

## Increases in food availability can tempt oribi antelope into taking greater risks at both large and small spatial scales



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Differences in food availability and predation risk can influence how herbivores use landscapes. As a result, trade-offs between costs and benefits can influence habitat and patch selection. To determine how oribi antelope, *Ourebia ourebi*, weigh up costs and benefits when making habitat and patch level foraging decisions, we measured giving-up densities in artificial patches. First, we determined large-scale habitat use, and then explored how different variables explained patch use within habitats. When the availability of food within patches across the different habitats was equal, oribi preferred to feed in short and tall grasslands and avoided woodlands. Furthermore, the avoidance of woodlands extended into the surrounding grasslands, resulting in oribi feeding less intensively in grassland areas within 15 m of the woodlands. Within the safe grassland habitats, oribi preferred to feed in patches close to tall grass (i.e. escape cover), and where they could see beyond 2 m. These results suggest that oribi select habitats and patches in relation to perceived predation risk (i.e. predation costs outweigh potential food intake benefits). However, when we increased food availability within woodlands, oribi increased their large-scale risk-taking behaviour and fed in these woodlands. Furthermore, this increased risk taking extended to small-scale foraging decisions whereby an increase in food availability within woodlands caused oribi to increase their relative usage of patches that had sight lines as well as patches that were closer to potential ambush sites. Ultimately, these results highlight how changes in food availability can determine the degree to which herbivores are willing to increase their risk-taking behaviour, and how these changes can affect overall landscape use.

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Spatial and temporal variability of food (i.e. quality and availability; Milne, Johnson, & Forman, 1989; Whittingham, Devereux, Evans, & Bradbury, 2006) and predation risk (Druce et al., 2009; Shrader, Brown, Kerley, & Kotler, 2008) are key factors that influence how animals use landscapes. The quality and availability of food is an important factor that can affect habitat and patch use (Langvatn & Hanley, 1993). For example, African elephants, *Loxodonta africana*, make foraging decisions at large scales (i.e. landscapes and habitats) that provide high food availability and then select for tree species within habitats (Shrader, Bell, Bertolli, & Ward, 2012). At a smaller scale, elk, *Cervus elaphus*, selected for grass patches with intermediate biomass, which allowed them to maximize their daily rate of energy gain (Wilmshurst, Fryxell, & Hudson, 1995).

Food, however, is not the only factor that influences the landscape use of herbivores. Predators also play a vital role. The spatial utilization of the landscape in response to perceived predation risk is termed a 'landscape of fear' (Laundré, Hernández, & Altendorf, 2001). The fear of being eaten can influence the behaviour as well as the foraging and fitness costs of herbivores (McArthur, Banks, Boonstra, & Forbey, 2014). From a behavioural perspective, many species reduce their predation risk by avoiding or altering their use of habitats as well as their small-scale use of patches within habitats. They do this because habitat structure affects visibility (Tchabovsky, Krasnov, Khokhlova, & Shenbrot, 2001), ease of escape (Lima, 1992) and predator ambush opportunities (Hopcraft, Sinclair, & Packer, 2005). When different habitats within a landscape differ in their predation risk, this may result in distinct boundaries between these habitats (Abu Baker & Brown, 2012). However, the risk associated with a habitat may extend beyond that habitat's boundaries into preferred habitats (Lidicker, 1999). For example, four-striped grass mice, *Rhabdomys pumilio*, fed less intensively in suitable grassland patches close to dangerous woodlands compared

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with similar patches far from these woodlands (Abu Baker & Brown, 2012).

It is generally assumed that the abundance of prey is the main driver of habitat use for predators (Lima, 2002). However, this assumption is based on a predator seeking out sessile prey (Sih, 1984). Realistically, herbivores are mobile and base their foraging decisions on the trade-off between food (quality and availability) and predation risk (Arias-Del Razo, Hernández, Laundré, & Velasco-Vázquez, 2012; Lima & Dill, 1990; McArthur et al., 2014). As a result, predators can hunt either in areas where prey are more abundant (Lima, 2002) or in areas where prey are less abundant but have higher vulnerability (Hopcraft et al., 2005; Laundré, Calderas, & Hernández, 2009). Therefore, the decisions driving habitat use of predators and prey have to balance not only food, but also the reciprocal levels of predation risk and predation success (Arias-Del Razo et al., 2012). This balance results in a landscape of fear that is very dynamic and greatly influenced by habitat characteristics.

Because of the dynamic heterogeneity in food availability and predation risk, foraging decisions cannot be based on food availability or predation risk alone. Rather, these factors are intertwined and foragers often make a behavioural trade-off between food and fear that maximizes food resources and protection from predators (Arias-Del Razo et al., 2012; Lima & Dill, 1990; McArthur et al., 2014). To do this, a forager must assess risk in terms of energy and/or other resources (Brown & Kotler, 2004). Prey species can find a trade-off between food and fear through a number of behavioural strategies, including spatial and temporal variation in activity patterns, and the selection of safe habitats (reviewed in Lima, 1998). For example, wild boar, *Sus scrofa*, increased their use of safe refuge areas within their home range over two temporal scales (within a day and over the year) in response to changes in predation risk, such as during the hunting season (Tolon, Dray, Loison, Fischer, & Baubet, 2009). By avoiding certain habitats, a forager may feed in areas that provide low energy gain but also low predation risk. For example, when wolves, *Canis lupus*, were present, elk fed on lower quality vegetation that was closer to safe forest habitats (Hernández & Laundré, 2005). Alternatively, a forager may feed in a risky habitat if it offers greater benefits (e.g. higher energy gains). This highlights the diversity of responses that foragers use to balance food and fear. As a result, we ask under what circumstances will potential food benefits outweigh the potential costs of predation? Exploring this question ultimately allows us to explore the conditions under which animals are willing to increase risk-taking behaviours.

To quantify trade-offs between food and safety, we focused on both the large- (habitat) and small-scale (patch) use of Africa's smallest pure grazing ungulate: the oribi antelope, *Ourebia ourebi*. Oribe live primarily in open grasslands but are sometimes seen in woodlands (Mduma & Sinclair, 1994; Perrin & Everett, 1999). Generally, they prefer to feed on gradual slopes (5–10°) in grasslands (Perrin & Everett, 1999). With regard to aspect, oribi tend to prefer feeding on north- and east-facing slopes because these slopes are drier and thus tend to have a higher percentage of palatable grasses (Perrin & Everett, 1999).

To measure habitat-specific foraging costs of oribi, we measured giving-up densities in artificial feeding patches (e.g. Abu Baker & Brown, 2012; Shrader et al., 2008). We tested landscape use across two scales: (1) large-scale habitat use between three habitats (tall grass, short grass and woodlands) and (2) small-scale patch use within habitats. In addition, at the patch scale, we explored how both large- and small-scale variables affected foraging within patches. Owing to their small size (ca. 14 kg), oribi are susceptible to a range of predators (e.g. caracal, *Caracal caracal*, and black-backed jackal, *Canis mesomelas*). Moreover, their small

body size, and thus high mass-specific metabolic requirements (Jarman, 1974), means that the availability of high-quality food influences both habitat and patch selection (Brashares & Arcese, 2002).

#### Giving-up Densities

To determine large-scale habitat use and small-scale patch use, we measured giving-up densities (GUDs) in artificial patches (Brown, 1988). A GUD is the amount of food that a forager leaves behind after it has ceased feeding in a patch (Brown, 1988). Theoretically, a forager should feed in a patch until its harvest rate ( $H$ ) no longer compensates for the energetic ( $C$ ), predation ( $P$ ) and missed opportunity costs (MOC) of foraging in that patch ( $H = C + P + \text{MOC}$ ; Brown, 1988, 1992). Given that harvest rate is a function of patch quality, GUDs are a reflection of the forager's quitting harvest rate (Schmidt, Brown, & Morgan, 1998). Because artificial patches are set up the same (i.e. the same amount of food and diminishing returns), they can be set out across the landscape to determine both spatial and temporal differences in perceived costs (Druce et al., 2009). The MOC can be controlled for by providing the forager with additional patches in each habitat that is being tested (Brown, 1988). In doing so, a forager feeding in a patch has the same set of alternative activities. Therefore, the forager experiences the same MOC in each habitat (Brown, 1988). Thus, lower GUDs (i.e. greater feeding effort) reflect greater preference (Brown & Kotler, 2004). Moreover, by measuring habitat characteristics around the patches, it is possible to understand how different landscape features affect foraging decisions (Morris, Kotler, Brown, Sundararaj, & Ale, 2009; Shrader et al., 2008).

#### Hypotheses and Predictions

##### Large-scale habitat use

We predicted that oribi would feed in habitats according to their predation risk. For example, when food availability is constant between habitats, oribi would select habitats with the lowest predation risk. Moreover, because of the high predation risk associated with woodlands (Thaker et al., 2011; Valeix et al., 2009), we predicted that oribi would feed less within this habitat. In addition, as the negative effects of avoided habitats can extend into surrounding habitats (Abu Baker & Brown, 2012; Lidicker, 1999), we predicted that there would be a negative buffer zone around woodlands, extending into the preferred grasslands, where oribi would not feed.

##### Small-scale patch use

Within habitats, predation risk can vary over small spatial scales. As a result, we predicted that oribi would feed less intensively in patches where landscape variables increased predation risk. We predicted that oribi would feed in patches where landscape variables, such as structure and the availability of refugia, would increase the ability of oribi to detect and escape from predators.

##### Changes in Risk-taking Behaviours

If food availability was greater in a high-risk habitat, we predicted that oribi would, at some point, increase their risk-taking behaviour and forage in the high-risk habitat (i.e. potential benefits outweigh costs) by feeding in the safest patches within these habitats. Alternatively, if the potential benefits from feeding in a patch far outweigh predation risk, then oribi could potentially feed in all patches irrespective of risk. This would result in an increase in their small-scale risk-taking behaviour.

## METHODS

### Study Site

We conducted our experiments from 1 June to 30 August 2013 at Arundel Farm (ca. 770 ha) in Ixopo, KwaZulu-Natal, South Africa (30°11.557S, 30°12.199E). Both the University of KwaZulu-Natal and Ezemvelo KZN Wildlife approved all aspects of the research design (Ethics code: 058/14/Animal and W/2052/01). Although the study spanned 3 months during the dry season, the availability of high-quality vegetation (i.e. green grass) remained relatively constant throughout the study period (K. Stears, personal observations). This was due to the higher than average rainfall during the previous wet season, and the low density of herbivores during the dry season.

Most of the property (ca. 700 ha) comprises grasslands consisting of a mosaic of short and tall grass dominated by species such as *Aristida junciformis*, *Hyparrhenia hirta*, *Themeda triandra* and *Sporobolus africanus*. However, scattered throughout the grasslands were woodland patches (0.36–0.72 ha). Grasses within these woodlands comprised *Pennisetum clandestinum*, *Paspalum dilatatum*, *H. hirta*, *A. junciformis*, *T. triandra* and *S. africanus*. The woody component of woodlands was dominated by *Acacia karroo*, *Acacia nilotica*, *Acacia mearnsii*, *Rhus rehmanniana*, *Ziziphus mucronata* and *Rubus cuneifolius*. Woody species varied in size from small shrubs (ca. 1.5 m) to large trees (2–6 m). Other herbivores found on the farm included common duiker, *Sylvicapra grimmia*, springbok, *Antidorcas marsupialis*, impala, *Aepyceros melampus*, kudu, *Tragelaphus strepsiceros*, reedbuck, *Redunca arundinum*, zebra, *Equus quagga*, and bushpig, *Potamochoerus larvatus*. Potential predators of oribi included black-backed jackal, caracal and stray/feral dogs, *C. lupus familiaris*. Black-backed jackals have a bigeminous activity pattern (crepuscular and nocturnal periods) and are cursorial pack hunters (Kaunda, 2000). In contrast, caracal are solitary and mainly nocturnal hunters that stalk and ambush their prey (Kingdon, 1997). In the study site, feral dogs were active throughout the 24 h period.

We conducted our experiment at three sites within Arundel Farm. To ensure that each site contained a separate group of oribi, we selected sites that were least 1 km apart. Because this distance was greater than the territory size of male oribi (0.1–0.9 km<sup>2</sup>; Brashares & Arcese, 1999), it ensured that the animals did not move between the sites. Site 1 contained three oribi, while both sites 2 and 3 had four oribi. These group sizes are normal for oribi populations across the species' distributional range (Skinner & Chimimba, 2005). Each site contained short grass, tall grass and

woodland habitats. The proportional availability of each habitat was similar across the oribi territories in each site. The tall and short grass habitats had roughly equal availabilities and dominated each site (ca. 70% combined). In comparison, the woodland habitat had a lower availability (ca. 30%), but was also similar between sites. Based on the literature (e.g. Thaker et al., 2011; Valeix et al., 2009) and personal observations (by K.S), we assumed higher predator abundance and prey vulnerability in the woodland habitats.

Before the start of the experiments, we habituated the oribi to the artificial food patches. We did this by exposing them to these patches and used camera traps to identify consistent oribi foraging. Once this had happened, we considered the oribi to be fully habituated to the patches, and only then collected data. However, to be sure, we explored whether 'day' influenced oribi feeding intensity (i.e. GUDs). If the oribi were not fully habituated to the artificial patches, we would expect them to feed more intensively (i.e. achieve lower GUDs) as the experiment went on. If this were the case, then this would result in 'day' being an important factor in the model. However, for the first experiment, the model that included 'day' as a random effect was not the best model (i.e. lowest Akaike information criterion (AIC) value; Table 1). This indicates that the feeding intensity of the oribi from the patches (i.e. GUDs) did not differ between days. Therefore, we were confident that variation across days, as a result of habituation, was unlikely.

The artificial patches consisted of plastic trays (500 × 340 mm and 120 mm high) with a 1 × 2 grid of 2 mm galvanized wire over the top of each tray. To create diminishing returns (Kotler & Brown, 1990), we filled each patch with 9 litres of an inedible medium of dried corncobs. For all experiments, we put in 300 g of commercial sheep pellets (Complete Sheep Finisher, Meadow Feeds, South Africa) into each patch. Because other herbivores were present in the study site, we used trail cameras (Bushnell Trophy Cam) in the habituation period as well as throughout the experiments to ensure that we only measured the GUDs of oribi. In addition, each camera trap was positioned on a pole ca. 1 m above the ground a few metres from an artificial patch to avoid changes in foraging behaviour caused by the camera. Because multiple experiments were run at the same time, each experiment had two cameras. However, these cameras were oriented such that they covered six of the nine patches. In addition, we rotated the positions of the cameras every other day to maximize the probability of photographing a herbivore feeding at the patches. When we reset the artificial patches with food, all the photos from the trail cameras were analysed. If a herbivore other than an oribi was captured by

**Table 1**

Results of the model selection procedure to assess which model best predicts large-scale oribi habitat use in relation to predation risk and which model best predicts grassland use surrounding woodlands

Factors included in the model		Number of parameters	AICc	ΔAICc
Large-scale habitat selection				
Fixed structure		Random structure		
Habitat	Day and site	5	–227.54	2.218
Habitat	Day	4	–188.78	40.976
Habitat	Site	4	–229.76	0
Fear of woodlands transect				
Fixed structure		Random structure		
Woodland size and Distance from woodland	Day and Site	6	–338.44	4.237
Woodland size and Distance from woodland	Day	5	–336.58	6.09
Woodland size and Distance from woodland	Site	5	–340.6	2.07
Woodland size	Site	4	–82.933	259.741
Distance from woodland	Site	4	–342.67	0

The model with the lowest AICc value provides the best fit to the data. ΔAICc = AICc<sub>i</sub> – AICc<sub>min</sub>.

the trail camera, the data from that day would be excluded from the data set. However, only oribi were photographed feeding from the artificial patches throughout the experimental period. As a result, we did not exclude any data, and thus all data were collected over consecutive days.

Because we placed the artificial patches at ground level, it is possible that some rodents may have fed from the patches without triggering the trail cameras. However, as very few of the patches in each of the habitats contained rodent droppings, it is unlikely that rodent foraging from the patches in the different habitats was extensive. Moreover, as the frequency at which we found rodent droppings in the patches did not differ between the habitats, the potential small removal of food is unlikely to have biased our results.

#### *Large-scale Habitat Use*

To test for habitat use, we placed a  $3 \times 3$  grid of artificial patches in the three different habitat types at each site replicated across the three sites (i.e.  $N = 9$  grids of artificial patches). Within each grid, we spaced the different artificial patches 15 m apart. Habitats comprised: (1) tall grass that ranged from 38 to 113 cm in height; (2) short grass that ranged between 5 and 28 cm in height; and (3) woodland areas that contained both grass and trees. Within the woodlands, shrubs and broken branches provided potential ambush sites for predators and reduced visibility for oribi, both potentially increasing predation risk (Lima & Dill, 1990).

To determine habitat use, we collected data for 7 consecutive days. We obtained GUDs by leaving the artificial patches out for 24 h. During the habituation period, before data collection, we found that oribi finished their morning foraging bouts by about 0700 hours. Therefore, just after 0700 hours every day we sifted out the remaining food and refilled the patches with 300 g of food. We then weighed the remaining food in each patch to determine the GUDs.

As predicted, we found that oribi moved through the wooded areas, but they did not feed there (see Results). As a result, we tested to see whether risks associated with wooded areas extended into the surrounding grassland habitats and influenced the foraging behaviour of oribi. We did this by running two transects of four patches from opposite sides of a wooded area into the surrounding grassland. We placed the first artificial patch of each transect at the edge of the wooded area (0 m) and the others extending 15 m, 30 m and 45 m into the surrounding grassland. We set up two transects at each of the three sites ( $N = 3$  wooded areas). We then collected GUDs using the same experimental protocol as in the previous experiments (i.e. 300 g of food per patch, patches left for 24 h, experiment run for 7 consecutive days).

#### *Small-scale Patch Use*

Within all three habitat types, we used the same  $3 \times 3$  grid of artificial patches as in the previous experiment and recorded patch variables that could influence foraging decisions at each patch within the grids. For the tall grass habitat, these variables included aspect (whether the patch faced north, south, east or west), slope ( $0-5^\circ$ ,  $6-10^\circ$ ,  $11-15^\circ$ ,  $16-20^\circ$  or  $>20^\circ$ ) and sight lines (whether or not the visibility from the patch was blocked within a 2 m radius of the patch by tall grass or shrubs). For the short grass habitat the variables were aspect, slope and distance to tall grass (escape cover), while for the woodland habitat we used the variables aspect, slope, sight lines, distance to edge of woodland and distance to ambush site. As in the previous experiment, we used 300 g of food and obtained GUDs after leaving the artificial patches out for 24 h. The experiment ran for 7 consecutive days.

#### *Changes in Risk-taking Behaviour*

The key experiment that we ran was to determine whether oribi would overcome their fear of woodlands as food availability increased (i.e. potential benefits outweighed predation costs). To make direct comparisons between this experiment and the habitat and patch use experiment, we used the same wooded areas and artificial patch grids. To determine whether greater food availability would increase risk-taking behaviour, we increased the amount of food in each patch within the woodlands to 500 g. As above, we left the artificial patches out for 24 h before collecting the GUDs, and ran the experiment for 7 days. We then ran the experiment again, but increased the amount of food to 750 g. We followed the same experimental protocol, but were only able to run this experiment for 3 days.

The above experiments were run sequentially. However, there was a habituation period of 2 days between each experiment. We limited the period to 3 days, as within that time the oribi expanded their use of the artificial patches (i.e. lower GUDs and feeding from previously avoided patches). This suggested that they had adjusted their use of the patches in response to the increase in food availability. Data collected during the habituation periods were not included in the analysis.

As in the first experiment, we collected patch variables that could influence patch use. These variables included distance to edge of wooded area, distance to potential ambush site, and sight lines. Because we used the same wooded areas and patch positions from the first experiment, we were able to compare the importance of the landscape variables across the different food availability treatments.

#### *Data Analysis*

We analysed our data using a model selection procedure. The use of model selection criteria enables inferences to be drawn from several models simultaneously to consider the 'best' model. Once the best model has been selected, maximum likelihood parameter estimates or predictions from that model can be made (Johnson & Omland, 2004). Model selection was based on AIC; (Burnham & Anderson, 1998). Owing to small sample sizes, we used small sample AIC or AICc for model comparison (Burnham & Anderson, 1998).

The data we collected did not conform to the assumptions of normality and contained fixed and random effects. As a result, we used generalized linear mixed models (GLMMs) in our model selection procedure. Once the correct distribution and link function were identified (see below), it was important to first determine the optimal random structure in the model (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). To do this, we included all biologically relevant fixed-effect variables in a model (the beyond optimal model). We then ran the beyond optimal model with the different combinations of random-effects variables included. We compared these models using their AIC values. The model with the lowest AIC value had the optimal random structure. The next step was to determine the optimal fixed structure of the explanatory variables, based on the optimal random structure that was calculated in the previous step. To do this, we compared the beyond optimal model with simpler biologically relevant models derived from the beyond optimal model. The model with the lowest AIC value ( $\Delta AICc = 0$ ) had the optimal fixed and random structure and provided the best fit for the data. A detailed outline of this model selection process can be found in Zuur et al. (2009). We followed this procedure for each of the experiments outlined below. For some experiments there was only one random-effect variable. As a result, there was no need to determine the optimal random structure, so we skipped

this step and only determined the optimal fixed structure using the single random-effects variable.

#### Large-scale habitat use

To determine oribi habitat use in relation to perceived predation risk, we analysed GUDs (dependent variable) with a GLMM. We used a gamma distribution with a log-link function. Habitat (short grass, tall grass and woodlands) was included in the model as a fixed effect. The GUDs of the nine patches per habitat were averaged for each day, because we were interested in how oribi use a habitat and not how they use each patch. To account for variation across days, we included day as a random effect, which accounts for the variability due to daily differences and tested for the main effect, the influence of habitat on foraging intensity (Altendorf, Laundré, González, & Brown, 2001). It is possible that the different sites varied in food availability, predation risk, the number of oribi and competition. To account for these potential differences, we included site as a random effect. We followed the model selection procedure outlined above and the best model achieved the lowest AIC value (see Table 1).

To explore whether the negative effects of the avoided woodland habitat extended into the surrounding favoured grassland habitat and influenced the feeding intensity (i.e. GUDs) of oribi, we ran a GLMM (gamma distribution and log-link function). We calculated mean GUDs for each patch position per day from the two transects in each wooded area. In the analysis, mean GUD was the dependent variable, the size of the wooded habitat and distance to wooded area (0 m, 15 m, 30 m, 45 m) were fixed effects and day and site were included as random effects. We followed the model selection procedure outlined above and the best model achieved the lowest AIC value (see Table 1).

#### Small-scale Patch Use

To determine the influence of environmental variables on small-scale patch use, a separate GLMM (gamma distribution with a log-link function) was performed for each habitat (tall grass, short grass and woodlands). We generated mean GUDs (dependent variable) for each patch in each habitat from the data collected over the 7 days. We averaged GUDs across days because we were interested in how landscape variables influenced feeding effort overall, and not how feeding effort varied in the different patches across days. As a result, we did not include day as a random effect, but rather used

mean GUDs across days, thus avoiding possible nonindependences between days.

For the tall grass habitat, slope, aspect and sight lines were fixed effects and site was a random effect. For the short grass habitat, slope, aspect and distance to cover were fixed effects and site was a random effect. Finally, for the woodland habitat, aspect, slope, sight lines, distance to edge of woodland and distance to ambush site were fixed effects and site was a random effect. To determine which model, and therefore which landscape variables, best explains small-scale patch use of oribi, we followed the model selection procedure outlined above. For each habitat, the model with the lowest AIC value is considered the best model given the data (see Table 2).

#### Changes in Risk-taking Behaviour

To explore whether oribi increased their large-scale use of wooded areas as food availability increased, we analysed GUDs using a GLMM. We converted the GUDs to proportion of food left to make the three treatments of increasing food availability (300 g, 500 g and 750 g) comparable. As a result, we used a binomial distribution and a logit link function. The GUDs of the nine patches per treatment were averaged for each day and the mean proportion of food left was included in the model as the dependent variable. Treatment was included as a fixed effect and day and site were included as random effects. We followed the model selection procedure outlined above and the best model achieved the lowest AIC value (see Table 3).

To determine the influence of the landscape variables on small-scale patch use and thus risk-taking behaviour, we used another GLMM (gamma distribution and log-link function). We limited this analysis to the wooded areas across the different treatments (i.e. 300 g, 500 g, 750 g). We converted the GUDs to proportions of food left (dependent variable) to make the three treatments comparable. We generated mean GUDs (dependent variable) for each patch from the data collected over the 7 days within the wooded habitat for each treatment and combined them into a single data set. Independent variables included treatment, sight lines, distance to edge of wooded area, distance to potential ambush site, treatment \* sight lines, treatment \* distance to edge and treatment \* distance to potential ambush site. To determine which model, and therefore which landscape variables, best explains small-scale changes in risk-taking behaviour of oribi, we followed the model selection procedure outlined above. The model with the lowest AIC value is

**Table 2**

Results of the model selection process to determine which model, containing different landscape variables, best explains small-scale patch use in tall and short grass habitats

Factors included in the model		Number of parameters	AICc	$\Delta$ AICc
<b>Tall grass habitat</b>				
Fixed structure		Random structure		
Aspect, Sight lines and Slope	Site	6	-29.255	17.199
Aspect and Sight lines	Site	5	-39.1	7.354
Aspect and Slope	Site	5	-18.446	28.008
Slope and Sight lines	Site	5	-32.73	13.724
Aspect	Site	4	-25.311	21.143
Slope	Site	4	-26.359	20.095
Sight lines	Site	4	-46.454	0
<b>Short grass habitat</b>				
Fixed structure		Random structure		
Slope, Aspect and Distance to cover	Site	6	-52.792	12.798
Slope and Aspect	Site	5	-38.574	27.016
Slope and Distance to cover	Site	5	-59.473	6.117
Aspect and distance to cover	Site	5	-58.801	6.789
Slope	Site	4	-44.179	21.411
Aspect	Site	4	-43.027	22.563
Distance to cover	Site	4	-65.59	0

The model that provides the best support for the data has the lowest AICc value.  $\Delta$ AICc = AICc<sub>i</sub> - AICc<sub>min</sub>.

**Table 3**  
Results of the model selection procedure to determine which model best supports both large- and small-scale changes in risk-taking behaviour

Factors included in the model		Number of parameters	AICc	$\Delta$ AICc
Large-scale changes in risk-taking behaviour				
Fixed structure	Random structure			
Treatment	Day and Site	5	68.438	2.18
Treatment	Day	4	79.035	12.777
Treatment	Site	4	66.258	0
Small-scale changes in risk-taking behaviour				
Fixed structure	Random structure			
Treatment, Sight lines, Distance to edge, Distance to ambush site, Treatment*Sight lines, Treatment*Distance to edge and Treatment*Distance to ambush site	Site	12	731.451	15.79
Treatment, Sight lines, Distance to edge, Distance to ambush site, Treatment*Sight lines and Treatment*Distance to ambush site	Site	10	724.305	8.644
Treatment, Sight lines, Distance to ambush site, Treatment*Sight lines and Treatment*Distance to ambush site	Site	9	715.661	0

The model with the lowest AICc value provides the best fit to the data.  $\Delta$ AICc = AICc<sub>i</sub> – AICc<sub>min</sub>.

considered the best model given the data (see Table 3). All statistical analyses were done using SPSS version 22 (SPSS Inc., Chicago, IL, U.S.A.).

## RESULTS

### Large-scale Habitat Use

The model selection procedure to test our hypothesis that oribi select habitats in relation to perceived predation risk is summarized in Table 1. The model that provided the best fit to the data included habitat as the fixed effect and site as the random effect. This model provides support that the feeding intensity (i.e. GUDs; estimated mean  $\pm$  SE g) of oribi differed significantly across the three habitats (Fig. 1). Oribi fed with equal intensity in the short (estimated mean GUD = 252  $\pm$  1 g) and tall (mean GUD = 253  $\pm$  1 g) grass habitats, but fed less intensively in woodlands (i.e. high GUDs; estimated mean GUD = 299  $\pm$  1 g).

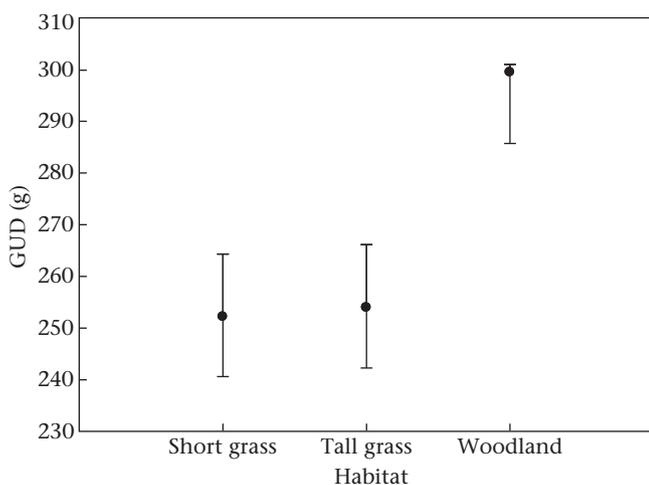
Oribi showed very little feeding within woodlands. The model selection procedure to determine whether the negative effects of woodlands extended into the surrounding grasslands is summarized in Table 1. The model that provided the best fit to the data included distance from the woodland habitat as a fixed effect and

site as a random effect. Oribi did not forage at the edge of the woodlands, and only increased their feeding intensity (i.e. lower GUDs) as they moved further away from the woodlands (Fig. 2). The model selection procedure shows that models that included the size of the woodlands did not provide good support for the data (see Table 1). This suggests that this pattern of avoidance around woodlands occurs irrespective of the size of the woodlands.

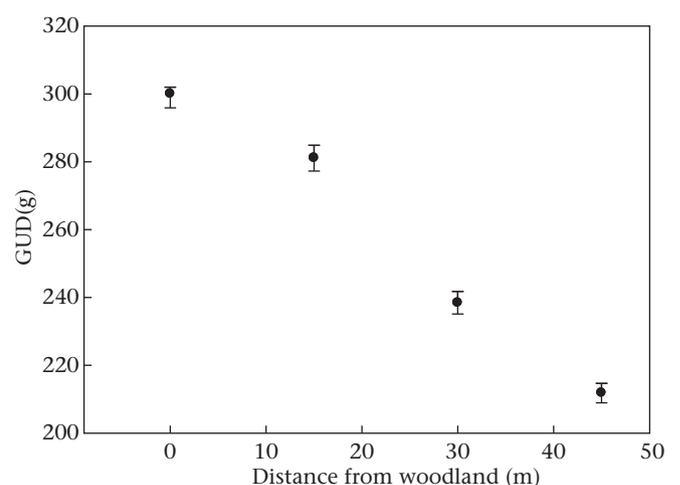
### Small-scale Patch Use

The model selection procedure that was used to predict which landscape variables influence small-scale foraging decisions of oribi in tall grasslands is summarized in Table 2. The model that provided the best fit to the data included the landscape variable sight lines as a fixed effect and site as a random effect. Within tall grasslands, oribi ate more intensively (i.e. achieved lower GUDs) from patches where they could see >2 m (estimated mean = 235  $\pm$  1 g) compared with patches where they could only see <2 m (mean = 280  $\pm$  1 g).

The model selection procedure that was used to predict which landscape variables influence small-scale foraging decisions of oribi in short grasslands is summarized in Table 2. Within the short grass habitat, the model that provided the best fit to the data included



**Figure 1.** Giving-up density (GUD, in g; estimated mean  $\pm$  95% confidence interval (CI)) for oribi across habitats. Overlapping CIs show equal preference. Estimated means and CIs are calculated from model predictions and have been back-transformed from the log scale to create asymmetrical CIs.



**Figure 2.** Giving-up density (GUD, in g; estimated mean  $\pm$  95% confidence interval (CI)) in artificial food patches in relation to distance from woodlands. Estimated means and CIs are calculated from model predictions and are back-transformed from the log scale to create asymmetrical CIs.

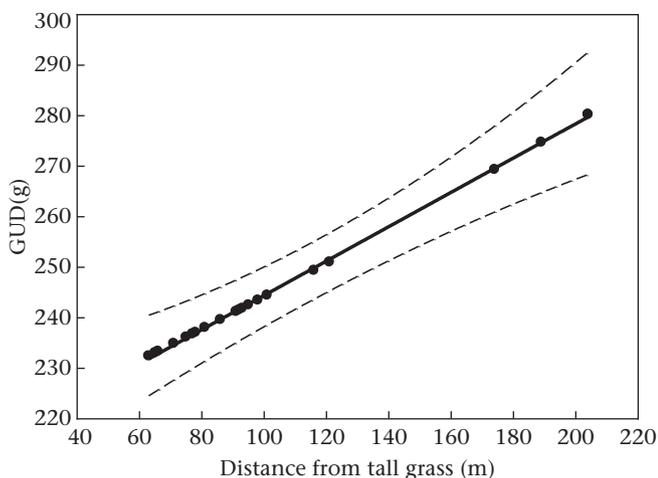
distance to tall grass (i.e. cover from predators) as a fixed effect and site as a random effect. As the distance to tall grass increased, oribi fed less intensively from the patches (Fig. 3).

For the woodland habitat, we were not able to determine which landscape variables influenced small-scale patch use, because the lack of feeding did not create enough variance to fit a model. However, the lack of variance due to low feeding is a result in itself. For the given food availability (300 g), oribi showed very little feeding in this habitat because of the high perceived predation risk. Ultimately, the cost of predation was too high to feed within the safest patches in this habitat.

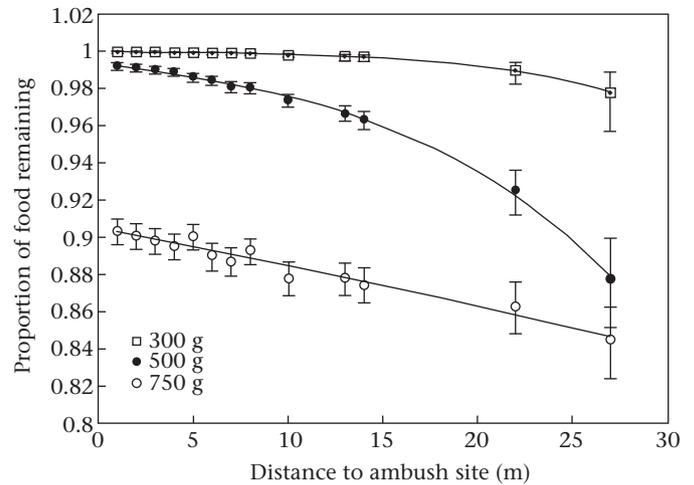
#### Changes in Risk-taking Behaviour

The model selection procedure that was used to determine whether oribi increase their use of avoided woodlands as food availability increased (i.e. large-scale changes in risk-taking behaviour) can be seen in Table 3. The model that best supported the data included treatment as a fixed effect and site as a random effect. As food availability increased in the woodlands, oribi increased their use of this habitat. The mean percentage of food left in the patches declined as food availability increased from  $99.8 \pm 0.57\%$  (for 300 g), to  $97.7 \pm 0.52\%$  (for 500 g), and finally to  $89.6 \pm 0.51\%$  (for 750 g).

Table 3 provides the model selection procedure that was used to determine which landscape variables influence small-scale patch use in woodlands and whether an increase in food availability influences their small-scale patch use (i.e. small-scale change in risk-taking behaviour). This model included treatment, sight lines, distance to ambush site and their interaction with treatment as fixed effects and site as a random effect. As the distance from potential ambush sites increased, oribi fed more intensively (i.e. obtained lower GUDs; Fig. 4), especially when feeding in patches containing 500 g and 750 g. Furthermore, the interaction of food availability and distance to ambush site influenced the small-scale patch use of oribi. Specifically, oribi ate closer to ambush sites (especially when food availability was 750 g), and ate more (i.e. achieved lower GUDs) from these artificial patches as food availability within the patches increased (Fig. 4). In addition, as food availability increased,



**Figure 3.** The mean giving-up density (GUD) for each artificial food patch (solid line) in relation to distance to tall grass (escape cover) from short grass habitats. The dashed lines represent 95% confidence bands around the predicted line. All data were back-transformed from the log scale. Low GUDs indicate greater feeding intensity and thus greater preference, whereas high GUDs indicate low feeding intensity (i.e. avoidance). Estimated means and 95% confidence bands are calculated from model predictions.

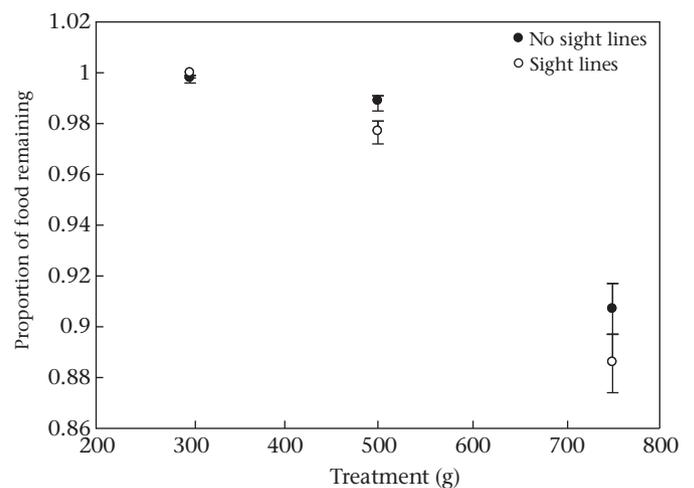


**Figure 4.** The estimated mean proportion of food remaining from three initial food densities (300 g, 500 g and 750 g) in artificial food patches in relation to distance to ambush sites. All data were back-transformed from the logit scale to create asymmetrical confidence intervals.

oribi fed more, and preferred to feed from patches that had sight lines (Fig. 5).

#### DISCUSSION

Two key factors that influence both large- and small-scale foraging decisions of herbivores are food (quality and availability) and predation risk (Bakker, Reiffers, Olf, & Gleichman, 2005; Whittingham et al., 2006). Animals tend to make foraging decisions (e.g. where, when and what to eat) using both large- and small-scale decisions (Lima & Dill, 1990). For example, where to feed includes both habitat (i.e. large-scale) and patch (i.e. small-scale) choices. Because foraging decisions can occur over a range of scales, one would expect that an animal's risk-taking behaviour would also occur over these scales. However, the majority of studies we found focus on risk-taking behaviour at a single spatial scale (e.g. Bakker et al. 2005; Kotler & Blaustein, 1995), and thus overlook the multilevelled decisions that animals make. By using GUDs to



**Figure 5.** The estimated mean proportion of food remaining from patches that had sight lines compared to patches without sight lines across three initial food densities (300 g, 500 g and 750 g). All data were back-transformed from the logit scale to create asymmetrical confidence intervals.

measure habitat and patch use our results are the first, to our knowledge, to quantify changes in risk-taking behaviour across multiple scales.

#### Large-scale Habitat Use

Similar to other studies (Perrin & Everett, 1999; Shackleton & Walker, 1985), we found that oribi preferred feeding in grasslands and avoided woodlands. However, contrary to these studies, we found that oribi did not just use the tall grass to hide in, but rather they foraged equally in both short and tall grass habitats. The oribi probably avoided woodlands owing to higher levels of perceived predation risk. Although oribi may not feed within woodlands, these habitats still have high predation risk, because predators select habitats in relation to prey vulnerability and not prey abundance (Laundré et al., 2009). Thus, our results support our initial hypothesis that when the food availability is equal, oribi will prefer to feed within safer habitats.

In addition, the perceived predation risk associated with woodlands was not restricted to woodlands. The negative effects extended into the preferred surrounding grasslands, creating a negative buffer zone around the woodland patches. This buffer zone was present around all of the woodland patches we tested, irrespective of size. Therefore, even small woodlands can reduce the total amount of suitable grasslands across the landscape for oribi. This effect is likely to be a result of increased predation risk at the edge of these two distinct habitats. Thus, the oribi did not use the entire grassland habitat within the study area. Abu Baker and Brown (2012) found similar results for the four-striped grass mice living in a grassland and woodland mosaic.

#### Small-scale Patch Use

The variability in the structure of habitats can influence the level of predation risk (Hannon, Jenkins, Crabtree, & Swanson, 2006), and thus small-scale patch use. Within tall and short grasslands, distance to cover and sight lines were the only variables that influenced small-scale patch use in our study. Distance to tall grass (escape cover) is important for oribi, because they have a cover-dependent escape tactic and normally hide in grass to avoid predators (Jarman, 1974). If oribi forage in short grass, they would need to retreat to tall grass to hide and thus reduce predation risk. The further away from tall grass oribi forage, the earlier they would have to flee to avoid a predator (Dill & Houtman, 1989). Although fleeing may enable a forager to escape predation, it incurs a cost in terms of reduced foraging (Ydenberg & Dill, 1986). As a result, foraging further away from cover increases predation risk, which would result in an increase in vigilance at the expense of foraging efficiency (i.e. higher GUDs; Brown, 1999; Lima & Dill, 1990). Therefore, it is not surprising that oribi fed more intensively near tall grass. Similarly, Nubian ibex, *Capra nubiana*, perceive cliffs as areas of safety and GUDs increased as the distance from the refuges increased (Kotler, Gross, & Mitchell, 1994). This avoidance of open areas far from cover may explain why oribi tend to avoid homogeneous agricultural land, such as oats, *Avena sativa*, and rye grass, *Lolium perenne*, pastures, as a source of supplementary food during winter (Perrin & Everett, 1999).

One of the main ways in which prey species reduce predation risk is through early detection of predators before they attack (Sorato, Gullett, Griffith, & Russell, 2012). Thus, objects that block sight lines can increase predation risk (Camp, Rachlow, Woods, Johnson, & Shipley, 2012; Shrader et al., 2008). In our study, oribi reduced feeding intensity in grassland patches where they could not see beyond 2 m. Thus, by avoiding patches with limited visibility, oribi probably reduced their predation risk because they

would be better able to assess the characteristics of approaching predators (e.g. speed and direction of approach), and thus make better escape decisions (Bateman & Fleming, 2011; Braun, Baird, & LeBeau, 2010). Similarly, bighorn sheep, *Ovis canadensis*, prefer to feed in open areas where they can easily detect approaching predators (Risenhoover & Bailey, 1985). Moreover, by feeding in patches with unrestricted sight lines, oribi would be able to observe other group members, and thus further reduce predation risk via collective detection (Elgar, McKay, & Woon, 1986; Metcalfe, 1984).

One of the main predators of oribi is caracal (Coverdale et al., 2006; Grey-Ross, Downs, & Kirkman, 2009), which is an ambush predator (Kingdon, 1997). Thus, caracal could take advantage of the ambush sites, provided by woodlands, which increases predation risk to oribi. In response to this possibility, when feeding within woodlands oribi fed more intensively in patches further away from ambush sites. However, in grasslands, oribi did not avoid feeding next to tall grass, which could also act as an ambush site. This may be due to the lower predator density found within the grasslands and thus a lower perceived risk. However, it may also be that, unlike shrubs and fallen branches found within woodlands, grass tufts are less of an obstacle preventing the oribi from fleeing cursorial predators such as jackal. The density of predators, as well as the encounter rate between predators and prey, can influence the antipredator response of herbivores. Owing to prey uncertainty about predators, prey should generally avoid risky areas (Sih, 1992). Therefore, predator density or encounter rate between predator and prey does not necessarily have to be high to illicit strong antipredator behaviour and avoidance of risky areas.

#### Changes in Risk-taking Behaviour

Despite greater perceived predation risk, woodlands can sustain greener vegetation, with increased production and increased nitrogen, longer into the dry season compared with open grasslands due to the microhabitats they create (Treydte, Heitkönig, Prins, & Ludwig, 2007). As a result, this higher quality vegetation could attract oribi to feed within these habitats. We simulated these conditions by increasing the amount of food within woodlands and found that oribi increased both their large- and small-scale risk-taking behaviour. Specifically, when food availability increased, oribi shifted and fed within the woodlands (i.e. large-scale habitat shift).

Within woodlands, small-scale risk-taking behaviour was influenced by food availability. Specifically, when the patches contained 300 g of food, oribi did not adjust their feeding effort in patches that had sight lines or as the distance from ambush sites increased. As a result, it is likely that at 300 g of food, the oribi perceived the cost of predation to be too high to feed intensively (i.e. achieve low GUDs) at any patch. However, when we increased food availability to 500 g, oribi fed more intensively from patches that had sight lines and from patches that were further away from ambush sites. Yet, their feeding intensity close to ambush sites did not increase with this increase in food availability. Ultimately, this suggests that, similar to 300 g, when the oribi fed close to ambush sites the cost of predation risk was greater than the benefits obtained from feeding in those patches. Nevertheless, in patches further away from ambush sites, feeding benefits outweighed perceived predation costs and the oribi fed more intensively (i.e. lower proportion of food remaining).

Finally, when we increased food availability in the patches to 750 g, the lower intercept indicated a greater overall feeding effort across all patches, irrespective of distance to ambush sites. In addition, oribi fed more intensively from patches, irrespective of whether they had sight lines or not. This greater feeding effort of the oribi (i.e. smaller proportion of food remaining) suggests that at

750 g of food the benefits of greater food availability outweighed the potential costs of predation at all patches. This risk-taking behaviour of oribi is surprising, because if they are trying to reduce predation risk, we would expect them to feed in the safest patches within the more dangerous woodland habitat. However, our results suggest that the perceived benefits of greater food intake outweighed the potential costs of predation (Brown, 1992).

There are two explanations that could explain this increase in small-scale risk-taking behaviour. First, by taking advantage of high-quality patches within risky habitats, oribi may increase their short-term predation risk. However, this may allow them to meet their energetic requirements faster than when feeding in safer habitats with lower food availability. Once oribi have finished foraging they tend to hide in tall grass to reduce predation risk (Mduma & Sinclair, 1994). Thus, if oribi quickly meet their energetic requirements by feeding in unsafe areas they may reduce the amount of time they are exposed to predators, and thus, potentially reduce their long-term daily predation risk (i.e. time-minimizing foraging behaviour; Bergman, Fryxell, Gates, & Fortin, 2001). Second, it is possible that the potential ambush sites within woodlands acted as escape cover and therefore had a similar function as tall grass refugia in short grass habitats. A number of studies have shown that landscape features that increase habitat structure (i.e. shrubs) can have contrasting functions (Camp et al., 2012; Hannon et al., 2006; Tchabovsky et al., 2001). These shrubs reduce predation risk by providing cover for the forager. Alternatively, these shrubs can increase predation risk by providing cover for the predator and by reducing the ability of a herbivore to detect approaching predators.

Although we did include 'day' as a random-effect variable in the model for this experiment, this model did not provide the best fit for the given data (see Table 3). However, because of the sequential nature of the experiments there is temporal variation that cannot be accounted for in the statistical model (i.e. it is possible that temporal changes in food quality and availability may be influencing habitat and patch use). However, this is unlikely to have a significant effect because these experiments were run over 23 days within the same season. As a result, the availability and quality of food across the landscape did not vary extensively throughout the experimental period (K. Stears, personal observations). Because of this, we are confident that the changes in risk-taking behaviour recorded are most probably due to the increase in food availability in the patches and not to temporal changes in the availability and quality of food across the landscape. Because oribi were fully habituated to the artificial patches before data collection occurred, it is unlikely that variation across days is a result of habituation.

One factor that might push animals to take greater risks is body condition (Brown, 1999). This is unlikely to explain our findings, however, because we conducted all our experiments over a relatively short period (i.e. 58 days). Over this period, the availability of food across the environment did not change dramatically. Moreover, we did not notice any changes in the body condition of any of the animals. As a result, the energetic state of oribi was unlikely to have changed excessively throughout our experiments. Therefore, our results demonstrate that benefits of greater food availability can even tempt animals in good condition to increase risky behaviour over both large and small scales.

Although we conducted this research on a working farm, there were no livestock present during the dry season when our study took place. In addition, there was no control of natural predators on the farm. As a result, the predator densities reflect those expected under natural conditions where oribi occur. Furthermore, the majority of predators of oribi occurred on the farm as well as low densities of additional herbivores. Therefore, the results of this study can be used to predict habitat use of oribi under natural conditions.

## Conclusions

Our results indicate that predation risk is a major factor that influences herbivore foraging behaviour (Kotler, 1984; Laundré, Hernández, & Ripple, 2010; Tolon et al., 2009). To understand predator–prey dynamics it is important to determine how habitat characteristics influence the landscape of fear by influencing predation risk for herbivores as well as the predation success of predators (Arias-Del Razo et al., 2012). As a result, herbivores have a trade-off between food and fear to maximize food resources and protection from predators (McArthur et al., 2014). The spatial and temporal variation in food availability and predation risk can vary simultaneously across both large and small spatial scales and therefore influence this trade-off. However, previous studies have only shown that food availability and/or quality can influence the risk-taking behaviour of herbivores at either a large spatial scale (i.e. habitats; Whittingham et al., 2006) or small spatial scale (i.e. patches; Bakker et al., 2005), but have never recorded simultaneous changes in risk-taking behaviour at both scales. However, we found that changes in food availability can tempt oribi to increase their risk-taking behaviour over both large and small spatial scales. Ultimately, our results highlight that potential benefits gained from increased food availability can override the costs associated with predation risk, and thus alter how prey species use landscapes.

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