbons indicate the 95% confidence interval for the different protected areas (based on fixed effects uncertainty).

The GLMM for hyaena RAI results showed that the RAI of hyaenas increased with the RAI of large prey, large predators and, to a lesser extent ($P < 0.05$), that of small predators (Fig. 5; Table 6). The RAI of hyaenas however decreased with an increase of small prey RAI (estimate = -0.0085, $p = 0.0016$). The most important driver was the RAI of large predators (estimate = 0.0174, $p < 0.001$), and it subsequently caused an exponential increase in the RAI of hyaenas over a large predator RAI of 50 (Fig. 5). The relative abundance of medium prey and predators had little effect on the RAI of hyaenas, as neither had significant probability values. HIP was had the largest RAI of hyaena of the four protected areas (1316.131), whilst Somkhanda community reserve appeared to have almost no hyaena present (Fig. 5; Appendix III).

Table 6: Summary of the GLMM results for results for factors determining hyaena RAI.

Independent Variable	Estimate	Standard Error	Z Value	Pr(>|z|)
Intercept	-2.8232	0.5430	-5.1990	0.0000
Small prey	-0.0085	0.0027	-3.1620	0.0016
Medium prey	0.0003	0.0005	0.5070	0.6123
Large prey	0.0008	0.0002	3.6550	0.0003
Small predator	0.0067	0.0032	2.1200	0.0340
Medium predator	0.0153	0.0206	0.7420	0.4582
Large predator	0.0174	0.0019	9.1400	0.0000

RANDOM EFFECTS: Protected area estimated variance ± SD=1.14±1.07

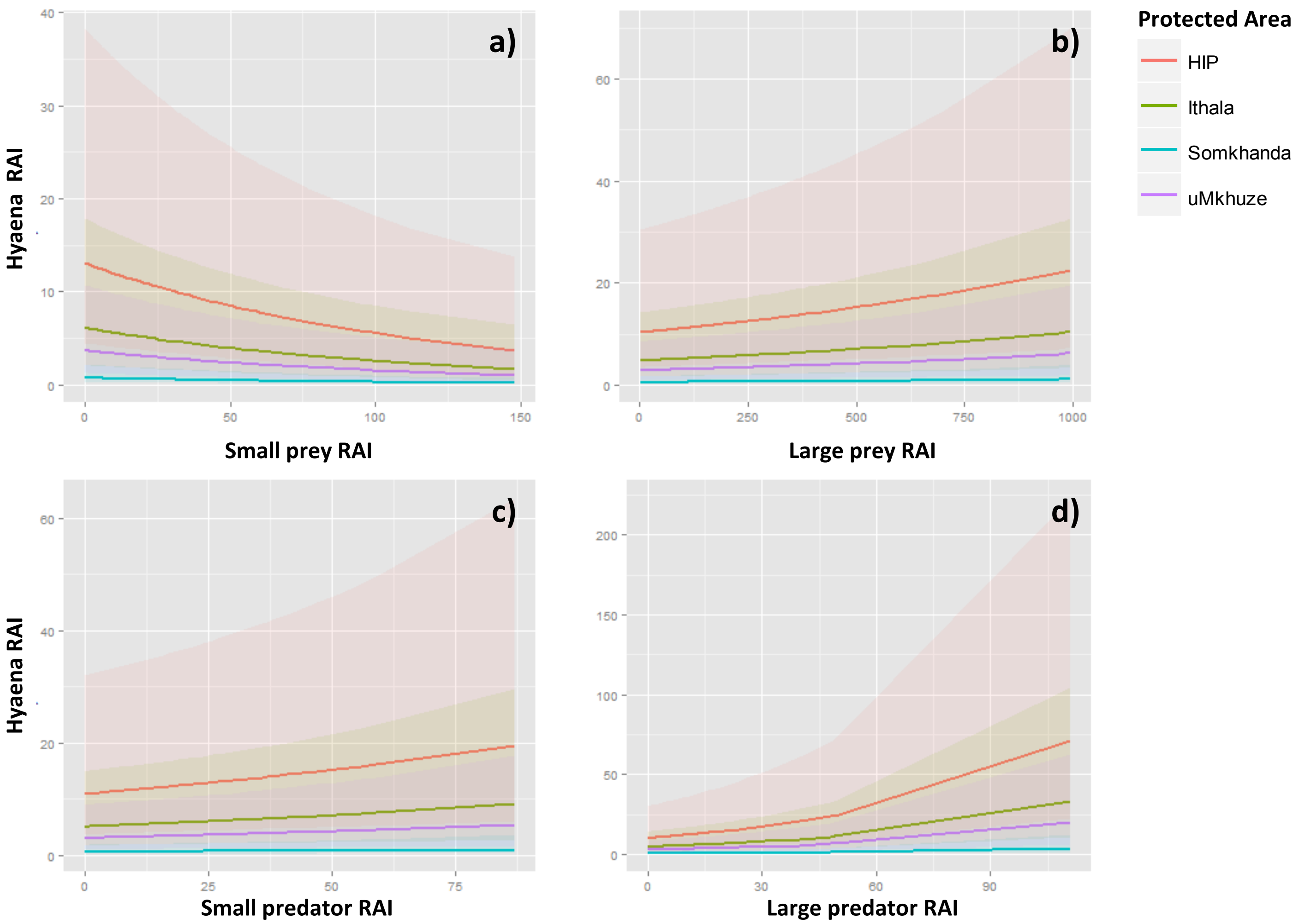

Figure 5: Probability of hyaena RAI across a range of prey size categories RAI a) small prey, b) large, and a range of predator size categories RAI c) small and d) for all four protected areas. Shaded ribbons indicate the 95% confidence interval for the different protected areas (based on fixed effects uncertainty).

The results from the final GLMM showed that the RAI of leopards positively increased with the relative abundance of large predators, small and medium prey (Fig. 6; Table 7). The RAI of large prey, small predators and large predators had little influence on the RAI of leopards. The RAI of large predators had the greatest influence on the RAI of leopards (estimate=

0.0125, $p < 0.001$), and leopard RAI was predicted to increase exponentially with an increase in large predator RAI (Fig. 6). Ithala game reserve had the largest RAI of leopards, and also had the largest increase with respect to the RAI of small, medium prey and large predators (Fig. 6). HIP and uMkhuze had very similar RAIs for leopards.

Table 7: Summary of the GLMM results for factors determining leopard RAI

Independent Variable	Estimate	Standard Error	Z Value	Pr(>|z|)
Intercept	-2.7330	0.2749	-9.9410	0.0000
Small prey	0.0068	0.0019	3.6690	0.0002
Medium prey	0.0018	0.0004	4.2410	0.0000
Large prey	0.0001	0.0002	0.4090	0.6822
Small predator	0.0012	0.0032	0.3660	0.7146
Medium predator	-0.0052	0.0185	-0.2830	0.7769
Large predator	0.0124	0.0019	6.6900	0.0000

RANDOM EFFECTS: Protected area estimated variance ± SD=0.28±0.52

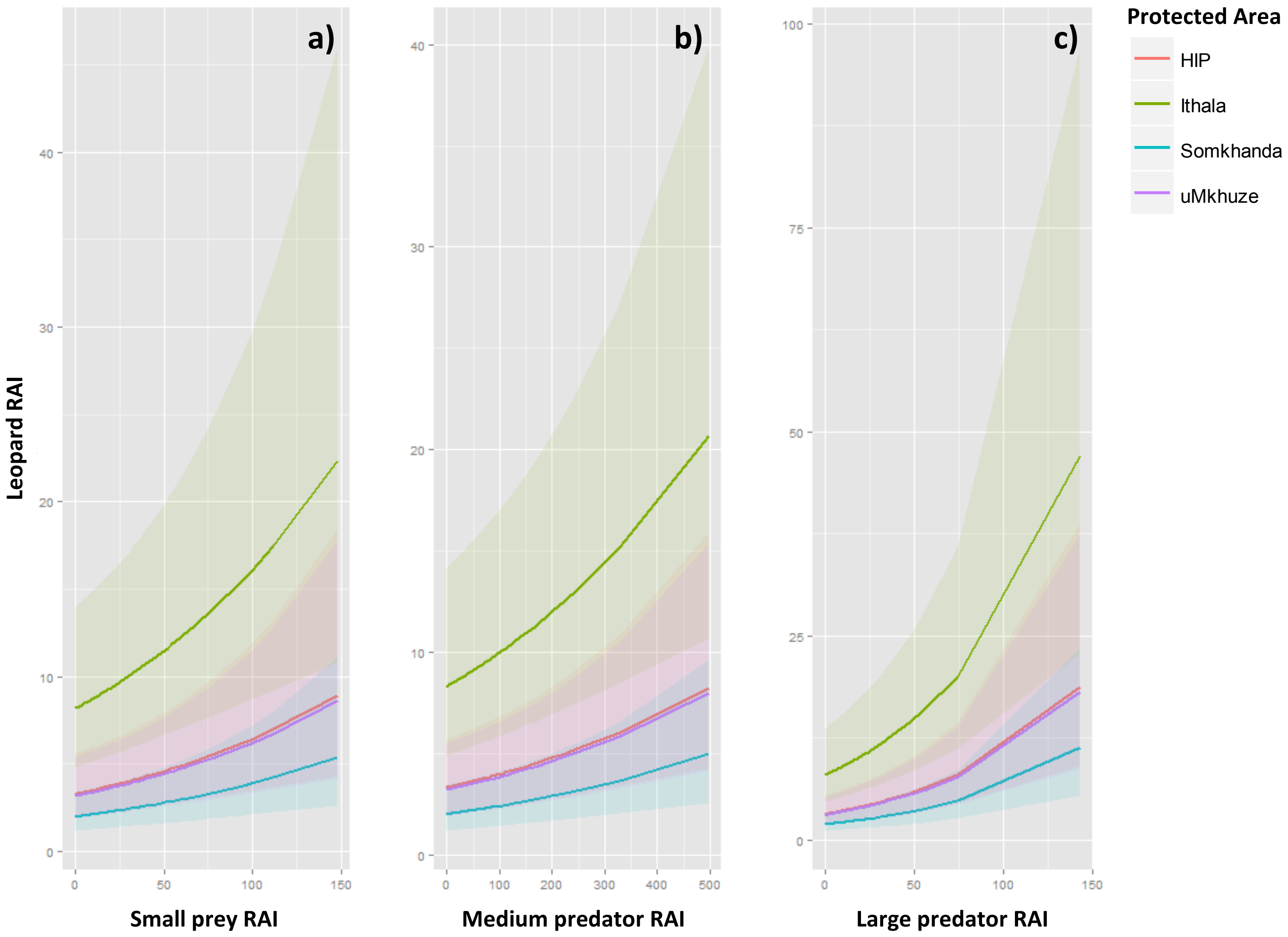

Figure 6: Probability of leopard RAI across a range of prey size categories RAI a) small prey, b) medium, across c) large predator size RAI for all four protected areas. Shaded ribbons indicate the 95% confidence interval for the different protected areas (based on fixed effects uncertainty).

DISCUSSION

Top-down controls (large predator abundance) were not the dominant processes driving changes in mesopredator, hyaena (facultative scavenger) and leopard (apex predator) RAIs. However, bottom-up ecological processes (prey abundance and competition) were shown to have a significant effect on all three trophic classes. As competition is linked to prey availability, it can be broadly stated that a large and diverse prey population within a protected area will support a large number of predators. This has practical repercussions for reserve management across Southern Africa, particularly when considering the monitoring of predator species in protected areas.

Initial data exploration suggested the occurrence of mesopredator release in protected areas with incomplete mammalian predator guilds (Appendix III; Table 3; Table 4). However, further analysis revealed that large predator RAI did not significantly contribute to mesopredator RAI. In light of this, large predator RAI was dropped from the final GLMM of mesopredator RAI (Appendix VII). These findings are incongruent with those of several European and Australian studies, which showed that when primary productivity was high, top-down controls were more important in mesopredator population regulation (Elmhagen & Rushton 2007; Prugh et al. 2009; Pasanen-Mortensen et al. 2013). Despite comprising slightly different, although structurally similar vegetation, types, the four protected areas included in this study all fall under the savannah biome (Appendix I), which has high levels of primary productivity (Grange & Duncan 2006; Gandiwa 2013).

In spite of the putatively high levels of primary productivity at our study localities, we were unable to show evidence of interference and/or predation by larger predators driving mesopredator RAI. It has been suggested that more diverse predator guilds exert weaker, more diffused top-down controls on herbivore populations than less diverse predator guilds (Elmhagen & Ludwig 2010). It can be subsequently implied that top-down controls on predator populations might also be limited in the more species rich predator guilds of Southern Africa, a *post hoc* hypothesis that finds support in our findings. The drivers of mesopredator abundance proposed by Pasanen-Mortensen et. al. (2013), and Elmhagen and Rushton (2007), may thus not be applicable to a savannah ecosystem, and the generality of their findings needs to be reviewed. In addition, as the GLMM for mesopredator RAI did not include a factor for medium sized predators, competition strength within the trophic class was not evaluated. Competition within the mesopredator trophic class is potentially an important regulator of its abundance, as it has been observed prior amongst subordinate predators in a similar predator guild (Hayward & Kerley 2008). I thus recommend that further studies in this field critically evaluate competition within the mesopredator trophic class by either focusing on a single, representative species or broadening their specifications.

Hyaena RAI was shown to be positively related to that of large predator RAI. This finding is in agreement with those of Yarnell et al. (2013). In their research the reintroduction of lions into protected areas not only created novel scavenging opportunities for brown hyaenas, but they also suppressed populations of blackbacked jackals via persecution. As brown hyaenas are facultative scavengers they compete with both mesopredators and apex predators for resources. The creation of new feeding niches by lions thus allowed for the co-occurrence of brown hyaenas and blackbacked jackals by preventing dietary overlap and subsequent competition, as blackbacked jackals predominantly hunt small prey for their food (Merwe et al. 2009). Our study's findings showed that the abundance of large mammalian predators, such as lion or leopards, allowed for protected areas to support higher densities of hyaena species alongside potentially competing mesopredators.

Our study shows that both leopard and hyaena RAI correlate positively with that of large predator RAI. Therefore it can be concluded that competition, a bottom-up regulatory process, is an important driver of abundance. Yet the results indicate that high levers competition increases the abundance of predators, which is an unexpected result (Hayward & Slotow 2009). Ferreira and Hofmeyr (2014), emphasized the importance of mimicking social processes in their approach to large predator conservation in small protected areas. They also noted that the sizes of cheetah and lion populations were positively correlated with that of large prey. The results of our study are in support with both of Ferreira & Hofmeyr's (2014) findings. A possible explanation for the positive correlation is that in the presence of other large predators, leopards and hyaenas may alter their activity periods or feeding behaviours in order to successfully co-occur. Levels of competition are, however, also dependent upon the abundance of prey species, and is expected to relax as prey availability increases. Therefore it can be stated that the strength of competition is dependent on the prey population's size. We propose that as the abundance of prey increases, so does the abundance of large predators, yet due to the high levels of food competition within a trophic class decreases (Fig. 5; Fig. 6).

An alternative (although not mutually exclusive) explanation for the positive relationship between leopard and hyaena RAI with that of large predator RAI may be that a sizeable population of large predators is reflective of a well-managed protected area. Despite explicit regulations, poaching is often rife in game reserves with poor management or few resources. The results of the GLMM of leopard RAI showed that Somkhanda Community Reserve had both the lowest leopard RAI (Fig. 6), and the weakest relationship between leopard and large predator RAI, of all four protected areas investigated in this study. Not only is poaching a substantial issue for the reserve management, but trophy hunting is permitted to generate income (Balme G., pers. comm). These activities have been previously implicated as influential drivers in both prey and predator population dynamics (Gandiwa 2013). Such anthropogenic impacts often blur the true picture of top-down or bottom-up control on predator populations. The influence of poaching thus needs to be kept in mind when evaluating our conclusions. Future studies should attempt to include a quantitative proxy for poaching pressure, such as snare density or observed anthropogenic kills, in their analyses.

Prey RAI was an important driver of the RAI of all three trophic classes in the four protected areas investigated in this study. Large prey RAI was of particular importance in driving fluctuations in both leopard and hyaena RAIs. Previous studies have highlighted how local primary productivity and foraging availability were the primary determinants of herbivore populations in African ecosystems (Grange & Duncan 2006; Gandiwa 2013). Consequently, as all three trophic classes RAIs were closely related to that of prey RAI, it can be proposed that bottom-up drivers, such as primary productivity levels, are important in determining predator population size. Our study is in agreement with Sinclair and Krebs (2002) conclusions, which suggested that bottom-up processes are the dominant controls of all terrestrial vertebrate populations which have the potential to overridden by strong top-down controls. However, it is acknowledged that there are issues associated with the use of prey abundance as a proxy for bottom-up control, and that other factors, such as the Normalized Difference Vegetation Index (NDVI), might provide more accurate alternatives.

Interference, direct competition with, or predation by apex predators on mesopredators, hyaenas and even leopards could alter patterns of behaviour rather than actual abundances, an effect which cannot be directly assessed from this study’s data (Linnell & Strand 2000). It is well known that mammalian predators have the potential to affect not only the abundance of herbivores, but also their behavioural patterns (Ripple et al. 2010). For example, studies in

Yellowstone National Park have illuminated the influence of wolf predation on elk feeding behaviour (Ripple & Beschta 2004). Elk avoided grazing in areas that the new wolf populations commonly utilised, leading to a structuring of landscape usage by elk based on the fear of predation. This ‘ecology of fear’ has been successfully adapted and applied to many landscapes, including that of African savannahs (Riginos & Grace 2008).While the presence of larger predators might not directly impact mesopredator and hyaena (facultative scavenger) populations in terms of density or abundance, it may alter their periods of activity in order to avoid confrontation (Hayward & Hayward 2007; Yarnell et al. 2013). Temporal partitioning of predators was observed in India between two large felids, allowing for coexistence of two sympatric species (Ramesh et al. 2012). It has also been observed between subsidiary and apex predators in Southern Africa, primarily to avoid potential competition (Hayward & Slotow 2009). Our study did not analyse the potential for temporal or spatial portioning, because it focused rather on variation in abundance, and thus this top-down population control was excluded from the results. Such partitioning is likely to be present in KwaZulu-Natal’s protected areas, however this has yet to be demonstrated. Any further investigation should strive to include behavioural analyses, in order to fully encapsulate any type of top-down regulation by predators.

Distinguishing between bottom-up and top-down drivers of predator abundance is a notoriously difficult process. Various studies from Europe have shown that they are rarely independent of one another, and thus determining which is the more influential driver of predator abundance is problematic (Elmhagen & Rushton 2007; Elmhagen & Ludwig 2010; Pasanen-Mortensen et al. 2013).Often only prey size is used to try understand the complexity of predator trophic classes, however this fails to encapsulate the influence of predator-prey or predator-predator relationships in structuring trophic guilds (Owen-Smith & Mills 2008). In our study, the decline of mesopredator RAI as medium prey RAI increases may be the result of a complicated trophic cascade, whereby reduced predation classes, due to decreased mesopredator numbers, allow medium prey species to increase in abundance (Fig. 4). Additionally, prey population size may be influenced by the management of a protected area. In parks with more resources available, snaring, which primarily targets ungulates for consumption purposes but potentially traps predators, may occur at a lowered frequency. As anthropogenic drivers such as poaching or reserve management are considered to be top-down controls on predator populations, this further complicates the process of separating bottom-up from top-down controls.

Aside from having localised conservation management implications, this study's results have practical repercussions for mammalian predator management in protected areas across Southern Africa. Traditionally protected area size is used as a proxy for which predator species at what densities a reserve could potentially support. However this study illuminates the utility of long and short term camera trap surveys in assessing prey populations, and thus monitoring the health of local mammalian predator populations.

CONCLUSIONS

The findings of this study provide evidence in support of bottom-up processes, reliant on primary productivity, for structuring mammalian predator guilds. Mesopredator, facultative scavenger and an apex predator's RAI were strongly influenced by prey RAI in all four protected areas included in this study. These findings highlight the importance of maintaining healthy populations of large prey for improved mammalian predator conservation. This study also emphasizes the importance of long-term monitoring of both large predator and prey populations using landscape level camera trapping surveys.

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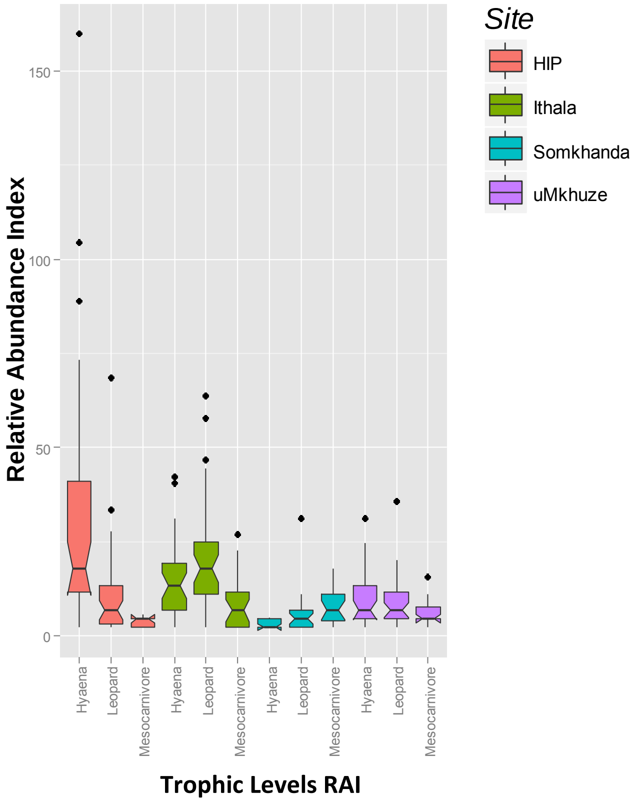
APPENDIX

Appendix I: Main characteristic of the four protected areas

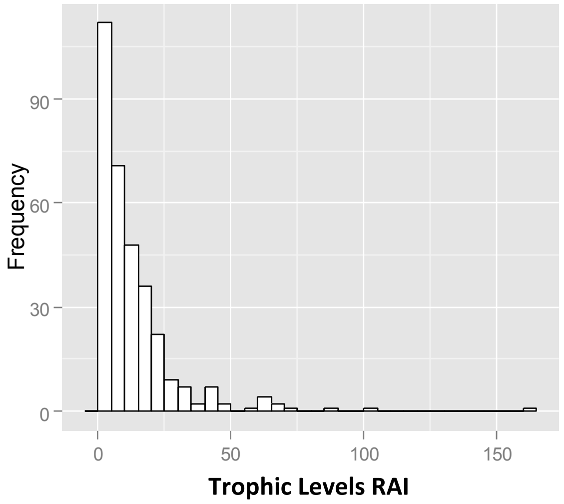
Site	**Carnivore Guild**	**Vegetation Type** (Scott-Shaw & Escott 2011)
Hluhluwe-iMfolozi Game Reserve	Intact	Zululand lowveld & coastal thronveld
iSimangaliso Wetland Park - Mkhuze section	Intact	Western Maputo Land clay bushveld & sandy bushveld
Somkhanda Community Reserve/ Zimanga Game Reserve	Incomplete	Zululand lowveld
Ithala Game Reserve	Incomplete	Ithala quartzite sourveld & Mabela sandy grassland

Appendix II: Packages utilized in this study, loaded into R studio 3.1.0

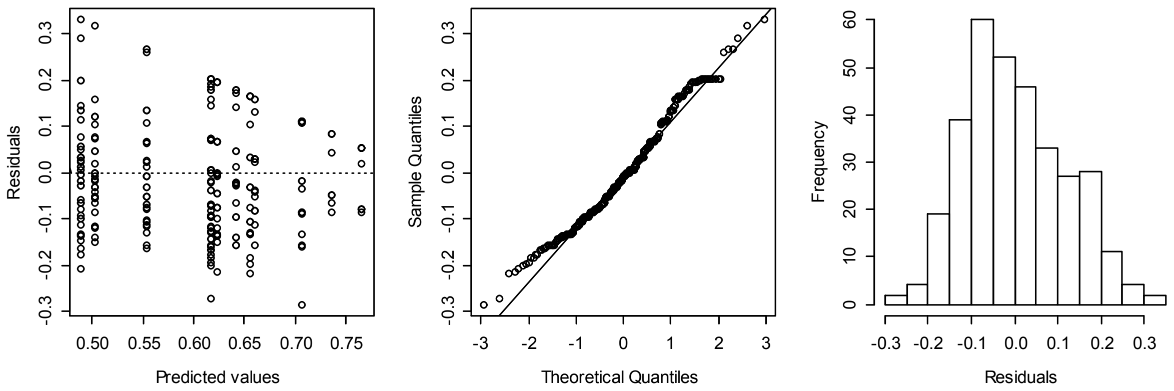
Package	**Author**
Gplots	Wickham (2009)
Ggplot2	Warnes et al. (2014)
Lme4	Bates et al. (2014)
AICmodavg	Mazerolle (2014)
nlme	Pinheiro et al. (2014)
gridExtra	Auguie (2012)
MASS	Venables & Ripley (2002)



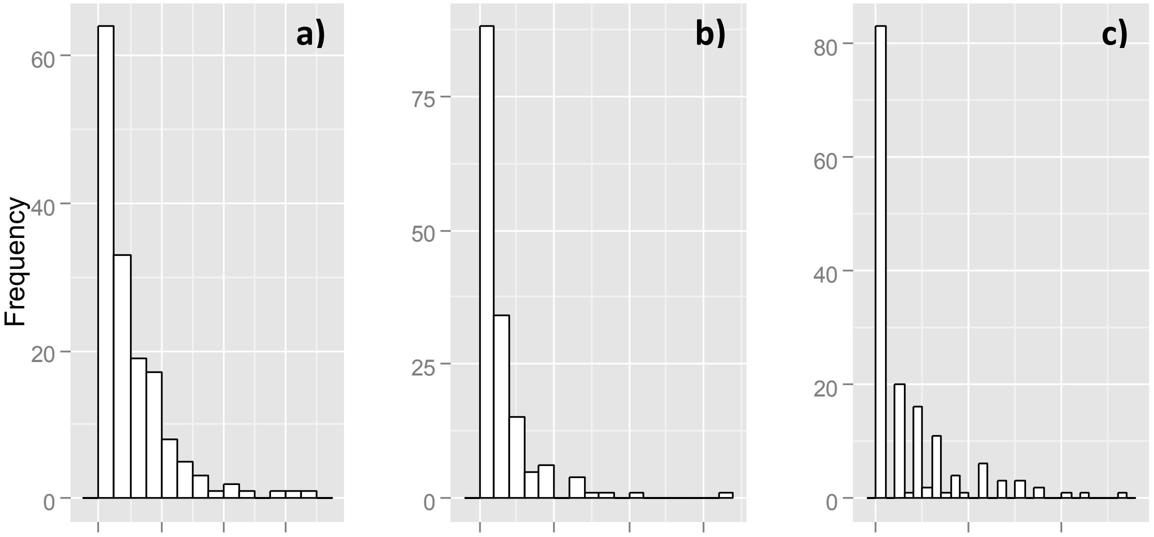
Appendix III: Boxplots showing variation in the RAI of trophic in relation to protected area. Notches are representative of approximate 95% confidence intervals of the median.



Appendix IV: Frequency distribution over a full range of protected areas RAI values for trophic classes species .



Appendix V: Model diagnostic plots for trophic classes. Slight bias present, but acceptable for the purposes of this study.



Appendix VI: Frequency distribution over a full range of protected areas RAI values for a) leopard, b) hyaena and c) mesopredators.

Appendix VII: Model selection values for mesopredator GLMM (where y is mesopredator RAI).

Model	AIC	BIC
$y = \beta_0 + \beta_1 small\ prey + \beta_7 (offset) trap\ days$	588.486	597.636
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_7 (offset) trap\ days$	581.198	593.398
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_7 (offset) trap\ days$	580.045	595.294
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_4 small\ carnivore + \beta_7 (offset) trap\ days$	577.863	596.163
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_4 small\ carnivore + \beta_5 large\ carnivore + \beta_7 (offset) trap\ days$	579.684	601.033

FINAL MODEL: $y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_4 small\ carnivore + \beta_7 (offset) trap\ days$

Appendix VIII: Model selection values for hyaena GLMM (where y is hyaena RAI).

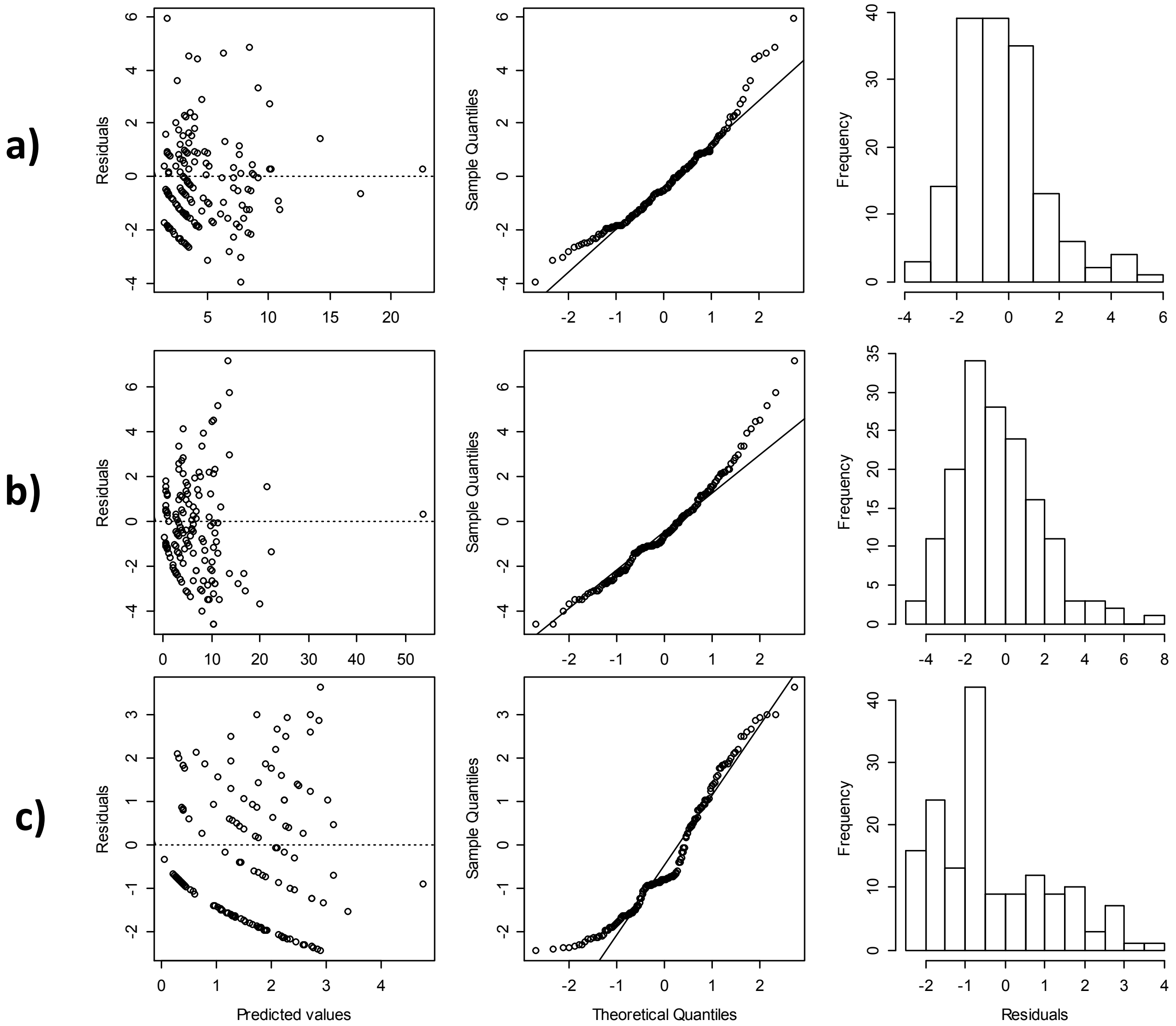
Model	AIC	BIC
$y = \beta_0 + \beta_1 small\ prey + \beta_7 (offset) trap\ days$	1265.084	1274.234
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_7 (offset) trap\ days$	12220.412	1232.611
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_7 (offset) trap\ days$	1212.254	1227.503
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_4 small\ carnivore + \beta_7 (offset) trap\ days$	1208.738	1227.038
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_4 small\ carnivore + \beta_5 medium\ carnivore + \beta_7 (offset) trap\ days$	1209.241	1230.590
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_4 small\ carnivore + \beta_5 medium\ carnivore + \beta_6 large\ carnivore + \beta_7 (offset) trap\ days$	1129.656	1129.656

FINAL MODEL: $y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_4 small\ carnivore + \beta_5 medium\ carnivore + \beta_6 large\ carnivore + \beta_7 (offset) trap\ days$

Appendix IX: Model selection values for leopard GLMM (where y is leopard RAI).

Model	AIC	BIC
$y = \beta_0 + \beta_1 small\ prey + \beta_7 (offset) trap\ days$	980.237	989.387
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_7 (offset) trap\ days$	940.774	952.973
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_7 (offset) trap\ days$	942.721	957.970
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_4 small\ carnivore + \beta_7 (offset) trap\ days$	944.408	962.707
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_4 small\ carnivore + \beta_5 medium\ carnivore + \beta_7 (offset) trap\ days$	946.404	967.753
$y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_4 small\ carnivore + \beta_5 medium\ carnivore + \beta_6 large\ carnivore + \beta_7 (offset) trap\ days$	910.274	934.673

FINAL MODEL: $y = \beta_0 + \beta_1 small\ prey + \beta_2 medium\ prey + \beta_3 large\ prey + \beta_4 small\ carnivore + \beta_5 medium\ carnivore + \beta_6 large\ carnivore + \beta_7 (offset) trap\ days$



Appendix X: Model diagnostic plots for a) leopard, b) hyaena and c) mesopredator GLMM's. Slight bias present in a) and b), but acceptable for the purposes of this study (homoscedastic for the most part). Model diagnostics acknowledged to not be ideal in c), however as the theoretical quantiles correlate well, and there is an acceptable spread of residuals around predicted values, the final model is accepted.