

significantly influence the 'catchability' of prey, and predators simply hunted in areas where prey was more common. The theoretical framework behind both hypotheses is similar: predators should select habitats in which to hunt where energy requirements can be met at minimum energy expenditure and, at times, that pose the least risk (Hayward & Kerley 2005). Depending on the payoff realized by a hunting predator, either the abundance of prey or its catchability (or some combination of both) is likely to be the prevailing factor driving decisions on where to hunt.

Using 44 months of data on radiocollared leopards, *Panthera pardus*, we tested the relative importance of these two selective approaches. Leopards are the most widespread of large felids, occurring throughout sub-Saharan Africa, the Middle East, and much of tropical and temperate Asia (Nowell & Jackson 1996). Leopards occupy a diverse variety of habitats, ranging from tropical rain forests to semideserts, and from alpine mountains to the edges of urban areas. Their ability to inhabit such a variety of landscape types is largely due to a highly adaptable foraging strategy. Leopards have an extremely catholic diet and have been recorded feeding on 92 prey species in sub-Saharan Africa alone, varying in size from small arthropods to adult male eland, *Taurotragus oryx* (Bailey 2005). To capture prey, leopards use a range of hunting methods that vary with prey species and habitat type but almost always rely on cover to hide their approach (Hunter et al., in press). To have any chance of success, they need to approach their prey closely (mean \pm SE: 4.4 ± 0.25 m in Kaudom, northeast Namibia; Stander et al. 1997) before initiating a charge. Leopards are therefore dependent on some form of cover, although Bothma & Le Riche (1984) found that vegetation as low as 200 mm was sufficient to effectively conceal them. Attempts only ended in kills in 5% of hunts in the Serengeti (Bertram 1982), 16% of hunts in the Kruger (Bailey 2005) and 38% of hunts in Kaudom, Namibia (Stander et al. 1997). Furthermore, between 5 and 10% of kills are lost to other predators, especially lions and spotted hyaenas, *Crocuta crocuta* (Bailey 2005). Leopards minimize kleptoparasitism by caching carcasses in trees, caves and large burrows or dragging them into dense vegetation (Sunquist & Sunquist 2002).

In this study we investigated the selection of feeding habitats by leopards in the Phinda Private Game Reserve, South Africa. We address two main questions: (1) do leopards select certain habitat types over others in which to hunt and, if so, (2) what factors determine whether an area is preferred or avoided? For the prey abundance hypothesis to be supported, leopards should hunt in areas with the greatest abundance of available prey, regardless of landscape attributes. In contrast, according to the landscape hypothesis, leopards should select feeding habitats where prey catchability is highest. In this paper, we assess the relative importance of these two hypotheses to leopard hunting behaviour by assessing how often leopards hunted and killed prey in various habitat types, and how successfully they hunted in different habitats. We also assessed the influence of interspecific competition on feeding habitat selection by leopards.

METHODS

The Study Area

The study was conducted in the Phinda Private Game Reserve, South Africa ($27^{\circ}44'–27^{\circ}55'S$, $31^{\circ}12'–32^{\circ}26'E$; Fig. 1), from April 2002 to December 2005. Phinda is located in the Southern Maputaland coastal plain region, which runs from the Umfolozi River north into Mozambique and is bounded in the east by the Indian Ocean and the west by the Lebombo Mountains (Maud 1980). For the first 2 years of the study, the reserve was approximately 145 km²; in July 2004, it was increased in size to 180 km². The entire perimeter of Phinda is surrounded by electric game fencing as prescribed by the local conservation authority, Ezemvelo KwaZulu-Natal Wildlife.

The climate in this region is described by Schulze (1965) as warm to hot, humid subtropical. There are essentially two distinct seasons: the warm, arid winter from April to September and the hot, humid summer from October to March, which includes the rainy season. The average annual rainfall is 550 mm. Mean monthly temperatures ranged from 33°C in January to 19°C in July.

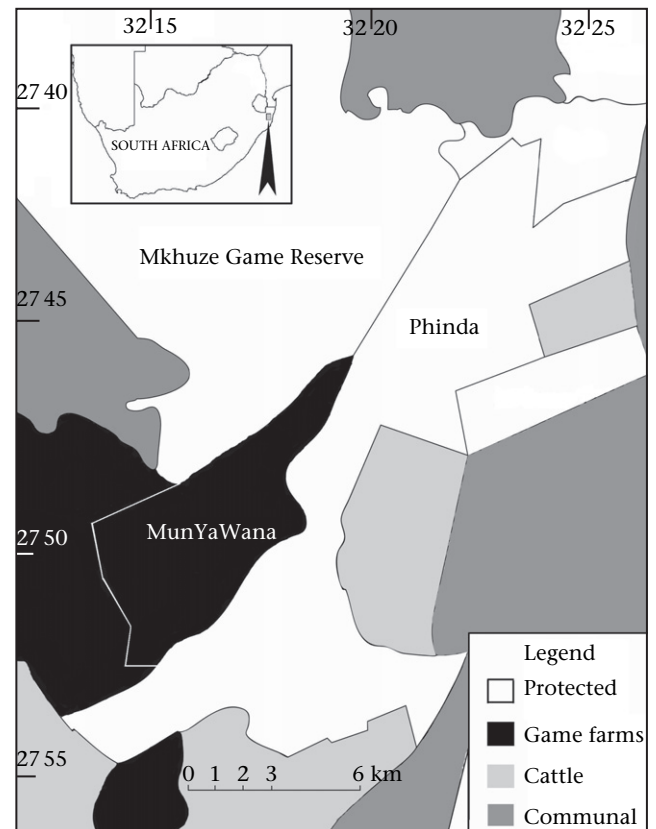


Figure 1. Map of study site showing land-use types in the region. Game farms commercially harvest wild, free-ranging ungulates. Cattle areas are indicated where farming of domestic livestock is the dominant use, although these areas also have significant wild ungulate populations, and mixed livestock-game farming is widespread. Human populations on communal land subsist primarily from domestic livestock. The Munyawana area was used for game-farming until July 2004, after which it was consolidated with Phinda. Inset: arrow indicates region shown.

Phinda is situated in Natal lowveld bushveld, coastal and bushveld-grassland vegetation zones (Low & Rebelo 1996). Nine distinct vegetation types were classified by Hunter (1998; see for detailed descriptions of vegetation types): open red sand bushveld (ORB), closed red sand bushveld (CRB), palmveld (PV), grassland (G), sandforest (SF), open mixed bushveld (OMB), closed mixed bushveld (CMB), dry mountain bushveld (DMB) and riparian woodland (RW). A detailed digitized habitat map (ArcView 3.2) generated by Hunter (1998) covering the entire reserve was used for the analyses. We updated and modified this map to reflect significant habitat alterations since 1998, chiefly the result of artificial clearing of habitats by Phinda management.

Forty-two large mammal species (excluding bats and small rodents) have been recorded from Phinda. Both lions and cheetahs, *Acinonyx jubatus*, were reintroduced following anthropogenic extirpation (Hunter 1998; Hunter et al. 2007), while leopards and spotted hyaenas had persisted in the area during years of heavy persecution preceding the formation of the reserve. Leopards are fully protected in Phinda. At the time of the study, leopard densities within Phinda were approximately 5.9 leopards per 100 km², as determined by mark–recapture models applied to data from camera trapping (G. Balme & L. Hunter, unpublished data). Leopards are not constrained by the boundary fence and move freely between neighbouring properties. The surrounding land is made up of a mosaic of local Zulu communities, livestock farms and private game farms, where leopards are generally perceived as potential problem animals or as targets for commercial trophy hunting (Fig. 1; Balme & Hunter 2004).

Feeding Ecology Data

We captured 27 leopards using a combination of free-darting, baited cage traps and soft-hold foot snares (Frank et al. 2003; Balme & Hunter 2004). Snare assemblies were modified to minimize the chance of injury and to reduce the possibility of catching smaller-footed, nontarget species. Leopards were immobilized using a tiletamine–zolazepam combination at 3–5 kg/mg (Zoletil, Virbac, RSA) and fitted with VHF radiocollars weighing approximately 250 g (Sirtrack, Havelock North, New Zealand; Hunter et al. 2003). We attempted to locate every radiocollared animal at least once daily and recorded their location to the nearest 50 m using a hand-held GPS receiver or by radiotriangulation when close approach was not possible.

We collected data on feeding ecology by three means. First, where possible, we followed leopards by vehicle for extended periods to observe hunting behaviour and kills as they happened. Leopards were followed at the greatest distance possible that enabled us to maintain contact with the cat without interfering with the hunt. In open environments, this distance was up to 150 m, but in woodland and forest, it was reduced to 30–50 m. When following leopards at night, we used night vision binoculars (Rigel 2350, Rigel Optics, Portland, OR, U.S.A.) and a spotlight with a red filter to minimize the impact on leopards and their prey. As soon as a leopard encountered

prey, we switched off the spotlight and waited in silence, switching on the red-filtered light intermittently for a few seconds at a time to ascertain whether the leopard had begun stalking; we only kept the spotlight on once the leopard had initiated a charge or was detected by the prey. We did not start the vehicle again until the attempt was over. When we lost sight of a leopard during its final rush, we waited in silence for 3–5 min before attempting to locate it again. In successful hunts, we observed or more often heard the moment of capture, or we re-located the leopard in the act of killing the prey. A hunting attempt was defined as any occasion where a leopard initiated a stalk on a prey species. Opportunistic hunts, in which a leopard surprised a prey species and gave chase without a preceding stalk, were also included as a hunting attempt. Following leopards for extended periods had limited applicability in Phinda because of the thickness of the vegetation. When a leopard was lost in dense bush, we moved ahead of its path of travel until we resumed contact, then we followed it again for as long as possible.

Leopards were also regularly located either feeding on or very near to a carcass. We included only those cases where we were certain the leopard had made the kill. As leopards often drag carcasses a considerable distance from where they make the kill (Smith 1977), we attempted to follow the drag-mark back until we found the kill site and recorded this as the kill location. Scavenged carcasses were identified by evidence that included their level of decomposition, the lack of evident bite wounds to the neck or back of the head, and the lack of any signs of a struggle.

Finally, when we were unable to drive to a leopard (excluding known nursing females and mating pairs) that remained in the same position for two or more days, we calculated the location by radiotriangulation and walked into the site to search the area for a carcass once the cat had moved off. Again, we included only those kills where we were certain that the leopard was responsible.

For all kills, we recorded the species, sex (where possible), age (juvenile, subadult and adult, where possible), estimated time of the kill, location and surrounding vegetation type. We also recorded whether a kill was cached in a tree or stored in dense vegetation and whether it was scavenged by other species.

Prey Abundance and Landscape Attributes

A road strip sampling technique (Hirst 1969; Hunter 1998) was used to calculate prey density estimates for each habitat type on Phinda. We surveyed two separate transect routes, totalling 70 km, that passed through all of the reserve's vegetation types. A single survey involved driving each route a minimum of three times over a 6–8 day period (i.e. six counts), alternating the direction on each count. The population estimate for each survey was derived from the mean number of each prey species counted in the 6–8 day period. Vehicle speed was maintained at 10–15 km/h, and all counts were conducted in the early morning between 0600 and 1100 hours. Only animals on the driver's side were counted because visibility was not consistent for both sides of the vehicle and

vegetation types often differed markedly on opposite sides of the road, mainly because of artificial bush-clearing (Hunter 1998). We counted six herbivore species known to be the most important leopard prey from a previous study (Walker 1999); nyala, *Tragelaphus angasii*, impala, *Aepyceros melampus*, warthog, *Phacochoerus aethiopicus*, red duiker, *Cephalophus natalensis*, grey duiker, *Sylvicapra grimmia*, and reedbuck, *Redunca arundinum*. Each species was classified by age (juvenile, subadult, adult) and sex. Within each habitat type, the mean visibility limit of each species was determined by measuring the distance (using range finders) from the road that they disappeared from view. This resulted in an effective strip width for each species in each habitat type. We measured the distance driven through each vegetation type per transect and multiplied this value by the number of times that each transect was driven to give total distance driven per habitat type. Density of each prey species was then calculated in each habitat according to the following formula: density = number of animals counted / (total distance driven in each habitat type × effective strip width).

Abundance figures were generated for each vegetation type by multiplying the mean density of each species in each habitat type by the total area covered in the reserve by each habitat calculated in ArcView 3.2. Biomass estimates of available prey in each habitat type were calculated from abundance estimates (mean weights for prey species from Skinner & Chimimba 2005). Surveys were carried out in both the dry (July) and the wet season (December) to assess whether herbivore numbers varied seasonally.

We conducted five vegetation transects (Krebs 1999) in each of the nine habitat types to quantify the extent of woody cover for each. Each transect line was 100 m long and all woody plants higher than 200 mm and within 2 m of either side of the line were counted. The effective sampled area was therefore 400 m² per transect. Woody plants were divided into two categories: between 200 mm and 2 m tall (shrub) and >2 m tall (tree). Only plants over 200 mm were counted because this was considered sufficient cover to conceal a hunting leopard (Bothma & Le Riche 1984). Mean total woody vegetation density for each habitat was calculated by summing the total number of shrubs and trees counted in each vegetation type and dividing this value by the total area sampled in that habitat type. Mean percentage grass cover was estimated in 1-m² plots every 10 m along each transect line. Grass cover was divided into four categories: no grass, short (0–200 mm), medium (200–600 mm) and long (>600 mm).

Distance from kills to the nearest permanent water source was calculated in ArcView 3.2 with the Spatial Analyst extension (projection: UTM; units: metres; datum: ARC 1960; spheroid: Clarke 1880).

Statistical Analyses

We used traditional chi-square goodness-of-fit tests to assess whether leopards were selecting particular habitat types in which to hunt. The data were corrected for

search bias because it may have been easier for us to locate carcasses in certain habitat types than in others. The expected number of carcasses found was adjusted according to an index of the number of sightings of leopards in a particular habitat type divided by the total number of locations obtained in that habitat type. We always attempted to view leopards during daily radio-tracking and hence this index provided an accurate indication of how accessible leopards were in each vegetation type. We found the majority of carcasses while watching leopards (see Results), so this index also provided an accurate estimate of the likelihood of locating a kill in a particular habitat type. Dry mountain bushveld was excluded from the analysis because of very low sample sizes in both numbers of locations and kills recorded. We assessed seasonal differences in the number of kills found in different habitat types using Wilcoxon matched-pairs signed-ranks tests.

We applied binary logistic regressions to model the relative probability of a kill occurring in the remaining eight vegetation types and to predict kill location using prey abundance and landscape attributes. A used–availability design was used to calculate the odds ratio for each covariate that was proportional to the probability of use (Manly et al. 2002). When the odds ratio is greater than 1, β (the coefficient for each habitat type) is positive, suggesting an increased occurrence of a kill. Alternatively, when the odds ratio is less than 1, β is negative, suggesting a decreased occurrence of a kill (Tabachnick & Fidell 1996). Used units were characterized as 1 and unused units as 0. Availability was defined as all areas in which either the predator or prey occurred (Hebblewhite et al. 2005), which in this case included the entire reserve. We compared corrected (according to the search bias index) kill locations (used units) to 1000 random locations (available units) within the reserve that excluded dry mountain bushveld. The covariates in our model were habitat type, prey biomass, shrub density, tree density, total vegetation density, grass cover and distance to water. The logistic regressions used the stepwise backward-elimination process based on the Wald statistic. The Wald statistic and the corresponding significance level test the significance of each of the covariate and dummy independents in the model (Manly et al. 2002). The ratio of the logistic coefficient β to its standard error, squared, equals the Wald statistic. If the Wald statistic is significant, then the parameter is significant in the model. Significance was set at $P \leq 0.1$ because of collinearity between independent variables. This level of significance excludes the possibility that potentially important variables will be dropped from the multivariate analysis (Hopcraft et al. 2005). Keating & Cherry (2004) highlighted the potential problem of a high contamination rate, or false-negative rate (units that were used but misclassified as available because of sampling) in used–availability designs in logistic regressions. Because the number of available units in this analysis was much larger than the number of units used, contamination was unlikely. Nonlinear relationships in the logistic models were tested by including squared functions (Hopcraft et al. 2005). If a continuous variable was behaving quadratically, we expected the squared function

β to be opposite (either positive or negative) to the normal β . Model fit was assessed using Nagerleke's R^2 test.

Nonparametric G tests (Sokal & Rohlf 1995) were used to assess the relative success of observed hunts, the number of kills lost to other predators and the percentage of kills hoisted in the different habitat types. All statistical tests were conducted using SPSS 11.5 (SPSS, Chicago, IL, U.S.A.).

RESULTS

Between April 2002 and December 2005, we located 217 leopard kills. The mean \pm SE number of kills found per individual leopard was 7.37 ± 2.20 . Eighty-six per cent ($N = 185$) of kills comprised the six herbivore species that we counted. Nyala ($N = 94$) made up almost half of the carcasses found, followed by impala ($N = 34$), warthog ($N = 22$), grey duiker ($N = 14$), red duiker ($N = 11$) and reedbuck ($N = 10$). Most kills were found while watching leopards (94%). On 26 occasions (12%), we observed leopards make the kill, on 174 occasions (80%), leopards were found either feeding on or close to a carcass, and on 17 occasions (8%), we found the kill once the leopard had moved off.

We collected 2709 daily locations of radiocollared leopards in Phinda during the study and viewed collared cats on 1018 occasions (Table 1). Leopards used most habitat types according to their relative availability except for grassland, which they avoided ($\chi^2_7 = 243$, $P \leq 0.001$). Leopards were most accessible to viewing in grassland and least accessible in sandforest ($\chi^2_7 = 68.1$, $P \leq 0.001$).

Prey Abundance and Landscape Attributes

We completed four surveys for prey abundance, two in the dry season and two in the wet season. The road strip method appeared to provide reasonable population estimates for each species, with confidence intervals ranging

Table 1. Number of locations, sightings and kills of six major prey species recorded for radiocollared leopards, and mean prey biomass and vegetation density by habitat type

Habitat type*	Number of locations	Number of sightings	Number of kills	Prey biomass (kg/km ²)	Vegetation density (number of woody plants/km ²)
CRB	1097	392	50	2048	101 584
ORB	337	130	30	2311	67 917
PV	192	137	39	515	54 500
G	97	71	11	796	31 417
SF	204	25	3	2031	115 250
CMB	474	137	22	3077	89 773
OMB	210	82	25	1790	42 625
RW	98	44	5	3848	137 205
Total	2709	1018	185		
Mean \pm SE				2052 \pm 386	80 034 \pm 13 113

*See Methods for habitat type codes.

between 2 and 18% (Table 2). We probably underestimated grey duiker numbers ($N = 97$, $CI = 2\%$), because this species is primarily nocturnal and tends to remain hidden during daylight hours. There was a large discrepancy between the wet and dry season counts for warthogs, presumably because, at the time of the summer surveys, most adult female warthogs were in their burrows giving birth or nursing new litters. There was no significant difference, however, between seasonal surveys for all species combined (Wilcoxon matched-pairs signed-ranks test: $Z = -0.520$, $N = 6$, $P = 0.497$), nor was there a difference between results from the 2003–2005 surveys and those conducted by Hunter (1998) in 1992–1995 ($Z = -0.674$, $N = 6$, $P = 0.500$).

Mean group size for all prey species combined decreased in relation to total woody vegetation density ($F_{1,5.784} = 6.952$, $P = 0.039$, $R^2 = 0.538$; Fig. 2). Within the social species, average group size for impala (mean \pm SE = 7.70 ± 2.06) was significantly higher in the more open vegetation types (Kruskal–Wallis test: $\chi^2_6 = 12.64$, $P = 0.047$), as was nyala group size (2.64 ± 0.29), although the difference was not significant ($\chi^2_7 = 5.802$, $P = 0.563$).

Confidence intervals for the vegetation density surveys ranged from 8 to 27%. Vegetation types including large areas that had been modified by artificial clearing (grassland, open red sand bushveld and open mixed bushveld) had the greatest variation.

There was a strong linear relationship between leopard prey biomass and vegetation density (Pearson correlation: $r_7 = 0.772$, $P \leq 0.05$; Fig. 3). The greatest abundance of available leopard prey was found in habitat types with the highest percentage of woody cover (Table 1).

Feeding Habitat Selection

Leopards did not hunt in habitats at random ($\chi^2_7 = 38.5$, $P \leq 0.001$). More kills than expected occurred in open red sand bushveld, palmveld and open mixed bushveld. In contrast, predation was marginally less than expected in the denser vegetation types (closed red sand bushveld, closed mixed bushveld and sandforest/riparian woodland), and significantly less than expected in grassland. There was no seasonal difference in the distribution of leopard kills (Wilcoxon matched-pairs signed-ranks test: $Z = -0.700$, $N = 8$, $P = 0.484$).

Results of the logistic regression models were similar to those of the univariate analyses in that only open red bushveld, palmveld and open mixed bushveld led to an increased probability of a kill (Table 3). However, grassland was the only significant variable ($P \leq 0.1$), with $\beta = -1.185$, and the overall model fit was poor (Nagerleke's $R^2 = 0.039$).

The logistic regression model that best predicted the location of carcasses using prey abundance and landscape attributes included the three variables associated with woody vegetation cover (shrub density, tree density and total woody vegetation density) and their squared functions, suggesting a nonlinear relationship between woody cover and kill location (Table 4). Variables not included in the final model were prey biomass, grass cover and

Table 2. Mean density (animals/km²) and total population estimates of six major prey species by habitat type at Phinda Game Reserve

Habitat type*	Species					
	Grey duiker	Impala	Nyala	Red duiker	Reedbuck	Warthog
CRB	0.74	3.94	30.29	3.93	0	0.34
ORB	3.12	27.00	15.47	0	0.21	5.35
PV	1.08	0	3.51	0	2.42	3.69
G	0.54	10.21	2.64	0	0.56	4.26
SF	0	0	30.59	14.88	0	0.46
CMB	0	15.66	36.41	2.77	0	5.19
OMB	1.17	29.05	5.44	0	0	6.27
RW	0	3.82	60.08	7.67	0	0
Total population size (±SD)	91±3	1432±321	3117±460	375±50	31±2	402±112
Confidence intervals for counts (%)	2.34	15.17	10.23	9.49	5.35	17.79

*See [Methods](#) for habitat type codes.

distance to water. Model fit and overall predictability were again poor (Nagerleke's $R^2 = 0.067$).

Figure 4 shows a quadratic relationship (ANOVA: $F_{1,6} = 0.76$, $P = 0.514$, $R^2 = 0.233$) between kill probability (odds ratio) and vegetation density. The greatest chance of a kill taking place did not occur in the densest vegetation types, as may have been expected, but rather in habitat types with medium cover levels (range 40 000–80 000 woody plants/km²).

We observed 134 hunting attempts while following radiocollared leopards. We went to considerable effort to minimize possible disturbance to both leopards and prey, and believe that our influence on hunts was minimal. Ungulates at Phinda are continually exposed to vehicles and mostly ignore them (Hunter & Skinner 1998), but to err on the side of caution, we excluded five attempts (one successful, four unsuccessful) from all analyses where we felt that the proximity of the vehicle might have influenced the outcome. During four unsuccessful hunts, the prey moved away after looking in our direction and the leopard stopped stalking. On one occasion, a leopard killed a warthog that we had unintentionally flushed from its burrow. Of the remaining 129 hunting attempts that we observed, 26 (20.2%) were successful (Table 5). There was no significant difference in the outcome of hunts in different habitat types (G test: $\chi^2_5 = 0.705$, $P = 0.990$). Although not significant, more hunts than average were successful in closed red sand bushveld, open

red sand bushveld, palmveld and open mixed bushveld, and less hunts than average were successful in grassland and closed mixed bushveld (Table 5).

Eighteen per cent ($N = 23$) of observed hunts were opportunistic (Table 5). More opportunistic hunts than expected took place in the denser vegetation types (closed red sand bushveld and closed mixed bushveld), while fewer than expected opportunistic hunts were recorded in open red sand bushveld and grassland ($\chi^2_5 = 11.624$, $P = 0.041$).

Interspecific Competition and Avoidance

Seventeen (8%) leopard kills were lost to scavengers (Table 6). Spotted hyaenas were the most common perpetrators ($N = 6$), followed by bushpigs, *Potamochoerus larvatus* ($N = 5$), lions ($N = 4$) and other leopards ($N = 2$). There was no significant difference in the frequency that kills were pirated in particular habitat types to their relative occurrence in those habitat types (G test: $\chi^2_5 = 6.856$, $P = 0.220$), but our sample size for pirated kills was small.

The majority of leopard kills in Phinda were stored in dense vegetation on the ground ($N = 198$), with only 9% ($N = 19$) of carcasses hoisted into trees (Table 6). There was no significant difference in the number of kills hoisted in different vegetation types relative to the occurrence in those habitats (G test: $\chi^2_5 = 5.704$, $P = 0.336$).

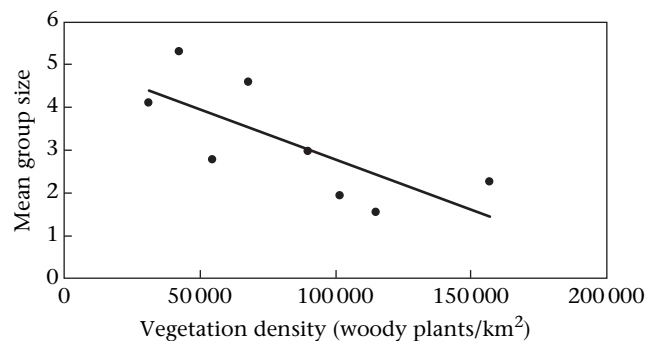


Figure 2. The effect of total woody vegetation density on mean group size of leopard prey species in Phinda Private Game Reserve.

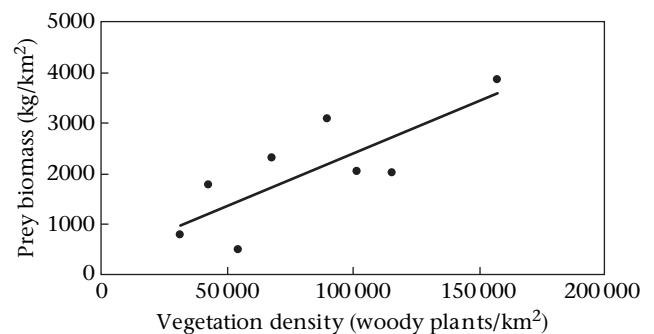


Figure 3. The effect of total woody vegetation density on leopard prey biomass in Phinda Private Game Reserve.

Table 3. Results of the logistic regression models predicting the probability of a kill in different habitat types

Habitat type*	Kill probability		
	Odds ratio	SE	<i>P</i>
CRB	0.923	0.508	0.875
ORB	1.964	0.528	0.201
PV	1.580	0.541	0.398
G	0.306	0.644	0.066†
SF	0.986	0.589	0.981
CMB	0.845	0.523	0.748
OMB	1.400	0.336	0.528
RW	0.951	0.525	0.921

Parameter estimates are presented as relative odds ratios; standard errors and associated *P* values are based on the Wald statistic for independent variables.

*See **Methods** for habitat type codes.

†*P* ≤ 0.1.

DISCUSSION

Leopards at Phinda hunted in habitats where it was easier to catch prey rather than where prey was more common. However, in contrast to expectations, the apparent 'catchability' of prey was not directly proportional to the amount of cover present within a vegetation type. Leopards are widely perceived to favour the densest habitats available for hunting (Hes 1991; Sunquist & Sunquist 2002; Bailey 2005). For example, of 50 kills recorded in the Kruger National Park (Bailey 2005), 46% were found in dense riparian vegetation, 44% in medium to dense thorn-bush thickets and 10% in open habitats. Hayward et al. (2006) suggested a similar trend, with leopards preferring to hunt in dense environments. However, our results show that the probability of a kill occurring was greater in habitat types with intermediate cover levels, even though areas with the densest vegetation also had the highest abundance of available prey.

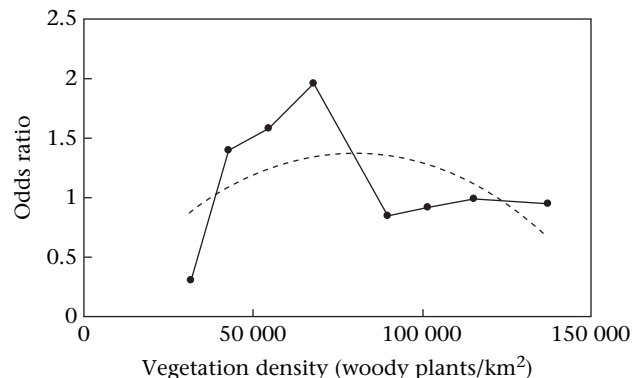
Leopards are visual hunters, relying heavily on sight and to a lesser extent on hearing to detect prey (Sunquist & Sunquist 2002; Bailey 2005). Thicker habitat types on Phinda (closed red sand bushveld, closed mixed bushveld,

Table 4. Results of the logistic regression analyses predicting kill location using landscape and prey abundance attributes

	Kill probability		
	Odds ratio	SE	<i>P</i>
Prey biomass	1.001	0.001	0.382
Shrub density	1.183	0.272	0.083
Tree density	0.978	0.429	0.065†
Total woody vegetation density	1.176	0.331	0.081†
Grass cover	1.020	0.582	0.290
Distance to water	0.999	0.001	0.317

Parameter estimates are presented as relative odds ratios; standard errors and associated *P* values are based on the Wald statistic for independent variables.

†*P* ≤ 0.1.

**Figure 4.** The effect of woody cover on the probability of a kill occurring (expressed as odds ratios) as determined by logistic regression analyses. Dotted line is a second-order polynomial trend line.

riparian woodland and sandforest) may have reduced the chance of an encounter with prey sufficiently to negate any benefits accrued from increased cover for stalking. Additionally, even if prey is successfully detected, increased vegetation density may not always benefit a stalking predator. Too much cover can either impede the progress of a stalk by obstructing a clear view of the target, or increase the chance of detection by prey (because of a noisier approach by the predator), and may hamper the final chase even if a predator gets within charging distance (Leyhausen 1979). At Phinda, leopards appear to favour habitats that strike a balance between these factors. Preferred habitat is not so dense as to significantly reduce encounter rates with prey or hinder stalking cats, but at the same time must provide sufficient cover to allow leopards to approach to within charging distance undetected. In Phinda, open red sand bushveld, palmveld and open mixed bushveld (mean ± SE prey biomass = 1539 ± 533 kg/km², mean ± SE total woody vegetation density = 55014 ± 7306 woody plants/km²) appeared to be the optimum habitat types that met these criteria.

Table 5. The number of successful, unsuccessful and opportunistic hunts observed while following radiocollared leopards by habitat type

Habitat type*	Hunt outcome			Number of opportunistic hunts
	Unsuccessful	Successful	% Successful	
CRB	27	7	25.93	10†
ORB	25	7	28.00	2†
PV	19	5	26.32	4
G	11	2	18.18	1†
SF	1	0	0	0
CMB	7	1	14.29	4†
OMB	13	4	30.77	2
RW	0	0	0	0
Total	103	26	20.16	23

*See **Methods** for habitat type codes.

†*P* ≤ 0.05.

Table 6. Number and percentage of kills lost and carcasses hoisted by radiocollared leopards by habitat type

Habitat type*	Kills lost		Kills hoisted	
	Number	%	Number	%
CRB	3	6	3	6
ORB	3	10	6	20
PV	3	8	6	15
G	4	36	1	18
SF	0	0	0	0
CMB	2	9	1	0.5
OMB	2	8	2	8
RW	0	0	0	0
Total	17	8	19	9

*See [Methods](#) for habitat type codes.

We found no significant difference in the success rate of observed hunts in different habitat types ([Table 5](#)), suggesting that reduced detectability of prey in denser vegetation types was more important in governing the decreased occurrence of kills there. Within the dense habitat types, group size was smaller for all species of herbivores and there was also a higher prevalence of solitary species ([Fig. 2](#)). A reduction in group size may yield antipredator benefits for prey by reducing their detectability to and their encounter rates with predators ([Dehn 1990](#)).

When leopards occur in dense environments, they may use alternative hunting strategies rather than the typical stalk-chase-kill approach as most often used by Phinda leopards. In the Ituri Forest, Democratic Republic of Congo, leopards hide close to fruiting trees, which attract duikers, red river hogs and groups of foraging monkeys, and then ambush their prey from a few metres away ([Hart et al. 1996](#)). Similarly, [Jenny & Zuberbühler \(2005\)](#) observed a Cote D'Ivoire female leopard hide in dense vegetation near monkey groups, then wait for the monkeys to move close before launching her attack. [Hes \(1991\)](#) also recorded South African leopards apparently favouring an ambush-pounce technique in dense, riverine woodland. In contrast, in open, northeastern Namibia ([Stander et al. 1997](#)), 100% of recorded leopard hunts ($N = 100$) included a stalking phase. In our study, we recorded more kills from opportunistic chases (where a leopard surprised prey and no stalk took place) in thicker vegetation types. Because prey detectability was significantly reduced in these areas, leopards may rely more on ambushing or flushing prey than on a prolonged stalk.

Grassland was the only vegetation type that was significantly avoided by leopards, as reflected both in how often leopards were found there and in their probability of making kills there. The level of cover within grassland habitat may have been below a critical threshold that leopards considered worthwhile areas in which to hunt. Even if a hunt was initiated, the chance of a successful outcome was reduced. Predator detectability by prey was probably enhanced by lack of available cover, as well as by the formation of larger group sizes by prey species. Both nyala and impala herds are typically larger in grassland than in more dense habitats, which may result

in an increased likelihood of spotting a predator before it can pose a serious threat ([Dehn 1990](#)). Leopards may also have avoided grassland because of the increased presence of other competing carnivores, which represent a potential threat to them and their kills. Lions can outrun leopards on open ground (L. Hunter, unpublished data) and, in Phinda, lions use grassland more often than expected by chance ([Hunter 1998](#)).

The lack of seasonal variation in both the distribution of carcasses and the prey biomass can probably be attributed to Phinda's mesic climate and relatively uniform distribution of prey throughout the reserve, which may, in part, be influenced by the reserve's small size, total enclosure by fences and presence of artificially maintained water sources. These factors may also explain why distance to water was not a significant variable in the logistic regression models, although waterholes at Phinda were also targeted as areas of high use by lions ([Hunter 1998](#)), especially in the drier months, possibly forcing leopards to avoid them. It is unclear whether fencing and the provision of water affected leopard hunting behaviour. Leopards are not constrained by fences ([Balme & Hunter 2004](#)), nor are they dependent on standing water ([Hunter et al., in press](#)) but these factors might influence the distribution of prey and therefore the hunting patterns that we describe. However, all six key species of leopard prey in the region are naturally resident rather than migratory or nomadic, and they occur at mostly comparable densities in the neighbouring Mkhuzi Game Reserve ([Goodman 1990; Hearne et al. 1996](#)). Furthermore, habitat-specific densities of key prey species during our study did not differ from those in 1992–1995, even though management regimes (including the provisioning of water) varied widely during these two periods ([Hunter 1998](#)). In addition, during our study, water was artificially available only during the dry season and only at two waterholes for no more than 90 days each year, and Phinda management rotated the provision of water through various sites so that no single site or habitat type was overused. Accordingly, we think that significant effects of management practices on leopards' hunting patterns are doubtful and that leopards elsewhere are likely to show some degree of selectivity in hunting habitat as shown here. It would be valuable to investigate this question in more arid habitats where the distribution of water (and possibly also of fences; see [Marker & Dickman 2005](#)) is more likely to significantly influence the spatial occurrence of prey and hence where leopards choose to hunt.

Fewer carcasses were hoisted at Phinda compared to other studies from woodland savanna environments. In Kruger, 84% of carcasses were stored in trees ([Bailey 2005](#)) and 76% of kills were hoisted in the adjacent Londolozi Game Reserve ([Le Roux & Skinner 1989](#)). However, studies in forested habitat have shown that the majority of kills are cached on the ground in dense vegetation ([Karanth & Sunquist 2000](#)) and in areas where scavenger densities are low, and that very few carcasses are hoisted in trees ([Smith 1977; Bothma & Le Riche 1984](#)). It appears that landscape attributes and the degree of interspecific competition determine the likelihood of a kill being hoisted. In our study area, there was no significant difference in the

probability of kills being hoisted in different habitat types (Table 6), presumably because of the relatively low densities of lions and spotted hyaenas (Hunter 1998; G. Balme & L. Hunter, unpublished data) on the reserve.

Carnivore foraging decisions are driven by natural selection to optimize nutrient intake at the minimum energy expenditure and at the least risk to the predator (Krebs & Davies 1993). These decisions are tempered, however, by a wide range of ecological constraints. As long as individuals can overcome these constraints and increase their chances of survival and reproductive success by hunting more efficiently, natural selection will favour optimally foraging predators (Hayward & Kerley 2005). Leopards at Phinda achieved this by selecting particular habitats in which to hunt. Their preferred vegetation types had intermediate cover levels where prey was easier to catch rather than where prey was more abundant, thereby supporting the landscape hypothesis for feeding habitat selection. As the success rates for hunts did not vary significantly between the different habitats, reduced detectability of prey was presumably the main reason driving leopards away from denser vegetation types.

Our results help inform meaningful conservation planning for leopards. Although the leopard has the widest habitat tolerance of any African felid and is more resilient than other, sympatric large cat species in the face of anthropogenic threats (Sunquist & Sunquist 2002), the widely held perception that leopards are 'supergeneralists' with little need for dedicated conservation action is increasingly viewed with suspicion (Spong et al. 2000; Balme & Hunter 2004; Ray et al. 2005). Our results indicate that leopards show some degree of specialization, at least in their choice of hunting habitat. On a larger scale than our study site, this specialization likely translates to important differences in population densities and resilience to threats. Indeed, Norton (1990) first doubted that dense habitat was a refuge for leopards, challenging published density estimates as high as 40 leopards/100 km² for primary rainforest (Martin & De Meulenaer 1988). Subsequently, it has been shown that prey biomass in rainforest is too low to support such densities (Jenny 1996; Henschel 2001; Maisels et al. 2001) and that, more widely, leopard numbers correlate with prey abundance (Stander et al. 1997; Marker & Dickman 2005). Our results suggest that prey catchability will further influence the suitability of habitat for leopards and that, beyond a certain threshold of vegetation density, prey abundance alone will fail to accurately reflect its value for leopards.

This finding might have surprising implications for large areas in Africa that are generally considered to be highly suitable for leopards, such as the dense miombo woodland, which is the dominant vegetation type across most of south-central Africa, from central Mozambique through Tanzania and west through Malawi, Zambia and Angola. It would be valuable to produce density estimates from miombo habitat to test this idea; these data currently do not exist, but they could be easily generated by mark-recapture models applied to camera-trapping results (Henschel & Ray 2003). More generally, our results highlight the importance of detailed ecological studies in

elucidating the conservation needs of large cats. Despite their comparative success, leopards have disappeared from at least one-third of their historical range in Africa (Ray et al. 2005), in part, because of indirect threats that are poorly understood (Henschel 2001; Henschel & Ray 2003). A greater understanding of the leopard's subtle ecological requirements will help researchers to inform this question and plan wisely for the species' conservation.

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