

## 12 • Foraging female baboons exhibit similar patterns of antipredator vigilance across two populations

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### Introduction

Predation pressure has long been considered a powerful selective force on primate behavior (Alexander 1974, Anderson 1986, Crook and Gartlan 1966, Dunbar 1988, Isbell 1994, van Schaik 1983, 1989). However, most studies that have investigated the importance of predation on primates have tended to focus on either patterns across different species (Anderson 1986, Cheney and Wrangham 1987, Goodman *et al.* 1993, Hill and Lee 1998, Isbell 1994) or patterns across individuals within a given population (e.g., Cowlishaw, 1997a, Isbell and Young 1993, Stanford 1995). In contrast, little attention has been paid to the consistency of antipredator strategies across different populations of the same primate species. Nevertheless, such patterns can potentially shed valuable light on intraspecific variation in tolerance to predation risk and the strategies used to reduce that risk, together with the differential costs and benefits of such strategies in different populations.

Baboons represent an ideal taxon for such an investigation, since predation risk in this species is relatively well understood (e.g., Cowlishaw 1994, 1997a) and the wealth of data available on their ecological and behavioral flexibility (Barton *et al.* 1996) permits detailed assessments on the impact of predation risk across a wide array of ecological conditions (e.g., Dunbar 1996). The evidence already available for baboons indicates that antipredator behavior is not fixed but that individuals invest differentially with response to the degree of predation risk. For example, baboons that live in small, high-risk, groups are more active in their use of refuges, such as tall trees and cliff faces, than are larger groups. Importantly, this pattern has been reported in more than one population: Amboseli, Kenya (Stacey 1986) and Tsaobis, Namibia (Cowlishaw 1997b). Likewise, similar patterns of avoidance of food-rich but high-risk

habitats by baboons has been reported in two different populations: Tsaobis (Cowlishaw 1997a) and De Hoop, South Africa (Hill 1999). These studies thus emphasize not only the flexibility of baboon antipredator behavior, but also the consistency of antipredator responses between different populations.

The purpose of the present study is to conduct a systematic and detailed investigation of the consistency of antipredator behavior across two different baboon populations: De Hoop in South Africa and Tsaobis in Namibia. We focus our analysis on vigilance, since this is an easily recognizable and quantifiable antipredator behavior that can be directly compared across populations. Moreover, it is a highly flexible behavioral response to predators, and we have a good understanding of the different factors that can affect vigilance in primates. These include group size (Isbell and Young 1993, de Ruiter 1986) and composition (Rose and Fedigan 1995, van Schaik and van Noordwijk 1989), habitat visibility (Chapman 1985, Cowlishaw 1998), refuge proximity (Cowlishaw 1998), and distance to nearest neighbors (Cowlishaw 1998, Treves 1998). Although vigilance might also have functional roles that are not related to predation, for example the detection of potential mates and competitors (Cowlishaw 1998, Treves 2000), the current evidence suggests that this is primarily the case only in male baboons (who are therefore not included in this analysis), and that female vigilance is predominantly related to predation risk (Cowlishaw 1998).

Our analysis first examines whether the performance of antipredator vigilance in foraging females is similar in the two populations. Our analyses show that it is not. In fact, foraging female baboons at De Hoop spend about twice as much time vigilant as those at Tsaobis. Assuming that all foraging baboons respond in a similar way to predation risk, and assuming further that all such individuals will strive to maintain a similar level of safety across populations, we hypothesize that this pattern can best be explained by differences in the relative costs and benefits of antipredator vigilance between the two sites. Specifically, these differences might be accounted for by (a) higher fitness costs of vigilance during foraging at Tsaobis, perhaps due to reduced compatibility between foraging and vigilance at this site, and/or (b) higher fitness benefits of vigilance during foraging at De Hoop, perhaps due to higher predation risk at this site. If our hypothesis is correct, then we should find that the differences in vigilance between the two populations disappear once the local differences in costs/benefits have been statistically controlled.

In order to test this hypothesis, our analysis attempts to control for the different costs and benefits of vigilance that might exist between the two populations. First, we evaluate the costs of vigilance. Specifically, we investigate whether vigilance is more costly during foraging at Tsaobis because the Tsaobis baboons spend more of their foraging time feeding rather than traveling between feeding events. Vigilance is likely to be most costly when performed during the feeding component of foraging time, since it interrupts feeding activities and hence reduces food intake rates (Treves 2000); in contrast, vigilance during the traveling component of foraging is not associated with this cost. Second, we investigate the benefits of vigilance. In order to do this we examine four measures of local predation risk that might cause foraging female baboons to adjust their vigilance (see Cowlishaw 1998 for review and explanation). The first measure is the size of the social group, given that females in smaller groups perceive a higher risk of predation. The second is the distance to refuge, given that baboons closer to refuges are typically safer from predators. The third is the visibility of the habitat, given that leopards attack from close cover, thus making low-visibility habitats more dangerous for baboons. The fourth is the proximity of the nearest neighbor, given that individuals will be at less risk of predation if they are in company rather than alone.

## Methods

The data presented here are drawn from females across five groups of chacma baboons (*Papio cynocephalus ursinus*): one group from De Hoop Nature Reserve, South Africa, while the remaining four groups are from Tsaobis Leopard Park, Namibia (see Table 12.1).

### Study sites

De Hoop Nature Reserve (20° 24'E, 34° 27'S) is a coastal reserve within the Overberg region, Western Cape Province, South Africa. The reserve is characterized by limestone hills on the western regions, with the Potberg Mountains rising in the northeast. The baboons ranged in an area surrounding the De Hoop Vlei, a large landlocked body of brackish water that is also fed by several freshwater springs. Vegetation is dominated by coastal fynbos, a unique and diverse vegetation type comprising four primary vegetation groups: Proteaceae, Ericaceae, Restionaceae and geophytes. De Hoop experiences a Mediterranean climate and receives most of its rainfall during the austral winter. Mean annual rainfall is 428 mm

Table 12.1. Study group compositions for the two populations

Population	Group	Age/sex class				Group size
		Adult Male	Adult Female	Juvenile	Infants	
De Hoop	VT	4	12	19	7	42
Tsaobis	A	1	8	10	3	22
	B	2	11	10	1	24
	C	4	13	15	4	36
	D	6	15	30	4	55

with a mean annual temperature of 17.0 °C. The reserve ranges in altitude from 0 to 611 m. A more detailed description of the ecology of the reserve is given in Hill (1999).

Tsaobis Leopard Park (15° 45' E, 22° 23' S) is located in the semi-desert Pro-Namib region of Namibia. The reserve is characterized by mountains and ravines, fringed by steep rocky foothills and rolling gravel and alluvial plains. The site is bordered by the ephemeral Swakop River, which supports patches of riparian woodland dominated by *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica*. Beyond the woodland, vegetation is sparse with dwarf trees and low shrubs dominated by *Commiphora virgata*. The climate is extremely arid, with a mean annual rainfall of 85 mm and mean annual temperatures of 24.8 °C. Altitude ranges from 683 to 1445 m. A full description of the site is given in Cowlshaw and Davies (1997).

#### Data collection and analysis

Data for the De Hoop baboons were collected by means of instantaneous point samples (Altmann 1974) of all visible individuals at 30-minute intervals during full day follows, while those for Tsaobis result from instantaneous point samples (Altmann 1974) of a focal individual at 5-minute intervals over multiple one-hour periods per focal. All adult males and females were sampled for De Hoop, with all adult males and selected adult females sampled at Tsaobis. The De Hoop data were collected over a period of 10 months (Mar–Dec 1997); in contrast the Tsaobis data were collected over an intensive 2-month period (Sept–Nov 1991). More detailed descriptions of the study methods at each site are given in Hill (1999) and Cowlshaw (1998). It is unlikely that the differences in methodology between the two studies will lead to significant biases in the data collected, and thus

Table 12.2. Classification of behavioral and habitat variables incorporated in the analyses

Behavioral category	Summary of categories
Activity	Foraging (defined as feeding and moving activity combined) or Nonforaging
Vigilance	Yes or No
Habitat type	Closed (visibility < 30 m) or Open (visibility > 30 m)
Refuge distance	Close (0–20m) or Distant (> 20 m)
Neighbor distance	Aggregated ( $\geq 1$ individual within 5 m) or Dispersed (no individuals within 5 m)

for the remainder of this chapter the data for the two populations are considered wholly comparable. However, the difference in sampling effort between the two populations does appear to result in the Tsaobis females exhibiting a much greater range of values than the De Hoop females. The relationships presented may thus be tighter for the De Hoop females than for the Tsaobis females because they were sampled more extensively, although the broader range of social and ecological conditions at Tsaobis is also likely to contribute to this pattern. At each sample point, the vigilance state of the individual was recorded (an animal was considered vigilant when its head was up and its eyes open), together with its current activity and three measures of its present state of risk: its surrounding habitat type, its distance to refuge and its proximity to neighbors (Table 12.2). In the case of current activity, an animal was considered to be foraging when its activity consisted of either feeding or traveling. Although some traveling time may be unrelated to foraging, for example on the route between the last feeding event of the day and the sleeping site, the great majority of traveling is time spent reaching the next food item or patch. In the case of habitat type, the habitats were divided into two categories on the basis of visibility: closed habitats, where mean visibility at baboon-eye level was below 30 m, and open habitats, where mean visibility was at least 30 m. Three of six habitat types at De Hoop (see Hill 1999), and one of four at Tsaobis (see Cowlshaw 1997a), were thus classified as low visibility. In the case of refuges (trees or cliffs of at least 8 m height and inclined at an angle of at least 75° to the horizontal: Cowlshaw 1997b), two conditions are recognized: individuals in close proximity are defined as those

within 20 m of a refuge (including those on a refuge), whereas those distant are at least 20 m away from the nearest refuge. Finally, in the case of neighbor proximity, two categories are once again defined: aggregated, where at least one adult individual is within 5 m of the focal animal, and dispersed, where no adult baboons are within 5 m of the focal individual. Although previous studies have shown primates to be sensitive to the number of near neighbors they have (Treves 1998), it is likely that isolation is the key effect and several previous studies have reported a simple decline in vigilance in the presence of near neighbors (Robinson 1981, van Schaik and van Noordwijk 1989, Steenbeck *et al.* 1999).

If an individual was poorly sampled during foraging, such that five or fewer instantaneous scans were recorded, then this individual was excluded from the analysis (see Cowlishaw 1998, Isbell and Young 1993). All of the proportional data are angular transformed (Sokal and Rohlf 1981) to ensure normality for parametric analysis. However, all figures are drawn utilizing the untransformed data for ease of interpretation (while these figures may only approximate the statistical relationships described in the text, they differ only very slightly from those produced with transformed data). To control for the multivariate nature of vigilance in bivariate plots, the graphs presented typically plot the residual foraging time spent vigilant from the preceding analysis rather than the absolute values, although population identity is not included as a factor in the computation of the residual values.

## Results

### General patterns of vigilance during foraging

Strong differences exist in the vigilance levels of foraging females between the De Hoop and Tsaobis baboon populations (Fig. 12.1: *t*-test,  $t=5.90$ ,  $df=42.0$ ,  $p<0.001$ ). Males, who are included here for comparative purposes, also show the same pattern ( $t=4.66$ ,  $df=19$ ,  $p<0.001$ ). In both sexes, the De Hoop baboons spend approximately twice as much time vigilant as the Tsaobis baboons.

### Costs of vigilance during foraging

An analysis of the costs of vigilance during foraging indicates that vigilance appears to be incompatible with feeding, since females that spend more of their foraging time feeding are also less vigilant (Fig. 12.2:  $r^2=0.61$ ,  $F_{(1,46)}=70.7$ ,  $p<0.001$ ). This cost of vigilance

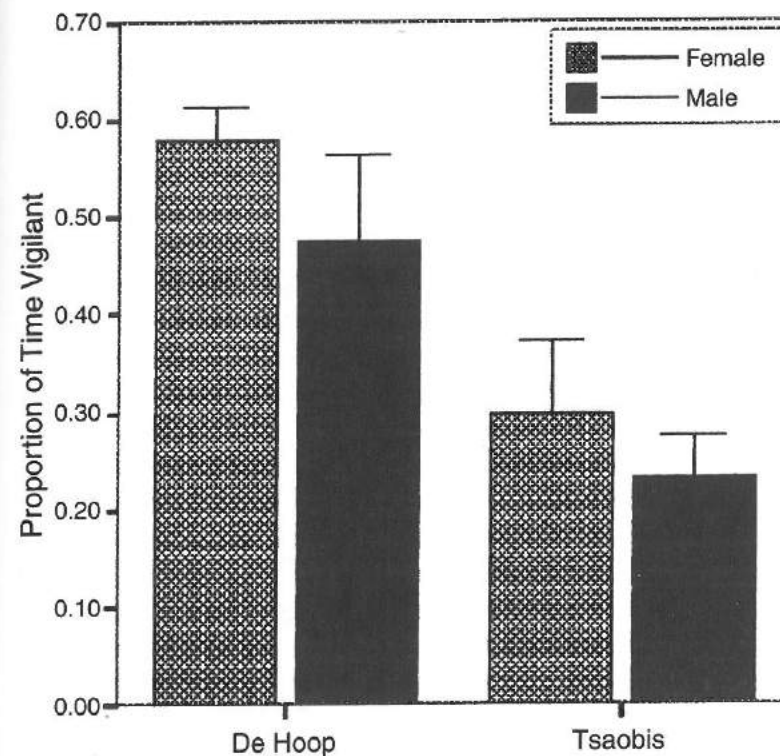


Fig. 12.1. Vigilance rates during foraging for the De Hoop and Tsaobis populations. Mean values and standard errors are shown.

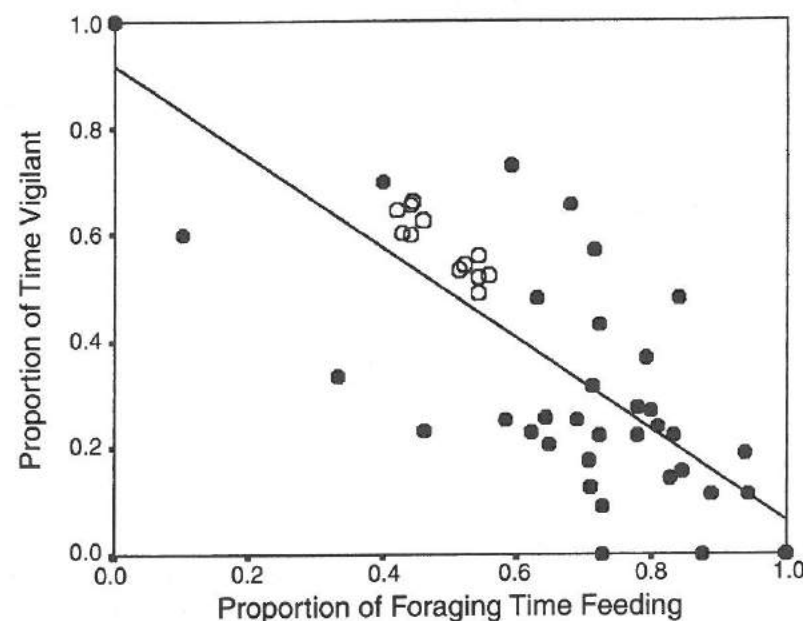
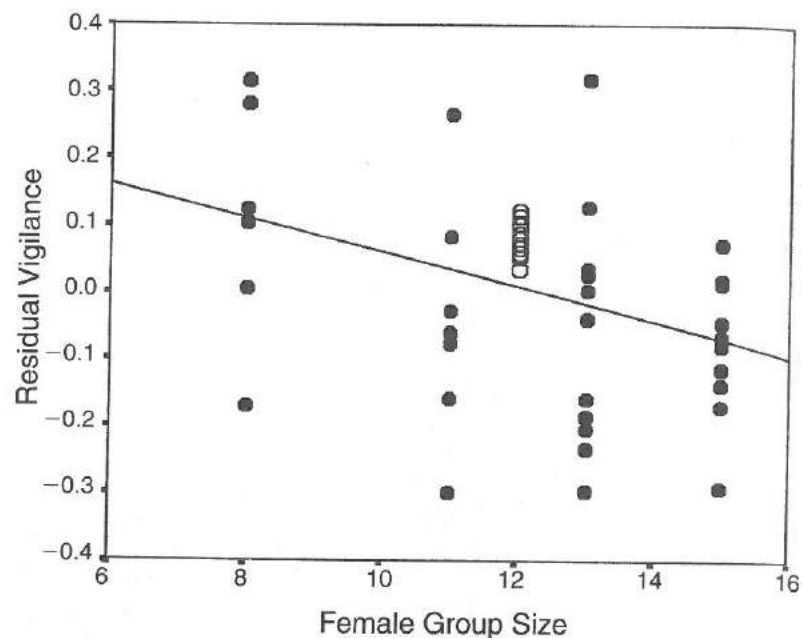


Fig. 12.2. Relationship between proportion of foraging time spent vigilant and proportion of foraging time spent feeding (De Hoop females, open circles; Tsaobis females, solid circles). The line is a best fit least-squares regression for the entire data set.

Fig. 12.3. Relationship between residual proportion of foraging time spent vigilant (calculated from Fig. 12.2) and female group size (De Hoop females, open circles; Tsaobis females, solid circles). The line is a best fit least-squares regression for the entire data set.



appears to be particularly heavy at Tsaobis, since these baboons spend considerably more of their foraging time feeding compared to De Hoop (De Hoop:  $0.49 \pm 0.05$ , Tsaobis:  $0.69 \pm 0.21$ , t-test:  $t = -4.60$ ,  $df = 41.5$ ,  $p < 0.001$ ). However, the fact that all the De Hoop females lie above the regression line indicates that these costs alone are not sufficient to explain the relatively high vigilance rates at De Hoop, such that there remains a significant difference between the two populations (analysis of covariance (ANCOVA):  $r^2 = 0.64$ ,  $F_{(2,48)} = 40.0$ ,  $p < 0.001$ ; feeding covariate:  $F_{(1,48)} = 53.0$ ,  $p < 0.001$ ; population factor:  $F_{(1,48)} = 4.27$ ,  $p < 0.05$ ).

### Benefits of vigilance during foraging

#### Effects of group size

Vigilance should become increasingly beneficial to females in smaller groups (indexed here as the number of adult females) due to the greater risk of predation in such groups. Investigation of this pattern (Fig. 12.3) reveals that as predicted, baboons in smaller groups do spend more of their foraging time vigilant. However, there is no apparent difference in average group size between the De Hoop and Tsaobis populations, indicating that this cannot explain the differences that still remain in vigilance between the populations. Indeed, the De Hoop females still exhibit levels of vig-

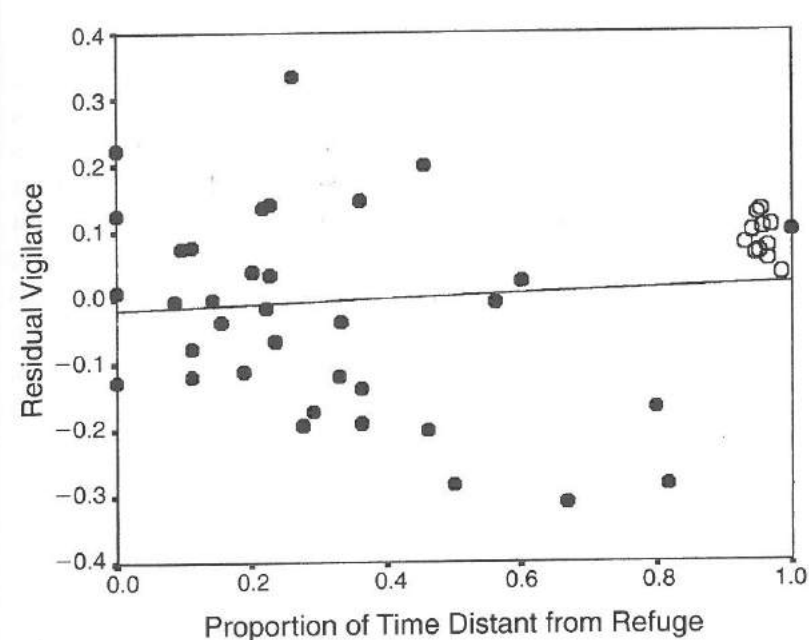


Fig. 12.4. Relationship between residual proportion of foraging time spent vigilant (calculated from Fig. 12.3) and proportion of time spent distant from refuge (De Hoop females, open circles; Tsaobis females, solid circles). The line is a best fit least-squares regression for the entire data set.

ilance that consistently exceeded the trend (ANCOVA:  $r^2 = 0.69$ ,  $F_{(3,48)} = 32.6$ ,  $p < 0.001$ ; feeding covariate:  $F_{(1,48)} = 46.6$ ,  $p < 0.001$ ; group size covariate:  $F_{(1,48)} = 7.07$ ,  $p < 0.02$ ; population factor:  $F_{(1,48)} = 5.10$ ,  $p < 0.03$ ). These results do not differ substantially if total group size is used instead of the number of adult females.

#### Effects of refuge proximity

Vigilance should also become increasingly beneficial to females who are distant from refuge. This is precisely the relationship observed (Fig. 12.4), although the effect is slight. Nevertheless, baboons that are more distant from refuge spend a greater proportion of their foraging time vigilant. Notably, the De Hoop females spend about three times as much foraging time distant from refuge than do the Tsaobis baboons (De Hoop:  $0.95 \pm 0.01$ , Tsaobis:  $0.30 \pm 0.25$ , t-test:  $t = -4.60$ ,  $df = 41.5$ ,  $p < 0.001$ ). However, once again, the effects of this additional measure of predation risk are not sufficient to account for the remaining population differences, with the De Hoop females still exhibiting vigilance levels in excess of that predicted (ANCOVA:  $r^2 = 0.75$ ,  $F_{(4,48)} = 31.5$ ,  $p < 0.001$ ; feeding covariate:  $F_{(1,48)} = 47.0$ ,  $p < 0.001$ ; group size covariate:  $F_{(1,48)} = 10.8$ ,  $p < 0.005$ ; refuge distance covariate:  $F_{(1,48)} = 9.44$ ,  $p < 0.005$ ; population factor:  $F_{(1,48)} = 15.4$ ,  $p < 0.001$ ).

#### Effects of habitat type

Baboons that spend more time in closed habitats should be more vigilant than others, due to the danger of leopard attack in such habitats. However, evaluation of this predicted relationship suggests that it is absent across these two baboon populations, and it is clearly insufficient to explain the persistent differences that remain between the two populations (ANCOVA:  $r^2 = 0.75$ ,  $F_{(5,48)} = 24.8$ ,  $p < 0.001$ ; feeding covariate:  $F_{(1,48)} = 46.3$ ,  $p < 0.001$ ; group size covariate:  $F_{(1,48)} = 10.7$ ,  $p = 0.002$ ; refuge distance covariate:  $F_{(1,48)} = 7.25$ ,  $p = 0.01$ ; habitat covariate:  $F_{(1,48)} = 0.22$ ,  $p > 0.60$ ; population factor:  $F_{(1,48)} = 15.4$ ,  $p < 0.001$ ). This latter point though is perhaps not surprising given the fact that there is no difference in the amount of time that the two populations spend in high-risk habitats (De Hoop:  $0.40 \pm 0.04$ , Tsaobis:  $0.49 \pm 0.32$ , t-test:  $t = -1.38$ ,  $df = 36.6$ ,  $p > 0.10$ ). Nevertheless, this cannot account for the lack of significance of habitat visibility as a factor determining baboon vigilance levels.

#### Effects of nearest neighbor proximity

Finally, baboons that spend more time distant from their neighbors should spend more time vigilant because of the higher risk of predation that such dispersed spacing behavior entails. A plot of the proportion of foraging time spent vigilant against the proportion of time spent dispersed (Fig. 12.5) suggests that this is indeed the case. Notably, the De Hoop baboons spend three times as much foraging time in such dispersed positions (De Hoop:  $0.75 \pm 0.05$ , Tsaobis:  $0.21 \pm 0.15$ , t-test:  $t = 14.61$ ,  $df = 46.3$ ,  $p < 0.001$ ). Crucially, the inclusion of this final component of predation risk appears to be sufficient to account for any remaining differences in the proportion of foraging time spent vigilant between females in the two populations (ANCOVA:  $r^2 = 0.77$ ,  $F_{(5,48)} = 28.6$ ,  $p < 0.001$ ; feeding covariate:  $F_{(1,48)} = 49.2$ ,  $p < 0.001$ ; group size covariate:  $F_{(1,48)} = 15.0$ ,  $p < 0.001$ ; refuge distance covariate:  $F_{(1,48)} = 8.50$ ,  $p < 0.01$ ; neighbor proximity covariate:  $F_{(1,48)} = 5.05$ ,  $p = 0.03$ ; population factor:  $F_{(1,48)} = 2.80$ ,  $p > 0.10$ ).

### Discussion

Our results indicate that female baboons at De Hoop spend about twice as much time vigilant when foraging than females at Tsaobis, and that these differences may be explained by differences in the costs and benefits of antipredator vigilance between the two populations. In total, four of the five different measures of the costs and

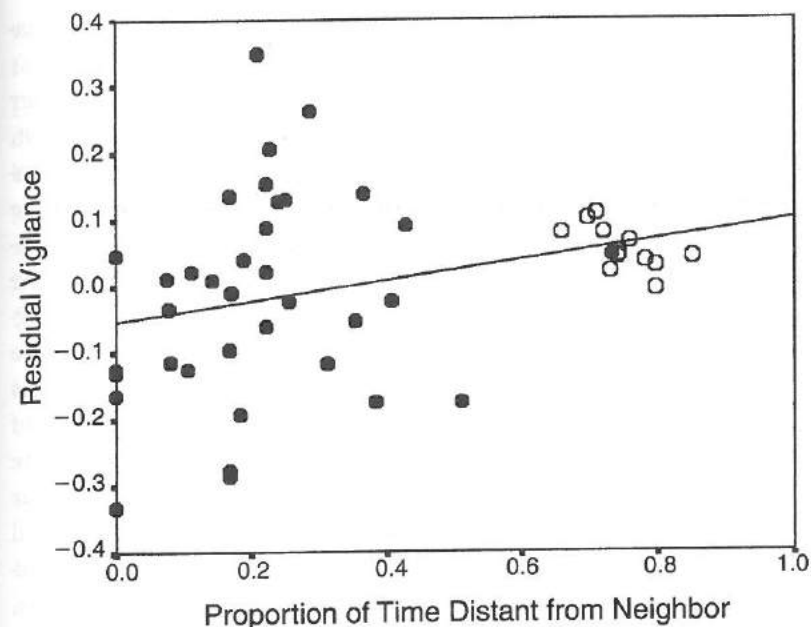


Fig. 12.5. Relationship between residual proportion of foraging time spent vigilant (calculated from Fig. 12.4) and proportion of time spent distant from nearest adult neighbor (De Hoop females, open circles; Tsaobis females, solid circles). The line is a best fit least-squares regression for the entire data set.

benefits tested in this analysis were found to independently contribute to the overall variance in vigilance among foraging females: these were the size of the social group and the proportion of foraging time that was spent feeding, spent distant from refuges, and spent distant from neighbors. The most important of these four measures appears to be the proportion of foraging time spent feeding, which alone accounts for 61% of the variance. Together, the four variables explain over 75% of the variance in the proportion of foraging time spent vigilant, and account for the observed differences between the two populations.

One complication in the interpretation of these results relates to the finding that vigilance during foraging becomes increasingly costly as the proportion of foraging time spent feeding increases. There is an alternative explanation for this pattern: that vigilance becomes increasingly beneficial as the proportion of feeding time declines. In fact, this is exactly what theory would predict, because as feeding time declines during foraging so traveling time increases, and traveling is associated with the highest risk of predation of all baboon activities (Cowlshaw 1998). Unfortunately, it is not possible to distinguish between these two explanations in this analysis; indeed, both might apply equally. Fortunately, though, these explanations are effectively two alternative sides of the same

coin; the only key difference between them is their relative emphasis on costs versus benefits.

During foraging, the De Hoop females appear to be at greater risk of predation than the Tsaobis females for two key reasons. First, the De Hoop baboons spent more time distant from refuges in comparison to the Tsaobis baboons. This almost certainly relates to the fact that De Hoop is a virtually treeless environment (a characteristic of fynbos vegetation: Campbell *et al.* 1979). In contrast, the baboons at Tsaobis had access to abundant tree refuges while foraging in the woodland habitat (Cowlishaw 1997a,b). Second, the baboons at De Hoop spent more time distant from neighbors. This is most likely the result of differences in the spatial distribution of food at the two sites. At Tsaobis, foraging was largely confined to the riverine woodland, where the baboons gathered together in or under the trees to feed on their seeds, pods, flowers, leaves and bark. At De Hoop, the baboons were often widely dispersed, particularly when foraging in the grassland or burnt fynbos habitats, where food was at relatively low density in the herb layer, or where foraging was confined to dispersed digging sites in the vlei habitat.

No relationship was found between vigilance and time spent in low-visibility habitats. This is surprising, given the importance of visibility in determining habitat choice in both populations (Cowlishaw 1997a, Hill 1999) and the fact that such relationships have been reported in other studies (Chapman 1985; Underwood 1982). However, an analysis of daily vigilance among the Tsaobis females similarly found no pattern (Cowlishaw 1998). There are two possible explanations for this. First, this result might be a consequence of the costs of vigilance while feeding, because the closed habitats are often those with greatest food availability (Cowlishaw 1997a, Hill 1999). Indeed, there is a positive correlation between time spent in closed habitats and the proportion of foraging time spent feeding ( $r=0.58$ ,  $n=48$ ,  $p<0.001$ ). This in itself could be taken as a means to reduce predation risk, since it would reduce the amount of time an individual needed to spend in high-risk environments; moreover, there is evidence from both populations that the high-risk habitats are not exploited as heavily as would be anticipated on the basis of food availability (Cowlishaw 1997a, Hill 1999). Second, the measure of vigilance used here is not sufficiently detailed to capture subtle variation in the way vigilance is performed, and that alternative indices such as glance rates (e.g., Alberts 1994) might provide greater insight. It is possible that, rather than increasing vigilance in closed habitats, baboons

might maintain the same level of vigilance but 'parcel' it in a different fashion. For example, in closed habitats, long vigilance periods followed by prolonged feeding bouts might be an inefficient way of monitoring the environment, since the area that can be scanned is small and the additional information that can be gained by long scans will be minimal. However, the visible area needs to be monitored as constantly as possible, since approaching predators must be detected immediately if a successful attack from such close proximity is to be prevented. As a consequence, frequent glances may be a better strategy in low-visibility habitats, because they would allow regular checks for predators. Such a change in vigilance strategy may not be captured by this analysis, since it does not necessarily require any change in the overall time spent vigilant.

It is also important to note that the relationship described here between group size and vigilance rates was not reported in a previous study of vigilance among the Tsaobis baboons (although there was a trend in the predicted negative direction: Cowlishaw 1998). However, this previous work examined daily patterns of vigilance across all activities, and other studies have reported group size effects to be present for certain activities and not others (Blumstein 1996). Indeed, since vigilance patterns differ markedly between activities in the Tsaobis baboon population (Cowlishaw 1998), variation in activity budgets between groups might serve to weaken patterns of covariation between vigilance and group size, hence leading to the failure to detect a clear relationship when data from several different activities are combined.

Overall the results suggest that the baboons at De Hoop are twice as vigilant as those at Tsaobis when foraging because the Tsaobis baboons spend more foraging time feeding (and/or the De Hoop baboons spend more foraging time traveling: see above) and the De Hoop baboons spend more foraging time distant from refuges and neighbors. The longer distances to both refuges and neighbors at De Hoop suggest that foraging was a more dangerous activity there than at Tsaobis, and that the De Hoop baboons responded appropriately with higher levels of vigilance. Given that the presence of leopards, the primary predators of baboons (Cowlishaw 1994), was only confirmed at Tsaobis and not at De Hoop during these studies, these data suggest that baboons may react more sensitively to the conditions that predispose to leopard predation, rather than the presence of leopards themselves. In fact, this may be the most adaptive strategy for baboons, given the difficulties in reliably assessing the

presence/absence of leopards and, particularly, given the relatively rapid changes in presence/absence that can occur (e.g., leopards were reported at De Hoop following this study: Henzi *et al.* 2000).

The findings of this study are based on two key assumptions: (a) that baboons in different populations strive to maintain similar levels of safety, and (b) that baboons in different populations respond in similar ways to predation risk. The results presented here lend considerable support to these assumptions, since there was no difference in vigilance between the two populations once the differences in costs and benefits between them were statistically controlled, and both populations follow the same general trend in their response to predation risk (baboons across both populations increase their vigilance in response to a decline in group size, an increase in distance to refuge, and an increase in distance to nearest neighbor). Nevertheless an element of caution must be exercised in this interpretation. For example, although the higher levels of vigilance at De Hoop might be thought to indicate that foraging activities are twice as dangerous there than at Tsaobis, it might instead be argued that foraging is actually more dangerous at Tsaobis, specifically because the baboons are less vigilant during this activity. Similarly, it is possible that one of the reasons why the De Hoop baboons foraged at greater distances from refuges and neighbors was because they have a higher tolerance to the same level of local predation risk than those at Tsaobis; that is, they are not striving to maintain similar levels of safety (perhaps because leopards are less common residents at De Hoop).

In relation to this latter point, however, it might be possible to make some estimate of the levels of risk that the two populations should be willing to experience. Hill and Dunbar (1998) showed that across species, observed predation rates are closely related to the reproductive rate of that species. Predation rates were thus suggested to represent the rate of loss that animals could accommodate within their life history strategies, such that the animals were adopting behavioral strategies that reduced risk to some undefined 'acceptable' level. Such relationships should hold true within species, with the level of risk a population should be willing to experience being related to potential reproductive rates at that site. Mean interbirth interval at De Hoop is 25 months (Barrett *et al.* 1999). Although similar data are not available for Tsaobis, it is possible to estimate the interbirth interval for this population using the equation given in Hill *et al.* (2000). On the basis of the available ecological and demographic data for Tsaobis, the predicted mean

interbirth interval would be 23.0 months. Some caution needs to be employed with this estimate, since the available temperature data for Tsaobis are drawn from Karibib, a locality about 65 km to the north of the study area. Nevertheless, the predicted value is not substantially different from the figure for De Hoop, and given the error margins involved, such differences are unlikely significantly to affect the levels of risk that the two populations perceive as acceptable. As a consequence, it seems likely that risk tolerances of the two populations should be virtually the same. However, such conclusions must be considered preliminary at best, and merely serve to highlight one possible way in which risk tolerances might be assessed. As a consequence, the preceding discussion clearly highlights that our understanding of interpopulation differences in risk tolerance, and the impact this has on the consistency of anti-predation strategies, is still somewhat limited. Thus, while our analyses support the notion that baboons (and other primates) are following a species-typical antipredation strategy that is tailored to the local environmental conditions, such conclusions are contingent on our starting assumptions. A primary goal for future research should therefore be to determine whether such assumptions can be justified.

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### 13 • Foraging and safety in adult female blue monkeys in the Kakamega Forest, Kenya

MARINA CORDS

#### Introduction

Finding food and avoiding being someone else's food are two problems every primate must solve. The trick is finding a solution to each problem which does not simultaneously compound the other one. For example, being in close proximity to conspecifics, who can reduce the chances of being preyed upon in various ways, may also lead to increased competition for resources. Feeding on the newly emerged leaves of a deciduous tree, a relatively easily harvested source of protein, may mean forsaking protective cover. Understanding how animals balance the sometimes conflicting demands of efficiency and safety in food acquisition can help us clarify their biological priorities. Comparisons of the various solutions across taxa can help us determine the extent to which behavioral solutions are phylogenetically canalized, or flexible responses to local environmental conditions.

This chapter considers the relations between foraging and anti-predator strategies in an African forest guenon, the blue monkey (*Cercopithecus mitis stuhlmanni*). Blue monkeys are omnivores whose major dietary constituents are fruits, leafy matter (including leaf blades, petioles and buds), and invertebrates. They also eat flowers, nectar, gum, seeds, galls, and fungi. They harvest their foods from a broad array of plant species. For example, Cords (1986) reported that blue monkeys at Kakamega used at least 104 plant species as sources of plant food over a 12-month period, and at least 80 plant species (many of which did not double as sources of plant parts) as sources of invertebrates. In addition, blue monkeys show considerable variation in diet over various spatial and temporal scales. Lawes (1991) has described dietary variation that occurs over a broad geographical scale, while Rudran (1978) and Butynski (1990) have compared blue monkey groups that inhabit different parts of