Animal Behaviour 115 (2016) 107–114

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Strong reactive movement response of the medium-sized European hare to elevated predation risk in short vegetation

Martijn J. A. Weterings [a, c, *], Marco Zaccaroni [b], Nikki van der Koore [c], Linda M. Zijlstra [c], Henry J. Kuipers [c], Frank van Langevelde [a], Sipke E. van Wieren [a]

[a] Resource Ecology Group, Wageningen University, Wageningen, The Netherlands
[b] Department of Biology, University of Florence, Sesto Florence, Italy
[c] Wildlife Management, Department of Animal Management, Van Hall Larenstein University of Applied Sciences, Leeuwarden, The Netherlands

ARTICLE INFO

Article history:
Received 28 October 2015
Initial acceptance 9 December 2015
Final acceptance 24 February 2016

MS. number 15-00922R

Keywords:
habitat characteristics
Lepus europaeus
nonlethal predator
risk effect
stretch length
vegetation structure

Reactive movement responses of prey are affected by habitat characteristics, such as cover, which determine predation risk. Open habitats with low cover facilitate predator detection, movement and escape, while closed habitats reduce the ability to detect predators and hinder movement. We performed a field experiment using nonlethal predators to study the reactive movement responses of medium-sized prey in patches with different vegetation characteristics related to elevated predation risk. Ten GPS-collared, free-ranging European hares, *Lepus europaeus*, were repeatedly subjected to a leashed dog and two humans in an experimental cross-over design. Linear mixed models were used to assess the effect of the treatment and its interaction with vegetation parameters on the movement behaviour of the European hare. The reactive movement response was best explained by the model that included the interaction between elevated predation risk and vegetation structure. A strong immediate response was found in short vegetation up to 1 h after the treatment ended. The effect extended beyond the duration of the treatment and was synchronized with the resting and foraging period over the next 24 h. The distance covered between resting and foraging grounds was negatively affected, while use of less risky, low-quality vegetation during resting and foraging was favoured. Medium-sized prey species exhibit strong behavioural responses to the perceived predation risk, which we demonstrate here for the European hare. An elevated predation risk, for example by dogs, can trigger costly behavioural responses in these medium-sized prey species.

Predators affect prey by increasing mortality and altering behaviour (Creel & Christianson, 2008; Lima & Dill, 1990). The impact of predators scaring prey (risk effects) is at least as strong as or stronger than predator density effects (Preisser, Bolnick, & Benard, 2005). These risk effects induce antipredator behaviour, such as predator avoidance, and negatively affect foraging efficiency (Møller, 2008).

Prey can show both predictive and reactive responses to perceived predation risk. Predictive responses are based on previous knowledge and are thus not immediate, but are expressed by long-term habitat selection (Valeix et al., 2009). Reactive responses are based on current knowledge resulting in immediate responses during an encounter with a predator. Habitat characteristics are expected to affect reactive movement responses (Broekhuis, Cozzi, Valeix, McNutt, & Macdonald, 2013; Ydenberg & Dill, 1986) and the rate at which predators succeed in preying upon animals (Gorini et al., 2012). Previous studies have characterized the riskiness of habitats (i.e. amount of cover) by vegetation density, height or structure (Bissett & Bernard, 2007; Riginos & Grace, 2008). In general, open, less structured, relatively homogeneous habitats with little cover lead to high visibility for both prey and predators. This type of open habitat reduces the opportunity for hiding and concealment, but will cause prey to be more easily alerted (Focardi & Rizzotto, 1999). Little cover facilitates movement or escape. In contrast, closed, structured, relatively heterogeneous habitats provide cover, but they reduce the ability to visually detect predators and hinder movements (Lima, 1992).

Studying movement offers the potential to understand the relative riskiness of habitats (Valeix et al., 2010). Movement allows animals to optimally use their habitat by trading off energy investment and expenditure (Johnson, Wiens, Milne, & Crist, 1992). Overall, faster movement can be expected in open habitats when predation risk is elevated than in closed habitats (Hauzy, Tully,

* Correspondence: M. J. A. Weterings, Resource Ecology Group, Wageningen University, 6708 PB Wageningen, The Netherlands.
E-mail addresses: Martijn2.Weterings@wur.nl, Martijn.Weterings@hvhl.nl (M. J. A. Weterings).

http://dx.doi.org/10.1016/j.anbehav.2016.03.011
0003-3472/

Spataro, Paul, & Arditi, 2010). Although reactive responses have been the focus of various correlative field studies (Valeix et al., 2009) and experimental laboratory studies (mostly aquatic, Waggett & Buskey, 2007), the interaction between elevated predation risk and cover on reactive movement responses of mammal prey has not as yet been tested experimentally in a field setting.

Predation effects are dependent on body mass. Small (e.g. rodent) and medium (e.g. lagomorph) prey species are expected to be top-down regulated by predation, whereas population sizes of large prey species (e.g. bovines) will be determined by food availability (Hopcraft, Olff, & Sinclair, 2010; Sinclair, Mduma, & Brashares, 2003). For medium-sized prey, elevated predator encounters in open habitats are expected to result in a reactive movement response characterized by increased speed, or longer stretches (Waggett & Buskey, 2007) alternating with small angle directional changes to allow prey to escape predators. In closed habitats, prey are expected to remain motionless due to the presence of cover.

The European hare, *Lepus europaeus*, is a medium-sized, solitary, noncentral-place herbivore found in open areas. Most medium-sized mammals like the European hare are nocturnal or crepuscular and share visual and auditory adaptations for living in low light conditions (Ashby, 1972); thus they presumably perceive predation risk in a similar way. Hare populations have decreased consistently and substantially in Europe since the 1960s (Tapper & Parsons, 1984). A broad spectrum of possible causes has been postulated (Smith, Jennings, & Harris, 2005), including recent increases in their main predator, the red fox, *Vulpes vulpes* (Knauer, Küchenhoff, & Pilz, 2010). Smith et al. (2005) identified agricultural intensification as the ultimate cause of their decline, leading to more homogeneous landscapes that are lacking in cover. As a consequence, hare populations could experience greater predator impact (Schneider, 2001). Risk effects are especially profound in hares, as they cannot rely on aggregation or a burrow to reduce predation risk (Creel, 2011). Hares have developed a very strong active antipredator strategy; they are built for flight, while at the same time they can be immobile, vigilant and cryptic.

We hypothesized that the reactive movement response of medium-sized prey in low cover habitats would increase in speed with an elevated predation risk compared with movement in high cover habitats. To test this hypothesis we performed a field experiment and manipulated predation risk using nonlethal predators. European hares were used as the medium-sized prey species and were affixed with GPS collars to more accurately track movement.

METHODS

Study Area

The study was conducted on the island of Schiermonnikoog (53°30′N, 6°10′E), The Netherlands. Two 200 ha experimental areas were selected, both at least 1 km apart to prevent overlap of hare territories between the two sites (Fig. 1). The sites had similar vegetation types and structures, containing successional stages from pioneer to climax stage, with a patchy distribution of both homogeneous and heterogeneous dune and salt marsh habitat. The salt marsh was a lowland area under tidal influence positioned parallel to the coastline. Currently, a fluctuating population of between 300 and 600 sedentary European hares live on the island (Van Wieren, Wiersma, & Prins, 2006), with an average home range (values are given as mean ± SD throughout the manuscript) of 27.3 ± 9.0 ha (Kunst, van der Wal, & van Wieren, 2001).

On the island of Schiermonnikoog, birds of prey such as the marsh harrier, *Circus aeruginosus*, goshawk, *Accipiter gentilis*, and common buzzard, *Buteo buteo*, and feral cats prey upon hares (Van Wieren et al., 2006), albeit mainly on leverets and juveniles during the reproductive season. Thus, adults experience low natural predation risk. Moreover, hunting has not been allowed since 1996.

Experimental Design

European hare body weights increase from midway through the autumn to overcome the reduction in resource quality and quantity in winter and to build up fat reserves. These reserves are necessary for reproduction; hares are capital breeders, at least during their first litter (Valencak, Tataruch, & Ruf, 2009). It can be assumed that, owing to their accumulated body fat, European hares respond maximally to predation risk in autumn and the onset of winter (Luttbeg, Rowe, & Mangel, 2003), making antipredator behaviour more pronounced. The study was therefore conducted outside the reproductive season, from 17 November to 22 December 2012.

To test reactive movement responses to elevated predation risk, an experimental cross-over design with three nonlethal predators (i.e. a dog and two humans) was performed. Because both predators and disturbers can cause similar antipredator behaviour (Frid & Dill, 2002), such behaviours are thought to be a generalized response to stimuli that indicate potential predation risk (Koops, 2004). Sheriff, Krebs, and Boonstra (2009) demonstrated that nonlethal dog exposure had a negative effect on the reproductive output of snowshoe hares. It was thus likely that exposure to a nonlethal dog in this study would trigger antipredator behaviour of our prey species. Reactive movement responses of European hares were measured using GPS data loggers that stored one position fix every 6 min for 2×12 days. Previous work demonstrated that patterns of activity and movement of brushtail possums, *Trichosurus vulpecula*, were affected by tagging and could persist for at least 4 days (Dennis & Shah, 2012). Therefore, the initial experiment was preceded by a 5-day settling down period (Petrovan, Ward, & Wheeler, 2013) and subsequent experiments were separated by a 5-day washout period, during which the hares did not receive any treatment. We assumed that our treatment did not impact the hares more strongly than the tagging itself. Thus, we assumed that a 5-day washout period eliminated previous treatment effects and minimized carry-over effects (Ruxton & Colegrave, 2011).

In each of the two experimental areas, five healthy European hares (three females and two males) with an average body weight of 3291 ± 237 g ($N = 10$) were caught and equipped with a GPS transmitter positioned on a neck belt. We used lightweight GPS transmitters (69 g, 2.11 ± 0.15% of body weight) with a radio link for wireless communication (Type A, E-obs GmbH, Gruenwald, Germany) to minimize disturbance of the experimental subjects. Body weight was measured, as it can influence movement patterns and habitat use (Prevedello, Forero-Medina, & Vieira, 2010). To capture study animals, hares were flushed by a line of beaters and caught using eight Speedset static hare nets (ca. 90 m × 45 cm, with 13 cm full mesh; JB's Nets, Alexandria, U.K.) positioned in a T shape. Hares that were captured in the nets were removed within 2–3 min by trained experts standing under cover in front of the nets. After capture, the hares were temporarily kept in darkened wooden boxes (20 × 30 cm and 25 cm high) with ventilation holes to reduce excess body heat and were blindfolded by a hood to reduce visual stimulation and stress (Paci, Ferretti, & Bagliacca, 2012). Tagging proceeded immediately after all hares in the area were flushed. The hooded hares were gently stabilized by two persons and tagged without sedation (Gerritsmann, Stalder, Seilern-Moy, Knauer, & Walzer, 2012); handling was kept to a minimum and took 4 min or less on average. Experimental design, capturing and tagging of hares were approved by the Wageningen University Animal Experiment Committee (no. 2012083) and followed the EU Directive 2010/63 on the protection of animals used for scientific purposes.