



# Long- and short-term state-dependent foraging under predation risk: an indication of habitat quality

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Animals living in environments of different quality will have different expectations of their future reproductive success and survival. This may affect the individual's risk-taking behaviour as manifest in the cost of predation. We investigated the foraging behaviour of starlings, *Sturnus vulgaris*, when perceived predation risk varied between patches. Short-term food availability varied between treatments and long-term differences in perceptions of environmental quality varied between groups of individuals. This corresponds to variation in the three components of the cost of predation ( $P$ ): the predation risk ( $\mu$ ); the change in reproductive value with energy gain ( $\partial F/\partial e$ ); and the reproductive value or fitness factor ( $F$ ). The birds showed that they experienced a higher cost of predation while using the risky food patches ( $\mu$  component) and in the high food treatment ( $\partial F/\partial e$  component). Furthermore, birds from a high-reward habitat revealed a higher  $P$  than birds from a poor habitat ( $F$  component). The results show that the costs of predation are possible to tease apart by using behavioural indicators. The method presented allows measurement of fitness prospects of individuals, which may have consequences for conservation, for example, to identify low-quality habitat.

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The fitness of an animal should be positively influenced by both increased energy gain and increased survival. In most cases the behavioural option that yields the highest energetic reward will not also be the safest option (Lima & Dill 1990). This leads to a trade-off between energy gains and predation risk. For a foraging animal, the optimal behaviour may then vary both with the nature of the foraging patch, and with the animal's internal state (McNamara & Houston 1986; Houston et al. 1988; Mangel & Clark 1988). State-dependent foraging emerges as a consequence of the cost of predation (Brown 1988, 1992; Houston & McNamara 1989; Clark 1994; McNamara & Houston 1994). A formal definition of the cost of predation involves three terms: the risk of predation ( $\mu$ ); the cost of being killed, which is the expected fitness if surviving ( $F$ ); and the rate of change in expected fitness with energy intake (i.e. the marginal value of energy,  $\partial F/\partial e$ ; Brown 1992; McNamara & Houston 1994). The cost of predation,  $P$ , measured in units of energy, is then  $P = \mu F / (\partial F/\partial e)$ . Thus, the cost of predation is not the same as the risk of predation. An animal's allocation of time among food patches, its level of awareness of

predation while foraging and the food density at which it leaves a foraging patch (giving-up densities of prey, GUD, Brown 1988) should respond to differences in predation risk, in fitness if surviving and in the marginal value of energy:  $\mu$ ,  $F$ , and  $\partial F/\partial e$ , respectively.

Through the cost of predation, the optimal behaviour of an animal should depend on its future expectations, which depend on the long-term quality of the environment (Olsson & Holmgren 1999), as well as on short-term changes in environmental state (McNamara & Houston 1994). Animals used to a habitat of a given quality may respond differently to animals used to a habitat of another quality when exposed to the same short-term environmental state (Wilson 1976). All else being equal, animals with a low expected fitness ( $F$ ) should be willing to take higher risks and work harder to gain energy, whereas animals with high fitness expectations should be more protective about their lives (e.g. asset protection principle, Clark 1994). That is, their cost of predation ( $P$ ) is higher, even when the risk of predation ( $\mu$ ) is the same.

Here, we are concerned with the patch use behaviour of European starlings, *Sturnus vulgaris*, in a closed economy (sensu Houston & McNamara 1989) feeding experiment. That is, only the experimental treatment and their own behaviour determined the starlings' energy intake, as they did not get any food outside the experiments. The

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starlings searched for food in foraging patches and we measured patch residence times, patch harvest rates, vigilance behaviour and final prey densities (which can be used as a surrogate of GUDs, e.g. Brown 1988 see Methods). The experiment tested for three scales at which the cost of predation can vary: (1) between patches within a foraging bout; (2) short-term changes in food availability between treatments; and (3) long-term differences in perceptions of environmental quality between groups of individuals.

(1) Within a foraging bout we offered the birds food patches with low and high perceived risk of predation. Only  $\mu$  should vary between patches. GUDs should be higher in the patch with higher perceived predation risk. The total feeding effort should also be lower in the riskier patch. However, since there may be several different ways for animals to modify their predation risk while foraging (Brown 1999; Lima & Bednekoff 1999), explicit a priori predictions about foraging time are difficult to make.

(2) To vary short-term environmental state, we exposed the birds to treatments with either high or low food availability. Within a food treatment there should be little change in the forager's perception of its fitness if surviving,  $F$ , as the experimental time is relatively short. However, there can be large changes in the marginal value of energy,  $\partial F/\partial e$ , that is, when food is scarce energy should be more valuable. GUDs should be higher, and the feeding effort in the patches should be lower, when food availability is high.

(3) To test for differences in foraging behaviour in response to long-term differences in environmental quality, we used starlings from two different habitats that varied in population density and average reproductive success, probably because of differences in long-term food availability (Smith & Bruun, in press). We expected birds from the higher-quality environment to have higher perceived fitness prospects,  $F$ . Theory (Brown 1999) predicts that these birds, relative to those from the lower-quality habitat, will have higher costs of predation, leading to higher GUDs, higher rates of vigilance and lower harvest rates. We refer to this factor as habitat of origin.

We aim to further our understanding of foraging under predation risk in general by providing conceptual and methodological tools for measuring animals' own predictions of their future. This approach may also provide us with a way to measure the fitness prospects of non-reproducing animals.

## METHODS

### Aviaries, Birds and Husbandry

We caught 12 female starlings in early May 1999, after they had completed laying a clutch and had just started to incubate. (The eggs were redistributed among other nests as part of a different experiment, and were accepted by the foster parents.) The birds were caught under licence from the Swedish Environmental Protection Agency and the Malmö/Lund ethical committee for animal research approved the experiment. Each bird was

captured in a separate breeding colony, which were at least 500 m, but most often several km, apart. Six of the birds were taken from a good (high reproductive success) and six from a bad (low reproductive success) habitat. In this study, good habitats constituted part of the Revinge study area (55°43'N, 13°30'E), a large grazed permanent grassland that offers good foraging habitats. The bad habitat was the surrounding agricultural plain, mostly comprised of arable fields, with for example, grain, rape, beet and potato, with few and dispersed grazed pastures.

There are more opportunities to feed and gain fitness in the grazed grassland than in the agricultural plain (Smith & Bruun, in press). Consequently, starlings from the grassland should perceive a lower marginal value of energy, value safety more and have a higher marginal rate of substitution of energy for safety from predation. Any of these effects predict that starlings from the good habitat should, under controlled circumstances, experience a higher foraging cost of predation than the starlings from the bad habitat. This habitat-specific difference in the cost of predation occurs independent of any habitat differences in predation risk.

The birds were kept in groups of three in four separate outdoor aviaries (8 m<sup>2</sup> floor area, 2.5 m high). The aviaries were shaded against direct sunshine in the mid-day and afternoon, and the temperature never exceeded 30°C. In the aviaries, the birds had a continuous supply of fresh water. They fed with negligible aggressive interactions, as determined from videorecordings. As they had four feeding patches available, of which three were without edges (see below) there was little possibility for one individual to exclude another from feeding opportunities. In each aviary the starlings had shrubs available for perching, and three nestboxes which they used for cover and roosting. The birds were weighed when caught and thereafter several times per week. At capture they weighed on average 84 g and then declined to 78 g. This weight loss is regarded as normal as the females were reducing the size of their reproductive organs at this time. After this initial weight loss they kept a constant weight and weighed ca. 78 g when released.

The birds in each group originated from the same habitat such that two aviaries held birds from one habitat and two held birds from the other habitat. Prior to experiments, birds were kept in the aviaries for 2 weeks for habituation to the experimental protocols. A group size of three can be small relative to potential flock sizes in nature, but this group size falls well within the range of typical feeding groups (Feare 1984). All birds would be familiar with foraging as a group of three.

After the experiment we released the birds as a group, in a suitable habitat, not far from where they were caught.

### Experimental Protocol

Each aviary had four food patches, which consisted of trays (25 × 25 cm wide, 3.5 cm deep) stocked with freeze-killed mealworms, hidden beneath moist sand. To stock a tray with food, we covered its bottom with 1 cm of moist sand, on which we distributed the worms. We then buried the worms under an additional 2.5 cm of moist

sand. Patches were stocked in the mornings (between 0900 and 1200 hours). After a randomly selected time (4–9 h), we stopped the experiments and collected the remaining mealworms from the patches (see below).

The experimental treatments were high (36 g per patch, mean initial prey density, IPD, 567 mealworms) and low (24 g per patch, mean IPD 376 mealworms) short-term food availability. In a first experimental run (7 days), we randomly assigned one aviary with birds from the good, and one with birds from the bad, habitat to the high food availability. The other two aviaries received the low food availability. After this, we reversed the food treatments in a second experimental run (6 days). At this time we moved the groups of birds to remove any aviary effects: the birds from the good habitat that initially had high food availability were moved to the aviary where the birds from the bad habitat had low food availability and vice versa.

To vary predation risk between patches within an aviary, we erected a 10-cm-high wall around one of the patches in each aviary. The barrier could increase perceived predation risk in three ways. First, the barrier should hamper a bird's ability to escape ambush by a predator. Second, it reduces the bird's sight lines for detecting potential threats. Third, the obstruction of vision also hinders a bird's ability to see other birds and gain valuable information from their behaviour.

In each aviary, we used a dummy sparrowhawk (a piece of construction board cut to the shape of a hawk silhouette) to maintain a sense of predation risk in the starlings. The 'hawk' was positioned in cover (out of sight of the birds) and, using a remote control, we could 'fly' it across the aviary by sliding it along a wire. This was done two or three times a day, at irregular intervals.

## Behavioural Observations

We collected three types of data: (1) time spent in patches as recorded by transponder driven data loggers; (2) observations from videorecordings of patch use, prey captures and vigilance; and (3) density of prey remaining at the end of each day.

### *Transponder data*

All birds were equipped with a passive glass encapsulated transponder ( $2.2 \times 11.5$  mm), attached with electrical tape to the birds' leg rings. The transponders weighed ca. 0.1 g and did not constrain the birds' mobility. Under each food tray we placed an antenna connected to a transponder decoder with a data logger (Trovan). In this way we got individual readings of birds when they were in the patches. For each individual that was in a patch, one reading was recorded every sixth second. From these data we could evaluate when, and for how long, the different patches were occupied. However, these data do not determine if the birds were actively feeding or engaged in other activities while in the food patch. Transponder data could be collected in two aviaries at a time. Hence, activity data for a given aviary was recorded every second day.

### *Video observations*

Every other day (in the aviaries without transponder readers), we used video cameras to record the actual behaviour of birds in food patches. For individual identification, we applied acrylic paint (red, white or green) to the wing coverts of the birds. We scraped off the paint with our fingers before the birds were released, which had a marginal effect on the feathers. We started the filming when the food was presented to the birds. The cameras then ran for 2–4 h, that is, only during the first part of each day's experiment.

The videotapes were analysed with Noldus Observer Video Pro 4 (Noldus Information Technology 1995). In the analyses we kept track of one focal bird at a time. That is, the first bird that started to use the patches became the first focal bird. We recorded its activity until it left that patch (mean patch visit duration 34 s, range 1–178 s). The next bird that entered a patch became the new focal bird, until it left that patch, and so on. For the current non-focal birds, we kept track of their time spent in food patches, but we did not record their specific behaviour while in the patches.

Behaviours recorded were active searching for prey (probing or walking with bill pointed below horizontal), handling prey and scanning (looking up with bill horizontal or above). From this we could estimate instantaneous harvest rates of prey, and the proportion of time spent vigilant or handling prey (Olsson et al. 2001). Instantaneous harvest rates were calculated as the inverse of the time spent actively searching for a given prey item. Unfortunately, these behavioural variables could be reliably estimated only in the patches without walls around them.

### *Final prey density*

At the conclusion of a day's experiment, we collected the food patches and weighed the remaining mealworms. As the sand used was moist, simple sifting did not work. Instead we dumped the tray's contents into a bucket of salt water (ca. 1 kg of NaCl per 10 litres of water), in which all mealworms float. The sand/water/worm mix was stirred, and the water was then skimmed to retrieve all remaining mealworms. These were subsequently weighed to the nearest 0.1 g on an electronic balance. We converted this weight to the weight of dry (not-soaked) worms by multiplying by 0.857 (regression coefficient from calibration weighing:  $r^2=0.99$ ,  $P<0.005$ ,  $N=16$  groups of 1, 5, 10 and 20 g).

Varying the length of the experiments allowed us to estimate the rate at which prey were harvested. The final prey densities also varied with time, but could be used as a surrogate of true GUDs (Brown 1988) under some conditions. Ideally, GUDs estimate the forager's quitting harvest rate. This requires that harvest rates increase with prey density, that is decrease with time spent searching. Our data allow us to test for this. To be useful, this also requires that the quitting harvest rate equals the sum of the foraging costs (metabolic, predation and missed opportunity; Brown 1988). Within a day's experiment, the patches did not replenish, and the birds had no

**Table 1.** The experimental protocol

Habitat	Group			
	Good	Good	Bad	Bad
Run 1	H	L	H	L
Run 2	L	H	L	H
Runs group	HL	LH	HL	LH

Each group contains three birds. See text for details. H: High food availability; L: low food availability.

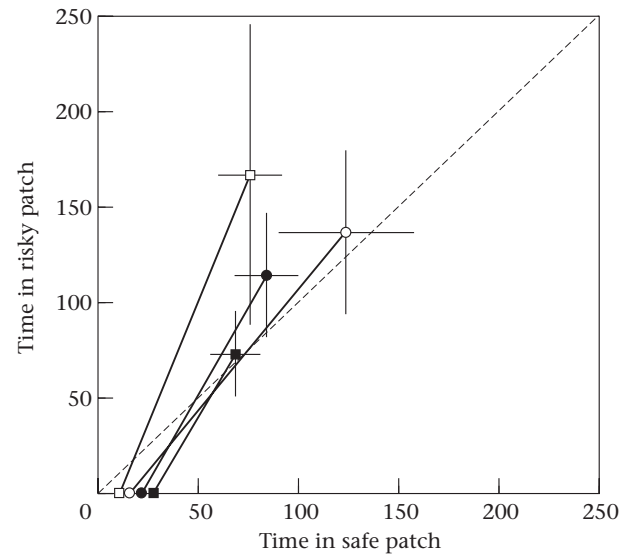
alternative food sources. Thus, the value of energy could change within a day, and the prey densities finally approach zero. At any given time, however, each bird should have exploited the individual patches until its quitting harvest rate at that time had been reached. Thus, we argue that the final prey densities as we have measured them can be used as a surrogate for GUDs. For simplicity, we refer to these densities as GUDs hereafter.

## Statistics

The birds were randomly assigned to the four groups of three: two groups with birds from the bad, and two with birds from the good, habitat (Table 1). The birds were randomly assigned to these groups. In the first experimental run we randomly assigned the groups of birds to one of the food treatments (high or low), according to Table 1. In the second run the treatments were reversed. This assignment hence identifies the 'runs group' (HL or LH) to which the group of birds belonged.

A sample size of 12 birds will unavoidably lead to a low power of the tests to be performed. This means that we must refrain from making any conclusions about lack of relationships from nonsignificant results. However, results that turn out to be significant are as valid when based on a small sample size as when based on a large one.

When we analysed individual behaviour, observed with video or transponder equipment, could identify individual birds and consequently made the analyses at the individual level. This was done in nested ANOVAs (SPSS 1999), where the individual was considered a random factor, and habitat of origin, food treatment, runs group and safety (patches with high or low walls) were considered fixed. The individuals were nested within habitats and runs groups. In some cases observations are missing for one or more individuals in some treatments, and therefore degrees of freedom are not always the same between analyses. When we analysed final prey densities, GUDs and total number of prey caught, we could not identify individuals and so did the analyses at the group level. We used ANOVAs with only the fixed factors habitat, food treatment, runs group and safety. When we analysed the start of foraging, proportion of total time spent in the foraging patches and proportion of time spent scanning, we did the analyses on the mean values of individuals, for each food treatments. Proportions were



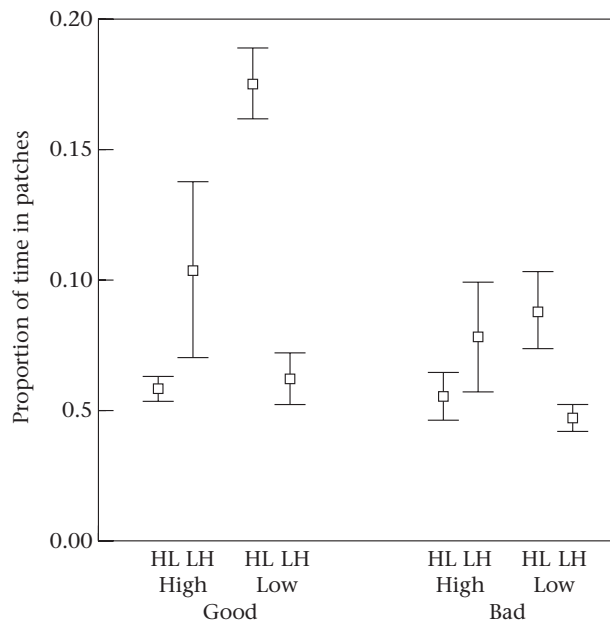
**Figure 1.** Use of the two types of foraging patches. The axes show the times (seconds per individual and patch) spent in the safe and risky patches. The lower set of points shows the situation in the instants when the risky patch was first being used. The upper set of points shows the situation when the experiment was terminated.  $\square$ ,  $\blacksquare$ : bad habitat;  $\circ$ ,  $\bullet$ : good habitat.  $\square$ ,  $\circ$ : Low food availability;  $\blacksquare$ ,  $\bullet$ : high food availability. Vertical and horizontal lines indicate 1 SE. The dashed line connects the points where both patches have been used for the same amount of time.

arcsine square-root transformed before analysis. When we analysed the relations between instantaneous harvest rate and foraging time, GUDs and experimental time, and number of prey caught and time in patches, we first made separate regression analyses for each individual and food treatment. We then used the obtained model coefficients for analysis in ANOVAs as described above. In all analyses we did preliminary analyses of the saturated models, and subsequently removed all interaction terms that were not significant at  $P < 0.1$ . We present only final models with main effects and possible significant interactions.

## RESULTS

### Transponder Data

Overall, the birds started foraging significantly later in the risky patch, that is, the average difference in start time between the risky and the safe patch (start in risky – start in safe) was greater than zero ( $F_{1,9} = 48.96$ ,  $P < 0.0005$ ; Fig. 1). High food availability tended to increase the delay of the start in the risky patch ( $F_{1,11} = 3.88$ ,  $P = 0.075$ ). The birds' habitat of origin did not influence the overall delay of the start in the risky patch ( $F_{1,9} = 0.08$ ,  $P = 0.8$ ). There was no difference between the runs groups ( $F_{1,9} = 2.24$ ,  $P = 0.17$ ) and there were no individual differences between the birds in their start time in the patches (individual nested within habitat and runs group:  $F_{9,11} = 0.87$ ,  $P = 0.6$ ). A direct comparison showed that 10 of the 12 birds had a later start time in the risky patch when food was high than when it was low (sign test:  $P = 0.039$ ). Figure 1 summarizes these results. Initially the safe patch was used



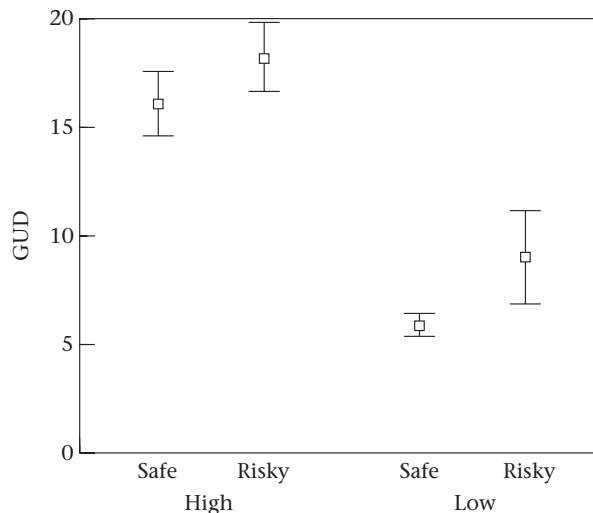
**Figure 2.** The proportion of time spent in the patches by the starlings, from the different habitats (good and bad), in the different food treatments (high and low food availability) and in the different runs groups (see Table 1). Means are shown  $\pm 1$  SE.

more than the risky one. The use of the risky one then increased faster than the use of the safe one (higher than 1:1 slope), so that at the end of the experiment both patches had been used approximately equally.

On average  $\pm$  SD the birds spent  $8.3 \pm 3.01\%$  ( $N=12$  individuals) of the total experimental time in the patches (Fig. 2). This percentage was approximately the same regardless of food treatment ( $F_{1,10}=2.67$ ,  $P=0.13$ ) and also for the two runs groups ( $F_{1,9}=2.06$ ,  $P=0.18$ ). However, there was a strong interaction between food treatment and runs group ( $F_{1,10}=27.53$ ,  $P<0.0005$ ). That is, all groups of birds spent less time in the patches in the first run than in the second. There was a tendency for the birds from the good habitat to spend more time in the patches ( $F_{1,10}=4.13$ ,  $P=0.069$ ), but this was not significant. There were no significant differences between individuals (nested within habitat and runs group:  $F_{9,10}=1.87$ ,  $P=0.17$ ).

### Video Observations

The starlings faced diminishing returns while foraging. We showed this by separate regression analyses between the (log-transformed) instantaneous harvest rate of prey and time spent searching, for each individual and food treatment. All 12 individuals had slopes less than zero in both treatments (average slope  $-0.00082$ ,  $F_{1,9,6}=24.67$ ,  $P=0.001$ ). These slopes differed between runs groups ( $F_{1,10,1}=6.45$ ,  $P=0.029$ ) but not between individuals, habitats or food treatments ( $F_{9,8}=2.33$ ,  $P=0.12$ ;  $F_{1,9,6}=0.02$ ,  $P=0.9$ ;  $F_{1,8}=2.23$ ,  $P=0.17$ , respectively). Using the assumption that slopes differed between runs groups but were homogeneous between individuals, habitats and food treatments, we made new regression analyses. In



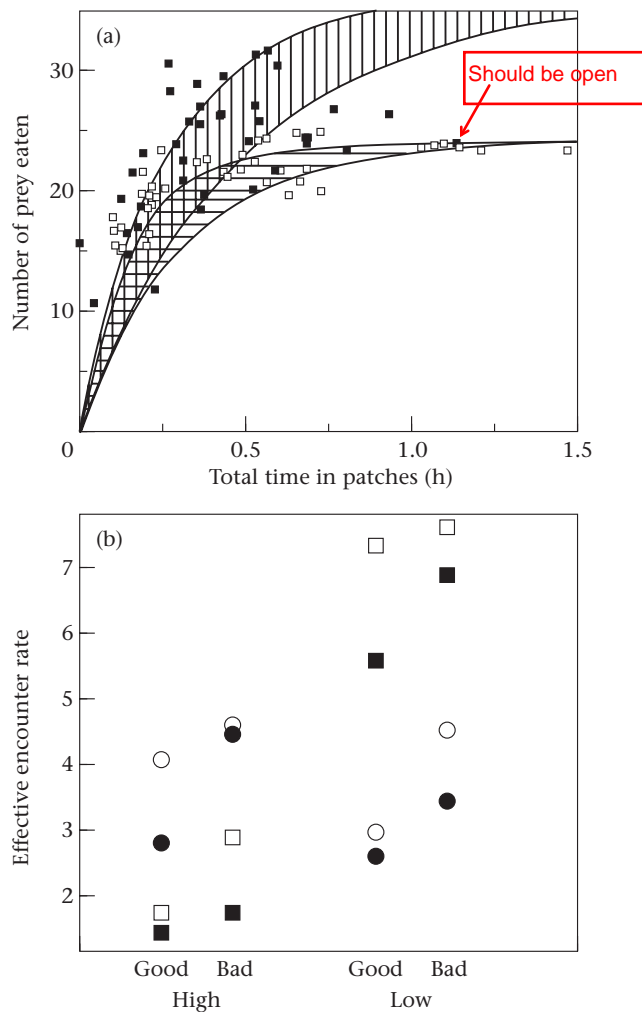
**Figure 3.** Giving-up densities (GUD) of prey in the safe and risky patches. Means are shown  $\pm$  SE; the values are estimated values after 6 h of the experiment. High and low refer to high and low food availability.

these we kept the slope fixed (to the average values of the runs groups,  $-0.00047$  for runs group 1 and  $-0.00114$  for runs group 2) to calculate the zero intercepts for each individual and food treatment. This approach is in lieu of a standard ANCOVA procedure. The birds from the bad habitat had slightly, albeit not significantly, higher intercept ( $F_{1,9,4}=3.85$ ,  $P=0.08$ ), that is, a higher instantaneous intake rate. Food treatment, however, did not influence the instantaneous intake rate ( $F_{1,7}=0.075$ ,  $P=0.8$ ; there was no difference in the intercepts between runs groups ( $F_{1,10,0}=1.59$ ,  $P=0.2$ ). The between-individual differences were close to significant ( $F_{9,7}=3.59$ ,  $P=0.053$ ).

The proportion of time in the patches that was devoted to scanning or handling (that is (scanning+handling)/total time), did not differ between habitats, food treatments, runs groups or individual birds (ANOVA on arcsine square-root transformed values:  $F_{1,9,8}=1.07$ ,  $P=0.3$ ;  $F_{1,9}=0.36$ ,  $P=0.6$ ;  $F_{1,10,3}=0.53$ ,  $P=0.5$ ;  $F_{9,9}=1.06$ ,  $P=0.5$ , respectively).

### Final Prey Densities

The GUDs were higher in the risky patches than in the safe patches. Not unexpectedly, the GUDs were also higher with high food availability (Fig. 3). We found this by calculating the intercept and slope for the linear regression between GUD and total time of the experiment, separately for each aviary, food treatment and patch type. Also not surprisingly, GUD declined with length of experiment ( $F_{1,11}=162.62$ ,  $P<0.0005$ ). In the risky patches, GUD was in general higher after an experiment of a given length (higher intercept;  $F_{1,10}=5.83$ ,  $P=0.034$ ), and the decline in GUD with time was stronger (steeper slope;  $F_{1,11}=6.96$ ,  $P=0.023$ ). That is, the difference in GUD between risky and safe patches declined with time. With high food availability, GUDs were initially higher and declined more rapidly than with low



**Figure 4.** (a) The number of prey items taken during an experiment as a function of the total time spent in the patches. ■: High food availability; □: low food availability. The hatched areas are the 95% confidence regions for the relation between number of prey caught and time in patch, for high (| | |) and low (≡) food availability. The particular regions shown are for birds from the bad habitat, foraging in safe patches during the second experiment. (a) the effective encounter rate, estimated from the above data. ○, ●: First experiment; □, ■: second experiment. ○, □: safe patches; ●, ■: risky patches.

food availability. That is, the intercept of the relation was higher ( $F_{1,11}=21.50$ ,  $P=0.001$ ) and the slope was steeper ( $F_{1,11}=9.30$ ,  $P=0.011$ ). There was no difference between birds from different habitats, for either of the two variables (intercept:  $F_{1,11}=1.77$ ,  $P=0.2$ ; slope:  $F_{1,11}=1.66$ ,  $P=0.2$ ). Similarly, there was no difference between the two runs groups (intercept:  $F_{1,11}=0.68$ ,  $P=0.4$ ; slope:  $F_{1,11}=2.60$ ,  $P=0.14$ ). All possible interactions had  $P$  values 0.5 or higher.

For each aviary and food treatment we fitted the total number of prey consumed (as measured from the final prey densities) to the total time (using transponder data) spent in each patch, using a negative exponential function (Olsson et al. 2001; Fig. 4a). That is, we fitted  $n=IPD(1 - e^{-at})$ , where  $n=IPD - GUD$ ,  $t$  is total time

spent in the patches (i.e. searching, scanning and handling) and  $a$  the effective encounter rate with prey. The values of  $a$  for each cage, food treatment and patch type (safe versus risky) were then used as the dependent variable in an ANOVA. A low effective encounter rate indicates that the birds are less attentive to foraging and more attentive to vigilance, potential risks and to other birds.

The birds from the bad habitat had higher encounter rates than those from the good habitat ( $F_{1,10}=30.74$ ,  $P<0.0005$ ; Fig. 4b). Encounter rates were higher in the safe than risky patches ( $F_{1,10}=24.20$ ,  $P=0.001$ ) and lower when food availability was high ( $F_{1,10}=155.90$ ,  $P<0.0005$ ; Fig. 4b). However, when habitat, safety and food treatment were accounted for, the encounter rates also differed between the two experimental groups that started with high, and the two that started with low, food availability ( $F_{1,10}=16.51$ ,  $P=0.002$ ; Fig. 4b). Furthermore, there was a highly significant interaction between food treatment and experimental group ( $F_{1,10}=254.02$ ,  $P<0.0005$ ). That is, all four groups of birds lowered their effective encounter rates in their second experimental run, but the group that started with low food availability decreased the rates much more. Nevertheless, within each experimental run, the encounter rates were lower with high food availability (Fig. 4b). None of the other possible two-way interactions was significant ( $P>0.35$  in all cases).

## DISCUSSION

Based on time allocation patterns, GUDs and attentiveness to foraging, we can make three main conclusions from this study.

(1) The birds showed that they experienced a higher cost of predation while using the risky food patch, as: (a) risky patches were not used until the safe patches had been somewhat depleted; (b) risky patches had a higher GUD than safe patches; and (c) the birds had a lower effective encounter rate on mealworms in the risky patches.

(2) The birds showed that they experienced a higher cost of predation with high food availability, that is food was perceived as less valuable when abundant, as: (a) GUDs were higher when food was more abundant; (b) with high food availability, the birds increased the delay in initiating use of the risky patch relative to the safe patches; and (c) the birds had a lower effective encounter rate of mealworms when food was abundant.

(3) The birds from the good habitat showed that they experienced a higher cost of predation, that is, they were less willing to take risks, as they chose a lower effective encounter rate than the birds from the bad habitat. The difference in instantaneous harvest rate between the groups was in the same direction (lower in the good habitat), but this difference was not significant.

The above three results correspond to the three components of the cost of predation:  $\mu$ ,  $\partial F/\partial e$  and  $F$ , respectively. Below, we consider how within-bout variation in predation risk (conclusion 1), short-term changes in food availability (conclusion 2) and long-term variation in environmental quality (conclusion 3) operate at

different spatial or temporal scales; and how each influences a different component of the foraging cost of predation.

### Within-bout Variation in Predation Risk

The starlings responded to our manipulation of risk in patches in an appropriate manner. The patches should be exploited until the expected harvest rate equals the sum of metabolic, missed opportunity and predation costs of foraging (Brown 1988). In a patch with higher perceived predation risk, the cost of predation should be higher. Thus, starlings should have, as they did, higher GUDs in the risky patches. Similar results have been found for desert rodents (Kotler et al. 1991; Hughes & Ward 1993), squirrels (Thorson et al. 1998) and ungulates (Kotler et al. 1994).

We could not measure directly the vigilance behaviour of the birds from the risky patches. However, based on the number of prey caught and the total time spent in the patches, we know that starlings lowered their effective encounter rates of food in the risky patches. This reduction accords with the birds becoming less attentive to patch exploitation as a consequence of greater attentiveness to predation (Fraser & Gilliam 1987). This result fits with literature showing increased vigilance (and hence decreased foraging efficiency) with higher predation risk (e.g. Lima & Dill 1990). The starlings' lowered effective encounter rates in the risky patch provide clues to how walls render a food patch scarier for a starling. (1) The walls may decrease the value of vigilance in which case vigilance may decline in the walled patch as the birds attempt to manage risk by minimizing time there. (2) Alternatively, the walls may increase the predator's lethality either by encumbering the starling's escape or by preventing it from gaining useful information from its flockmates. If this is the case, then starlings, as they did, should become more attentive to predators in the risky patch (Brown 1999).

The starlings began feeding by using the safer patch first. Later, after some resource depletion in the safe patch, the starlings switched to the risky patch. This seems a straightforward result and it is consistent with density-dependent habitat selection when habitats vary in some qualitative manner such as risk (Morris 1992). It is straightforward only if the birds are focusing primarily on current rather than future rewards. The order of patch use would not have been so predictable if a single bird had sole ownership of all patches and if the bird knew it would have sufficient time to complete its desired depletion of each patch. In our case, several factors probably encouraged the starlings to focus on current rather than future opportunities. First, multiple foragers nullify or dilute the gains to an individual that tries to postpone foraging (Mitchell 1989). Second, the birds may not have absolute confidence in the duration of the foraging bout. They may expect that weather, the experimenter, or other chance natural events will abruptly terminate some foraging bouts. Given multiple foragers and the expectation that foraging might end prematurely, the birds should begin by using the safe

patches first and then only later incorporating the risky patch into their feeding activities.

### Short-term Manipulation of Food Availability

When the experimental food level was high the birds delayed using the risky patch further and appeared to be feeding in a more relaxed manner. That is, when food was easier to find, the birds decreased their effective encounter rate. Thus, the GUDs are not merely a trivial consequence of initial food abundance, but can be seen as an outcome of the foragers' behavioural decisions. As can be inferred from Figs 3 and 4, the end result was that the number of prey consumed over a whole day was almost constant between food treatments.

A decline in the marginal value of food,  $\partial F/\partial e$ , with increased food availability probably explains the above results (Brown 1988; Abrams 1993; McNamara & Houston 1994). An increase in perceived survivor's fitness,  $F$ , could also produce these results. However, it is highly unlikely that a weeklong increase in food availability would have or be perceived as having much impact on the birds' future prospects (Frey-Roos et al. 1995; Svensson & Nilsson 1995; Olsson et al. 1999). When food is less valuable (owing to high availability) then foragers transfer attentiveness from foraging towards reducing risks.

The above results show how the scale at which resource availability varies matters to foraging and the costs of predation (Abrams 1993). During a foraging bout our birds experienced either all high-quality or all low-quality patches. In a different experiment, we offered the same starlings a mix of high- and low-quality trays within a foraging bout (Olsson et al. 2001). Under these circumstances, birds biased their activity towards the rich patches and did not change their level of attentiveness to foraging with food level. Similar patterns have been found when the value of energy varies with the availability of food (Brown et al. 1992; Morgan et al. 1997) and manipulated predation risk (Abramsky et al. 1997). In addition, via changes in the marginal value of food and its effect on the cost of predation, patches should be exploited less thoroughly in rich than poor circumstances (day-to-day variability in overall patch quality). For a fixed circumstance, rich patches should be exploited more thoroughly than poor patches.

Direct measures of vigilance behaviour (e.g. Jennings & Evans 1980) may underestimate the true attention that a forager is giving to predation risk while exploiting a food patch. Based on effective encounter rates with food, the starlings were much less attentive to foraging when food availability was higher and when risk was higher. This indicates that they shifted their foraging tactic from a more efficient one to a safer one. If so, we would expect to see an increase in vigilance behaviour between food treatments and between safe and risky patches. However, based on video analysis, we could detect no differences in time devoted to observable vigilance activities (scanning and handling) between food treatments. We also could not detect any strong differences in instantaneous intake rates (food items per unit search time) between food

treatments. Nevertheless, within a foraging bout, the intake rate declined with declining prey availability in the patches.

We therefore conclude that feeding activities, that is searching, probing and handling of food, may provide some collateral opportunities for scanning as well as food consumption. That is, while apparently searching for food within a patch, the starlings may be less attentive to finding food and more attentive to predators when the cost of predation increases. Thus, simple measurements of obvious vigilance behaviours may not fully measure an animal's attentiveness to predators. Fraser & Gilliam's (1987) tenacity index, which measures the overall decline in the forager's harvest rate within a food patch as the risk or cost of predation rises may provide a better measure.

### Long-term Differences in Environmental Quality

The individuals caught in the worse habitat seemed to work harder to obtain food, or were less bothered by risks. They had higher effective encounter rates and almost higher instantaneous intake rates. This should probably not be interpreted as that they were inherently more efficient foragers. In contrast, the results from the food manipulations show that effective encounter rate is a behaviour chosen by the foragers, in relation to the cost of predation. Therefore, we conclude that the observed behaviours are in agreement with the idea that the starlings adopted a behaviour that was influenced by their expectations of long-term environmental quality, that is, their fitness prospects,  $F$ . That is, the birds from the better habitat perceived a higher cost of predation. This made them adopt a foraging strategy that increased their chances of survival, but decreased their energy intake (McNamara & Houston 1994; Brown 1999).

The starlings in our study area produce more recruits when the availability of pasture is high (Smith & Bruun, in press), that is, in the good habitat. By the difference in foraging behaviour between habitats, this study thereby adds to the, still rather short, list of studies showing that foraging behaviour is related to subsequent reproductive success (Ritchie 1988; Lemon 1991; Frey-Roos et al. 1995; Martin 1995; Olsson et al. 1999). The behaviour of the starlings from the two habitats implies that they are expecting different reproductive outcomes at the time of egg laying, even though the differences in success appear at later stages. There are several other studies of birds (Källander 1974; Daan et al. 1988; Svensson & Nilsson 1995; Olsson et al. 1999; Reid et al. 2000) showing that food availability or energy expenditure before or during the early phases of breeding may affect the outcome during the later stages.

As pasture is the starlings' preferred foraging habitat (e.g. Dunnet 1955; Whitehead et al. 1995) the difference in reproductive success is likely to be due to food availability. Thus, we find it reasonable to believe that the long-term food availability in the habitats where the birds had settled and were caught is that which governs their fitness prospects.

### Research and Conservation Prospects

The cost of predation is expected to be the single factor most strongly influencing animals' behaviour (e.g. Brown 1992; McNamara & Houston 1994). Our results show that it is possible to tease apart this cost by using behavioural indicators, that is, by collecting data on time allocation, patch depletion and feeding attentiveness. The components of the cost of predation are important to understand.

As we have shown that there are measurable behavioural differences between individuals from habitats of different quality, our method can be used to estimate this difference. For conservation purposes this is important as one needs to identify good and bad, or source and sink, habitats (Brown & Pavlovic 1992). The behavioural differences do not merely correlate with the outcome of, for example, breeding success; instead, they reflect the individual's reproductive value directly, and are the animal's own estimate of this factor. Therefore, this measure should be close to the actual population growth rate, which a proximate measure such as clutch size is not necessarily (Smith & Bruun, in press). This method can thereby be applied to estimate ongoing or future population responses to habitat differences or habitat deterioration, at stages much earlier than with many other methods.

Furthermore, our method does not require the individuals under study to reproduce, to measure their fitness prospects. One can therefore compare the fitness prospects of juveniles born in different habitats, or adults wintering in different areas, or compare floaters with reproducing males. In many cases these comparisons may be the important ones for effective conservation strategies.

Finally, it may often be preferable to do studies like this one in the field. As artificial patches can be provided (Brown & Alkon 1990), there is no need to catch the animals under study, and they can remain in the environment that is to be investigated.

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