Starling foraging success in relation to agricultural land-use

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Changes in agricultural land-use have been suggested to contribute to the decline of several bird species through negative effects on their food supply during breeding. One important change in land-use has been loss of pastures, especially permanent pastures. In this study we investigated how different forms of agricultural land-use affected foraging success of a declining bird species, the European starling *Sturnus vulgaris*. We let caged starlings forage in different forms of agricultural fields and determined time spent foraging and foraging success. The starlings' activity level (time spent actively foraging) as well as the number of prey caught per time unit was strongly related to the abundance of prey in soil samples. Also the body mass change during the experiment was positively related to activity level and prey capture rate. We found consistent differences in foraging variables between habitats. In spring sown grain starlings were least active and found fewer prey items at a lower rate than in any other habitat. The other three habitats differed less, but in general mowed hay fields appeared slightly more valuable than the cultivated and natural pastures. We did not find any differences between natural and cultivated pastures in foraging variables. Thus, starling foraging success is higher in grass-covered fields than in cultivated fields, but the management of the grass-covered fields mattered less. The results are consistent with starlings having higher population densities and breeding success in areas with higher availability of pasture. We suggest that the physical structure of the habitat (sward height) and moisture may be additional variables that need to be taken into account to explain starling breeding density and success in the agricultural landscape.

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Agricultural intensification has been suggested as a major reason for the decline of several bird species associated with the agricultural landscape in northern Europe (O'Connor and Shrubb 1986, Chamberlain et al. 1999). Agricultural intensification, a process whereby a larger production of crops has been achieved per unit of area, has been achieved through increased use of pesticides and inorganic fertilisers, increased size of fields, removal of natural habitat fragments, changes in land-use and increased regional specialisation (e.g. O'Connor and Shrubb 1986, Campbell et al. 1997, Chamberlain et al. 1999). However, except for a few bird species, the mechanisms by which agricultural intensification affects population density are poorly known (Fuller et al. 1991, Chamberlain et al. 1999).

One major change, suggested to be important for some bird species associated with the agricultural landscape, is loss of pastures, especially natural pastures (Fuller et al. 1991, Chamberlain et al. 1999). Agricultural development has resulted in increased regional specialisation and thus concentration of dairy farming and meat production (O'Connor and Shrubb 1986, Chamberlain et al. 1999). A larger proportion of the fodder for cattle is produced in hayfields in rotation with grains or other crops, i.e. in fields that are regularly ploughed and fertilised (Chamberlain et al. 1999). In addition, many natural pastures are now improved, e.g. by being fertilised (Chamberlain et al. 1999). For birds dependent on soil-living invertebrates during breeding, these changes may have significant effects on

population trends if they in turn affect the abundance and/or accessibility of prey (Wilson et al. 1999).

Some studies have shown that the abundance of soil-living invertebrates may depend on agricultural land-use (Wilson et al. 1999). However, abundance and accessibility may not be linearly related across habitat types, because vegetation structure, soil texture and moisture all may affect how available prey are. It has recently been suggested that measuring foraging rates of caged birds in different habitats may be a reasonable method to measure prey availability (Whitehead et al. 1996).

The European starling *Sturnus vulgaris* is associated with man and the agricultural landscape. Starlings predominantly forage in open grassland where soil-living invertebrates constitute the most important food (Dunnet 1955, Tinbergen 1976, 1981, Moore 1986). During recent decades the starling has declined over large parts of northern Europe (e.g. Møller 1983, Svensson 1990, Solonen et al. 1991, Feare et al. 1992, Feare 1996). In the most northerly parts of Europe the starling's range has contracted (e.g. Carlsson 1979, Orell and Ojanen 1980, Solonen et al. 1991). Tiainen et al. (1989) suggested that the decline of the starling population was caused by the reduction of pasture in the modern agricultural landscape and Solonen et al. (1991) demonstrated that declines in Finland often were related to changes in the availability of pasture. In southern Sweden, starling reproductive success has been found to be associated with the availability of pastures near breeding colonies (Smith and Bruun 2002).

In this study we use caged wild starlings in experiments, where they are allowed to forage in different agricultural habitats. We study how the foraging activity and success varies between these habitats. We also evaluate how the measured foraging variables can be related to measured prey abundance in soil samples. We can then determine if the suggestion, that the population decrease of the starling is related to loss of good foraging habitat, is a reasonable one.

Methods

We used ten female starlings for a foraging cage experiment in four types of grass-dominated habitat. The birds were caught in the beginning of May 1998 in the Revinge study area in southern Sweden. The experiment was carried out during the subsequent six weeks, corresponding to the starling's breeding season, on farmland in and around the Revinge area. Between experiments the birds were kept in two aviaries (five birds in each), each with a surface area of 12.8 m² and a height of 2.2 m, that had some shrubs for perching and six clean nest boxes for roosting. They were given continuous access to fresh water.

Natural pasture (NP) was defined as grazed (although not necessarily during the experiment) grassland that were unploughed, unfertilised, or that at least had a flora that indicated that such activities had not occurred in the last ca 10 yr (Anon. 1997). Cultivated pasture (CP) was defined as grazed grassland that had clear signs of ploughing on the ground structure (e.g. low walls around the edges) and of fertilising on the flora (mainly nitrogen tolerant species present). Mowed hayfield (MH) was agricultural fields that were presently used for hay harvest (including silage). Fields used had either been mowed for grass harvest within the previous week, or when this had not occurred we manually cut the grass to a height similar to that obtained by agricultural mowing (ca 7–10 cm). These fields were usually fertilised several times per year and were normally in a rotation with other crops. Hence, the grass vegetation was in most cases not more than two to three years old. Spring-sown grain fields (SG) were both ploughed and fertilised in the present year. In the study area sowing took place in the last week of March and first two or three weeks of April in the year of study. In most cases they were also treated with herbicides and pesticides. Hence, they lacked most natural vegetation.

Nest box colonies, used for other studies (Smith and Bruun unpubl.), were randomly selected for the experiments. Adjacent to each colony one plot of each of the four study habitats, natural pasture, cultivated pasture, mowed hayfield, and spring-sown grain field was chosen. The plots were chosen such that for each habitat the closest place where it was found, was used for the experiment. Such plots were never > 500 m away from colonies, and usually much closer. Within colonies, plots had similar surrounding vegetation, soil characteristics and water table.

The experiments took place in cages with 1 m² bottom surface (100 × 100 cm wide, 50 cm high). These were made of a wood frame with nylon fish net for walls and roof, and open bottom. Before the actual experiments started, we habituated the starlings to the foraging cage, by performing at least three sham experiments per individual.

Each experimental day one group of five birds (from one of the aviaries) was used in the experiment. That is, each bird was never used two days in a row. Prior to an experiment the birds in the group to be used that day were deprived of food from the afternoon before. During the days when they were not used they were given mealworms and dog food pellets ad lib. On experiment days we checked the condition of the birds by weighing them.

The experimental period was divided into two runs (14–28 May and 3–12 June, respectively) and the starlings were split into two groups of five birds in each. Only one of the starling groups participated in the experiment in a given day, and never two days in a row.

Each day a group of starlings was taken to a new colony where the birds visited one habitat each, according to a rotational schedule. Over the whole experiment each individual starling visited each habitat twice – once in the first run and once in the second. The colonies visited by the first group of starlings in the first run was revisited by the second group in the second run, and vice versa, i.e. each starling only visited each colony once, and only in one habitat.

After being weighed a bird was released in one out of two adjacent cages for ca 12 min. During this time it was filmed using a video camera at a distance of ca 2 m. The person carrying out the experiment moved out of sight of the bird during the experiment. After the 12 min the bird was moved to the other cage for a new trial, equal to the first in all respects. After the second trial the bird was weighed again.

In the cages, the birds usually settled and started to feed within 2 min. The subsequent 10 min of activities were recorded and analysed using Noldus Observer Video Pro 4. Using this technique it was possible to separate between time spent actively foraging (searching or probing for prey), time spent handling prey (indicating prey capture) and time spent scanning for predators. The behavioural observations were grouped into ten 1-min intervals for each cage. Within these intervals we hence estimated: the proportion of time foraging actively, the number of prey caught, and the intake rate (number of prey/per time unit actively foraging). As the grain (SG) grew during the six weeks of the experiment, video analysis of the behaviour in this habitat was impossible in several experiments. This prevented some of the data analyses (see Results).

We sampled the soil in the cages by taking eight cylindrical (diameter = 72 mm, depth 50 mm) cores, including the top vegetation. The depth of the cores is greater than the probing depth of the starlings. However, preliminary evaluation of the method revealed that using a smaller depth there was a risk of losing e.g. earthworms that were located horizontally even if their one end was located close to the surface. Thus, the value of our soil samples is based on the assumption that the number of prey found in them correlate well with the numbers available to the starlings. The invertebrates in these soil cores were counted by sifting (sieve mesh size 0.64×0.64 mm) the soil samples under running water. For the analyses we used the total numbers of invertebrates per individual bird and day. Preliminary analyses showed that using the biomass instead of numbers of invertebrates produced similar results. However, the statistical distribution of biomass was extremely skew and could not be normalized using transformations. Hence, we chose to base all results on the analysis of number of invertebrates.

We analysed the data by repeated measures ANOVA, and when that method was not applicable by univariate linear models analysis (ANOVA, ANCOVA,

regression). In the repeated measures analyses we used the Huyn-Feldt corrected degrees of freedom for significance testing, due to the fact that deviations from sphericity sometimes occurred. In these analyses, all interactions terms that are not reported are not significant at the p = 0.1 level.

Three planned contrasts were performed on these repeated measures ANOVAs: contrasting the two types of pasture (NP vs CP), contrasting the pastures against the mowed hayfields ({NP, CP} vs MH), and contrasting the three grass bearing habitats against the grain fields ({NP, CP, MH} vs SG). These contrasts are orthogonal and their significance levels need not be adjusted.

When performing the linear model analyses on individuals' behaviour we first made separate analyses for each individual and then tested the individuals' model coefficients against zero using paired t-test, hence avoiding pseudo-replication. In all these cases we verified the assumptions of linear model analysis using Levene's test.

Results

Within-individual differences in foraging behaviour

In order to study how the foraging success and activity varied between habitats and in time we performed a series of repeated measures ANOVAs of the different foraging variables using the observations of the individuals as the subjects and repeated measurements over experimental run (two levels), habitats (four levels), cage (two levels), and time from start of experiment in the cage (ten levels, i.e. discrete 1-min intervals) as the within-subjects factors.

Time in active foraging
We found that the proportion of time during a 1-min interval that a bird was actively foraging varied significantly by the time from the initiation of the experiment ($F_{7.32,65.9} = 7.91$, $p < 0.0005$; Fig. 1d), varied between habitats ($F_{3.0,27.0} = 5.59$, $p = 0.004$; Fig. 1a), and was lower in the second run of experiments ($F_{1.0,9.0} = 13.36$, $p = 0.005$; Fig. 1b). Furthermore, the experimental run seemed to have slightly different effect on the different habitats (interaction term $F_{2.62,23.6} = 3.25$, $p = 0.045$). However, the time spent actively foraging was the same in the first and second experimental cage ($F_{1,9} = 0.146$, $p = 0.7$; Fig. 1c).

In order to look closer at these relations we computed the within-subjects contrasts of the above analysis. Making three planned contrasts among the habitats we found that the activity levels were the same in the two types of pasture (NP and CP, $F_{1,9} = 0.48$, $p = 0.5$), almost significantly higher in the MH than in the pastures ($F_{1,9} = 4.93$, $p = 0.054$), and clearly lower in

SG than in the other habitats ($F_{1,9} = 8.58$, $p = 0.017$; Fig. 1a). The decrease in activity level in the second experimental run was more pronounced in MH than in the two pasture habitats ($F_{1,9} = 6.47$, $p = 0.031$) whereas it was the same across the other two contrasts studied (NP vs CP: $F_{1,9} = 1.79$, $p = 0.2$; {NP, CP, MH} vs SG: $F_{1,9} = 2.28$, $p = 0.2$).

Finally, the level of activity was highest during the fourth minute of the experiment (Fig. 1d), and then decreased again. The second order contrast for the time intervals, that corresponds to a humped relationship, was clearly significant ($F_{1,9} = 15.3$, $p = 0.004$) and stronger than the linear contrast ($F_{1,9} = 5.80$, $p = 0.039$).

Number of prey caught per minute
The number of prey caught per 1-min interval differed clearly between habitats ($F_{2.63,23.64} = 10.98$, $p < 0.0005$; Fig. 2a) and also significantly varied with the time since the start of the experiment in the cage ($F_{7.94,71.41} = 3.06$, $p = 0.005$; Fig. 2d). However, number of prey caught per minute varied with time slightly differently in different habitats ($F_{22.0,197.7} = 1.604$, $p = 0.048$).

Number of prey taken per minute was the same in the two experimental runs ($F_{1.0,9.0} = 1.72$, $p = 0.2$; Fig. 2b), and in the first and second experimental cage ($F_{1.0,9.0} = 2.43$, $p = 0.15$; Fig. 2c). That is, in a given habitat and a given time after the bird was released in the cage, the number of prey taken per minute was the same in both cages.

We computed the within-subjects contrasts of the model to study the relationships more thoroughly. As for the level of activity, we found that out of three planned contrasts the number of prey caught per minute was not different between NP and CP ($F_{1,9} = 0.31$, $p = 0.6$) but it was higher in MH than in the pasture habitats ($F_{1,9} = 5.90$, $p = 0.038$) and much lower in SG than in the other three habitats ($F_{1,9} = 42.11$, $p < 0.0005$; Fig. 2a). The effect of time was clearly not linear (linear contrast $F_{1,9} = 0.006$, $p = 0.9$), but rather quadratic (quadratic contrast $F_{1,9} = 12.43$, $p = 0.006$; Fig. 2d), that is humped. The only significant contrast for the habitat time interaction was that in SG the number of prey taken per minute appeared to be virtually unaffected by time since start of experiment (quadratic contrast for SG vs {NP, CP, MH}: $F_{1,9} = 11.32$, $p = 0.008$). The two other quadratic contrasts were insignificant ($p > 0.1$).

Prey capture rate
The number of prey items caught per unit active foraging time per 1-min interval, i.e. the instantaneous prey capture rate, differed between habitats ($F_{3.0,27.0} = 9.37$, $p < 0.0005$; Fig. 3a). This rate was independent of time since start of experiment (Fig. 3d), experimental run (Fig. 3b), or cage (Fig. 3c) ($F_{6.62,59.6} = 1.05$, $p = 0.4$; $F_{1.0,9.0} = 0.015$, $p = 0.9$; $F_{1.0,9.0} = 0.49$, $p = 0.5$ respectively).

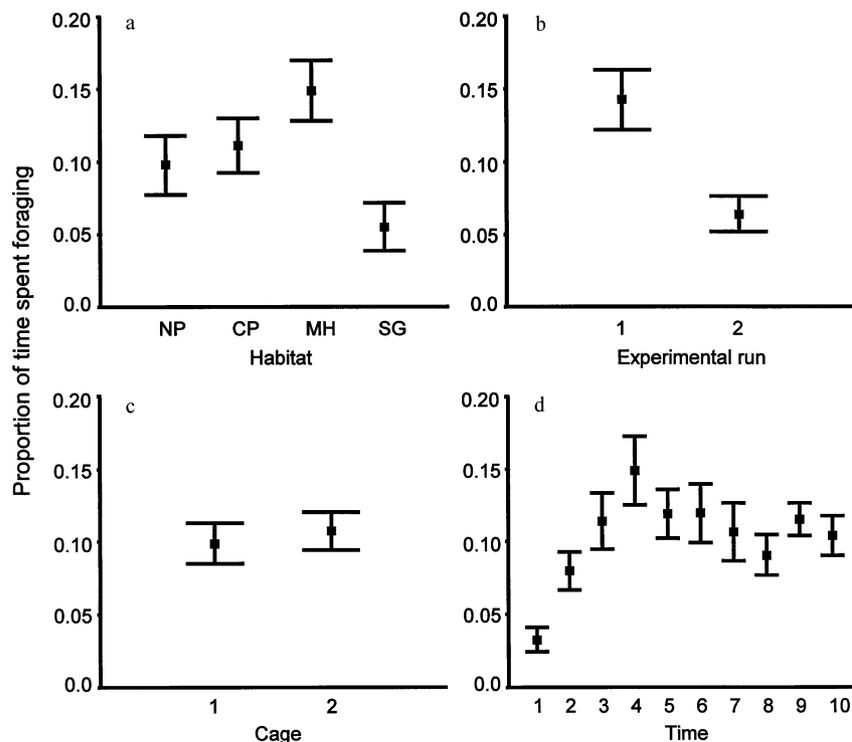We found the three planned within-subjects contrasts computed for the among-habitat comparisons similar

Fig. 1. The proportion of time spent actively foraging per 1-min interval during the experiments. Values are means (per bird and minute) ± 1 SE of the 10 birds in the experiment. The four panels show values for the four studied habitats (NP, natural pasture; CP, cultivated pasture; MH, mowed hayfield; SG, spring-sown grain field), the two experimental runs (1, second half of May; 2, first half of June), the two experimental cages (1, first 10 min; 2, latter 10 min of the experiment), and the 10 1-min intervals of the experiment in each cage.

Fig. 2. Number of prey caught per 1-min interval during the experiments. Values are means (per bird and minute) ± 1 SE of the 10 birds in the experiment. The four panels show values for the four studied habitats (NP, natural pasture; CP, cultivated pasture; MH, mowed hayfield; SG, spring-sown grain field), the two experimental runs (1, second half of May; 2, first half of June), the two experimental cages (1, first 10 min; 2, latter 10 min of the experiment), and the 10 1-min intervals of the experiment in each cage.
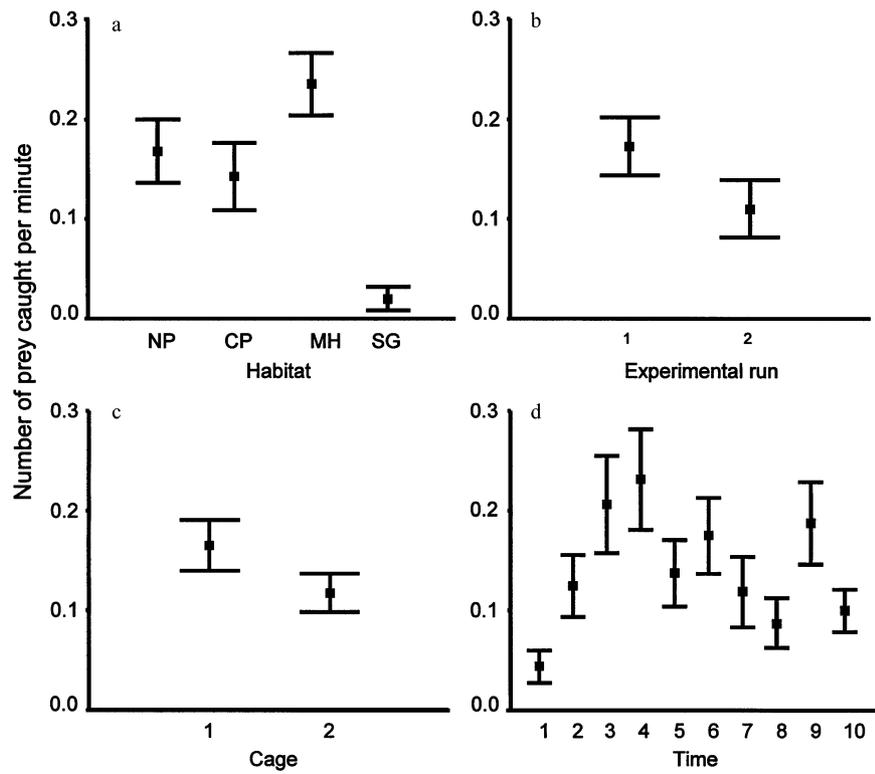

Fig. 3. Prey capture rate, i.e. number of prey caught per second active foraging time. Values are means (per bird and minute) ± 1 SE of the 10 birds in the experiment. The four panels show values for the four studied habitats (NP, natural pasture; CP, cultivated pasture; MH, mowed hayfield; SG, spring-sown grain field), the two experimental runs (1, second half of May; 2, first half of June), the two experimental cages (1, first 10 min; 2, latter 10 min of the experiment), and the 10 1-min intervals of the experiment in each cage.
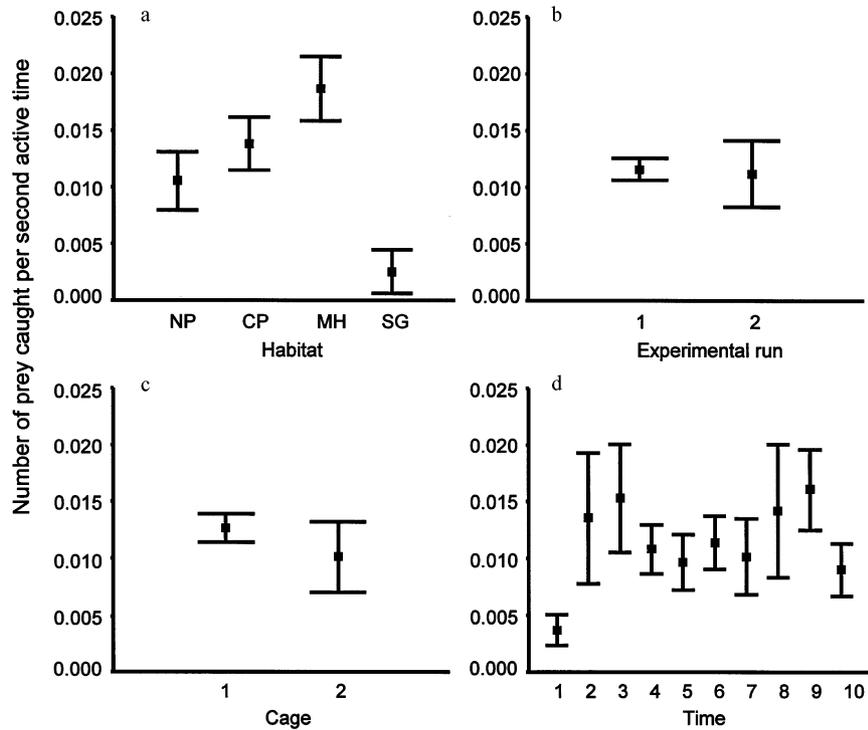
to the previously analysed foraging variables. That is, the prey capture rate was not different between the two pasture habitats (NP vs CP: $F_{1,9} = 0.95$, $p = 0.4$), but slightly higher in MH than in the pastures (MH vs {NP, CP}: $F_{1,9} = 5.20$, $p = 0.049$), and much lower in the SG than in the other habitats (SG vs {NP, CP, MH}: $F_{1,9} = 28.16$, $p < 0.0005$; Fig. 3a).

Changes in activity within experiments

The activity level in a given minute increased with the number of prey caught during the previous minute
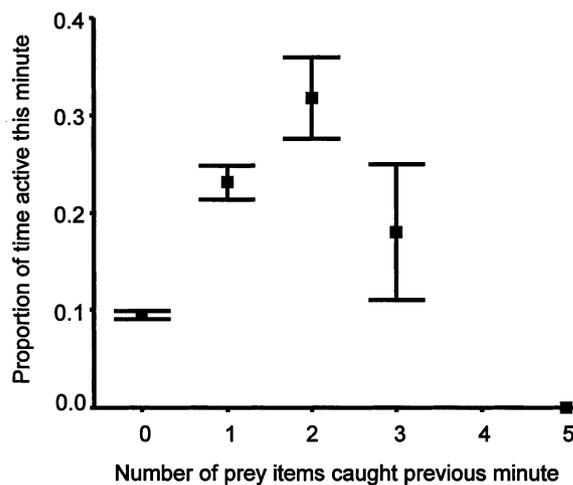

Fig. 4. The activity (proportion of time spent actively foraging) in a given 1-min interval as a function of the number of prey items caught during the previous minute of the experiment. Mean and 1 SE. The number of intervals that these descriptive statistics are based on is 1271, 138, 23, 7, 0 and 1 for 0 to 5 prey items caught, respectively.
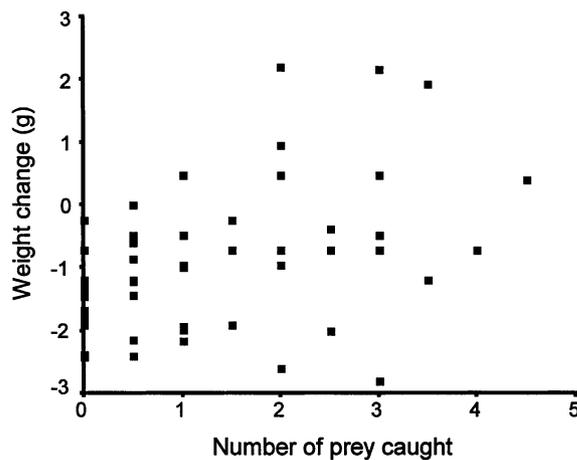

Fig. 5. The change in body mass by the starlings during an experiment (two cages, 20 min) plotted against the number of prey caught during the same time. Each point represents one experiment and an individual bird.
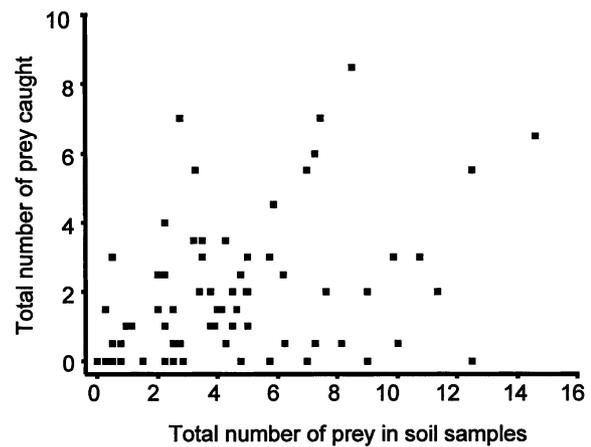

Fig. 6. The total number of prey caught during an experiment (two cages, 20 min) plotted against the total number of invertebrates found in the soil samples from the experiment.

$(t = 4.48$, $n = 10$, $p = 0.002)$ and decreased with this number squared $(t = -3.85$, $n = 10$, $p = 0.004)$, that is the relation was humped with a maximal activity level if two items were caught during the previous minute (Fig. 4). The regression coefficient computed for each individual was found by performing an ANCOVA with number of prey taken during the previous minute, and its squared value, were covariates, and habitat, experimental run, and cage were factors. By including these factors we ruled out the possibility that generally high activity levels were associated with experiments that were generally highly rewarding.

Individuals' changes in body mass

By subtracting the individuals' initial body mass, prior to an experiment, from their final body mass, after the experiment we estimated the average change of weight that the birds experienced. We excluded weight records from days when the vegetation was wet, as any water in the plumage otherwise could have influenced the result. On average the individual starlings lost 0.91 g (SD = 0.48, n = 10 individuals) of their body mass per hour of experiment time.

Within individuals, we found that the mass-change was positively influenced by the proportion of time spent foraging actively $(t = 2.27$, $p = 0.049)$, number of prey caught during the experiment $(t = 2.82$, $p = 0.020$; Fig. 5), and the prey capture rate $(t = 2.88$, $p = 0.018$, $n = 10$ in all cases). That is, they lost less weight, or even gained weight, when active, finding many prey or foraging at a high rate.

Between-habitat prey abundance

We found that there was a significant difference in prey abundance between habitats $(F_{3,67} = 9.78$, $p < 0.0005)$

when the effect of colony where the experiment was performed ($F_{8,67} = 2.43$, p = 0.023) was accounted for. Three planned contrasts showed that the only habitat deviating from the others was SG (SG vs {NP, CP, MH}: $F_{1,67} = 27.95$, p < 0.0005; NP vs CP: $F_{1,67} = 0.71$, p = 0.4; MH vs {NP, CP}: $F_{1,67} = 0.66$, p = 0.4).

Both the proportion of time spent in active foraging, and the number of prey caught per experiment (Fig. 6) increased with the prey abundance in the soil samples (t = 3.08, p = 0.013 and paired-t = 3.09, p = 0.013 respectively, n = 10). The prey capture rate, however, was not significantly influenced by prey abundance (t = 1.41, p = 0.2).

Discussion

Throughout, we found a consistent difference in the behavioural variables between the habitats. In the spring-sown grain (SG) the starlings were least active and found fewer prey items at a lower rate, than in any other habitat. The other three habitats differed less, but in general recently mowed hayfields (MH) appeared slightly more valuable than the cultivated pasture (CP) or natural pasture (NP). We did not find any differences between the pasture habitats.

The starlings' activity level (measured as the proportion of time spent actively foraging) as well as the number of prey caught per minute of experiment was strongly related to the abundance of prey in the soil samples. Also, the rate of body mass change during the experiment was positively related to activity level and prey capture rate.

Foraging patterns and agricultural practices

On a coarse scale our results corroborate the idea that the decline of the starling populations is due to loss of good foraging habitats (Tiainen et al. 1989, Solonen et al. 1991). That is, the trend over the last decades is that pastures and meadows are either abandoned, and finally forested, or converted into ploughed grain fields (Anon. 1990, Chamberlain et al. 1999). Our findings indicate that the conversion of pasture to grain field diminishes the starlings' feeding rate five- to sevenfold (Fig. 3a). A very crude estimate is thus that using grain fields, the starlings would need to spend the same amount of time feeding one nestling, as they would feeding six nestlings if using pasture or mowed hay meadows. This is a dramatic difference.

On a finer scale, we found no differences between the two types of pastures, and only a weak difference between pastures and meadow. Our inability to find a difference between natural and cultivated pastures may very well reflect reality. However, in much of the study area, the agriculture is intensive and much of the habitat loss may already have taken place. That is, what is left of natural pasture is often only small fragments, and often poorly managed (Berlin 1998, Chamberlain et al. 1999). In this study we did not compare grazing regimes within habitats. Such a comparison could potentially resolve some of the within-habitat variation, as starlings seem to prefer foraging on short swards (Williamson and Gray 1975, Feare 1984).

The finding that mowed hay meadows yield high foraging returns to starlings is supported by observations that flocks of feeding starlings often use newly mowed hayfields (Bruun unpubl.). Our analysis of the soil samples, however, did not indicate that hay meadows had a higher abundance of invertebrates than pastures. It may be the case that some of the prey caught in the hay meadows (that were mostly freshly mowed by ourselves) occur in the vegetation, and are exposed to the starlings by the mowing.

The hay meadows are usually not mowed until the very end of the starlings' breeding season. During the early stages of the breeding (end of April beginning of May) they may be as accessible to the starlings as are pastures. They then grow very rapidly, however, and are not used by the starlings until they are mowed (Bruun and Smith unpubl.). Modern agricultural practices may have a twofolded impact, as the meadows are cut earlier than previously, which ought to be positive. At the same time, however, they are more heavily fertilised, and grow faster (Chamberlain et al. 1999), which is likely negative to the starlings.

Foraging as a behavioural indicator

The different foraging variables correlated well with the abundance of potential prey in soil samples, and with the change in body mass during the experiment. Thus, all of these measures seem to provide the same, and relevant information. The method easiest to use, although perhaps also most crude, is obviously the change in body mass.

Studying the foraging behaviour, rather than directly sampling food abundance, may be a more efficient means of estimating habitat value (Hutto 1990, Whitehead et al. 1995, Poulin and Lefebvre 1997, Olsson et al. 1999). Ideally, a behavioural indicator may reveal the fitness value of a given habitat, or activity (Brown 1988, Olsson and Holmgren 1999). This requires that the animal's behaviour is a trade-off between the costs and benefits of foraging, not constrained by the experimental procedure. In the present study, this is only partly true. The starlings probably had the same feeding possibilities in the cages, as they would have had in the same spots without a cage. They were also free to forage or sit idle in the cages. However crucially, they were not given alternative useful activities, such as moving to a better foraging site (e.g. MacArthur and

Pianka 1966), or flocking together with conspecifics to reduce predation risk (e.g. Lima and Dill 1990). Thus, our method is likely to overlook other costs and benefits, associated with foraging in a habitat, than energy gain itself.

However, it seems likely that the four habitats we have studied, that always were closely together (within a few hundred meters from one another), differed mainly in energetic reward. The difference between them, in e.g. predation risk, is likely much less. Thus, in a case like ours, using only measures of the animal's foraging gains is probably a good way of obtaining information about how the animals would rank the alternative habitats.

Foraging and information use

The humped relation between time of experiment and activity level (Fig. 4) could potentially have three causes: satiation, depletion or motivation. The first two are already ruled out from the analyses of within-individual differences in foraging behaviour, as satiation would lead to a lower activity in the second cage, and depletion would lead to a decrease in prey capture rate with time. If motivation, e.g. driven by the individual's estimate of patch quality, caused the relation then a prediction would be that the level of activity should increase with recent experience. The decline in activity after having found more than two preys in the previous minute, may indicate that the starlings may have constraints in processing prey, a constraint that may not occur for starlings providing food to nestlings.

Conclusion

The present study demonstrates that agricultural land-use may have dramatic effects on the food available to foraging starlings. Thus, changes in agricultural land-use may have contributed to the recent decline of the starling. The study failed to find differences related to management of grass-covered fields. It may, however, be premature to conclude that this indicates that management of meadows and pastures has no consequences for foraging starlings. Different grassland management regimes, e.g. grazing with different stocks or density or at different times, affect the height and density of swards, thus affecting foraging efficiency (Williamson and Gray 1975). Furthermore, an important variable not considered in the present study is moisture, which may affect a starling's ability to probe for prey. Only additional studies can resolve these issues.

References

Anon. 1990. Betesmarker – historiska data. – Statistics Sweden, Stockholm.

Anon. 1997. Ancient meadows and pastures in Sweden. – Swedish Environmental Protection Agency, Solna.

Berlin, G. 1998. Semi-natural meadows in southern Sweden. – Ph.D. thesis, Lund Univ., Sweden.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk and competition. – Behav. Ecol. Sociobiol. 22: 37–47.

Campbell, L. H. et al. 1997. A review of the indirect effects of pesticides on birds. – Joint Nature Conservation Committee, Rep. No. 227, Peterborough.

Carlsson, U. T. 1979. Något om starens *Sturnus vulgaris* minskning i Värmland. – Värmlandsornitologen 7: 48–51.

Chamberlain, D. E. et al. 1999. The effects of agricultural management on farmland birds. – British Trust for Ornithology, The Nummery, Thetford, Norfolk.

Dunnet, G. M. 1955. The breeding of the starling *Sturnus vulgaris* in relation to its food supply. – Ibis 97: 619–662.

Feare, C. 1984. The starling. – Oxford Univ. Press.

Feare, C. J. 1996. Studies of West Palearctic birds 196. Common starling *Sturnus vulgaris*. – British Birds 89: 549–568.

Feare, C. J., De Franssu, P. D. and Peris, S. J. 1992. The starling in Europe: multiple approaches to a problem species. – In: Borrecco, J. E. and Marsh, R. E. (eds), Proc. 15th Vertebrate Pest Conf. Univ. of California, Davis, pp. 83–88.

Fuller, R., Hill, D. and Tucker, G. 1991. Feeding the birds down on the farm: perspectives from Britain. – Ambio 20: 232–237.

Hutto, R. L. 1990. Measuring the availability of food resources. – In: Morrison, M. L. et al. (eds), Studies in avian biology 13. Cooper Ornithol. Soc., Los Angeles, pp. 20–28.

Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – Can. J. Zool. 68: 619–640.

MacArthur, R. H. and Pianka, E. R. 1966. On optimal use of a patchy environment. – Am. Nat. 100: 603–609.

Møller, A. P. 1983. Changes in Danish farmland habitats and their populations of breeding birds. – Holarct. Ecol. 6: 95–100.

Moore, J. 1986. Dietary variation among nestling starlings. – Condor 88: 181–189.

O'Connor, R. J. and Shrubb, M. 1986. Farming and birds. – Cambridge Univ. Press.

Olsson, O. and Holmgren, N. M. A. 1999. Gaining ecological information about Bayesian foragers through their behaviour. I. Models with predictions. – Oikos. 87: 251–263.

Olsson, O. et al. 1999. Gaining ecological information about Bayesian foragers through their behaviour. II. A field test with woodpeckers. – Oikos 87: 264–276.

Orell, M. and Ojanen, M. 1980. Zur Abnahme der Stars (*Sturnus vulgaris*) in Skandinavien. – J. Ornithol. 121: 397–401.

Poulin, B. and Lefebvre, G. 1997. Estimation of arthropods available to birds: effect of trapping technique, prey distribution, and bird diet. – J. Field Ornithol. 68: 426–442.

Smith, H. G. and Bruun, M. 2002. The effects of pasture on starling (*Sturnus vulgaris*) breeding success and population density in a heterogeneous landscape in southern Sweden. – Agricult. Ecosyst. Environ., in press.

Solonen, T. et al. 1991. Dynamics of Finnish starling *Sturnus vulgaris* populations in recent decades. – Ornis Fenn. 68: 158–169.

Svensson, S. 1990. The decline of the starling *Sturnus vulgaris* population. – In: Viksne, J. and Vilks, I. (eds), Baltic birds II. Proc. of the fifth conference on the study and conservation of migratory birds of the Baltic basin, Riga, 5–10 October 1987. Zinatne Publishers, Riga, pp. 180–191.

Tiainen, J. et al. 1989. Clutch size, nestling growth and nestling mortality of the starling *Sturnus vulgaris* in south Finnish agroenvironments. – Ornis Fenn. 66: 41–48.

Tinbergen, J. M. 1976. How starlings (*Sturnus vulgaris* L.) apportion their foraging time in a virtual single-prey situation on a meadow. – Ardea 64: 155–170.

Tinbergen, J. M. 1981. Foraging decisions in starlings (*Sturnus vulgaris* L.). – Ardea 69: 1–67.

Whitehead, S. C., Wright, J. and Cotton, P. A. 1995. Winter field use by the European starling *Sturnus vulgaris*: habitat preferences and the availability of prey. – J. Avian Biol. 26: 193–292.

Whitehead, S. C., Wright, J. and Cotton, P. A. 1996. Measuring the impact of parental foraging by starlings (*Sturnus vulgaris*) on soil invertebrate prey availability: an exclosure experiment. – Oikos 76: 511–521.

Williamson, P. and Gray, L. 1975. Feeding behavior of the starling (*Sturnus vulgaris*) in Maryland. – Condor 77: 84–89.

Wilson, J. D. et al. 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. – Agricult. Ecosyst. Environ. 75: 13–30.