Patch use, apprehension, and vigilance behavior of Nubian Ibex under perceived risk of predation

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Foraging theory predicts that animals will sacrifice feeding effort in order to reduce predation risk. Once a forager chooses a habitat, it must decide how to allocate its foraging effort. Nubian Ibex are diurnal, social, cliff-dwelling herbivores. Many of their characteristics seem to have evolved as responses to predation risk. In order to assess the effects that perceived risk of predation might have on foraging behavior of free-ranging Nubian Ibex in the Negev Desert, Israel, we measured giving-up densities (GUDs) in artificial food patches and used them to gauge apprehension level. (Apprehension can be defined as a reduction in attention devoted to performing an activity as a consequence of reallocating attention to detecting or responding to predation risk. A forager can also be vigilant. Vigilance is often defined as time spent scanning the surroundings with the head up.) We also quantified time budgeting using focal observation of individual Nubian Ibex. Habitat preferences and patch selectivity as a measure of apprehension were considered. In particular, we tested the effect of distance from refuge on GUDs, the effect of micropatch structure on selectivity, and the effect of distance from the refuge and group size on Nubian Ibex vigilance level and apprehension. Nubian Ibex allocate their foraging effort more toward patches closer to the escape terrain. At the same time, Nubian Ibex are more apprehensive at intermediate distances from the cliff edge than nearer the cliff, and their use of vigilance increases with distance from the cliff edge. These results suggest that Nubian Ibex may switch from apprehension to a more extreme behavior of vigilance at greater distances from the refuge. This study demonstrated the use of antipredatory behaviors, apprehension, and vigilance by a forager. Estimating apprehension and vigilance levels of a forager simultaneously gives a more complete and accurate picture of how the habitat is perceived by them and combined with measurements of GUD allow a more accurate assessment of habitat quality. Key words: apprehension, foraging behavior, giving-up densities, Nubian Ibex, patch use, predation risk, vigilance. [Behav Ecol 18:368–374 (2007)]

An individual foraging under predation risk has several options for resolving the conflicting demands of food versus safety. One is its degree of time allocation and foraging effort (Brown 1999). While foraging, an individual must choose not only when and where to eat but also how long it should stay in a food patch (Lima and Dill 1990). In regard to patch use, a forager should exploit a patch until its harvest rate falls to equal its foraging cost (Brown 1988). Typically, because a forager prefers to harvest food from safe patches, and should deplete food from there first, there will be a choice between a risky patch with high harvest rates versus a safe patch with lower energetic returns. If risk increases, then an individual should devote less time to foraging, especially in the riskiest locations (Brown 1999).

A second option for managing risk is the choice of apprehension level. Apprehension can be defined as a reduction in attention devoted to performing an activity (e.g., patch exploitation) as a consequence of reallocating attention to detecting or responding to predation risk (Dall et al. 2001). An animal can increase safety by increasing its level of apprehension. A forager can also be vigilant. Vigilance is often defined as time spent scanning the surroundings with the head up during which time no foraging takes place. Unlike vigilance, apprehension allows a forager to harvest food while it is more alert for predators. However, apprehension may come with a cost resulting from reduced food intake rate and poorer assessment abilities. Thus, there should be an optimal level of apprehension (Kotler et al. 2002). Even when there is no imminent attack, an individual should keep a baseline level of apprehension given the constant possibility of an attack (Brown et al. 1999).

Changes in apprehension as a response to different levels of predation risk can be revealed in several ways. For instance, they can be quantified by offering a forager artificial food patches (feeding trays) that differ in micropatch (sections within the feeding tray) structure or complexity (Kotler et al. 2002). An increase in apprehension should be detected as a rise in selectivity for those food patches in which it is more difficult to make mistakes, for example, in which it is easier to assess boundaries or easier to handle the food resource. An artificial food patch with a higher level of complexity implies that information on some aspect of patch characteristic is harder to acquire and there is a greater likelihood to either over- or underestimate the value of the characteristic (e.g., micropatch size). A forager is more prone to make mistakes there. A mistake in estimating the micropatch size reduces the harvest rate and therefore value of the patch (Schmidt and Brown 1996). The more apprehensive a forager is, the more mistakes it will make. This is especially so in a patch comprised of micropatches. This decreases the value of the patch with micropatch structure especially when compared with a more homogeneous patch. Therefore, the value of the patch with micropatches will decrease relatively more than that of the patch without micropatch structure.

Related to apprehension is vigilance. A more vigilant forager might be safer but does not feed while actually being...
vigilant. Excessive vigilance might imply unnecessary loss of feeding opportunities (Frid 1997). Therefore, a forager must choose an optimal level of vigilance while feeding. Vigilance is not mutually exclusive with processing food but usually is with food searching and handling (Frid 1997). Many studies on ungulates have assumed that the risk of being killed by a predator is the primary reason for vigilance behavior (Hunter and Skinner 1998).

Several studies with other species have analyzed behavioral responses to predation risk by estimating only the vigilance level of individuals either by measuring scanning rates or by measuring the duration of the scanning bouts (e.g., Lima 1995b; Hunter and Skinner 1998; Laundré et al. 2001). Altendorf et al. (2001) measured how mule deer (*Odocoileus hemionus*) allocate their foraging effort while foraging under predation by applying the giving-up densities (GUDs) technique and measuring their vigilance level at feeding trays. However, in that study, the vigilance level was measured through photographs taken of deer exploiting the feeding trays. Even the most thorough of these studies provides an incomplete picture because apprehension was not examined. This is the first time to assess the manner in which a forager uses time allocation and both apprehension and vigilance to manage predation risk. For instance, the concept of antipredatory apprehension to study how predation risk affects foraging decisions has only been applied to gerbils, animals that cannot use vigilance (e.g., Dall et al. 2001; Kotler et al. 2002; Kotler et al. 2004).

Summing up, a forager must choose a strategy that maximizes feeding rate while minimizing predation risk (Sih 1980). In order to achieve this, a forager can, for instance, reduce its activity times, change its apprehension level, and change its vigilance behavior. It is then of interest how a forager uses these tools.

Nubian Ibex, *Capra nubiana*, are wild social goats that live on steep terrain and cliffs (Gross et al. 1995a). Males average 62.5 kg whereas females average 26.5 kg (Gross et al. 1995a). The social groups are mainly 1) Female-based groups, including young individuals in herd sizes up to 20 individuals or more. In the study area, groups numbering more than 100 individuals have been recorded (Levy and Bernadsky 1991); 2) Males more than 3 years old and adult males (Levy and Bernadsky 1991; Müller et al. 1995). Nubian Ibex are diurnal foragers and are mostly active during morning and afternoon hours. Resting and ruminating occur around noon and at night (Levy and Bernadsky 1991). Even though they are adapted to desert conditions, they drink water almost everyday. The possible predators of Nubian Ibex include leopards (*Panthera pardus*), wolves (*Canis lupus*), striped hyenas (*Hyaena hyaena*), and humans. The neonates can be depredated by golden eagles (*Aquila chrysaetus*) and eagle owls (*Bubo bubo*) (Levy and Bernadsky 1991). Mountain ungulates appear to be dependent on steep terrain to avoid predators (Kohlmann et al. 1996). Predation risk is affected by the distance to a refuge, and for Nubian Ibex, a refuge is represented by the cliff edge and slope that provide escape terrain (Kotler et al. 1994; Gross et al. 1995b).

We applied the GUD technique (Brown 1988; Kotler et al. 1994) using artificial food patches to free-ranging Nubian Ibex in the Negev Desert, Israel to test the effects of perceived predation risk on their foraging behavior. We (1) measured the effects of distance from cliff edge on Nubian Ibex foraging effort allocation, (2) quantified changes in their selectivity for artificial food patches that differed in complexity as a way to gauge changes in their apprehension level, and also (3) quantified the effects of distance from cliff edge on time spent in vigilance using direct observations.

### METHODS

#### The study area

The study was carried out in the vicinity of Midreshet Ben-Gurion, in the highlands of Central Negev Desert, Israel (30°52’N, 34°46’E). The topography of the area is highly varied with elevations ranging from 320 to 580 m.a.s.l. The area is dominated by a large drainage and its tributaries and includes dry riverbeds and steep-walled canyons. All the experiments and direct observations were carried out within Ein Avdat National Park and Zin Nature Reserve.

The region is a warm arid zone (UNESCO 1977), with hot, dry summers and cold, wet winters. Winter rainfall averages 100 mm per year and is extremely variable within and between years (Gross et al. 1995a). Major plant communities on the slopes and plateaus are dominated by shrubs from 30 to 100 cm tall, especially white bean caper (*Zygophyllum dumosum*), white worm wood (*Artemisia herba-alba*), and articulated anabis (*Anabis ariculata*) (Kotler et al. 1994; Gross et al. 1995a).

#### The GUD technique

A forager exploiting a depletable food patch should use the patch until the marginal cost of foraging and the marginal benefits of exploitation are equal. For a forager in a risky environment, this occurs when \( H = C + P + MOC \), where \( H \) is the harvest rate of energy in the patch and \( C, P, \) and \( MOC \) are the energetic cost of foraging, the foraging cost due to predation, and the missed opportunities cost, respectively (Brown 1988). This last cost arises from not being able to forage elsewhere or perform other fitness enhancing activities during the time spent in the patch. The resource density at which an individual stops foraging is called the GUD (Brown 1988). GUDs can be measured using depletable food patches in which food is mixed into a nonedible substrate in a tray, for example, using feeding trays as artificial resource patches (Brown 1988, 1989).

In these experiments, we applied the GUD technique to free-ranging Nubian Ibex following Brown (1988) and Kotler et al. (1994). Using feeding trays as artificial resource patches allows manipulations of variables while foragers remain in the natural environment (Brown 1988). The feeding tray gives the GUD for the most efficient forager to have visited it, typically the last animal to have exploited it thoroughly. If less efficient foragers visit the tray later on, they will not find profitable opportunities to exploit. If a more efficient forager visits the tray later, it will find profitable opportunities and will then exploit the tray. The GUD will reflect the animal’s foraging costs at the time it leaves the patch. Consequently, the GUD is insensitive to the number of foragers that have visited the tray, per se. In addition, if guts of foragers fill rapidly while exploiting feeding trays and become less efficient in handling food as they fill, and animals do not revisit patches, then the order of visitation may matter. But there is no reason that animals will always visit patches close to the cliff first and patches more distant from the cliff later unless distance from the cliff is related to foraging costs.

We presented to the Nubian Ibex premeasured amounts of food in wooden trays (46 × 30 × 12 cm) filled with the nonedible substrate. The food consisted of 100 g of compressed alfalfa pellets, with the mean mass of 1.5 g per individual pellet. The nonedible substrate consisted of 1400 g of 1 cm diameter black plastic irrigation tubing cut into lengths of approximately 3 cm. To avoid animals pushing the substrate out of the trays and to better mimic natural foraging, we covered the trays with chain link fencing. This forced the Nubian Ibex to insert their muzzles between the links of the fence mesh much as they do when reaching for leaves inside...
shrubs. For each foraging bout, the trays were left for 24 h in the field for animals to discover and feed from prior to collecting data. In order to verify that only Nubian Ibex removed food from the trays, we identified the tracks left around each tray over the previous 24 h before collecting the remaining food in the trays.

The experiments were conducted at 2 locations on the plateau above Zin Canyon and separated by more than 2 km. The locations were far enough apart that those individuals feeding at one location that day did not feed at the other. At each location, 2 stations separated by 100 m were selected.

Foraging effort
To test whether individual ibex foraging farther from the safety of the cliff edge have higher GUDs, we placed feeding trays at 3 distances from the cliff edge: adjacent to the cliff, intermediate, and far away (10, 60, and 90 m away from the cliff edge, respectively). At each distance, we offered 3 trays that differed in the micropatch structure to the foragers. Hence, a station contained a total of 9 trays. Each day, we offered a total 36 trays to Nubian Ibex (2 stations × 3 trays × 3 distances × 2 locations = 36 trays). The different types of micropatch structures differed in the distribution of the food resources within the tray. We created the first type of micropatch structure by mixing all the food with all the substrate (full tray), the second type by mixing the food with half of the substrate from a tray, placing this in the bottom of the tray, and covering it with the remaining (food-free) substrate (bottom tray), and the third type (half tray) by mixing the food with half of the substrate, pouring this into the middle half of the tray, and placing the remaining substrate in the remaining 2 quarters of the tray. The half tray is more demanding than the full tray in that it has 2 vague boundaries, boundaries defined by a change in the resource density) and 2 distinct boundaries (boundaries clearly recognizable by a change in the substrate or border of an experimental patch, Brown 1988). On the other hand, the full tray has 4 distinct boundaries only, that is, the 4 sides of the tray and no vague boundaries.

When the apprehension level of a forager increases, the presence of vague boundaries reduces the value of the half tray relative to the full tray because of its effect on the forager's ability to allocate their foraging effort to areas of higher resource density (Schmidt and Brown 1996). Similarly, bottom trays are also more demanding than full trays. If multiple visits occur, the microstructure of a patch might change. However, if the earlier forager is a less efficient forager, it has little effect on either GUDs or selectivity. Nevertheless, if the earlier forager is more efficient, then the second individual would not find profitable opportunities and would quickly leave the patch after removing little or no resources. We allowed Nubian Ibex to access to trays for 24 h and then collected the remaining food to obtain the GUDs. We ran this experiment for 39 days in July and August 2003.

Selectivity
Changes in the apprehension level can be assayed by means of detecting changes in the selectivity for those artificial food patches (e.g., food trays) where food density is easier to assess. Changes in selectivity were measured through changes in Manly’s index.

In the present experiment, we applied the GUD technique previously described.

We used only 2 types of artificial food patches (feeding trays) that differed in complexity: the full and the half trays previously described. As apprehension increases, the value of the full tray should increase relative to the half tray. When apprehension increases, the forager should be less able to distinguish the vague boundaries of micropatches. Therefore, changes in the selectivity for the full tray relative to the half tray allow us to measures changes in apprehension (Kotler et al. 2002). As before, the trays were left 24 h in the field for animals to discover and feed from, and the same 3 distances from the cliff edge were considered (10, 60, and 90 m from cliff). Each day, we offered a total 24 trays to Nubian Ibex. We conducted the experiment at 2 locations. At each location, 2 stations were selected at each distance, with 2 trays that differed in their micropatch structure per station (2 stations × 2 trays × 3 distances × 2 locations = 24 trays).

We used selectivity for the full tray as a measure of apprehension. An increase in apprehension should be detected by an increase in the selectivity for this tray relative to the half tray. We used Manly’s index to calculate the selectivity for the full tray (Chesson 1983; Schmidt and Brown 1996; Kotler et al. 2002):

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S = \frac{\ln \left( \frac{\text{remaining food full tray}}{\text{initial food full tray}} \right)}{\ln \left( \frac{\text{remaining food half tray}}{\text{initial food half tray}} \right)},
\]

where \( S \) is the selectivity for the full tray. This index can be used to measure preferences because the measure itself does not change with the food density (Chesson 1983). In addition, this measure of selectivity is appropriate when food resources decline with harvest (Brown and Morgan 1995).

The selectivity index takes values from 0 to 1. \( S = 0 \) indicates that no foraging occurred in the full tray, \( S = 1 \) indicates that no foraging occurred in the half tray, and \( S = 0.5 \) indicates that food is being consumed equally from both trays. We expected that selectivity for the full tray to be less than 0.5 (food is more concentrated in the half tray) but to increase with distance from cliff edge as apprehension increases.

Vigilance levels
Generally, foraging individuals tend to experience a trade-off between the risk of being killed by a predator and the risk of starvation (Repasky 1996). Foraging will be costly when scanning for behaviors that reflect the risk of predation while foraging is by measuring changes in vigilance levels (Repasky 1996). In addition, a social forager’s vigilance level can be also affected by the herd size. When foraging in larger groups, each individual can afford to be less apprehensive, while the total vigilance of the group will be higher thanks to the “many eyes” and “dilution” effects (Lima and Dill 1990; Lima 1995a; Brown et al. 1999).

The goal of this experiment was to measure the vigilance level of Nubian Ibex as an indicator of predation risk. Nubian Ibex vigilance level should be lower in locations closer to cliff edge (which should represent escape substrate to ibex) and in larger group sizes. In these situations, it is expected that Nubian Ibex feeding bouts will be longer.

In order to estimate the vigilance level of Nubian Ibex, we observed and recorded the behavior of individual Nubian Ibex. Data were collected within 2.30 h after sunrise and 2.30 h before sunset, a period when Nubian Ibex are most active and therefore are more easily observed (Gross et al. 1995b). Focal samples (Altmann 1974) were carried out to assess Nubian Ibex vigilance level. Each focal sample bout lasted 3 min. A Palm Pilot Zaire programmed with the F.I.T. Manager software was used as an event recorder. Observations were done with the aid of 20 × 50 binoculars. In order to minimize any effect caused by the presence of the observer,
we let the groups of ibex calm down for a minimum of 5 min before starting observations. Observations were conducted at a mean distance of approximately 35 m.

Behaviors were classified into three categories:

1) Vigilance: The animal stands on 4 legs with its head raised, the ears are directed forward, and it is looking intently at the surroundings. The head might be turned a little from side to side (Alados 1985). Also, an animal was considered to be vigilance when it interrupted its feeding to lift its head briefly without chewing. However, we made no distinction between the different possible levels of vigilance.

2) Feeding: The animal stands clipping vegetation with its mouth or walks from the vegetation patch it had just exploited from to the next patch where it continues cropping (Frid 1997).

3) Other behaviors: These activities include lying down, walking, and social interactions such as fighting and courting.

Apprehension may not be measurable using the focal sample technique as the individuals can be harvesting and still be able to detect predators, and they can alter this ability (i.e., they can become more apprehensive). For all point observations, distance from cliff edge, group size, sex and age class, and habitat type (plateau or slope) were noted. Note that we observed and quantified vigilance from ibex on the plateau and also on the steep slope of the cliff face (60° or more). We performed only one focal sample per individual per observation session. As vigilance was estimated as a proportion of time, data were arsine transformed (Sokal and Rohlf 1981).

We performed all data analysis using the Systat software version 10.

RESULTS

To test the effect of distance from cliff edge on GUDs, we used analysis of variance (ANOVA), with tray type (full, bottom, and half tray), location, distance from cliff, and the interactions between tray type and distance from cliff, location and distance from cliff, and location and tray type as the factors and daily mean GUD as the dependent variable.

Tray type, distance from cliff, and the interactions between location and distance from cliff and location and tray type significantly affected the daily mean GUD (mean square [MS] = 15207.802, $F_{2,563} = 37.382$, $P < 0.001$; MS = 5358.954, $F_{2,563} = 13.173$, $P < 0.001$; MS = 89038.454, $F_{1,563} = 218.868$, $P < 0.001$; MS = 2833.688, $F_{2,563} = 6.965$, $P = 0.001$; MS = 1560.582, $F_{2,563} = 3.863$, $P = 0.022$, respectively; Figure 1). Mean GUDs increased with distance from the cliff edge, suggesting that Nubian Ibex treated predation risk as a foraging cost (Figure 1). This experiment also allows us to examine how foraging effort changed with variation in the micropatch structure. As predicted, Nubian Ibex showed lower GUDs in the half trays, showing that they respond to the micropatch structure. They allocated their foraging effort most to those trays where the food items were easier to discover (Figure 1).

To test the effect of distance from cliff and location on mean selectivity, we used ANOVA, with location, distance from cliff, and their interactions as the factors and the daily mean selectivity index as the dependent variable. We used data from full trays and half trays only because of the greater sensitivity they offer; comparisons between bottom trays and full trays provide less sensitive measures because of the tendency of food pellets in full trays to sink to the bottom during exploitation by ibex.

Both distance from cliff edge (MS = 0.074, $F_{2,134} = 4.456$, $P = 0.013$; Figure 2) and location (MS = 0.404, $F_{1,124} = 25.185$, $P = 0.001$; Figure 2) significantly affected selectivity. Furthermore, Tukey HSD posteriori contrasts show that selectivity is lower at the far distance that at the medium distance ($P = 0.01$) but does not differ at near and far distances from the cliff (Figure 2). This shows a change in ibex behavior as distance from cliff edge increases, at least when going from 60 to 90 m away from the cliff edge.

We performed multiple linear regressions to evaluate the effects of distance from cliff edge and group size on Nubian Ibex vigilance level. The data analyses were performed for data from each of the 2 habitat types, for example, plateau or cliff slope. While foraging on the plateau, distance from cliff edge had a significant effect on the vigilance level ($n = 45$, $r^2 = 0.153$, $P = 0.016$, Figure 3). Vigilance level increased as distance from cliff increased. However, while foraging on the slope, distance from cliff edge had no significant effect on Nubian Ibex vigilance level ($n = 65$, $r^2 = 0.01$, $P = 0.627$, Figure 4). This result suggests that the entire slope is perceived a safe area where risk of predation is constant. In addition, while foraging neither on the plateau ($n = 45$, $r^2 = 0.153$,...
1994). Our result supports the notion that 'fear' of predation Nubian Ibex population density and distribution (Kotler et al. from predators, predation risk could be a factor that limits does not only affect foraging behavior of animals but may also selective force (Sih 1987; Lima and Dill 1990). Predation risk found near steep terrain and cliff edges (Kotler et al. 1994 and GUDs as distance from the cliff edge increased. This is con- tistent with the observation that Nubian Ibex are most often timberline, the perceived danger of foraging in patch has been demonstrated for several species such as desert rodents (Brown 1988; Kotler and Brown 1988), mule deer (Altendorf et al. 2001), and fox squirrels (Brown 1992; Brown et al. 1992).

The results of the experiments indicate that Nubian Ibex treated predation risk as a foraging cost. They showed higher GUDs as distance from the cliff edge increased. This is consistent with the observation that Nubian Ibex are most often found near steep terrain and cliff edges (Kotler et al. 1994 and references therein). Predation has been recognized as a strong selective force (Sih 1987; Lima and Dill 1990). Predation risk does not only affect foraging behavior of animals but may also affect the evolution of behaviors not necessarily related to feeding. These may include sociality, vigilance, and group size (Lima and Dill 1990). Even in the absence of direct mortality from predators, predation risk could be a factor that limits Nubian Ibex population density and distribution (Kotler et al. 1994). Our result supports the notion that "fear" of predation (Brown et al. 1999) is a major factor in the feeding ecology of prey species. GUDs reflect foraging costs of all sorts. However, when energetic costs are accounted for and miss opportunity costs are controlled for, the leftover is most likely due to risk of predation (Brown et al. 1994; Nolet et al. 2006).

The results of the experiments support the prediction that Nubian Ibex will increase their vigilance level when predation risk increases. However, this situation is only noted in the plateau habitat, an open flat area. Here it is important to remember that Nubian Ibex are better climbers than runners, and therefore for this species, the slope represents refuge. On the slope, a Nubian Ibex is better suited to escape any potential predator. Consequently, Nubian Ibex keep their vigilance level constant on the slope.

It was predicted that apprehension as measured by the selectivity for the full tray would increase as distance from cliff increased. Distance from cliff had a significant effect on selectivity, suggesting that apprehension is used by Nubian Ibex to manage predation risk. However, Nubian Ibex showed their greatest selectivity value at the middle distance for example 50 m from cliff edge (Figure 2). Therefore, if Nubian Ibex use apprehension, they may do so mostly at intermediate distances. An apprehensive forager can be alert for predators yet still maintain much of its harvest rate. Yet, an apprehensive forager can likely detect predators only at relatively short distances. Otherwise, apprehension may be effective only up to the middle distances from the cliff edge and still allow enough time to escape and reach the refuge. When a forager goes farther, apprehension may not be able to provide early enough detection to allow escape. At longer distances, it may then switch to vigilance. A vigilant forager is better able to use all of its attention and senses (e.g., sight) to scan for predators from a distance and more thoroughly than is possible using only apprehension. We note that this interpretation depends on an extrapolation of vigilance rate beyond the 30 m from cliff edge that we were able to observe.

The results of the present study show a change in foraging behavior between the middle and farthest distances. One possible explanation for this type of response may be that Nubian Ibex are social foragers, and they might also use group vigilance as a tool to manage predation risk. Reduction in the time spent in predator vigilance is a major benefit from living in groups. An individual forager can afford to allocate less time to being vigilant without reducing the group's collective activity to detect predators (for a review, see Lima and Dill 1990; Lima 1995b). Consequently, individuals can devote more time to foraging. However, our results show that Nubian Ibex do not alter vigilance level with group size and do not alter group size with distance from cliff edge. In addition while foraging in groups, it could be expected that subordinate individuals would be sent by the dominant individuals to forage farther from the cliff. This situation could be reflected in higher GUDs farther from the cliff.

In regard to vigilance rate and groups sizes, it has been shown for some ungulates and bird species that the vigilance of other group members is not considered as efficient as an individu- al's own vigilance (Roberts 1996 and references therein). Perhaps, Nubian Ibex do not rely on group vigilance.

Several authors have reported a negative correlation between vigilance level and groups size in ungulates (group size effect) (e.g., Elgar 1989; Hunter and Skinner 1998; Caro 2005). However, our data do not support that the group size affects the way Nubian Ibex deal with predation risk, even though Nubian Ibex do use vigilance in risky situations. Similarly, Laundré et al. (2001) noted that even though elk (Cervus elaphus) and bison (Bison bison) respond to predation risk by increasing their vigilance level when predators were reintroduced in their habitat, there was no correlation it was predicted that apprehension as measured by the selectivity for the full tray would increase as distance from cliff increased. Distance from cliff had a significant effect on selectivity, suggesting that apprehension is used by Nubian Ibex to manage predation risk. However, Nubian Ibex showed their greatest selectivity value at the middle distance for example 50 m from cliff edge (Figure 2). Therefore, if Nubian Ibex use apprehension, they may do so mostly at intermediate distances. An apprehensive forager can be alert for predators yet still maintain much of its harvest rate. Yet, an apprehensive forager can likely detect predators only at relatively short distances. Otherwise, apprehension may be effective only up to the middle distances from the cliff edge and still allow enough time to escape and reach the refuge. When a forager goes farther, apprehension may not be able to provide early enough detection to allow escape. At longer distances, it may then switch to vigilance. A vigilant forager is better able to use all of its attention and senses (e.g., sight) to scan for predators from a distance and more thoroughly than is possible using only apprehension. We note that this interpretation depends on an extrapolation of vigilance rate beyond the 30 m from cliff edge that we were able to observe.

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between group size and vigilance level. Lima (1995b) described similar results in juncos (Junco hyemalis) and in American sparrows (Spizella arborea). He noted that the evidence for the collective detection of these species was weak. Alternatively, it may be that the number of individuals in each group in our study is largely fixed regardless of the distances where the observations took place, and therefore, we did not take into consideration the interference and scrounging factors. Another possible explanation might be that the number of groups considered was not large enough, and we could not fairly test group size hypotheses.

Overall, Nubian Ibex respond to predation risk while feeding in an open area by increasing their vigilance level. However, they do not use the group size to manage predation risk. These results are consistent with a few examples such as Laundré et al. (2001) where the expected decrease in vigilance level with group size is not supported (for a review, see Beauchamp 2003).

It is of interest how Nubian Ibex use 2 behaviors that involve the allocation of attention between foraging tasks and predator detection: apprehension and vigilance. The results show that these foragers use both apprehension heavily at 60 m from the cliff edge but less near the refuge or at 90 m from the cliff edge. There are at least 2 possibilities to explain the Nubian Ibex behavior at the farther distance. Perhaps, using any sort of apprehension or vigilance at 90 m does not provide for early enough detection of predators to allow Nubian Ibex retreat to the cliff, and foragers who dare to venture there stay only long enough to exploit the food patches as fast as they can. Lima et al. (1985) observed similar behavior in gray squirrels (Sciurus carolinensis) exploiting food patches far from the cover. Alternatively, the trend of increasing vigilance with increasing distance from the cliff edge displayed by these Nubian Ibex from 0 to 30 m may continue at greater distances. If so, perhaps Nubian Ibex at 90 m switch from using apprehension to using vigilance. Apprehension and vigilance both are used more away from the cliff than at the cliff edge, but their uses may peak at different distances. As it was difficult to obtain focal observations for Nubian Ibex at greater distances, we could not test if the vigilance level was affected by the hierarchical position of the individuals within the group.

The results of the present study showed that Nubian Ibex use several tools to manage predation risk. Nubian Ibex forage in patches of higher quality to offset the cost of predation: they reallocated their foraging effort toward those patches that were located closer to the escape terrain. The most notable result from this study is that Nubian Ibex use both apprehension and vigilance as behavioral responses to predation risk, along with time allocation.

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