Fear factor: prey habitat selection and its consequences in a predation risk landscape

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Predation risk influences prey use of space. However, little is known about how predation risk influences breeding habitat selection and the fitness consequences of these decisions. The nest sites of central-place foraging predators may spatially anchor predation risk in the landscape. We explored how the spatial dispersion of avian predator nests influenced prey territory location and fitness related measures. We placed 249 nest boxes for migrant pied flycatchers *Ficedula hypoleuca*, at distances between 10 and 630 m, around seven different sparrowhawk nests *Accipiter nisus*. After closely monitoring flycatcher nests we found that flycatcher arrival dates, nest box occupation rates and clutch size showed a unimodal relationship with distance from sparrowhawk nests. This relationship suggested an optimal territory location at intermediate distances between 330 and 430 m from sparrowhawk nests. Furthermore, pied flycatcher nestling quantity and quality increased linearly with distance from sparrowhawk nests. These fitness related measures were between 4 and 26% larger in flycatcher nestlings raised far from, relative to those raised nearby, sparrowhawk nests. Our results suggest that breeding sparrowhawk affected both flycatcher habitat selection and reproductive success. We propose that nesting predators create predictable spatial variation in predation risk for both adult prey and possibly their nests, to which prey individuals are able to adaptively respond. Recognising predictable spatial variation in perceived predation risk may be fundamental for a proper understanding of predator-prey interactions and indeed prey species interactions.

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The non-lethal costs of predation risk to individuals, caused by the stress of anti-predator decision making, have proved as important as the lethal costs themselves (Lima 1998b). Within this, the use of space by prey has received a generous amount of attention. Investigations, however, have largely persisted in the small-scale use of habitat (e.g. feeding sites) and little information exists about predation risk effects on territory location (Lima 1998a). Understanding the implications of predation risk on habitat selection decisions would be crucial in understanding population dynamics.

Breeding habitat selection is a vital step for settling birds. It not only determines the foraging areas for the entire breeding season, but a poor choice may negatively affect the life-time reproductive success of an individual. Evidence has suggested that individuals from various

taxa gather information prior to habitat selection decision-making in order to be flexible and control for unpredictability in the environment (Stamps 2001). Individuals are known to use cues such as the presence or density of conspecifics and heterospecifics (Stamps 1988, Mönkkönen and Forsman 2002) or public information based on monitoring conspecific performance (e.g. reproductive success) in making habitat selection decisions (Danchin et al. 2004). These cues may provide a reliable indication of overall environmental quality and incorporate the influence of numerous factors. Nevertheless, direct information regarding predation risk would be highly beneficial prior to habitat selection and reproductive investment decisions. Direct cues of predator presence or density may be far more reliable than indirect (and potentially outdated) cues such as public information. However, little is known about how predation risk influences breeding habitat selection, what cues are used in decision-making, and what the fitness consequences of these decisions are (Lima 1998a).

Central-place foraging avian predators can either directly or indirectly affect the spatial dynamics of their prey, resulting in diminished adult prey abundance around their nests (Suhonen et al. 1994, Norrdahl and Korpimäki 1998). In contrast, several avian predators are not a nest predation threat and could potentially provide protection for nests against destructive nest predators. Several studies have shown that breeding avian predators are sought as neighbours because they provide such protection (Norrdahl et al. 1995, Bogliani et al. 1999, Quinn et al. 2003). From a prey perspective, by using nesting avian predators as cues, predictable gradients in adult predation risk and nest predation risk may exist throughout the breeding season. We coin this spatially predictable predation risk gradient a "predation risk landscape" which may affect habitat selection of prey individuals which attempt to optimise reproductive success relative to direct and perceived predation (Lima 1987).

We test for the existence of a predation risk landscape using migrant pied flycatcher *Ficedula hypoleuca* nests relative to those of sparrowhawk *Accipiter nisus*. Sparrowhawk exert severe predation pressure on small passerines (Rytkönen et al. 1998) and may decrease adult survival (Geer 1978, Dhondt et al. 1998). Earlier we found that willow tit *Parus montanus* breeding in proximity to sparrowhawk (and other avian predator) nests raised fewer and smaller nestlings (Thomson et al. 2006). Willow tit, however, appeared to settle randomly in the landscape relative to avian predator nests. Pied flycatchers arrive after sparrowhawks have initiated breeding, and from this context one would expect flycatchers to avoid nesting near sparrowhawks. However, using artificial nests, Mönkkönen et al. (2000) found that nests placed closer to breeding goshawk *A. gentilis* were less likely to be predated than those

further away. In addition, Forsman and Mönkkönen (2001b) found that passerine birds occurred in a unimodal density pattern relative to distance from sparrowhawk nest. Therefore, we predicted that the optimal nest location for flycatchers would be at intermediate distances from sparrowhawk nests. This prediction integrates the effects of the potential costs and benefits of breeding in proximity to a sparrowhawk nest. By using pied flycatcher arrival dates, nest box occupation rates and the resulting breeding success, we investigated the predictions of the predation risk landscape concept.

Material and methods

Study site and methods

Active territories of seven sparrowhawk pairs were located in the forests near Oulu, northern Finland (65°N, 25°30′E) in summers 2002–2004. Mixed forests with varying proportions of Scots pine *Pinus sylvestris*, Norway spruce *Picea abies* and birch *Betula* spp. were found around sparrowhawk nests. All sparrowhawk territories, one in 2002, three in 2003 and three in 2004, were each used only once. Pied flycatchers arrive at their breeding grounds once sparrowhawk nesting has already begun. 249 identical nest boxes for flycatchers were placed in a grid format within active sparrowhawk territories. The distance between consecutive boxes was roughly 60–70 m in all directions in order to keep box densities constant. Due to the fragmented nature of the forests, the number of nest boxes varied from 20 to 46 per territory. Ten nest boxes were occupied by late nesting great tits *Parus major* and were excluded from analyses.

In a 23 km² portion of the study area, the highest recorded sparrowhawk densities occurred in 1996 (Thomson et al. 2006). In this year, sparrowhawk nests average 1.32 km to their nearest neighbours. Nest boxes, therefore, varied between 10 and 630 m from sparrowhawk nests. We believe these distances were sufficient to test our predictions due to the geometric increase in area with increasing distance, which will quickly dilute predation risk (Forsman et al. 2001). In addition, at larger distances the influence of unknown avian predator nests became increasingly possible. After flycatcher arrival, egg-laying, clutch size, hatching and resulting nest success were closely monitored. Occupied boxes were defined as boxes in which at least one egg was laid. Although early arriving individuals wait longer to start egg-laying than later arriving individuals, we used the date of the first egg laid (laying date) as an indication of arrival date and hence parental quality (Lundberg and Alatalo 1992, pp. 63–68, Kokko 1999). The earliest day an egg was laid was assigned a value of 1, the next day 2 and so on, separately standardised for each year. A successful nest was defined where at least one nestling fledged and nestlings were measured at 12 d of age by the

same observer (RLT) using standard procedures across all nests. The measures, used as an indication of nestling quality, included tarsus length, wing length, tail length and body mass. Unsuccessful nests were classified as nest predated if we observed disappearance of eggs or chicks combined with a disturbance of nest material. Other unsuccessful nests contained dead chicks or a clutch of cold eggs, indicating that parents had either abandoned or were taken by predators. If only the same adult bird was repeatedly observed at a nest, the nest was classified as a single parent nest. Single parent nests may result from the other parent being taken by a predator. However, single females can also be secondary females that receive very little parental help from the male (Lundberg and Alatalo 1992). Nevertheless, 33% of single parent nests were male only nests suggesting that secondary female nests were rare. Each flycatcher nest was used as the sampling unit, and nestling quality measures were averaged within each nest.

Statistical analyses

Logistic regression and nested ANOVA models were used for testing binary and continuous variables respectively. The binary response variable was nest box occupation, while the continuous variables included laying date, clutch size, nestling size variables (mass, wing length, tarsus length) and the number of fledged chicks. In logistic regression models, sparrowhawk territory was used as a random factor, in nested ANOVA models the effect of distance (or squared distance) is nested within hawk territory, which controls for the effect of specific sparrowhawks and habitat types on response variables and therefore provides a stronger representation of the responses in the wider population. Predation risk was incorporated into analyses by using the distance and squared distance to sparrowhawk nests. Squared distance to hawk nest was included in order to check for non-linear, unimodal relationships. In the clutch size ANOVA, laying date was controlled for by entering it as a covariate. Furthermore, because the laying date and clutch size may affect nestling number and quality variables, they were included as covariates in these models in order to control for their effect and reveal the true effect of predation risk. In order to simplify models, backward elimination was used if the quadratic term of distance was non-significant. Parameter values (B) are calculated from normal ANOVA models with territory entered as a random factor (distance not nested within territory). Unequal error variances in clutch size and nestling mass ANOVAs were due to the unbalanced sampling design. Underwood (1997) suggests such a design decreases the possibility of making Type I error, thereby making the test conservative. In addition, our sample size was large decreasing the possibility that our result was due to chance. We therefore did not transform these variables. Normality of residuals was checked in ANOVA models. All p values are two-tailed and statistical significance is defined as $\alpha = 0.05$. Analyses were performed using SPSS 12.0.1 software.

Results

Occupation rates

Of the 239 flycatcher boxes around sparrowhawk nests included in analyses, 145 (60.7%) were occupied by breeding pied flycatchers. The distance to sparrowhawk nest clearly affected flycatcher box occupation rate. The model showed a clear quadratic relationship of box occupation rates with increasing distance around sparrowhawk nests (Table 1) with a peak in occupation rates predicted around 400 m (Fig. 1). The model correctly predicted 55.3% of unoccupied boxes and 82.1% of occupied boxes, giving overall 71.5% of states correctly predicted. There was a large difference between the mean distance from sparrowhawk nests of empty and occupied boxes (empty (mean $\pm$ SE) $= 189$ m ± 0.15; occupied $= 264$ m ± 0.12; $t_{237} = -3.952$, $p < 0.001$). The significant quadratic term indicates that flycatchers avoided settling very close to and far from sparrowhawk nests (Table 1).

Parental choice and quality

Of the 145 occupied flycatcher nest boxes around sparrowhawk nests, 19 were not followed and are excluded from analyses hereafter. Laying date (n $=126$) is used as an indication of the order of nest box occupation. There was a highly significant quadratic relationship between laying date and increasing distance around sparrowhawk nests (model: $F_{14,111} = 3.91$,

Table 1. Logistic regression model of nest box (n $=239$) occupation rates with distance from sparrowhawk nests. Distance to nest and squared distances are entered as continuous covariates while territory is categorical.

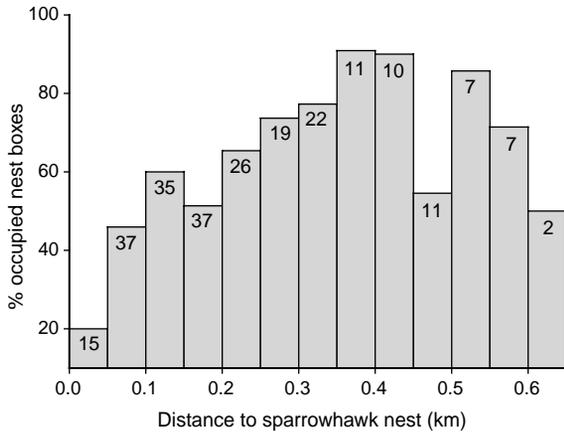| Variable	B $\pm$ SE	χ^2	Wald statistic	DF	p
Model		46.06		8	0.000
Distance to nest	13.53 $\pm$ 3.89		12.14	1	0.000
(Distance)^2	-15.95 ± 6.46		6.10	1	0.013
Territory			20.38	6	0.002
Constant	-1.07 ± 0.56		3.70	1	0.054

Fig. 1. Distribution of mean nest box occupation rate of pied flycatchers in relation to distance from sparrowhawk nests. Nest box sample sizes relevant to each distance category are indicated within the bars.

p < 0.001; distance (territory): B = −36.29, $F_{7,111}$ = 5.79, p < 0.001; squared distance (territory): B = 53.64, $F_{7,111}$ = 4.33, p < 0.001). The earliest arriving individuals were selecting boxes at an intermediate distance of 338 m from the sparrowhawk nest (Fig. 2). Pairs breeding at this distance laid their first egg approximately six days earlier than pairs settling very close to sparrowhawks and four and a half days before pairs settling at 630 m (the maximum distance in our study).

Direct (lethal) effects of predation risk

Few nests failed (n = 14) and only three failures were due to nest predation, as indicated by disturbance or disappearance of nest contents. Mean distances from sparrowhawk nest of successful versus failed nests did not differ significantly (successful = 0.26 km ± 0.001; failed = 0.24 km ± 0.01; t_{124} = −0.46, p = 0.65). Similarly, no difference in mean distances from sparrowhawk nest of single parent (n = 9) versus both parent (n = 103) nests were found (single = 0.29 km ± 0.01; both = 0.26 km ± 0.001; t_{110} = 0.60, p = 0.56).

Indirect (non-lethal) effects of predation risk

To look at the indirect effects of predation risk on nestling quality, all nests that had been directly affected by predation (failed or single parent nests) were removed. The nested ANOVA (n = 103) for clutch size showed that laying date, distance to sparrowhawk nest and squared distance to sparrowhawk nest significantly influenced flycatcher clutch size. Earlier arriving flycatcher pairs laid larger clutches than later arriving pairs. However, even with laying date controlled for, there was a significant unimodal relationship with distance from sparrowhawk nest (model: $F_{15,87}$ = 4.35, p < 0.001; distance (territory): B = 3.31, $F_{7,87}$ = 3.80, p < 0.001; squared distance (territory): B = −3.90, $F_{7,87}$ = 2.74, p = 0.013). Largest clutches were laid at intermediate distances, with the peak at 424 m from sparrowhawk nests. At 424 m clutch sizes were 11.6% larger than in nests 10 m from sparrowhawks, however, only 2.6% larger than nests situated 630 m from sparrowhawks (Fig. 3).

With clutch size and laying date controlled for, distance from sparrowhawk nest significantly explained the number of fledged nestlings (cubed transformation). The quadratic term of distance was not significant and number of fledglings linearly increased with distance from sparrowhawk nests (model: $F_{9,93}$ = 9.15, p < 0.001; distance (territory): B = 57.44, $F_{7,93}$ = 3.03, p = 0.006). This increase results in 5.1% more fledglings across the range of nest box distances.
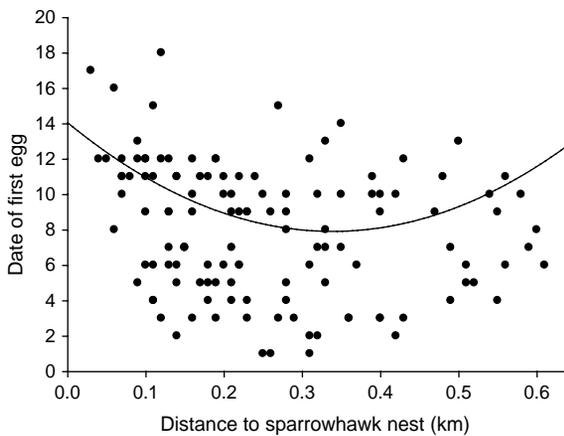

Fig. 2. Relationship between pied flycatcher laying date and distance from sparrowhawk nests. Laying date represents parental quality, the earlier the first egg is laid (low values) the higher the parental quality.
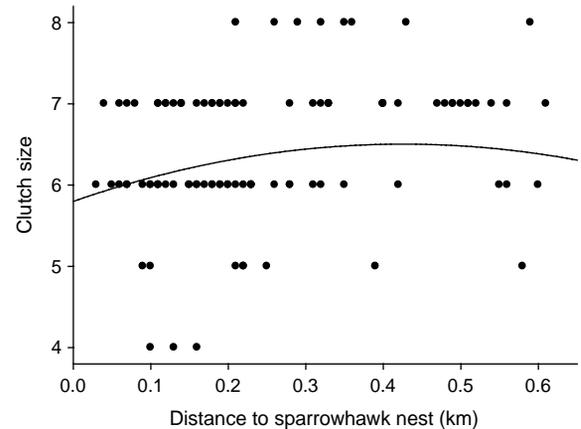

Fig. 3. Relationship between pied flycatcher clutch size and distance from sparrowhawk nests.

Results of nested ANOVA models for nestling quality measures ($n = 103$) showed that, even with clutch size and laying date controlled for, distance to sparrowhawk nest significantly linearly influenced nestling tarsus length (model: $F_{9,93} = 3.28$, $p = 0.002$; distance (territory): $B = 1.09$, $F_{7,93} = 4.03$, $p = 0.001$), wing length (model: $F_{9,93} = 2.77$, $p = 0.006$; distance (territory): $B = 5.89$, $F_{7,93} = 2.67$, $p = 0.014$), tail length (model: $F_{9,93} = 3.11$, $p = 0.003$; distance (territory): $B = 5.35$, $F_{7,93} = 3.09$, $p = 0.006$) and nestling mass (model: $F_{9,93} = 2.70$, $p = 0.008$; distance (territory): $B = 1.35$, $F_{7,93} = 2.32$, $p = 0.032$). All relationships were positively linear and translate into increases of 3.7 mm (7.8%) in wing length, 3.3 mm (25.7%) in tail length, 0.7 mm (3.9%) in tarsus length and 0.8 g (6.1%) in nestling mass for nests situated between 10 and 630 m from sparrowhawk nests (Fig. 4).

Discussion

Our results suggest that variation in perceived predation risk caused by the spatial dispersion of sparrowhawk nests may have multiple affects on breeding pied flycatchers. Distance to sparrowhawk nests was found to correlate with flycatcher territory location and initial reproductive investment. In addition, proximity to sparrowhawk nest also correlated with the quantity and quality of flycatcher nestlings produced. While earlier work has demonstrated linear effects of predator nests on prey territory location, i.e. avoidance due to increased adult risk (Norrdahl and Korpimäki 1998), or aggregation due to protection benefits (Norrdahl et al. 1995), this is to our knowledge the first study to integrate these effects.

Flycatcher breeding habitat selection appears to support the idea of prey avoidance of breeding avian predators (Meese and Fuller 1989, Sodhi et al. 1990, Suhonen et al. 1994, Norrdahl and Korpimäki 1998, Tryjanowski 2001, Hromada et al. 2002, Roos and Pärt 2004). This is the first suggestion of this strategy from forested, structurally diverse, habitats. However, we found that flycatcher habitat selection showed a unimodal relationship with distance from sparrowhawk nest (Fig. 1 and 2). Flycatchers preferentially selected nest boxes at intermediate distances from breeding sparrowhawks. On average, these nest boxes were occupied 6 d before nest boxes close to hawk nests. This result suggests an optimal territory location at intermediate distances from a sparrowhawk nest.

In addition, initial reproductive investment decisions (clutch size) mirrored those of habitat selection. Largest clutches were laid at intermediate distances from sparrowhawk nests. Animals have been shown to have adaptive phenotypic plasticity in reproductive traits, such as clutch size and mass, relative to proximate environmental
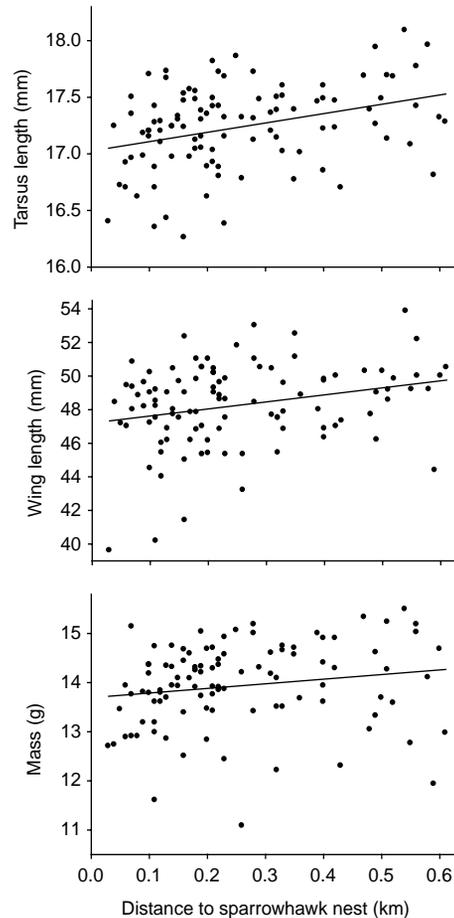

Fig. 4. Relationship between pied flycatcher nestling quality measures (tarsus length, tail length, wing length and mass) and distance to sparrowhawk nests.

factors (Sinervo and DeNardo 1996, Seigel and Ford 2001, Doligez and Clobert 2003). Here we observed marked differences in clutch size between birds breeding within 630 m of each other, after accounting for the quality of the birds. Low clutch size in the vicinity of sparrowhawk nests may be explained by parents' perceived capability to feed the chicks under a high risk of predation. During settlement, a female may perceive the level of predation risk and might adaptively adjust clutch size relative to the burden of nurturing the chicks under a given predation risk. Too many chicks relative to environmental conditions usually results in low number and low quality chicks (Roff 2002). Therefore, largest clutches should be laid where conditions are most favourable. In all, these results imply that female flycatchers gather information on the quality of the environment (predation risk) and adjust their investment in offspring according to the expected trade-off.

Optimal territory location relative to breeding predators suggests a trade-off between the costs and

benefits of such an association (Quinn and Kokorev 2002). Breeding sparrowhawk represents a large predation threat to adult flycatchers (Dhondt et al. 1998, Rytkönen et al. 1998), this entails the cost. However, sparrowhawk may potentially provide protection from other sparrowhawks or avian predators, this entails the benefit. For example, sparrowhawks defend their territory against conspecifics (Newton 1986) and avoidance in habitat selection has been shown within the avian predator guild (Sergio et al. 2003). In addition, sparrowhawks could provide protection against nest predation by decreasing the abundance of nest predators in the vicinity of their nests. Sparrowhawks may hunt potential nest predators, such as squirrels *Sciurus vulgaris* or woodpeckers, and also prey on small mammals (Sulkava 1964), which may also decrease the number of mammalian predators in the area. Several studies have shown that avian predators provide protection against destructive nest predators (Ueta 1994, Norrdahl et al. 1995, Bogliani et al. 1999, Quinn et al. 2003, Sergio et al. 2004). Therefore, the trade-off between the costs and benefits of the association could produce the unimodal relationship between nest site/success and distance from avian predator nest that this study documents. An optimal territory location may then exist at intermediate distances (Fig. 5). We term this a predation risk landscape. The distance of optimal territory location from the predator nest will be determined by the relative strengths of adult or nest predation risk curves for that particular prey species, and also the spacing between avian predator nests. We would further expect that species under higher predation risk would be increasingly fine-tuned in decision making (cue using) to optimise territory location.

These results suggest that the nest sites of breeding predators may be used as cues in prey habitat selection decisions in order decrease the unpredictability relative to ambient predation risk. Important properties of such cues are that they must be reliable and easy to assess. Firstly, it is unlikely that avian predators could fabricate an alternative nest site. Secondly, the foci of (adult or nest) predation risk, the nests of avian predators, are likely to announce themselves, making their use as cues ideal. Nesting *Accipiter* hawks have noisy pair formation and territory defence, and will be readily detectable by prey (Newton 1986). Birds may also use information gathered through acoustic cues such as mobbing behaviour by neighbours (Forsman and Mönkkönen 2001a). In fact, birds are suggested to correctly assess levels of nest predation risk from mammalian predators and respond adaptively (Forstmeier and Weiss 2004). We suggest that assessment with regards to predation risk from nesting avian predators could be quicker, easier and more reliable than for mammalian nest predators. Because breeding avian predators are central-place foragers, spatial variation in predation risk resulting from the spatial dispersion of their nests will be predictable throughout the breeding season.

Our study further aimed to determine the fitness consequences of habitat selection decisions relative to breeding predators. The low number of missing parent birds implied that direct adult predation did not significantly increase closer to sparrowhawk nests. However, there appeared to be strong non-lethal predation risk effects as expressed by the reproductive output of flycatcher nests. Flycatchers breeding close to sparrowhawks produced fewer and smaller nestlings relative to those further away (Fig. 4); an increase in nestling size of between 3.9 and 25.7%. Similar nestling quality results relative to the distance from predator nests have been found for willow tits nesting in the same study area (Thomson et al. 2006), even though the distances to predator nests examined in the previous study were far larger than in the present. Unlike flycatchers, however, willow tits nested in naturally excavated cavities. Furthermore, willow tits are residents, which initiate nesting early in spring (prior to sparrowhawk arrival), and appear unable to avoid the proximity of avian predator nests during territory location.

Decreasing offspring condition in proximity to sparrowhawk nests may be due to various reasons. Closer to sparrowhawk nests, parent birds may forage in a heightened anti-predator state (Lima 1998a), decreasing foraging efficiency through altered activity, vigilance, foraging sites and food handling times i.e. the sum of all small scale anti-predator behaviours. Breeding in high risk areas may also induce physiological stress responses in adults causing decreased parent condition and less efficient provisioning (Thomson et al. unpubl.) and may result in reluctance by parents to invest too much in the current breeding attempt (Verboven and Tinbergen 2002). In contrast, smaller nestling size may be adaptive (fit-for-flight) in order to evade sparrowhawk attack
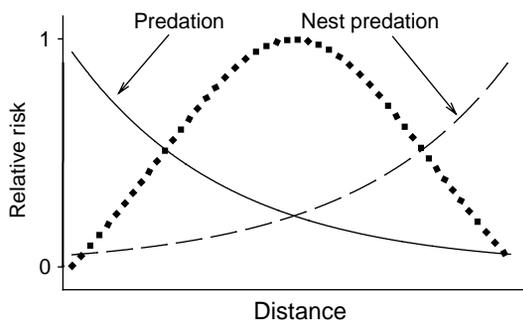

Fig. 5. Relative risk curves in relation to distance from a predator's nest for adult (solid line) and nest predation (dashed line). The dotted line refers to optimality of site-selection and here indicates a true trade-off situation between the two predation types which results in the predicted unimodal relationship between distance and relative optimality of nesting sites. Optimality is expressed as the inverse of the sum of the two types of predation.

(Adriaensen et al. 1998) although we suggest it is unlikely that fledglings can escape hunting sparrowhawks (see also Newton 1986, pp. 117). The above reasons suggest negative implications for the fitness of parents because nestling size, resulting from early development, determines future survival and fecundity (Lindström 1999).

A paradox, however, exists in our results. Initial flycatcher reproductive decisions (territory location and clutch size) support an optimal territory location idea, whereas, actual reproductive output (quantity and quality of nestlings) show a linear increase where farther is better. This apparent conflict may be the result of historically high nest predation rates typical when flycatchers bred in natural cavities (Walankiewicz 2002). High nest predation risk may still be perceived by flycatchers and incorporated into territory location decisions, even though nest predation in our nest boxes was extremely rare (only 1.5%). Flycatchers, may therefore select intermediate distances in order to gain protection from potentially destructive nest predators as predicted by our landscape (Fig. 5). An alternative explanation is that this parental behaviour stems from a strategy to ensure a predictable, as opposed to unpredictable, predation risk caused by unknown predator nests and floating individuals (Sergio et al. 2003). Admittedly, protection provided by sparrowhawks against nest predators requires further study. However, the unimodal passerine density pattern relative to distance from sparrowhawk nests (Forsman and Mönkkönen 2001b), and the decreased predation of artificial nests close to the similar goshawk (Mönkkönen et al. 2000), suggests that sparrowhawks may indeed provide a protective umbrella against nest predators around their nests. Such protection may contribute to the recently reported association between raptor nests and high biodiversity value (Sergio et al. 2005).

The current study, however, was not experimental and sparrowhawks were free to settle in the landscape. Nest locations were thus not randomly located and we cannot exclude the possibility that habitat characteristics relative to settlement cues used by sparrowhawks account for observed flycatcher settlement and reproductive success. However, pied flycatchers are habitat generalists, and it is unlikely that such large and consistent effects on both territory location and reproductive success could result from habitat quality alone. Furthermore, an experimental test we have conducted, where flycatcher habitat selection decisions have been manipulated relative to sparrowhawk nests, suggests that at least flycatcher reproductive output is correlated with distance to sparrowhawk nest (Thomson et al. unpubl.).

The predation risk landscape concept may be important in prey habitat selection in any system where central-place foraging predators occur. Although nesting in association with a regular predator has to our knowledge never been documented, such associations may be more widespread than realised. Our study demonstrates that individual fitness depends on habitat selection decisions relative to avian predator nests, which suggests an impetus to the evolution of habitat selection strategies. By incorporating spatial variation in predation risk at a landscape scale, the concept of the predation risk landscape offers a fruitful pathway to study predator-prey interactions, variation in prey anti-predator behaviour and population dynamics.

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