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

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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.
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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,

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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.
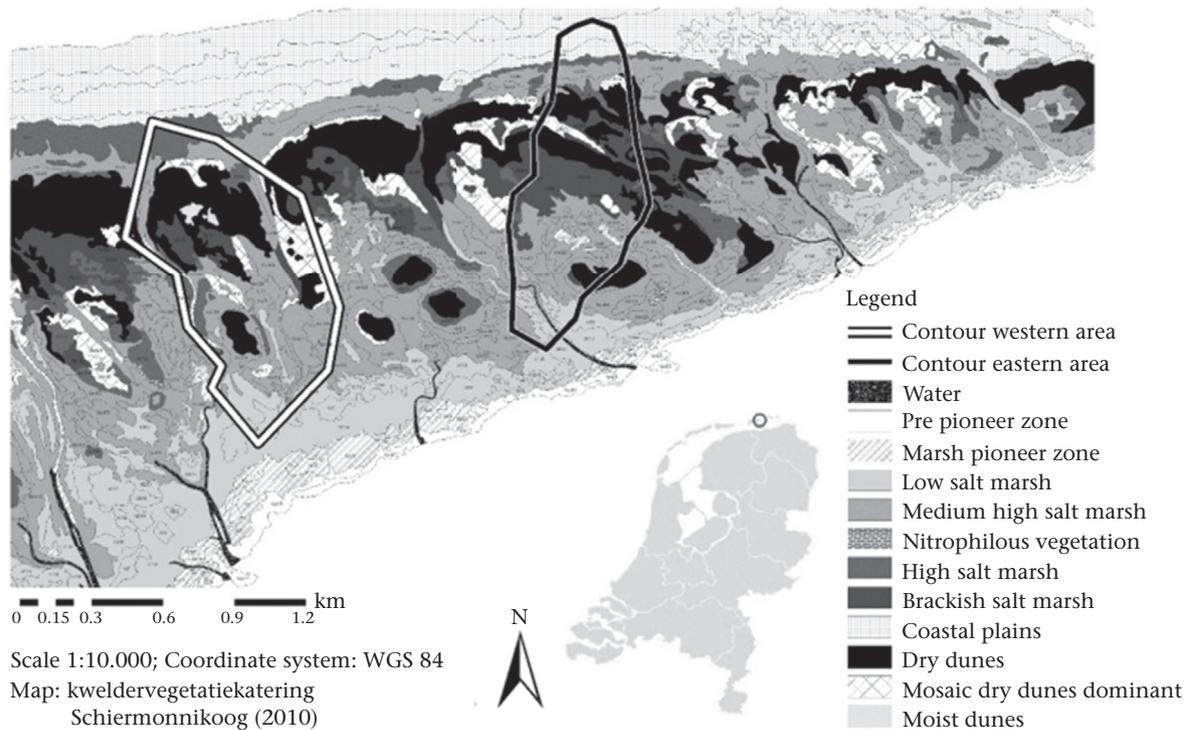
Figure 1. Delineation of the study area on Schiermonnikoog, including the two experimental areas in the salt marsh; the western (left) and eastern (right) areas are shown with white and black contour lines, respectively.

During the experimental treatment, two persons walked with a nonbarking and leashed (±5 m long line) 4-year-old dog (black labrador retriever) through the centre of hare activity for 57 ± 11 min. The centre of hare activity (determined by the locations of all individuals) was updated daily using new remotely recorded GPS locations obtained from the hares' transmitters; locations were determined using a BaseStation (b5, E-obs GmBH, Gruenwald, Germany). During the first 12 days, the treatment was executed in the western area every day and the eastern area served as the control area. After the 5-day washout period, the treatment was executed in the eastern area for 12 consecutive days, while the western area served as the control area. Hares did not move between study areas because the minimum distance that separated the GPS locations of the collared hares in the two study areas was 537 m. The onset of the experiment was on average 72 ± 35 min before sunset (i.e. during peak hare movement (Schai-Braun, Rödel, & Hackländer, 2012)), which began at 1623 hours (GMT+1). At that time of the day hares become active (Schai-Braun et al., 2012). This timing allowed us to measure potential reductions as well as increases in movement activity as a response to the treatment.

Data Preparation

Accuracy of all GPS collars was measured in the habitats studied prior to animal tagging. After data collection, we used only those GPS (E-obs GmbH GPS loggers, Ublox LEA-4T) locations with a horizontal inaccuracy of less than 10 m, improving the GPS accuracy from 8.63 ± 9.62 m to 5.82 ± 4.06 m. Spatial data were corrected for location errors (Bjørneraas, van Moorter, Rolandsen, & Herfindal, 2010; Friar et al., 2004), which reduced the original data set to 66.5% of its original size. First, GPS data were averaged over two subsequent GPS locations around a single gap when their Euclidean distance was smaller than 18 m (mean GPS accuracy ± 3 SD). Subsequently, we removed 'spikes' where the angle between three successive GPS locations was greater than 150° and smaller

than 210°. Lastly, we removed cases where calculated speed over ground was greater than 15 m/s or the distance travelled between the 6 min intervals was greater than 1000 m.

We parameterized the riskiness of habitats in classes based on the dominant vertical vegetation structure (VST), primarily using vegetation height (0−1 m). Low cover represented high-risk vegetation with a short height, while high cover implied the opposite. Habitats were placed on an ordinal scale from low cover to high cover as follows: bare soil (BS, 0 cm); short herb/grass layer (SO, 0−30 cm); tall herb/grass layer (TA, 30−100 cm); shrubs (SH, 0−50 cm). Geographical analysis (ArcGIS 10.1) was used to obtain the vegetation structure from landscape maps (1:10 000 with an accuracy of 2 m, based on false-colour aerial photography, average patch size 0.66 ha; Pranger & Tolman, 2012). We also included two additional vegetation parameters: the Euclidean distance (DIS) between European hare GPS location and the nearest vegetation patch edge, and patch edge length (EDG). Not only do structure-rich landscapes have a high edge to area ratio (Gorini et al., 2012), European hares prefer edge habitat, and their body weight (condition) is related to edge length (Wincentz-Jensen, 2009).

Data Analysis

We ran multiple linear mixed models (LMM) to assess the effects elevated predation risk, and its interaction with all three vegetation parameters, on the movement behaviour of European hare. We quantified the movement behaviour by calculating the stretch lengths of the movement paths (i.e. the distance between two fixed points), which indicates the net displacement distance covered by the hares during the 6 min interval between the GPS fixes. Predictor variables were grouped into three categories: (1) treatment (and its interaction with the 1 h time span before, during and after the treatment); (2) vegetation parameters; and (3) control variables. Vegetation parameters consisted of VST, DIS and EDG. We included the two plausible control variables most relevant

for hare movement, namely the time to sunset (Schai-Braun et al., 2012) and weight (Prevedello et al., 2010). We generated 14 candidate models from the combinations of these categories, including an intercept- and treatment-only model for comparison (Table 1). Small sample Akaike information criterion (AICc) values were used to select the best fitting 95% weighted models. Candidate models were used to assess the relative strength of our hypothesis, following Grueber, Nakagawa, Laws, and Jamieson (2011). To prevent overprediction, the maximum number of predictor variables in any model never exceeded five, following Burnham and Anderson (2002).

Individual hares on separate days were used as subjects in the LMM to overcome autocorrelation in the covariance matrix between consecutive days. The GPS interval was set as the repeated measure. The autoregressive moving average (ARMA(1,1)) covariance structure was selected using restricted maximum likelihood (REML) estimation based on minimum AICc values. Maximum likelihood (ML) was used to compare the different models.

RESULTS

We found that the reactive movement response of European hares was best explained by the model including the interaction between the treatment and vegetation structure, with the time until sunset and body weight as controlling variables (Table 1; see Appendix I for beta coefficients and standard errors of the best fitting model).

Models that included VST had a better fit than models that included the DIS, while EDG performed worst of the vegetation parameters. Models that included an interaction between the treatment and the vegetation structure outperformed similar models containing only the main effects of the treatment and vegetation structure. In contrast, models including the main effects of DIS and EDG had a better fit than models that included the interaction of these parameters with the treatment. There was no significant difference in movement response between the two study areas ($F_{1,442} = 1.17$, $P = 0.28$). Day, as a random factor, was not significant (Wald = 0.51, $P = 0.61$), suggesting that habituation to the treatment was not relevant.

Elevated predation risk increased stretch length compared to control areas in habitats with little structure (i.e. bare soil, low and tall herb/grass layers) during the treatment. This behavioural change was similar 1 h after treatment, but only in vegetation with low and tall herb/grass layers (Fig. 2). Remarkably, the behavioural response was strongest in shrub vegetation 1 h before the treatment commenced. Stretch length in the treated areas during the time of treatment was significantly higher in the low herb/grass layers compared with the tall herb/grass layers. Stretch length in the former was also significantly greater compared with stretch length in the same vegetation structure 1 h before the treatment took place.

In the control area, the average 6 min stretch length was shortest in shrub vegetation 1 h before the treatment. Stretch length was also significantly different in shrub vegetation compared with bare soil or vegetation with low and high herb/grass layers during the same time period. Furthermore, in shrub vegetation, stretch length differed between the time of treatment and the subsequent 1 h time period.

The effect of the predation risk treatment on the Euclidean distance between the position of the hares at the start of the dog walk and positions during the rest of the day (Fig. 3) roughly followed the day–night cycle. This cycle could be split in three distinct phases. During the first 2 h and last 7 h of the day, the Euclidean distance moved by hares exposed to elevated predation risk was larger compared to hares in the untreated area, but distances were lower for treated hares during the night (Fig. 3). The same pattern was observed for hares in vegetation with tall herb/grass layers (Fig. 4a) and in shrub vegetation (Fig. 4b). Compared with the control group, hares in the treated area were more often present in vegetation with tall herb/grass layers during the night (Fig. 4a), but were less frequently present in this type of vegetation structure during the day. Hares were found in vegetation with tall grass/herb layers in 58.4% of the total number of fixes. Hares in the treated area were present in shrub vegetation less often during the night, but more often during the day, compared with the control (Fig. 4b). In addition to the increased presence in the shrub layer during the day, treated hares exhibited a larger average stretch length in shrubs 1 h prior to treatment (Fig. 2). Hares were in shrub vegetation in 15.1% of the total number of fixes. The difference (treatment − control) in the fraction of time spent by hares on bare soil and in vegetation with short herb/grass layers did not show the distinct pattern seen in the vegetation with tall herb/grass layers and shrub vegetation.

Table 1
Results of the linear mixed model selection, the effect of elevated predation risk and its interaction with vegetation parameters on the movement response of European hares

Model type	Rank	Model	K	AICc	ΔAICc	w_i
Intercept	14	Intercept	4	8995.0	294.0	<0.01
T	10	(T∗HR)	9	8782.2	81.2	<0.01
T+vegetation parameter	8	(T∗HR)+VST	12	8767.7	66.7	<0.01
	9	(T∗HR)+DIS	10	8779.7	78.7	<0.01
	11	(T∗HR)+EDG	10	8783.2	82.3	<0.01
T+vegetation parameter+control	2	(T∗HR)+VST+TS+W	14	8710.1	9.1	0.01
	3	(T∗HR)+DIS+TS+W	11	8716.9	15.9	<0.01
	5	(T∗HR)+EDG+TS+W	12	8722.6	21.6	<0.01
T∗vegetation parameter	7	(T∗HR∗VST)	27	8760.5	59.5	<0.01
	12	(T∗HR∗DIS)	13	8784.2	83.2	<0.01
	13	(T∗HR∗EDG)	13	8786.4	85.4	<0.01
T∗vegetation parameter+control	1	(T∗HR∗VST)+TS+W	29	8701.0	0.0	0.99
	4	(T∗HR∗DIS)+TS+W	14	8722.5	21.5	<0.01
	6	(T∗HR∗EDG)+TS+W	15	8726.7	25.7	<0.01

AICc: Akaike information criterion corrected for small sample size; ΔAICc: delta AICc with regard to best fitting model; DIS: distance to nearest edge; EDG: patch edge length; HR: h block (1 h data segment before, during and after the experiment); K: number of estimated parameters; T: treatment; TS: time to sunset; VST: vegetation structure; W: body weight; w_i: Akaike weight or relative weight of each model.
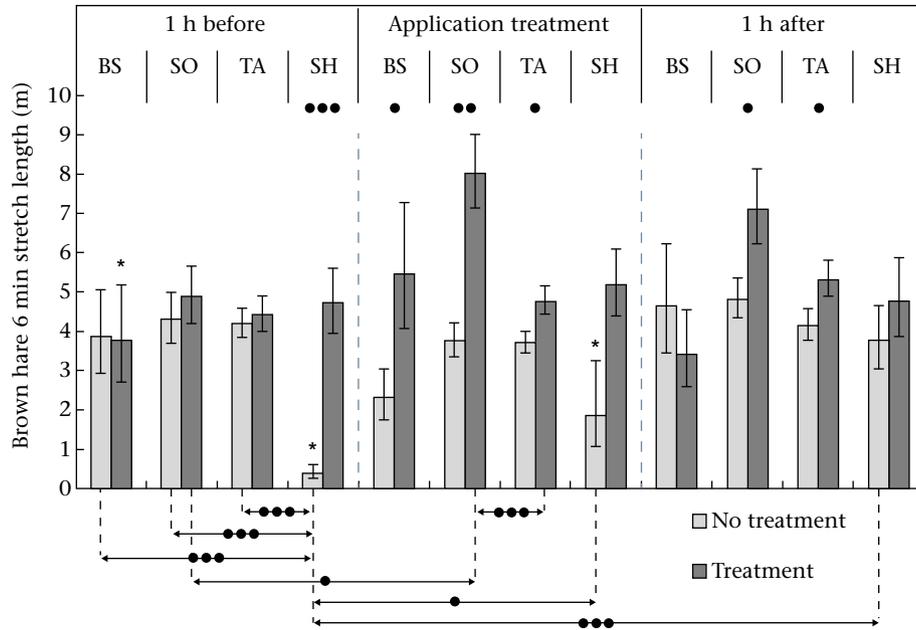
Figure 2. Six-minute stretch length of European hare 1 h prior to, during and after predation risk treatment in different habitats (marginal means + 95% confidence intervals). Vegetation structures (% used) are as follows: BS = bare soil, 0 cm (4.4%); SO = short herb/grass layer, 0–30 cm (26.4%); TA = tall herb/grass layer, 30–100 cm (62.1%); SH = shrub, 0–50 cm (7.2%). Dots above the bar graph indicate differences between treated and untreated groups, whereas the dots underneath the columns show differences between types of vegetation structure within a treatment group. •$P < 0.05$; ••$P < 0.01$; •••$P < 0.001$ (Sidak test). Marginal means were evaluated 0.69 h before sunset for a European hare with a weight of 3322 g (average $N = 25.5$, * < 5 samples).

DISCUSSION

We investigated the reactive movement response of European hares following exposure to an elevated predation risk, that is, a leashed dog with two humans, in a mosaic of salt marsh vegetation. Our study is the first to experimentally manipulate and measure the short- and longer-term effects of predation risk on the movement activity of a medium-sized mammal in a field setting (Ferrari, Sih, & Chivers, 2009).

We showed that there was a strong reactive movement response to elevated predation risk in short vegetation. Vegetation structure was the most important vegetation parameter affecting the reactive movement response of hares, followed by the distance to the nearest vegetation patch and patch edge length. Finally, the effect of the elevated risk treatment extended beyond the immediate time of the treatment. Although the effect roughly followed the night and day activity cycle, risk exposure primarily influenced the time spent in vegetation with high cover
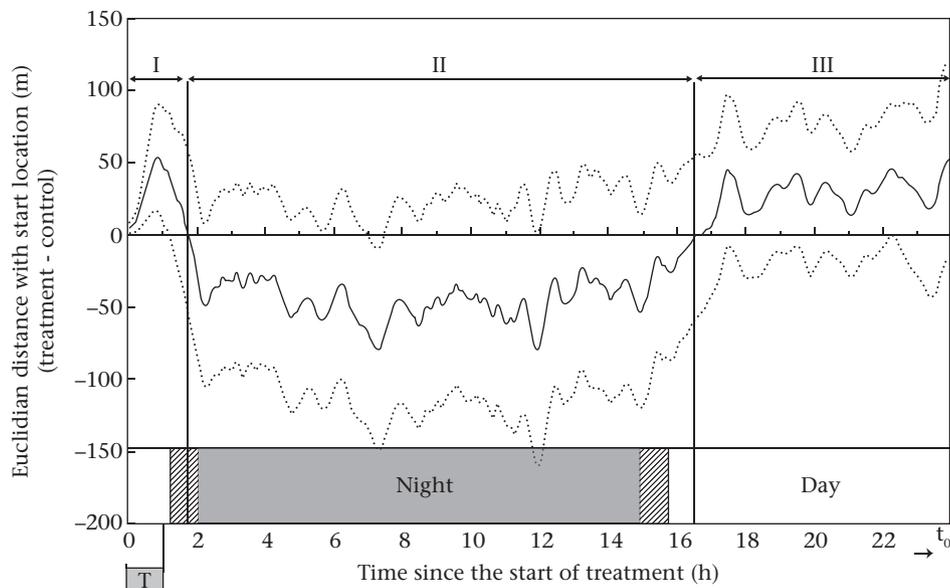
Figure 3. Time since the start of the treatment and the Euclidean distance between the start location at t_0 and the location of European hares at t_x (average $N = 50.1$; treatment – control); the bold black line indicates the mean, the broken lines indicate the upper and lower 95% confidence intervals. T = application of treatment. Three phases can be distinguished: I and III, where treatment > control, and II, where treatment < control. The light grey areas indicate dusk and dawn.
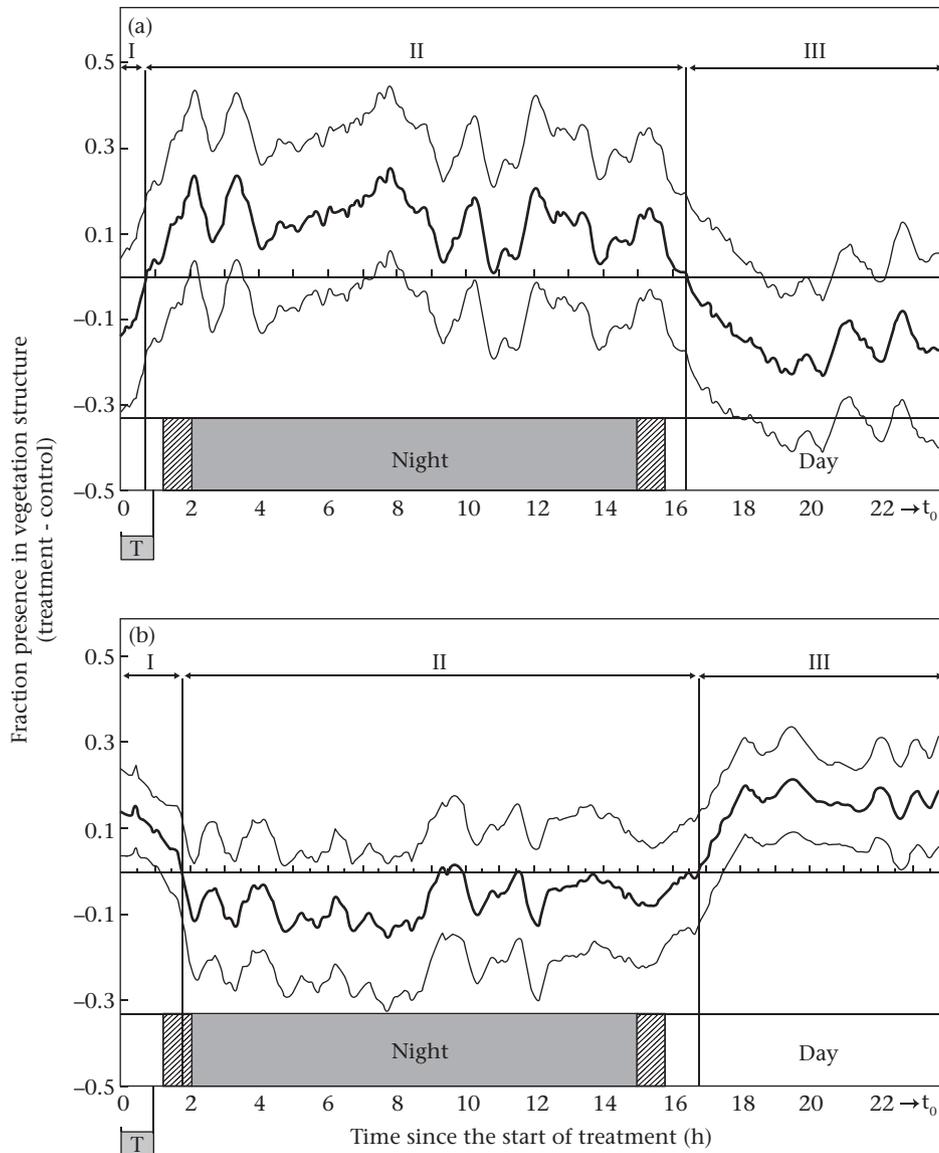
Figure 4. The time since the start of the treatment and the fraction of time spent in (a) vegetation with tall herb/grass layer (30–100 cm) and (b) shrub vegetation (0–50 cm) by European hares (average $N = 50.1$; treatment – control); the bold black line indicates the mean, the broken lines indicate the upper and lower 95% confidence intervals. T = application of treatment. Three phases can be distinguished: I and III, where treatment > control, and II, where treatment < control. The light grey areas indicate dusk and dawn.

(shrub), in which prey was found after the sunrise following the treatment.

Reactive Response

As hypothesized, the reactive response increased prey average speed only in areas of low cover, while the average speed in high cover did not show a significant increase. There are several explanations for these responses. First, low cover is correlated with high visibility and more frequent encounter rates (Gorini et al., 2012). An imminent predation threat can encourage prey to avoid the attention of the predator (Broom & Ruxton, 2005; Ydenberg & Dill, 1986) by moving to a safer location with more cover. Second, the spatial distribution of vegetation patches in the salt marsh mosaic may affect habitat-dependent escape tactics (Heithaus, Wirsing, Burkholder, Thomson, & Dill, 2009). Compared to a more open area, a patchwork of small vegetation patches decreases the detection distance of approaching predators. Prey present in low

cover patches seem to increase speed, resulting in movement to new vegetation patches, where 'its escape tactic is most effective' (Lima, 1992, p.598). Third, the interaction between predator type and vegetation structure is important for the perceived predation risk by prey. For example, Hewson (1977) emphasizes the importance of low cover to enable European hares to see approaching predators and thus facilitate flight. High cover benefits stealth-dependent predators (i.e. ambush or stalker), while low cover benefits coursers. During our experiment, prey that recognized the nonlethal predator as a courser could have been avoiding low vegetation to reduce predation risk.

We found an increase in the speed of hares in shrub vegetation over time in the untreated areas around the time of treatment application (i.e. just prior to sunset). At that time of day, European hares increased locomotion to translocate from resting areas to foraging grounds (Schai-Braun et al., 2012). For unknown reasons, the stretch length of hares in shrub vegetation in the treated area 1 h before the application of the treatment was significantly higher

than the control. For the treated prey, the perceived predation risk in shrub vegetation during treatment did not increase the benefits of fleeing to outweigh the benefits of staying (Ydenberg & Dill, 1986). Vegetation with high cover reduces fear in animals (Stankowich & Blumstein, 2005). In addition, European hares make use of morphological crypsis in covered vegetation to effectively reduce flight distance (Focardi & Rizzotto, 1999).

Our results show a clear influence of the daily activity cycle, as seen in the transition from one phase to another, on the effect of treatment over the subsequent 24 h. Although marginally significant, treated prey tended not to move as far as the control group from their original position at dusk during the start of the treatment; nor did they return as close to that position at dawn. Cooper and Sherbrooke (2013) showed that cryptic prey take their own recent movement into account in assessing predation risk, explaining the reduction in speed after an initial flight response. According to models of patch use under predation risk, animals either reduce behaviours that attract predators, such as moving, or increase the encounter rate with predators (Brown, 1999). European hares leave their resting areas just before sunset and move to foraging grounds, where they forage during the night (Tapper & Barnes, 1986). Just prior to sunrise, they relocate to their shelters again. It seems that these transitions from shelter to foraging ground and back are affected several hours after the application of the treatment, resulting in shorter translocations, possibly in an attempt to avoid predator attention. Compared with the control group, prey that experienced an elevated predation risk favoured the high cover vegetation patches during their daily activities over the subsequent 24 h. These patches contained a lower quality of forage, but were less risky (Gorini et al., 2012; Hauzy et al., 2010), and thus indicate an antipredator benefit (Lima & Dill, 1990).

Continuous disturbance resulting in antipredator behaviour and the effects of behavioural changes on lower trophic levels (i.e. trait-mediated indirect effects) require further attention (Kuijper et al., 2013). Kuijper and Bakker (2005), for example, showed that exclusion of European hares allows the invasion of late successional plant species in some habitats, with shifts in species composition being most pronounced in unproductive areas. Trait-mediated indirect effects of prey may thus have a strong effect in dunes or other unproductive habitats.

Here we used a nonlethal dog as a (cursorial) predator, because we see this experiment as a first step towards evaluating the risk effects on medium-sized prey (Luttbeg et al., 2003). The question remains as to whether these effects were the result of the direct exposure to the humans or the dog, or the result of the dog's odour. Odours can cause habitat shifts, alter activity patterns or reduce nondefensive behaviours, and skin- and fur-derived odours have a stronger long-lasting effect on prey species than those from urine or faeces (Apfelbach, Blanchard, Blanchard, Hayes, & McGregor, 2005). However, according to Thaker et al. (2011), ungulates did not avoid areas of high utilization by cursorial predators, probably as olfactory cues associated with coursing predators were not related to predator proximity (Wilkenros, Kuijper, Behnke, & Schmidt, 2015; but see Kuijper et al., 2014).

Smaller prey species exhibit stronger behavioural responses to perceived predation risks than larger species (Creel, 2011). Nevertheless, it is not uncommon for prey to compensate behaviourally for losses, for example in foraging, due to risk effects (Luttbeg et al., 2003). Repeated exposure to elevated predation risk, as well as disturbance (Frid & Dill, 2002), could make the effects on medium-sized prey shown here more long lasting, with potential demographic consequences (Sheriff, Krebs, & Boonstra, 2011). European hares are sensitive to disturbance, especially by dogs (Hoeksma, 1950) and roads (Roedenbeck & Voser, 2008). Frequent disturbances could have contributed to the population declines of European hares near human populations (Cromsigt et al., 2013). Young, Olson, Reading, Amgalanbaatar, and Berger (2011) suggested that dogs should be excluded from critical wildlife habitats, as they and their accompanying humans can affect prey habitat choice and movement activity, and can bring about a costly stress response (Lenth, Knight, & Brennan, 2008).

Conclusions

We found an interaction between elevated predation risk and cover on the reactive movement responses of a medium-sized prey, the European hare, in a field experiment. Hares show a strong reactive response to elevated risk in low cover. Vegetation structure most strongly affected the reactive response of hares. We also observed an extended effect of the treatment used in this study, with hares spending more time in high cover vegetation during resting and feeding for at least 24 h following predator exposure.

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APPENDIX

The coefficients (β) and standard errors (SE) of the best fitting model (the three-way interaction between the treatment, vegetation structure and h block) were generally higher during the control phase of the experiment than during the treatment phase (Table A1). Time until sunset was positively related to European hare 6 min stretch length, while a higher European hare body weight was related to shorter stretch lengths.

Table A1
Beta coefficients and SEs of the best fitting model [(T ∗ HR ∗ VST) + TS + W] variables related to European hare 6 min stretch length

Model variable*	HR		
	1 h before	During treatment	1 h after
T (control)∗VST			
1. BS	2.55±0.62	3.16±0.79	2.38±0.81
2. LO	0.077±0.43	0.67±0.67	0.076±0.69
3. HI	0.15±0.46	1.16±0.69	0.35±0.71
4. SH	Ref	0.88±0.54	−0.27±0.58
T (treatment)∗VST			
1. BS	Ref	2.10±0.68	2.11±0.61
2. LO	Ref	0.39±0.38	−0.20±0.41
3. HI	Ref	0.37±0.40	−0.070±0.43
4. SH	Ref	Ref	Ref

HR: h block (1 h data segment before, during and after the experiment); T: treatment; TS: time until sunset (h); VST: vegetation structure [BS, bare soil (0 cm); LO, low herb/grass layer (0–30 cm); HI, high herb/grass layer (30–100 cm); SH, shrub (0–50 cm)]; W: body weight (g); ref: reference category = shrub vegetation 1 h before treatment.
* Without main effects of three-way interaction. Intercept: β ± SE = −2.37 ± 0.49; TS: β ± SE = 0.34 ± 0.043; W: β ± SE = −0.0002 ± 0.0001.