

# Patch use and vigilance behaviour by Nubian ibex: the role of the effectiveness of vigilance

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## ABSTRACT

**Background:** Brown (1999) presented a model for optimal levels of vigilance in foragers exploiting depletable resource patches. This theory includes vigilance along with time allocation, patch use, resource depletion, and energetic costs in a fitness-maximizing model. It predicts a humped-shaped relationship between the optimal level of vigilance and the effectiveness of vigilance.

**Aim:** To test Brown's model with free-ranging Nubian ibex (*Capra nubiana*). Use specific predictions for ibex, including vigilance levels increasing and patch use decreasing with predation risk and with energetic state of the forager.

**Site of experiments:** Negev Desert, Israel.

**Methods:** Manipulate sight lines (lines between food and safety) to reduce the effectiveness of vigilance of Nubian ibex. Evaluate the resulting effects on foraging costs, patch use, and risk management behaviour (vigilance and apprehension). Quantify ibex vigilance by direct observations. Quantify patch use and apprehension by measuring giving-up densities (GUD, the amount of food left in a patch following exploitation) in artificial food patches that differ in complexity. We couple our manipulation of sight lines (effectiveness of vigilance) with placement of feeding trays near and far from a refuge (to manipulate the risk of predation) and with augmentation of food (to manipulate the energetic state of the forager).

**Results:** Brown's model was supported. Nubian ibex were more vigilant and/or more apprehensive, and depleted food patches less thoroughly (left higher GUDs) in patches farther from a cliff (risky), in the presence of sight-line obstructions (low effectiveness of vigilance), and when food was augmented (low marginal value of energy).

*Keywords:* foraging theory, giving-up densities, Nubian ibex, optimal patch use, optimal vigilance, risk management, time allocation, trade-offs of food and safety.

## INTRODUCTION

Feeding animals should forage in a manner that balances the demands for energy intake and the long-term probability of survival through avoiding predators and starvation. To balance these conflicting demands, foraging animals may use various tools. First, they can vary time

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allocation to patches that differ in the levels of risk and feeding rates to determine where, when, and for how long to forage (Abramsky *et al.*, 2002; Wirsing *et al.*, 2007). Second, feeding individuals can use vigilance and apprehension while foraging. Apprehension occurs when an individual redirects some of its attention from foraging to detecting predators (Dall *et al.*, 2001). This may be achieved by directing greater attention towards hearing, olfaction, and/or peripheral vision while continuing to feed. Vigilance can be considered the highest level of apprehension: when an animal stops feeding entirely, lifts its head, and switches all the attention from harvesting food to looking for predators (Lima, 1987).

What determines a forager's optimal level of vigilance? Higher levels of vigilance and/or apprehension provide more safety but result in more mistakes and lower feeding rates. Choose a rate of vigilance too high and the forager loses valuable feeding opportunities needlessly. But choose a rate too low, and a predator will more likely kill the forager. Those individual foragers which are sensitive to the current level of risk and which accordingly adjust their anti-predator responses should have evolutionary advantages (Lima and Dill, 1990). Brown's (1999) model predicts optimal vigilance for foragers exploiting depletable resource patches. It views vigilance as part of a larger foraging strategy in which there are multiple inputs into fitness; foragers have alternative fitness-enhancing activities; and they manage risk using time allocation and vigilance.

According to the model, foragers should use an optimal level of vigilance,  $u^*$  (equation 1):

$$u^* = \sqrt{\frac{mF}{bf_{\max} \left( \frac{\partial F}{\partial e} \right)}} - \frac{k}{b}. \quad (1)$$

Thus vigilance should increase with the encounter rate with predators,  $m$ ; with predator lethality,  $1/k$ ; and with survivor's fitness,  $F$  ( $F$  is the fitness return that a forager in a given energetic state receives should it live until the next reproductive season).  $u^*$  decreases with the forager's quitting harvest rate of resources in a patch,  $f$ , and with the marginal value of energy,  $\partial F/\partial e$ . The latter signifies that an animal that gains little from an additional unit of energy (e.g. a satiated animal) should be more vigilant and less willing to take risks to get extra energy than an individual that has much to gain [e.g. a hungry animal (McNamara and Houston, 1986; Lima, 1988)].

Of special interest is  $b$ , the effectiveness of vigilance in reducing mortality. Brown's model predicts a humped-shaped relationship between  $u^*$  and  $b$ . When vigilance is highly effective in reducing risk, individuals require little vigilance; when vigilance is ineffective, individuals want little. The highest levels of vigilance should thus occur when vigilance is of intermediate effectiveness. Thus, reducing the effectiveness of vigilance when it is highly effective should lead foragers to increase their rate of vigilance (e.g. diurnal foragers in open environments). However, reducing the effectiveness of vigilance when it is of intermediate or low effectiveness should lead foragers to reduce their rate of vigilance yet further.

Embar *et al.* (2011) used Brown's theory to make predictions about the optimal level of vigilance in Allenby's gerbil, *Gerbillus andersoni allenbyi*. Allenby's gerbils forage at night, collecting seeds and suffering risk of predation from fast, stealthy predators, which implies their vigilance is only moderately effective in reducing mortality. So reducing the effectiveness of vigilance should lead the gerbils to perform vigilance less. Embar *et al.* reduced the effectiveness of vigilance by using obstructions to block sight lines to feeding

trays. In response, vigilance levels dropped. These results argue for a section of positive slope in the graph of optimal vigilance level versus effectiveness of vigilance, at least when vigilance is of intermediate effectiveness. While this is consistent with Brown's model, much stronger support would arise were there also evidence for a section of negative slope where vigilance is highly effective.

Here we seek to provide such evidence by examining patch use, vigilance, and apprehension in free-ranging Nubian ibex (*Capra nubiana*). Vigilance in Nubian ibex should be highly effective. They are diurnal, live in extremely open habitats close to cliffs that provide escape refuge, and have excellent vision. They keep close to cliffs at all times, and so can quickly reach refuge as soon as a predator is spotted.

We reduced the effectiveness of vigilance for ibex by partially blocking their sight lines. Increasing rates of vigilance in response to this sight line manipulation would provide evidence for the negative slope of the optimal vigilance versus effectiveness of vigilance relationship. It would also suggest how vigilance has evolved by natural selection.

### OPTIMAL FORAGING THEORY

Foraging theory provides a framework that allows for a better understanding of the evolution of animal behavior. Brown's (1988) optimal patch use model predicts that in food patches where foragers experience diminishing returns (a decline in the harvest rate as the forager depletes the sources of the patch), an optimal forager should remain in the patch until costs and benefits of foraging are equal. This point occurs when the harvest rate,  $H$ , in the patch equals the sum of metabolic,  $C$ , predation,  $P$ , and missed opportunity,  $MOC$ , costs of foraging [ $H = C + P + MOC$  (Brown, 1988)]. The cost of predation,  $P$ , is a complex cost that involves the risk of predation,  $\mu$ . When  $\mu$  varies with vigilance as in equation (1), predation is more complex (Brown, 1999) and more involved. The equation for optimal patch use then becomes:

$$f_i \left( 1 + \frac{k_i}{b_i} \right) = c_1 - 2 \sqrt{\frac{m_i f_i F}{b_i \frac{\partial F}{\partial e}}} - c_0, \quad (2)$$

where  $f$  is the quitting harvest rate in the absence of vigilance,  $c_1$  is the energetic cost of foraging,  $c_0$  is the resting metabolic rate, and all other parameters are as in equation (1).

### MATERIALS AND METHODS

#### General methods and predictions

To measure patch use and vigilance in ibex, we made feeding trays to create artificial resource patches and used them to measure ibex giving-up densities [GUD, the amount of food left in a patch after exploitation (Brown, 1988, 1992)]. To measure vigilance, we performed focal animal observations and recorded time budgets. We reduced the effectiveness of vigilance by partially blocking sight lines surrounding feeding trays. We also manipulated the marginal value of energy (energetic state) for the ibex by providing, on alternating days, food augmentations. We created foraging opportunities under both low and high risk of

predation by placing feeding stations close to and far from the refuge (cliff edge). We then evaluated ibex foraging and anti-predator responses to these manipulations. From equations (1) and (2), we predicted that ibex would have higher costs of predation and therefore higher GUDs when foraging farther from the cliff or when sight lines were blocked to reduce the effectiveness of vigilance. Furthermore, because the predation cost of foraging increases as an animal's marginal value of energy decreases [i.e. when the animal is in a high-energy state (Brown, 1988)], we also predicted that ibex would have higher GUDs when we added extra food. We also predicted that ibex would have higher rates of vigilance farther from the cliff due to the higher risk experienced. Since vigilance in ibex should be highly effective, we predicted that blocking sight lines would therefore lead ibex to increase vigilance. Finally, we predicted that ibex would increase their vigilance in response to the food augmentation and the decreased marginal value of energy it causes. Apprehension should change in much the same way for much the same reasons, with the exception that we did not expect the sight line manipulation to affect apprehension to the extent that it does vigilance, if at all, because apprehension in ibex may partially or wholly involve the sensory modalities of hearing and olfaction rather than (or in addition to) peripheral vision (Hochman and Kotler, 2007).

### Study area

We conducted the study in the vicinity of Midreshet Ben-Gurion, in the Central Negev Desert Highlands of Israel (30°52'N, 34°46'E). We carried out our experiments within the Ein Avdat National Park and Zin Nature Reserve. The elevation in the region varies from 320 to 580 m above sea level. A large drainage (Nahal Zin) and its tributaries dominate the area (Gross *et al.*, 1995a). The region is a warm arid zone (UNESCO, 1977) with a Mediterranean climate of hot, dry summers and cool, wet winters. Rainfall averages 100 mm per year and is extremely variable within and between years. Major plant communities on the slopes and plateaus are dominated by shrubs 30–100 cm tall, especially white bean caper (*Zigophyllum dumosum*), white wormwood (*Artemisia herba-alba*), and articulated anabasis (*Anabasis articulata*) (Kotler *et al.*, 1994; Gross *et al.*, 1995a).

### Study organism

Nubian ibex are wild, social goats restricted to desert habitats with steep terrain and cliffs (Gross *et al.*, 1995a). They forage diurnally and are active mostly during the morning and afternoon hours. They rest and ruminate during midday and at night (Levy and Bernadsky, 1991). Nubian ibex are sexually dimorphic; adult males average 74.7 kg and females 32.7 kg (Gross *et al.*, 1995b). Since females take care of the young and are more vulnerable to predators, they are usually confined to safer habitats with higher food quality than are males (Gross *et al.*, 1995b; Kohlmann *et al.*, 1996). The possible predators of Nubian ibex include leopards (*Panthera pardus*), wolves (*Canis lupus*), striped hyenas (*Hyaena hyaena*), and humans. Newborn ibex can also fall prey to golden eagles (*Aquila chrysaetus*) and eagle owls (*Bubo bubo*) (Levy and Bernadsky, 1991). The perceived risk of predation of Nubian ibex increases with distance to the cliffs (Kotler *et al.*, 1994; Gross *et al.*, 1995a).

### GUD measurements

To measure Nubian ibex GUDs, we used artificial food patches (Kotler *et al.*, 1994) made from wooden boxes (46 × 30 × 12 cm) containing an initial amount of 100 g of food (compressed alfalfa pellets with a mean mass of 2 g per pellet) mixed into 1400 g of non-edible substrate (1 cm diameter tubes cut into 3 cm long pieces). As ibex removed the alfalfa pellets, the rising proportion of non-edible tubes caused diminishing returns for the ibex. To further ensure diminishing returns, we covered the feeding trays with a 7 cm wire mesh. The mesh prevented the ibex from pushing the substrate out of the trays and obliged them to insert their muzzles repeatedly between the links of the mesh to reach the food, much as they do in nature when trying to reach leaves inside shrubs (Kotler *et al.*, 1994). In addition to the 'GUD trays', we also used 'augmentation trays' of similar size. They differed from the GUD trays in that they were provisioned with 1000 g of alfalfa pellets, and had neither the non-edible substrate nor the wire mesh cover. Note that we measured GUDs only from the GUD trays.

We placed the feeding trays at four stations in the ibex's natural environment: two close to the cliff edge and two at 75 m from the cliff edge. An observer could see all trays simultaneously. At each station, we placed one augmentation tray and two GUD trays: a full tray and a half tray (see below). This allowed us to measure GUDs and apprehension. We added the alfalfa pellets early in the morning (05.00–06.00 h) and collected the food that remained just before dusk (18.00–19.00 h). We collected GUD data from 27 September to 27 October 2007. To ensure that the ibex were familiarized with the experimental layout, we placed the feeding trays provisioned with food at the stations every day for more than one month prior to the first measurements.

### Apprehension measurements

One way to measure the apprehensiveness of a forager is by using the GUD technique and providing two food patches that differ in complexity (Kotler *et al.*, 2002). Apprehensive animals will allocate less attention to foraging and more to detecting predators. Thus more apprehensive animals should increase their selectivity for the less complex patch where it is more difficult to make foraging-related mistakes, even when attention is redirected to other tasks.

To measure apprehension, we used the selectivity of ibex for feeding trays that differed in the complexity of finding the food. We created a less complex food patch by evenly mixing the alfalfa pellets with the non-edible substrate and spreading it evenly in the GUD tray (hereafter called the 'full tray'). We created a more complex food patch by mixing the food with only half of the non-edible substrate and pouring it into the centre of the tray, and then filling the remaining half of the tray with the remaining food-free non-edible substrate (hereafter called the 'half tray'). The half tray was more demanding than the full tray in that it had two vague patch boundaries where the resource density changed. Thus the half tray presented more opportunities for foraging-related mistakes, which reduce harvest (Schmidt and Brown, 1996). Therefore, changes in the selectivity for the full tray relative to the half tray should allow us to quantify changes in Nubian ibex apprehension (Kotler *et al.*, 2002).

We estimated the selectivity for the full trays relative to the half trays by using Manly's selectivity index,  $S$  (Chesson, 1983; Kotler *et al.*, 2002):

$$S = \frac{\ln\left(\frac{\text{remaining food}}{\text{initial food}} \text{ Full tray}\right)}{\ln\left(\frac{\text{remaining food}}{\text{initial food}} \text{ Full tray}\right) + \ln\left(\frac{\text{remaining food}}{\text{initial food}} \text{ Half tray}\right)}. \quad (3)$$

This index was specifically developed to deal with selectivity for different types of resource patches when the forager depletes these patches during foraging bouts. In our case, an increase in apprehension level should be detected as an increase in selectivity of the full tray. This selectivity index can vary from 0 to 1, where  $S = 0$  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 consumed equally from the two trays. We expected selectivity for the full tray to be less than 0.5 (due to food being more concentrated in the half tray), but to increase as apprehension increased (Kotler *et al.*, 2002).

### Predation risk manipulation

We manipulated predation risk by placing feeding stations close to and far from the cliff edge (Nubian ibex's refuge). The experimental set-up consisted of four stations. We placed two low-risk stations at 0 m from the cliff separated by 100 m from each other, and two high-risk stations at 75 m from the cliff, again separated by 100 m.

### Marginal value of energy manipulation

We altered the ibex marginal value of energy by manipulating their energetic state. We did this by offering animals supplemental food that we placed in augmentation trays at each station. We worked in three-day sequences: on Day 1 we provisioned with food in GUD trays; on Day 2 we provisioned GUD trays and also filled augmentation trays; on Day 3 we provided only food in the GUD trays, but we did not collect data. This allowed the energetic state of the ibex to return to normal levels after days in which augmented food was provided. As a result, the ibex should have started every day of data collection with similar marginal values of energy. Nubian ibex fed from the augmentation trays first, and so during days when augmented food was provided should have had lower marginal values of energy than on days when food was offered only in the GUD trays.

### Effectiveness of vigilance manipulation

We manipulated the effectiveness of vigilance by interfering with sight lines surrounding feeding tray stations. We placed three visual obstructions comprised of 90% black mesh shade cloth suspended vertically in a U-shaped pattern around each feeding station. In addition to the unobstructed side, we also left unobstructed space in each corner between the junctions of two obstructions that allowed the ibex to enter and to leave the feeding stations freely from different directions. Each obstruction was 4.5 m long and 0.85 m high and was placed with its lower edge suspended 25 cm above the ground. This allowed the ibex to pass underneath it, and could help to minimize any feeling of confinement that the obstructions might cause to the ibex.

We were able to manipulate sight lines by either furling or unfurling the black cloths. When furlled, the obstructions presented 10 cm wide strips of shade cloth. This provided

some confinement similar to that from the unfurled obstructions and helped to ensure that the two different experimental levels (furled and unfurled) mostly differed in how they altered sight lines. When unfurled, the obstructions blocked sight lines at least in part.

On any given day, we furled obstructions at one station at a given distance and unfurled the other one at the same distance. We exchanged the state of the visual obstructions after every two days of collecting data: furled to unfurled, and vice versa. In this way, the experimental design allowed us to alter the combinations of effectiveness of vigilance (furled or unfurled obstructions) and food state (augmentation or no augmentation) at each station (close and far from the cliff edge).

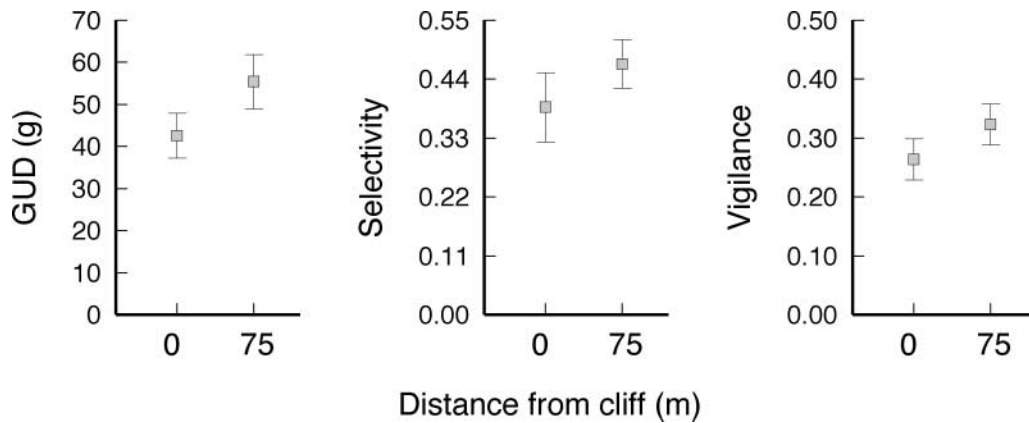
### Behavioural observations

We observed individual ibex at the feeding stations from inside a blind that was placed equidistant from the four stations. We categorized the behaviours to three groups – vigilance, feeding, and other activities – and measured the proportion of time ibex spent involved in each one of them. An ibex was considered to be ‘vigilant’ when it had its head raised, its ears erect, and appeared to be looking attentively at the surroundings, or when it interrupted feeding to lift its head briefly without chewing. We classified an ibex as ‘feeding’ when it had its head down while extracting or searching for food from the feeding trays, or had its head up while chewing. ‘Other activities’ included walking, scratching, grooming, observing other ibex, and playing with the shade cloth.

The study area was visited by herds of females with their young, but we restricted our measurements to a single individual at a time, the focal animal. The size of the visiting groups varied from 2 to 14 individuals. Ibex were unmarked, but the small group sizes helped us to avoid collecting multiple samples on the same animal on any given day and at any given station. We restricted our observations to actively foraging ibex within the area of the feeding station delimited by the sight line obstructions. The choice of the focal animal for observation was arbitrary, but we attempted to distribute samplings evenly among the four stations. The observations were done approximately 2½ h after sunrise and 2½ h before sunset. During these times, Nubian ibex are most active and most easily observed (Gross *et al.*, 1995b). The focal samplings lasted from 3 to 5 min. We collected the behavioural data from 27 September to 19 October 2007. We performed a total of 160 observations, which we averaged for each station each day to yield a sample size of 44.

### Statistical analyses

To test the effects of distance from the cliff edge, food augmentation, sight obstructions, and their interactions on the GUD and selectivity level of Nubian ibex, we used analyses of variance (ANOVA) with daily-mean-GUDs and daily-mean-selectivity-index as the dependent variable respectively. To evaluate the effects of distance from the cliff edge, food augmentation, sight obstructions, and their interactions on Nubian ibex vigilance level, we used multivariate analysis of variance (MANOVA), with daily-mean proportion-of-time-spent-vigilant and proportion-of-time-spent-feeding forming the vector of dependent variables.



**Fig. 1.** Giving-up density (GUD; left), level of selectivity according to Manly's index (centre), and fraction of time devoted to vigilance (right) for Nubian ibex when foraging at 0 and 75 m from the cliff (mean  $\pm$  95% confidence intervals).

## RESULTS

### Distance from the cliff

Nubian ibex altered their foraging behaviour markedly when feeding at different distances from the cliff. When foraging at stations at 75 m from the cliff edge, Nubian ibex displayed higher GUDs ( $F_{1,159} = 12.461$ ,  $P < 0.000$ ; Fig. 1) and were more selective towards the full tray (i.e. more apprehensive;  $F_{1,77} = 7.183$ ,  $P < 0.000$ ; Fig. 1) than when foraging in the stations at the cliff edge. But they did not adjust their vigilance level depending on whether they were foraging far from or close to the cliff ( $F_{1,36} = 0.902$ ,  $P = 0.348$ ; Fig. 1).

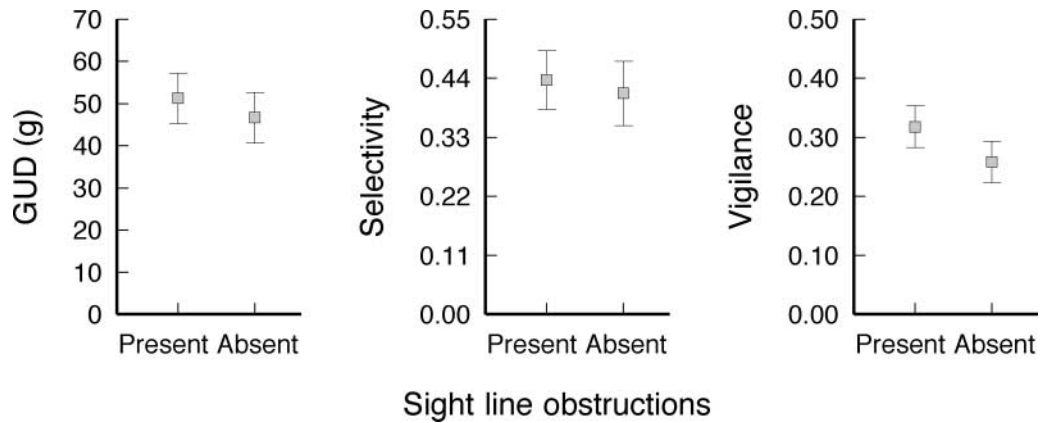
### Sight line obstructions

Ibex responded significantly to the visual obstructions. They increased their vigilance level ( $F_{1,36} = 4.659$ ,  $P = 0.037$ ; Fig. 2) when foraging at stations with unfurled sight line obstructions, i.e. when the obstructions obscured sight lines. Ibex also left feeding trays at higher GUDs in stations with obstructions ( $F_{1,159} = 2.882$ ,  $P_{\text{one-tailed}} = 0.047$ ; Fig. 2). Visual obstructions had no effect on apprehension, as indicated by selectivity ( $F_{1,77} = 1.150$ ,  $P = 0.287$ ; Fig. 2).

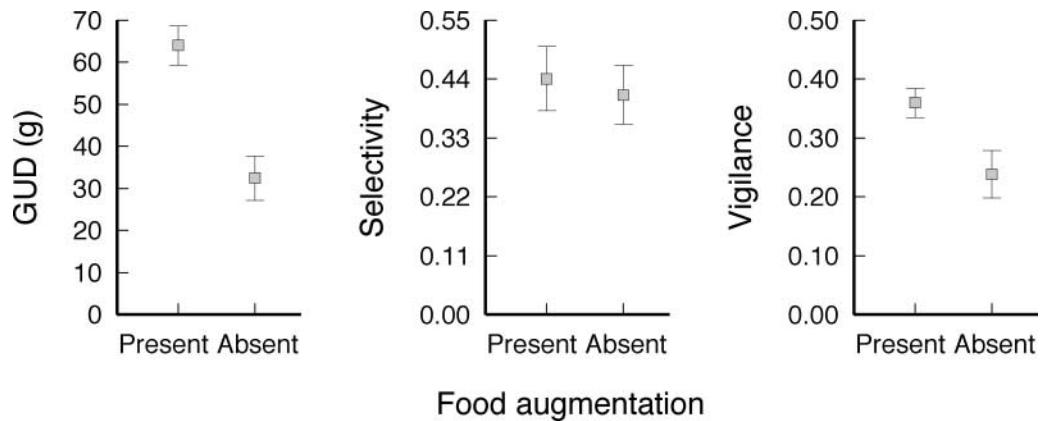
### Food treatment

Increasing the food availability strongly affected ibex foraging behaviour. Mean GUDs were higher on food augmentation days ( $F_{1,159} = 64.536$ ,  $P < 0.000$ ; Fig. 3), as was ibex vigilance ( $F_{1,36} = 11.186$ ,  $P = 0.002$ ; Fig. 3). The interactions of food augmentation with both sight line obstructions and distance from the cliff were not significant (ANOVA, food  $\times$  distance:  $F_{1,159} = 2.460$ ,  $P = 0.1187$ ; food  $\times$  sight:  $F_{1,159} = 0.003$ ,  $P = 0.959$ ; MANOVA, food  $\times$  distance:  $F_{1,36} = 0.008$ ,  $P = 0.927$ ; food  $\times$  sight:  $F_{1,36} = 0.664$ ,  $P = 0.420$ ), nor were the three-way interactions (ANOVA, food  $\times$  distance  $\times$  sight:  $F_{1,159} = 0.010$ ,  $P = 0.919$ ; MANOVA, food  $\times$  distance  $\times$  sight:  $F_{1,36} = 2.131$ ,  $P = 0.153$ ). The effect of food augmentation on apprehension was not significant ( $F_{1,77} = 2.345$ ,  $P = 0.287$ ; Fig. 3).





**Fig. 2.** Giving-up density (GUD; left), level of selectivity according to Manly's index (centre), and fraction of time devoted to vigilance (right) for Nubian ibex in the presence and absence of sight line obstructions (mean  $\pm$  95% confidence intervals).



**Fig. 3.** Giving-up density (GUD; left), level of selectivity according to Manly's index (centre), and fraction of time devoted to vigilance (right) for Nubian ibex when foraging in the presence and absence of food augmentations (mean  $\pm$  95% confidence intervals).

## DISCUSSION

We undertook this study primarily to test Brown's (1999) optimal vigilance model, but to do so in an environment and with an organism for which vigilance is highly effective in reducing mortality risk. The theory tells us that for such conditions and organisms, the relationship between optimal vigilance and effectiveness of vigilance should have a negative slope and result in an increase in vigilance when its effectiveness is reduced. Nubian ibex at Ein Avdat National Park in the Negev Desert of Israel should provide such a context. Indeed, in response to experimental reductions in the value of  $b$  using shade cloth, ibex did increase their vigilance. This result lends support to Brown's theory. At the same time, previous work on gerbils that found only moderately effective vigilance provides evidence for a section of the curve with positive slope (Embar *et al.*, 2011). Together, they imply that the

relationship between  $u^*$  and  $b$  is humped-shaped. This is a unique prediction of Brown's theory. Appropriately predicting how organisms as different as gerbils and ibex should respond to sight line manipulations increases our confidence that Brown's theory captures something fundamental about optimal vigilance behaviour and the factors affecting its evolution. Studies of vigilance that focus on vigilance behaviour to the exclusion of feeding and patch use may be missing vital aspects of the story.

In addition to how ibex respond to sight lines, we also examined the effects of distance to the cliff edge and to resource augmentations on their patch use behaviour. Their responses to these factors were similar to those reported earlier in similar work with ibex (Kotler *et al.*, 1994; Hochman and Kotler, 2006) and will not be considered further here.

The behaviour of other species seems to be consistent with a humped-shaped relationship between  $u^*$  and  $b$ . For example, house sparrows (*Passer domesticus*) decreased their scanning rate when farther away from protective cover (Lima, 1987). Lima suggested that this behaviour could be a consequence of a low effectiveness of vigilance at preventing predation (because the greater the distance to protective cover, the lower the probability to escape). If the effectiveness of vigilance of the sparrows drops to intermediate/low values in patches far from safety, then the presence of visual obstructions should eventually result in even lower scanning rates. Indeed, when foraging in the patch far from the protective cover and in the presence of visual obstructions, the sparrows further lowered the use of their vigilance.

In addition to the higher levels of vigilance, and as argued by equations (1) and (2), we also expected ibex to have a higher cost of predation and therefore higher GUDs when sight lines were blocked to reduce the effectiveness of vigilance. Our results support this prediction. Whittingham *et al.* (2004) reported similar results to ours in demonstrating that chaffinches (*Fringilla coelebs*) responded to visual obstructions by increasing their vigilance, and by lowering their foraging efficiency. Ebensperger and Hurtado (2005) studied another species in which the foraging costs increase with visual obstructions, the degus (*Octodon degus*). The ability of degus to detect predators is reduced in high vegetation. As a result, when they forage near tall vegetation, degus allocated more time to bipedal vigilance in spite of the fact that bipedal vigilance incurs a higher foraging cost (quadrupedal vigilance in degus is compatible with foraging while bipedal vigilance is not).

Nubian ibex also use apprehension to manage predation risk. As predicted, they increased their selectivity towards the full trays when foraging farther from the cliff edge, which implies higher apprehensiveness. When near the cliff, the ibex were less apprehensive, allocating their foraging effort more towards the trays in which the food was more concentrated (the half trays). As distance from the cliff increased, ibex became more selective towards the trays where less attention was needed to find the food (the full trays). Hochman and Kotler (2006) also showed that ibex are more apprehensive when foraging far from the cliff. Similarly, Molvar and Bowyer (1994) observed that the foraging selectivity of Alaskan moose declined when the distance to the refuge increased, which may be interpreted as an increase in apprehension.

In contrast to their effects on vigilance, the sight line obstructions did not affect the apprehension levels of ibex, despite the otherwise similar aspects of vigilance and apprehension. Why the difference? We suggest it is because vigilance and apprehension rely on different senses. We previously suggested that apprehension in ibex is mediated mostly through the sensory modes of hearing and olfaction (Hochman and Kotler, 2007), whereas vigilance relies mostly on vision. Since we used mesh shade cloth as obstructions, our manipulation

mainly affected vision and should have made vigilance less effective. Indeed, ibex altered their vigilance in response to the sight lines manipulation. At the same time, the shade cloth should have had little effect on hearing and olfaction, and therefore little effect on apprehension. Thus our manipulation should have altered the effectiveness of vigilance in reducing mortality risk, but not the effectiveness of apprehension in doing the same. Thus sight line manipulations cause ibex to alter vigilance, but not apprehension. Still, the obstructions may have had an indirect effect on the apprehension level of the ibex by increasing the perceived risk of predation (because apprehension is expected to increase with predation risk). However, ibex appear to compensate for the sight line obstructions by reducing time allocation and using greater vigilance instead.

To summarize, our results support Brown's (1999) model that the effectiveness of vigilance in reducing risks helps determine the amount of vigilance displayed, and that variations in the effectiveness of vigilance can also impact an animal's foraging behaviour. When the effectiveness of vigilance is reduced by visual obstructions, Nubian ibex use greater vigilance, and display higher GUDs in resource patches. We also showed that food abundance has a strong effect on foraging decisions; the ibex greatly reduce their foraging efforts, employ higher levels of vigilance, and therefore have higher GUDs when the availability of food is high. The present study contributes not only to the knowledge of Nubian ibex ecology by determining how different environmental variables affect their patch use and anti-predator behaviour, but also provides a better understanding of how animals use time allocation, vigilance, and apprehension in relation to environmental factors that affect risk and the effectiveness of vigilance. Together with previous studies of gerbils, our ibex study provides support for a humped-shaped relationship between optimal vigilance and the effectiveness of vigilance in reducing mortality risk. The ibex study and the gerbil study together provide strong support for Brown's theory and argue for a more comprehensive approach to studying vigilance and its evolution that includes feeding, patch use, and apprehension.

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