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Original article

Foraging patterns of habitat use reveal landscape of fear of Nubian ibex *Capra nubiana*

Cecilia Iribarren & Burt P. Kotler

Different environmental features may serve as cues of the risk of predation. Therefore, when foraging in heterogeneous landscapes, the costs of predation for optimal foragers should vary along with the environmental features. In our study, we describe how foraging costs of predation vary spatially for Nubian ibex *Capra nubiana* with respect to characteristics of their natural environment, i.e. we quantified their 'landscape of fear'. To do so, we established a five by five array of feeding trays within the natural environment of free-ranging Nubian ibex and measured the variation of giving-up densities (GUD, i.e. the amount of food remaining in a resource patch following exploitation) in relation to the landscape variables. The ibex' perceptions of risk of predation increased with distance from cliff and slope edges, and decreased with vegetation cover. Although several environmental variables are probably involved in the determination of an animal's foraging behaviour, with our study we revealed the most prominent features influencing the landscape of fear of Nubian ibex. Since Nubian ibex are endangered, this information is relevant for planning their conservation and management.

Key words: Capra nubiana, environmental features, foraging behaviour, giving-up density, landscape of fear, Nubian ibex, patch use, predation risk

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When making foraging decisions, animals evaluate the quality and quantity of different food patches in the landscape, as well as the likelihood of being killed by a predator. As the perceived risk of predation increases, feeding animals resort to use anti-predator behaviours that confer safety at the expense of a reduction in the foraging efficiency and intake (Sih 1980, Fortin et al. 2005, Hernández & Laundré 2005). Such anti-predator responses usually involve reducing the time of foraging activity, shifting activity from risky to safe patches, and/or using higher levels of vigilance (Lima & Dill 1990, Kotler et al. 1994, Brown 1999). If the level of danger varies among patches throughout the landscape, the food resources left in each resource patch should reflect the foragers' perceptions of risk. The patches with higher food resources should be the ones that are perceived to confer higher risk of predation. In this way, one can quantify the animals' 'landscape of fear', which describes how the animals' foraging cost of predation varies spatially with respect to landscape features (Laundré et al. 2001, 2010). Such information can be very useful in understanding the distribution of species in the face of predators, as well as helpful for providing more accurate predictions concerning the effect of anthropogenic development and other changes in the environment. Hence, the identification of those environmental variables that are more likely to influence the behaviour of the target species may be valuable for meeting conservation goals.

Several studies have shown that ungulate habitat use has a strong association with abiotic factors that might influence the perceived risk of predation. For instance, when foraging, many animals reduce their use of habitat patches as the distance from a refuge increases (Berner et al. 1992, Molvar & Bowyer 1994, Kotler et al. 1999, Gates et al. 2005). Other species, though, prioritise visibility when selecting foraging habitats (e.g. mountain sheep *Ovis canadensis*; Risenhoover & Bailey 1985) because good visibility means that an animal has higher probability of detecting an approaching predator, and thus, more time to escape. Still, others prefer to forage on slopes with lower visibility than on plateaus since the safety of the slopes offsets the reduced visibility (e.g. soay sheep *Ovis aries*; Hopewell et al. 2005). Vegetation can be another important feature influencing habitat use (Fortin et al. 2005), and its effect may be determined by its obstructive or concealing and protective functions, depending on the anti-predator strategies of the species (Pays et al. 2009, Beauchamp 2010). The distance to a human-induced disturbance is also likely to affect habitat selection and foraging behaviour of certain wildlife species, with the magnitude of its effect varying greatly among species (Berger et al. 1983, Frid & Dill 2002).

Nubian ibex *Capra nubiana* is an endangered species protected by law in Israel (IUCN Red List, November 2005). These wild social goats forage during daylight hours, are more active during mornings and afternoons, and rest and ruminate during midday and at night (Levy & Bernadsky 1991). Differences in the vulnerability to predation risk and in forage requirements lead to sexual segregation in this species. Since females take care of the young and are more vulnerable than males, they are usually confined to safer and richer habitats (Gross et al. 1995a, Kohlmann et al. 1996). Potential predators of this species are leopards *Panthera pardus*, wolves *Canis lupus*, striped hyenas *Hyaena hyaen*a and human beings *Homo sapiens*. The neonates can fall prey to golden eagles *Aquila chrysaetos* and eagle owls *Bubo bubo* (Levy & Bernadsky 1991). Nubian ibex are exceptional climbers so they are restricted to desert habitats with steep slopes and cliffs that provide escape terrain (Kotler et al. 1994, Gross et al. 1995b). As they venture farther from the cliff edges, their use of anti-predator behaviour increases (Kotler et al. 1994, Hochman & Kotler 2007).

The goal of our study was to quantify the Nubian ibex' landscape of fear. That is, we want to better understand how the ibex perceive features of their environment and how these features affect their use of the landscape with respect to the risk of predation. To this end, we used the giving-up density (GUD) technique to map the landscape (Brown 1988, Kotler et al. 1994, van der Merwe & Brown 2008, Druce et al. 2009). By measuring the variation in GUDs (i.e. the amount of food left behind after foraging exploitation) among patches, we drew contours of equal foraging costs of predation in the physical space occupied by the ibex.

Material and methods

Measuring patch use under risk of predation

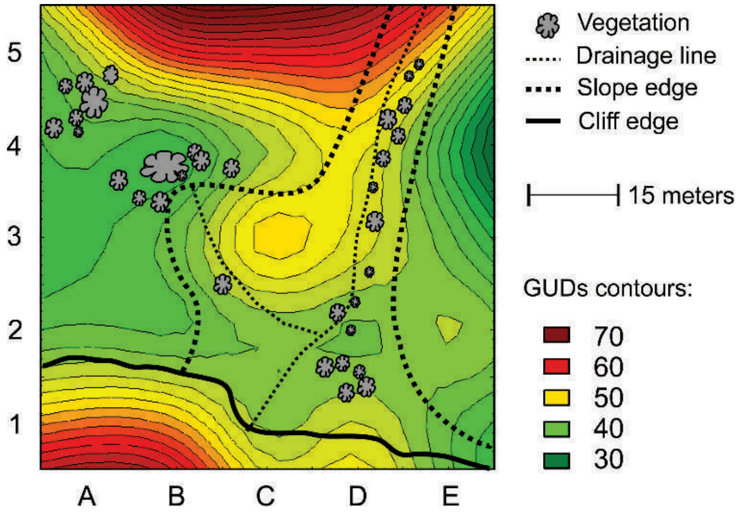
Optimal foragers feeding under risk of predation should leave depletable food patches when the marginal benefits of exploitation no longer exceed the marginal cost of foraging. This occurs when H = C + P + MOC, where H is the harvest rate of the forager while exploiting the patch, C is the metabolic cost of foraging, P is the predation cost arising from the mortality risk and MOC is the missed opportunity costs of foraging. The quitting harvest rate can be estimated empirically by measuring the GUD (Brown 1988). If the different resource patches in the same habitat or microhabitat do not differ in the energetic costs of foraging nor in the missed opportunity costs (e.g. when the same forager has access to similar food patches across the habitats of its home range), the differences in the quitting harvest rates (the GUDs) should represent differences in patch specific risks of predation. However, if all the patches share the same predation risk, the quitting harvest rates should be the same.

Landscape of the GUDs

Our study area was located near the entrance to Midreshet Ben-Gurion, in the Negev Desert of Israel (30°52'N, 34°46'E), within Ein Avdat National Park and Zin Nature Reserve. We selected this location due to its characteristic wide range of environmental features. The elevations in the region vary from 320 to 580 m a.s.l. A large drainage (Nahal Zin) and its tributaries dominate the area, including dry riverbeds, steep walled canyons and slopes, loess plains and plateaus, and limestone hills (Gross et al. 1995b). The region is in the warm arid zone (UNESCO 1977) with Mediterranean climate of hot, dry summers and cool, wet winters. Rainfall averages 100 mm/year but is extremely variable within and between years. 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 anabasis *Anabasis articulata* (Kotler et al. 1994, Gross et al. 1995b).

For the purpose of determining how various

Figure 1. Nubian ibex' landscape of fear. The contour lines represent mean GUDs (i.e. grams of food left on the trays) at each food patch. Higher GUDs reflect higher perceived risk of predation. The artificial food patches were located at the intersections of the x and y axes, i.e. A1, B1, C1 etc.



habitat variables influence the ibex' foraging costs of predation, we established a five by five array of feeding trays, with each tray located 15 m from each other. This constituted the experimental landscape. Because one of the trays (A1; Fig. 1) repeatedly fell down the cliff, we removed this station from the data analysis. We measured the GUDs of free ranging Nubian ibex in each artificial feeding patch during six consecutive days during fall (from 4 November to 10 November 2007). The GUD technique consists of offering the target animals standardised artificial feeding patches in which they experience diminishing returns. To create the artificial food patches, we used wooden feeding trays (46 × 30 × 12 cm). Each tray was provisioned with an initial amount of 100 g food (compressed alfalfa pellets with a mean mass of 2 g/pellet) which we evenly mixed with 1,400 g non-edible substrate (1-cm diameter black plastic irrigation tubes cut into 3-cm long pieces). Mixing the food into a non-edible substrate creates a situation where an ibex can easily find and extract the alfalfa pellets near the surface of the trays. However, as the ibex spend more time harvesting food from a patch, they deplete the food near the surface and have to expend greater effort to extract the remaining pellets buried more deeply in the trays. This creates a decelerating gain of energy with time spent foraging from the tray, i.e. diminishing returns. To further ensure diminishing returns, we covered the feeding trays with a 7-cm wire mesh. The mesh prevents the ibex from pushing the substrate out of the trays and assures that the ibex repeatedly insert their muzzle in between the links of the mesh to reach the food, much as they would do in nature when trying to reach leaves inside the shrubs (Kotler et al. 1994). The food was left in the trays for 12 hours (from approximately 5-6 a.m. to 6 p.m.) in the field for Nubian ibex to discover and feed from it. To quantify patch use behaviour of Nubian ibex, we measured their GUD. We did so by weighing the remaining food pellets in a tray at the end of the day. After refilling the trays in the morning, we smoothed the substrate around each tray to detect and identify animal tracks of foragers visiting and exploiting the tray, and thus to ensure that the GUD only reflected foraging of Nubian ibex. Only ibex spoor were found in the soil around the feeding areas. We set up all food patches and provisioned them with food several days before the experiment in order to alert and familiarise the ibex with all the artificial feeding patches prior to the start of data collection. Our study area was visited by small herds (around 12 individuals) of females with their young. Ibex fed from all the feeding trays during each day of the experiment.

Features of the landscape

We collected detailed environmental information from the location of each artificial food patch so that we could characterise the different combinations of environmental variables associated with each location. These measures included distances to the main cliff and to the nearest cliff or slope. The difference between these two is that the main cliff is characterised by a steep slope, and this is the one to which Nubian ibex tend to move to when highly disturbed. The nearest slope could be either the main cliff or any other abrupt change in the elevation of the topography such as the slope leading into a gully. We measured the distance to the nearest human disturbance with aid of a metre tape, i.e. either the main entrance road of Midreshet Ben-Gurion or the fence of a small military camp located alongside our study area and adjacent to the main road. These distances varied from 3 m (the shortest distance to the military fence) to 63 m (the largest distance registered to the main road). We determined the elevation at which each feeding patch was located by using a GPS. We also measured the distance from the feeding trays to the lowest points along the drainage line. Vegetation cover was measured as the percentage of cover found within a 5 × 5 m square surrounding each feeding tray. The vegetation in the area typically consisted of bushes < 60 cm in height, with the exception of two trees located in two different patches. We estimated the percentage of ground covered by sand and pebbles, medium rocks ($10 \text{ cm} < \text{size} < 50 \text{ cm}$), or big rocks ($\text{size} > 50 \text{ cm}$) in the 5×5 m square. We also measured the steepness of the terrain, and the visibility at each patch. This last variable could vary from 0° when all sight lines were obstructed to 360° when sight lines were open in all directions. The measurements were done by using a compass at 1-m height, the average height of Nubian ibex females, and we considered any object located within 10 m of the tray that blocked the view an obstruction. Since the bushes in the area were all < 1 m tall, they were not considered to be obstructions. The main sightline obstructions were two trees located outside the gully and the slopes of the gully (the latter obstructed sight lines from feeding patches located near the bottom of the gully). We could then correlate features of the landscape to the patch use (GUDs) of the ibex underlying the landscape of fear.

To identify the habitat features influencing the costs of predation of Nubian ibex, the environmental variables were regressed on the GUDs by using a linear multiple regression. We also used polynomial regression to identify non-linear patterns. With the purpose of avoiding pseudoreplication, we performed the analyses using the average value of the six daily GUDs measurements, thus reducing the sample size to 24, since one of the 25 initial trays was left out of the analysis. The level of statistical significance was set at 0.05 and all P-values were two-tailed. To optimise the model performance and reduce potential effects due to multicollinearity, we used a collinearity diagnostic. Tolerance is a measure that can be used to detect multicollinearity in regression models, and values may vary between 0 and 1. The closer to zero the tolerance value is for a variable, the stronger the relationship between this and the other predictor variables. Variables with very low tolerance contribute with little information to a model, increasing the instability of the b and beta coefficients. Tolerance values < 0.1 are likely causing serious collinearity problems (Hair et al. 1995).

Landscape of fear

We quantified the Nubian ibex' landscape of fear by overlapping two maps: one with the features of the landscape and the second with the landscape of the GUDs. The last one was created by determining contour lines of equal GUDs representing the Nubian ibex' perceptions of fear. We did this using the distance weighted least squares (DWLS) smoothing method that fits the lines through a set of points by least squares. Every point on the smoothed line requires a weighted quadratic multiple regression on all the points.

Results

The tolerance values indicated multicollinearity problems in the model. In order to overcome these problems and to reduce the number of predictors, we dropped some of the intercorrelated variables from the model. Among these variables were 'elevation' and 'pebble', which had tolerance levels < 0.1. 'Visibility' was also involved in high intercorrelation, but since we have special interest in this variable, due to results from an experiment which we have recently conducted and due to the fact that it also evaluates visibility, we kept it in the model. Since 'drainage' and 'big rocks' were highly correlated with 'visibility', we dropped them instead.

Patch use by Nubian ibex varied significantly with environmental features along the landscape. The percentage of vegetation cover, the distance to the main cliff and the distance to nearest slope significantly influenced the GUDs of Nubian ibex. The polynomial regression analysis suggested no non-linear problems, therefore, we only report the results of the linear multiple regression (Table 1). Vegetation cover had a negative influence on the GUDs (see Table 1 and Fig. 2A). The distance to the main cliff and to the nearest slope both affected the GUDs positively (see Table 1 and Fig. 2B-C). The rest of the environmental variables were not significant.

We created a map with contour lines of equal GUDs. The lines represent areas that differ in the predation risk perceived by the ibex and can be viewed as the Nubian ibex' landscape of fear. Then, we determined the contours of the GUD on the map of the features of the landscape (see Fig. 1). The

Table 1. Results of the linear multiple regression model testing the effect of environmental variables on the Nubian ibex perception of risk of predation as measured by GUDs (overall model was significant: $P = 0.006$, $N = 24$, $R^2 = 0.63$). Beta = standardised β-coefficient, B = regression coefficient.

	Beta	B	t	P
Constant	0.000	31.743	3.0769	0.007
Main cliff	0.632	0.276	3.793	0.002
Vegetation cover	-0.459	-0.243	-2.441	0.025
Nearest slope	0.388	0.406	2.251	0.038
Visibility	0.111	0.019	0.319	0.754
Disturbance	-0.046	-0.033	-0.329	0.746
Medium rocks	0.048	-0.006	0.047	0.963
Steepness	0.221	0.083	0.792	0.439

features of the landscape were drawn based on a satellite photo. Areas of lower GUDs correspond to areas of greater safety. These correspond to areas near the cliff and more heavily vegetated areas.

Discussion

Different environmental features may serve as cues of predation risks to foraging animals. If so, animals should alter their foraging and anti-predator behaviour in response to these cues as they move within a landscape. In our study, we demonstrated that the foraging behaviour of Nubian ibex varies according to different characteristics of their environment. The behaviour of the ibex reveals that they perceive greater predation risk as they venture farther from the cliff areas. This was reflected in the increasing GUDs with the distance from both the main cliff and the nearest cliff or slope. The observation of Nubian ibex leaving higher GUDs as the distance to the main cliff increases has been shown by Hochman & Kotler (2007). However, our work provides a more complete view of the most important environmental features working together to shape the Nubian ibex behavioural responses to the risk of predation, revealing the animals' preferences for escape routes and cover while foraging.

In 19 out of 24 artificial feeding patches, the nearest cliff was represented by a small and shallow slope, while in only five occasions, the nearest cliff coincided to be the main cliff. The small slopes have a smaller effect than the main cliff and at a smaller scale. This suggests that less steep and shallower slopes provide less protection for the ibex. Still, when venturing farther from the main cliff, an ibex may gain some protection by being close to a slope. The last observation is consistent with how an ibex responds to threats such as dogs or humans. The moment that the threat is detected, the ibex stop their current activity and becomes vigilant. If the agent of threat comes closer, the ibex retreat towards the nearest slope edge, and if it becomes even more threatening, the ibex retreat to the main cliff and may even descend the slope in extreme cases (C. Iribarren, pers. obs.).

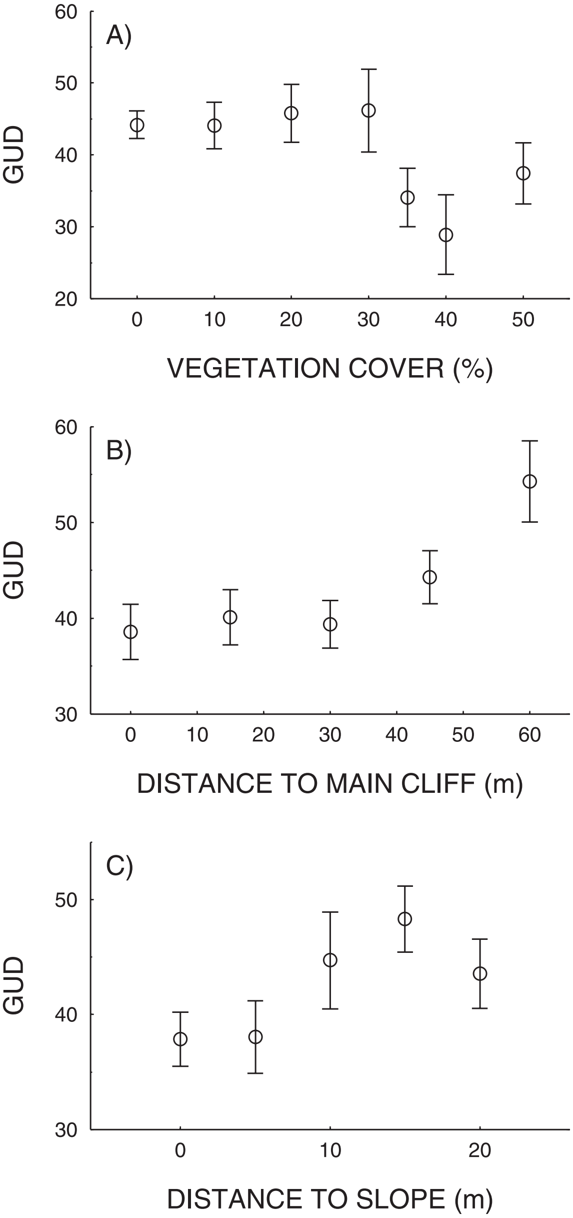


Figure 2. Effect of vegetation cover (percentage; A), distance from the main cliff (metres; B), and distance from the nearest slope (metres; C) on Nubian ibex' giving-up densities (GUD, i.e. grams of food left on the trays; mean ± SE).

The fact that a reduction of foraging effort by ibex occurs as the distance from the refuge increases, suggests that this species behaves like a central place forager. A central place is a location such as a nest, a refuge, a burrow or any other site to which an animal returns between foraging bouts. In general, the cost of foraging increases as the forager travels to farther areas from the central place (Thorson et al. 1998, Druce et al. 2006). As a consequence, patches that are closer to the central place are more valuable. This leads the foragers to harvest those patches more thoroughly. The pattern of increasing perceived predation risk with the distance from the refuge has been shown previously in several other species where the strategy of avoiding predators consists on fleeing to a refuge (see review by Stankowich & Blumstein 2005).

GUDs were lower when thick (40%) vegetation cover was present, i.e. Nubian ibex increased their foraging efforts in the presence of vegetation. This suggests that the costs of predation when the ibex forage far from the cliff might be assuaged by an increase in the vegetation cover. Such effect was especially evident at station A5 (see Fig. 1), located in the row farthest from the cliff (60 m). This station had considerably higher vegetation cover than the other four stations located at approximately 60 m from the main cliff. Nubian ibex always left lower GUDs at this station compared to the other four.

Two possible explanations may help explain the habitat preference of Nubian ibex for patches with higher vegetation. One explanation is that patches with higher vegetation are more attractive to the ibex simply because they offer greater feeding opportunities. This agrees with Searle et al. (2008), who demonstrated that after altering the natural environment of brown bandicoots *Isoodon macrourus*, the animals spent more time foraging in feeding stations within areas of the landscape that had greater resource density, independent of the predation risk. In this example, bandicoots harvested food only from feeding trays. However, in our case, the extra food was found outside of trays and would more likely have diverted ibex from feeding trays.

A second explanation may be related to a reduction in the perceived risk of predation. The vegetation present in the area was not tall enough to restrict the ibex' sight lines, but in most cases it was sufficiently tall to wholly or partially conceal an ibex. Moreover, vegetation was distributed in a manner that did not represent a barrier to the ibex, ensuring a safe escape route if necessary. Therefore, vegetation could increase the ibex' concealment without impeding their vigilance. In this way, the vegetation in our study area may play a role in reducing risk of predation, leading the ibex to forage more thoroughly from areas where vegetation was abundant. Note that GUDs were lowest at 40% cover, indicating that really thick vegetation might obstruct vigilance or escape opportunities. If so, very dense vegetation should have the opposite effect compared to the moderate (40%) vegetation, hence increasing the ibex' perception of predation risk.

Sight lines per se did not affect the ibex' patch use significantly. This is in contrast to a recent experiment in which we obstructed sight lines surrounding food patches for the same population of ibex (C. Iribarren & B.P. Kotler, unpubl. data). In response to reduced sight lines, ibex increased their GUDs and increased their vigilance. What may explain these differences? A possibility is that the criterion used to measure the visibility in our current work was inappropriate. We assumed that all sightline directions were of equal importance. However, it is possible that some visual directions are more relevant for reducing risk of predation than others, especially those sight lines directed to escape routes or to areas where the risk increases (e.g. with higher human disturbance or opposite to the cliff area). Similarly, Arenz & Leger (1997) suggested that the position of visual obstructions within the visual field is important to thirteen lined ground squirrels *Spermophilus tridecemlineatus*, even more than the amount of occlusion per se. In addition, the perceived risk of predation may also depend on the distance to the obstruction. However, in our study, we assumed that all visual obstructions within 10 m were equally important.

An alternative explanation for the lack of correlation between visibility and risk of predation is that, in general, the ibex forage in groups where individuals are separated from each other by a few metres. This means that the presence of sentinels located in areas that offer better visibility (e.g. at higher elevations) may reduce the predation risk of the whole group. Numerous works have shown that ungulates rely on the vigilance of others, and that it leads to a reduction of vigilance of group members in several cases (Alados 1985, Roberts 1996, Hunter & Skinner 1998). If this is the case with Nubian ibex, it is possible that visibility has a stronger effect when individuals forage solitarily or in very small groups. However, we note that ibex do not appear to alter their vigilance behaviour according to group size (Gross et al. 1995b, Hochman & Kotler 2007).

Our study provides information about the important role that habitat structure plays in the ecology of Nubian ibex, even when considering a small area (relative to their home range). Environmental features influenced the ibex' perceptions of predation risk. They ranked the patches based on these perceptions and varied their foraging efforts among the patches accordingly. This means that any manipulations of the natural environment of the Negev Desert could strongly influence the ibex' fear of predation leading to changes in their patch use and foraging efficiency. As previously noted, Nubian ibex are endangered (IUCN Red List, November 2005) and a reduction in their foraging efficiency or in the easy access to escape terrain could affect the future of the local population. Midreshet Ben-Gurion and environs (the location where this research was carried out) has become a popular recreational destination and it has been in continuous development during the last several years. Therefore, proper conservation planning and management is needed. Based on this work, special attention should be paid to the most prominent environmental features that affect the Nubian ibex landscape of fear, which are the distance to the cliff and edge slopes that offers escape terrain, and the vegetation cover that provides concealment to these animals.

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