

Predator-hunting success and prey vulnerability: quantifying the spatial scale over which lethal and non-lethal effects of predation occur

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Summary

1. The shape of the function linking predator-attack success rate with distance to predator-concealing cover, or prey refuge, will affect population dynamics, distribution patterns and community trophic structure. Theory predicts that predator-attack success should decline exponentially with distance from predator-concealing cover, resulting in a threshold distance value above which there is little change in risk. Animals should then completely avoid areas of otherwise suitable habitat below this threshold, except when starvation risk exceeds predation risk.

2. We measured the shape of the function linking attack success with distance from cover in a system of Eurasian Sparrowhawks *Accipiter nisus* attacking ($n = 445$) and killing ($n = 71$) Redshanks *Tringa totanus*. We then determined if there was a threshold value and whether redshanks avoided areas below this threshold.

3. Sparrowhawk success rate with distance to predator-concealing cover declined exponentially with a threshold value of approximately 30 m. Redshanks used habitat above the threshold according to profitability and only fed below it, on average, in cold weather when starvation risk can be imminently high. Above about 5°C, 26% of available habitat was avoided.

4. Our data support the hypothesis that predators create discrete areas with respect to cover that are avoided by prey. Large areas of suitable habitat may be unused, except in times of high starvation risk, when such areas may provide a foraging reserve, with large implications for population distribution and dynamics.

5. Our results are generated from a system in which predators attack their prey from concealing cover. But in the theoretically identical reverse scenario where the prey animal's distance from protective cover determines predation risk, such non-lethal effects will be equally important, especially in heavily fragmented landscapes.

Key-words: cover, hunting success, predation risk, refuge, trait-mediated interactions

Introduction

Explaining the outcome of predator–prey interactions is fundamental to understanding behavioural variation, population dynamics and community structure (Lima 1998; Werner & Peacor 2003; Caro 2005). Changes in prey density and the associated cascading effects on other trophic levels can occur through both lethal effects, where prey is eaten by predators and by non-lethal effects, where prey avoid predators (Abrams 1984). Several studies have shown that such non-lethal effects can have major effects on behaviour, on habitat

use and on community structure (Cowlshaw 1997; Schmitz, Krivan & Ovardia 2004; Owen-Smith & Mills 2006; Ripple & Beschta 2006; Schmidt 2006; Thomson *et al.* 2006; Creel *et al.* 2007). Similarly, the influence of distance to protective cover on predation risk and its ecological effects as a consequence of foragers avoiding risky areas (i.e. the ‘landscape of fear’ Brown, Laundre & Gurung 1999) has also been shown by several studies indirectly using ‘giving-up densities’, where degree of patch depletion indicates perception of risk (e.g. see Brown 1988; Olsson, Brown & Smith 2002; Brown & Kotler 2004). The shape of the function relating predator-attack success with distance from predator-concealing cover, or distance of prey from a refuge, will be particularly important

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because this determines the spatial and trophic scale over which predators and prey interact, and which habitats will be avoided by prey (Abrams 1993; Lima 1998; Brown *et al.* 1999; Cresswell 2008; Griesser & Nystrand 2009).

Cover can be perceived by the prey as being dangerous because it conceals surprise hunting predators (e.g. Cresswell 1994a; Devereux *et al.* 2006) or the reverse, when animals have a preference for foraging close to cover because it presents a refuge (e.g. Walther & Gosler 2001; Lee, Kuo & Bollinger 2005). In both cases, attack success depends on the relative distance (or time) that a predator has to approach the prey to catch it, relative to the distance (or time) that the prey has to reach safety (Blumstein 2003; Lind 2004; Stankowich & Coss 2006). Non-lethal effects related to distance from protective, rather than predator-concealing, cover should therefore be the same. Whether cover conceals predators or acts as a refuge for prey will determine whether areas close or far from cover are avoided, but the size and importance of these zones will be determined in both cases by the average attack success, the speed of the exponential decline in the attack success function, and the proximity of cover and foraging areas.

In this study, we consider the case of where cover hides the predator. Theory and some empirical data suggest that attack success rate declines with increasing distance to cover with an exponential function (Fig. 1a) (Cresswell 1994a; Whitfield 2003; Cresswell & Quinn 2004); see Caro (2005) for review. This is simply because animals further from predator-concealing cover have more time to detect an approaching predator and so to make an effective escape. Above a threshold of distance to cover however, detection probability becomes close to one so that further increases in distance to cover will make little difference to the probability of detection (Pulliam 1973; Roberts 1996; Fig. 1a). Therefore, attack success should remain reasonably constant above this threshold separating 'risk' distances from 'safe' distances (Fig. 1a). Here, we examine a large quantity of observational data of Redshank *Tringa totanus* (L.) flocks being attacked by Eurasian Sparrowhawks *Accipiter nisus* (L.) at different distances to cover (see Cresswell & Whitfield 2008 and references therein for details of the long term study). We determine whether any observed threshold in attack success decline results in habitat avoidance and so quantify how a non-lethal effect of predation risk determines prey distribution.

If there is a clear threshold where attack success levels off with distance to cover a number of predictions arise. Firstly, if energy budgets can be met in areas above the threshold, then animals should not feed in areas below the threshold, instead concentrating in areas that have the highest profitability within the 'safe' distances. In our redshank system, feeding rate increases with proximity to predator-concealing cover (Cresswell 1994b; Sansom *et al.* 2008) because prey is larger and more profitable (Cresswell 1994a), and also more available (Minderman, Lind & Cresswell 2006). Therefore, we predict that redshanks should feed most commonly close to the threshold, where risk is minimized and intake rate

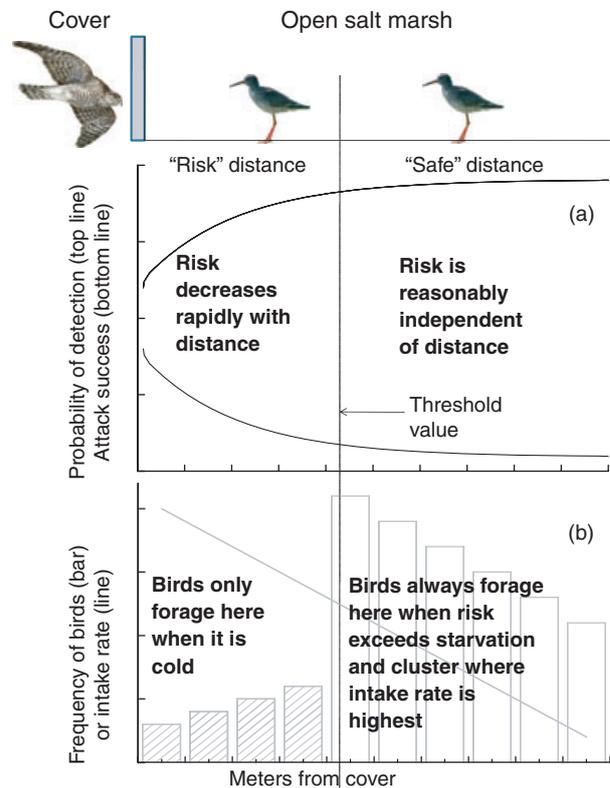


Fig. 1. Predictions of the study. Probability of detection increases with distance from predator-concealing cover but rapidly reaches an asymptote of 1 (top line a), so capture success rate of a predator emerging by surprise from cover is predicted to follow a negative exponential function reflecting this (bottom line a). By its nature, an exponentially declining function will have a period of rapid change followed by a period of very slight change, resulting in two distinct regions: 'risk' distances where risk decreases rapidly with distance, and across a threshold value, 'safe' distances where risk is reasonably independent of distance (a). When animals can meet their energy budgets without taking risks, they occupy habitats above the threshold, dependent on their profitability (b). If habitats below the threshold are more profitable, then as energy demands increase, as with decreasing cold, then individuals may be forced to feed within 'risk' areas (b).

maximized (Fig. 1b). Secondly, when energy budgets cannot be met in areas above the threshold, then animals should then feed below the threshold at 'risk' distances. For redshanks, we predict that they should only forage below the threshold in cold weather and so the proportion of birds feeding within 'risk' distances should increase as temperature declines (when redshank energy budgets increase, see Yasue, Quinn & Cresswell 2003).

Materials and methods

The study area consisted of saltmarsh habitat backed by woodland or dunes at Tynninghame Estuary, East Lothian, Scotland (see Whitfield 1985 for further study site details). Data were collected September to early March, 1989–1992, and 2001–2006. The salt marsh (c. 15 ha) provides a feeding habitat for wintering redshanks, in particular for juvenile animals (Cresswell 1994a).

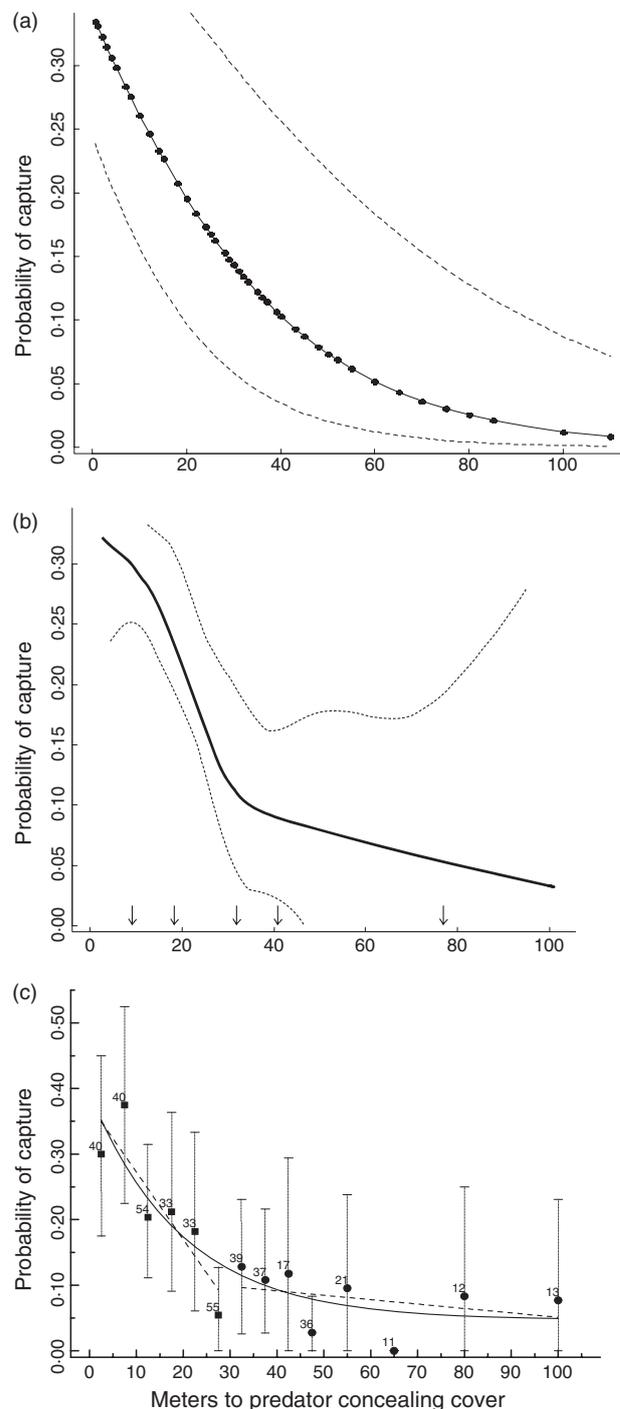
ATTACK DATA

All sparrowhawk attacks and kills were recorded during observation periods on flocks of redshanks. Sparrowhawk attacks were seen on 288 separate days over nine winters (2.5 ± 0.3 attacks per day recorded for any day when attacks were recorded). During the initial more intensive study in the first three winters (2557 h spent at the study site), we estimated that at least six different sparrowhawks were recording attacking during each winter. Some individuals were adults and it is likely that some individuals were recorded across winters (see Cresswell & Whitfield 1994). The 16-year period over which observations took place, however, makes it likely that many different birds were involved. An attack was defined as a rapid flight directed towards a flock or a single bird. A 'kill' was defined as when the raptor captured a redshank. For each attack, flock size and distance from predator-concealing cover were estimated when possible. A flock was defined as a cluster of birds in which the maximum nearest neighbour distance was < 25 m and less than one tenth of the distance between clusters, with inter-cluster distance always being > 25 m, and varied in size from 1 to 200 birds. Markers were placed at regular intervals around the edge of the saltmarsh to facilitate estimating distances. Because redshank flocks were also being studied, flock size and distance to cover details were usually recorded before attacks. For some attacks details were obtained from videos (see Quinn & Cresswell 2006). In total, we saw 441 surprise attacks by sparrowhawks (where sparrowhawks attacked directly from concealing cover see Cresswell 1996) where distance to cover was accurately recorded which resulted in 71 captures.

The relationship between sparrowhawk attack success rate and distance to cover may be confounded by flock size, which also strongly affects capture success rate in our system (Cresswell 1994b; Cresswell & Quinn 2004). To most simply demonstrate the function linking attack success with distance from cover, attacks were pooled within distance to cover classes to approximately equalize sample sizes and so that any variation in attack rate because of distance to cover or flock size, respectively, was uniform and should not bias the estimate of the mean. On average, there was no significant variation for attacking sparrowhawks in group size across different distances from cover of (e.g. Kruskal–Wallis $\chi^2_{13} = 18.1$, $P = 0.15$; see Fig. 2c where data were pooled within 14 classes of increasing distance to cover). There was also no evidence for biases in flock size dependent on temperature (see Fig. 5a). Flock size was therefore ignored as a confounding variable in all subsequent analyses.

Fig. 2. Function describing attack success and distance to cover. (a) The predicted values of a logistic regression plus 95% confidence limits (dashed lines). (b) The best fit spline fitted to the logistic regression data. Arrows indicate the knots (significant changes in direction). (c) Capture success rate with distance to cover with attacks pooled into distance classes so rates of capture can be calculated; numbers of attacks in each class are stated beside each point; 95% confidence limits are shown (estimated by bootstrapping – random sampling with replacement 1000 times). The solid line is the exponential decay function of best fit. The dotted lines represent linear regression lines for data above and below 30 m. Capture rate depended significantly on distance to cover overall $\chi^2_{13} = 35.8$, $P = 0.001$: above 30 m there was no change in capture rate across distance classes, $\chi^2_7 = 4.0$, exact $P = 0.81$; below 30 m there was a large change in capture rate across distance classes, $\chi^2_5 = 16.6$, exact $P = 0.005$; capture success rate was significantly different above and below 30 m, $\chi^2_1 = 10.4$, exact $P = 0.001$.

The function linking attack success and distance from cover was determined in several ways. Whether distance to cover was a significant predictor of attack success or failure was determined using logistic regression (Fig. 2a). The shape of the function, and any 'threshold' changes in it, were then determined using the 'rcspline' function in the Hmisc library of R (R Development Core Team 2009), which calculates a restricted cubic spline function of five knots (where the function makes significant changes of direction; Fig. 2b). Finally, attack success rate was pooled into 14 distance to cover classes (5 m classes until 50 m, then 10 m classes until 70 m and then 20 m classes until 100 m, classes becoming larger as sample sizes decreased for large distances from cover) and the best curve fitted using the exponential curve fitting function in Origin 8 (Origin Lab Corporation,



Northampton MA, USA). Linear regression functions were also fitted to this curve, split by the threshold value identified during spline fitting (Fig. 2c): if there is a clear threshold change in the function then there should be a linear relationship between attack success and distance to cover, that will be much steeper and significantly negative below the threshold, vs. shallow or flat and non-significant above the threshold.

DISTANCE TO COVER DATA: OCCURRENCE OF REDSHANKS AND HABITAT AVAILABILITY

Data on the occurrence of redshanks on the saltmarsh with respect to cover were collected by scan samples during the winter of 2001–2002 (see Quinn & Cresswell 2004) during 1–6 h observation periods from fixed locations overlooking the whole saltmarsh. During observation periods, the total number of redshanks and the number of flocks were recorded on the saltmarsh every 30 min, along with the mean distance to predator-concealing cover for each flock and air temperature ($^{\circ}\text{C}$) was recorded every 15 min using an automatic logger placed 1.5 m above ground level at a weather station in an open field 1 km southwest of the study site. Mean values were then calculated for each observation period, and then the means of these values was calculated to obtain a single mean for each observation day. Flocks were defined as above and varied in size from 1 to 200 birds (mean \pm SE = 28.8 ± 1.2 ; see Fig. 5a). Observations were carried out on 39 separate days, with 6.5 ± 0.5 scan samples a day, with 41.4 ± 4.7 birds being sampled per scan sample on average.

Availability of different distances to cover was determined because the saltmarsh is an enclosed, irregular shape, several hundred meters across (see inset in Fig. 3a), so that distances further from cover were less common. An aerial photograph of Tynninghame was traced and a 100 m^2 grid was superimposed over it. The grid then was then given x and y coordinates so that individual 1 m^2 could be identified by a unique six figure number. A total of 150 random numbers were then obtained between the x and y coordinate limits and the 150 points were then plotted on the map. The closest distance to cover for each point was then measured using a ruler to obtain an accuracy within 10 m.

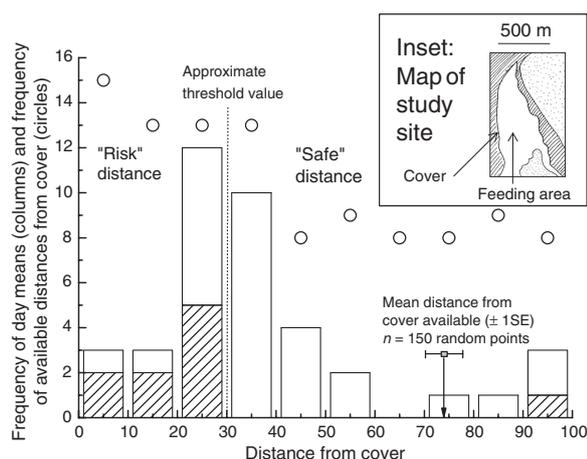


Fig. 3. Availability of habitat at different distances to cover (top circles, based on $n = 150$ random points sampled from the enclosed saltmarsh area illustrated as an inset top right) and the daily average use of these different distances to cover by redshanks at temperatures 5°C or above (unhatched area of bars) and below 5°C (hatched areas of bars). The 'threshold' value at 30 m is indicated by a dotted vertical line: 26% of saltmarsh occurs below the threshold.

The frequency of day means of distance to cover was then plotted to examine the distribution of distances to cover with respect to habitat availability (Fig. 3), habitat profitability (see below) and any interactions with respect to temperature and any threshold distance in risk function discovered above (Figs 5 and 6).

FEEDING DATA

Feeding data with respect to distance to cover were collected from colour-ringed redshanks to confirm the exact relationship between distance to cover and habitat profitability. In the winter of 2004/05, a total of 32 redshank were ringed after capture using a 5 by 15 m whoosh net (Cresswell *et al.* 2007). Birds were caught and ringed under British trust for Ornithology licence (permit no. 4486). Observations of foraging colour-ringed birds were made in the winter of 2004/05 on 23 days between the 6th of December and the 8th of February. Individuals were identified using a telescope (20–60 \times zoom Swarovski: ATM 80) and then videoed using a digital 8 video camera (Sony DCR-TRV330E; 2CCD; $\times 25$ optical zoom). Information on the birds' identity, time of day, flock size, distance of the bird from predator-concealing cover and position in the flock (edge or centre bird) was dictated directly onto the video at the time of the observation. Flock spacing was obtained later from the video recordings. All focals lasted for 1 min. An individual was not recorded more than three times during a single day and focals of the same individual were never conducted consecutively whilst the bird fed in the same flock. All birds recorded were within 150 m of the observer, because behavioural information became less reliable in videos of birds further away. In total, we recorded 151 observations from 22 individuals, on 24 separate days. Behavioural data were extracted from the videos using JWATCHER™ behavioural recording software (version 0.9; Blumstein, Evans & Daniel 2000). Videos were played back in slow motion and the number of pecks, swallows and steps were recorded, along with average distance between birds in the flock and the time spent vigilant. Birds were considered to be vigilant only when their head was above their back (see Sansom *et al.* 2008).

The relationship between distance to cover and feeding rate (swallows per minute) was tested using a Generalised Linear Model in SPSS 16 (SPSS, Inc., Chicago, IL, USA). In the model bird (individual) and Julian date were included as random factors (to control for variable number of focals per individual per day) and position in the flock (edge or central) was a fixed factor. Time of day, flock size, distance to cover, mean flock spacing, number of steps, number of pecks and time spent vigilant were included as covariates. The rationale behind including these variables was to control statistically for as many of the other potentially confounding variables that may lead to variation in feeding rate so that any variation in feeding rate accounted for by distance to cover was likely to be an index of profitability of the habitat. Alternatively, however, it can be argued that regardless of prey availability, actual prey intake rate by redshanks is the crucial factor in determining a redshank's perception of habitat profitability, and so we also considered the univariate average relationship between feeding rate and distance to cover (Fig. 4).

Results

Attack success was predicted by distance to cover (logistic regression distance to cover $B = -0.037 \pm 0.009$, $P < 0.001$, $n = 371$ attacks, 70 captures; Fig. 2a. Adding flock size to this model improved its predictive power (Nagelkerke R^2 15%, from 10%), but the effect of distance to cover

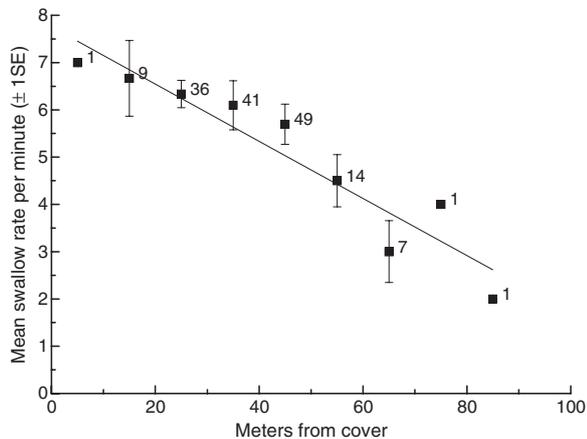


Fig. 4. Variation in mean swallow rate per minute for redshanks feeding at different distances from cover. The numbers by each square mean (± 1 SE) point indicate the sample sizes of 1-min videoed focal samples.

remained similar (logistic regression distance to cover $B = -0.034 \pm 0.009$, $P < 0.001$, flock size $B = -0.026 \pm 0.007$, $P < 0.001$, constant -0.065 ± 0.28 , $n = 362$ attacks, 69 captures, sample sizes smaller because in 2% of observations flock size could not be accurately assessed). A spline fitted to the logistic relationship resulted in a first major change direction of the function at about 30 m (Fig. 2b). Overall the function was well-expressed by an exponential decay [attack success rate = $0.173 \times \exp(-\text{distance to cover}/19.9) + 0.046$, $n = 14$ flock-size classes, $F = 24.3$, $P < 0.001$, adjusted $R^2 = 0.71$; Fig. 2c]. Splitting the data by the approximate threshold of 30 m to cover gave a significant negative linear relationship below 30 m ($y = -0.01x + 0.38$, $F_{1,4} = 13.8$, $P = 0.021$, $R^2 = 0.72$), and a non-significant relationship above 30 m ($F_{1,6} = 0.8$, $P = 0.40$; Fig. 2c). The slopes of the lines were significantly different (class; 1, above and 2, below threshold) \times distance from cover, $F_{1,10} = 14.2$, $P = 0.004$).

The frequency distribution of mean daily distances from cover produced a clear peak around the threshold distance of about 30 m (Fig. 3). Overall the availability of saltmarsh habitat decreased with distance from cover ($y = -0.058x + 13.7$, $P < 0.001$, $R^2 = 0.81$) because of the enclosed nature of the saltmarsh (inset Fig. 3): the relative availability of saltmarsh at different distances from cover was independent of mean daily distances from cover at which redshanks fed ($\chi^2_5 = 21.3$, $P < 0.001$), and this was the case even above the threshold of 30 m ($\chi^2_3 = 19.1$, $P < 0.001$): both analyses pooling distance above 50 m because of low expected values (Fig. 3).

There was a strong negative relationship between distance to cover and feeding rate, with a 10.6% increase in average feeding rate (5.75 ± 0.22 swallows per minute, $n = 151$ focal samples) every 10 m closer to cover ($F_{1,98} = 7.3$, $P = 0.008$, $B = -0.061 \pm 0.023$; model including bird identity, date, time of day, flock spacing, position with respect to the edge of the flock, number of pecks, number of steps and time spent vigilant; Fig. 4). There was a significant negative correlation

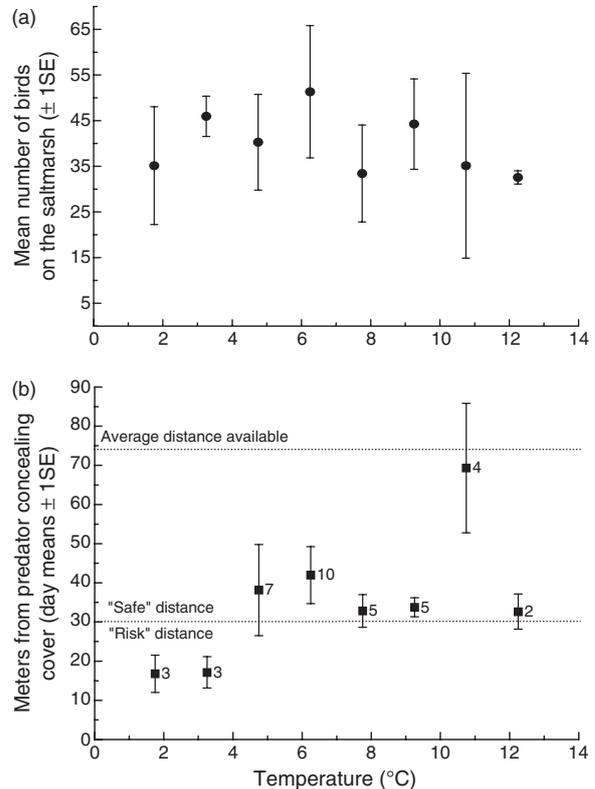


Fig. 5. (a) Mean (± 1 SE) daily number of birds (the mean number of all birds recorded in each scan samples during a day) and (b) mean (± 1 SE) daily distance from cover (the mean of all individual bird's distances from cover per scan sample, then averaged across all scan samples in a day) on the saltmarsh at different temperatures. Numbers by the side of the square points are the numbers of day means plotted in each temperature class.

between distance to cover and feeding rate ($R_s = -0.94$, $P = 0.005$) above the threshold of 30 m (Fig. 4). There was a significant negative correlation between feeding rate and frequency of daily mean distances to cover ($R_s = -0.90$, $P = 0.015$, $n = 6$) above the threshold of 30 m, showing that broadly, redshanks were found most often where feeding rate was the highest except below 30 m from cover (Figs 3 and 4).

Redshanks occurred more often below 30 m to cover when it was colder. Considering days where the temperature was below 5°C , there were a greater proportion of colder days which had distance to cover day means below the threshold than expected ($\chi^2_5 = 12.0$, exact $P = 0.028$; Fig. 3). On average, distance to cover on days below 5°C was well below the threshold and just above the threshold on warmer days ($t_{9,28} = -2.0$, $P = 0.05$); on even colder days, i.e. below 4°C , this relationship becomes stronger ($t_{5,32} = -2.5$, $P = 0.019$; Fig. 5). The proportion of birds at 'risk' distances – i.e. below the threshold of 30 m – increased as temperature declined ($F_{1,37} = 4.9$, $P = 0.033$; Fig. 6).

Conclusions

We found a clear exponential decline in attack success rate with increasing distance from predator-concealing cover,

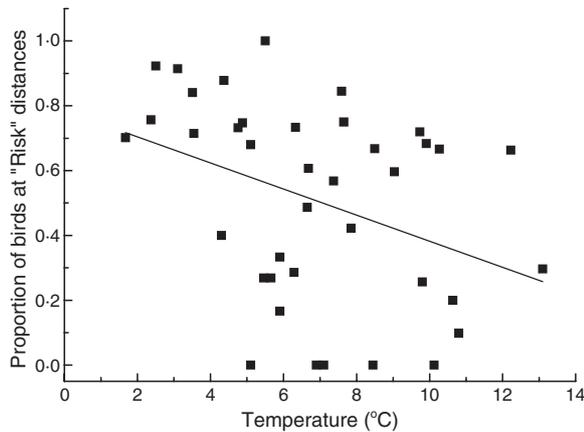


Fig. 6. The proportion of birds feeding at 'risk' distances (i.e. below the 'threshold' of 30 m) with temperature. $n = 39$ daily means (the mean of all individual bird's distances from cover per scan sample, then averaged across all scan samples in a day) are plotted.

where beyond a threshold of 30 m, selection according to risk of predation was reasonably uniform. There are a large number of studies which show the importance of protective or concealing cover to the hunting success of predators (e.g. Rohner & Krebs 1996; Reinhardt & Healey 1997; Funston, Mills & Biggs 2001; Kunkel & Pletscher 2001; Balme, Hunter & Slotow 2007). However, this contrasts with the very few studies, that we know of, that examine how predator-attack success changes with distance to cover, presumably because attack success rate is only very rarely observed (or seen frequently enough to be measured) in natural systems. Other studies have suggested that availability of cover in the landscape, and how it can facilitate predator avoidance or hunting success, determine the distribution and density of animals to a large degree (e.g. Griesser & Nystrand 2009), but none have quantified this in terms of proportion of habitat avoided. In our system, cover is perceived by the prey as being dangerous because it conceals surprise hunting predators, but in many systems animals may have a preference for foraging close to cover because it presents a refuge. Theoretically, this makes no difference to our conclusions: the size and importance of areas avoided with respect to cover will be determined by the average attack success, the speed of the exponential decline in the attack success function, and the landscape configuration between cover and foraging areas.

The attack success function shows us how the trade-off between the risks of predation and starvation can influence prey habitat choice, so resulting in large lethal and non-lethal effects. In our system, redshanks generally avoid areas close to cover because of predation risk (Cresswell 1994a) but when increased starvation risk outweighs the higher capture risk, they feed in risky but highly profitable areas close to cover (Yasue *et al.* 2003). The spatial scale of these non-lethal effects is therefore determined by the attack success function, so that 26% of habitat (and indeed the most profitable habitat) is typically not used. The lethal effects are then determined by the interaction with temperature increasing starvation risk, and so use of areas where capture on attack is

more likely. Clearly though, the fraction of unavailable habitat will depend on the ratio of availability of cover, which will in turn depend on the heterogeneity or fragmentation of the habitat (and of course the use of cover by either predators for hunting, or by prey as part of its anti-predation behaviour). We would predict, therefore, that non-lethal effects, where prey avoid suitable habitats, to be greatest in heterogenous, or transition zones of habitats such as open woodland, savannah, coral reefs, coastal fringes and urban habitats. At larger spatial scales, in habitats that incorporate these transition zones, it may then appear as if prey is co-existing with high predator density (Lima 1992), yet because prey are on the safe side of a predation risk threshold, there may be little actual direct predation mortality. We also predict that in heavily fragmented landscapes, for example in European farmland dissected by hedgerows or in heavily fragmented forests, the scale over which non-lethal effects are likely to apply could be substantially larger than those in open habitats where cover is typically relatively scarce.

Our data also support the hypothesis that the non-lethal implications of predation risk for structuring communities are potentially important. If areas are avoided, the prey of the species avoiding the area will have lower predation rates, higher density and different community structure because of corresponding changes in competition between the lower trophic level species (e.g. Leibold 1991). Higher trophic levels will then be affected because changes in the distribution of the focal prey affect competitive interactions and distribution of alternative prey and their predators (see discussion in Abrams 1993). Our study adds to the growing evidence that non-lethal effects of predation risk are equally if not more important than lethal effects in influencing habitat availability, prey distribution patterns and impacts on the community as a whole (see Werner & Peacor 2003). Again the shape of the function is critical to identifying the scale of these non-lethal effects. If the point at which further changes in distance to cover makes little further difference to attack success (i.e. where the point of inflection of the function) occurs at high values, large areas of potentially suitable habitat might be avoided, therefore having a major effect on prey distribution patterns and potentially on population size. Also, if large areas of habitat are avoided by a species this may result in increased stability of its population. This is because a large reserve feeding area may be protected from depletion, so effectively buffering starvation risk for times when the costs of starvation risk exceed those of predation (see Bolker *et al.* 2003). In contrast, such non-lethal effects may however be weak if the point at which further changes in distance to cover affect risk is small relative to the scale of the area.

The generality of non-lethal effects across different systems arising from attack success functions has yet to be demonstrated but we suggest that the distribution of most animals that are attacked by surprise by predators from cover, or that use cover as a refuge, will be profoundly affected by the steepness of the function linking their predators' attack success rates with distance from cover, be it predator concealing or protective. The relative importance of these effects will

undoubtedly vary across communities dependent on a whole range of factors, for example on the relative abundance of different predators, the structural complexity of habitats that allow prey to avoid predators and the relative abundance of habitat features exploited by predators to enhance their attack success.

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