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Using path analysis to explore vigilance behavior in the rock hyrax (*Procavia capensis*)

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Group size and vigilance are tools that animals can use to mitigate predation risk, and many studies have reported a negative relationship between them. Vigilance studies often investigate the direct effect of group size on vigilance, but they ignore the effect of ecological factors on group size. As a consequence, these studies can overlook important indirect effects of ecological factors on vigilance via group size. We investigated how ecological factors affect vigilance behavior in rock hyraxes (*Procavia capensis*), both directly and indirectly via group size. First, we showed a direct negative relationship between group size and vigilance behavior by measuring vigilance behavior before and after a change in group size. Second, we conducted a path analysis that included group size and several ecological factors (distance from shelter, distance from center of kopje, vegetation cover, and time since start of foraging session). Similar to the 1st analysis, the path analysis identified a strong negative relationship between group size and vigilance behavior; however, the other variables had little effect on group size or vigilance behavior, or both.

Key words: group size, predation risk, structural equation modeling

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Vigilance is one of the most important behaviors that animals can use to monitor their environment (Caro 2005; Lima and Dill 1990; Quenette 1990). Because increased levels of vigilance should lead to a greater probability of evading a predator attack, animals should invest considerable time in vigilance. However, vigilance generally is viewed as incompatible with other fitness-enhancing behaviors, such as foraging, mating, and resting; therefore, animals need to balance the costs and benefits of vigilance (Caro 2005; Lima and Dill 1990; Quenette 1990). Recent examinations of empirical data have suggested that animals can forage and be vigilant simultaneously (Lima and Bednekoff 1999; Makowska and Kramer 2007). However, the effectiveness of this vigilance appears diminished, probably due to cognitive interference and obstructed views (Makowska and Kramer 2007; Marois and Ivanoff 2005; Tombu and Jolicoeur 2005). Although vigilance might not be completely incompatible with other activities, in general, it probably reduces feeding rates, as has been shown for various species (Beauchamp and Livoreil 1997; Cowlshaw et al. 2004; Fritz et al. 2002).

Because vigilance is vital to survival, much research has been devoted to understanding factors affecting vigilance

strategies (Caro 2005; Lima and Dill 1990; Roberts 1996). Several factors have been identified, including ecological and environmental factors (e.g., distance from shelter, visual obstructions, time of day, and group size) and characteristics of the individual (e.g., age, sex, and position of the individual in the group—Caro 2005; Elgar 1989). Furthermore, these factors can impact vigilance behavior directly or indirectly. For example, vegetation can affect vigilance levels directly by creating a visual obstruction and reducing the effectiveness of vigilance. Alternatively, vegetation can affect vigilance behavior indirectly by causing individuals to cluster around a food source. This clustering can alter an individual's perceived predation risk and thereby impact its vigilance. Because of this network of relationships, it can be difficult to understand the relationship between individual characteristics, ecological factors, and vigilance behavior.

The effect of group size on vigilance has been one of the most thoroughly investigated relationships in vigilance studies



(Beauchamp 2003; Favreau et al. 2010; Lima and Dill 1990; Poysa 1994; Roberts 1996; Shi et al. 2010). Researchers have repeatedly reported a negative relationship between vigilance and group size in both birds and mammals. However, Elgar (1989) cogently argued that most of these studies lacked sufficient control of other variables to establish a direct relationship between group size and vigilance. After Elgar's (1989) review, several studies tried to control for some of these other variables, either through study design (Beauchamp 2006; Beauchamp and Livoreil 1997; Burger and Gochfeld 1992; Roberts 1995) or statistical analysis (Dalmau et al. 2010; Favreau et al. 2010; Périquet et al. 2010; Shi et al. 2010; Watson et al. 2007). Many of these studies supported earlier findings that group size directly affects vigilance.

The above approaches to studying vigilance behavior fail to elucidate indirect effects that might be influential in the system. The statistical techniques commonly used (e.g., multiple regression) examine only direct relationships between vigilance and ecological factors and not interactions among the ecological variables. Similarly, the experimental methods control for other factors by holding them fixed, allowing only analysis of direct effects. Many factors influence vigilance, but many of these variables also could affect group size, which indirectly affects vigilance. By looking solely at direct effects, we miss the complex web of interactions in which evolution occurs.

We sought to develop a more comprehensive understanding of how ecological variables affect the vigilance behavior of the rock hyrax (*Procapra capensis*). To accomplish this goal we used path analysis, a statistical technique designed to quantify both direct and indirect effects (Shipley 2000). This technique has been used primarily in the social sciences, but path analysis also has been used in ecological studies in recent years (e.g., sexual selection [Bart and Earnst 1999; Sih et al. 2002] and community ecology [Dyer and Stireman 2003; Pearson and Dyer 2006]). Path analysis presents a flexible linear model design, allowing the researcher to specify direct and indirect paths among variables (Shipley 2000).

We adopted a multistep approach to understanding how ecological factors affect vigilance. First, we tested for a direct relationship between vigilance and group size using an experimental method in which we measured vigilance levels before and after a change in group size (Roberts 1995). We then constructed a causal path diagram of factors affecting vigilance behavior in the rock hyrax, which was based on the literature and our results from the 1st step. Finally, we used observational data to estimate the strength of direct and indirect pathways of the path diagram.

MATERIALS AND METHODS

Study species and site.—Rock hyraxes are small, social mammals, ranging throughout parts of Africa and the Middle East (Olds and Shoshani 1990). Hyraxes are diurnal herbivores with a very diverse diet, and they conduct the majority of their foraging in the midmorning and late afternoon (Sale 1965; Turner and Watson 1965). Hyraxes generally form polygynous

family units and they inhabit kopjes (rock outcroppings). They seek shelter from predators (mainly raptors and felids) in the rock crevices (Sale 1965; Turner and Watson 1965). Group feeding is a characteristic aspect of hyrax foraging ecology, and the majority of all foraging is done in groups of ≥ 2 (Sale 1965; Turner and Watson 1965). During these group foraging bouts, occasionally 1 hyrax will act as a sentinel, watching for predators from a lookout (Kotler et al. 1999).

This study was conducted on an isolated kopje near the east gate of the Ngulia Rhino Sanctuary in Tsavo West National Park, Kenya ($2^{\circ}58'17.82''S$, $38^{\circ}17'0.41''E$). The kopje (~ 15 m tall \times 100 m long \times 75 m wide) is surrounded by semiarid savanna–bush habitat, and the nearest kopje is ~ 2 km away. Pockets of grasses and shrubs are scattered across the kopje, and the edge is mostly surrounded by low-growing grasses. Based on the maximum number of hyraxes observed, we estimated the population of hyraxes on this kopje to be approximately 50 individuals. We did not observe any sentinel behavior in this population.

Data collection.—This study was conducted from March through May 1999. Hyraxes foraged mostly on the lower part of the kopje, so observations were made from the elevated, central part of the kopje. The estimated observer–subject distance was a minimum of ~ 15 m. Direct observations were made from approximately 0730 to 1100 h and 1400 to 1730 h, the times of most-intense foraging activity. We ended each session when most hyraxes had retreated to the inner crevices of the kopje or if they became aware of the observer.

Focal subjects were chosen at random from among observable and active hyraxes. Because hyraxes were not marked, we chose subsequent subjects that were spatially removed from each other to avoid repeated sampling of an individual in the same foraging session. Focal subjects were watched through binoculars, and behaviors were recorded using a microcassette recorder. Tapes were replayed later, and a stopwatch was used to time the length of each behavior. Observations were terminated at 10 min or when the subject was lost from sight (mean observation length = 4.12 min; range = 1–36 min). Occasionally, when very little activity occurred on the kopje, observations were conducted for >10 min. If group size changed during the observation, it was noted so we could compare the behavior of the subject before and after the change in group size. Animals were not trapped or handled; our research was consistent with guidelines of the American Society of Mammalogists (Gannon et al. 2007) and was approved by Kenya Wildlife Services.

For each observation we recorded 8 ecological variables and the relative size of the focal individual (Table 1). We used vegetation to define group boundaries. Because vegetation on the kopje was patchy and clumped, hyraxes foraged in fairly distinct groups that were easily defined. Rock hyraxes do not exhibit any obvious sexual dimorphisms, so we were unable to include sex.

Vigilance variables.—Approximately 97% of our observations consisted of 3 behaviors (alert, incompatible foraging, and compatible foraging); therefore, we restricted our analyses

TABLE 1.—List of ecological variables recorded for each observation ($n = 161$).

Variable	Description	$\bar{X} \pm SD$	Range
Continuous variables			
Center	Distance from the center of the kopje (m)	20.89 \pm 11.27	1–47
Shelter	Distance from the nearest rock shelter (m)	6.42 \pm 4.91	0.5–15
Duration	Time since start of foraging session (h)	2.00 \pm 0.76	0–3.92
Ordinal variables			
Group size	No. hyraxes in the immediate area (within ~ 3 m)	2.81 \pm 1.67	1–8
Vicinity size	No. visible hyraxes on or around the kopje (scale: 1 [1 or 2 hyraxes] to 4 [>10 hyraxes])	2.33 \pm 0.94	1–4
Veg cover	Relative density of overhead vegetation cover (scale: 1 [none] to 5 [thickest])	2.91 \pm 1.46	1–5
Body size	Size of focal individual (scale: 1 = small, 2 = medium, 3 = large)	2.59 \pm 0.96	1–3
Categorical variables			
Location	On or off kopje		
Time period	Morning or afternoon		

to these behaviors. Alert was when the hyrax had its head raised and was scanning, with no ingestion of food. Following the framework of Cowlshaw et al. (2004), incompatible foraging was defined as foraging behavior that did not permit any visual detection of predators (e.g., head down in vegetation). Compatible foraging was when the head of the hyrax was raised and alert but the hyrax was ingesting vegetation. These 3 variables have different vigilance values, so to summarize the vigilance of an individual during an observation we constructed 2 composite variables: percent time vigilant and rate of vigilance.

Percent time vigilant ($V_{\%}$) represents the overall proportion of time that the individual spent being vigilant. To calculate $V_{\%}$ each of the 3 behaviors was weighted based on its vigilance value. Alertness was given full value because the animal appeared to be fully vigilant. Compatible foraging was given only half value because the effectiveness of the vigilance likely is reduced by cognitive interference (Marois and Ivanoff 2005; Tombu and Jolicoeur 2005). Incompatible foraging was assigned a vigilance value of 0. All 3 behaviors were then combined into a single response variable using the following equation:

$$V_{\%} = [(if_p \times 0) + (cf_p \times 0.5) + (a_p \times 1)] / (if_p + cf_p + a_p) \times 100,$$

where if_p is proportion of time devoted to incompatible foraging, cf_p is proportion of time devoted to compatible foraging, and a_p is proportion of time devoted to alertness. Therefore, if an individual was alert for the whole observation, $V_{\%} = 100$. Mean $V_{\%} \pm SD$ was 15.1% \pm 20.53% (range = 0–96.41%). We reran all analyses giving compatible foraging the same vigilance value as alert. The qualitative conclusions remained the same, but with larger regression coefficients. Treating compatible foraging the same as incompatible foraging resulted in smaller regression coefficients.

For rate of vigilance (V_r) we calculated the number of vigilance bouts (either compatible foraging or alertness) per minute. Following the assumption that compatible foraging and vigilance bouts both require the diversion of focus away from searching for and gathering food, we treated both vigilance and compatible foraging bouts as equal. Mean $V_r \pm SD$ was 1.25 \pm 1.02 bouts/min (range = 0–5.83 bouts/min).

Hypotheses about the relationship between variables (path diagram).—Path analysis can be used to test hypotheses about both direct and indirect relationships between variables. These relationships are represented in a path diagram (Fig. 1). For the path model we defined 3 response (endogenous) variables: vicinity size, group size, and vigilance (either $V_{\%}$ or V_r). We also included 4 independent (exogenous) variables: center, shelter, veg cover, and duration (Table 1).

The path diagram predicted that vigilance behavior was affected directly by the number of surrounding conspecifics, because our real-time analysis (below) indicated that group size has a direct effect on vigilance behavior (see “Results”). We included 2 different measurements of the number of conspecifics: group size (number of hyraxes in immediate area, as defined by vegetation boundaries) and vicinity size (total number of visible hyraxes on or around the kopje; i.e., in the vicinity). We also included a path between vicinity size and group size, because group size was determined at least in part by the total number of hyraxes on the kopje (K. V. Fanson, pers. obs.).

The timing of the observation with relation to the start of the foraging session (duration) could affect vicinity size, group size, and vigilance, and thus these 3 paths were included in the model. Although hyraxes are group foragers, they do not initiate or terminate their foraging activity simultaneously. Therefore, hyraxes that emerge 1st will necessarily have smaller group and vicinity sizes. Additionally, Druce et al. (2006) found that predation costs can change throughout the day for rock hyraxes.

Vegetation structure can affect the exposure of an animal to predators, grouping patterns, and effectiveness of vigilance. Therefore, we included paths from veg cover to group size and vigilance. We ranked veg cover from 1 (indicating little or no stem structure, such as a grassy patch) to 5 (a shrub or tree with dense foliage). Visual obstructions can compromise the effectiveness of vigilance (Makowska and Kramer 2007); however, visual obstructions also can hide the animal from predators. Druce et al. (2006) found that hyraxes appear to have lower predation costs under cover. Additionally, vegetation can affect the spatial dynamics of groups and

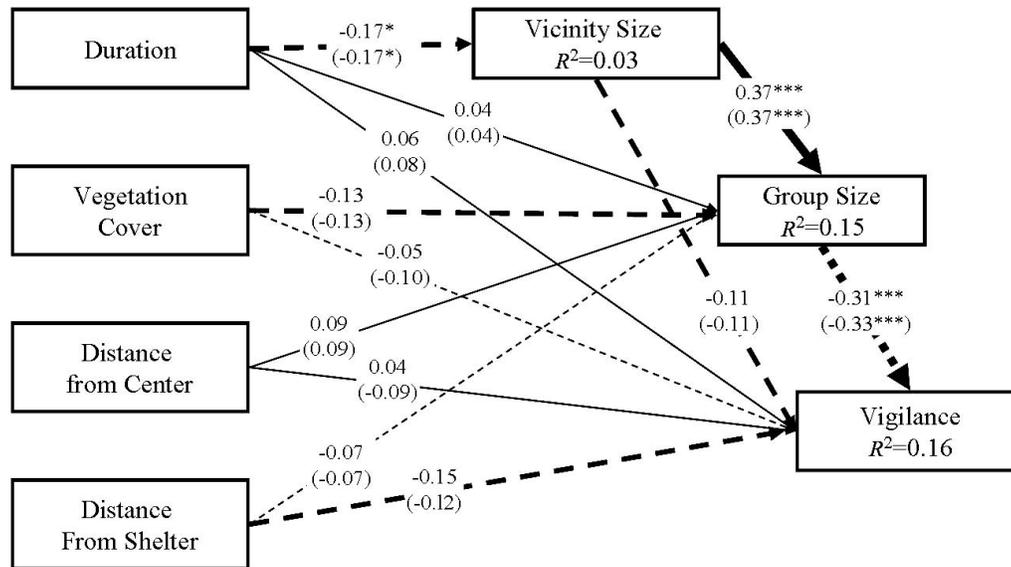


FIG. 1.—Path diagram illustrating the effects of different ecological factors on vigilance behavior. Path coefficients are given for both percent time vigilant ($V_{\%}$; top number) and rate of vigilance (V_r ; bottom number, in parentheses). Positive effects (+) are shown with solid lines and negative effects (–) with dashed lines. The relative strength of the path coefficient is indicated by the weight of the line, and asterisks indicate significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). R^2 -values are provided for only $V_{\%}$, but values were similar for V_r .

group size, because the vegetation on the kopje provides clustered resources that can vary in quality.

Hyraxes are central place foragers, initiating and terminating foraging sessions from a central refuge (Kotler et al. 1999; Sale 1965; Turner and Watson 1965). The farther an animal is from a refuge, the more time it requires to reach safety in the event of an attack. Hyrax foraging rates decrease with distance from the center of the kopje (Druce et al. 2006). Furthermore, hyraxes often leave the kopje in a single group (Kotler et al. 1999; Sale 1965). As environmental risk increases, it could be advantageous to form larger, more cohesive groups. Therefore, our model included paths from center to group size and vigilance.

Kopjes also usually have temporary rock shelters that hyraxes use when frightened (Sale 1965; Turner and Watson 1965). The distance from the nearest shelter affects predation risk and hence vigilance and group size (Caro 2005; Lima and Dill 1990). Distance to shelter and center correlate strongly near the center of the kopje, but the relationship degrades quickly beyond ~ 5 m from the center. Thus, it was possible to differentiate between the 2 spatial scales.

Data analysis: real-time changes in group size.—We 1st tested for a direct link between group size and vigilance using the “real-time change in group size” technique described by Roberts (1995). For this method vigilance behavior of a focal animal was recorded before and after a change in group size. This method helps control many potentially confounding variables, such as temperature, age, sex, and time of day.

We recorded 50 observations during which group size changed. We included only observations for which we had at least 1 min of data for each group size ($\bar{X} = 3.4$ min before and 2.7 min after change in group size). For each observation we recorded the directionality of the group size change (increase or decrease). To calculate the difference in vigilance

behavior (both $V_{\%}$ and V_r) before and after the change in group size, we subtracted the vigilance level of the smaller group size from that of the larger group size. The differences in $V_{\%}$ and V_r were log-transformed to meet assumptions of normality and homoscedasticity (Zar 1998).

Using the paired difference in $V_{\%}$ and V_r as the response variables, we ran a general linear model (SAS 9.1; SAS Institute Inc., Cary, North Carolina) to determine how the change in group size (increase or decrease) affected vigilance levels. We also included 4 fixed variables: period, body size, location, and group size (Table 1). We performed a backward selection process, removing any predictor variables for which $P > 0.10$. $V_{\%}$ and V_r were analyzed in separate models.

Data analysis: path diagram.—Path analysis provides a tool to quantify statistically the strength of indirect and direct pathways between variables. We constructed separate path models for both measures of vigilance ($V_{\%}$ and V_r). For observations that included more than 1 group size (see real-time analysis above) we randomly chose 1 group size to include in the path analysis.

Path analysis relies on a multivariate normal distribution, and inferences are strongly influenced by kurtosis of the data (Hatcher 1994). Data were log-transformed to meet assumptions of linearity and normality (Hatcher 1994). After the transformations a multivariate measure of kurtosis found that the Mardia value was -1.46 ($P = 0.14$), suggesting our data were normal (Hatcher 1994). All analyses were performed on the correlation matrix using PROC CALIS in SAS 9.1 (Hatcher 1994). We used Pearson correlations (r) for continuous variable pairings. We used polyserial and polychoric correlations for ordinal–continuous and for ordinal–ordinal pairings, respectively.

To evaluate the fit of the models we used goodness of fit (χ^2) plus 2 additional indices that are less susceptible to small

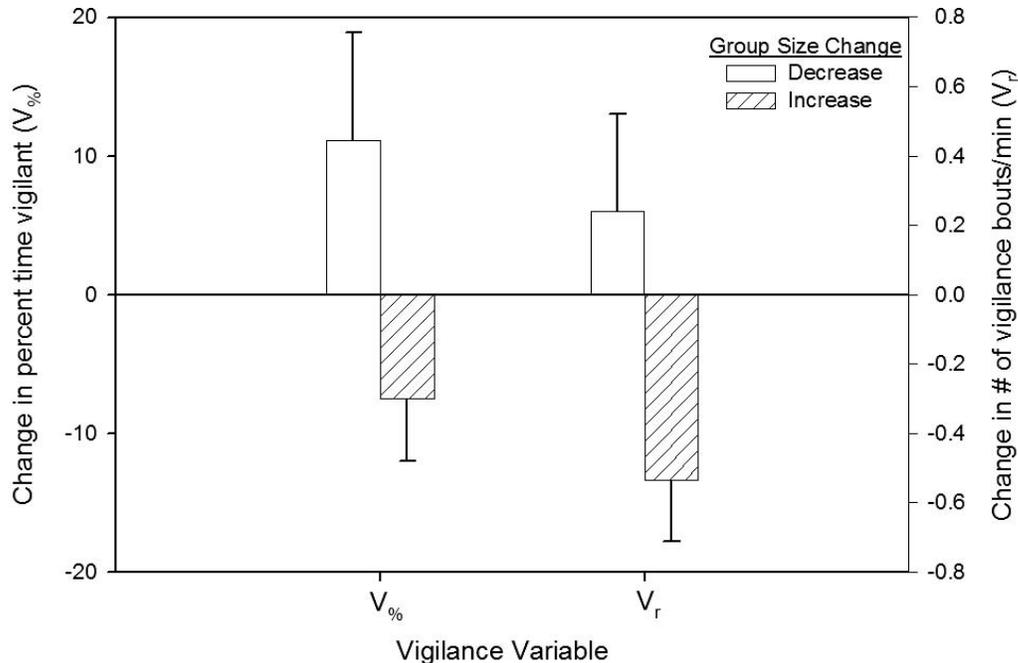


FIG. 2.—Effect of real-time change in group size on vigilance behavior (least-square means ± 1 SE). The direction of the change in group size (increase or decrease) did not significantly affect ($P > 0.05$) the magnitude of the change in vigilance (percent time vigilant [$V_{\%}$] and rate of vigilance [V_r]).

sample sizes: Bentler's comparative fit index and Bentler and Bonett's normed-fit index (Bollen 1989). A path diagram is determined to have support if the chi-square statistic is not significant ($P > 0.05$) and the comparative fit index and normed-fit index are >0.95 . Overall, we had 6.5 observations per parameter estimated in the model, exceeding the >5 per parameter recommended by Petraitis et al. (1996). Results are presented in terms of standardized regression coefficients (β) for each path. The β coefficients can be interpreted similarly to correlation coefficients (e.g., range from -1 to 1).

Accounting for repeated measurements.—Because we did not trap, handle, or mark the hyraxes, we were not able to identify individuals. We avoided repeated sampling of an individual during a foraging session; however, between foraging sessions and days we most likely measured the same individual repeatedly. To estimate the correlation between observations from the same individual we ran a mixed linear model with the real-time changes data set. We included both the before and after data instead of the paired data, and then included the identification of the hyrax as a random effect. The estimated within-individual correlation was 0.20 ($n = 50$, $P = 0.06$). Because $r = 0.20$ for repeated measures of an individual within several minutes, measurements farther apart in time (across days and weeks) should have much smaller correlations. Therefore, we suspect that assuming independence of observations should not be problematic to our overall conclusions.

RESULTS

Real-time changes in group size.—Changes in group size had a significant effect on the percentage of time hyraxes

devoted to vigilance ($V_{\%}$: $F_{1,49} = 4.7$, $P = 0.017$). The addition of a hyrax to a group caused $V_{\%}$ to decrease by $7.5\% \pm 4.5\%$ ($\bar{X} \pm SE$; $n = 35$), and when a hyrax left a group, $V_{\%}$ increased by $11.1\% \pm 7.8\%$ ($n = 15$). However, the magnitude of these differences did not differ significantly whether a group member was added or subtracted ($F_{1,43} = 0.06$, $P = 0.81$; Fig. 2). Furthermore, the total group size in which the hyrax was foraging did not affect the magnitude of the change in $V_{\%}$ ($4.2\% \pm 3.1\%$ /hyrax, $F_{1,43} = 1.85$, $P = 0.18$). In other words, whether group size was 2 or 8, the addition of an individual caused a similar decrease in $V_{\%}$. $V_{\%}$ was not affected by time of day, body size, or whether the hyrax was on or off the kopje ($F_{3,43} = 0.23$, $P = 0.87$; $F_{1,43} = 0.04$, $P = 0.85$; $F_{1,43} = 0.16$, $P = 0.69$, respectively). Inspection of the data revealed no indications of nonlinear trends between group size and $V_{\%}$ (quadratic term, $P > 0.10$) and thus were not included in the final model. The interaction between direction of change in group size and total group size was not significant ($F_{1,42} = 2.28$, $P = 0.12$).

The rate of vigilance (V_r) also was significantly affected by changes in group size ($F_{1,49} = 8.8$, $P = 0.002$). When group size increased, hyraxes reduced the number of vigilance bouts by 0.53 ± 0.18 bouts/min ($\bar{X} \pm SE$; $n = 35$); when group size decreased, hyraxes increased V_r by 0.24 ± 0.28 bouts/min ($n = 15$). The direction of the change in group size (i.e., whether group size increased or decreased) did not appear to affect the magnitude of the change in V_r ($F_{1,43} = 0.01$, $P = 0.93$; Fig. 2). Additionally, we found no strong statistical support that body size, location, time of day, or group size affected the magnitude of the change in V_r ($F_{3,43} = 1.92$, $P = 0.14$; $F_{1,43} = 0.00$, $P = 0.96$; $F_{1,43} = -0.39$, $P = 0.69$; $F_{1,43} = 0.08$, $P = 0.77$, respectively).

Evaluation of path diagrams.—Overall, both path models ($V_{\%}$ and V_r) fit the data. The Bentler's comparative fits were 0.97 and 0.98 for $V_{\%}$ and V_r , respectively, and Bentler and Bonett's normed-fit indices were 0.96 for both models. Although the data support the causal structure proposed in the path models, much variation still remained unexplained (Fig. 1). Many of the paths proposed in our path diagram had only minimal influences on the 3 response variables (vicinity size, group size, and vigilance behavior). Below, we present $\hat{\beta}$ for each path in the $V_{\%}$ model. The V_r model had very similar regression coefficients (Fig. 1).

With respect to vicinity size, our results indicated a negative effect of time since start of the foraging session on the total number of hyraxes foraging ($\hat{\beta} = -0.17$, $P = 0.03$). Of the paths leading to group size, results suggested that only vicinity size had a strong positive effect ($\hat{\beta} = 0.37$, $P < 0.001$). Time since start of the foraging session ($\hat{\beta} = 0.04$, $P = 0.34$), distance from center of kopje ($\hat{\beta} = 0.09$, $P = 0.24$), vegetation cover ($\hat{\beta} = -0.13$, $P = 0.15$), and distance from nearest shelter ($\hat{\beta} = -0.15$, $P = 0.14$) were not significant.

Similar to the results from the real-time change in group size analysis, the path model suggested that group size had a negative effect on $V_{\%}$ ($\hat{\beta} = -0.31$, $P < 0.001$). We did not find strong support for an effect of distance from nearest shelter on $V_{\%}$ ($\hat{\beta} = -0.15$, $P = 0.14$). Time since start of the foraging session ($\hat{\beta} = 0.06$, $P = 0.28$), distance from center ($\hat{\beta} = 0.04$, $P = 0.36$), vicinity size ($\hat{\beta} = -0.11$, $P = 0.18$), and vegetation cover ($\hat{\beta} = -0.05$, $P = 0.35$) did not affect $V_{\%}$ significantly.

DISCUSSION

Our study provides an in-depth analysis of ecological factors affecting the vigilance behavior of rock hyraxes inhabiting a kopje. We performed 2 sets of statistical analyses to explore the interconnectedness of various ecological factors, group size, and vigilance behavior. We 1st showed a direct effect of group size on vigilance levels in rock hyraxes using paired comparisons. This analysis provided experimental support for a direct link between group size and vigilance levels, which has not been demonstrated before for rock hyraxes. Next, we quantified the strength of the relationships in our path diagram, providing insights into the importance of various factors, directly and indirectly, on vigilance levels. These results substantiated a strong effect of group size on vigilance behavior and revealed only minor influences of the other variables.

Analysis of real-time changes in group size showed that rock hyraxes alter their vigilance behavior in response to changes in group size. A decrease in group size resulted in an increase in both $V_{\%}$ and V_r . Hyraxes not only increased the total time spent being vigilant but also how often they interrupted their foraging to scan their environment. Frequent shifts between foraging and vigilance can reduce foraging efficiency and reflect an animal's perception of predation risk (Dall et al. 1999, 2001; Kotler et al. 2002). Overall, these results strongly suggest that rock hyraxes were aware of changing group sizes and changed their vigilance levels in response.

Although hyraxes were responsive to changes in group size, the overall size of the group did not appear to influence the magnitude of the change in vigilance behavior. Both the "many eyes" and "dilution" hypotheses predict that as group size increases, the addition of another animal results in a smaller decrease in predation risk compared with the arrival of the previous animal (Beauchamp 2003). This is because perceived predation risk is calculated as risk divided by group size ($1/N$). If the group size is large, the addition of an individual causes only a small decrease in predation risk, and therefore individuals should modify their vigilance behavior only slightly. Conversely, if the group size is small, the addition of an individual causes a much greater reduction in predation risk, and theory predicts a greater reduction in individual vigilance levels. Thus, we expected a negative slope between group size and the difference in $V_{\%}$ or V_r before and after a change in group size. However, we did not find strong support for a negative relationship between group size and the magnitude of the change in vigilance behavior. Similarly, Roberts (1995) found no effect of current flock size on the magnitude of change in vigilance behavior with crested terns. Therefore, our results suggest that hyraxes might be monitoring only the arrival or departure of other hyraxes and not the total number present.

Path analysis provides a more comprehensive understanding of vigilance behavior than would be obtained from looking solely at direct relationships. We were able to ask if different ecological variables affected vigilance through indirect processes. Similar to the real-time results, path analysis revealed a strong negative effect of group size on both measures of vigilance. Hyraxes spent more time being vigilant and interrupted their foraging more frequently to be vigilant when they were in smaller groups. In contrast to group size, other factors had only small effects on $V_{\%}$ and V_r . The small effects of distance from cover and distance from shelter are particularly interesting. Based on patch use, Druce et al. (2006) suggested that rock hyraxes perceive lower predation risk under rocks or shrubs and farther away from the center of the kopje. Therefore, if vigilance can mitigate predation risk, we expected a strong positive effect of these variables on vigilance. Our path analysis revealed no strong support for such a relationship, either directly or indirectly through group size.

The patchy distribution of vegetation on the kopje resulted in patchy distribution of hyraxes. Therefore, neighbor-distance was bimodal, with the 1st mode ~ 1.5 m and the 2nd mode ~ 15 m. Studies have found that distance to nearest neighbor affects vigilance level (Fernandez-Juricic et al. 2007; Poysa 1994; Rolando et al. 2001). Our path diagram revealed that vigilance was affected strongly by the distance to nearest neighbors (group size) but not by farther neighbors (vicinity size). This suggests that visual cues could be very important for assessing predation risk. The topography on the kopje hindered visual observation of conspecifics that were further away. Therefore, hyraxes might decrease their individual vigilance levels only when conspecifics are close. Alarm calls should be detectable anywhere on the kopje, but we rarely observed the use of alarm calls by this population of hyraxes.

Time since the start of the foraging session (duration) had a direct positive effect on vicinity size but had little direct effect on vigilance. The indirect effect of duration on vigilance is also very small, because the path coefficients between vicinity and group size and group size and vigilance are only moderate. As a consequence, vigilance levels increased only slightly throughout the foraging session ($\hat{\beta} = -0.17 \times 0.37 \times -0.33 = 0.02\%$ increase in vigilance). Thus, although the time since the start of a foraging session does affect the number of hyraxes active on the kopje, it does not have a strong effect on vigilance behavior.

Although vigilance was affected significantly by some factors, our model explained only a small proportion of the total variance in hyrax vigilance. Vigilance is a complex behavior that likely is affected by numerous factors. A recent review of avian studies found that group size accounted for <20% of the variance in vigilance (Beauchamp 2008). Although we included several ecological factors that we thought might influence vigilance, undoubtedly important ecological variables exist that we did not or could not quantify (e.g., presence of predators—Périquet et al. 2010). Furthermore, several characteristics of the individual animal, such as age, sex, physiological state, and dominance level have strong effects on vigilance behavior (Caro 2005; Dalmau et al. 2010; Elgar 1989). Because we were unable to mark individuals, we could not incorporate these individual attributes in our analysis. Finally, vigilance can function as not only a means of predator detection, but also as a mechanism for monitoring conspecifics (social monitoring—Caro 2005; Favreau et al. 2010). We still have much to learn about how different factors influence vigilance behavior, but path analysis could prove useful in understanding this complex web of interactions.

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