

Factors influencing pride dominance, space-use and hunting success of sympatric lion prides in a semi-arid savanna landscape (#89660)

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Factors influencing pride dominance, space-use and hunting success of sympatric lion prides in a semi-arid savanna landscape

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Understanding lions' (*Panthera leo*) space-use is important for the management of multi-species wildlife systems because lions can have profound impacts on ecosystem-wide ecological processes. Semi-arid savanna landscapes are typically heterogeneous with species space-use driven by the availability and distribution of resources. Previous studies have demonstrated that lions select habitats close to water as encounter rates with prey are higher and hunting success is greater in these regions. Where multiple lion prides exist, landscape partitioning is expected to follow an ideal despotic distribution in which competitively superior prides occupy high-quality ~~key resource~~ areas while subordinates select poorer habitats. In this study, Global Positioning System collar data and logistic regression were used to investigate space-use and kill distribution among three lion prides at Malilangwe Wildlife Reserve, Zimbabwe. Our findings show that lion space-use was driven by surface water availability and that home range selection was hierarchical with the dominant pride occupying habitat in which water was most abundant. In addition, we found that the effect of shrub cover, clay content and soil depth on kill probability was habitat specific and not influenced by hierarchical dominance. Where multiple lion prides are studied, we recommend treating prides as individual units because pooling data may obscure site and pride specific response patterns. Given that lion space-use can be indirectly impacted by the manipulation of surface water, our findings could have management relevance for both lions and their prey.

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Abstract

Understanding lions' (*Panthera leo*) space-use is important for the management of multi-species wildlife systems because lions can have profound impacts on ecosystem-wide ecological processes. Semi-arid savanna landscapes are typically heterogeneous with species space-use driven by the availability and distribution of resources. Previous studies have demonstrated that lions select habitats close to water as encounter rates with prey are higher and hunting success is greater in these regions. Where multiple lion prides exist, landscape partitioning is expected to follow an ideal despotic distribution in which competitively superior prides occupy high-quality key resource areas while subordinates select poorer habitats. In this study, Global Positioning System collar data and logistic regression were used to investigate space-use and kill probability among three lion prides at Malilangwe Wildlife Reserve, Zimbabwe. Our findings show that lion space-use was driven by surface water availability and that home range selection was hierarchical with the dominant pride occupying habitat in which water was most abundant. In addition, we found that the effect of shrub cover, clay content and soil depth on kill probability was habitat specific and not influenced by hierarchical dominance. Where multiple lion prides are studied, we recommend treating prides as individual units because pooling data may obscure site and pride specific response patterns. Given that lion space-use can be indirectly impacted by the manipulation of surface water, our findings could have management relevance for both lions and their prey.

Introduction

Understanding why animals occur where they do is a cornerstone of ecology (Burt 1943; Krebs 1980; Powers and McKee 1994). ~~Where animals spend most of their time in a habitat is~~ determined by a complex interplay of social and environmental factors (Davies et al. 2016;

Moyer et al. 2008). Prey availability and catchability are major factors driving patterns of space-use among large carnivores (Davidson et al. 2012; Hopcraft et al. 2005; Ogutu and Dublin 2004), but for gregarious species, access to profitable areas may be moderated by social pressures (Struhsaker 1967). Lions (*Panthera leo*) are an important focal species in most conservation and tourism-based systems (Loveridge et al. 2009) and as an apex predator, understanding their space-use patterns and predation dynamics is important for informing management decisions on carrying capacities and herbivore stocking rates (Webb et al. 2008; Tambling et al. 2010; McPhee et al. 2012). Despite extensive research on lion ecology, the determinants of space-use and hunting success in savanna environments are not fully understood. Furthermore, generalizations can be misleading because prey assemblages, social and demographic factors as well as environmental conditions differ between prides, home ranges and protected areas. As such, studies that consider both environmental and social factors at the inter-pride level could provide valuable insights into lion behaviour; an aspect of lion ecology that has been under explored.

Semi-arid savanna landscapes are typically heterogeneous, with resources patchily distributed and habitats varying in quality (Gaillard et al. 1998; Jetz et al. 2004). Habitat quality is determined by environmental conditions with surface water availability being the primary factor limiting the distribution of herbivore populations (Owen-Smith 1996; Redfern et al. 2003; Valeix et al. 2009). Most herbivores need to drink regularly and, as such, areas close to water sources are usually associated with large aggregations of game and, in turn, have a pull effect on predators (De Boer et al. 2010; Cain et al. 2012). Several studies have demonstrated that lions select habitats close to water as these provide increased encounters with prey and associated hunting success (Duncan et al. 2012; Harrington et al. 1999; Kittle et al. 2022; Owen-Smith 1996; Valeix et al. 2010). Intrinsically, such areas are profitable to lions as they provide the least energetic cost to acquire food (Mitchell and Powell 2004). Where multiple prides exist, landscape partitioning is expected to follow an ideal despotic distribution (Fretwell and Lucas 1969) in which competitively superior prides occupy high-quality key resource areas forcing subordinates into sub-optimal habitats. When this occurs, prides are expected to respond to environmental determinants of space-use in accordance with their position in the dominance hierarchy. For example, distance from permanent surface water is predicted to have a strong negative effect for the dominant pride, a medium negative effect for prides mid-way in the dominance hierarchy, and a weak negative or even a positive effect for the most subordinate prides, meaning that dominant prides are expected to be positively associated with surface water. Knowledge of this effect is important because where it occurs, analyses of space-use that pools data across prides may yield spurious results. The aim of this study was to test this hypothesis at the scale of home range and kill site selection.

~~Global Positioning System (GPS) collar data were used to investigate choice of home range and the distribution of kills among three lion prides at Malilangwe Wildlife Reserve (MWR), Zimbabwe. Specific objectives were to examine the functional relationships between~~

lion home range selection and hunting success, and likely determinants of prey density viz. (i) distance to permanent surface water, (ii) shrub canopy cover and (iii) soil properties. Previous studies have shown that the presence of surface water in an environment improves conditions for lion kill success (De Boer et al. 2010; Hopcraft et al. 2005; Orsdol 1984; Venter et al. 2003) and that group size plays a role in shaping hierarchy dynamics among prides, with large prides routinely outcompeting smaller ones (Alexander 1974; Hamilton 1971; Packer et al. 1990; Wilson 1975). This study hypothesized that the availability of surface water has an influence on lion space-use and kill location, and that the dominant lion pride would occupy the key resource habitat within the study area, with subordinate prides occupying decreasingly profitable habitats with associated declines in hunting success. ~~Our findings may provide useful information for the analysis of space-use by predators and for managing the landscape, its components and prey populations.~~

Method

Study area

The study was conducted at MWR which is located in the south-eastern lowveld of Zimbabwe between 20°58' and 21°15'S and 31°47' and 32°01'E (Figure 1). MWR is a non-hunting property whose main objectives are conservation and community development (Ball et al. 2019). The reserve is approximately 490 km² in size and altitude ranges from 290 m, in river systems, to 500 m above sea level on hills (Traill and Bigalke 2007). Rainfall (mean ≈ 560 mm per year) is seasonal with approximately 84 % of precipitation occurring between November and March and the average minimum and maximum monthly temperatures ranging from 13.4 °C (July) to 23.7 °C (December) and 23.2 °C (June) to 33.9 °C (November) respectively (Clegg and O'Connor 2012). The southern boundary, bordering Gonarezhou National Park has a short fence that allows some movement of carnivores and plains game but restricts the movement of large herbivores.

Although soils vary, they are principally derived from alluvium, sandstone, gneiss and basalt (Clegg and O'Connor 2012). Vegetation types at MWR can be broadly classified as riverine, hill miombo, mopane (*Colophospermum mopane*) veld, thorn thicket and open woodland (Clegg and O'Connor 2012). Hills are largely dominated by redwood (*Brachystegia tamarindiodes*) and mmondo (*Julbernardia globiflora*) tree species, while low lying areas are characterized by mixed broadleaf woodland. The grass layer on MWR is mostly composed of *Urochloa mossambicensis*, *Heteropogon contortus*, *Digitaria eriantha* and *Aristida spp.* A wide variety of prey species inhabit the heterogenous landscape including Cape buffalo (*Syncerus caffer*), zebra (*Equus burchellii*) and impala (*Aepyceros melampus*) among other antelope species. Competing predators of lions include leopards (*Panthera pardus*), spotted hyenas (*Crocuta crocuta*) and wild dogs (*Lycaon pictus*).

Collaring of animals

Three independent lion prides (Banyini $n = 12$, Nduna $n = 6$ and Hlamba mlonga $n = 4$) were identified for collaring at MWR. Between February 21 and August 02, 2004, three GPS/drop-off collars (Televilt, Lindesberg, Sweden) were fitted onto either an adult male or female member of each pride. Subjects were chemically immobilized with a combination of Zoletil-Medetomidine (1.0-20 mg/kg body mass), with the anaesthetic being darted into the muscular region of the hindquarters. Reversal was achieved by subcutaneous injection of Antisedan (at 2.5 mg/mg of Medetomidine) or Yohimbine (at 1 ml/50 kg of body weight) and subjects were monitored until they fully recovered from the effects of the anaesthesia. Safe, professional, and humane animal care guidelines stipulated by the Scientific Experiments on Animals Act of Zimbabwe (Chapter 19:12 of 1963) and Olfert et al. (1993) were adhered to. The National Animal Research Ethics Committee of Zimbabwe approved the study protocols (permit number: NAREC/008/23) and all animal handling procedures were performed by a licensed practitioner (with Zimbabwean Dangerous Drugs License number: 034/2004). Three other lion prides were present in the study area [Matsanga ($n = 10$, north-western section), Chiloveka ($n = 8$, south-western section) and Tennis Court ($n = 6$, south-eastern section)] over the period under investigation but were not included in this study.

Collar and kill data collection

Collars were programmed to fix a GPS position at 30-min intervals from 16:15 to 07:15 and at two 3-hourly intervals during the hottest part of the day, when lions are presumed to be less active (i.e., 33 positions per day). For all prides, collars broadcasted Very High Frequency (VHF) signals on Mondays, Wednesdays and Fridays. The lion prides were tracked in the field using VHF telemetry and GPS data were remotely downloaded and stored onboard a Televilt RX-900 terminal (Followit, Lindesberg, Sweden). Downloaded points were transferred onto a laptop computer and uploaded into CartaLinx v1.2, a GIS software, for the identification of potential kill sites.

A potential kill site was defined as a cluster of ≥ 3 consecutive GPS positions located within a 50 m radius of each other i.e., a location where a pride spent at least one and a half hours without moving. A single point that was central within the cluster was chosen as a reference for the location of the site. The coordinates of potential kill sites were relayed to field scouts who visited the locations. At the site, the surroundings were inspected for evidence of a kill. Data recorded included the presence or absence of a kill, the species of animal killed, identification method (bones, fur, horns etc.), estimated time of kill and possible lion pride composition.

Data analysis

This study posited that broad-scale (study area) ranging and fine-scale (kill site) hunting success of lions at MWR were influenced by both environmental and social factors. The following underlying assumptions were made: (i) surface water availability influenced the distribution of prey and consequently space-use and hunting success of lions, (ii) home range selection among prides was predicated on competitive dominance and (iii) vegetation cover influenced lion hunting strategy and success. In addition, we theorized that soil depth and clay content determine plant available moisture and hence forage quality thereby influencing herbivore and lion distributions. For an environmental variable to be considered important, it must be statistically significant and able to elicit a consistent response across all prides. Because previous studies have demonstrated that large groups outcompete smaller ones (Adams 2001; Carlson 1986; Cheney 1992; Grinnell et al. 1995; Packer et al. 1990; Wilson and Wrangham 2003) and occupy higher quality territories (Kauffman et al. 2007; Mosser and Packer 2009; Woolfenden and Fitzpatrick 1984), we used pride size as a proxy for social dominance.

Landscape level home range selection

Minimum convex polygons (MCPs) delineating each lion pride's home range were constructed using GPS presence data in Quantum GIS v3.26 (QGIS Development Team 2022) and their sizes calculated. Resource selection models that incorporate both presence and absence data generally outperform presence-only methods in explaining ecological variation among data (Brotons et al. 2004; Engler et al. 2004). Logistic regression is used extensively to explain variation in binomially distributed data (McCullagh and Nelder 1989), but because GPS collar data reports only presence information, the data is non-binomial, precluding the use of logistic regression on the raw data. To address this issue "pseudo-absence" points are generated to produce a combined presence-absence dataset for use in the logistic regression analyses (Odendaal-Holmes et al. 2014).

To determine which environmental parameters were important for home range selection, each pride's location fixes were overlaid onto MWR's base map as training sites for spatial distribution modelling in MaxEnt v3.4 (Phillips et al. 2006). MaxEnt uses presence data together with environmental variables to model an approximation of a species' niche within the geographical bounds of its environment (Phillips et al. 2006). Presence locations and the associated environmental attributes (distance to surface water, shrub canopy volume, soil depth, clay content) were used to model the suitability of MWR's landscape in relation to each pride's space-use choices. Habitats classified as suitable were those in which 95 % of a pride's presence positions were recorded. Using this threshold, a habitat suitability map was created for each pride and reclassified to produce two categories: suitable and unsuitable.

Using QGIS, a set of spatially independent randomly distributed points (absence data) equal to the number of each pride's presence points was generated within the unsuitable habitat of each pride. The full extent of MWR's landscape was considered available to each pride when generating the absence data. Next, a raster surface of permanent water locations across the study area was created by mapping point (permanent pans, springs and dams) and linear (perennial streams and rivers) sources from digital aerial photographs and the DISTANCE module of TerrSet (Eastman 2015) was used to calculate Euclidean distances between the presence and absence points and their nearest water sources. Similarly, data for shrub canopy volume, soil depth and clay content were extracted for the presence and absence points using respective maps created from a 2003 dataset [see Clegg and O'Connor (2012) for how these maps were created].

The R statistical platform was used to perform logistic regression analysis to determine the effects of the environmental variables on the outcome of each pride's ranging behaviour (Bates et al. 2014; R Development Core Team 2017). *Presence probability* (presence or absence) was used as a response variable while *distance to water, shrub canopy volume, soil depth and clay content* were treated as fixed effects:

Presence probability ~ *distance to water + shrub canopy volume + soil depth + clay content.*

From model results, significance values (at $\alpha = 0.05$) were used to identify environmental factors that were important in determining the ranging choices of each pride and the relationships plotted using marginal effects.

Home range level kill site selection

Within each pride's home range, we theorized that the location of sites where lions made kills was not random but that kill locations were a result of a combination of favourable environmental conditions. Following the methodology described above, kill data and environmental variables were used in MaxEnt to model fine-scale habitat suitability for kill success for each lion pride. An equal number of pseudo-absence points as kill locations were placed in the no-kill habitat and values of environmental variables extracted for use in logistic regression with *kill probability* being used as the response variable.

Game encounter within home ranges

The density of prey present in an environment influences the hunting success of resident prides (De Boer et al. 2010; Mitchell and Powell 2004). We assumed that prey encounter rates (number of groups identified per search effort) were positively correlated to lion kill rates, with home ranges having high encounter rates expected to have correspondingly higher kill rates. Prey

species population and distribution data were obtained from MWR's 2004 census data. Malilangwe Wildlife Reserve conducts annual aerial game surveys where the entire property is flown by helicopter at a height of 90 m above the ground at an average air speed of 50 knots along predetermined transects spaced 1 km apart (Clegg 2011). The number of groups of eligible prey species encountered during the 2004 aerial game census were recorded and values for prey encounter rates were derived and allocated to each of the subject pride's home ranges for comparison with lion hunting success and space-use.

Results

A total of 2 994 presence points (Banyini $n = 1\,935$, Nduna $n = 323$, Hlamba mlonga $n = 736$) and 146 confirmed kills (Banyini $n = 67$, Nduna $n = 42$, Hlamba mlonga $n = 37$) were recorded over the study period (Figure 2). The Banyini pride, being the largest in size, was considered the most dominant, followed by the Nduna pride and lastly, the Hlamba mlonga pride which was smallest in size. Analysis showed that the most dominant pride (Banyini) occupied a home range in which the average distances to water was shortest, while the least dominant (Hlamba mlonga) was found in habitats where the average distance to water was longest (Table 1). In addition, intervals between kills decreased with increasing pride size and home range size was negatively correlated with pride size (Figure 3), meaning that larger prides kill more often despite inhabiting smaller home ranges.

Influence of environmental factors on home range selection

The Banyini pride showed a strong ($P < 0.01$) negative response to distance from surface water (most presence points for this pride were < 4 km from water) (Table 2, Figure 5). The Nduna pride, which was next in the dominance hierarchy, also showed a negative response to distance from water but the effect was weaker ($P < 0.15$). In contrast, the Hlamba mlonga pride, which was least dominant, showed a strong ($P < 0.01$) positive response to distance from water. The change in direction and strength of the response across the prides was consistent with our predictions of how position in the social hierarchy would modify the response to an environmental variable, with the dominant pride selecting habitats closest to surface water and the least dominant pride relegated to marginal landscapes where surface water was relatively scarce, and the middle pride occupying a home range with conditions somewhere in between the two extremes.

Home range selection appeared to be influenced by shrub cover, soil clay content and soil depth but responses to these variables were neither consistent among prides, nor aligned with the predicted effects of hierarchical dominance.

Influence of environmental factors on kill location

Soil clay content ($P < 0.001$), soil depth ($P < 0.01$) and shrub canopy cover ($P < 0.05$) were significantly associated with kill site for the Banyini pride, while shrub cover ($P < 0.01$) and clay content ($P < 0.05$) were significant for the Nduna and Hlamba mlonga prides respectively (Table 3). Distance to water was not significantly associated with kill location for any of the prides (Table 3). Lion prides' responses to the environmental variables measured were not consistent, for example kill location was negatively and positively related to shrub canopy volume for the Banyini and Nduna prides respectively. Overall, the relationship between environmental variables and kill probability was weaker (large confidence intervals around the mean) compared to that with presence probability (Figures 5 and 6).

Discussion

Understanding where animals spend their time in an environment is a central tenet of ecology (Powers and McKee 1994; Stephens and Krebs 1986). The factors that underpin home range choice and hunting success among carnivores have been extensively explored (Brown and Kotler 2004; Davies et al. 2016; Fryxell 1991) yet knowledge gaps remain. Investigating animal behaviour in the field is challenging as monitoring is often invasive and can affect spatial and social behaviour as well as the foraging success of subjects (Carney and Sydeman 1999; Queiroz and Young 2018). Advances in GPS technology have facilitated the remote collection of data on dangerous game and study animals in inaccessible terrain (Knopff et al. 2009; Zimmermann et al. 2007); and it has eliminated the need for regular disturbance of subject animals. This study used GPS data to investigate the influence of environmental conditions and hierarchical dominance on the space-use and hunting success of three lion prides at MWR, Zimbabwe. Our findings showed that surface water was a key determinant of lion space-use and that pride dominance influenced home range selection among sympatric prides.

Factors influencing lion ranging and feeding ecology at MWR

Our study demonstrated that of the environmental variables measured, only distance from water reflected the predicted pride hierarchical response. Areas close to water are ordinarily associated with large aggregations of game thereby facilitating higher prey encounter and kill rates (Redfern et al. 2003; Valeix et al. 2009). Our findings were consistent with the work of Owen-Smith (1996), Harrington et al. (1999), Valeix et al. (2010), De Boer et al. (2010), Cain et al. (2012), Duncan et al. (2012) and Kittle et al. (2022) who have also shown that lions preferentially select habitats in which surface water is abundant. The ideal free distribution model (Fretwell and Lucas 1969) has been widely used to demonstrate how resource availability and competition influence animal space-use where habitat quality varies. Our findings support our hypothesis that pride dominance determines home range selection among lions at MWR with the Banyini pride,

which was the most dominant in size, occupying the central section of the reserve, which was well-endowed with water, while the Nduna (intermediate dominance) and Hlamba mlonga (least dominant) prides selected the northern and southern sections with intermediate and low levels of surface water, respectively. Group size is a key determinant of pride strength (Packer et al. 1990) and this is supported by earlier studies that document large prides routinely outcompeting smaller ones in inter-pride conflicts (Bertram 1978; Packer et al. 1990) to occupy higher quality territories (Kauffman et al. 2007; Mosser et al. 2009). Where unrestricted, a pride is expected to select the most profitable habitat the landscape offers (Larson 1980; Mitchell and Powell 2004; Morris 2003) and we postulate that had either the Nduna or the Hlamba mlonga pride had sole jurisdiction over the study area, they too would have selected the home range occupied by the Banyini pride.

Shrub cover, soil clay content and soil depth exhibited neither a consistent pattern nor hierarchical dominance in response to space-use by the three prides studied at MWR. As such, these variables were regarded lower order, and the associated responses inconsequential. We posit that once a home range has been selected based on the availability of surface water within the constraints of dominance hierarchy, a pride must make do with the configuration of lower order environmental attributes found in that habitat. At the resolution of our data, home range level responses were more ecologically significant while kill site responses were weaker and habitat specific. This was probably because explanatory data for kills were not collected at the actual kill sites but were coarse averages derived at the scale of a vegetation map unit [see Clegg & O'Connor (2012)]. Within a vegetation unit there are variations in shrub canopy cover, clay content and soil depth. Obtaining kill site specific measurements would have improved the resolution of these data but resources for the study were limited. Contrary to our hypothesis, proximity to surface water did not significantly influence kill probability. This outcome may be explained by prey species associating areas close to water with higher predation risk and so increasing vigilance in these areas (Tuytens 2019; Valeix et al. 2007).

Where a generalized population-level response is required, it is common practice to pool observations from several groups belonging to the same population (Barker et al. 2023; Machlis, et al. 1985). However, in this study it was observed that while the lions belonged to the same ecological system, the interaction of individual prides with their immediate environments differed and in this case pooling data would hide pride and habitat specific response patterns and produce flawed inferences. This is because pooling data assumes non-independence among intergroup observations and where such does not hold true the approach is likely to obscure functional differences that may exist between groups (Aebischer, et al. 1993; Kuhar 2006; Pollet et al. 2015). For example, an earlier analysis that was run using a pooled dataset produced a no relationship response between lion position data and distance from water, yet this was a key factor which lost significance when averaging directly opposing response patterns. Where lion ecology is studied and multiple prides are investigated, we recommend treating study prides as individual units. This is because the configuration of components and resources found in each

pride's home range vary and, likewise, each pride's adaptations and interaction with its bounding habitat may be different. Where baseline information is not available, it is advisable to model ecological interactions from primary parameters (soil, water, vegetation) as secondary data (e.g., game census statistics) may not be readily available or are costly to generate.

Management implications

In this study we show that surface water availability is a key driver of lion space-use in semi-arid environments, and as such it can be manipulated to control lion ecology across the landscape. The introduction of permanent water in previously arid environments favours population growth of water-dependent game species thereby improving conditions for lion success (De Boer et al. 2010; Kittle et al. 2022). For example, in Kruger National Park, South Africa the number of water points was increased across the park between 1939 and 1989 with a view to improving conditions for game, but this triggered an increase in lion numbers precipitated by a proliferation of prey over a wider area of the landscape (Bryden 1976; Grant et al. 2002; Harrington et al. 1999; Mills et al. 1995; Owen-Smith 1996; Smuts 1978). Access to prey is a key determinant of home range size among carnivores (Brown and Kotler 2004; Loveridge et al. 2009; Mosser et al. 2009). Where prey is abundant (synonymous with habitats that are well-endowed with water), lion home range sizes are generally small and vice-versa (Joshi et al. 1995; Macdonald and Carr 1989; Mills and Knowlton 1991).

Even though study prides did not show consistent responses to soil clay content, soil depth and shrub cover, the additive effect of these factors is important in defining habitat quality and, by extension, prey abundance and catchability (Hopcraft et al. 2005). Among the lower order variables, shrub cover is the one that can be easily manipulated by property managers either to open up or revegetate sections of veld depending on management's goals. Earlier studies have shown that vegetation cover is an important factor in predator-prey interactions with both predators and prey using the cover of vegetation to their advantage, i.e., either to aid or evade predation (Davidson et al. 2012; Hebblewhite et al. 2005; Hopcraft et al. 2005; Orsdol 1984; Spong 2002). In this study, lion prides made kills in both open and closed habitats thus exhibiting behavioural plasticity with respect to hunting habitat selection and strategy. This implies that in heterogenous environments management should maintain open and closed habitats as both are functionally important to the space-use and feeding ecology of lions.

The lion population at MWR follows an ideal despotic distribution with the dominant pride inhabiting the key resource habitat and the most inferior pride occupying marginal habitat where surface water availability was limited. While marginal areas may be less profitable in terms of lion hunting, they are ecologically important to conservation managers as they serve as foraging grounds and refugia for species such as sable (*Hippotragus niger*) and Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*). Sable and hartebeest prefer taller grass which is usually found further from surface water due to reduced grazing pressure. In addition, the limited

utilisation of these areas by water-dependent species results in reduced competition for food, low tick loads and low predator presence (Cain et al. 2012; Capon et al. 2013; Harrington et al. 1999). The existence and preservation of such habitats at MWR is considered to have contributed to the persistence of sable and Lichtenstein's hartebeest's populations on the property (Capon et al. 2013; Clegg et al. 2013).

Conclusions

This study has demonstrated that both social and environmental factors influence the ranging decisions and hunting success of lions at MWR. Most studies have focused on top-down processes of predator-prey interactions as the primary drivers and determinants of carnivore space-use choices. However, considering space-use and predation patterns in isolation from environmental and social factors does not provide a holistic understanding because ranging decisions are influenced by an interplay of biotic, abiotic and co-existence factors. Our findings confirm the hypothesis that the availability of surface water across the landscape influences space-use decisions of lions and shows that social dominance determines where in the landscape individual prides acquired their nutrition. Given that landscape level surface water availability can be manipulated by property managers to direct lion space-use, our findings have management relevance for both lions and their prey.

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Figure 1

Location of the study area.

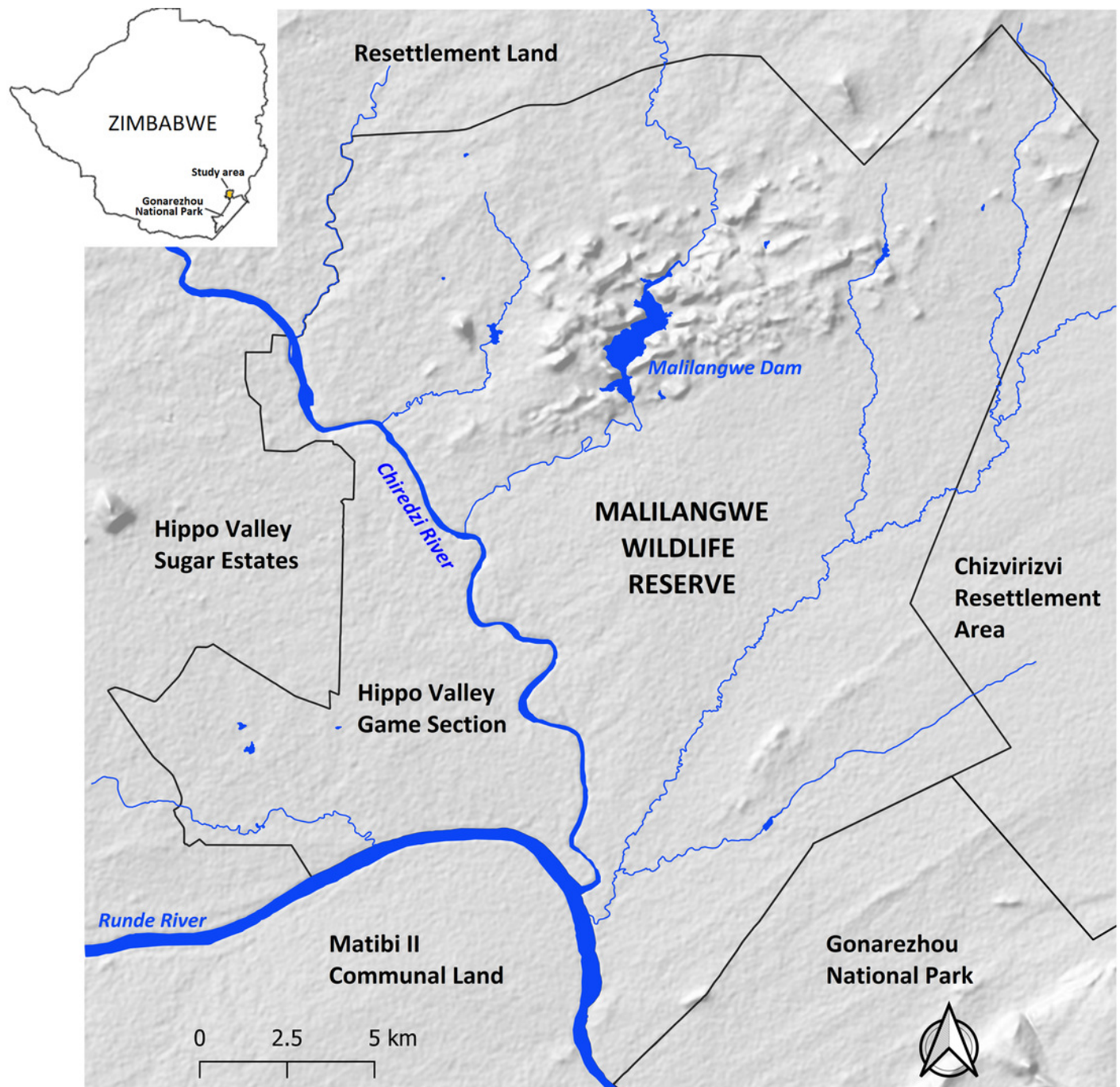


Figure 2

Map showing the location of home ranges and kill locations of the three study lion prides.

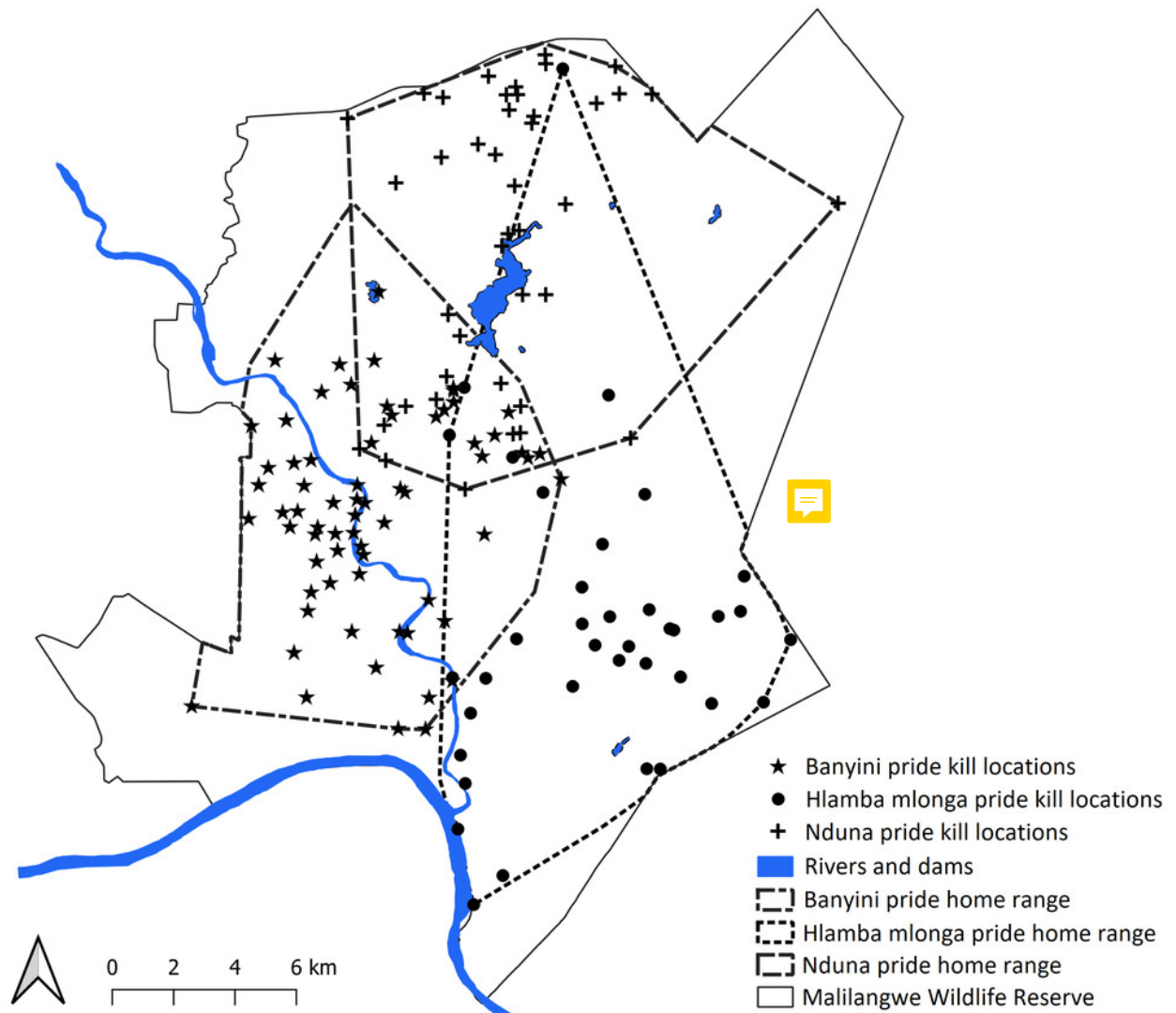
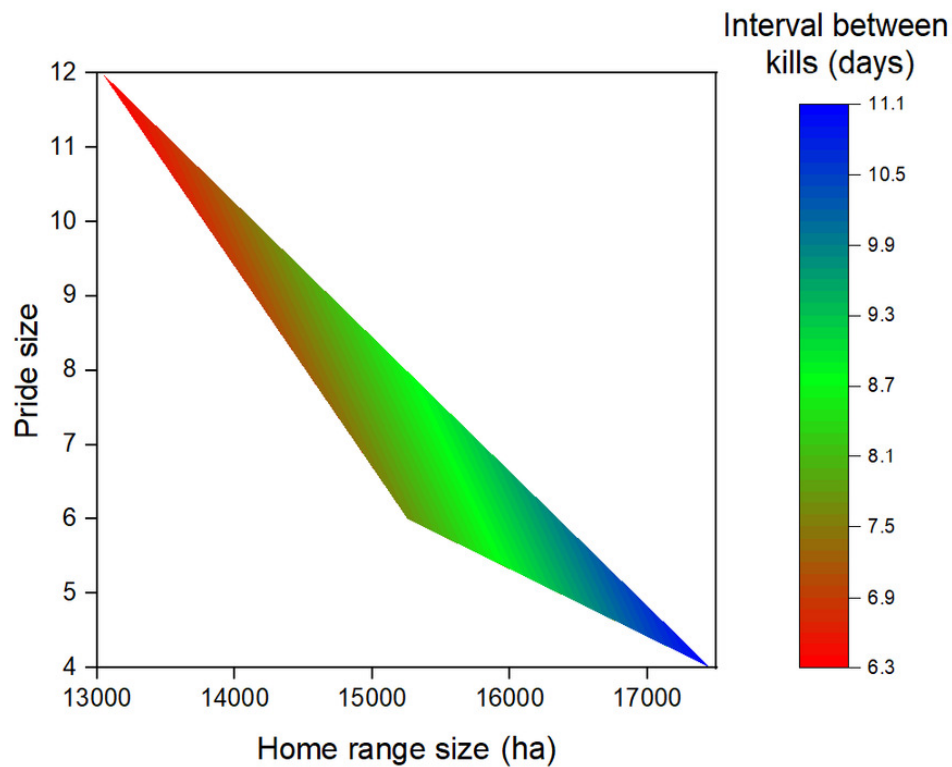
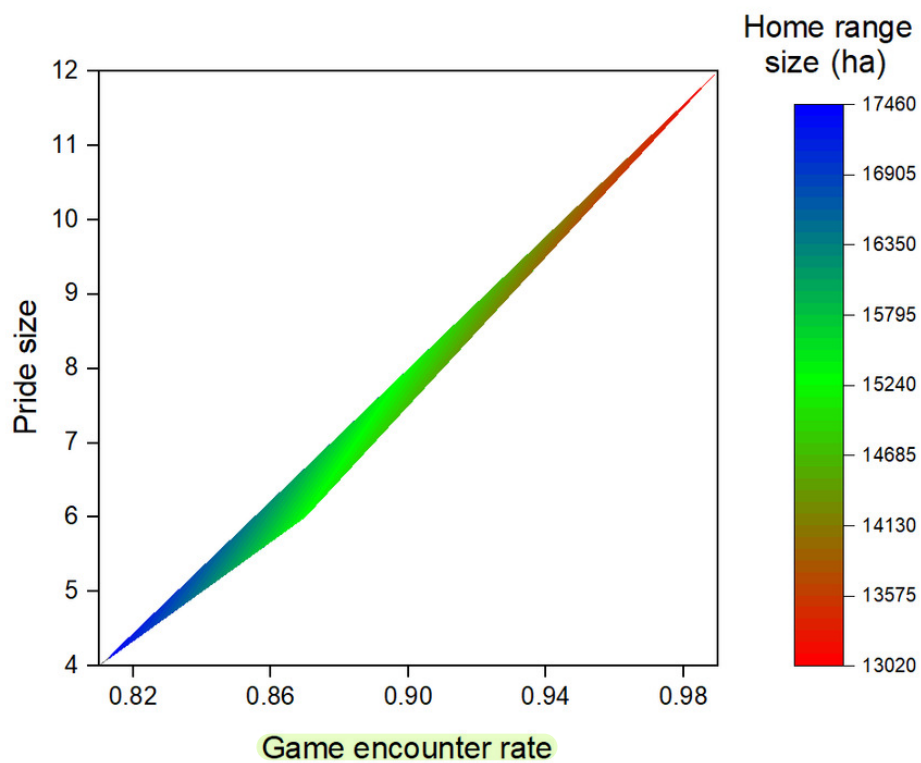


Figure 3

Contour plots showing the relationships between pride size, home range size, interval between kills and game encounter rate.



A



B

Figure 4

Panel chart showing the relationship between the probability of lion presence and the logistic regression marginal effects of distance to water, shrub canopy volume, soil clay content and soil depth.

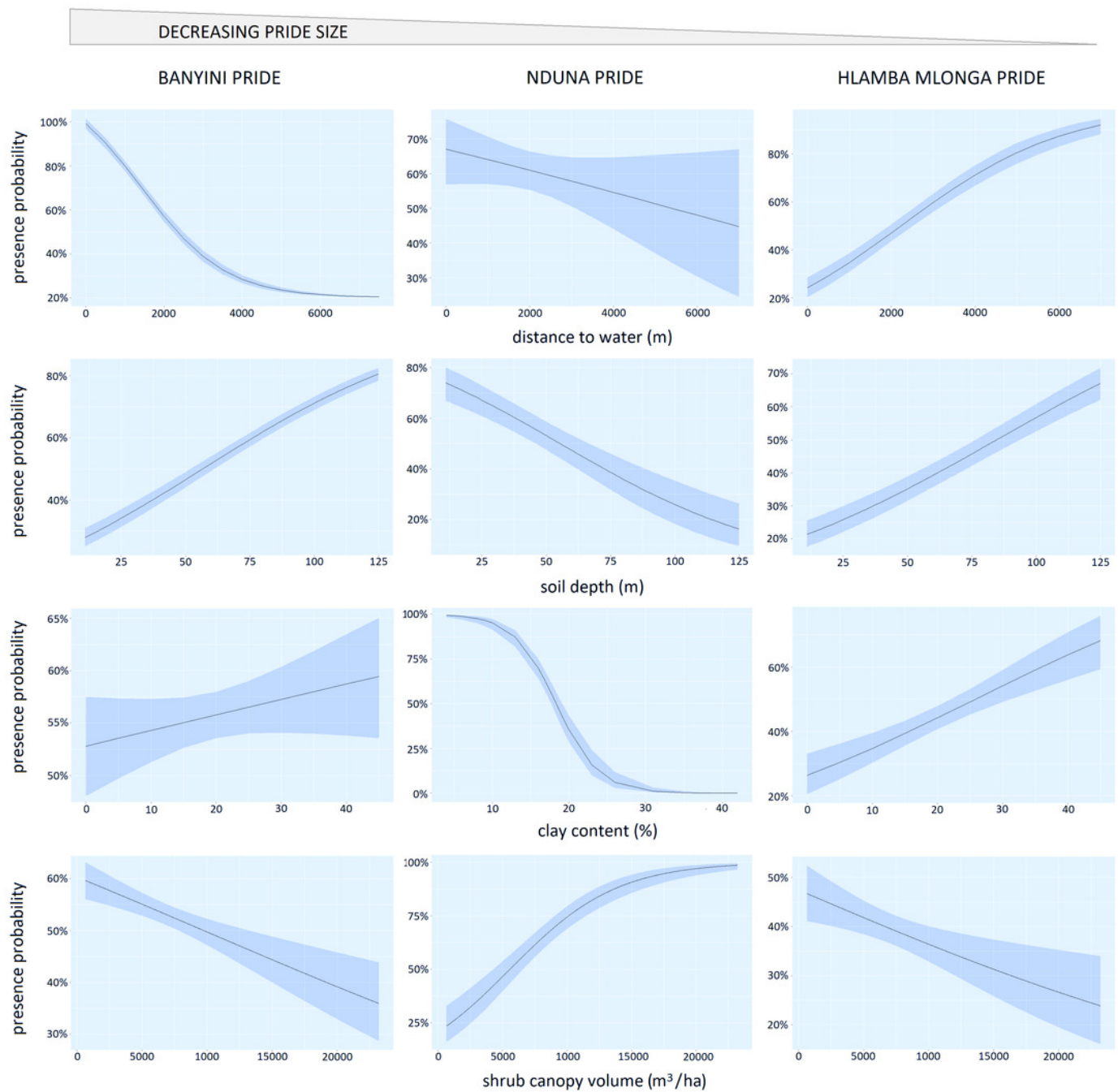


Figure 5

Panel chart showing the relationship between kill probability and the logistic regression marginal effects of distance to water, shrub canopy volume, soil clay content and soil depth.

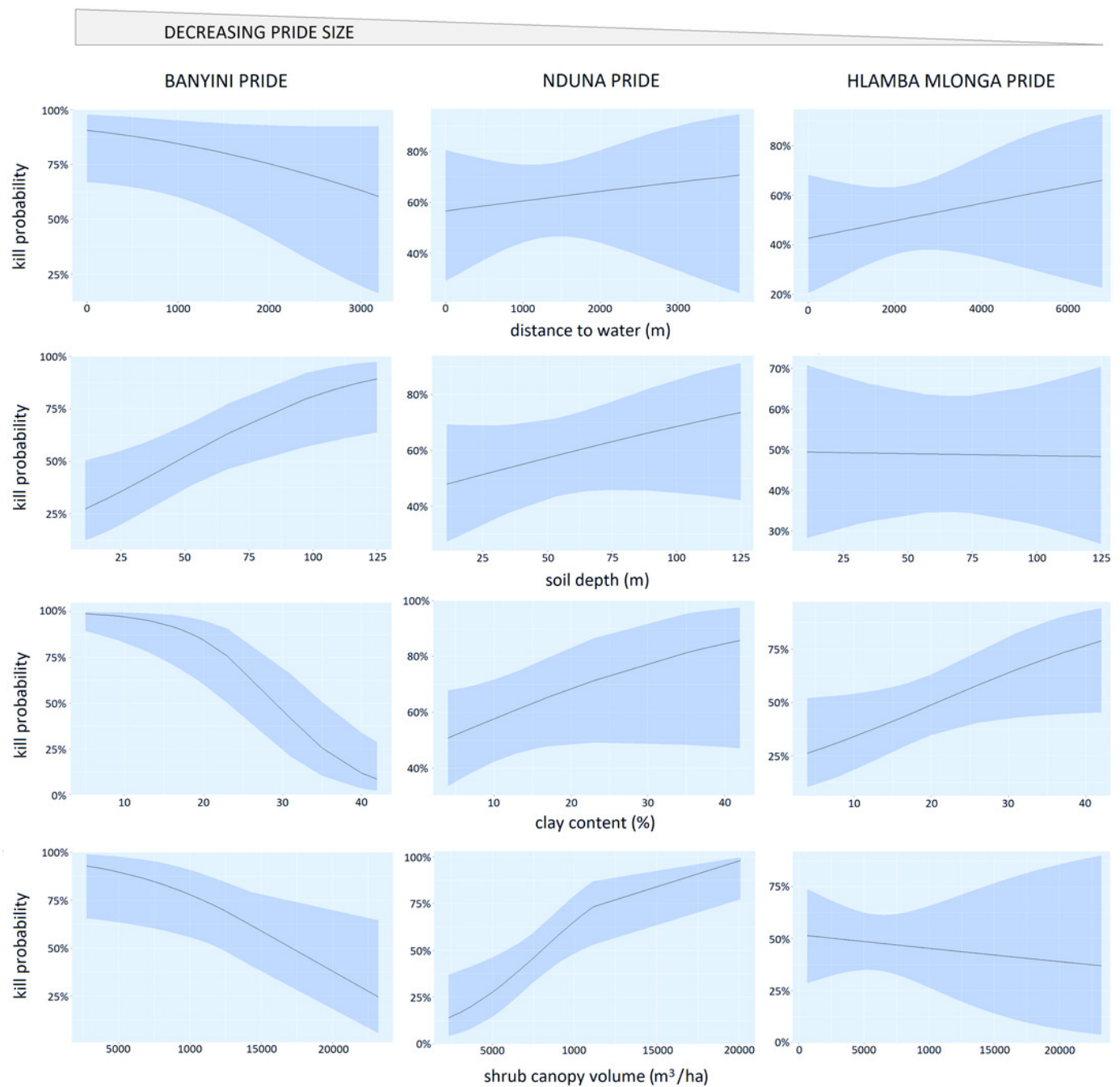


Table 1 (on next page)

Home range characteristics for the three study lion prides

Pride	Pride size (<i>n</i>)	Home range size (ha)	Average distance to water (km)	Average shrub canopy cover (m ³ /ha)	Average clay content (%)	Average soil depth (m)	Game encounter rate (groups/km ²)	Interval between kills (days)
Banyini	12	13 035	1.1	8537	21	77	0.99	6.3
Nduna	6	15 259	1.3	7843	14	66	0.87	7.7
Hlamba mlonga	4	17 460	2.4	5876	20	71	0.81	11.1

1

Table 2 (on next page)

Results of logistic regression analysis: Presence probability ~ *distance to water + shrub canopy cover + clay content + soil depth*. $\text{Pr}(>|z|)$ values <0.05 were considered significant

	Fixed effects	Estimate	Std. Error	z value	Pr(> z)
Banyini pride	Intercept	0.05	0.15	0.36	0.720
	<i>distance to water</i>	-9e-04	4e-05	-21.67	2e-16
	<i>shrub canopy cover</i>	-4e-05	1e-05	-4.26	2e-05
	<i>clay content</i>	0.01	4e-03	1.356	0.175
	<i>soil depth</i>	0.02	9e-04	22.409	2e-16
Nduna pride	Intercept	5.81	0.85	6.86	7e-12
	<i>distance to water</i>	-1e-04	9e-05	-1.44	0.150
	<i>shrub canopy cover</i>	2e-04	3e-05	8.101	5e-16
	<i>clay content</i>	0.36	0.04	-8.851	2e-16
	<i>soil depth</i>	0.02	4e-03	-6.35	2e-10
Hlamba mlonga pride	Intercept	-2.84	0.25	-11.28	2e-16
	<i>distance to water</i>	5e-04	4e-05	12.24	2e-16
	<i>shrub canopy cover</i>	-5e-05	2e-05	-3.02	0.003
	<i>clay content</i>	0.04	0.01	5.40	7e-08
	<i>soil depth</i>	0.02	2e-03	11.40	2e-16

Table 3 (on next page)

Results of logistic regression analysis: Kill probability $\sim$ *distance to water + shrub canopy cover + clay content + soil depth*. $\text{Pr}(> |z|)$ values < 0.05 were considered significant

	Fixed effects	Estimate	Std. Error	z value	Pr(> z)
Banyini pride	Intercept	4.53	1.19	3.66	>0.001
	<i>distance to water</i>	-6e-04	4e-04	-1.43	0.152
	<i>shrub canopy cover</i>	-2e-04	8e-05	-2.25	0.025
	<i>clay content</i>	0.18	0.04	-4.22	2e-05
	<i>soil depth</i>	0.03	0.01	2.76	0.006
Nduna pride	Intercept	-4.00	1.56	-2.57	0.010
	<i>distance to water</i>	>0.01	>0.01	0.41	0.679
	<i>shrub canopy cover</i>	>0.01	>0.01	2.96	0.003
	<i>clay content</i>	0.05	0.03	1.59	0.249
	<i>soil depth</i>	0.01	0.01	1.15	0.112
Hlamba mlonga pride	Intercept	-1.39	0.98	-1.41	0.158
	<i>distance to water</i>	1e-04	2e-04	0.69	0.490
	<i>shrub canopy cover</i>	-3e-05	8e-05	-0.34	0.738
	<i>clay content</i>	0.06	0.03	1.97	0.049
	<i>soil depth</i>	-4e-04	0.01	-0.06	0.950