



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.

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