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HOW STARLINGS (*STURNUS VULGARIS* L.) APPORTION THEIR FORAGING TIME IN A VIRTUAL SINGLE-PREY SITUATION ON A MEADOW.

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CONTENTS

1. INTRODUCTION

In the study of feeding behaviour the important questions are when, where, how and what does an animal eat. Recent studies on foraging in birds have emphasized the 'where' question. The problem is, how do birds adapt their foraging behaviour to the distribution of the prey. Prey distribution will be either random, over- or under-dispersed. In nature we normally find dispersed or clumped populations (Southwood 1967). This means that prey tend to occur in small groups, more or less separated by areas without prey. These groups I will term clusters. On a much larger scale, we can expect density differences between different parts of the habitat. Ideally one could subdivide the habitat into small parts within which prey density is constant. I will call these idealised subdivisions units of the habitat. One unit thus contains a prey species at a certain density.

In birds hunting for a hidden prey type, detectable only at a short distance, we can distinguish two levels of behavioural adaptation to the distribution of the prey species: one within, and one between habitat units. Adaptation within a unit concerns searching for a clustered prey population. Two extremes can be distinguished: (a) If no clues reveal the border of a single cluster, search can only be adapted to the situation in a diffuse way, as in area restricted searching (Smith 1971). Area restricted searching is an effect of eating a prey item on the search path (and/or search intensity) of a bird, resulting in more intensive searching in the immediate vicinity of a place of capture than in areas where no prey were found. Since the prey is clustered, this behaviour increases the chance of finding another prey. Smith (1971) has detected this behaviour in Blackbirds, *Turdus merula,* hunting for earthworms in a field. The same behaviour has been observed in laboratory experiments with Sticklebacks, *Gasterosteus aculeatus,* and in some insects (Thomas 1974). (b) If the boundaries of a cluster can be detected by the predator, search can be adapted in a more specific way, even when no clues exist for the individual prey locations. This recognizable type of cluster has been named a patch by Charnov (1973) and the term has been so applied by Krebs *et al.* (1974). Since the predator can recognize boundaries and hence is aware of the extent of the patches, it can decide when to leave one to go on to the next. For this kind of situation Charnov (1973) predicted on the basis of an optimal foraging model that birds should leave a patch at the moment that the intake rate in that patch has dropped (by depletion) below the 'average intake rate in the habitat'. This means that patches of like density should be treated differently in environments of differing average intake rates. Krebs *et al.* (1974) did laboratory experiments with Black-capped Chickadees, *Parus atricapillus,* to test this prediction. They showed that tits that had foraged in a rich habitat would leave a certain patch type (a cup with a fixed number of hidden prey) more quickly than they did when encountering the same patch type in a poor habitat. The difference was thus in the direction predicted by Charnov's model.

Since birds respond to the general 'richness' of the habitat, it is likely that they may be able to remember the quality of the different units within the feeding range, and make use of this information when deciding where to go to feed. This brings us to what may be termed the second level of behavioural adaptation of the predator to the prey distribution: choosing between habitat units. Royama (1970) has presented a model for this situation. Although originally developed for a situation with more than one prey type, the idea can usefully be applied to the one-prey case as we shall see. In the model, Royama regarded the habitat as divided into different units, each containing one prey species at a certain density (it is perhaps unfortunate that he chose to call these units 'niches'). The predator, Royama supposed, would measure the profitability of the different units while hunting there, for example, by relating energy gain to energy expenditure or something of that nature. By comparing profitabilities of the different units the predator would arrive at a decision as to where to spend most of its hunting time. Because prey densities change with time, Royama expects the predator to spend a certain amount of time in the non-optimal units in order to keep informed about changes ('sampling'). To test this model, one has to know whether birds use a measure of intake in making a choice between units of the habitat, and in addition the cardinal question must be solved, of what the bird itself recognizes as a unit of the habitat.

There is evidence from laboratory experiments that tits can in fact measure intake rates (Krebs 1973; Krebs *et al.* 1974; Krebs & Cowie 1976). Whether they can make use of this in a choice situation has been tested in the laboratory by Smith & Dawkins (1971). They gave individual birds the choice between different areas with different food densitites of one prey-type, mealworms. The area was recognizable by the position in the aviary. The birds did learn to go to the best places. Since no other clues were given, they must have accomplished this by measuring the profitability differences between areas. Similar results were obtained by Alcock (1973) in the Red-winged Blackbird, *Agelaius phoeniceus*.

In field experiments Croze (1970) and Smith (1971) showed that Carrion Crows *Corvus corvus* and Blackbirds *Turdus merula* spend more time at places baited by the experimenter. Goss-Custard (1970) showed that Redshanks *Tringa totanus* in a natural one-prey-situation (*Corophium* on the mudflat) foraged at a higher density at sites where the intake rate was highest. The 'average' Redshank thus spends more time at places with most food.

The aim of this study is to see whether the profitability model can explain the relation between the time spent foraging and food abundance in a certain area for the Starling under field conditions. Testing a model in the field must always be preferred where it is feasible, and one always has the hope that intensive observation in the field may yield insights about mechanisms involved in natural foraging, that may have been neglected in the model. Starting in a relatively simple situation, I chose a part of the habitat for intensive study where very largely only one prey type (*Tipula paludosa*) was taken by the Starlings.

A major difficulty in testing the profitability model is to decide on what scale to describe prey densities on the one hand and foraging visits on the other. Since we do not yet know what constitutes a 'unit' for a foraging Starling, we divided the intensive area into plots of 20×20 meters, and determined potential food supply by sampling each plot. In fact, prey density varied greatly between plots, and our question became, do Starlings in their natural environment spend more time foraging in the plots with more food? If so, the next problem is to analyse the mechanisms responsible for the observed time allocation, as revealed by the behaviour of the birds. In essence we are trying to find out to what extent learning plays a role in determining the relation between time spent foraging in a part of the habitat and the food supply at that site.

2. ACKNOWLEDGEMENTS

This project originated as part of my study in Biology at the University of Groningen, and I am very grateful to Dr. R. H. Drent who has been the stimulator behind this work in all its phases.

The study was done on Schiermonnikoog in a field administered by the 'Dienst der Domeinen' and in use by the local farmers. Mr. R. Nieuwenhuis, local head of 'Domeinen', and

Mr. F. Visser, chairman of the farmers' cooperative, gave kind permission to erect the observation tower, insert marker stakes, and carry out the soil sampling on their field.

The help of numerous zoology students from the University of Groningen has been absolutely indispensable, and I wish to thank Mr. J. Prop in particular, who devoted both the 1974 and 1975 seasons to the starling project and contributed a major share of the observations. My thanks also go to Mr. R. Vodegel for help with the computer analysis, Mr. J. van der Laan en Mr. J. Koenes for making the nestboxes, Mr. D. Visser for carefully preparing the figures and Mrs. H. Lochorn-Hulsebos for typing the manuscript.

I am indebted to several colleagues at Groningen for critical comments on the manuscript (Dr. S. Daan, Dr. R. H. Drent, Drs. B. Ebbinge and Dr. G. Thomas) and it is a pleasure to acknowledge the further help of Dr. H. Klomp.

3. STUDY OBJECT AND STUDY AREA

The question raised can best be answered by studying a bird that forages in open country so that it can be followed while feeding. The Starling (*Sturnus vulgaris* L.) meets this requirement and offers further advantage as a hole breeding species.

The research was done with a group of eight pairs in nestboxes on the biological station 'De Herdershut' on Schiermonnikoog, a small island in the extreme north of the Netherlands. (Fig. 1). The Starlings forage on the meadows, dunes, and saltmarsh. Their prey mainly lives between grassy vegetation or in shallow burrows. Flying prey was rarely taken during the observations reported.

The intensive study area was chosen on the basis of preliminary observations over a large part of the habitat. A place was selected where regular visits of Starlings were recorded, but where group foraging was not frequent. This turned out to be close to the nestboxes. The exact area chosen was part of a rough meadow with small differences in level. The higher parts were more sandy than the lower. As there were also differences in sward height we expected that these differences would correlate with variations in food supply. The size of the study area was 70 x 80 m in 1974 (divided in 10 x 10 plots) and 60 x 80 m in 1975 (divided in 20 x 20 m plots). For analysis four adjacent 1974 plots were taken together; hence for both years I deal with 20 x 20 m plots. The plots were recognizable by colour coded stakes at the corners.

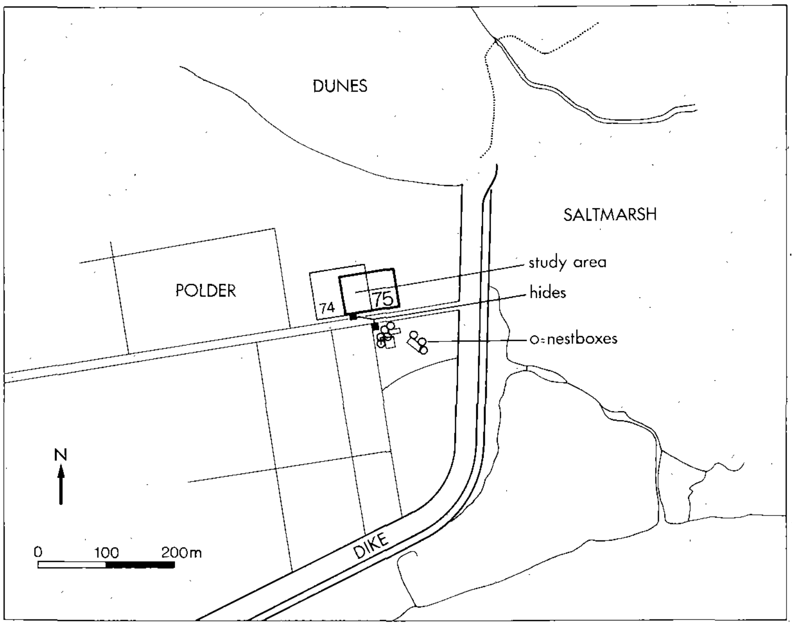

Fig. 1. Map of the study area.

4. METHODS

To clarify the relation between food supply and foraging time we also measured additional properties of the plots (soil moisture-content, grass-length and distance to the colony) that might be important in influencing this relation.

Moisture-content and grass-length might on the one hand have an influence on the abundance of the prey species. On the other hand these factors can influence the behaviour and the visibility of the prey, i.e. they might influence catchability.

The distance to the nestboxes was included in the analysis, because if the Starling incorporates flight in its cost-benefit balance one would expect that plots further away from the nestboxes are visited less, other things being equal.

4.1. THE ESTIMATION OF THE FOOD SUPPLY

Since we do not know exactly what Starlings eat we had to estimate the potential food supply. We did this by taking soil samples. This method was preferred to pitfalls or sweepnets, because it gives a density estimate per surface for all insects living in the sod. The sampling was done by taking soil cores to a depth of 3 cm. The samples were brought to the field laboratory for extraction of the animals.

The number of samples that has to be taken per plot depends on the density and the degree of aggregation of the insects (Southwood 1967). Because we were limited in our capacity to extract the animals (see on), and our study area had to be fairly large to incorporate large differences in food supply, we had to pool samples taken in different weeks, to improve the reliability of estimation as much as possible.

The insects were extracted from a sample with a simple Tullgren funnel (Fig. 2). This apparatus consists of a funnel placed in a bottle with alcohol (70%). The inlet is covered with wire netting (7 mm) on top of which the sample is placed upside down. To prevent the escape of flying insects a PVC cylinder covered by mosquito netting was placed on top. A carbon filament lamp was hung above the apparatus to heat the surface of the sample. The lamp causes a moisture and temperature gradient through the sod from which the insects and other organisms flee. Eventually they fall out of the sod and through the funnel. The whole process takes a week on average.

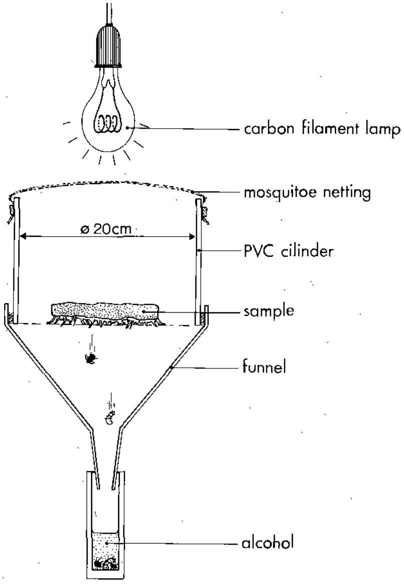

Fig. 2. The Tullgren funnel (for explanation see text).

Extraction by this method is relatively complete according to Edwards & Fletcher (1971). A drawback is that only actively mobile animals are extracted. We checked some samples, after extraction, for pupae remaining in the soil and found their number to be negligible, so this step was omitted.

We worked with 55 funnels in 1974 and with 96 in 1975. Because a sample contains a lot of species, we took the dry-weight of all potential prey animals (defined as all animals larger than 0.5 mm) as a measure for the food supply. This weight cannot be measured directly from the preserved specimens since alcohol dilutes fat. Therefore we measured the lenght of each animal under a dissecting microscope. The weight was then reconstructed from calibration curves we made for fresh material. Weights of species that could not be collected in quantity were estimated from the weight of more common insects with the same shape and size. The soil samples were taken on 30 April and 10 May in 1974, and on 25 April, 8 and 16 May in 1975.

The insect dry weight was computed per sample. Variability between samples was large (Table 1). The number of samples taken on one day per plot was not high enough for a good estimate of mean dry weight. Therefore the different sample days within years were taken together. Since there might have been changes in the course of the season we work with an average in space and

Table 1: Mean and standard deviation of dry weight (in mg) per sample (0.15 m^2 1974, 0.18 m^2 in 1975, taken to a depth of 3 cm) per plot, given per sampling date and taken together for the whole year. An average dry weight per sample for the whole study area is given as well.

1974	30 April			10 May			1974		
plot	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
1	20	21	4	14	12	4	17	16	8
2	26	36	4	16	8	4	21	25	8
3	15	12	4	29	36	4	22	26	8
4	23	16	4	20	17	4	22	16	8
5	16	10	4	15	6	4	15	8	8
6	4	1	4	18	24	4	11	18	8
7	20	6	4	19	19	4	19	12	8
8	13	4	4	24	22	4	19	16	8
9	9	4	4	6	3	4	7	4	8
10	10	9	4	12	12	4	11	10	8
11	9	1	3	25	34	3	17	23	6
12	15	6	4	10	2	4	13	5	8
13	3	2	4	8	9	4	5	7	8
14	8	4	4	4	3	4	6	4	8
total area	14	15	55	16	20	55	15	17	110

1975	25 April			8 May			16 May			1975		
plot	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
1	46	19	4	60	31	8	82	65	8	66	49	20
2	40	25	4	50	44	8	32	37	8	41	37	20
3	34	16	4	36	34	8	39	30	8	37	24	20
4	96	58	4	24	20	8	24	6	8	39	40	20
5	21	19	8	44	42	8	42	23	8	36	31	24
6	9	7	8	16	12	8	94	63	8	39	53	24
7	50	43	8	41	28	8	64	60	8	52	44	24
8	64	36	8	67	36	8	42	37	8	58	36	24
9	19	13	8	12	20	8	29	24	8	20	20	24
10	10	16	8	16	15	8	65	44	8	30	29	24
11	15	12	8	43	35	7	38	31	8	32	30	23
12	49	26	8	51	26	8	58	37	8	53	29	24
total area	38	33	80	38	32	95	50	47	96	42	39	271

time. This does not reduce the variability but gives, because of the higher number of samples, a more reliable estimate for average dry weight. An average dry weight per plot per year was finally computed. This was called the 'biomass' and was expressed in grams dry weight per m^2.

4.2. MOISTURE CONTENT

To obtain a relative measure of moisture content, each soil sample was weighed before and after drying in the Tullgren funnel. The percentages of the wet weight that disappeared was called the moisture content. Because prey weights were very small these were neglected. Again a yearly average was computed per plot.

4.3. GRASSLENGTH

Grass length was estimated with a ruler placed perpendicularly in the grass. From a distance of ten meters and at a height of one meter the ruler was read with the aid of a pair of binoculars. That centimeter was recorded that just disappeared below the grass. In 1974 the grass length was measured twice (with respectively 16 and 36 points per plot) on 30 April and 10 May, in 1975 once (16 points) on 14 May. For both years an average figure per plot was computed.

4.4. DISTANCE TO THE COLONY

The distance from the middle of the colony to the middle of each plot was taken as the distance to the colony.

4.5. ESTIMATION OF FORAGING TIME AND INTAKE RATE

From a hide placed on a two-meter-high frame it was possible to closely observe the Starlings on the intensive study area. We estimated the time spent foraging by scanning the whole study area every two minutes. In fact birds spent most of their time actively foraging when visible on the study area. Between 10-20% of the time was normally devoted to looking around, and much less frequent behaviours were collecting nesting material, singing, copulating, preening and sleeping, together accounting for 2-5% of the total time spent on the foraging area.

Observation of time devoted to foraging and location were combined by scanning the study area every two minutes, and drawing in symbols on a map for each Starling present. Different symbols were used for foraging and non-foraging birds. The sum of the number of foraging symbols per plot, multiplied by two (the observation interval in minutes) yielded our estimation of the total number of minutes spent foraging on each plot.

A second observer in the hide measured intake rate. Using a telescope (15—60 ×) on a tripod, individual foraging Starlings were followed over the study area. The number and size-class of the prey taken, the time spent foraging, and the plot where the visit occurred were noted with a tape recorder. The crossing of plot boundaries was recorded as well. The prey taken was recorded in sizeclasses relative to bill-length, or for very small prey, as revealed by the behaviour of the birds. The classes, with associated mean prey dry weight, were as follows: large (longer than bill-length, 60 mg), medium (0.25—1.0 bill-length, 12 mg), small (less than 0.25 bill-length but visible as such, 2.6 mg) peck (short peck high in the vegetation followed by swallow, 1 mg). The mean dry weight of the prey was estimated from the samples of what was available at that time, and from very close observation of the Starlings under favourable conditions allowing prey recognition by the observer. Fortunately a single prey species (larvae of *Tipula paludosa*) made up the bulk of the intake (as measured by weight, 68% in 1974 and 90% in 1975 of total prey extracted from the study area). Therefore we feel that the effect of observational error involving the smaller prey is relatively unimportant.

Whenever more than two Starlings flew and landed together, and foraged within about 10 m of one another, we designated these birds as constituting a 'group'. Groups were treated separately and will not be incorporated in this discussion.

The observations were collected on ten observation days in 1974 (between 28 April and 12 May) and on seven observation days in 1975 (between 2 and 8 May). For Starlings on Schiermonnikoog this is the time of nest-building, egg-laying and incubation. No young hatched in this period so we have to do with parents foraging for themselves. Observations were done between 0500 and 1900 hrs, with observers being relieved every 2-3 hours.

Table 2: Percentage of the variation in foraging time explained by different variables (FT = foraging time in min, B = biomass in g dry/m^2, D = distance to the colony in m, M = moisture content in percent, G = grass length in cm).

Regression	Variable added	Percentage of the variation of FT explained by adding an independent variable (100r^2)	
FT-B	B	1974: 40.2	1975: 69.3
FT-B, D.	D	30.0	1.8
FT-B, D, M.	M	12.1	0.0
FT-B. D. M. G.	G	0.3	0.6

1974 FT = 69.6 + 114B — 3.88D + 5.50 M
(± 231) (± 132) (± 2.14) (± 4.66) (95% conf.int.)
1975 FT = — 76.4 + 122 B
(± 141) (± 57) (95% conf.int.)

5. THE RELATION BETWEEN FOOD SUPPLY AND FORAGING TIME

To find out which of the properties of the study area correlate with the foraging time I used multiple linear regression analysis. Under the assumption that the foraging time on a plot has a normal distribution for all properties of the study area and under the assumption that the relationships are linear this model can be used (Wonnacott & Wonnacott 1970). When a multiple regression is computed for certain variables it is possible to say how much (in per cent) of the variation of the measured foraging time is 'explained' by those variables. By computing the regression with each additional independent variable sequentially one can see how much each variable explains by itself. This method was used to determine which variables had influence on the regression (Table 2). It is shown that in 1974 biomass, distance to the colony and moisture-content all contribute to variation in foraging time. In 1975 the biomass was the only factor significantly affecting the foraging time. The regression formulae are shown at the foot of the table.

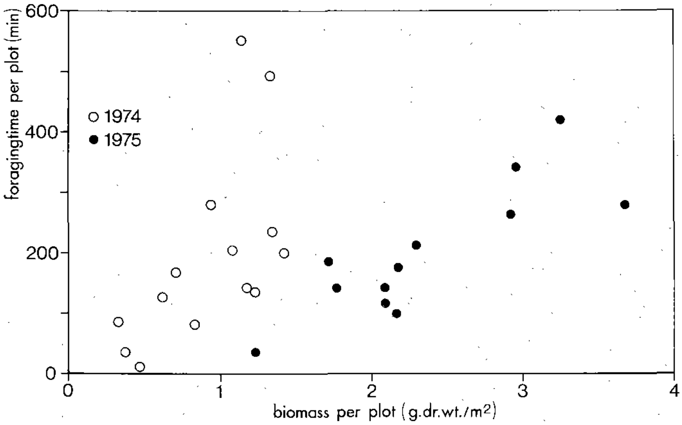

Fig. 3. Relation of total foraging time spent on a plot and the food supply in that plot (for 1974 and 1975).

In both years there was a positive relation between foraging time and biomass, although this was not significant in 1974 (Fig. 3). In 1974 the moisture content had an influence on foraging time. In 1975 there was no relation, probably because 1975 was overall a much wetter summer (av. moisture content 53% as compared to 41% in 1974). In both years no influence of the grass length could be found although grass length differed clearly between plots. The influence of the distance to the colony differed markedly between the years. Therefore it can be suspected that we did not measure effects of distance to the colony alone.

Summing up, in both years the foraging time of Starlings was positively related to the biomass. Moisture content and distance to the colony might have a relation with foraging time as well, although their effects were not consistent between years.

6. ARTIFICIAL BAITING: THE MEALWORM EXPERIMENT

If variations in biomass between plots are causally involved in the variations in foraging time one would expect an artificial increase of biomass to result in an increase in foraging time.

To test this, we carried out the following experiment. After the observations on the natural feeding situation in 1975 we added food to a plot known to have about the average biomass. Ideally we should have added natural food to the plot, but as this is difficult to collect, we chose mealworms. On each square of 2 × 2 meters about thirty mealworms were added, concentrated on 1 m^2. This clumping was done because we were afraid that the mealworms would crawl under the grass, as they had done in a pilot experiment, and avoid detection by the Starlings.

The observations revealed a strong increase in total time spent foraging on the baited plot (Fig. 4). The addition of food thus caused an increase of

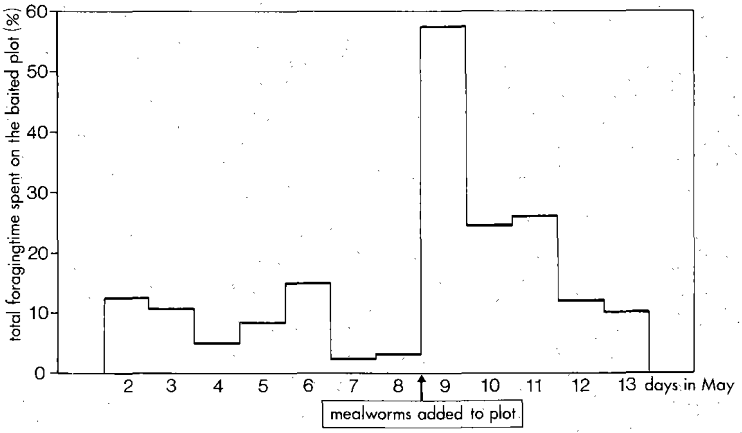

Fig. 4. The increase in percentage of the total foraging time on the study area spent on the plot that was baited with mealworms.

foraging time, but I cannot say whether the causal factor was quantity or quality of the food. Social attraction was in a later stage of the experiment responsible for part of the increase.

7. IN SEARCH OF THE UNDERLYING MECHANISM

7.1. EXTENDED VISITS OR RECURRING VISITS?

Starlings can spend more time on plots with more food either by staying longer or by coming more often or both. This difference is relevant if we wish to say something about the mechanism. If Starlings stay longer per visit, short term effects (like the positive feedback from finding a prey) alone can be responsible for the relation between biomass and foraging time. If they return more often to places with more food, they must use information gathered during a visit, combined with some place parameter, in selecting the spot visited next.

We were able to distinguish between those two extremes because it was possible to follow the same individual during the time it spent on the study area.

To estimate the average duration of a visit we recorded an individual the first time it was seen during scanning (every two minutes for estimating the total foraging time) differently to subsequent sightings (see 4.5.). Visits turned out to be very short. This means that scanning every two minutes, although giving a good estimation for total time spent foraging, is not suitable for measuring visit frequency. In 1975 we therefore measured the number of landings independently of the scanning time, to get a more accurate estimate of number and duration of visits per plot.

The average duration of visits does not markedly differ between plots in both years, but the number of visits Starlings pay to plots is strongly correlated with the biomass of that plot (Fig. 5). Starlings divided their foraging time by returning often to plots with a higher biomass. As said

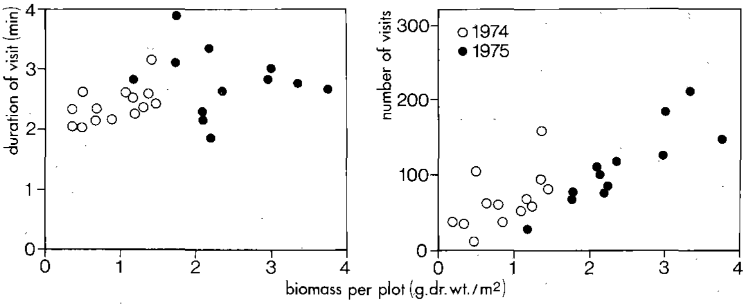

Fig. 5. Left: The relation of the duration of an average visit on a plot and the biomass in that plot (for 1974 and 1975).
Right: The relation of the total number of visits on a plot and the biomass in that plot (1974 and 1975 taken together).

previously the basis for this choice must be some parameter correlated with biomass and acting at least from one visit to the next. For instance the bird might remember intake rate as a basis for their choice.

7.2. IS INTAKE RATE A POSSIBLE CRITERION FOR SITE SELECTION?

If intake rate is the selection criterion, we would expect it to be highest on the plots where most of the foraging time is spent. We therefore measured intake rate for each plot, as has been described previously (4.5). Fig. 6 shows that in both seasons the time spent foraging tended to be higher in plots where a higher rate of food intake was recorded. Unfortunately, the 1974 intake observations were more limited than those of 1975 (240 and 382 minutes respectively). This is one reason why the relation is less clear in the 1974 data. Possibly other effects associated with the much lower intake rates characteristic for the 1974 season (influence of adjacent plots, presence of nest material) further complicated the picture.

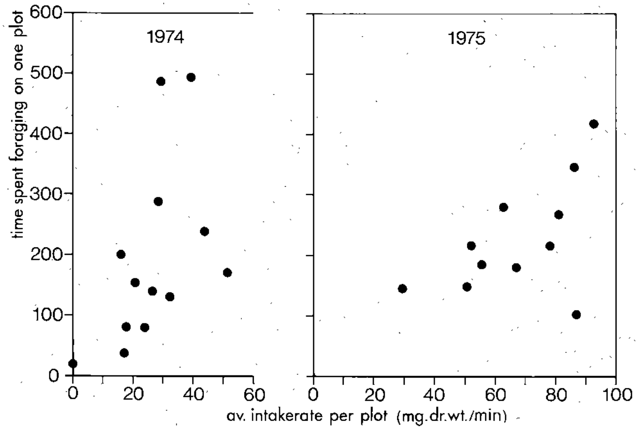

Fig. 6. The relation between foraging time and intake rate (1974 and 1975 separately).

7.3. ON WHAT TIME SCALE DOES MEMORY OPERATE?

We have two additional observations from the mealworm experiment that support the idea that Starlings learn where to go, although I cannot be sure that the intake rate is causally involved. The day after adding the mealworms, at 0500 hrs, visits to the plot that had been baited were extremely frequent in comparison to pre-experiment days, even though all mealworms had in fact been eaten by this time (see Fig. 7). Since Starlings forage exclusively by day, they had been away all night. The birds must have learned the previous day where the 'good' place was, and remembered this the following morning.

More direct evidence comes from following a marked individual. On the experimental day this individual was the first to happen upon the baited plot

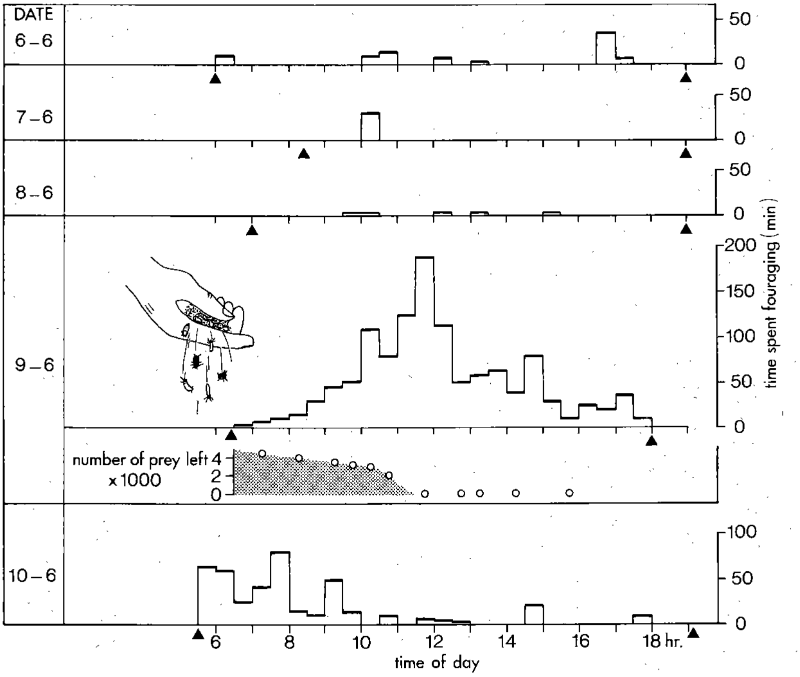

Fig. 7. The influence of adding mealworms to a plot on Starling visits: foraging time on the baited plot before and during the experiment on a half-hour time base. Prey depletion is shown in the inset.

as he walked foraging over the study area. After finding and testing the first mealworm it ate 12 mealworms in 78 seconds and flew off. The intake rate was much higher than normal for that place. After some ten minutes the same individual landed at the same place in the baited plot. It must have remembered the place as such in combination with the intake rate. Even after other individuals had also found the mealworms, the marked individual kept returning later on to the same place.

8. DISCUSSION

The results of this field study support the profitability model of Royama (1970): the Starling spends more time at places with more food. This seems a common pattern and has been measured in the field situation for the Redshank (Goss-Custard 1970) and in both field and laboratory experiments in several other birds (see introduction).

The mechanisms by which the bird achieves this concentration of foraging time in places with more food is poorly understood. The data in this study show that Starlings pay more visits to plots with more food. Since average duration of visits as we defined them varied only slightly with food density, the Starlings allocated their foraging time by going more often to the better plots. This probably means that individual Starlings remember the profitability of a certain place they visited, and use this information in making a choice of site for the next visit. In other words: Starlings learn where to go. The only alternative explanation could be that Starlings react to some factor other than intake rate, that was related to food density. From the regression analysis we know that grass length, moisture-content and distance to the colony do not play such a rôle. This explanation is, moreover, unlikely because the mealworm experiment showed that the pattern of visits can change drastically under influence of a change in food supply.

Our observations are too crude to reveal a possible role of area restricted searching in foraging. I believe that the birds could not discover a patch at first sight, and in fact experience difficulty in determining the boundaries. To look at the fine distribution of leatherjackets I took at two places, chosen at random in the study area, a pattern of 37 contaguous samples as shown in fig. 8. The figures give the impression that the clusters of leatherjackets, if they exist at all, are rather large with poorly defined boundaries. From our sample program we know that some places do not have any leatherjackets at all. It is therefore not surprising that the birds experience variable intake rates over rather short distances. Such variation might account for the fact that the birds do not concentrate solely on the best plots. Horizontal and vertical movements of the leatherjackets from day to day (it will be recalled that *Tipula* larvae are night-active) if extensive, may contribute to the difficulty a Starling apparently experiences in recognizing prey clusters.

Alternatively it is possible that the Starlings avoid depleting food resources close to the nestboxes (the intensive study area) until the young demand a lot of food, and time becomes a limiting factor in foraging. Perhaps the birds search close to the nestboxes mainly to learn where the good places are, with a view to efficient food gathering for the young later on. Another functional reason for avoiding frequent visitation to the best plots, is that this might

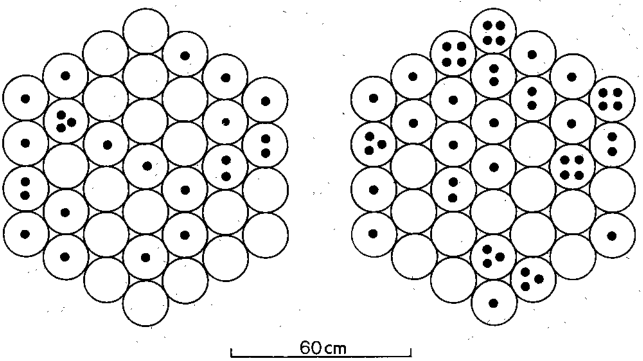

Fig. 8. The distribution of leatherjackets (*Tipula paludosa*) in two parts of the study area. Each circle indicates a sample(177 cm^2); each dot indicates a leatherjacket extracted from that sample. For further explanation see text.

increase the risk for the Starlings themselves to be caught by birds of prey (such as the Hen Harrier, *Circus cyaneus*, patroling the study area regularly).

Since Starlings prefer the best plots within the study area to some extent, they must do this outside the study area as well. So the time Starlings spent in the study area will not be a function of the richness of this area alone. Although the biomass in 1975 was twice as high as in 1974, the time spent on the study area did not increase proportionally (1975 = 4/3 1974).

To evaluate the absolute importance of our study area for the Starlings we have to observe what individual Starlings do throughout the day. In fact we do not know what our birds did outside the area. Still I will try to say something about the importance of the area in terms of food supply. Our observations on the intensive study area indicated that total daily prey capture by all the Starlings amounted to 9.5 g (dry) in 1974, and 26.9 g (dry) in 1975. We can estimate roughly to what extent this covered the daily food requirement of the colony by the following extrapolations. Prop (pers. comm.) measured the intake rate of a captive bird feeding on natural sod (taking mainly leatherjackets). The intake was measured as described in 6.2. throughout the whole day. Every two hours the cage was shifted to avoid depletion. On two observation days the bird ate 12 g (dry) per day without loss of weight. The wild birds fly a lot and will therefore use more energy. A crude estimate for wild birds can be taken as 1.5 times the cage rate, thus about 18 g (dry) per day. The amounts taken from the study plot thus account for 1/32 to 1/8 of the estimated requirements of the eight pairs nesting in the colony close to the study area.

The influence on the prey population by Starlings that are able to learn where to go deserves special attention. Since the birds spend more time on better places than if they would forage at random, they might have a locally variable influence on the prey population. From the 1975 figures I have extrapolated which percentage of the prey in a plot was removed in three weeks of foraging by the Starlings (Fig. 9). Starlings had a higher impact on

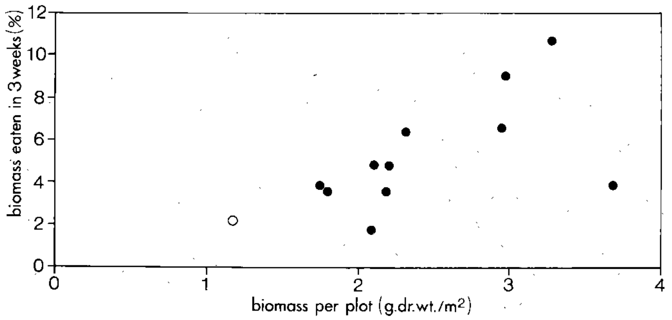

Fig. 9. Percentage of the prey eaten in relation to prey weight available (biomass). For the open circle no intake rate estimate was available; the average value for the whole study area was taken as a crude estimate. For the black points intake rate estimates were available.

prey in plots with higher densities. Those places are probably optimal for the prey as well, in the sense that reproduction might be higher for an individual living there. If so, the local impact of the predator on the prey population would be even more significant for the prey.

For future work we need more data on individual birds over longer periods to be able to find out what makes a bird come back to a profitable area. In the laboratory we are trying to find out what criteria can be used by Starlings in deciding where to forage and how these change under influence of experience.

Fieldwork on individual Starlings feeding young will be the subject of a later report. It is already clear that apart from learning where to go by intake rate alone, in a natural multiple prey situation the influence of prey type on choice of site is of great importance as well.

9. SUMMARY

This study deals with the question of whether free living Starlings (*Sturnus vulgaris* L.) spend more time foraging in places with more food in a field situation. As in fact they do, the next problem is to investigate the mechanism. Special attention is given to the profitability idea of Royama (1970).

Observations were collected in two seasons, and data from egg-laying and incubation phase are presented here. The place selected for intensive study was close to the nesting colony, but consisting only of a part of the foraging area used by the Starlings. In this area the major prey was the larvae of *Tipula paludosa*.

This study area was divided in plots of 20 x 20 m. Per plot the dry weight of insect prey, the grass length, the moisture-content and the distance to the colony was measured. Starlings were observed from a hide on a tower. The time spent foraging, the number of visits and the intake rate were estimated per plot.

The observations revealed that in both years the Starlings spent more time on plots with more food (Fig. 3). In one season distance to the colony and moisture-content of the soil played a role in determining foraging time as well.

The positive relation between foraging time and food quantity resulting from more frequent visits to places with more food, and not by a longer duration of visit (Fig. 5). It is argued that this means that the birds obtain information about the profitability of the place during a visit and use this information later in choice of foraging site.

In both years intake rate was higher in places where most visits occurred, although this trend was not significant (Fig. 6). So far as the data go, they do not conflict with Royama's model that birds should chose the best places to forage on the basis of intake rate, at least when hunting for the same prey at different sites, as in this study.

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11. SAMENVATTING

Dit werk probeert een antwoord te geven op de vraag of Spreeuwen (*Sturnus vulgaris* L.) zich aanpassen aan de verspreiding van hun voedsel door hun voedselzoektijd, in plaats van lukraak te verdelen, te concentreren op de plekken met het meeste voedsel.

Als dat waar blijkt is de volgende vraag achter het mechanisme van deze plaatsvoorkeur te komen. Speciale aandacht werd besteed aan het 'profitability' model van Royama en de toepasbaarheid daarvan op onze gegevens. In het kort behelst dit model dat vogels op basis van ervaring met hun opnamesnelheid op verschillende plekken in hun fourageergebied, hun tijd zo over die plekken verdelen, dat ze een zo hoog mogelijk rendement halen. Een deel van hun tijd zou moeten worden besteed aan 'meten' van het rendement van de verschillende plekken omdat de prooidichtheid meestal niet constant blijft.

Wij deden onze waarnemingen op Schiermonnikoog aan een kleine kolonie Spreeuwen die in de nestkasten aan het biologisch station de Herdershut broedden (Fig. 1). Het proefterrein (60 x 80 m) werd dicht bij de kolonie gekozen en verdeeld in vakken van 20 x 20 m. Per vak werd de hoeveelheid voedsel, de graslengte, het vochtgehalte en de afstand tot de kolonie gemeten. Vanuit een schuiltent op een stellage (2 m hoog) werden waarnemingen aan de Spreeuwen verricht. Gemeten werden de fourageertijd, het aantal bezoeken en de opnamesnelheid per vak.

Het bleek dat er in beide waarnemingsjaren een positief verband bestond tussen de hoeveelheid voedsel ('biomass)' en het spreeuwenbezoek (Fig. 3). Om na te gaan of dit verband mogelijk toevallig was hebben we een experiment gedaan. We verwachtten dat toevoeging van voedsel (meelwormen) op een bepaald vak een toename in spreeuwenbezoek zou veroorzaken als het verband niet toevallig was. Het bleek dat onze verwachting klopte (Fig. 4).

Om meer te weten te komen over de manier waarop Spreeuwen hun voedselzoektijd op de 'beste' plekken concentreren splitsten we het totale bezoek aan het proefveld in aantal en duur van de bezoeken (Fig. 5). Het bleek dat Spreeuwen vooral vaker terug komen op de goede plekken, maar daar niet duidelijk langer blijven. Dat de dieren terug komen op een goede plek moet betekenen dat ze van die plek kunnen onthouden dat hij goed was.

Om te kijken of de plekken met meer voedsel ook werkelijk beter voor de Spreeuwen waren, maten we de opnamesnelheid op de verschillende vakken. Het bleek inderdaad dat de opnamesnelheid hoger was op vakken met meer bezoek, hoewel dit verband niet significant was (Fig. 6).

Spreeuwen kunnen dus waarschijnlijk aan de hand van de gemeten opname leren waar ze naar toe moeten gaan om met het hoogste rendement naar voedsel te zoeken.

In onze veldsituatie lijkt het erop dat Royama's model, dat vogels op basis van het rendement van een gebied kiezen voor de beste plekken, voor Spreeuwen opgaat wat betreft de keuze tussen plekken met verschillende dichtheden van eenzelfde prooisoort.