

Habitat and patch use by hyraxes: there's no place like home?

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Abstract

Models of central place foraging predict that animals should forage more thoroughly in resource patches located closer to the central place. Travel time, cost of transporting food back to the central place, and exposure to predators should all act to increase foraging costs with increasing distance from the refuge. We examined habitat and patch use in rock hyraxes (*Procavia capensis*) inhabiting a group of kopjes in a semiarid savanna, Augrabies Falls National Park, South Africa. We tested the prediction of more intense patch use closer to the central place by measuring giving-up densities (GUDs) in experimental resource patches set at four different distances from the kopje and in two microhabitats differing in cover. Surprisingly, hyraxes had their lowest GUDs at intermediate distances from the kopje. These unexpected results suggest that the sentinel behaviour of hyraxes alters the probability of detection of predators for animals foraging away from the kopje.

Keywords

Central place foraging, coloniality, habitat selection, hyrax, optimal patch use, predatory risk.

Ecology Letters (1999) 2: 82–88

INTRODUCTION

Under diverse situations, feeding animals make decisions affecting the amount of energy harvested and the likelihood of being killed by a predator (Lima & Dill 1990). Central place foraging can provide one such situation (Orians & Pearson 1979; Schoener 1979). Central place foraging occurs when an animal initiates and ends foraging bouts from a set location such as a perch, nest, den, burrow, refuge, or hive. In general, a forager should forage more thoroughly and demand a lower minimum harvest rate from patches nearer the central place than farther away, providing both near and far patches are simultaneously present. This preference for feeding location near the central place can occur for two reasons. First, the feeding animal may make frequent trips to and from the food patch as it builds a larder hoard or transports food to its young or to colony members. The travel time to and from more distant patches reduces the average rate of net energy return to the central place, and hence depletable food patches near the central place should be more valuable and harvested more thoroughly than patches farther away. Second, many animals must retreat to a refuge, nest, or colony to successfully escape an attacking predator. For such animals, the risk of predation increases with distance from the refuge; again,

patches near the refuge or central place are more valuable than those farther away. For these reasons, it is often the case that there is no place like home.

Rock hyraxes (*Procavia capensis*; Pallas 1766), medium-sized (up to 4.3 kg, with adult mass related to maximum summer temperatures; Yom-Tov 1993) herbivores, occur in rocky shrub lands throughout Africa and the Middle East (Olds & Shoshani 1982). Colonies of up to 80 individuals and more inhabit cliff faces, rock outcroppings, and kopjes (Coe 1962; Mendelssohn 1965). Hyraxes use rocks for shelter, leaving the protection of the rocks to forage for a variety of plants (Sale 1965; Hoeck 1975; Fourie & Perrin 1990). When they do, they are subject to predation (Davies 1994). In places, hyraxes comprise the most common prey of leopards (*Panthera pardus*, Linnaeus 1758; Stuart & Stuart 1993), crowned eagles (*Stephanoaetus coronatus*, Boshoff *et al.* 1994), and black eagles (*Aquila verreauxii*; Davies 1994).

In accord with simple models of central place foraging, foraging costs should be least on the kopje and increase with distance from the kopje. In fact, such a gradient in foraging effort and costs causes pikas (*Ochotona princeps*, Link 1795) to deplete and change the community composition of plants (Huntly 1987) more intensively near rock refugia than farther away. Declining patch exploitation with distance from a refuge has been

documented for ibex (Kotler *et al.* 1993a), fox squirrels and grey squirrels (Brown *et al.* 1992; Bowers *et al.* 1993; Brown & Morgan 1995), guinea pigs (Cassini & Galante 1992), juncos (Lima 1988), and ground squirrels (Smith 1991).

Here, we assess how the cost of predation varies with distance from a colony of hyraxes inhabiting a series of kopjes in Augrabies Falls National Park, Northern Cape Province, South Africa, by quantifying their use (giving-up densities; Brown 1988) of experimental food patches set at four distances from the kopjes.

OPTIMAL PATCH USE

In food patches where the forager experiences diminishing returns (harvest rates decline with time spent exploiting the resource patch), an optimal forager should exploit a patch until its harvest rate, H , in the patch falls to equal the sum of its energetic, C , predation, P , and missed opportunity costs, MOC, of foraging (Brown 1988, 1992):

$$H = C + P + \text{MOC} \quad (1)$$

When an animal's harvest rate is a function of the amount of food remaining in the patch, then the forager's giving-up density (GUD, the amount of food remaining in a patch following an activity bout) provides a surrogate for its quitting harvest rate and for its foraging costs. In support of the theory, GUDs change appropriately in response to factors influencing harvest rates (Ziv *et al.* 1995), energetic costs (Kotler *et al.* 1993a), predation costs (e.g. Brown *et al.* 1988; Kotler *et al.* 1991, 1993b), food characteristics (Kotler *et al.* 1994), and the richness of the environment (Brown *et al.* 1992).

Here, we will use GUDs to measure the hyraxes' perceived costs of predation while foraging from resource patches. To do so, we give the same forager easy access to a number of food patches. By making the patches identical in food and structure, we control for the food patches' harvest characteristics (H). Because the same foragers have access to all of the food patches, we control for the missed opportunity cost. MOC is a property of the individual and its environment, and not a feature of a given food patch (Brown *et al.* 1992). By placing the food patches under similar microclimates, hyraxes should have the same metabolic cost of foraging in all of the food patches. Under these circumstances, food patches can only differ in P . For the hyraxes in our study, we expect predatory risk to increase with distance from their kopje or refuge. In response, hyrax GUDs should increase with distance from refugia.

GUDs in feeding trays should give us insights into the costs and benefits of patch use, providing the fitness of a forager is a function of its energy gain, its survivorship, and the amount of fitness enhancing activities it performs when not engaged in foraging (Brown 1988). The

underlying model is based on fitness maximization. Furthermore, a wide variety of fitness functions ranging from additive to multiplicative interactions of food and safety lead to the same patch use rule (Brown 1992). The diminishing returns may be caused by anything ranging from resource patch depletion to the changing marginal value of energy to limited capacity to convert energy into offspring. One limitation of the technique is that all foraging costs must be taken into consideration. For example, interference may also constitute such a foraging cost (Kotler & Brown 1988). A second limitation is that the researcher be aware about whether the resource provided in the feeding trays constitute substitutable or complementary resources (Schmidt *et al.* 1998). A third limitation concerns the context in which GUDs are measured. That is, the feeding tray must offer a foraging task that the animal can perform with a food type that it can consume, the patch size must represent a scale of heterogeneity to which it can respond, and the costs and benefits experienced in the feeding trays must be at the same temporal scale as those that shaped the evolution of the forager's behaviour.

MATERIALS AND METHODS

We studied a colony of hyraxes at Augrabies Falls National Park, South Africa (28°34' S, 20°19' E). The colony of ≈ 50 hyraxes occupied a group of three adjacent kopjes (hereafter referred to as the "kopje") isolated by more than a kilometer of semiarid savanna from the closest large rock formation. Woody vegetation near the kopje included blackthorn acacia (*Acacia mellifera*), camelthorn acacia (*A. erioloba*), *Ficus cordata*, *Ceraria namaquensis*, shepherd's tree (*Boscia albitrunca*), stinkbush (*B. foetida*), buffalo thorn (*Ziziphus mucronata*), quiver tree (*Aloe dichotoma*), *Euphorbia gregaria*, *Tamarix usneoides*, and *Rhus pendulina*. The common grasses include *Aristida* sp., *Stipagrostis ciliata*, and *S. uniplumus*. Vegetation in the immediate vicinity of the kopje, primarily *A. mellifera* trees and *Aristida* spp. grasses, had been heavily modified by hyrax herbivory. The kopje itself, entirely devoid of vegetation with the exception of one *F. cordata*, rises 10–15 m above the relatively flat surroundings. A few scattered dead or severely pruned *A. mellifera* comprise the only vegetation within 10 m of the kopje. From 10 to 50 m beyond the kopje, the impact of herbivory diminished, and the amount and stature of trees and grasses increased (Table 1).

From 15 June through 20 June 1995, we prebaited potential stations at varying distances from the kopje with small piles of a mix of foods (rabbit pellets, corn, alfalfa, raisins, and peanuts). Starting 20 June, we began placing pairs of food patches at each of 11 stations at each of four

Table 1 Vegetation structure in habitats that differ in their distance from the kopje

Habitat	Acacia % leaves left	Grasses None: light: heavy damage
Kopje	No trees	No grasses
Base of Kopje	All dead or severely browsed	No grasses
Ring at 20 m	35.45 (12.17)	31%:9%:60%
Ring at 40 m	74.55 (9.86)	49%:40%:11%

Measurements were taken at feeding tray stations. We estimated the percentage of leaves remaining (95% C.I. given in parentheses) on the branches of the closest *Acacia* tree to each of the 11 stations, and we scored 10 (or fewer if 10 were not present) grass plants within a 5-m radius of each station as to the degree of grazing damage.

distances from the kopje. The stations at a given distance were distributed in a ring around the kopje. The distances included (i) on the kopje at an elevation 3–5 m above the surrounding plains, (ii) at the base of the kopje along the rock–soil boundary (only 10 stations), (iii) \approx 20 m from the edge (18.7 m, 4.15 SD), and (iv) \approx 40 m from the kopje's edge (37.3 m, 6.77 SD). A food patch consisted of a circular plastic tray (22.5 cm diameter, 4.5 cm deep) filled with 40 pieces of peanuts (from whole peanuts cut into eighths: resulting in 3.3 g, 0.249 SD, per tray) mixed into 1.5 liters of sifted sand. We placed four peanut halves on the surface of each patch as an attractant and indicator of foraging activity. At a station, one patch of a pair was placed at the base of an *Acacia* tree ("bush" microhabitat) and the other was placed 2–3 m away from the same tree ("open" microhabitat). These microhabitats applied to all distances except for the ring of stations on the kopje, in which case: "open" being exposed on the outer ledge of a flat, stone shelf; "bush" being 1.5–2 m away on the inner side of the same shelf adjacent to crevices in the kopje. In both cases, "bush" trays offered concealment and/or physical protection while "open" trays did not. We filled trays with food each morning, counted the peanut pieces remaining in each patch in the evening following foraging by hyraxes, recorded the GUD (number of pieces), and added peanut pieces to trays to reconstitute the original amount of food. Foraging in trays by hyraxes was confirmed by the removal of the indicator peanuts from the trays' surface and by foot prints left in the trays' sand.

We let the days of 20–21 June be an acclimatization period for the hyraxes. On these days, the hyraxes learned to nuzzle and scrape through the sand in search of food items. On the days of 22–23 June, we had foraging activity at a sufficient number of patches to collect data from 18 stations, six at each of the three nearest distances (on the kopje, at the kopje base, and 20 m from kopje). On 23–24 June we had sufficient patches to cover all 43

stations of the four distances. We analysed the GUD data (number of peanut pieces remaining) as a partially hierarchical ANOVA with habitat as a group variable, station as a variable nested within habitat, and microhabitat as a variable fully crossed with habitat and station. To account for different numbers of days of data collected from different stations (2 versus 4 days), we used the average GUD at each station for the entire experiment as the dependent variable. We felt comfortable with this procedure because an analysis of the 18 stations with 4 days of data revealed no significant effect of day on GUDs.

RESULTS

Patch use varied significantly with distance from the kopje, although not in the manner predicted (Table 2, Fig. 1). Planned comparisons of adjacent distances indicated significantly higher GUDs on the kopje than at the kopje's base; GUDs did not differ significantly between the kopje's base and 20 m away; GUDs increased significantly from 20 m to 40 m away from the kopje. In summary, GUDs were highest on the kopje, declined to their lowest at the 20 m distance, and increased again at 40 m.

Patch use varied significantly with microhabitat, but only as an interaction effect with distance from kopje (Table 2, Fig. 1). On the kopje, hyraxes had lower GUDs in microhabitats far from cover. At 20 m distance, the opposite occurred: hyraxes had lower GUDs near cover than farther away. There were much less pronounced effects of microhabitat at the kopje's base and at 40 m.

DISCUSSION

For two reasons, central place foraging theory typically predicts that patch use should decline and GUDs should

Table 2 Analysis of variance for GUDs in feeding trays. Included under Habitat are the *F*-tests for the three planned comparisons of adjacent distance habitats

Group variable	Source			
	SS	DF	MS	F
Habitat	5179.03	3	1726.34	7.66***
1 versus 2		1	1713.74	7.60*
2 versus 3		1	680.57	3.02
3 versus 4		1	2186.91	9.70**
Nested variable				
station	8794.49	39	225.50	13.99***
Fully crossed variable				
Microhabitat	0.04	1	0.04	0.00
Microhabitat \times habitat	200.89	3	66.96	4.15*
Error	628.725	39	16.121	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

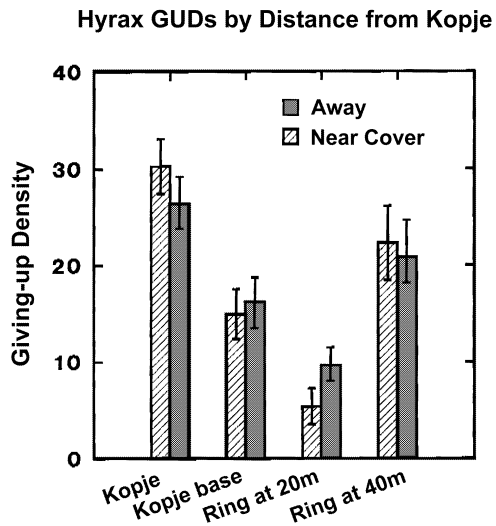


Figure 1 Mean GUDs (number of peanut eighths remaining), \pm SE, in feeding trays as a function of microhabitat and distance from the kopje.

increase with distance from the nest or refuge. If food must be transported back to the central place or if predatory risk increases with distance from the refuge, then nearby patches provide either higher average harvest rates or lower foraging costs than faraway patches, respectively. The latter situation probably applies to hyraxes: they do not transport food to the kopje, but they do escape from approaching predators by fleeing to the kopje. Patch use and GUDs of hyraxes did vary with distance from the kopje. Surprisingly, GUDs did not increase with distance; in fact, the pattern was not even monotonic.

In going from the kopje to 40 m away from the base, hyraxes produced a U-shaped pattern of GUDs. On the kopje, where we expected hyraxes to feel safest, they exhibited their highest GUDs. They exhibited their lowest GUDs at the 20 m distance. We interpret this to mean that hyraxes had their highest foraging costs on the kopje or far from the kopje and their lowest costs at intermediate distances. Despite the unusual pattern, we attribute these distance effects to predatory risk in the context of optimal patch use.

GUDs can be affected by metabolic costs of foraging, predation costs, and missed opportunity costs. Individual hyraxes had access to foraging patches at all distances, and this should equalize the missed opportunity costs among patches and distances. Also, because of the uniform nature of the feeding trays, metabolic costs of exploiting a feeding tray should have been the same at all distances unless thermoregulatory costs differed due to differences in microclimate. Save for on the kopje itself, all patches were on the same sandy substrate with the same range of

exposures to sun and wind. While we did not measure microclimate, it should have been similar across stations. Thus, we conclude that the differences in GUDs across distances resulted from differences in predatory risk.

The microhabitat effect near and away from cover was also unusual. Typically, near cover affords greater safety and lower predation costs (e.g. Werner *et al.* 1983; Lima 1988; Werner & Hall 1988; Lima & Dill 1990; Sweitzer & Berger 1992; Persson & Eklov 1995). Work with desert rodents (Brown *et al.* 1988, 1994; Kotler & Brown 1988; Kotler *et al.* 1991; Hughes & Ward 1993), squirrels (Bowers *et al.* 1995; Brown *et al.* 1992), and porcupines (Brown & Alkon 1990) have found lower GUDs in the "bush" microhabitat. This pattern of foraging applied to the hyraxes, but only at distances of 20 m from the kopje. The opposite occurred on the kopje, where GUDs were lowest on the exposed outer ledges of rock shelves and highest adjacent to vertical cracks and crevices along the inner portion of the shelf (see Brown 1989 and Kotler *et al.* 1993b for examples where desert rodents had a lower GUD in the open than in the bush microhabitat).

While we did not predict the pattern of foraging exhibited by the hyraxes, the data provide fascinating observations for developing new hypotheses regarding central place foraging in a social animal with sentinels. Consider first the effect of foraging in groups. The colonial habit of hyraxes may allow for the safe exploitation of resources away from the central refugia. The effectiveness of vigilance in hyraxes increases with group size (Barry 1994), as does the dilution effect and other antipredator escape tactics (Lima & Dill 1990). This may allow groups of hyraxes to forage more intensively and farther from refuge than can an isolated individual, but otherwise does not result in a U-shaped relationship of predatory risk and foraging costs with distance from the refuge.

Perhaps more importantly, hyraxes employ sentinels. When hyraxes venture away from the rocks, one or more group members remain behind and typically perch from a vantage point where they can see all of the exposed foragers; foraging away from the rocks only occurs in groups and in the presence of a sentinel (Davies 1994). When sentinels indicate approaching danger, the feeding hyraxes retreat to their kopje. Furthermore, the hyraxes leaving the kopje venture from their rock refuge in the same direction and as a single group (Sale 1965; Hoeck 1975; Davies 1994). This may enhance the effectiveness of their sentinels.

A sentinel acting as the eyes for a group of feeding hyraxes may bend the pattern of predation costs from the normal monotonic relationship between foraging costs and distance from refuge. It may be that on the kopje a hyrax has a more limited field of view because of the rocks and may therefore be more vulnerable to the stealthy

approach of a leopard from around the side of the kopje or to attack from a black eagle swooping over the kopje behind the hyrax's field of view (Davies 1994). In the absence of well placed sentinels, trying to feed on the kopje may be risky in the extreme. Furthermore, being on the inner face of rock shelves may further restrict a hyrax's vision and increase their susceptibility to sudden ambush. In the presence of a sentinel, the predation cost of feeding away from the kopje may be much lower than feeding on the kopje in the absence of effective sentinels. Recently, Bednekoff (1997) modeled the evolution of sentinel behaviour for when sentinel behaviour is part of a trade-off of foraging and predatory risk. This model shares many characteristics with our hypothesis and results. In particular, the model requires that nonvigilant animals occupying positions where sentinels are normally found are most at risk. This coincides with our results that GUDs are highest on the kopje.

One or several sentinels can provide an umbrella of vigilance for hyraxes feeding away from the kopje. The sentinels presumably establish this umbrella in response to feeding opportunities, which at our kopje start at about 20 m distance (although feeding opportunities are greater at 40 m than at 20 m). In this way, the structure of the vegetation (clear line of sight up to 20 m, but partially obscured by the vegetation beyond that point), and the behaviour of sentinels may minimize predation costs at 20 m. Beyond this distance, vegetation can obscure lines of sight, and escape time to the refuge increases. Under 20 m, there may be little feeding activity and consequently less coverage by the sentinels. Furthermore, at very close distances to the kopje, the same factors that presumably place sentinels at risk (limited field of view to the sides and to the rear—the forager's view is obstructed, and the sentinel either cannot see the forager or cannot see large areas close to the forager) can also act to endanger foragers. A U-shaped pattern of predation costs with distance from the kopje may represent the combined effects of the kopje, current vegetation structure, the vigilance behaviour of the sentinels, and optimal patch use by the hyraxes.

This interaction of vegetation structure and vigilance may also explain why the pattern of vegetation abundance (increased cover and decreased damage from hyraxes with increased distance from the kopje) follows closely the expectations of central place foraging (Huntly 1987), while the GUDs we measured did not. When vegetation cover is uniform with distance, feeding and vigilance should be directed at the kopje's base. As the vegetation becomes depleted and modified close to the kopje, the umbrella of vigilance and feeding shifts outward, eventually creating a barren strip until the rate of productivity can balance the rate of herbivory. A similar,

although less extreme, depletion of vegetation to the one hypothesized here was observed during a 17-year study of rock hyraxes in Kenya (Hoeck 1989) and annually during the dry season in the Karoo, South Africa (Davies 1994). Interestingly, in the Karoo study, productivity was higher than in the current study, and hyraxes ventured no further than 15 m from their refuge (Davies 1994). This suggests that in the Karoo, the greater seasonal regrowth of vegetation never allows the umbrella of vigilance to shift very far from the central place.

Alternatively, the U-shaped pattern of GUDs may be a response to differences among individuals in missed opportunity costs. Different classes of individuals may forage at different distances from the central place. Under this hypothesis, an individual is actually restricted to a narrower range of foraging opportunities according to its class than encompassed by our experiment. In which case, our U-shaped pattern manifests or includes individual differences in foraging costs caused by differences in individual state and missed opportunity (D.W. Morris, personal communication). While this possibility remains uninvestigated, the tendency of hyraxes to leave the kopje and forage as a group (Davies 1994) makes this hypothesis unlikely.

Our results may be somewhat idiosyncratic because they should be context dependent in time and space. With regard to time, if the foraging behaviours we observed are responses to episodic events, our experiment may not have included the actual events. With regard to space, varying the disposition of the rocky refuge, the structure of the vegetation, and the intensity and identity of predators may qualitatively vary the pattern of perceived predatory risk and GUDs around the central refuge. Nonetheless, these qualitative differences may provide additional advantages for coloniality. By reducing the perceived predatory risk of the foragers, coloniality allows for lower GUDs, the more thorough exploitation of resources, and the occupation of new or less favourable habitats. Of the many benefits of coloniality (e.g. Alexander 1974; Hoogland & Sherman 1976; Cote & Poulin 1995), this may be the most far reaching.

ACKNOWLEDGEMENTS

We thank the National Parks Board of South Africa for the opportunity to work in Augrabies Falls National Park. The friendly and helpful staff of Augrabies National Park provided accommodation and logistical support. Special thanks go to Barry Hopgood, Chief Ranger, Nico Van der Walt, Park Warden, and David Momberg, Camp Manager. This work was partially supported by the National Parks Board of South Africa and the United States-Israel Binational Science Foundation (grant number

93–00236). This is publication #262 of the Mitrani Center for Desert Ecology.

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BIOSKETCH

Burt P. Kotler tests predictions of foraging theory and mechanisms of species coexistence based on foraging theory. He has also done theory concerning the effect of foraging behaviour on species interactions and the effect of costly information on optimal diet.

Editor, R.D. Holt

Manuscript received 22 September 1998

First decision made 6 November 1998

Manuscript accepted 8 December 1998