Foraging and habitat specialization by female leopards (*Panthera pardus*) in the Waterberg Mountains of South Africa

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Carnivores that persist outside of protected areas are often deemed to have highly adaptable and generalist foraging strategies. Using data from three GPS-collared female leopards (*Panthera pardus*) and over an eight-month period, we attempted to establish whether leopards in a mountainous landscape display preferential behaviour (*i.e.* specialist) or not (*i.e.* generalist). We investigated whether female leopards used habitats in accordance with availability for both hunting and regular activities, and whether female leopards demonstrated preference for a particular prey species. Finally, we assessed tree caching behaviour and discuss leopard spatial dynamics in the context of superior competitors, such as lions (*Panthera leo*). Female leopards demonstrated selection for certain prey species. Mixed closed woodland (greatest vegetation density; lowest prey density) and tall open woodland (greatest vegetation biomass; high prey density) were preferred over other habitats. Female leopards on Welgevonden cached significantly larger prey species in trees. Our results suggest that female leopards in this landscape are selecting habitats – enabling the exploitation of certain ecological features – that balance energy expenditure against the likelihood of capturing prey in an attempt to maximize efficiency, whilst reducing inter-specific competition. We suggest that female leopards are limited in their foraging ability as a result of interference competition by superior species like lions, which in turn, affects their choice of prey. These findings highlight the potential importance of numerous ecological, spatio-temporal, and anthropogenic factors that influence leopard behaviour, and therefore have significant implications for leopard persistence and conservation.

Keywords: predation, kill site, carnivore, GPS cluster analysis, preference, optimal foraging.

INTRODUCTION

Due to their dietary plasticity and ecological adaptability, the leopard, *Panthera pardus,* is the most successful and wide-ranging large felid in Africa (Ray *et al.* 2005). Leopards often inhabit areas greatly modified by people or within close proximity to human settlements. Consequently, leopards are frequently regarded as opportunistic generalists, exhibiting wide habitat tolerances and resilience to anthropogenic threats (Hayward *et al.* 2006). However, research is beginning to reveal their specialized foraging behaviour (Balme *et al.* 2007; Hayward *et al.* 2007).

The positive relationship between prey biomass and leopard density is well established (Marker & Dickman 2005). However, leopards prefer prey species weighing an average of 23 kg (Hayward *et al.* 2006). Subsequent predictions of leopard density based on preferred prey biomass (Hayward *et al.* 2007) suggest that leopard populations are not just dependent on prey biomass alone, but rather, prey biomass within a suitable weight category.

Many factors can influence leopard diet (Steinmetz *et al.* 2013). For example, leopard prey density and composition can be affected by other predators, leading to dietary overlap resulting in increased competition for resources (Harihar *et al.* 2011). Additionally, anthropogenic pressure can alter food webs through activities such as overhunting of prey populations which can either drive leopards towards local extinction or force them to consume smaller prey (Henschel *et al.* 2011). Another factor affecting leopard diet is vegetation cover. Research has demonstrated that leopards have a greater probability of capturing prey when hunting occurs

in habitats with intermediate vegetation cover, even though these habitats contain lower prey densities than that of surrounding areas (Balme *et al.* 2007). These findings suggest that the likelihood of capturing prey and factors affecting this probability, like vegetation cover, are important determinants of leopard density and persistence. As a result of these recent studies, important questions are raised concerning leopard resilience in human-dominated landscapes and how adaptable these populations are. These issues are all the more pressing as the threats towards leopards are escalating due to extensive habitat loss (Ray *et al.* 2005), human–leopard conflict (Athreya *et al.* 2011), overhunting of leopards (Packer *et al.* 2011) and changes in prey composition due to human exploitation of leopard prey populations (Henschel *et al.* 2011).

The majority of scientific publications in southern Africa describing specialization by leopards have been conducted in open savanna systems (Stander *et al.* 1997; Hayward *et al.* 2006; Balme *et al.* 2007). Limited data exist regarding the preferences and ecological requirements of leopards in mountainous environments. This paper aims to answer one basic question: to what degree do leopards in a mountainous landscape show foraging and habitat specialization? We aim to 1) assess whether leopards prefer one species to another, 2) determine whether leopards use available habitats equally, and 3) assess whether predation occurs equally within available habitats, by monitoring three GPS-collared leopards over an eight-month period.

METHODS

Study area

The study was conducted in Welgevonden Private Game Reserve (24°10′–24°25′S and 27°45′–27°56′E; hereafter referred to as Welgevonden) situated on the Waterberg Plateau, Limpopo Province, South Africa, from August 2010 to March 2011. Welgevonden is characterized by mountains and flat hilltop plateaus dissected by steep valleys and ravines, and contains both natural rivers, artificial dams and permanent waterholes that sustain large populations of wildlife annually (Parker 2004). Fifty-two large mammal species are documented to occur on the reserve, including three primates, 17 ungulates and 19 carnivores.

The soil is sandy, acidic and nutrient-poor, giving rise to low-quality sourbush (Killian 2003). The

vegetation is classified as Waterberg Mountain Bushveld, dominated by wild seringa (*Burkea africana*), Transvaal beech (*Faurea saligna*), Transvaal milkplum (*Englerophytum magalismontanum*) and horn pod (*Diplorhynchus condylocarpon*) (Mucina & Rutherford 2006). Welgevonden lies in a summer rainfall region with an annual average precipitation of 613 mm and average temperature of 18.8°C (Institute of Soil, Climate and Water AgroMed section 2008). The dry season ranges from April to September and the wet season, from October to March.

Six vegetation types were classified by Parker (2004): grasslands (GR), open rocky woodland (ORW), mixed closed woodland dominated by *B. africana* with *D. condylocarpon* subcommunity (MCW), mixed woodland dominated by *B. africana* with *E. magalismontanum* subcommunity (MW), open woodland dominated by *B. africana* with *Terminalia sericea* subcommunity (OW), and tall open woodland dominated by *B. africana* with *F. saligna* subcommunity (TOW). A digitized vegetation map in ArcGIS v.9.2 (ESRI, Redlands, CA, U.S.A.) covering the entire reserve was used for the analysis (Fig. 1).

Capture and immobilization

The capture and collaring of leopards was undertaken as part of a larger study (Pitman *et al.* 2012). Leopards were captured using soft-hold foot snares (Frank *et al.* 2003), and immobilized using 4–5 mg/kg teletamine-zolazepam (Zoletil 100, Virbac RSA, Halfway House, South Africa). Three female leopards were fitted with remote drop-off global positioning systems (GPS) collars (Followit Tellus, Lindesberg, Sweden) and released within 3 km of the capture site after full recovery from the anaesthetic drug. GPS collars were remotely released after completion of the study. This study was approved by the University of Pretoria Animal Use and Care Committee ethics clearance protocol A022-06 with all its amendments and Limpopo standing permit (no. S13631) for scientific research.

Foraging activity

One hundred and twenty nine kills by three female leopards were located using contextual GPS cluster analysis (Tambling *et al.* 2010; Pitman *et al.* 2012). Each GPS collar was programmed to record 11 locations per day, totalling 6668 GPS locations for the study period. Leopard GPS clusters are locations in time and space, determined by a set of decision rules: 1) consecu-
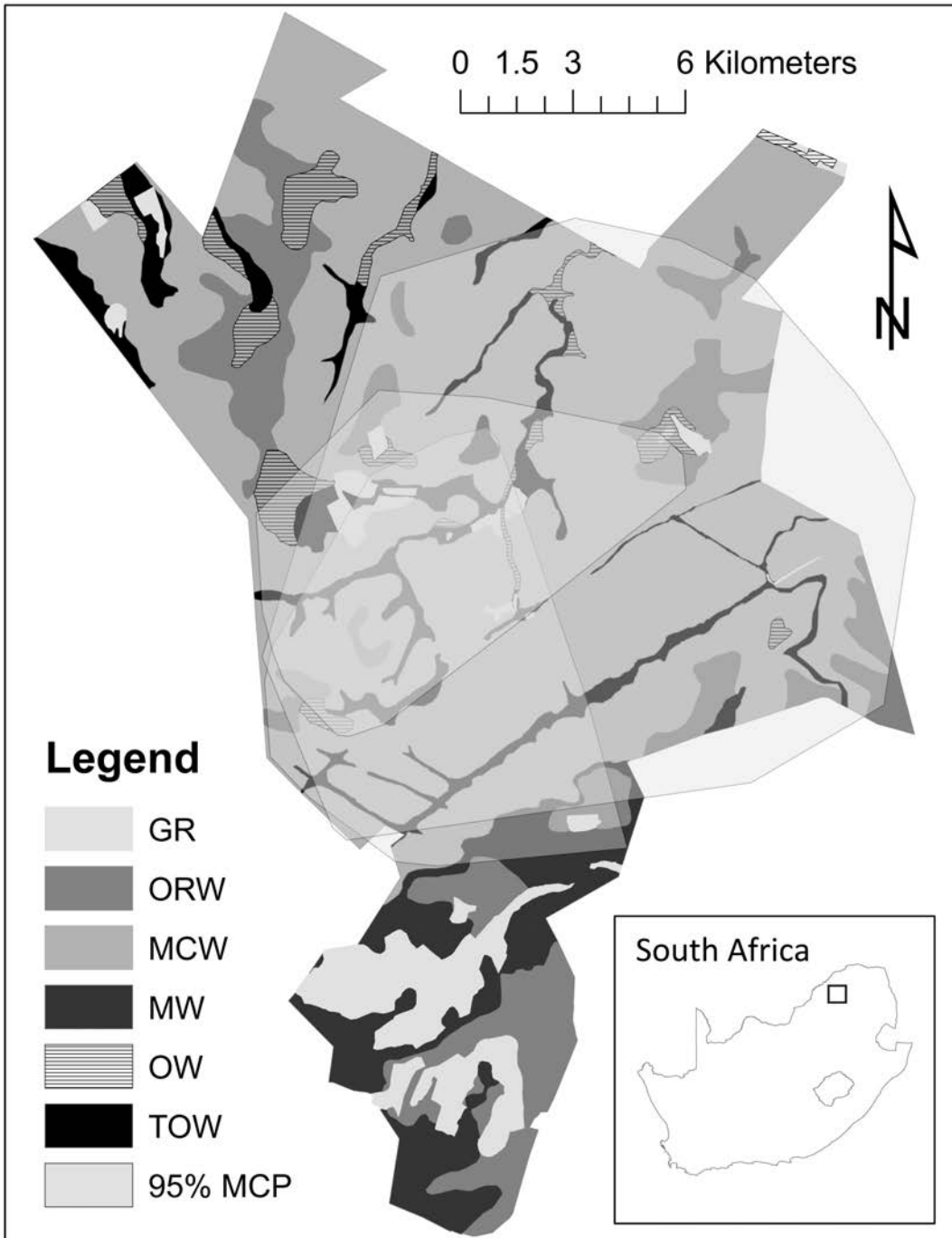
Fig. 1. Map of Welgevonden Private Game Reserve, Limpopo Province, South Africa, showing home ranges of three female leopards (95% minimum convex polygon; MCP) and six major vegetation types: GR = grasslands, ORW = open rocky woodland, MCW = mixed closed woodland dominated by *B. africana* with *D. condylocarpon* subcommunity, MW = mixed woodland dominated by *B. africana* with *E. magalismontanum* subcommunity, OW = open woodland dominated by *B. africana* with *Terminalia sericea* subcommunity, and TOW = tall open woodland dominated by *B. africana* with *F. saligna* subcommunity. Inset: square indicates the reserve's location within South Africa.

tive GPS locations within 50 m of each other were merged into one cluster, and 2) clusters within 100 m and 8 h (closest point to closest point) of other clusters were merged (refer to Pitman *et al.* 2012 for further details regarding these methods). These clusters (n = 356) were investigated in the field for kills. Leopard kill remains were identified macroscopically (e.g. horns, skull) or microscopically (cuticular hair scale patterns and cross-sections) using published references (Dreyer 1966; Keogh 19791983; Buys & Keogh 1984; Douglas 1989), and a reference collection housed at the Centre of Wildlife Management, University of Pretoria, South Africa. We measured the time predation occurred (diurnal = 6 am–4 pm; crepuscular = 4 am or 6 pm; nocturnal = 8 pm–2 am), taken at the start of a cluster and whether or not the carcass was cached. Vegetation density (woody stems/km^2) and vegetation biomass (kg/km^2) for each vegetation type on Welgevonden were obtained from (Parker 2004; Table 2). Leopard activity patterns were measured using Hawth's Analysis Tools v.3.27 (Beyer 2004) by averaging the distance moved between each consecutive GPS location and compared over a 24 h cycle.

Prey demographics

Twelve years of aerial count data (one count per year) were collated to create digital habitat utilization maps for each prey species on Welgevonden. Aerial counts were conducted at the end of the dry season, when wildlife is most easily detected. Welgevonden was systematically surveyed using a helicopter by flying 400 m transects in an easterly/westerly direction over a four-day period to ensure equal detection of prey species in each vegetation type.

Prey abundance was calculated by averaging the three most recent aerial counts (2008–2010) for each species. Aerial census techniques are biased against smaller, cryptic animals, and therefore correction factors (see Table 1) were applied to account for these species (Owen-Smith & Mills 2008). There was severe undercounting of klipspringer (*Oreotragus oreotragus*) and common duiker (*Sylvicapra grimmia*) as a result of the census technique. Therefore, their abundance estimates were calculated by multiplying the amount of suitable habitat available to each species (klipspringer = 318/km^2, entire reserve minus GR; common duiker = 340/km^2, entire reserve) by their average recorded densities (klipspringer = 0.3/km^2 and common duiker = 0.3 km^2) obtained from field

observations (Stuart & Stuart 2000; Skinner & Chimimba 2005).

Prey density estimates (animals/km^2) were generated for each vegetation type by dividing the average number of individuals (2008–2010) in each vegetation type by the available area within each vegetation type covering the entire reserve. Biomass estimates (kg/km^2) for each species in each vegetation type were calculated by multiplying density estimates by prey weights (Table 2). Average prey weights were determined by multiplying mean adult female weights by 0.75 to account for an assumed proportion of juveniles within the prey population (Stuart & Stuart 2000; Skinner & Chimimba 2005; Hayward *et al.* 2006). We did not evaluate seasonal variation of prey distribution. The short duration of the study (*i.e.* throughout the wet season), year-round availability of water, supplementary feeding of herbivores, and the small size of Welgevonden suggest that species migrations within the reserve are minimal (Parker 2004).

Statistical methods

We used *G*-tests to: 1) assess whether leopards were utilizing vegetation types at random (6668 leopard GPS locations were used to determine frequency of occurrence in each vegetation type), 2) whether leopards were hunting equally in each vegetation type, and 3) whether leopards were showing preference for particular prey. Only habitat and prey that fell within each collared leopard's home range (95% minimum convex polygon) was considered 'available', resulting in expected proportions of 'available' and 'used' habitat types and prey species derived from prey density and biomass estimates (see above). For example, to determine how many female leopard GPS locations should be located in GR habitat if this habitat is used randomly, we used the equation:

> Expected use = total number of GPS locations × (area of available GR habitat/total area of all habitats available) × 100)%

Resulting in *n* = 220 GPS locations (*i.e.* expected use) for GR habitat, where only *n* = 68 GPS locations were actually recorded. We used a Wilcoxon rank sum test with Yate's continuity correction to evaluate the difference between the average weight of cached and non-cached prey species. All tests were considered statistically significant at $\alpha \leq 0.05$. Analyses were conducted with R v.2.13.0 using preloaded packages (R Development Core Team 2011).

Table 1. Total population estimates (animals/km^2) of 17 leopard (*Panthera pardus*) prey species by vegetation type from Welgevonden Private Game Reserve, Limpopo Province, South Africa, for 2010.

Species	Vegetation types*						Total population size	Correction factor (Owen-Smith & Mills 2008)
	GR	ORW	MCW	MW	OW	TOW		
Chacma baboon	0.98	2.28	2.15	1.58	2.80	4.17	756	1.2
Blue wildebeest	8.16	1.98	0.93	0.40	8.20	3.24	668	1.2
Burchell's zebra	3.29	1.70	1.79	0.97	5.29	2.64	688	1.2
Bushbuck	0.10	0.02	0.01	0.01	0.00	0.25	12	3
Bushpig	0.12	0.02	0.09	0.10	0.00	0.21	30	3
Common duiker	0.84	0.26	0.21	0.96	0.23	0	102	1
Common reedbuck	5.22	2.63	0.04	0.41	0.00	0.89	279	3
Eland	1.30	0.98	0.56	0.84	0.98	0.34	234	1.5
Impala	11.87	3.22	1.48	2.33	7.44	12.75	1192	1.7
Klipspringer	0.19	0.19	0.77	1.5	0.3	0.95	239	1
Kudu	0.35	0.73	0.79	1.01	0.94	3.13	322	1.8
Mountain reedbuck	0.20	0.11	0.07	0.80	0.00	0.29	51	3
Red hartebeest	3.03	0.70	0.08	0.87	0.31	0.27	150	1.2
Steenbok	0.17	0.09	0.00	0.03	0.03	0.01	10	2
Tsessebe	0.08	0.03	0.00	0.01	0.02	0.02	5	1.7
Warthog	8.68	0.96	0.38	0.94	2.09	2.72	435	2.5
Waterbuck	2.53	0.28	0.26	1.32	0.85	1.87	214	1.7

*See Fig. 1 for vegetation type codes.

RESULTS

A total of 31 244 direct observations of prey species were recorded during aerial counts, comprising 17 species (Table 1). Grasslands were the most densely populated habitat and contained the highest prey biomass estimates. Mixed closed woodland was the most densely vegetated habitat and tall open woodland contained the highest vegetative biomass estimates (Table 2). Female leopards used mixed closed woodland and tall open woodland significantly more than expected, mixed woodland in accordance with availability and avoided grasslands, open rocky woodland, and open woodland (G_5 = 595.9, P < 0.001).

Most clusters (n = 227; 63%) did not have kills

associated with them, and may therefore have been resting sites, mating sites or areas frequented by female leopards for an unknown resource (*e.g.* scent-marking sites, patrolling routes; Pitman, *et al.* 2012). Kills (n = 129) were located and identified (six kills were unidentifiable) between August 2010 and March 2011 (Table 3). Average prey weight (median = 12.5 kg) was at the lower end of a leopard's preferred prey weight range (Hayward *et al.* 2006). Certain species were predated upon more than others (G_8 = 109.4, P < 0.001). Leopards killed common duiker, klipspringer and mountain reedbuck (*Redunca fulvorufula*) more than expected, chacma baboon (*Papio ursinus*) and impala (*Aepyceros melampus*) in accordance with

Table 2. Mean prey density, prey biomass, woody vegetation density, and vegetative biomass by vegetation type from Welgevonden Private Game Reserve, Limpopo Province, South Africa, for 2010.

	Vegetation types*					
	GR	ORW	MCW	MW	OW	TOW
Total prey density (animals/km^2)	47.12	16.17	9.61	14.08	29.49	33.75
Prey biomass (kg/km^2)	1744	574	355	506	1143	1226
Woody vegetation density (woody stems/km^2)	11 904	45 555	126 458	116 111	55 557	95 758
Vegetative biomass (kg/km^2)	1 161 801	298 168	1 129 009	481 161	1 083 833	4 813 323

*See Fig. 1 for vegetation type codes.

Table 3. Number of female leopard (*Panthera pardus*) kills of 18 prey species located using contextual GPS cluster analysis (Pitman *et al.* 2012) by vegetation type from Welgevonden Private Game Reserve, Limpopo Province, South Africa, during August 2010 – March 2011.

Species	Number of kills in each vegetation type*						
	Kills	GR	ORW	MCW	MW	OW	TOW
African civet	2	0	0	1	0	0	1
Chacma baboon	18	0	0	15	0	0	3
Banded mongoose	5	0	0	5	0	0	0
Blue wildebeest	5	0	0	2	0	0	3
Burchell's zebra	10	0	1	9	0	0	0
Bushpig	1	0	0	0	0	0	1
Common duiker**	7	0	0	3	0	0	0
Common reedbuck	1	0	0	1	0	0	0
Impala	23	0	0	18	1	2	2
Jameson's red rock rabbit	8	0	0	8	0	0	0
Klipspringer	19	0	0	15	0	0	4
Kudu	4	0	0	4	0	0	0
Leopard tortoise	1	0	0	1	0	0	0
Mountain reedbuck	12	0	0	12	0	0	0
Rock hyrax	1	0	0	1	0	0	0
Vlei rat	1	0	0	1	0	0	0
Warthog	1	0	0	1	0	0	0
Bird spp.	4	0	0	2	0	0	2
Unknown	6	0	0	5	0	0	1
Total kills	125	0	1	104	1	2	17

*See Fig. 1 for vegetation type codes.
**Four common duiker kills were located in areas outside Welgevonden for which habitat maps were not available.

availability, and avoided eland (*Tragelaphus oryx*), red hartebeest (*Alcelaphus buselaphus*), kudu (*Tragelaphus strepsiceros*), common reedbuck (*Redunca arundinum*), warthog (*Phacochoerus africanus*), bushpig *Potamochoerus larvatus*), waterbuck (*Kobus ellipsiprymnus*), blue wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*).

Female leopards preferred to hunt in mixed closed woodland and tall open woodland, making 96% of kills in these two habitats, and avoided all other habitats when hunting ($G_5 = 19.1$, $P = 0.001$). Thirty-one kills (24%) were cached in trees, these prey were significantly heavier ($z = -2.1$, $P < 0.05$; median = 31 kg) than non-cached prey (median = 12 kg). No kills were concealed with vegetation.

Most kills (53%) occurred during diurnal hours, peaking at mid-to-late afternoon, followed by nocturnal (25%) and crepuscular (22%) hours (Table 4). Female leopards were most active during daylight hours (Fig. 2).

DISCUSSION

Female leopards on Welgevonden did not use or hunt in habitats with the greatest abundance of prey. Leopards require not only high numbers of prey to hunt, but rather the appropriate ecological factors like vegetation cover, to ensure hunts are successful (Balme *et al.* 2007). On Welgevonden, female leopards may be exploiting high levels of vegetation cover (*e.g.* mixed closed woodland; greatest vegetation density) by using it to prevent detection during hunting, thereby increasing the probability of capturing prey (Hayward *et al.* 2006). Although mixed closed woodland contains the least number of prey species, this 'predator detection *versus* prey abundance' trade-off makes hunting in this habitat highly profitable and worthwhile for leopards – 83% of kills occurred here. It is plausible that these factors enabled leopards to successfully hunt species that are normally regarded as challenging or high-risk prey like chacma baboons (Cowlishaw 1994; Jooste *et al.* 2013), as most ($n = 15$; 83%) were killed in this habitat. The use of tall open woodland for hunting may be a result of some key factors that have been shown to facilitate successful leopard hunts: the abundance of prey (33.75 animals/km²; Table 2), suitable vegetation cover (*i.e.* greatest vegetation biomass; Balme *et al.* 2007), and the abundance
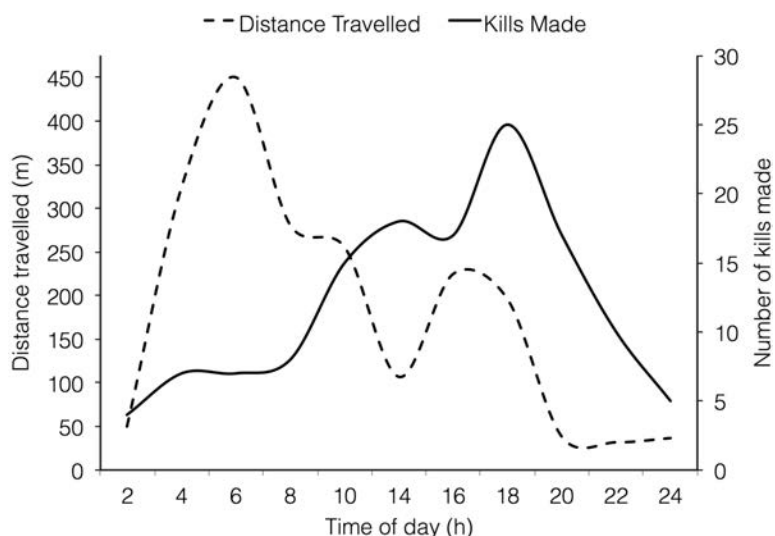
Fig. 2. The average distance travelled (m) and number of kills made by three female leopards (*Panthera pardus*) compared over a 24 h cycle from Welgevonden Private Game Reserve, Limpopo Province, South Africa, during August 2010 – March 2011. Note: midday data were not collected due to a GPS programming error.

of refuge trees – large wild seringa and Transvaal beech trees dominate this habitat (Pitman *et al.* 2012).

Leopards in our study selected certain prey species over others. This selection may not only be a result of dietary preference (Hayward *et al.* 2006), but rather the pursuit of certain prey in accordance with energy expenditure (Krebs & Davies 1993). Predation on kudu fits this hypothesis: leopards are reported to target and kill kudu in the Waterberg (Swanepoel 2009). However, the likelihood of capturing prey such as impala and klipspringer provide leopards with an easier, less risky option (Hayward *et al.* 2006). Kudu were most abundant in tall open woodland – a habitat frequently used by leopards – yet no kudu kills occurred here. Kudu are a tall, hyper-vigilant species (Périquet *et al.* 2010) that may be able to detect a hunting leopard in this habitat where environmental features like vegetation density and/or vegetation structure may be below a threshold that enables successful capture (Balme *et al.* 2007). In contrast, impala were least abundant in mixed closed woodland, yet most (n = 18; 78%) impala kills occurred here, suggesting this dense habitat offers leopards easier predatory opportunities possibly due to the presence of thick vegetation that permits a stealthier hunting approach.

Leopards are known to take refuge in rugged habitats when potential threats by superior competitors exist (Sunquist & Sunquist 2002), and then enter lower lying, prey abundant habitats to forage (Hayward *et al.* 2006). We hypothesize that the competitive pressure exerted by lions – which

Table 4. Number of female leopard (*Panthera pardus*) kills of 18 prey species by time of day (three phases) from Welgevonden Private Game Reserve, Limpopo Province, South Africa, during August 2010 – March 2011.

Species	Number of kills		
	Crepuscular	Diurnal	Nocturnal
African civet	0	1	1
Chacma baboon	2	13	3
Banded mongoose	2	3	0
Blue wildebeest	2	2	1
Burchell's zebra	2	6	2
Bushpig	0	0	1
Common duiker	2	4	1
Common reedbuck	0	0	1
Impala	5	11	7
Jameson's red rock rabbit	2	5	1
Klipspringer	5	8	6
Kudu	2	2	0
Leopard tortoise	0	0	1
Mountain reedbuck	1	8	3
Rock hyrax	0	0	1
Vlei rat	1	0	0
Warthog	0	1	0
Bird spp.	1	2	1
Unknown	2	2	2
Total	29	68	32

dominate these lower lying, open habitats (Kilian 2003) – force leopards to use rugged areas at greater frequencies that would normally exist, thus increasing the contact rates leopards have with species common to this environment, such as klipspringer and mountain reedbuck (Norton 1997a,b). This could explain why female leopards selected mountain reedbuck and klipspringer more than expected on Welgevonden whereas in other regions these species are not normally favoured (Hayward *et al.* 2006). Feeding sites were often located in rugged terrain (Pitman *et al.* 2012), which may be a direct result of our hypothesized inter-specific avoidance behaviour (*i.e.* leopards feel safer feeding here, where lions infrequently venture).

Other potential leopard prey species like common reedbuck, waterbuck, red hartebeest, blue wildebeest and zebra were avoided for two possible reasons: 1) these species are predominantly open habitat specialists and have lower encounter rates with leopards on Welgevonden, and 2) these species could inflict serious injury on leopards (Hayward *et al.* 2006). Nevertheless, given that aerial count data can misrepresent prey abundance, even after correction factors have been applied, it would be wise to interpret our prey preference results with caution. Though we are confident that twelve years of aerial counts provide a good representation of prey distribution, prey abundance within each vegetation type would have benefited from additional census techniques such as road-strip counts (Hirst 1969).

Predators are vulnerable during feeding and leopards are reported to climb trees not only to rest, but to avoid conflict with competitors (Bailey 2005). The high frequencies of refuge trees at kill sites on Welgevonden demonstrate the importance of ecological features like trees for leopard foraging and survival (Pitman *et al.* 2012). Caching of kills in trees on Welgevonden was fairly common (23%). This behaviour is thought to be a result of the competitive pressure exerted by scavengers (Balme *et al.* 2007). However, cached prey species were significantly heavier (mean = 68 kg) than non-cached prey species (mean = 33 kg), and may therefore be a response to an excess of food following satiation (Swanepoel 2009). Female leopards did not cover prey with vegetation as is so often seen in other studies (Grimbeek 1992; Karanth & Sunquist 2000). The high density and olfactory capabilities of scavengers on Welgevonden, particularly from brown hyaena (*Hyaena brunnea*) (Wiesel 2006), may suggest this hiding behaviour is ineffective.

Leopards are usually nocturnally active in savanna ecosystems (Bailey 2005), and mostly diurnal in forest ecosystems (Jenny & Zuberbühler 2005). In the Waterberg, leopards are predominantly nocturnal (L.H. Swanepoel, unpubl, data, 2012). On Welgevonden, female leopards were primarily active during the day and least active between 20:00 and 02:00 (Fig. 2). The reason for this decrease in activity during these nocturnal hours is unclear but may be a result of feeding activity (*i.e.* digestion) and/or intraspecific avoidance.

Although these findings suggest that leopards are adaptable, they are still governed to some extent by interactions with their environment, their prey, their competitors and people. In this mountainous landscape, female leopards demonstrate clear habitat preference. Their choice of hunting and refuge grounds are not determined simply by the availability of habitat, but rather by complex and subtle ecological dynamics. We suggest that these leopards are selecting habitats that balance energy expenditure against the likelihood of capturing prey in an attempt to maximize efficiency (Balme *et al.* 2007), whilst reducing inter-specific competition, which limits their foraging ability and affects their choice of prey (Creel *et al.* 2001). On Welgevonden, female leopards are not entirely opportunistic, nor generalist, but rather highly adapted to the pressures exerted upon them from within (ecological factors, inter-specific competition, human disturbance) and outside (persecution) the reserve.

Leopard predation is greatly affected by environmental factors (*e.g.* vegetation cover; Balme *et al.* 2007) and anthropogenic pressure (*e.g.* bush meat hunting in the Congo Basin; Henschel *et al.* 2011) which influence the suitability of available habitats and raise further questions regarding leopard population densities in other regions. Considerations need to be made that account for inter-specific interactions, habitat refugia, the likelihood of capturing prey, vegetation density and human disturbance when delineating suitable habitats and corridors for leopard conservation. These issues highlight our limited knowledge of leopard ecological requirements, and challenge our perceptions regarding the suitability of habitats.

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