

# 16

## Predation Risk and Habitat Use in Chacma Baboons (*Papio hamadryas ursinus*)

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### Introduction

Research into the importance of predation is underrepresented in primatology. Furthermore, the literature that does exist has produced inconsistent results. In part this reflects the difficulty one encounters in estimating predation pressure in natural environments. Here we present an introduction into how predation risk might be estimated in terrestrial environments, and we employ this model to explore patterns of habitat use in chacma baboons. The results suggest that baboons respond behaviorally to habitat-specific levels of predation risk, even in a low predator-density environment. This idea suggests that researcher primate perceptions of predation are not to be simply equated with what is observed in the predator-prey interactions; it is the breaking down of the predation process that offers considerable scope for understanding the impact of predation on primate behavior.

Predation pressure has long been assumed to be a powerful selective force on primate sociality (Alexander, 1974; van Schaik, 1983; Dunbar, 1988; Hill & Dunbar, 1998; Janson, 1998, 2003), although attempts at establishing its importance have reached contradictory conclusions. While some studies have reported positive relationships between group size and predation (Anderson, 1986; Dunbar, 1988; van Schaik & Hörsterman, 1994; Hill & Lee, 1998; Zuberbühler & Jenny, 2002), others have reported negative relationships (Isbell, 1994; Shultz et al., 2004), while still others have reported the absence of any relationship at all (Cheney & Wrangham, 1987). Much of the confusion in this debate, however, stems from a conflation of the effects of *predation risk* with *predation rate* to the extent that many of these studies have addressed fundamentally different aspects of predation (Hill & Dunbar, 1998).

Hill & Dunbar (1998) argued that “predation risk” and “predation rate” were separate elements of predation that generated disparate predictions about primate behavioral responses to the threat of predation. Observed predation rates in natural population *reflect* net predation risk *after* animals have invested in risk-reducing behavior; predation risk (or “*intrinsic predation risk*”) (see Janson 1998),

in contrast, represents “the probability that an animal living on its own and exercising no behavioral anti-predator strategies will succumb to a predator within a given time period” (Hill & Dunbar, 1998, p. 413). In essence, predation risk is an animal’s own perception of the likelihood of that it will be subject to an attack by a predator, and it is this that acts as both the proximate and ultimate constraint on primate behavior. Although in this sense the definition is somewhat abstract, it nevertheless suggests that an individual’s predation risk (as in its perception of that risk) is likely to be closely linked to its local environment. The challenge, therefore, is to identify the parameters within a primate’s environment that contribute to its perception of the level of intrinsic predation risk.

### *The Dynamics of Predation Risk in Terrestrial Environments*

Predation events are complex sequential dynamic processes that comprise a number of constituent elements (Lima & Dill, 1989; Endler, 1991). For the purposes of this chapter it is convenient to consider “predation risk” as a sequence of four components (Figure 16.1): (i) predator encounter; (ii) predator attack; (iii) prey capture; and (iv) individual capture probability. These categories are not necessarily exclusive and may overlap to a considerable extent. The order in which they are presented is also unlikely to be an accurate reflection of biological reality; predators are expected to select their target prey prior to attack and capture. Nevertheless, since here we are not interested in a specific individual per se, but rather in how predation risk averages out over individuals in a group, the current order at least provides a useful starting point. Thus, while it is recognized that the subdivision of predation risk into constituent components is not without its limitations, it is probably the most appropriate basis for a study of this type.

### *Probability of Encounter*

Few studies are able to obtain accurate encounter rates between primates and their major predators, particularly since the presence of observers may in fact reduce the

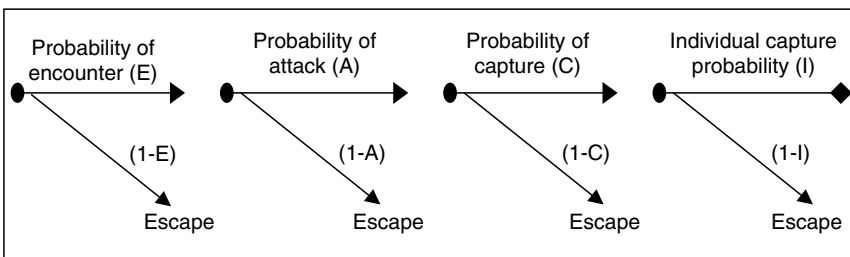


FIGURE 16.1. Schematic representation of individual predation risk in terrestrial primates. Predation risk is a sequence of four components: (i) predator encounter; (ii) predator attack; (iii) prey capture; and (iv) individual capture probability. Prey animals should attempt to interrupt the process as early as possible

frequency of predator-prey interactions (Isbell, 1991). Across populations, however, predator density is likely to provide a good working estimate of the frequency of interactions (Abrams, 1994; van Schaik & Hörsterman, 1994). While data on the density of predators are also limited, previous studies across populations and species have found positive relationships between primate group size and either estimated predator densities or categorical indices of the frequency of predator-prey relationships (Anderson, 1986; Hill & Lee, 1998; Hill, 1999). Within populations, predator habitat preferences are likely to provide a proxy for encounter rates. Leopards, for example, show preferences for dense vegetation and avoidance of open habitats (Bailey, 1993). Since leopards are the primary predators of baboons (Cowlshaw, 1994), it is likely that enclosed habitats present a high risk in relation to rates of encounters with predators.

### *Probability of Attack*

Once a predator has encountered and detected potential prey, an attack decision is made based on the likelihood of attack success (although other factors such as hunger levels and the availability of alternative prey are also important) (Schoener, 1971; Elliot et al., 1977; van Orsdol, 1984). Attack success is determined by the probability that a predator is able to approach within a critical striking distance of the prey (Underwood, 1982; van Orsdol, 1984). Primates attempt to detect predators before they approach this critical distance through monitoring their local environment, although the effectiveness of such vigilance is restricted by habitat visibility. In general, attacks by leopards and lions, which are both ambush predators, are more successful as the degree of cover increases (van Orsdol, 1984; Bothma & Le Riche, 1986). These observations suggest that, for terrestrial primates at least, predation risk and the probability of predator attack should together be a positive function of the level of ground cover and thus be negatively related to habitat visibility.

### *Probability of Prey Capture*

Once a predator attacks from ambush, prey will attempt to evade capture by trying to reach cover or a refuge (Dill & Houtman, 1990). Probability of escape is likely to be strongly influenced by the distance to a suitable refuge; this fact has been reflected in vigilance rates in baboons (Cowlshaw, 1998). Selective use of habitat may also be advantageous if the prey animal has greater agility over a substrate than its predator (Dunbar, 1986). In general, however, local refuge availability is likely to be the key parameter underlying the probability of prey capture for terrestrial primates.

### *Individual Capture Probability*

The “individual capture probability” for an animal simply relates to the probability that, given a successful attack upon a group, a particular individual is the

predated individual. This is a simple function of group size: the probability of an individual being the prey is a function of the number of individuals present, i.e.,  $1/N$ , where  $N$  is the prey group size; this is the *dilution effect* (Hamilton, 1971). Although it is counterintuitive to consider this the final stage of the predation process, since a predator will select its likely prey prior to attacking, it is useful to separate it from the other risk components since the level of risk is socially rather than environmentally determined. Across populations, therefore, group size (and thus individual capture probability) can be taken to indicate the degree to which individuals are responding to the perceived threat of predation. Observed variation in group size across populations should reflect the degree of risk resulting from the three habitat-related components (probability of encounter, probability of attack and probability of escape). Similarly, within populations, this approach allows us to examine the behavior of groups of different sizes in response to the habitat-specific levels of predation risk in that environment.

### *Predation and Habitat Use in Baboons*

Traditionally, studies of home range use in primates have tended to examine the relationship between intensity of habitat use and the spatial and temporal variability in food distribution. Several lines of evidence suggest, however, that predation risk may be an important influence on the ranging patterns of baboons. Stacey (1986) found that a small group at Amboseli remained in closer proximity to trees (refuges) than larger groups, and at Mkuzi the baboons tended to forage in areas of high tree density and avoid areas of tall grass where visibility was poor (Gaynor, 1994). In a more formal examination, Cowlshaw (1997a) found that at Tsaobis habitat use was influenced by group size, with smaller groups spending proportionately less time in high-risk habitats. There was also evidence that smaller troops spent more time on or close to refuges (Cowlshaw, 1997b).

Habitat choice may not be the only factor influenced by predation risk, and baboons appear to modify their behavior within habitats on the basis of the habitat-specific level of risk. At Tsaobis grooming and resting activity were almost exclusively restricted to the safest habitat, and moving was also predominantly confined to the safer areas (Cowlshaw, 1997a). Similarly, Stacey (1986) found that groups selected trees or other elevated areas while resting at Amboseli. In contrast, time spent in the high predation risk but high food availability habitat at Tsaobis was almost exclusively for feeding (Cowlshaw, 1997a). This suggests that where activities have no specific habitat requirements (such as sufficient food availability) these activities are conducted preferentially in low predation risk habitats.

The above studies provide general support that habitat characteristics—most notably visibility and refuge availability—influence perceived predation risk in baboons. The remainder of this chapter presents an examination of the role of predation risk in determining habitat use in a population of chacma baboons at De Hoop Nature Reserve, South Africa. In doing so, it further assesses the validity of the predation schema depicted in Figure 16.1 for determining habitat-specific predation risk.

TABLE 16.1. Home range composition, vegetation structure, habitat visibility, predation risk, and food availability of the major habitat types within the baboon home ranges at De Hoop.

| Habitat Type          | VT             | ST             | Bush Cover (%) | Tree Cover (%) | Visibility (m) | Visibility <10 m (%) | Predation Risk | Food Availability |
|-----------------------|----------------|----------------|----------------|----------------|----------------|----------------------|----------------|-------------------|
|                       | Home Range (%) | Home Range (%) |                |                |                |                      |                |                   |
| Acacia woodland       | 16.0           | 11.2           | 55.8           | 34.4           | 4.6            | 90                   | high           | high              |
| Burnt acacia woodland | 0.2            | 0              | 3.2            | 0.4            | 20.8           | 16.7                 | intermediate   | low               |
| Burnt fynbos          | 27.8           | 43.2           | 3.6            | 0.0            | 35.8           | 0                    | intermediate   | low               |
| Fynbos                | 25.9           | 32.0           | 54.0           | 3.4            | 13.7           | 72.5                 | high           | low               |
| Grassland             | 11.2           | 0.2            | 1.6            | 1.2            | 129.7          | 2.5                  | low            | intermediate      |
| Vlei                  | 18.9           | 13.4           | 0.0            | 0.0            | 251.7          | 0                    | low            | high              |
| Cliffs                | —              | —              | —              | —              | —              | —                    | very low       | very low          |

## Methods

### *Study Population*

De Hoop Nature Reserve, South Africa, is a coastal reserve situated close to Cape Agulhas, the southern tip of Africa. Vegetation on the reserve is classified as coastal fynbos, a unique and diverse vegetation type comprising Proteaceae, Ericaceae, Restionaceae, and geophyte species. Six distinct habitat types were classified on the basis of vegetation structure within the home range of the baboons (Table 16.1: see Hill (1999) for detailed descriptions and further information on the ecology of the reserve).

The data presented here were collected over a 10-month period (March to December 1997) from two groups of chacma baboons (*Papio hamadryas ursinus*): VT, which ranged in size from 40 to 44 individuals, and ST, which numbered 17 to 21 animals over the course of the study. Data were collected by means of instantaneous scan samples (Altmann, 1974) at 30-min intervals, with further 20-min focal samples with point samples at 2-min intervals collected for the all adults in VT. During 5 full day follows each month the position of the center of mass of the group (see Altmann & Altmann, 1970) was determined using a Magellan 4000 XL GPS for each scan sample. Cumulative home range areas and patterns of habitat use for the two troops were then established on the basis of the number and habitat composition of 4-ha quadrats entered by the groups during these day follows.

## Results

### *Habitat-Specific Predation Risk at De Hoop*

Although the *probability of encounter* with a predator is likely to be closely related to predator density across populations, within populations it is unlikely to be

a constant factor since predator preferences for specific habitat types will undoubtedly be important. The distribution of leopard (*Panthera pardus*) extends well into the Western Cape and the Cape Agulhas region (Stuart et al., 1985), although leopard numbers have declined significantly over the last century (Norton, 1986). As a consequence the region is characterized by low leopard density. But while no leopards were known to be resident on De Hoop during the study, they were recorded soon after (Henzi et al., 2000). Although this suggests the local leopard population is migratory, passing through the study area on an intermittent basis, these transient individuals should nevertheless be associated with the densest vegetation when on the reserve. Probability of encounter should thus be greatest in habitats with highest bush level cover (see Table 16.1).

The *probability of attack* also increases in enclosed habitats because the decreased visibility increases the probability that a predator can stalk to within a critical attack distance. Attack distances for leopards are recorded to range from 5 m to 10 m (Kruuk & Turner, 1967; Bertram, 1982). As a consequence, the proportion of visibility below 10 m rather than visibility per se may be the important factor, since this is the critical distance that delimits susceptibility to leopard attacks. The visibility distances and the proportion of visibility below 10 m for each De Hoop habitat are given in Table 16.1.

We expect the *probability of capture* to related to the availability of refuges within each habitat. De Hoop is a relatively treeless environment (a characteristic of fynbos vegetation; Campbell et al., 1979; Moll et al., 1980), however, and thus none of the habitat types contained a significant number of trees of a sufficient height to operate as refuges. As a consequence, refuge density is not a habitat-specific parameter but instead relates to the availability of cliffs that are topographic features of the landscape and independent of habitat type. Refuge density is not habitat-specific, therefore, and the probability of prey capture can thus be considered relatively constant between habitat types.

Estimates of habitat-specific predation risk for six habitats with the baboon home ranges at the De Hoop were thus quantified on the basis of two parameters: probability of encounter and probability of attack (Table 16.1). In both cases, risk increased in more enclosed habitats, and vegetation structure (bush cover) and habitat visibility were closely linked (visibility:  $r^2 = 0.816$ ,  $F_{(1,5)} = 22.18$ ,  $p = 0.005$ ; visibility < 10 m:  $r^2 = 0.879$ ,  $F_{(1,5)} = 36.16$ ,  $p = 0.002$ ). In addition A seventh habitat, regenerating fynbos, is included in this analysis (visibility: 14.7 m; visibility < 10 m: 47.5%; bush cover: 30.6%; tree cover: 0.2 %). For comparison, information on habitat-specific food availability is also provided since this is likely to be another important factor in habitat choice, and it is clear that both predation risk and food availability vary considerably between habitats. It is important to remember, however, that for any habitat-specific predation risk, the risk per individual in ST will be absolutely much greater relative to individuals in VT. As a consequence, we would expect the behavior of individuals in ST to show elevated responses to predation risk relative to individuals in VT.

### *Predation Risk and Habitat Choice*

In order to assess the relative preference for the different habitats by the two study troops, and thus determine the factors involved in habitat selection, it is important to control for the availability of the different habitat types. Monthly habitat preferences were therefore computed on the basis of Krebs' (1989) electivity index. The electivity index varies between +1 (strongly selected) and -1 (strongly avoided); it was calculated on the basis of the following formula:

$$EI = \frac{(h_i - p_i)}{(h_i + p_i)}$$

where EI is the electivity index,  $h_i$  is the observed proportion of time spent in habitat  $i$ , and  $p_i$  is the relative availability of habitat  $i$  in the home range of the troop. The mean electivity indices for the six habitat types are presented in Figure 16.2.

The relationships for three habitats are worth noting. As one would predict, both troops showed a clear preference for the high food availability, low predation risk vlei habitat. Similarly, both troops show avoidance of the low food availability, high predation risk climax fynbos. Interestingly, however, differences emerge when we consider acacia woodland, the high food availability but high predation risk habitat. While VT, the larger study group, showed a general preference for this habitat, ST avoided it. That individual capture probabilities were higher for the baboons in ST might suggest this group traded off food availability with predation risk in its patterns of habitat choice.

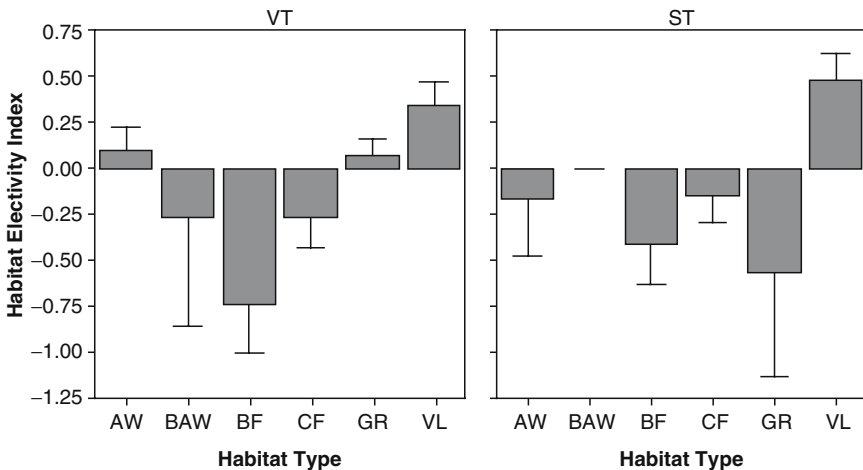


FIGURE 16.2. Mean monthly habitat electivity indices for each habitat type based upon the proportion of each habitat type within the home ranges of VT and ST. Data from quadrats containing sleeping sites are excluded to reduce artificial preferences for habitat types in close proximity to sleeping cliffs. AW: acacia woodland; BAW: burnt acacia woodland; BF: burnt fynbos; CF: climax fynbos; GR: grassland; VL: vle

TABLE 16.2. Stepwise linear regression equations relating monthly habitat electivity indices to monthly food availability and habitat visibility. EI: electivity index; HF: habitat food availability (defined as the proportion of total home range food available in each habitat type); V: habitat visibility.

| Troop | Equation   | $r^2$ | $F$            | $p$    |
|-------|--|-------|----------------|--------|
| VT    | $EI = 0.160 + 0.0795 \ln(\text{HF})$                       | 0.463 | (1, 40) 34.489 | <0.001 |
| ST    | $EI = -0.275 + 0.132 \ln(\text{HF}) + 0.143 \ln(\text{V})$ | 0.388 | (2, 27) 8.572  | 0.001  |

In order to determine whether this was the case, stepwise regression analysis was used to determine which factors best accounted for the observed monthly variation in habitat electivity indices. The best-fit models are given in Table 16.2. Both troops clearly show strong relationships between habitat electivity indices and relative food availability in that habitat. Furthermore, the coefficient is positive in both cases, indicating that high food availability habitats are more strongly selected relative to low food availability habitats. The best-fit model for ST also includes habitat visibility, suggesting that the baboons in this troop indeed traded food availability against predation and thus modified their habitat choice to minimize exposure to predation risk. Interestingly, if visibility is entered into the model for VT, a significant regression remains ( $r^2 = 0.481$ ;  $F_{(2,39)} = 18.103$ ;  $p < 0.001$ ), but although the coefficient for visibility is in the predicted positive direction, it is not itself a significant component of the model.

Two possible explanations could explain these troop-specific patterns of ranging behavior and habitat choice. Firstly, because VT was approximately twice the size of ST, individuals in this troop did not experience the same level of individual capture probability and thus may not have perceived acacia woodland as high predation risk habitat in the same way members of ST did. Alternatively, it may be that while individuals in VT may have attempted to avoid high predation risk habitats, their higher foraging requirements may have constrained them to foraging in the high food availability habitats. As a consequence, VT may have had little latitude with respect to predation risk in terms of its patterns of habitat choice. Although the data are not available to explicitly test these hypotheses, the available evidence does lend some support to the latter explanation.

An anecdotal feature of the foraging strategy of VT while in acacia woodland was an apparent preference for feeding in trees on the edge of this habitat. Since high visibility grassland and vlei primarily surrounded acacia woodland, such a strategy would have increased visibility in some directions, thus reducing overall predation risk. Figure 16.3 displays the mean intensity of use of acacia woodland against the distance of that quadrat to the nearest quadrat containing either grassland or vlei habitat. It is clear that acacia woodland is used more intensively when in close proximity to high visibility habitats, and the differences between the distance categories are significant (ANOVA:  $F_{(2,83)} = 6.028$ ,  $p = 0.004$ ). Post hoc analysis reveals that it is the 0–200m category that differs significantly from the other two (Scheffé: 0–200 v 200–400,  $p < 0.02$ ; 0–200 vs 400–600,  $p < 0.025$ ). This relationship cannot be interpreted as merely a by-product of



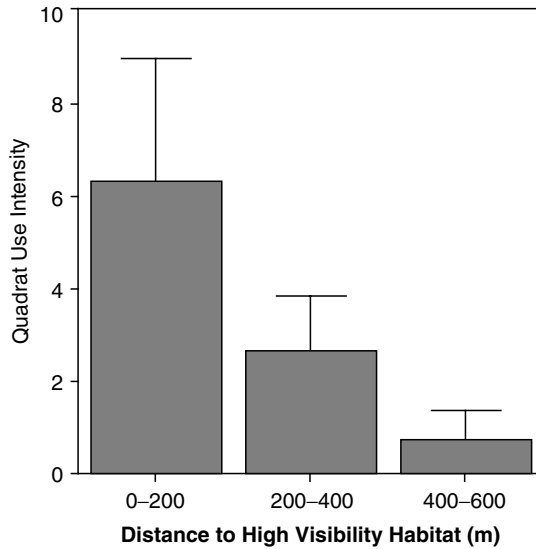


FIGURE 16.3. Intensity of use of acacia woodland quadrats in relation to the distance of this habitat from the nearest quadrat containing high visibility (low predation risk) habitat (either grassland or vlei)

declining intensity of habitat use with increasing distance away from sleeping sites and thus vlei habitat (which bordered many of the sleeping sites). A partial correlation controlling for distance to sleeping site maintains a strong negative correlation between intensity of acacia woodland use and distance to high visibility habitat ( $r = -0.321$ ,  $df = 83$ ,  $p = 0.003$ ). This provides compelling support for the idea that while the baboons in VT may have been forced to feed in this high food availability habitat to satisfy their daily nutritional requirements, they were able to ameliorate their exposure to predation risk to a certain degree by preferentially using the habitat fringes. In doing so, the troop was able to maintain a higher level of visibility while feeding within the acacia woodland. The role of predation in shaping the habitat use of the larger study group, therefore, appears to operate at the microhabitat level.

Similar relationships appear to explain why the *climax fynbos* is not more strongly avoided by the baboons, despite the fact that it is of low food availability and high predation risk. Since a large proportion of sleeping sites were fringed by climax fynbos, the habitat could not be completely avoided. Nevertheless, it is clear that the intensity of climax fynbos use declines markedly with distance from sleeping site for both groups (Figure 16.4). Thus, while the baboons often needed to use this habitat in order to access the sleeping sites, they only did so when they were in close proximity to these refuges. For both troops, therefore, it is clear that predation shapes patterns of habitat use at both the habitat and microhabitat level.

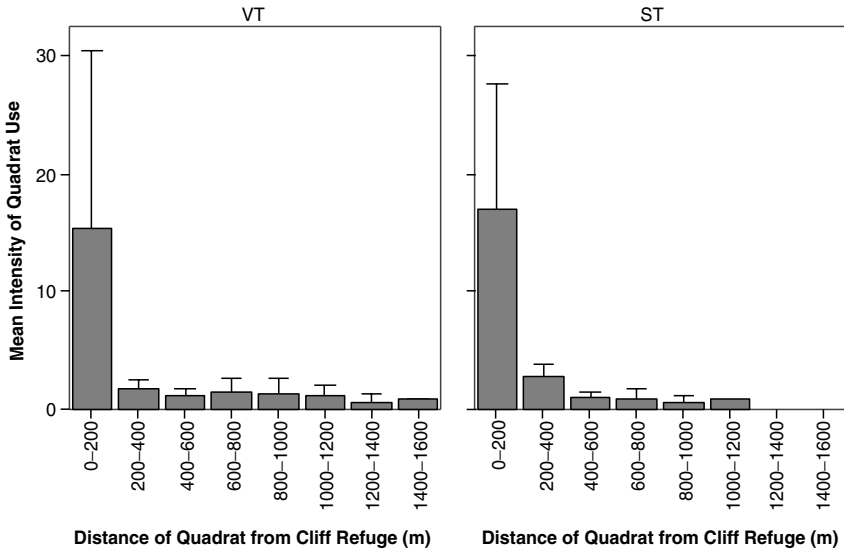


FIGURE 16.4. Intensity of use of climax fynbos habitat against distance from nearest cliff refuge for VT and ST

### *Predation Risk and Habitat Activity Patterns*

Predation risk might not only shape how frequently certain habitats are used and the microhabitats selected within habitats types, but could also influence behavioral profiles within habitats. Cowlshaw (1997a) found that at Tsaobis, the baboons utilised certain habitats preferentially for certain activities. Grooming and resting activity were almost exclusively restricted to the safest habitat, while moving was also predominantly confined to the safer areas. On the other hand, time spent in the high predation risk but high food availability habitat was used almost exclusively for feeding. This suggests that where activities have no specific habitat requirements, such as sufficient food availability, then they are conducted preferentially in low predation risk habitats. Due to the wide variation in habitat visibility and food availability at De Hoop, we might thus expect to find differences in activity budgets between the various habitat types.

One issue that we need to address before habitat-specific patterns of activity can be assessed, however, is the fact that a large proportion of resting and grooming occurs on sleeping cliffs, which are not associated with any specific habitat type. As Cowlshaw (1997a) concedes, the apparent use of the Namib Hills habitat at Tsaobis for non-foraging activity may arise from the fact that these activities are conducted preferentially at dawn and dusk while the animals are on their sleeping cliffs. It is certainly true that the De Hoop baboons use cliffs almost exclusively for resting and grooming (Figure 16.5). As a consequence, it is important that activity profiles be assessed in a way that allows behavior on cliffs to be removed.

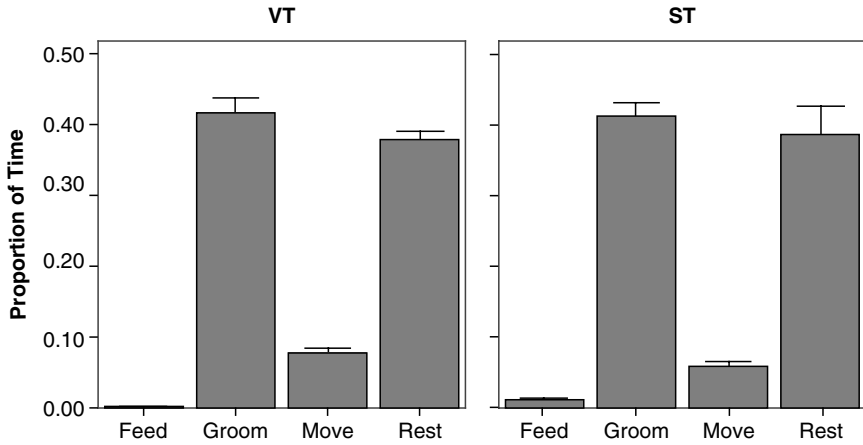


FIGURE 16.5. Mean time budgets while on cliffs for individuals in VT and ST

The importance of close cliff proximity on activity budgets can be seen in Figure 16.6, which displays the mean time budgets in the climax fynbos and vlei habitats for three distance to cliff categories: 0–10 m, 10–50 m, and 50 m+. Significant differences exist between distance categories for most of the activities in both habitats, although it is the non-foraging activities (grooming and resting) that show most pronounced effects. The relationships are most striking for grooming activity, particularly in climax fynbos where grooming represents almost sixty percent of activity within 10 m of a cliff. Such relationships do not appear to result from local resource depletion around sleeping sites causing animals to feed at greater distances from the refuge (and thus reducing feeding close to sleeping sites) since for fynbos in particular there is no relationship between proportion of time feeding and distance from sleeping site. It does appear, therefore, that where activities have no specific habitat requirements, such as sufficient food availability, then they are conducted preferentially in low predation risk habitats or in close proximity to refuges.

More complex analyses of habitat-specific activity patterns are complicated by the fact that, if percentage time budgets are considered, an increase in one activity must inevitably lead to an apparent decrease in other activities. It is thus difficult to determine whether high levels of a given behavior in a habitat reflect a preference for that activity or an avoidance of a different behavior. Furthermore, preferences for two activities are difficult to detect. It is also difficult to gauge what the expected level of activity should be in any habitat. One possible way to overcome this hurdle and assess preferences for conducting certain behaviors in different habitats is to restrict analyses to a single behavior. Feeding is a useful activity in this respect since we would expect the proportion of total feeding conducted in each habitat to correlate with the proportion of total home range food available within that habitat type. Figure 16.7 displays the mean preference for feeding

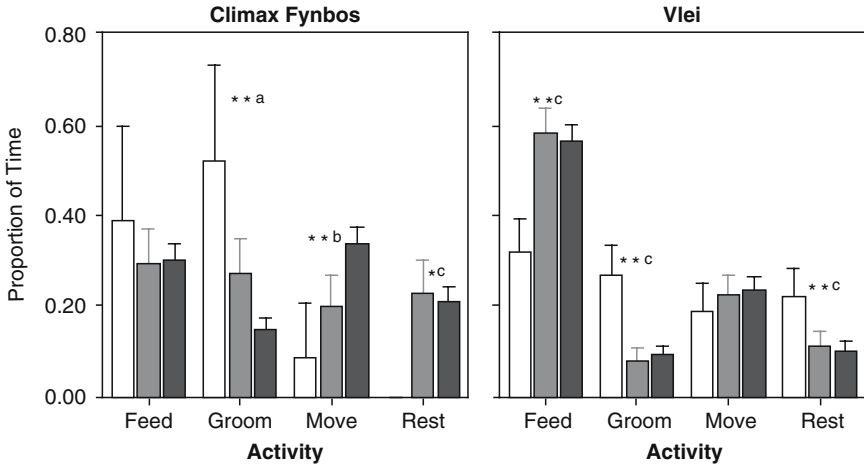


FIGURE 16.6. Comparison of the mean time budgets from focal samples for individuals in VT at various distances from the nearest cliff in the climax fynbos and vlei habitats. Open bars: 0–10 m; light bars: 10–50 m; dark bars: 50 m+. Asterisks indicate significant relationships (ANOVA: \*  $p < 0.05$ ; \*\*  $p < 0.001$ ; Scheffé,  $p < 0.05$ : a: 0–10 v 10–50; 0–10 v 50+, 10–50 v 50+; b: 0–10 v 50+; 10–50 v 50+; c: 0–10 v 10–50; 0–10 v 50+)

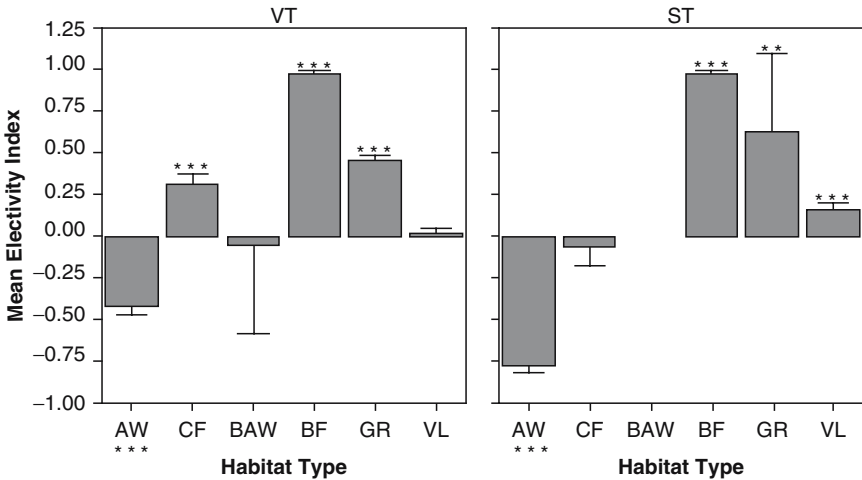


FIGURE 16.7. Mean individual electivity indices for feeding in each habitat type relative to food availability in these habitats. Asterisks indicate significant preferences or avoidances for feeding in that habitat (one-sample t-test: \*\*  $p < 0.025$ ; \*\*\*  $p < 0.001$ ). AW: acacia woodland; BAW: burnt acacia woodland; BF: burnt fynbos; CF: climax fynbos; GR: grassland; VL: vleii

in the different De Hoop habitats, where the electivity indices for each individual reflect the relative preference for feeding in each habitat against the baseline expected on the basis of food availability. The patterns are strikingly similar for both groups. Both troops show avoidance of feeding in high risk acacia woodland despite its high food availability, with preferences for feeding in the intermediate risk burnt fynbos and low risk grassland despite the lower food availabilities. ST also shows a significant preference for feeding in the high food availability, low risk vlei, although this preference is not significant for VT. While this again confirms a stronger predation response for ST due to higher individual capture probabilities, the fact that the preferences are not stronger for both groups probably reflects the fact that much of the food in this habitat is subterranean, with higher processing times and energetic costs of excavation. Finally, the apparent preference of individuals in VT for feeding in the low food availability, high risk climax fynbos almost certainly reflects the close proximity of this habitat to most of the sleeping sites within their home range. ST had fewer sleeping sites fringed by this habitat.

## Discussion

Predation risk is clearly an important constraint on primate behavior, although it is essential we break down the predation process into its constituent parts in order to fully understand its effects. Interestingly, the results presented here suggest that the frequency of predator-prey interactions is just one element of an individual's perception of predation risk since the strong responses to predation risk at De Hoop occur in an environment of low predator density. This confirms that predation risk is not a simple function of the frequency of predator-prey interactions, and that, at the very least, evolved responses may persist in populations following local reduction or extinction of primary predators (Bouskila & Blumstein, 1992). As a consequence it is essential that other elements of predation risk be adequately quantified in order to fully understand the importance of behavior on current patterns of primate behavior.

For terrestrial primates it is clear that habitat visibility and the distribution of refuges are important elements of predation risk, since these factors determine the probability of encounter, attack, and successful prey capture in any habitat or population. The baboons at De Hoop show a general avoidance of high-risk habitats, with this pattern generally stronger for the smaller study group. Furthermore, even when higher risk habitats cannot be avoided, due to the presence of sleeping sites or the need to forage in areas of high food availability, predation shapes habitat choice at the microhabitat level. Use of climax fynbos declines markedly with distance from sleeping sites, suggesting that this habitat was used due only to its proximity to refuges, while VT used the habitat fringes when feeding in acacia woodland in order to maximize visibility. These results suggest that baboons are responding to subtle elements of their environment in gauging their current levels of predation risk.

Behavioral profiles within habitats are also modified on the basis of predation risk. Both resting and grooming are preferentially conducted on cliff refuges. In both vlei and climax fynbos, levels of resting and, in particular, grooming decline as distance to refuge increases. These relationships are unlikely to be an artifact of local resource depletion on foraging activity, but instead suggest an active preference for conducting these behaviors close to refuges. Similarly, the proportion of feeding activity conducted in different habitats is also influenced by predation. After controlling for availability of food in different habitats, the baboons show strong preferences for feeding in the low and intermediate risk habitats and avoidance of areas of high risk, even though high-risk habitats must be used to satisfy the troops' nutritional requirement. Overall, these results provide robust support for the idea that predation shapes the behavioral decisions of baboons, with clear responses evident in activity choice and habitat selection at both the habitat and microhabitat levels.

Predation risk is clearly a complex parameter, although through breaking down the predation process into a number of components significant progress in understanding the impact of predation on primate behavior. Since many of these components are features of the environment that can be readily quantified, this approach also allows us not only the opportunity to examine behavioral differences of groups between habitats within populations, but also to see how differences between populations may arise on the basis of local variation in predation risk. Hill & Cowlishaw (2002) illustrated that differences in vigilance levels between the De Hoop and Tsaobis baboon populations disappear once ecological differences between the populations are controlled for, suggesting that baseline anti-predator responses to predation risk are relatively consistent across populations. Breaking down the predation process thus affords us considerable scope for understanding the importance of predation risk in shaping patterns of primate behavior.

*Acknowledgments.* We thank Anna Nekaris and Sharon Gursky for the invitation to contribute to this volume and three anonymous referees for their helpful and constructive comments on an earlier version of the chapter. We are grateful to Louise Barrett, Peter Henzi, and Cape Nature Conservation for assistance and permission to work at De Hoop Nature Reserve.

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