Foraging Decisions in Starlings (Sturnus vulgaris L.)

Author: Tinbergen, J. M.

Source: Ardea, 55(1–2) : 1-67

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/arde.v69.p1

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Ardea on 04 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

FORAGING DECISIONS IN STARLINGS (*STURNUS VULGARIS* L.)

J. M. TINBERGEN

Zoological Laboratory, University of Groningen, 9751 NN Haren, Netherlands

Received 28 July, 1980

CONTENTS

1. INTRODUCTION

1.1. BACKGROUND

The study of foraging is as old as ecology itself. Traditionally ecologists have been occupied with the question of impact: do predators regulate the numbers of their prey? Early work concentrated on measurement of predator consumption in relation to prey density, but it was soon evident that no simple relation could be found. Hence, it became necessary to study the behavioural mechanisms governing the response of the predator to prey densities, as a prelude to interpreting the role of predation in contributing to the stability of numbers in nature. With this goal in mind L. Tinbergen launched an extensive programme on the predation of the Great Tit, *Parus major*, and other forest birds on their insect prey, concentrating on the period when the birds were collecting food for their young. This project occupied the animal ecology group at Groningen University for eight consecutive years, and as summarized by L. Tinbergen (1960) led to the generalization that prey were often underrepresented in the diet when first appearing in the environment early in the season at low densities, were heavily exploited at intermediate densities, and again underrepresented when high densities were reached. To explain this relation Tinbergen introduced a new concept, and hypothesized that birds used a "searching image" when hunting their prey, the expression of a specialized form of learning. He contended that this searching image enhanced visual detection of the prey, but only when encounter rate with that prey species was above a threshold. This would explain why a prey species was ignored when at low densities, and why it suddenly would enter the diet in spectacular fashion at intermediate densities. Tinbergen evoked a second explanation for the underrepresentation in the diet as densities of that particular prey became very high, reasoning that the parent birds strive to provide the nestlings with a varied diet and hence would avoid concentrating too heavily on one or only a few prey species.

The next major effort to quantify vertebrate predation in the field was again devoted to the Great Tit in the nestling phase, this time in Japan and England (Royama 1966, 1970, 1971). Royama (1970) took a fresh look at the whole problem and proposed a general behavioural model on a different level to explain both his own and Tinbergen's data. Royama pointed out that prey species are not randomly distributed, but occur in specific types of sites: for example, some species are always on bark, others on leaves. This led him to introduce the functional concept of profitability, defined as the net rate of energy intake achieved on a particular type of site. Since by definition only one prey species occurs per site type (by narrowing the description of the site this is always possible, e.g. the bark of a certain species of tree, or the leaves of a certain class of trees at a given height in the canopy and so forth), prey choice is here considered dependent on the profitability of that site type at that moment.

Since the choice of a hunting site is dependent upon its relative profitability, Royama interpreted the sudden increase of a prey species in the tit's diet at intermediate densities as resulting from a sudden switch of site type utilized by the parent bird. He explained the relatively low predation on the prey species when it reached a high density by pointing out that handling time (the time to handle a prey item already caught, in the case of a parent bird the time needed to prepare it) will eventually limit intake rate. In common with Tinbergen's reasoning, Royama thus incorporated a threshold density in his model, but the essence of his contribution is that he made the relative "value" of each prey operational in terms of a measurable characteristic, its profitability.

The type of model Royama used is now widespread and is an example of an "optimal foraging model". These models are in the first place concerned with behaviour (MacArthur 1966, Charnov 1973, Pulliam 1975, Orians et al. 1979, for review see Pyke et al. 1977). To pick up the line of thought I will give a brief impression of the underlying theory. The theory of natural selection predicts that an individual will behave so as to maximize its inclusive fitness. Operationally, it is very hard to measure the effects of short-term behaviour changes on inclusive fitness, especially when the lifetime of an individual is relatively long. Therefore, we are forced to the expedient of formulating short-term goals for foraging, on the assumption that these bear some relation to inclusive fitness. This goal is maximizing intake rate. That intake rate, especially for small insectivorous birds, can be estimated over very short time periods and that this is very likely to bear a relation to inclusive fitness are two important reasons why foraging theory has been so successful.

At the moment three main questions are asked. Firstly, what are the constraints on the bird? Since different birds have evolved in different niches they differ in the performance of a particular task. Of course this basic performance has to be built in to predict foraging behaviour. Secondly, what are the foraging goals for an individual? This is studied by developing predictions on the basis of a foraging goal and testing these in the laboratory. Thirdly, what is the time scale over which the birds maximize these goals. Different predictions are generated by models when the time scale differs (Kacelnik 1979). A particular solution is therefore limited in value in space and time.

If a test of optimal foraging theory is not confirmed by the experimental results, there are two alternatives. Either a new foraging goal has to be formulated and tested, or the bird will never reach the theoretically optimal solution. Imagine a situation in which the bird has to measure a very complex situation to solve its problem. To reach the optimal solution it would have to invest so much that it will lower its overall fitness. In this case evolution might select for the measurement of some related variable that needs less investment, but only allows a solution close to optimal. Thus the mechanism the birds use to derive their optimal solution cannot be left out, if we want to predict foraging behaviour.

The task has thus two elements: Firstly finding optimization goals, secondly determining the mechanism the bird uses to achieve or nearly achieve the optimal solution.

An additional impetus to extend observations to birds foraging in the parental phase is provided by the body of theory amassed by Lack (1954, 1966). Lack argued that the family size of nidiculous birds has evolved to coincide with the optimal brood size, definable as yielding the highest return in offspring entering the breeding population. Lack's underlying premise, that the food situation is critical in determining clutch size either proximately or more indirectly via repercussions on adult survival and/or recruitment of resulting young, remains a central issue to biologists interested in the evolution of reproductive rates (Drent & Daan in press). To understand the relation between food supply and brood survival we again have to have knowledge of the foraging behaviour of the birds involved, as this imposes a limit on their capacity to raise young. The decisions that a bird takes during foraging at this time are thus of crucial importance to its overall fitness, and it is in this context that I have chosen to carry out my own work.

1.2. AIMS

Thus there are different ways to proceed with a study on foraging behaviour. We can consider problems that have been split up into digestable bits by optimal foraging theory and design experiments to test its predictions in the laboratory as is being done. Alternatively we may concentrate on experiments that can reveal more about the mechanism the bird actually uses in known optimality problems. The question here is, on what measurements are the decisions based.

The strategy I chose was to get as detailed data as possible on individual foraging birds in their natural environment. The aim was to verify whether the parameters and goals commonly used in the theory are indeed the most important ones, always keeping in mind that the mechanism the birds use is an important aspect.

The field situation is very complex in the sense that only few parameters can be controlled. On the other hand the birds have evolved in this type of complex habitat, and field observations are essential to determine important parameters.

Since foraging decisions are often influenced by learning, data are needed on individual birds. As observers have a limited capacity I had to decide whether to concentrate on one bird over a long time or divide my attention between different birds. Since I expected that long term information would play a role I decided to take the former possibility.

Since some general knowledge about the natural history of the predator is necessary to appreciate detailed facts I will start here. I then will narrow down the description to general foraging parameters e.g. diet and consumption. This sets the stage for the main part of this thesis, where I break up foraging behaviour into different foraging decisions. The question here is whether the different decisions are taken so as to maximize caloric intake rate alone.

Since I am dealing with the nestling stage, "intake rate" is here taken as including both prey items collected for the young and those consumed by the parent itself. Where possible I shall look at the mechanism and the functional aspects. Finally I shall touch briefly on the topic of impact. In the discussion I will compare the picture which emerges with that described by theory.

1.3. PREDATOR AND STUDY AREA

Starlings were selected as the experimental animal for several reasons. Since they breed in nestboxes it is possible to automate the recording of the diet of the young. Starlings forage in open pasture which allows almost continuous registration of their foraging behaviour. In Starlings it was possible to get detailed information on prey captures *etc.* for individual birds over an important part of the study area. This is in contrast to the Great Tit, the species on which we know most, which is virtually impossible to follow while foraging.

The work was done on Schiermonnikoog, a Dutch Waddensea island (Fig. 1). One colony consisted of about 15 nestboxes each year, of which 13 were in the close vicinity of a four meter high observation tower. A second colony 400 m to the northwest had around 25 nestboxes and was only used for general information on breeding success.

There was an important reason for chosing this study area. The colony is situated in the polder adjoining saltmarsh and dunes. This means that the Starlings could search for their food in different habitat types and allows us to analyse

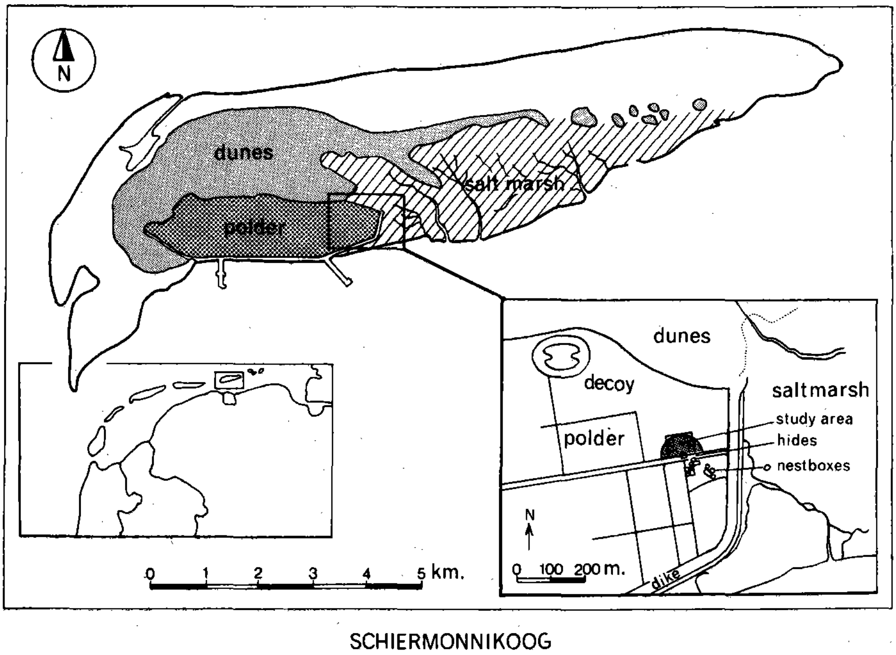


Fig. 1. Location of the study colony on the Waddenzee island Schiermonnikoog. Right inset shows detail of intensive study area on interface between saltmarsh and pastureland of the polder. (The area covered by range finder is stippled). Additional nestboxes were located in the former duck decoy.

habitat choice.

The field in the polder just north of the main colony is grazed, by yearling cattle during summer. The variation in elevation is around 1.60 m. In most observation years it was an important foraging area for the Starlings from the main colony. The saltmarsh area is totally different in that it is regularly flooded by the sea in Winter and early Spring. As it is also grazed, this results in varied vegetation with a clear zonation between the low water line and the dunes. Grasses are also important plants here, but areas with rushes and, higher up, Buckthorn bushes occur. On a small scale the plant distribution can best be described as a mosaic. The dunes are largely overgrown with marrem grass, Buckthorn bushes and in some places Elderberry trees. Starlings from the main colony visited all three habitat types to forage.

2. THE PREDATOR

2.1. ANNUAL CYCLE

In this section I shall give some general background information on the behaviour throughout the year. The first Starlings are seen in the breeding colony in the middle of February. Both the visits to the colony and the number of individuals have increased greatly by the end of March. In these months the birds can be seen foraging in small groups in the surroundings. Feeding is a very social event in this time of the year. Sometimes they spend the night in the nestbox and this is the time we catch and colourband them.

Nest building starts in April. Soon an occasional copulation can be seen. During this period the female sharply increases in weight, while the male remains the same. Gradually the pairs start to feed together more and the birds spend their foraging time closer to the colony. A birdwatcher can tell from this pairwise foraging whether the birds are about to lay eggs (end of April, beginning of May), since the female is seldom seen without her partner at this time. Copulations are now frequent (six per day).

Incubation starts directly after the last egg has been laid. This is a quiet time for the observer. Brooding bouts are interspersed with feeding bouts and male and female alternate. However, the female takes the major share in incubating.

When the young hatch the world changes yet again. Young have to be fed and the parents make regular trips to the foraging area. Brooding

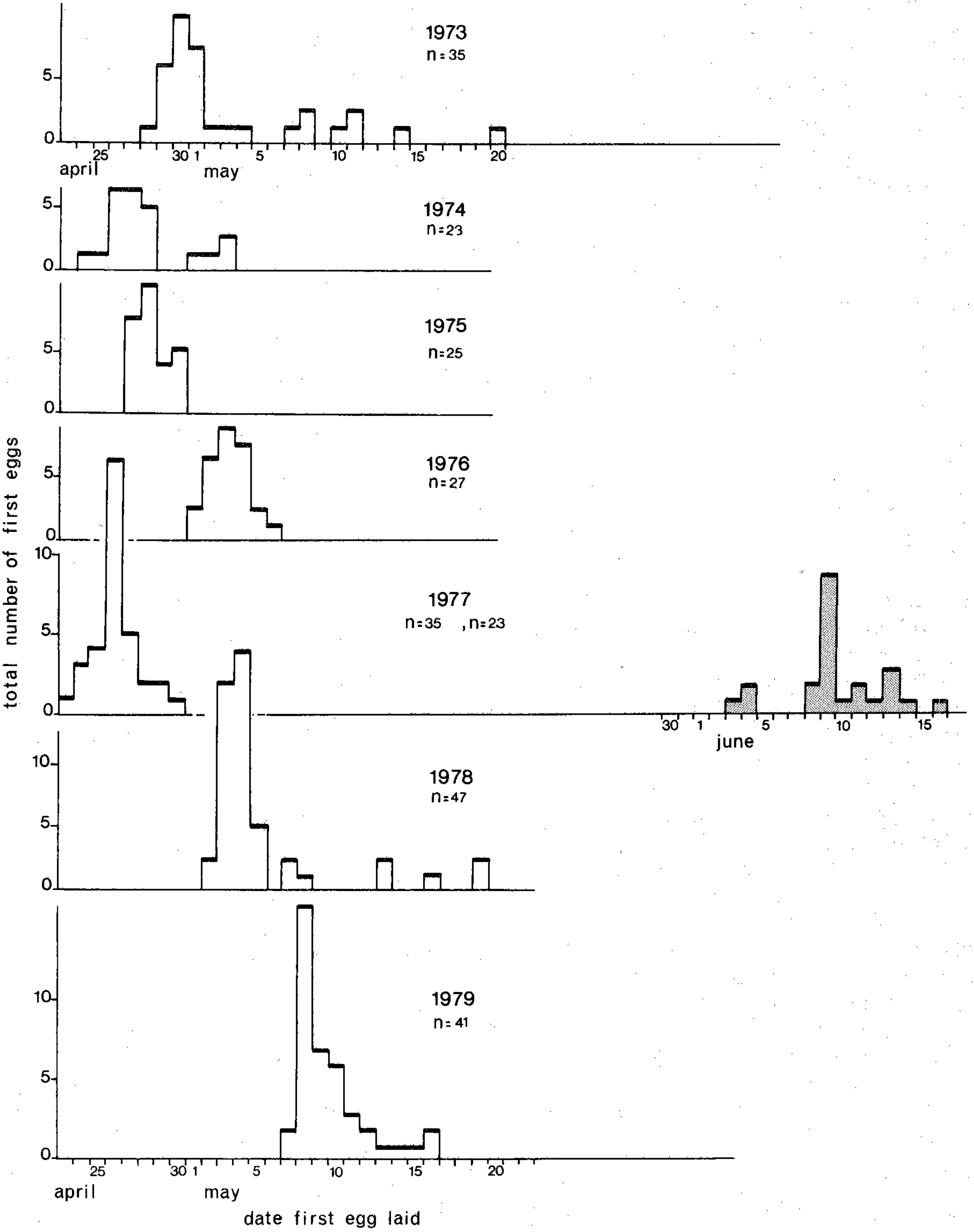


Fig. 2. Clutch initiation in the Schiermonnikoog Starling colony in 7 seasons. Second broods, observed only in 1977 are shaded. Sample size (number of nests) indicated.

the young declines in duration and frequency over the first six days. At this time of the year birds feed individually close to the colony, but more socially further away on the saltmarsh. When the young are six to ten days old the number of feeding trips has increased to its maximum, normally 300 trips daily. Parents do little else but foraging and flying in the daylight hours. Normally, both male and female take an equal share in feeding the young. As a result of this hard work the young grow from 7 to 70—85 g in 21 days.

When the young fledge they stay in trees close to the colony for one or two days and are fed regularly by the parents. Gradually they start following the parents, begging for food. It is interesting that the diet of the young now changes considerably. They receive many very small prey, presumably since travel to the young is no longer required. As time goes on the young follow their parents over larger distances, sometimes perching in bushes near the main foraging area, where they are fed. The members of the family recognize each other by using a special call note. After some two weeks, the young forage in juvenile groups, sometimes mixed with adults.

If a second brood is started, males begin to sing again just before the young of the first brood fledge. They then frequent the colony in the morning and the evening. Females are only seen there ten days later. The second laying starts around 3 weeks after fledging. Meanwhile the young of the first brood start roaming around more and some have been recovered on other Dutch Waddensea islands. Most of them will spend wintertime in mid-England. There, they also forage and roost socially, sometimes causing a plague for the local farmers. During this time Schiermonnikoog is exploited by Starlings from Scandinavia and Poland, weather conditions permitting.

If they have survived the Winter the birds return to the island in Spring and the cycle starts all over again.

2.2. BREEDING SEASON

2.2.1. Onset and survival of young

Starlings synchronize the laying of their first egg rather well (Fig. 2). Normally, more than 80% of all first eggs are laid within five days of the very first (Kluyver 1933, Dunnet 1955, Westerterp in press).

Laying dates differ between years. The maximum difference between peaks of first egg laying on Schiermonnikoog was 13 days in 7 years of observation. This is comparable to the data of other authors (Dunnet 9 days in 3 years, Andersen 10 days in 6 years, Schneider 13 days in 20 years, Kluyver 12 days in 7 years). Like Schneider (1972) we could not find a correlation between temperature in the 10 or 20 days preceding laying and onset of laying. However, an extensive analysis of the causation of the onset of laying will not be given here.

It is striking that large numbers of second broods only occurred in the 1977 season. This year egg laying started extremely early. Schneider (1972) concluded that there was no relation between the onset of the first brood and the probability of a second brood occurring. However, his data show a negative correlation of .50 (n = 13) suggesting that his conclusion might be premature.

Clutch sizes are relatively constant between years (Table 1). The overall average is 5.36 eggs per nest. This is relatively high as compared to clutch sizes in other places, although not the highest recorded (Schneider 1972, Lack 1948, 1954).

Table 1. Brood size of the Starling for the Schiermonnikoog study colony (I = first, II = second broods)

Year	Brood	n	x̄	S.D.
1973	I	28	4.96	0.43
1974	I	25	5.26	0.87
1975	I	25	5.12	0.83
1976	I	21	5.57	0.87
1977	I	17	5.53	0.80
1977	II	23	4.34	1.03
1978	I	31	5.52	1.20
1979	I	31	5.61	0.96

For the years 1974, 1977, 1978, 1979 and 1980 data are available on survival of the young. Fig. 3 shows the relation between initial brood size and the number of young fledged for the different years. The best clutch size in terms of the number of young fledged, differs between years.

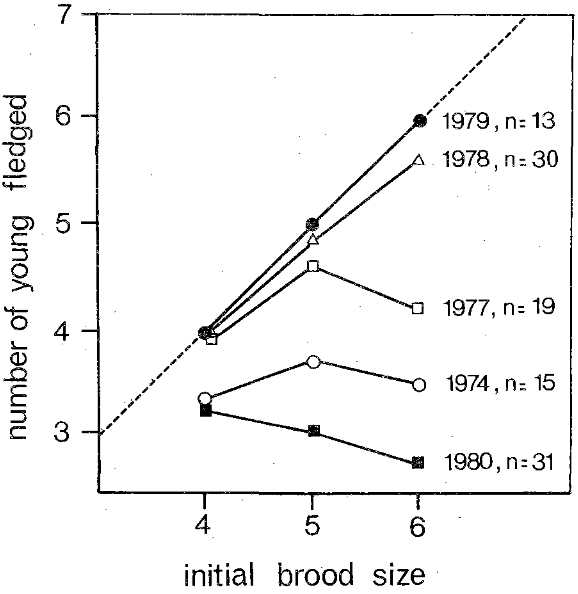


Fig. 3. Production of young (defined as number of young fledged) in relation to brood size at hatching in five seasons (n = number of broods studied). Dashed line shows maximal production (100% success) attained in one season.

Considerable differences in survival of the nestlings thus occur between years. As mentioned previously Lack thought that survival was correlated with the general food situation. Since we have data on intake rates of birds during the nestling phase we are in the position to verify this. We selected broods of six, as these would be expected to show the most pronounced effect. Fig. 4 gives the relation between nestling survival of these as a function of the intake rate on the main foraging areas. A clear relation indeed excists (r = 0.90, p < 0.05, Spearman rank correlation). The importance of the food situation is thus significant.

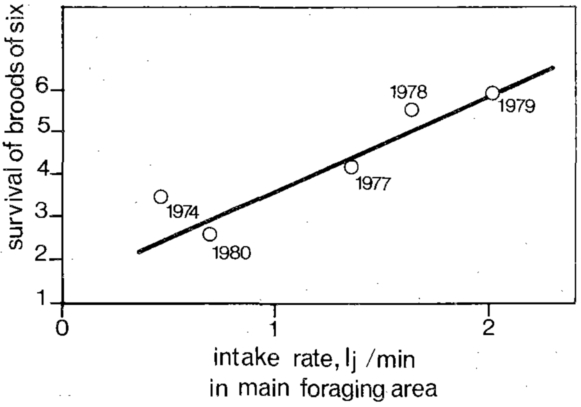


Fig. 4. Production (as measured by number of young fledged from broods of six) in relation to feeding conditions in the season concerned (as estimated by intake rate of parents while collecting leatherjackets, the predominant prey in the nestling diet, see text for methods). The line is drawn by eye. In this and following figures Leatherjacket is abbreviated as "lj".

Work on foraging behaviour will therefore enable us to unravel some of the factors governing survival of the nestlings and eventually fitness of the birds. When food situation is bad within a year this can be compensated for by taking the right foraging decisions, which will also increase fitness.

2.2.2. Time budget

Here I present data of how an individual female Starling ♀ 39, 1979) apportions her time between different behaviours throughout the breeding season. I chose the female because the male was involved more with behaviour other than foraging (chasing, singing) than the female. Since I was interested mostly in foraging behaviour this seemed to be the right choice. Of course we lose the opportunity of showing collaboration between the sexes, but for the moment we have to accept this drawback. We must remain aware of the fact that some conclusions are only based on one individual, but we first need these data, to be able to state the problem clearly before we collect data on the whole population.

I will use the time budget of the female from the onset of laying until halfway through the nestling period (Fig. 5). This example can be regarded as representative for an average female Starling for the nestling period. It is not typical for the incubation period, as differences can occur depending on the share the male takes in incubation. When he takes his full share, time on the nest for a female is around 50%.

The different behaviour categories making up the time budget are defined as follows.

Time spent in the nestbox: This is the time from entering the nestbox until leaving it. In the incubation period this is mostly incubating the eggs, when the young are small it is shared between feeding and brooding. After six days of age young

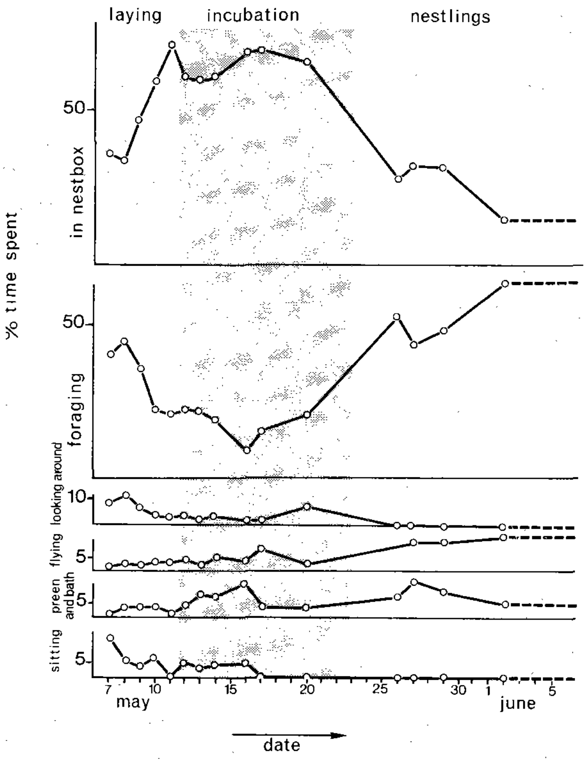


Fig. 5. Time budget of female Starling 39 while tending a clutch (later brood) of five in the 1979 season, as expressed in per cent of the daylight hours (based on continuous watch from the observation tower on 15 dates). After the 10th day of nestling life levels of activity can be considered constant (indicated by dashed lines). See text for definition of activities.

are no longer warmed and the time in the nestbox is spent feeding the young, cleaning the nest and waiting for faeces.

Time spent foraging: This includes only the time actually spent on the foraging area. Bouts of looking around lasting longer than 1 sec are not included.

Looking around: Defined as the time spent on long bouts (> 1 sec) of looking around while on the foraging area. It decreases throughout the season.

Time spent flying: Defined as the time from take-off to landing. Flying increases through the breeding season. The main increase occurs when the young have hatched since the female has to travel much more between nestbox and foraging area.

Bathing and preening: Since this is normally done at special places the whole time spent on these places was used. It was higher in incubation and nestling period than in the egg laying period.

Time spent sitting: Defined as the remaining time, not spent in any other category. It is high during egg laying and the first period of incubation. Later it is very seldom seen.

Exact data were available in the polder area, close to the nestbox. When the female went to the saltmarsh it was often possible to measure the time spent flying, but once she landed she could no longer be followed. The time budget on the saltmarsh was estimated by assuming that the flight back took as long as the flight out, and that the time actually spent on the saltmarsh had a comparable time budget to a polder visit. This is a reasonable assumption, verified by observations we were able to do on the saltmarsh.

The overall picture that emerges is that the length of the foraging day varies strongly through the breeding season. During incubation, the female only spends a small proportion of the day foraging. When she has young 90%—95% of her day is divided between time in the nestbox, time spent foraging and flying. The impression one gets is that the activities of the female are tightly fitted into the daylight period, and there will be a high selection pressure for efficiency.

It was impossible to measure the time budgets of the male simultaneously. My general impression is that during egg laying and incubation he spends more time singing and chasing other Starlings. In the nestling period his time budget is very similar to that of the female, but no precise data are available.

2.2.3. Foraging behaviour

Starlings can gather food on the ground, in trees and in the air. In the air they catch flying insects by chasing them, either with a short hop from the ground, or by flying continuously. This foraging mode has only been seen a few times. Since few trees occur in the area, the second mode is also only occasionally seen as for example, one year when Buckthorn bushes were infested with Geometrid caterpillars. Starlings are especially well adapted to search for food in the highest soil layers and in dense vegetation just

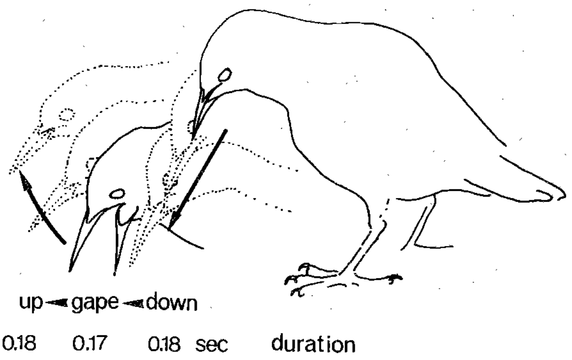


Fig. 6. Sequence of head movements involved in "gaping", a foraging technique typical for Starlings, whereby a hole is made at the soil/vegetation surface. Outlines generalized from ciné film (64 frames/second); the entire movement is completed within one second. See text for details.

above it. They use their bill in a peculiar way, called "Zirkeln" by Lorenz (1949), and here referred to as "gaping". A gape consists of a downward movement of the head, the actual opening of the bill and an upward movement. Film analysis shows that during the downward movement the bill is pointed exactly to the site of interest (Fig. 6). Due to the position of the eyes they look along the axis of the bill as it is moved down. As the bill hits the ground, or dense vegetation, it is opened, forcing a hole of one by two cm in the substrate. The position of the eyes and a special depression in the skull, lined with black feathers, ensure a binocular view into the hole while holding it open.

If prey is detected the Starling either grasps it immediately, or probes further for it. The last phase, the upward movement of the head is different from downward movement in that the bill and eyes are moved at an angle to the axis of the bill.

Starlings gape frequently (up to 3 times a min) when searching for Leatherjackets. However, they are also able to catch Leatherjackets without gaping, as can be seen on the short spring vegetation and on mowed pastures. We therefore used the total time spent searching as a measure for area searched instead of the rate of gaping.

Walking speeds are on average 1.5 m per min (for method see section 4.2.2.), but maximum speeds of 10 m per min have been recorded. The former is observed when the Starlings are searching for Leatherjackets. The higher speeds are seen when the birds occasionally forage exclusively on Bibionid flies.

In 1976 we carried out a detailed analysis of the foraging behaviour in the Leatherjacket area. Table 2 shows the frequencies of the different behaviours for males and females separately. The birds were randomly selected just before landing on the foraging area. Moments and duration of landing, digging, catching and handling time (this separately for eating and carrying to the nest) and take-off were recorded with an event recorder. As the duration of looking up was often very short (± 0.5 sec) only frequency was recorded.

The cause of the differences between the sexes in total time spent searching for a Leatherjacket and duration of digging might be due to differences in site choice. Alternatively there could be a difference in physical strength between the

Table 2. Foraging parameters for the Starling hunting Leatherjackets (1976 season)

	♂ (595 visits)		♀ (213 visits)	
	x̄	S.D.	x̄	S.D.
Time spent searching for one Leatherjacket (sec)	26.7	25.7	35.0	40.4 *
Handling time (sec) when prey is for:				
parent	1.4	1.2	3.8	3.3 *
young	2.6	2.9	5.3	4.1 *
Digging				
frequency/10 sec	2.0	1.0	2.0	1.1
duration (sec)	0.35	0.45	0.74	0.93 *
Looking up				
frequency/10 sec	0.4	0.9	0.4	0.8

* Differences between sexes significant, student-t test $p < 0.001$.

sexes. The latter could explain all differences found.

Both sexes spend more time handling a prey that is brought to the young than one which they eat themselves. Why this difference exists is not known. Since they often take the grub by its head and shake it vigorously, I believe that they immobolised it. The resultant tearing of the skin might allow digestive juces to penetrate the body quickly.

In subsequent years we simplified the measures to: foraging time (including handling time and digging time), the moment of prey catch, the prey species taken and bouts of looking around (> 1 sec), as these seemed the most feasible ones.

3. THE DIET

3.1. PARENTAL DIET

The diet of the parents was estimated in the polder area in 1976 by direct observation with telescopes (15—60×). Three categories of prey were distinguished a "peck", small prey, and large prey. A "peck" is defined by the behaviour of the bird in that a short peck is directed to the grass tips. From close range observations we know that one fly (Bibionidae for instance) is usually taken in each peck. It is interesting that the birds concentrate on pecking for a short time and than swallow the flies caught. Small prey were defined as prey visible from a distance but smaller than half the length of the bill. This category consists mainly of small grubs and beetles. Large prey were defined as prey longer than half the bill length and a very high percentage of these were Leatherjackets (in males 92%, in females 97%).

Table 3. Prey caught per foraging visit (1976 season) according to size category (see text for definitions) and according to destination (delivery to nest or self-feeding)

		♂ (n = 340)		♀ (n = 170)	
		x̄	SD	x̄	S.D.
Peck	parent	0.12	0.63	0.06	0.46
	young	0.12	0.97	0.01	0.08
Small prey	parent	0.16	0.46	0.17	0.82
	young	0.02	0.20	0.01	0.15
Large prey	parent	0.71	1.01	0.42	0.73
	young	1.51	0.67	0.93	0.65

The results are separated into the parents' own consumption and that taken to the young (Table 3). When small prey is caught, the parents consume a large proportion themselves, as has been shown for other birds (Oystercatcher, Lind 1965, Great Tit, Royama 1966). Many more Leatherjackets were brought to the young than smaller prey. If the total weight of prey is considered rather than the number, this difference is even more extreme as small prey weigh only a fraction of the large ones. In subsequent years we recorded the same prey categories during the observations, but the analysis of the data was restricted to the large prey only, since they were much more important.

3.2. NESTLING DIET

Various authors have reported on the diet of nestling Starlings. The emphasis is normally laid on the number of each species brought back to the nest. Kluyver (1933) gathered samples with the neck collar method and estimated that at least 313 species occurred in the diet. Pfeifer and Keil (1958, in Schneider 1972) also used this method, but categorized the number of prey items brought back into 17 groups, some single species, other mixed categories. Dunnet (1955) took photographs of the parent Starlings with prey in their bills, just before they entered the nestbox, and concluded that Leatherjackets and earthworms predominated in the diet. Westerterp (in press) used a balance under the nest to measure the weight of single feeds. However, he had to rely on visual observations to identify the prey species brought back.

In this study we measured the diet of the nestlings with an automatic camera as Royama (1970) did with tits. The aim was to get such good colour photographs that estimation of prey species, weight and time of the feed was possible. For this reason a photocell device was built into the entrance of the nestbox, so that, when the bird entered, it triggered the camera behind the nestbox to take a single frame. Light was supplied by an electronic flash unit (Fig. 7). A 35 mm still camera was used in 1976 but 16 mm filmcameras were used thereafter. These provide good resolution at reasonable cost. Prey species and length could be determined from the photographs for

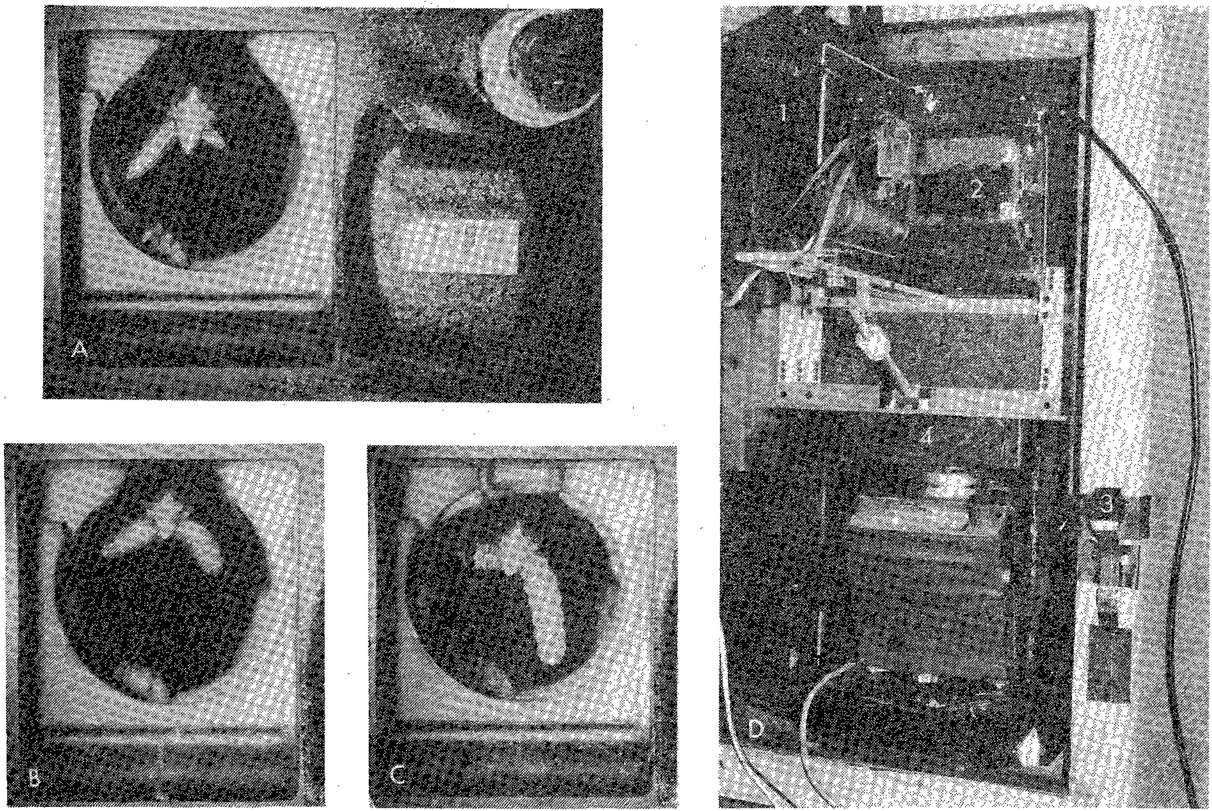


Fig. 7. Parent Starling entering the nestbox with a Carapteryx caterpillar (A), a Leatherjacket (B) and a Hadena caterpillar (C) (enlarged from 16 mm frames). On picture (A) the photocell that triggers the camera unit is visible on which a watch that gives the exact time is mounted. (D) gives the rear view of the observation nestbox showing the experimental setup. 1 = 16 mm cine camera (BOLEX) released automatically by photocell barrier in nest entrance via an electromagnet. 2 = viewing slit for observer, seated behind the nest entrance. 3 = watch for visual observations, running synchronously with second watch inside the nestbox appearing on each frame on cine film. 4 = Bottom of inner nestbox, containing the nestlings, resting on balance accurate to 0.1 g, whose scale is read off visually by the observer to allow determination of adult body weight.

most of the larger prey. The smaller species (flies and beetles) could not always be determined, but they only form a small proportion of the diet. In general, knowledge of the insects around helped a great deal in the analysis. The time of day, the sex of the parent and the number and length of each prey species were recorded from each picture.

Length-weight conversion graphs were constructed for the important food species from specimens freshly collected from the field. This was not done for the smaller species, where we used an average weight for all individuals. This allowed us to estimate the weight of the different food species in the diet from the photodata.

The percentage by weight for the different categories of prey brought to the young are given in Table 4. We can see at a glance that, although many species are brought, only a few contribute substantially to the diet. The main species are: *Tipula paludosa*, *Cerapteryx graminis*, *Crambus* spec., *Telephorus fuscus*, and in some years the caterpillars of *Hadena monoglypha*. Their natural history is described in the next chapter.

Tipulids are known to be an important prey species for Starling nestlings in many areas (Dunnet 1955, Kluyver 1933, Westerterp in press) but they are not obligatory (Pfeifer & Keil 1958). It is noteworthy that prey species important in the Schiermonnikoog area were also important in the area where Kluyver worked, indicating that certain insect species are particularly vulnerable

Table 4. Diet of nestling Starlings (data for all days combined) in percentage fresh weight, assembled from photo records (one nest in each year)

		1976		1977		1978		1979	
		♂	♀	♂	♀	♂	♀	♂	♀
Diptera									
Tipula paludosa	larva	36.9	48.7	76.1	76.3	75.7	67.6	45.3	50.5
	pupa	0.8	0.1	1.4	1.2	0.0	0.0	—	—
	adult	0.7	0.6	0.4	0.5	0.2	0.1	0.5	0.3
Bibionidae		0.0	0.0	0.4	0.6	0.0	—	—	—
Remaining Diptera		0.0	0.0	0.2	0.1	0.1	0.1	5.9	1.1
Lepidoptera									
Cerapteryx graminis	larva	41.0	43.5	1.0	3.9	15.5	25.5	26.7	34.4
	pupa	0.2	0.1	0.1	0.0	0.0	—	0.1	0.1
Hadena monoglypha		4.0	3.6	0.7	0.7	0.7	1.0	12.9	0.2
Crambus spp.		0.8	0.2	8.3	5.7	0.8	0.8	0.5	0.2
Remaining Lepidoptera		11.9	0.9	4.8	4.6	2.2	2.5	3.0	1.9
Coleoptera									
Telephorus fuscus		0.9	1.1	3.9	4.8	3.9	1.9	1.1	2.7
Remaining Coleoptera	adult	0.1	0.1	0.5	0.4	0.1	0.0	0.0	0.0
	imago	0.2	0.1	0.0	0.0	0.0	0.0	—	—
Arachnida		0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.1
Lumbricidae		0.0	—	0.7	0.5	0.3	—	—	—
Remainder		0.2	0.2	0.3	0.2	0.1	0.1	0.1	0.1
Unknown		2.0	0.6	0.9	0.6	0.6	0.3	3.9	3.6

0.0 = trace — = absent from diet

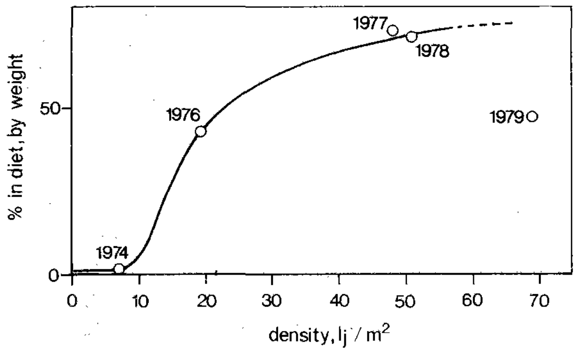


Fig. 8. Proportion of Leatherjackets (Tipula paludosa) in the diet of the nestling Starling in relation to the density of this prey in the area where most foraging occurred in that season. Diet is based on photographic records for one nest each season.

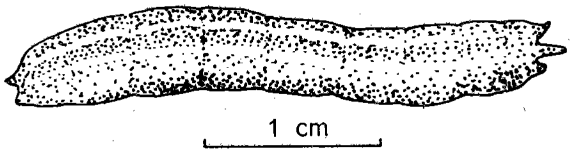
to predation by Starlings.

An essential ingredient in any foraging study is the measurement of prey density, in practice a difficult undertaking. In contrast to the extensive sampling undertaken by Tinbergen and his team (Tinbergen, 1960) in the Great Tit investigation, we only managed to assess densities for the principal prey species of the Starling, the Leatherjacket. This was repeated each year, and in all these years we collected data on the diet as well. If the diet data (percentage by weight in food brought to the nestlings) is plotted in relation to the density, an S-shaped curve emerges for the Leatherjacket (Fig. 8). Clearly, at very low density the parents did not take Leatherjackets to the young. The mechanism behind this effect will be the subject of a later section.

3.3. PREY TYPES

Tipula paludosa M. (Leatherjackets)

The larval stage of the crane fly occurs mainly in the polder and is called a Leatherjacket. It is a greyish, legless larva which grows up to 5 cm long. The annual cycle is as follows (de Jong 1922): Adult flies emerge in August and September and only live a few days. Females are



much less active than males. As soon as a male finds a female he copulates, after which the female starts laying up to 400 black, elongate eggs, which hatch after 18 days. The small Leatherjackets eat plants, mostly grass leaves and roots. Throughout September and October they are vulnerable to drying out, and correlations may exist between late dry Summers and few Leatherjackets the next year.

The larvae live between the grass. They pass the winter as the third or fourth (their last) instar. In early April they are still very small, but with increasing ambient temperatures in the next two months they grow extremely quickly. At this time the Leatherjackets start living in small J-shaped burrows. They reach their final weight at the end of May. By the middle of June the grubs are found in burrows up to 5 cm deep. They pupate in July and give rise to a new generation of crane flies in two months.

Each May we measured average densities for our 60×80 meter study area. These ranged from 5 to 69 per m² over six years. The distribution also differed between years. Different factors such as egg laying site, moisture and predation are believed to effect this. There are also short-term changes in distribution: during warm nights in early May some Leatherjackets leave their burrows and can be seen crawling around. Although only a small percentage of the population does so, this behaviour will change the distribution on a daily basis. Starlings predate on Leatherjackets during most of the Winter and in early Spring. They certainly take them a lot in May and June to feed their young.

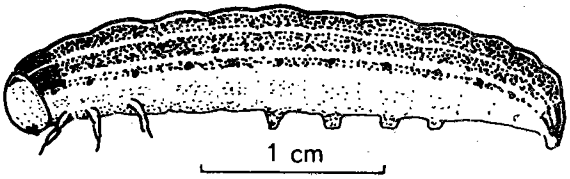
Table 5. Size of prey (in mm) brought to nestling Starlings, from the photo records in Table 4

			Tipula	Cerapteryx	Hadena	Crambus
1976	♂	x̄	29.3	29.8	29.5	17.2
		SD	5.0	4.4	7.3	3.6
		n	329	256	21	36
	♀	x̄	24.9	28.8	32.0	13.0
		SD	16.5	4.2	3.7	8.6
		n	659	353	21	217
1977	♂	x̄	30.4	26.2	33.5	17.3
		SD	5.4	4.0	3.5	3.3
		n	756	11	61	217
	♀	x̄	31.2	26.8	36.0	17.2
		SD	5.4	4.7	7.7	2.9
		n	2049	181	12	347
1978	♂	x̄	34.1	31.6	31.6	14.8
		SD	4.7	4.9	6.6	2.9
		n	1081	228	19	74
	♀	x̄	34.6	31.4	31.0	15.3
		SD	5.0	5.1	5.0	3.1
		n	818	356	20	78
1979	♂	x̄	29.9	28.6	34.0	14.2
		SD	4.1	4.9	6.0	2.1
		n	1159	576	162	49
	♀	x̄	31.9	30.1	32.1	13.6
		SD	4.2	5.3	7.0	2.2
		n	1529	782	83	29

The Leatherjackets taken for the young are between 2 and 3 cm long (Table 5) the mean differing between years. There is no systematic difference between those brought by male and female birds. The length-weight relationship is shown in Fig. 9.

Cerapteryx graminis

This is a moth belonging to the Noctuidae. Its caterpillar has a greenish-brown base with creamy, white, longitudinal stripes and a light belly.



Its yearly cycle runs more or less parallel to that of the previous species. The moths fly and the female lays her eggs in July and September. They overwinter as eggs or as caterpillars and May is their important growing time. By June they can reach a length of up to 5 cm and a weight of up to 1 g before they pupate. *Cerapteryx* caterpillars are mainly found in the saltmarsh and in the polder area they only occur in rough vegetation.

Analysis of the caterpillars' faeces has shown that they mainly eat *Festuca rubra*, a grass frequently occurring on the saltmarsh. Comparative data on yearly average densities of these caterpillars cannot be given. The best area we found had a density of 20 per m², while densities of 2—8 per m² were more normal. The occurrence of this caterpillar is related to the occurrence of *Festuca*. This grass alternates in a mosaic pattern with

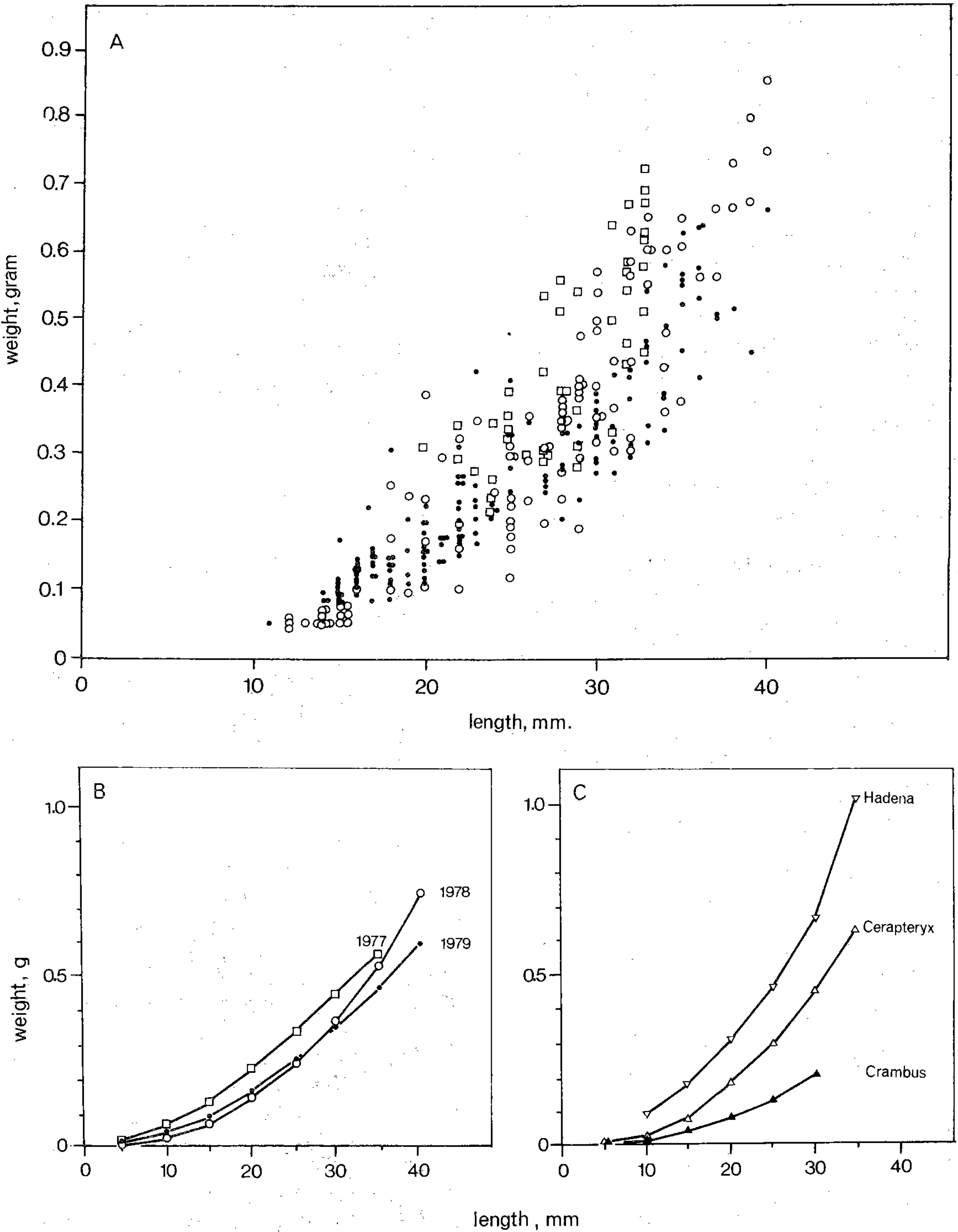


Fig. 9. Length-weight relationships for the principal prey insects of the Starling at Schiermonnikoog. Shown are *fresh* weights for individual insects collected where the Starlings foraged. Panel A shows the original data for *Tipula paludosa*, collected in three different seasons (points for 1976 omitted to avoid clutter). Panel B shows the curvilinear regression computed from these data, used for estimation of fresh weight of Leatherjackets whose length was known from the photo record. By way of example panel C shows the 1978 season curves for the other prey species *(Cerapteryx graminis, Hadena monoglypha, Crambus spp.)*.

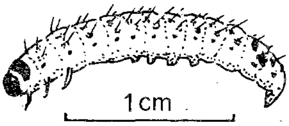
other vegetation types such as marram grass. Gradients in caterpillar density coincide with gradients in the vegetation.

During the day, when the Starlings prey on them, the caterpillars can be found under long tufts of dead vegetation. The older caterpillars are probably nocturnal, feeding in the vicinity of their shelters, which may result in small shifts in their distribution between days, possibly relevant in the context of Starling predation.

The Starlings prey upon them during the nestling phase, and even more heavily after the young have fledged. Large flocks of adult and young Starlings can be seen feeding on the caterpillars, just before they pupate. The pupae are some 3—5 cm under the ground so that they are not easily taken, although some occur in the nestling diet. When searching for caterpillars the Starling's foraging behaviour is rather similar to that when hunting for Leatherjackets except that they do not dig. The length of the caterpillars taken for the nestlings is around 2—3 cm, but varies between the years. Again no systematic difference between sexes occurs (Table 5). The length-weight relationship is shown in Fig. 9.

Crambus spp.

These are small, white caterpillars with a few hairs and black dots. They occur both in the polder and the saltmarsh.



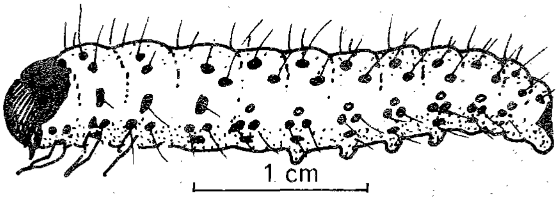
The caterpillar stage of these species is earlier than that of the others. The nocturnal grubs also live between *Festuca*, their food plant. They hide during the day in a loose web on the ground. Pupation occurs in the second half of May. They dig a burrow in the ground which is lined with silk. Emergence is from June onwards.

Starlings searching for these caterpillars again forage in the same way as when searching for Leatherjackets. When they collect them for their young they normally take more than one at a time.

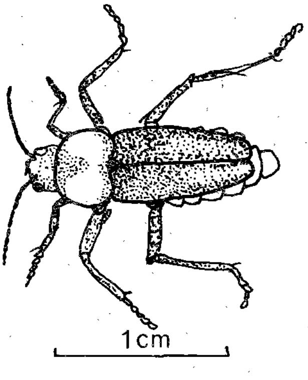
Comparative density data for these species are not available, but we know that they can occur locally at very high densities (60 per m^2). Again there is no systematic difference between sexes in length of prey brought. Differences between years do occur (Table 5). The length-weight relationship is given for one season in Fig. 9.

Hadena monoglypha

This big caterpillar grows up to 7 cm long. It is creamy-rose in ground colour with sparse, long hairs. Distinct black dots occur over the whole body and the head is dark-brown to black.



These caterpillars also pupate early, and in the years they are found in the diet, they only occur in the beginning of the season. Although mainly found in the saltmarsh, they also occur in the polder area. No density estimates are available. Average sizes brought to the young range from 2.5—3.5 cm (Table 5). The length-weight relationship is given for one season in Fig. 9.



Telephorus fuscus

This beetle is soft shelled. It has black wing cases and a red abdomen. Because of its colour it is easily recognized from the photographs. *Telephorus* can be found as pupae in the ground (4—10 cm deep) in April, from which they emerge in the second half of May and the first half of June.

They are very active during the day, walking around, presumably in search of prey.

Starlings add this species to their load after capturing a caterpillar. After they have found a caterpillar, their walking speed doubles and they move onto the shorter vegetation to search for the beetles. Running along with outstretched neck, the Starling picks up a beetle every now and then, without laying aside the caterpillar. An average weight of 66 mg was used for weight calculations.

3.4. WHERE THE PREY COME FROM

The Starlings forage in different habitat types, and the question arises whether they take a different prey species from each habitat. When we estimated the time budgets of the female Starling occupying the nestbox with the camera, we also recorded the landing sites. Since visits are relatively short, and site changes do not occur frequently, the landing sites are good estimates of the habitat from which the prey species brought back to the nestlings originate.

Comparing saltmarsh and polder, consistent patterns emerge (Fig. 10). Leatherjackets are almost invariably taken from the polder, while *Cerapteryx* originates mainly from the saltmarsh. *Telephorus*, the beetle, is brought more often from the saltmarsh than from the polder although this difference is less clear. This can be explained by the fact that as beetles fly, they thereby may disperse quickly after emergence. This is supported by the observation that in the beginning of the nestling period, beetles originate exclusively from the saltmarsh and only later are they taken from the polder area, especially on warm days.

Thus different prey species are brought from different habitat types. Sampling in these areas supports this distinction. This means that we cannot describe prey distribution for the Starling situation by a random model. Instead, prey distribution has to be differentiated into different habitat types. It is possible that the random model is applicable within the habitat type, but only on a very small scale (see section 6.1). I have already pointed out that within the saltmarsh Starlings search for caterpillars in places differing slightly from those they use for collecting *Telephorus*. Even within the polder area, the switch from Leatherjackets to Bibionid flies involves not only a switch in foraging mode (from normal walking to running) but also a switch in foraging site (from soil to grass tips).

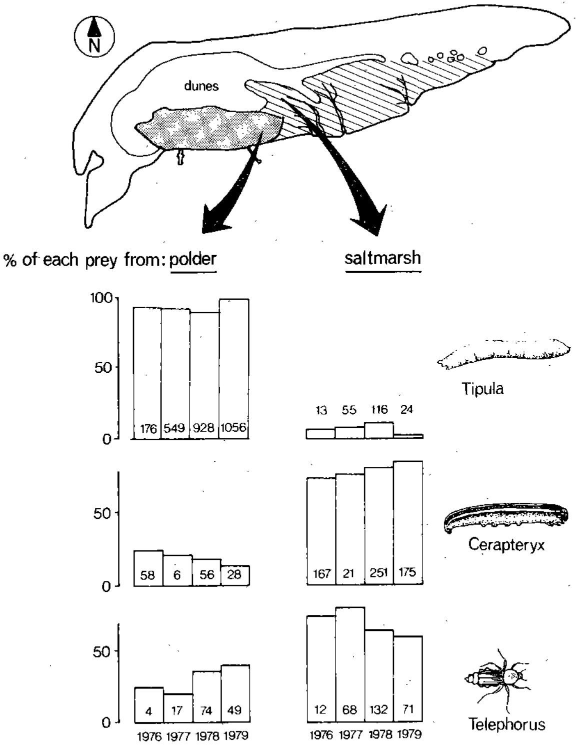


Fig. 10. Origin of prey brought to nestling Starlings: enclosed pastureland ("polder") and adjoining saltmarsh are contrasted. From top to bottom *Tipula paludosa, Cerapteryx graminis*, and *Telephorus fuscus*, with number of individual prey identified in the photo record each season (first broods only).

Royama's (1970) suggestion that for the Great Tit different prey species occur on spatially different sites fits the Starling situation on Schiermonnikoog very well, but there is however a difference in scale. Royama's units are much smaller than those I could discern in the field. Simultaneous encounters between prey species will thus not normally occur, since the probability of encountering a prey species is strongly correlated with the habitat chosen to forage in.

3.5. VARIATIONS WITH NESTLING AGE

The diet of the young varies with age. This is a known factor for Starlings and Great Tits, both of which are fed spiders more frequently in the first few days of life than later on (Kluyver 1933,

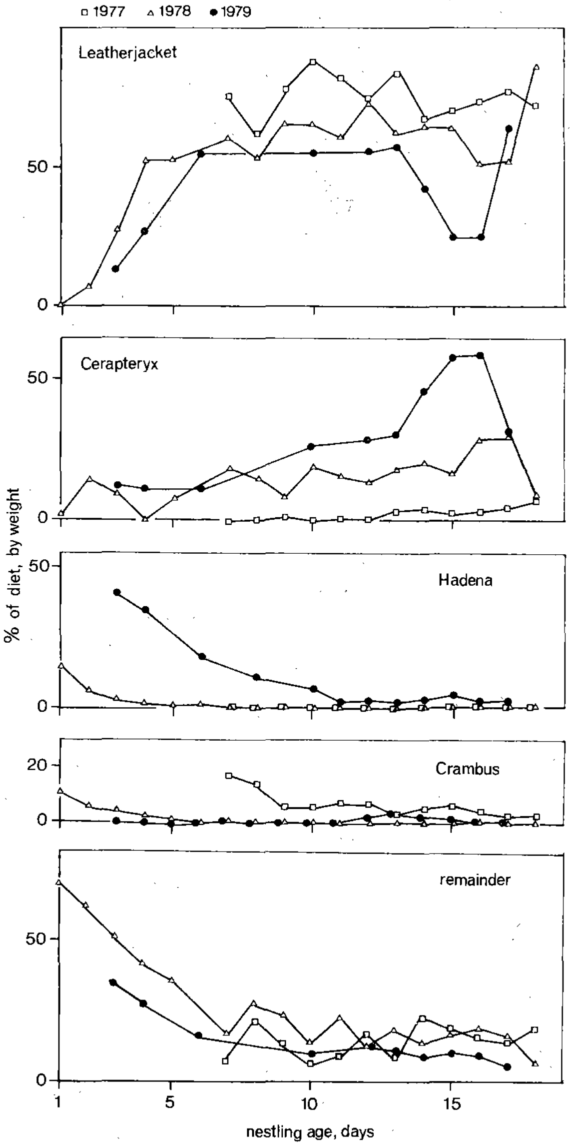


Fig. 11. Composition of the diet (per cent by weight) in nestling Starlings in relation to age (from top to bottom *Tipula paludosa, Cerapteryx graminis, Hadena monoglypha, Crambus* spp. and all other prey "remainder") for the three seasons with the most complete data (see key at top).

Royama 1970). This was also seen on Schiermonnikoog where the nestlings received more spiders in these first few days, although this was only a very small proportion of their diet by weight. Other food categories varied with nestling age as well, and I shall illustrate this with data from 1977, 1978 and 1979 (Fig. 11).

Leatherjackets are fed less frequently in the first few days of nestling life. Thereafter the percentage in the diet (by weight) increases rapidly to a relatively constant level. This is not caused by changes in Leatherjacket availability as parental capture rate ("intake rate" as directly observed, see section 1.2) does not change over this timespan.

Cerapteryx graminis provides, on average, an increasing share of the diet with increasing nestling age, *Hadena monoglypha* was fed relatively more frequently to the nestlings in the first few days of life. We do not know whether their availability changed. Our impression is that this is an early species, which might explain their decline in importance.

Crambus was brought more frequently the first few days in 1978, but was insignificant throughout 1979. Again we have no data on their availability. The rather mixed group forming the remainder category decreases with nestling age in two out of three seasons.

The general conclusion from this is that the nestlings get a more varied diet in the first few days of their lives but why this is so is not clear. Since we saw that the size of the *Cerapteryx graminis* fed to the young in the first days was very small in comparison to that fed a few days later it is possible that the small young could not swallow large prey, which would explain the effects found. However, size cannot be the only factor since *Hadena monoglypha*, the largest of the caterpillars, is brought to the young in this period. However, these caterpillars are much softer, and less tough than *Cerapteryx* which could explain why they can occur in the diet. It is also possible that small young need specific nutrients, as will be discussed later.

3.6. VARIATIONS WITHIN DAYS

Different prey types can vary significantly in a daily pattern (Orians & Horn 1969). In Starlings, Bibionid flies are taken mainly at mid-day (Tinbergen & Drent (1980). Presumably these flies emerge at this time, causing their availability to vary in a circadian rhythm. This was verified by sampling with a sweepnet. The number caught by sampling was strongly related to the number in the diet. However, this species is relatively unimportant in that its total weight brought to the nestlings is low. Here we will concentrate on those species that were important in the diet in most years, i.e. *Tipula paludosa* and *Cerapteryx graminis*, to verify whether the daily pattern of delivery can be explained from daily variation in availability. The Starling's daily pattern of collecting these species can be seen in Fig. 12.

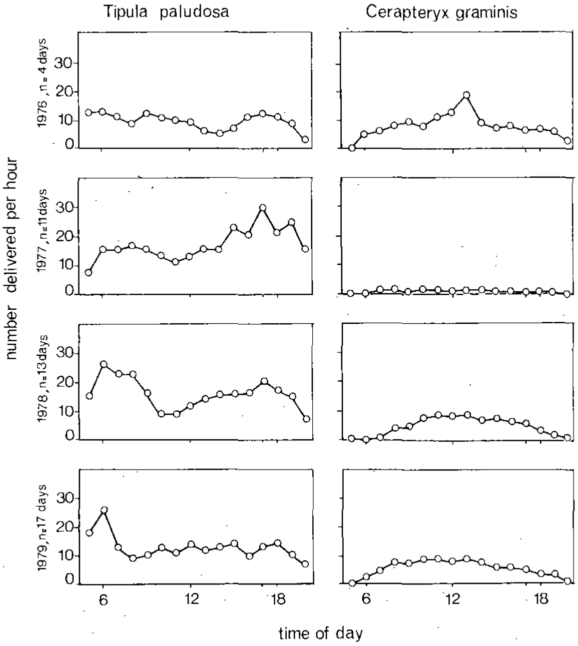


Fig. 12. Number delivered per hour of two important prey species (identified above) in relation to time of day for four consecutive seasons (derived from photo record). Contribution of these two prey to the nestling diet can be found in Table 4.

The number of Leatherjackets delivered per hour shows, more or less, a morning and an evening peak in all years. In contrast, *Cerapteryx* has a clear mid-day peak in the three years it was important. To explain these daily variations we would first of all think of daily changes in availability. Since we know roundtrip times and the weight brought back from the photographs, we can estimate the rate with which these different prey species were delivered to the nestlings. If we do this for Leatherjackets we see that the delivery rate is either constant or has a mid-day peak. Direct data on intake rates in the field, thus including parent consumption, confirm this picture (Fig. 13). Thus Starlings do not concentrate on Leatherjackets at the time of day they are most rapidly collected. This would not be expected for a Starling maximizing its intake rate. Possibly it occurs because of variation in availability of other prey species, such as *Cerapteryx*.

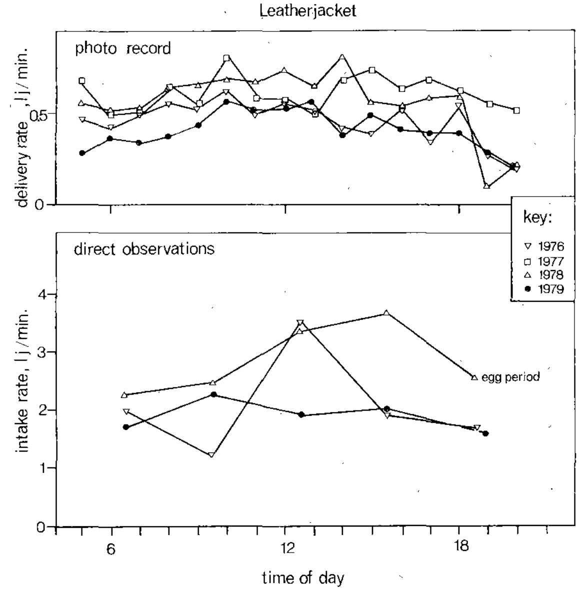


Fig. 13. Intake rate in relation to the time of day that parent Starlings collected Leatherjackets. The independent estimates shown are derived from the photo record (top panel, four seasons) and from direct observation of foraging birds (bottom, three seasons). Estimated intake during the egg stage is included for 1978. The two methods do not yield identical data because self-feeding is ignored in the photo method, but the daily pattern is evident in each.

Fig. 14 gives the delivery rates, as derived from the photographs, for the caterpillars. They are very low in comparison to the former species. The delivery rate, in the years that *Cerapteryx* was important, is either constant or decreases

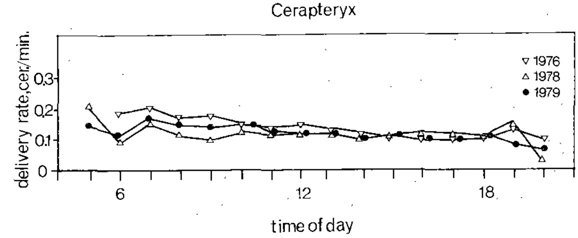


Fig. 14. Intake rate in relation to the time of day that parent Starlings collected *Cerapteryx graminis* on the saltmarsh, as derived from photo records made at the nest. There is no suggestion of a mid-day peak corresponding with the peak in delivery rate (compare Fig. 12).

during the day. But Starlings do bring *Cerapteryx* mainly in the mid-day period. Thus again, the Starlings do not take these prey species when they seem to be most readily available. Unfortunately intake rates of the birds on the *Cerapteryx* area could not be measured directly, so we cannot rule out the possibility that the parents eat more caterpillars for themselves in the middle of the day than they do in the morning.

In conclusion we can say firstly, it is difficult to see why caterpillars should be taken at all: since they give such a low delivery rate an explanation must be found. Secondly, we also have to explain why Starlings take Leatherjackets outside the time they are most available. For the moment we have to conclude that prey choice is not simply a function of prey availability, but we will follow up these questions in the section on prey choice (4.1.).

3.7. FOOD CONSUMPTION

One of the goals of this foraging study is to see how the Starling, in particular situations of supply and demand organizes its foraging behaviour. We therefore need to know what nestlings and parents consume daily as a basis for further study. We will estimate that of the parents as we go along, but the consumption of the nestlings will be considered here.

The information we will discuss here was taken from the photographs of the feedings. The visit frequency, the weight per visit and the diet could be derived for five different nests in four different seasons. For the Leatherjackets and the caterpillars (*Cerapteryx*) the energy content was estimated with a bomb-calorimeter. The final data will be given as a function of brood size since this affects the consumption per nestling.

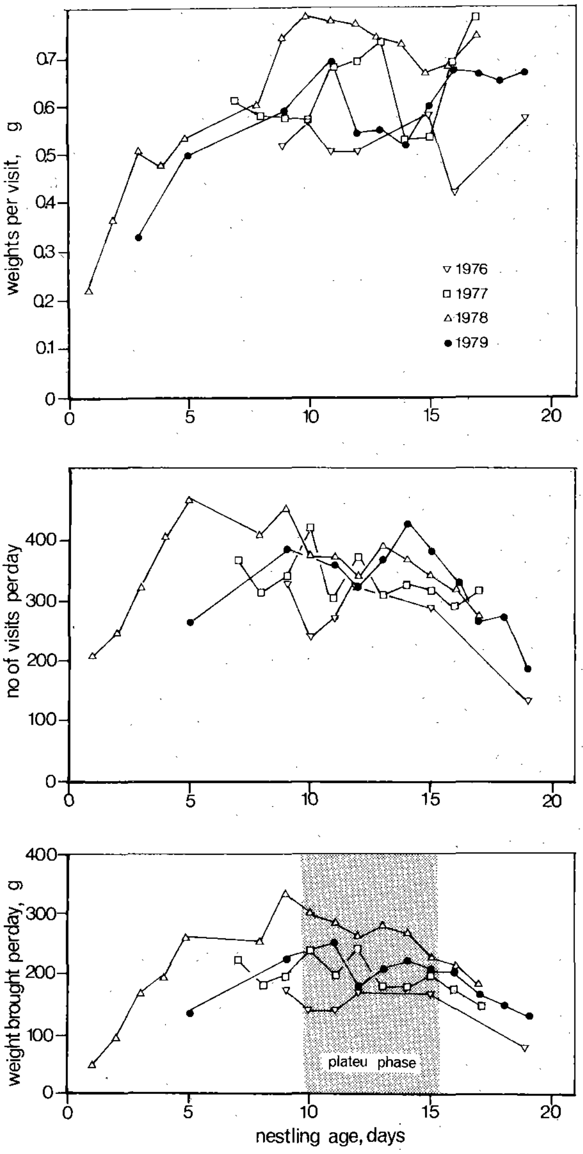


Fig. 15. Food input for four nests covered by photo record. (A) fresh weight of individual feeding, (B) number of visits per day, and (C) the product of these, namely total fresh weight of food delivered to the nest each day, all in relation to nestling age. Data from the plateau period are shown in relation to brood size in Fig. 16.

The daily number of visits made to the nestlings are given in Fig. 15B as a function of the age of the nestlings. Visit frequency increases strongly over the first five or six days, then stays relatively constant and decreases again after day 14. The weight per visit is also dependent on nestling age (Fig. 15A). It increases from .25 to .60 gram in the first seven days and stays more or less constant thereafter. The daily food consumption derived by combining Fig. 15A and 15B is seen in Fig. 15C. Since we do not have data over the whole nestling period for all years we will restrict our attention to the plateau phase, between day nine and day sixteen. The broods consume between 160 and 280 grams (fresh weight) of food. We are interested in the energy needs of the nestling to be able to understand the effect of brood size on parental feeding.

Converting data on total food consumption from fresh weight into energy value can only be done relatively, since the absolute level of our energy estimates is open to question on account of methodological shortcomings. Nevertheless we are confident that our estimates are mutually comparable. The diet was split up into two categories differing in energy content: Leatherjackets and the remainder. Data on the caloric value of these species were obtained from Schiermonnikoog specimens for the Leatherjackets and Caterpillars (Prop pers. comm.). We estimated gross consumption of the young by multiplying the weight per prey category by the caloric value but used an index value. Fig. 16 gives the relation between brood size and energy intake index per young per day for the plateau phase. Three types of data are given: Westerterp's data on Starlings breeding near Groningen, where brood size was manipulated, our own (1979) data on two manipulated broods one in the Polder and one in the Saltmarsh, and that for the four nests in four different seasons where the brood size was not manipulated.

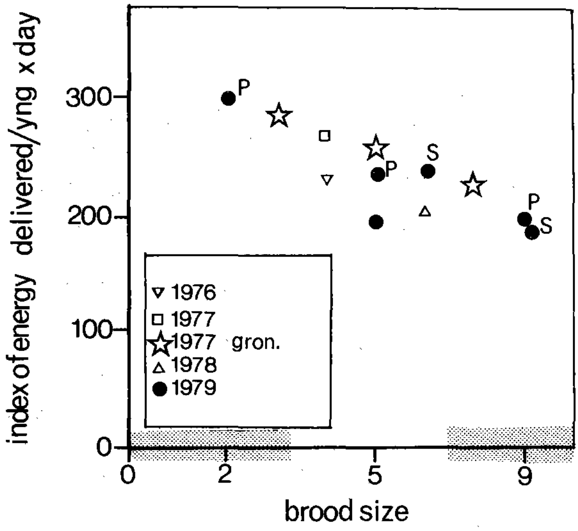


Fig. 16. Relative level of provisioning (energy units delivered per nestling per day) of nestling Starlings in the northern Netherlands during the plateau period (day 10-15, see Fig. 15) in relation to brood size. Data for polder (P), saltmarsh (S), and a colony near Groningen (Gron., from Westerterp *et al.*) are included. Energy content refers to gross energy content of prey, not metabolizable energy. Broods of 4, 5 and 6 are normal for this area, broods of 2, 3, 8 and 9 are experimental (indicated by stippled bar).

No large differences occur between the different sets of data. It is interesting that with larger brood sizes individual nestlings receive less food. This has been explained by the fact that young in larger broods need less energy for keeping themselves warm. However, it must be stressed that the weight of the nestlings is negatively correlated with size of the brood. This had also been shown for Great Tits by Perrins (1965) and for Starlings by Lack (1948). The number of surviving young has often been thought to be a good predictor for most productive brood size. However, since weight decreases with increasing brood size (Fig. 17), we have to be very careful in concluding that more young automatically means a higher fitness for the parents. Survival after fledging (i.e. expected fitness) probably depends on, among other factors, their weight at fledging. How number and quality of young combine in terms of fitness is not known, which makes it very hard to predict the most productive brood size. A further complication is that the parents' condition can also change as a result of brood size. The compromise the parent chooses to make is an interesting question that we will not go into here.

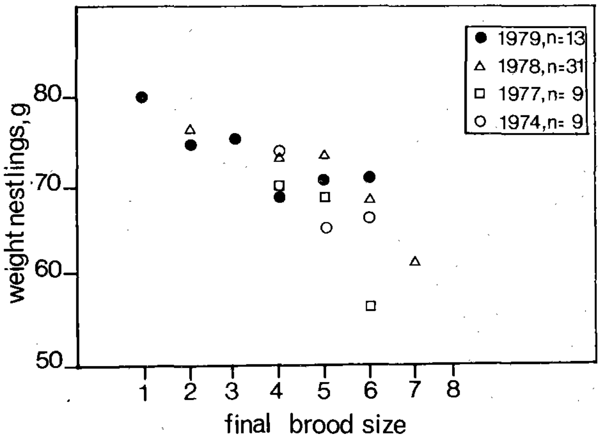


Fig. 17. Plateau weight of nestling Starlings at Schiermonnikoog (mean of day 14—18) in relation to brood size at fledging (n= number of nests studied per season).

4. FORAGING DECISIONS

An animal has to make a decision whenever its behaviour can continue via alternative pathways

(McFarland 1977). For instance, a Starling brooding its young in a nestbox has to make the decision whether to continue brooding or leave the nestbox to forage.

In this chapter I shall concentrate on foraging decisions, and assume for the time being that they are independent of one another. According to the definition given here, foraging decisions have to be made at those moments that alternatives appear. Whether these alternatives are there or not depends to a great deal on the options open to the bird itself and the organization of the foraging habitat of the bird.

We thus need a description of the foraging mode of Starlings and the foraging area they use to order the different decisions in a meaningful manner. In the breeding season, the Starling is a central place forager (Orians & Pearson 1979) that has to return to the nest site after a load of food has been collected for the young. The foraging day is therefore broken up into discrete units, the round trips (up to 250 per day).

An important aspect of the habitat in which the Starling breeds on Schiermonnikoog is that the two major prey species occur in different habitat types, the polder and the saltmarsh (see section 3.4). If a Starling makes the decision to collect a certain prey species, the flight direction should be chosen before the bird leaves the nestbox. Only once it has reached the appropriate habitat type has it to decide where to land. Decisions on how long to stay there, how many prey to take back etc. have to be made at least partly on the basis of information gathered on the site itself.

Observation of Starlings gives a strong impression that the different decisions are taken at different moments in the roundtrip. This is why the rest of this paper is organized in the sequence I think a Starling makes its decisions.

Various authors have discussed the chain of decisions that animals have to make when they are foraging (MacArthur 1966, Charnov 1973, Kacelnik 1979). All these arguments are partly based on theoretical assumptions regarding the foraging environment and the options open to the animal. Real measurements on how the foraging environment is organized are very scarce, at least in the detail necessary to analyse foraging decisions. Detailed measurements on what free living birds do in these environments are also scarce. Comparison of the Starling system with current views on decision chains in foraging behaviour will be given in the final discussion.

As the structure of the habitat forces the Starling to take the decision on prey choice first, I shall begin with this. The second part of this chapter concentrates on decisions taken once prey choice has been made. The bird is then essentially left with a single prey system. Decisions should be taken in such a way that the Starling maximizes fitness. Since it is almost impossible to measure the effect of individual foraging decisions on fitness, a subgoal for the foraging animal is used instead, namely intake.

What I shall investigate is whether the foraging decisions of free living Starlings are governed in such a way so as to maximixe the intake rate in Joules per time unit.

4.1. DECISION ON PREY CHOICE

Most models on foraging of insectivorous birds assume that the necessary factors to explain prey selection are: encounter rate, caloric content (gross energy value) and handling time (MacArthur 1966, Schoener 1971, Charnov 1973, Royama 1970). All these factors have proved to be important in a number of laboratory tests of prey selection in birds (Pulliam 1980, Krebs et al. 1974, 1977, Davies 1977). In addition, Zach and Falls (1978) have shown that the percentage chitin has to be incorporated to allow a good prediction of prey selection for ovenbirds in captivity. In general, birds tend to prefer those prey items that deliver the most net energy per time unit. For example, in Red Grouse it has been shown that a strong preference exists for the tops of heather plants: these contain significantly more protein than the rest of the plant (Moss et al., 1972). In Barnacle Geese, preference for certain vegetations can also be explained by protein content better than by caloric content alone (Prop pers.comm.).

The first suggestion that factors other than caloric content are important in prey selection in free living insectivorous birds comes from the work of Tinbergen (1960). In his extensive study on the Great Tit, he showed that certain prey species are underrepresented in the diet when the density of that prey in the environment is very high. Tinbergen suggested that Tits strive to bring the nestlings a varied diet. Later Royama (1970) criticized this idea and suggested that the underrepresentation was caused by another factor, namely the negative effect of handling time on intake rate at very high prey densities (see also chapter I).

Many people are currently aware of the fact that a bird may select on the basis of factors other than caloric value alone. Pulliam (1975) constructed a model which included nutrient constraints. McFarland (1978) published a model that predicts how an animal would choose between prey species containing different amounts of energy and a limiting nutrient, assuming that a certain amount of energy and nutrient are needed. Goss-Custard (1977) suggests that Redshank prefer Corophium to large worms although the latter would yield a higher return of net energy. The data are not conclusive, however, since on sites where Corophium and worm density is high some habitat character might make the large worms less vulnerable to predation. An experiment is necessary to evaluate the results properly.

Data from Kluyver (1933) and Royama (1970) show that nestling Starlings and Great Tits respectively get special food in the first few days of life. Both recieve spiders much more frequently in this period than later. Royama pointed out that this is not a seasonal effect since this also occurs with second broods. Whether this involves a nutrient constraint or simply an effect of limits such as prey size or consistence that the young can take, is not clear.

Data were collected to test the hypothesis that decisions regarding prey selection are taken on the basis of energy value alone. As we shall see this is not the case in Starlings and models that predict nestling diet in Starlings should incorporate constraints for some other food quality than energy value.

Because of the segregation into Leatherjacket and caterpillar habitats, study of prey selection in terms of caloric maximization is simplified. The prediction would be that the bird would select the prey species giving the highest amount of calories per time unit. The simplest approach to this question is to compare intake rates (nestling plus parental consumption) and time budgets in polder and saltmarsh for individual birds. I have shown however, that in the saltmarsh direct measurements of time budgets and intake rate are very hard to obtain. Those data we do have suggest that intake rate in the saltmarsh is low compared to that in the polder.

As we saw before, food delivery rates (prey collected for the young only, per unit time away) are extremely different (Figs. 13 & 14) for Leatherjackets and caterpillars but as long as we have no information on the parents consumption this is not convincing. Therefore, field experiments were done to test the Starlings preference in a simultaneous choice situation.

4.1.1. Field experiments.

An experiment involving feeding trays was done in 1976 on Starlings with young. Each of the six open compartments of a shallow box were filled with one Leatherjacket and one caterpillar. The box was placed 10 m from the nestbox. When approaching the box a bird had a high chance of seeing both prey types since they were not more than a few centimeters apart. Three Starlings discovered this rich foraging site. Table 6 shows that there is a clear preference for caterpillars. It was striking that the birds selected at first sight, implying that they already knew the difference between the species.

The Starlings brought caterpillars more often to the young than Leatherjackets (74% of the caterpillars and 53% of the Leatherjackets taken, were brought to the young) so Starlings show a strong preference for caterpillars.

Starlings do not normally encounter a simultaneous choice situation in the field as caterpillars occur on spatially different sites to Leatherjackets. Therefore, we designed a second experiment in which two feeding tables (placed 2 meters apart) were offered some 10 meters from a nestbox inhabited by a wild Starling family. Furthermore, as both caterpillars and Leatherjackets are hidden under grass and soil respectively, the two new feeding tables were designed to prohibit a direct view of the prey species, and had to be first investigated by the Starlings.

Table 6. Choice experiment involving Leatherjackets (*Tipula*) and caterpillars (*Cerapteryx*) offered near nestbox in food trays. Number of prey taken up to the point that 50% of the prey on offer had been captured is given, showing a clear preference for the caterpillars

test	test birds	number offered		number taken	
		Cerapteryx	Tipula	Cerapteryx	Tipula
1	$♂_z + ♀_{zz}$	10	10	9	1
2	$♂_z + ♂_{RG}$	10	10	8	2
3	$♂_z$	10	10	10	0
4	$♂_z$	6	6	5	1
5	$♂_z$	6	6	6	0
6	$♂_z$	6	6	6	0
7	$♂_z$	6	6	6	0

These tables, used throughout the study, have the following construction. The upper surface of the table contains a large number of holes arranged in a regular pattern. Each hole is covered by a rubber flap which had to be opened by the bird, in a similar way as when gaping, before it could inspect the hole. In our observations each inspection was equivalent to a peck. A sliding drawer was fixed under the table containing two to four times as many food cups as there were holes. Depending on the experiment either all holes were filled with prey, one prey per hole, or fifty percent were left empty. By moving this drawer laterally the observer was able to either replace eaten prey or produce any selected reward/no reward schedule.

Starlings were attracted to this new feeding place by putting mealworms and stuffed Starlings on top. The male was trained to forage in the morning on these tables for two hours. The bird became accustomed to foraging on both tables after several days. That was the moment for us to make a joint excursion to the saltmarsh to collect caterpillars to start the experiment. The next morning one table was filled with caterpillars, the other with the same weight of Leatherjackets, so that intake (weight) rate over time would be roughly equal on both tables.

The idea was to lower the density of caterpillars step by step, hence titrating the preference for caterpillars against Leatherjackets. One experiment was performed every day. Between days the caterpillar table was randomly exchanged for the Leatherjacket table, so that the bird had no way of predicting which table was which. The number and duration of visits were measured per table, as were the number of holes inspected, the intake rate and the number of prey delivered to the young.

The optimal solution for the birds based strictly on caloric maximization, would be to spend all their time on the table with the highest intake rate. If intake rate did not differ no preference was expected. In practice, our expectation was that the time spent on the caterpillar table would be proportional to the relative density of caterpillars to Leatherjackets. This is because we know from the literature (Krebs et al. 1978) that the time taken for a preference to develop is inversely related to the difference in intake rate between two areas.

The results of this experiment are shown in Fig. 18. A clear preference exists for the caterpillar table, which deviates strongly from the expectation for all tests. Unfortunately the experiments could not be continued as the nestlings of our male fledged. However the data are sufficient to conclude that a Starling foraging for its young has a high preference for caterpillars over Leatherjackets.

In conclusion, caterpillars are highly preferred to Leatherjackets. The male spent more energy to collect a caterpillar than a Leatherjacket in our experiments. The question arises why the nestlings are fed Leatherjackets at all. We can see from the diet of the nestlings (Table 4) that Leatherjackets account for a large proportion of the diet in most years. If it is true that the intake rate on caterpillar areas is low compared to the intake rate on Leatherjacket areas it is possible that the parents simply cannot meet the demands of the young by collecting caterpillars only. In this case we would expect that the demands of the young have an effect on their own diet. The

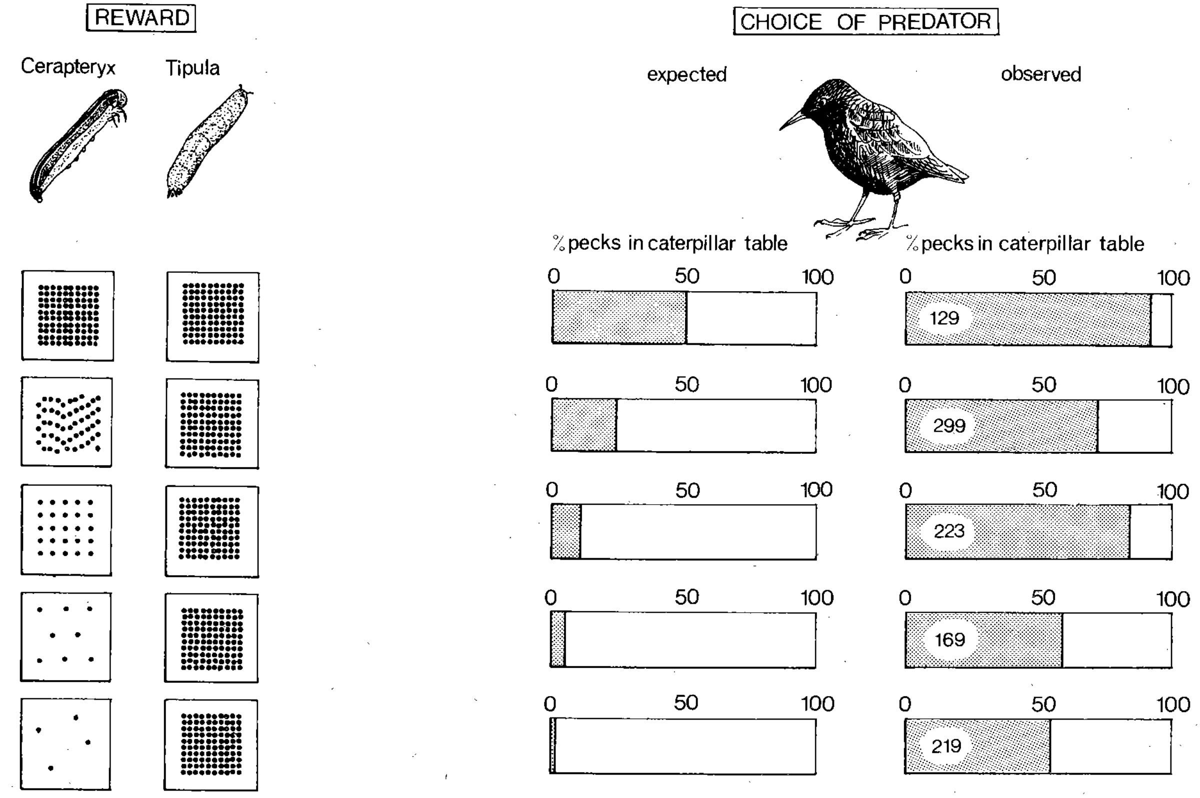


Fig. 18. Feeding table experiment on prey preference. Left: the test situation, a pair of tables situated close to the nestbox of male GH3. One table is stocked with *Tipula*, the other with *Cerapteryx* in the relative reward ratio depicted (on a *weight* basis). An expectation for per cent pecks directed towards the *Cerapteryx* (caterpillar) table was computed for each test (see text) and is given in the centre panel. On the far right the observed test outcome (n= number of total pecks per test).

basic decision for a parent would be to collect caterpillars but when the young get more hungry the parents have to switch to Leatherjackets to meet the caloric demand of the nest. We therefore designed two experiments to test this. In the first experiment I will show that the demands of the nest do influence the decision on prey choice. In the second I will try to explain part of the rationale behind this shift in the decision on prey choice.

4.1.2. The effect of brood demand on nestling diet

The nest demand was manipulated via hunger of the young (defined here as the time they had not received food) and the number of the young in the nestbox.

The nestboxes were equipped with drawers in which the birds could build their nests. These drawers could be manipulated from a hide directly attached to the nestbox. A second drawer with a man made nest that could be exchanged with the original drawer was available.

The experiment was performed as follows: just after the observer entered the hide the brood was separated into two groups of three, one was left in the nestbox, the other was kept in a spare drawer, nicely warm under a heat lamp or with a hot water bottle. The number of visits by the parents to the nest were recorded and in addition the feedings categorized into two types: with or without Leatherjackets.

After an hour of observation the young that had not received food were exchanged with those that had been in the nestbox. Registration of the number of feeds and the food type brought back to the nestbox was continued. After another hour

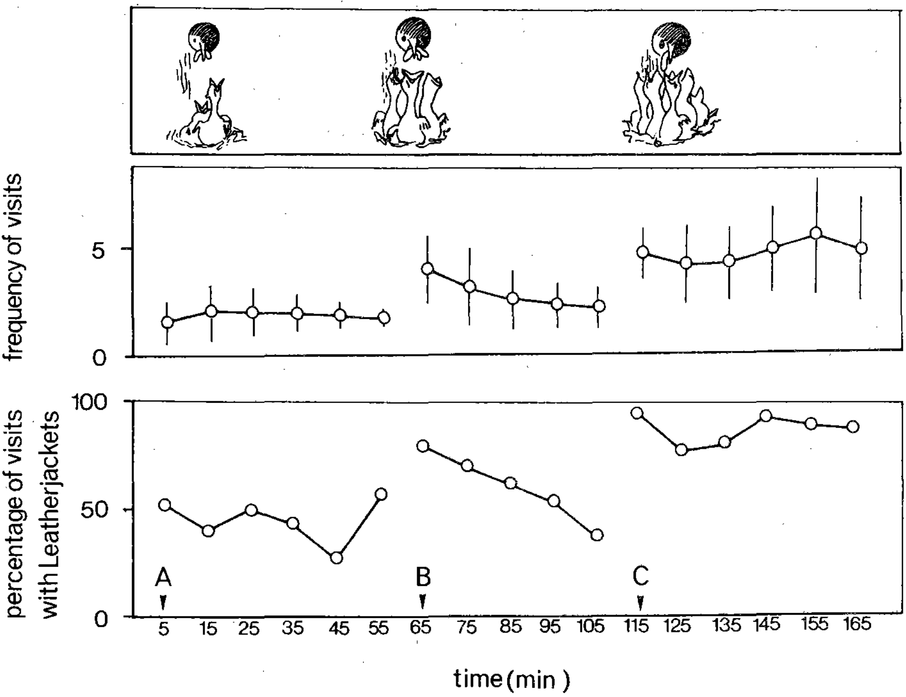


Fig. 19. Experiment demonstrating effect of nestling demand on their diet spectrum. Three experimental phases (see time scale in minutes along the bottom) are shown. At (A), three young of the original six-brood are removed and the parents need only provision the three relatively satiated young remaining. At (B) the three young removed at (A), now very hungry, are exchanged for the three well-fed young, which are again returned to the nest at (C). Depicted are frequencies of parental feeding visits (per ten minutes, vertical bars indicate 95% confidence intervals, middle panel) and per cent of feedings which included Leatherjackets (bottom).

of observation all nestlings were put together into the nestbox which thus contained three hungry and three well fed young. In most experiments another hour of registration followed. In total, ten experiments were done with three different pairs. The pooled results are shown in Fig. 19. There are clear effects of hunger and number of young on the number of feeds that are brought to the nestlings. But the diet of the young varies as well! After the first exchange from normal to hungry young there is an increase in the percentage of feeds with Leatherjackets. A significant increase in this percentage is seen after the exchange to twice the number of young in the nestbox.

Thus, the prey choice of parent Starlings is affected by the demands of their nest (hunger state and number of young). With an increasing nest demand the parents shift the diet of the nestlings to Leatherjackets which are easier to get (i.e. allow a higher delivery rate). The rationale behind this shift in prey choice could well be that the parent is limited in time. We must not forget that this time limit is not only imposed by nest demands and the parents ability to collect food, but also by the parents own demands. We thus need information on total intake rate (nestlings plus parents) prey choice and time budget. Therefore, we continued the same experiment, measuring these parameters over a longer time basis.

4.1.3. Will increasing brood demand cause parents to relinquish time consuming prey

The experiment was set up as follows. In 1979 a nest was equipped with a camera, so that the food brought to the young could be recorded as described in section 3.2. At the same time the female of this nest was followed from dawn to dusk, enabling time budgets and, where possible, intake rate to be ascertained. The normal number of young for this nest, five, was a basis for the experiment. Brood size was changed to two or nine. Care was taken that two of the young always stayed in the nest to give reference weights for growth. The exact dates of the nest manipulations can be found in table 7.

Figure 20 gives the diet of the young as a function of brood size. In this experiment also the diet of a nestling changes sharply with brood size. The more young in the nest the fewer cat-

Table 7. Experimental sequence, brood-size manipulations in 1979

Month	May				June											
Day	27	28*	29*	30*	31*	1*	2*	3*	4	5	6	7	8	9	10	11	12
Nestling age (days)	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
No young in nest	5	9**	5	2**	9**	9**	5	2**	5	5	5	5	5	5	5	5	5

* = all day observation
** = brood size changed

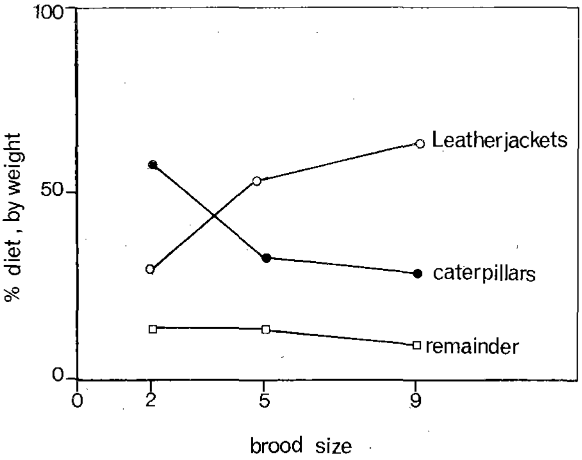


Fig. 20. Effect of brood size on diet (weight per cent) as shown by outcome of 7 tests over the daylight period (nestbox 39, 1979, both parents).

erpillars occur in their diet. The "remainder" category stays relatively constant. Thus the effect of the demands of the nestlings on their diet is also clear on a daily basis.

What we want to show is that the parent Starling, when confronted with a large and hungry brood, does more than simply expand foraging activities to fill the time available (the daylight hours). The major contrast between the brood of five and the brood of nine, as we shall see, is in where the foraging time is expended. This will become clear when more information on time budgets and intake rate has been given.

To estimate the total number of Leatherjackets and caterpillars collected by the female, both for the nestlings and for herself, is complicated since direct observations of the intake rate of the female on the saltmarsh are not available. The way we go about this is as follows. The number of Leatherjackets eaten by the female can be determined rather precisely. We have a great many observations on intake rates, and the time devoted to hunting Leatherjackets is also known from direct observations since the number delivered to the nest can be obtained from the photographic record, by subtracting this from the total intake we know the number consumed by the female. Consequently we can estimate (1) the total energy demand of the female, and (2) the energy obtained by the female from the Leatherjackets, and hence the contingent of the daily energy contributed by other prey can be approximated. Before entering on these computations two points must be stressed. Firstly, we realize that there are many shortcomings in our energetic approximations and by no means wish to suggest that our literature-based extrapolation is the ideal way to solve this problem. What we mean to do, is present a daily energy budget for the individual parent as a pursuasive argument to stimulate direct study of field energetics. Second, as will become apparent, the crux of the argument can be given on time budget considerations alone, i.e. the trends mentioned below do not depend on the exact level of the estimates employed.

Our first problem is thus to determine the daily energy requirement of the female during the nestling period. The energy required must be equivalent to the sum of the costs of different elements of her time budget, with in addition a correction for weight changes (obtained from direct measurement of parental body weight change in these experiments) and a correction for temperature regulation costs. As is common practice in this type of work, we will express costs as multiples of Basal Metabolic Rate (BMR). The cost of flight was taken as 9.9 BMR, as this is the value obtained for the Starling in wind tunnel experiments reported by Torre Buenos et al. (1978).

By analogy with other studies the cost of sitting, preening and sleeping was taken all as equivalent to 1.5 BMR (see discussion in King (1974)). A major problem is posed by active foraging, and here we are forced to resort to guesswork. Preliminary experiments with captive birds allowed to forage on the Leatherjackets grid, but prevented by the dimensions of the cage from flying, indicate that active foraging for Leatherjackets must cost in the order of 5 BMR (Prop, unpublished). An increase in weight was taken to cost 33.5 KJ. per g, a decrease was taken to Yield 20.9 KJ. per g (generalization from Kendeigh et al. 1977). Costs of temperature regulation were estimated from work of Gavrilow & Dolnik, cited in Kendeigh et al. (1977). Since the BMR has been measured for our Starlings (Biebach 1979, see also summary in Kendeigh et al. 1977) we can now compute the daily cost from our time budget data. To convert this to Leatherjacket units, we need to know the energetic content of one Leatherjacket (here estimated at 1.46 Kjoules) and the digestibility in order to convert metabolic requirement to given intake (determined by Prop as 0.65 in the experiment alluded to above, a figure in agreement with other work on insectivorous birds). How do these estimated Leatherjacket rations compare with the number consumed by the female according to the field data?

In Fig. 21 the estimated daily energy requirement (GMI, gross metabolic intake, derived from the time-budget approach) is compared to the energy content of the Leatherjackets consumed by the female according to the field data (computed from time spent in the Leatherjacket area, measured intake rate, and corrected for the number brought to the nest). The first conclusion we draw from this figure, is that the female's own diet varies according to brood-size: the smaller the brood (the less the pressure on the parent) the fewer Leatherjackets there are in her diet. When the brood is increased to nine, the female cuts out caterpillars entirely from her diet, in order to supply the young with an adequate diet. If we accept the conclusion that the female consumes no other food items apart from Leatherjackets when confronted with the supernormal brood of nine, we can now approximate her caterpillar consumption for other brood sizes, as the photorecord for the nine-brood in combination with the time-budget data for saltmarsh visits provide all the necessary data. The time to collect one caterpillar is the duration of a visit ($\bar{T}v$) minus the flying time ($\bar{T}f$) divided by the number of caterpillars delivered per visit ($\bar{N}$) which is:

$$\frac{\bar{T}v - \bar{T}f}{\bar{N}} = \frac{370 - 110}{1.21} = 215 \text{ seconds.}$$

Assuming that the time to collect a caterpillar does not vary with brood size, we can compute the total caterpillar intake for other brood sizes by simply dividing the time spent on the saltmarsh by the mean time spent searching for one caterpillar. By subtracting the number of caterpillars brought to the young from total intake, we see that the female's caterpillar consumption decreases with increasing brood-size (Fig. 22).

Further evidence for this can be seen in body weight data. Normally the female collects caterpillars in the middle of the day. Comparing her mid-day body weight for different brood sizes reveals a negative relation between these factors

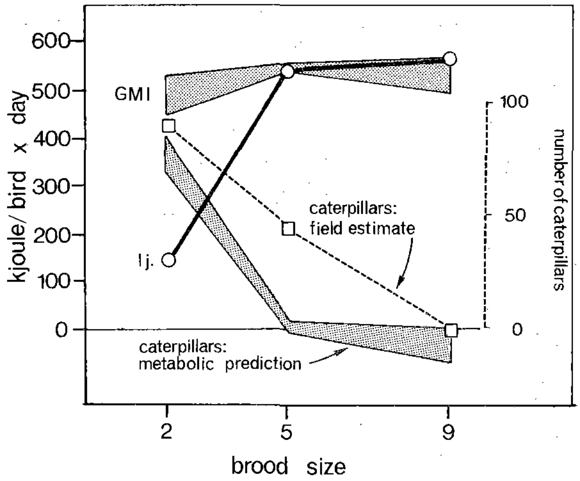


Fig. 21. The female's own consumption during the brood size manipulations. Time-budget data together with estimates of total daily energy requirement (stippled bar). The latter are based on the assumption that foraging costs are 5 BMR weight changes included. Actual intake of leatherjackets has been entered, based on continuous watch kept from the observation tower. The discrepancy between required and observed intake can be explained by intake of *Cerapteryx* caterpillars from the saltmarsh (note the close agreement between the number of caterpillars that could be caught in the time available, computation details in text, with the energy debt requiring explanation).

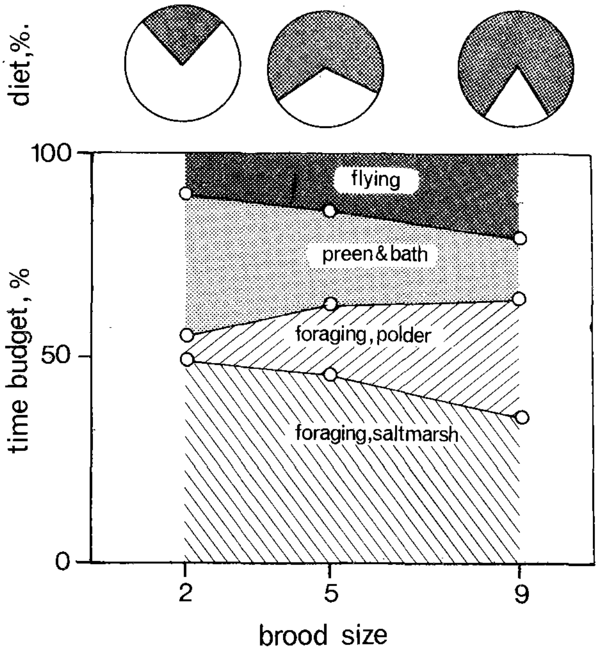


Fig. 22. How female 39 apportions her time between different activities when brood size is changed. It can be seen that foraging in the polder and flying increase at the cost of preening and bathing and foraging in the saltmarsh. As a consequence, percentage of Leatherjackets (by weight) in the diet of the parents and young increases with brood size, as shown in the pie diagram at top (stippled = proportion by weight of Leatherjackets in the diet).

(Drent & Daan 1980). Since female body weight at the end of the day is relatively constant, this indicates that with large broods the female's consumption is postponed until she forages for Leatherjackets.

The decrease of caterpillars in the female's diet resulting from increasing the pressure of nestling demand by enlarging the brood experimentally can of course be supported, albeit on a relative scale only, by restricting the argument to time-budget data and not speculating about energetics. We could not, however, resist including these speculations to emphasize the need for information on individual energy budgets in future studies on foraging behaviour.

The female is thus able to adapt her foraging to the demands of the nest in two ways. Firstly, in the transition from brood size 2 to 5 she increases the time spent foraging and the time spent flying, at the cost of the time spent preening (Table 8). This extra foraging time is spent in the polder. The total number of Leatherjackets caught increases correspondingly (Fig. 22). The transition from 5 to 9 nestlings shows hardly any increase in foraging time, but flying again increases at the expense of preening (Table 8). The female spends less time searching for caterpillars. The time so gained is devoted to Leatherjackets instead, and since time freed from one caterpillar will yield seven Leatherjackets of comparable weight, this tactic increases the amount of food delivered per unit time. Since the female is already utilizing the full daylight period when tending the brood of five, the replacement of caterpillars by the less time consuming Leatherjackets is the only avenue open if the female is to bring more food.

Secondly, she changes the destination of the caterpillars caught. Since she brings half as many caterpillars to a brood of two as compared to a brood of five, individual young in a brood of five get fewer caterpillars. Our time-budget extrapolation given above indicates that the caterpillar consumption of the female herself is still more sharply curtailed. Comparable trends exist between brood sizes 5 and 9. Apparently there is a premium on maintaining caterpillars in the diet of the nestlings, a problem we shall examine in the next section.

4.1.4. Effects of diet on the survival of the young

The question why the parents do not feed their young only with the most profitable prey (Leatherjackets) still has to be answered. One possibility is Kluyver's (1933) discovery of the effect of diet composition on the state of the young. He found that in some years a considerable number of nests were fouled by the nestlings and not sufficiently cleaned by the parents. Normally the

Table 8. Time-budget of Starling ♀ 39 in relation to brood-size (hr per 24 hr and %, see text for behaviour categories)

	foraging	preen etc.	flying	night
2 young	9.57 hr (39.9%)	5.87 hr (24.5%)	1.56 hr (6.5%)	7 hr (29%)
5 young	10.71 hr (44.6%)	3.77 hr (15.7%)	2.51 hr (10.5%)	7 hr (29%)
9 young	10.81 hr (45.0%)	2.70 hr (11.3%)	3.48 hr (14.5%)	7 hr (29%)

parents take the faeces away from the nest. When the nestlings are still small the parents wait after each feeding until a young defecates, and if it does so they remove the pellet. When the young are older they defecate on the rim of the nest, from where it is removed by the parent. Later his Starlings tended to defecate directly through the nesthole, leaving a white patch of faeces just in front of the nestbox.

The faecal pellet has to be quite compact in the first phase of the nestling period to enable the parents to pick it up. It then has a mucous sac around it, enabling it to be easily taken up whole.

In the years that fouled nests occurred Kluyver noticed that the faeces of these nestlings were exceptionally watery, making it impossible for the parents to clean out without also removing nest material. The young often end up sitting on the bottom of the nestbox in their own faeces. They became very wet and sometimes had clumps of faeces around their legs and feathers. Such birds must suffer a great heat loss and eventually their chance of survival would be low. Since Kluyver was a bird lover he made a fresh and higher nest enabling the young to defecate out of the nest opening hence preventing fouling. He claimed that these young survived the nestling period as well as the normal broods.

Kluyver found that there was a correlation between the percentage (in number) of Leatherjackets fed to the young and the chance of fouling (Fig. 23). To verify this he fed young different diets. The diet containing a high percentage of Leatherjackets caused the faeces to become very wet and loose. His conclusion was that if the nestlings get too many Leatherjackets the faeces become wet and the parents are not able to clean the nest. Eventually this can result in the young becoming fouled and finally dying. There is thus a clear negative effect of feeding too many Leatherjackets to the young, particularly with certain types of nests, implying that the preference for caterpillars in the Schiermonnikoog situation can have survival value.

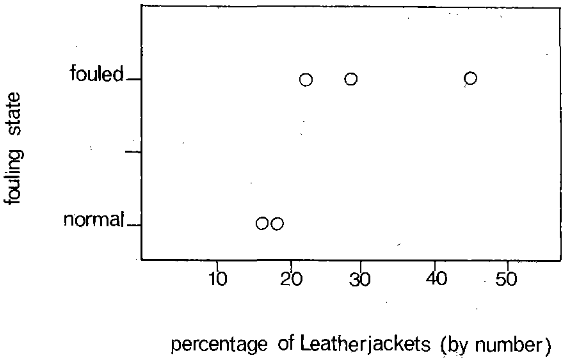


Fig. 23. Influence of nestling diet (numerical per cent of Leatherjackets in the total prey brought as determined from neck-collar samples on nest fouling. Each point represents one nestbox observed by Kluyver in 1931 (1933: 72).

To answer the question whether young can live on a diet of caterpillars alone we put up some nestboxes in the saltmarsh, two kilometers away from the polder. These birds lived in the middle of the caterpillar area. We recorded the feedings in one nest for 6 days with an automatic camera. The young were 10—15 days of age. It turned out that these young were fed 96% (by weight) caterpillars of which 94.4% was *Cerapteryx graminis*. Growth was good and no fouling of the nest occurred. Thus the young can survive on caterpillars alone.

Westerterp (in press) did a study following up the work of Kluyver. His primary interest was to quantify the parents reaction to different brood size. He observed the food type brought to the young and found that a brood of seven (normal brood size five) received a much higher proportion of Leatherjackets than a brood of three and were also more fouled. Despite the fact that this brood of seven received more Joules per nestling, mortality was considerable and replacement of young was necessary to maintain brood size. Oxygen consumption also turned out to be much higher for fouled young than for normal young of the same age. This is to be expected since the insulation provided by the feathers must be greatly reduced by fouling.

What causes the faeces to become wet is not clear. Westerterp's suggestion is that since Leatherjackets contain more water than caterpillars this might be the sole factor causing fouling of the nest. Another possibility is that a diet of Leatherjackets alone is not balanced and may affect water resorption. The fact that the parents also prefer saltmarsh food, suggests that fouling is not the only effect of a high percentage of Leatherjackets in the diet. However, we cannot be conclusive on this point and further work should be done to find the physiological basis for this preference.

For the moment we can only conclude that there is a negative effect of too high a percentage of Leatherjackets in the diet. This means that parent Starlings should avoid overly increasing the amount of Leatherjackets in the diet.

4.1.5. Discussion

It is clear that caloric maximization alone does not explain the prey choice in Starlings. Instead there is a preference for *Cerapteryx graminis* caterpillars which might be due to the fact that Leatherjackets alone cause fouling. However, mixed with caterpillars they can feed the young very well.

Royama's (1970) ideas that nestlings do not need a varied diet is wrong in the Starling situation. It is not known what the important difference between the prey species actually is. The need for analysis of this type of problem should have a high priority in the current work in foraging. As shown here it will be very hard to predict prey choice without this knowledge.

In the experiment with hungry young the parents reacted instantly by delivering more Leatherjackets for some period, even up to a higher percentage than is possibly good for them in the long run. This suggests that when parents switch prey they are switching their foraging goal. Presumably, in terms of fitness loss, the cost of being fed too few calories for some period is higher than the cost of being fed poor quality for the same period. If this is true a parent with hungry young should decide to maximize caloric intake over time and a parent with well fed young should decide to maximize "quality". This fits the data very well: with too large a brood size the parents will feed the young too many Leatherjackets, up to the point where the weakest dies. This causes the demands of the nest to decrease, allowing the parents to again increase the quality of the food.

We have already answered the question why caterpillars are taken despite their low delivery rate. Now that we determined hunger as a governing factor in prey choice we can explain the daily variations in delivery rates of Leatherjackets and caterpillars (see section 3.6) readily in terms of daily variations in hunger of the young.

When the foraging situation fluctuates, a similar mechanism might work. In bad times parents concentrate on quantity enabling the young to survive that period. When the foraging situation improves parents can concentrate on food quality again. This mechnism could be one of the reasons why insectivorous birds seldom seem to have any "spare time". As soon as the foraging situation becomes easier the birds are more selective for quality, with the result that they still spend their day mainly foraging.

4.2. DECISION WHERE TO LAND

In deciding which prey species to take a Starling also choses its foraging habitat: polder or saltmarsh. The next decision it has to make is where to land within that habitat type. Because of the spatial segregation of the different prey species, in most cases we can rule out the possibility that site choice within a habitat type is further governed by search for specific prey. In the polder situation around 90% (by weight) of the prey collected were Leatherjackets.

I have detailed data on site choice in the polder situation and therefore our discussion in this section will concentrate on this habitat. The question is, whether we can explain the site choice of Starlings in terms of caloric maximization alone. After suggesting which factors are likely to effect the decision on landing sites we will give a detailed description of the pattern of prey distribution and predator search, and analyse their relationship. Finally we will concentrate on some causal factors that are important by using experimental and field data.

To try and find an explanation for the pattern of landing sites we measured different properties of the study area. The methods have been largely described by Tinbergen (1976). Basically, the study area was divided into twelve 20 × 20 meter plots. For each plot we measured yearly the number of landings, prey density, grass length, moisture content and distance from the colony.

A multiple regression was performed on the data to correlate the number of landings per plot in relation to the factors: prey density, grass length, moisture content and distance from the colony for each year. The method assumes that the relationships are linear, the data normally distributed and the plots homogeneous. Since it later became apparent that the first and last assumptions are not valid we have to interpret the outcome of this method with great care. However, it does give an indication of possible important factors.

The results are given as a percentage of the total variance explained (R^2) by adding the variable involved to the equation (Table 9). In all years distance from the colony explains a considerable amount of the variation. Prey density is important in 1978 and 1979. Fluctuations in grass length and moisture content seem to be negligible, at least, within the range observed on our study area.

Table 9. Multiple regression analysis showing relation between frequency of landings per 400 m^2 plot and four variables (R^2 = amount of variation "explained" by including variable concerned in the analysis in the sequence from top to bottom, i.e. prey density alone, prey density plus distance from colony, etc.)

	1976	1977	1978	1979
prey density	+ 0.01	+ 0.00	+ 0.13	+ 0.32
distance from colony	— 0.19	— 0.62	— 0.45	— 0.08
grass length	—	+ 0.01	+ 0.00	+ 0.05
moisture content	+ 0.08	+ 0.01	—	+ 0.00

In the following I shall emphasize the effect of prey density on foraging decisions. Effects of the distance from the colony are only briefly touched upon.

4.2.1. Pattern of prey distribution

Prey density is obviously one of the major factors controlling intake rate of the Starlings. Local differences in prey distribution should therefore be relevant to a maximizing Starling. I shall thus first describe prey distribution, and then compare this with the Starling's pattern of search.

Methods

Since sampling techniques are labour intensive we only measured density and distribution of prey on the study area, where data on Starling visits were also collected. Each year we selected twelve 20 × 20 meter plots in one block of 60 × 80 meters for sampling.

Leatherjackets, the larvae of *Tipula paludosa* M. are the major prey in the study area. To sample them we used a soil corer with a surface area of 178.6 cm^2. After a sample was taken it was cut off to the standard depth of 5 cm, put into a plastic bag and taken into the laboratory where it was placed upside down in a Tullgren-funnel. After drying a week under a carbon filament lamp the samples were completely dry. By then the Leatherjackets had left the sample via the funnel and ended up in a collecting tube filled with alcohol. The number and length of the Leatherjackets was noted per sample. Samples were weighed before and after drying in order to estimate the moisture content of the soil. Generally, about a 100 samples a week could be processed.

Eight samples per plot (20 × 20) were taken per sampling day. Since the sampling method does not work so well when the grubs are older, they were all taken in May. We sampled two or three times each year. A regular grid pattern was used in taking samples which was changed each week in order to get even spacing over the area. The position of samples was carefully recorded in order to reconstruct the basic pattern of the prey distribution over the plot.

The average densities of Leatherjackets for the study area in four successive years are shown in Table 10. They vary considerably from year to year, ranging from 9 to 69 Leatherjackets per square meter, indicating that the food situation varies between years for Starlings. The standard deviations from the mean number of Leatherjackets are always larger than the mean, indicating that they are not randomly spaced, but occur more often in some sites than others.

For our problem it is very important to describe the exact distribution of Leatherjackets. Therefore we will look in more detail at the data for 1979, where density was so high that sampling problems were minimal.

One glance at Fig. 24 shows that there are areas with high prey densities. In other words prey in the study area is not distributed homogeneously on a large scale. Distinct boundaries, however, do not show up in the density picture.

Table 10. Leatherjacket sampling data for intensive study area for early (I), mid (II) and late (III) May in four consecutive years, expressed per core sample of 179 cm² area, and summarized per year as density of prey per m² area

	period	May I	II	III	I+II+III	Density per square meter
1976	$\bar{x}$ (number/sample)	0.73	0.26	0.15	0.39	
	SD	1.33	0.64	0.35	0.91	20.6
	n	96	96	96	288	
1977	$\bar{x}$ (number/sample)	0.17	0.11	0.17	0.17	
	SD	0.46	0.31	0.37	0.43	9.5
	n	92	94	84	270	
1978	$\bar{x}$ (number/sample)		0.79	0.49	0.65	
	SD		1.24	1.08	1.17	36.2
	n		94	96	190	
1979	$\bar{x}$ (number/sample)	1.51	1.22	0.69	1.24	
	SD	2.29	1.86	1.28	1.88	69.4
	n	94	96	94	284	

To get an impression of prey distribution on a fine scale, a strip 12 m long and 10 cm wide was sampled in an area used intensively by the Starlings. In these samples the exact positions of the Leatherjackets were measured by carefully dissecting the sod. To illustrate the distribution on this scale, a dispersion index was computed for different plot sizes within this strip (Southwood 1978; p.39). Table 11 shows that Leatherjacket distribution is significantly clumped independent of plot size.

Since prey distribution is clumped on all scales I conclude that the Starling will encounter gradients in the prey distribution rather than distinct boundaries.

Table 11. Degree of clumping in the distribution of Leatherjackets depending on size of plot sampled (see text for methods) I_D = dispersion index

plot size	N	$\bar{x}$	S^2	I_D	p
5 × 5	480	0.6	0.7	575	< 0.01
10 × 10	120	2.4	3.2	160	< 0.01
10 × 25	48	6	9.2	72	< 0.05
10 × 100	12	24	55	25	< 0.01
10 × 200	6	48	193	20	< 0.01

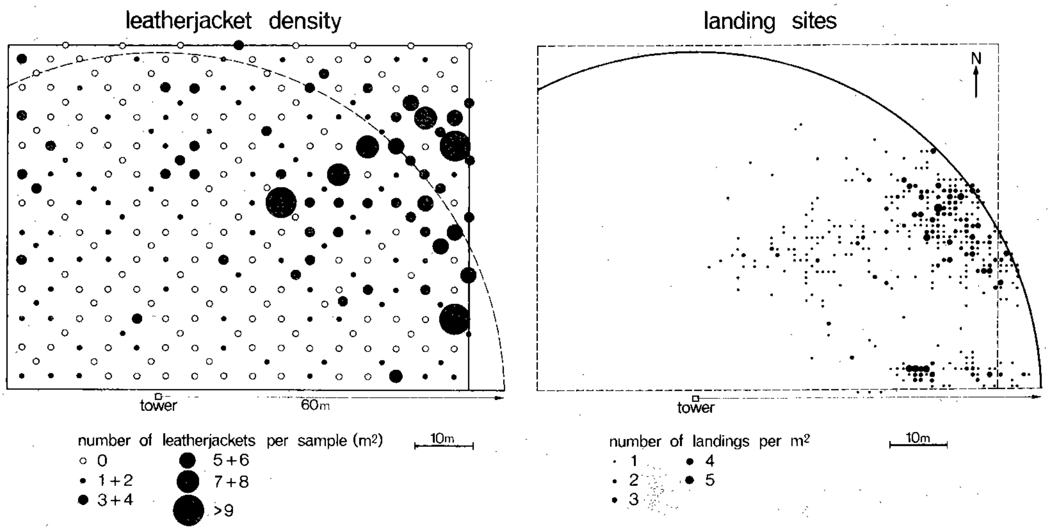


Fig. 24. Comparison of Leatherjacket density and landing sites of female 39 on the intensive study plot. Leatherjacket distribution in the 1979 season (based on 284 core samples) in the area covered by the sweep of the rangefinder is indicated. Right: distribution of her landing sites over a seven day period in that season.

4.2.2. Pattern of landing sites

From the observations of the landing sites of individual Starlings in the polder the following general picture emerges. Starlings visit different fields in the period that they have young, but have never been observed foraging in fields more than 800 m from the colony. Only fields that have been mowed or grazed can be utilized by them in this period of vigorous growth. The pattern of visits is therefore dependent upon where the farmers mow or graze their cattle (see also Tinbergen and Drent 1980). However, there was always a period in the year, when the study plot was used most by the Starlings, since grazing started here before the other fields were mowed. Consequently, this is where we have the most detailed data. Since the scale on which Starlings utilize the area might be very fine grained I shall present the most detailed data we have, that of female 39 in 1979. That year we also had an optical rangefinder available which enabled us to measure very accurately the position of a foraging Starling (± 50 cm) up to a range of 60 m. This contrasts with earlier seasons, where 20 × 20 m were the smallest units.

The rangefinder (Zeiss Jena) works on a triangulation principle (Fig. 25). The bird is seen as a "split image" through a 15 × telescope. To measure the direction of the bird the observer has to keep it on the mark in the center of the view finder. To measure the distance the two images have to be brought in line. A distinct advantage of this instrument is that the exact position of the bird can then be directly plotted on a map by means of a mechanical plotting device.

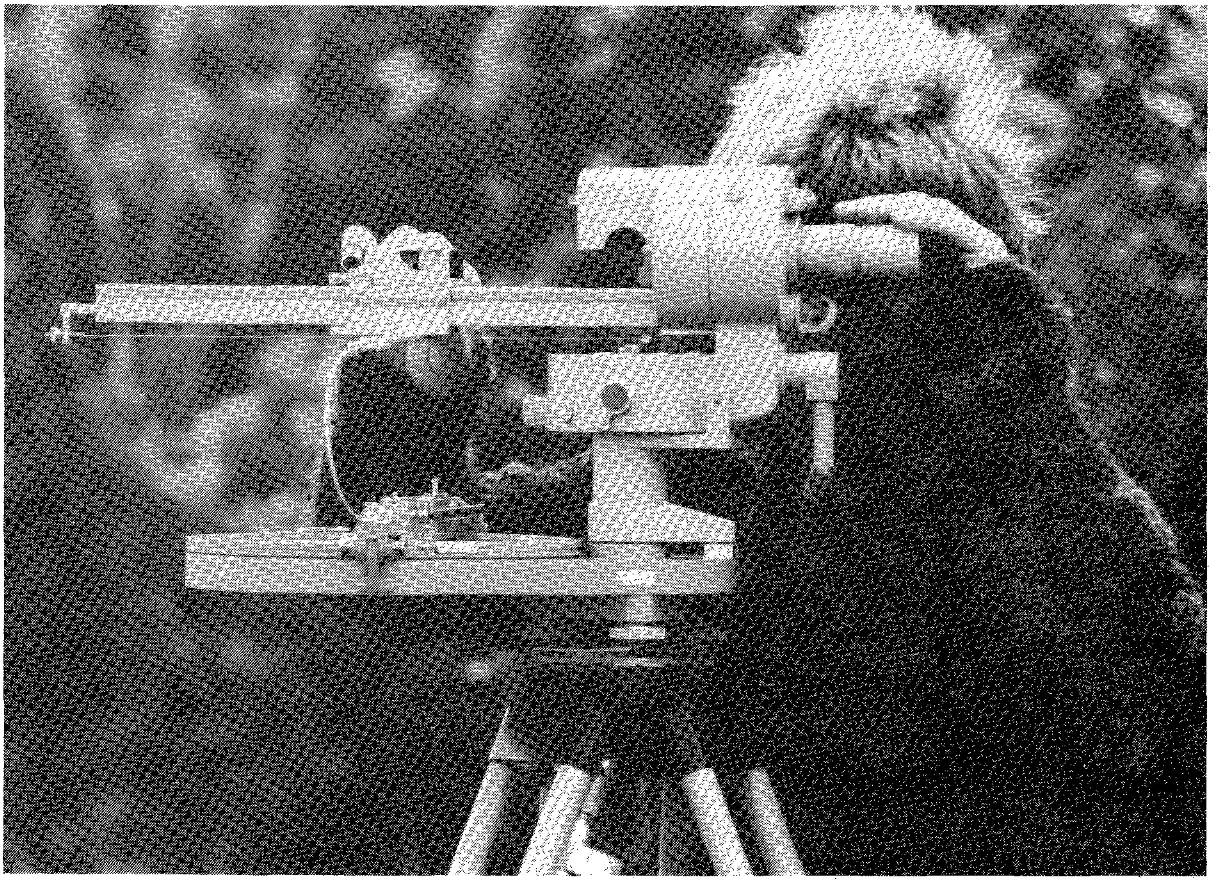


Fig. 25. Optical rangefinder in use for tracking a foraging Starling: the observer brings two images in line by adjusting the movable prism on the side-arm, and the position so obtained is plotted automatically on the circular chart immediately below the arm (sample record in Fig. 27).

The bird's position could be recorded every ten seconds and a second observer marked the order of the plotted points.

Data were collected during one week. In this period 968 visits were made to sites in the polder area, of which 678 were within the range of the rangefinder (488 were actually recorded).

The general picture of the female exploiting this area is that she made many short visits ($\bar{x}$ = 60.2 sec, SD = 44.0 sec, n = 449) either successively or alternated with visits to the saltmarsh. On all days, particularly in the first few days of nestling life, she spent some time in the nestbox, presumably warming the young and cleaning the nest.

Data on the spatial distribution of the landing sites and the search effort (all plotted points) were pooled for the week. Fig. 24 shows that the distribution of landing sites per square meter is strongly aggregated (normal deviate = 19.27, $p<0.001$, Southwood 1978 p.39). The landing sites of the female delineate the good Leatherjacket areas more clearly than the data on Leatherjacket distribution. The bird concentrated its landings on some areas and seemed to avoid others.

To describe the spatial pattern of these landing sites more formally an analysis was done to describe the scale on which landing sites are aggregated by determining the relation between dispersion index and sample area. We use Morisita's (1959, in Hairston et al. 1971) index of dispersion since it is relatively independent of type of distribution, the number of samples and the size of the mean. The higher the index the more aggregated the landing sites (Id = 1, random; Id > 1, aggregated; Id < 1, uniform). The data show that even with a sample size of one square meter (close to the precision of measurement) maximal aggregation is not yet achieved. This indicates that aggregation of Starling landing sites is on an even smaller scale (Fig. 26).

A second interesting effect can be seen. Although the general trend of the graph is that dispersion indices decrease with increasing plot size, there might be a pattern in the way this happens. The steep decrease for the small plot size is followed by a slower decrease for sizes between 36 and 100 m². With larger plot sizes the steeper decrease again appears. This suggests two levels of aggregation in the landing sites, one smaller than a square meter, the other between 36 and 100 square meters.

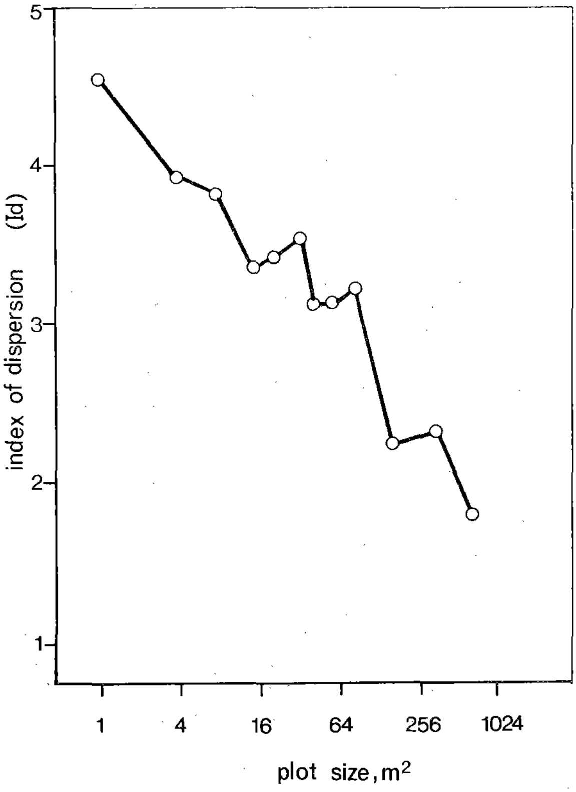


Fig. 26. Degree of clumping of landing sites as measured by Morisita's index of dispersion (Id), in relation to the area examined (plot size in m², note the logarithmic scale).

Splitting up the landing site data into daily totals gives the picture shown in Fig. 27. Comparing the figures between days shows that roughly the same areas are used every day, except for the 29th of May. This day was exceptional in that it was very rainy, and therefore not directly comparable. When we compare the other days in detail we see that minor changes do occur. Slight shifts in our female's major area of attention, point to some sort of systematic search. Another indication for systematic shifts occurring in the landing site pattern is that the daily aggregation is higher than the weekly aggregation. Taking the results together, the Starling shows a pattern of landing sites that is highly aggregated in space. The area is used with an a-

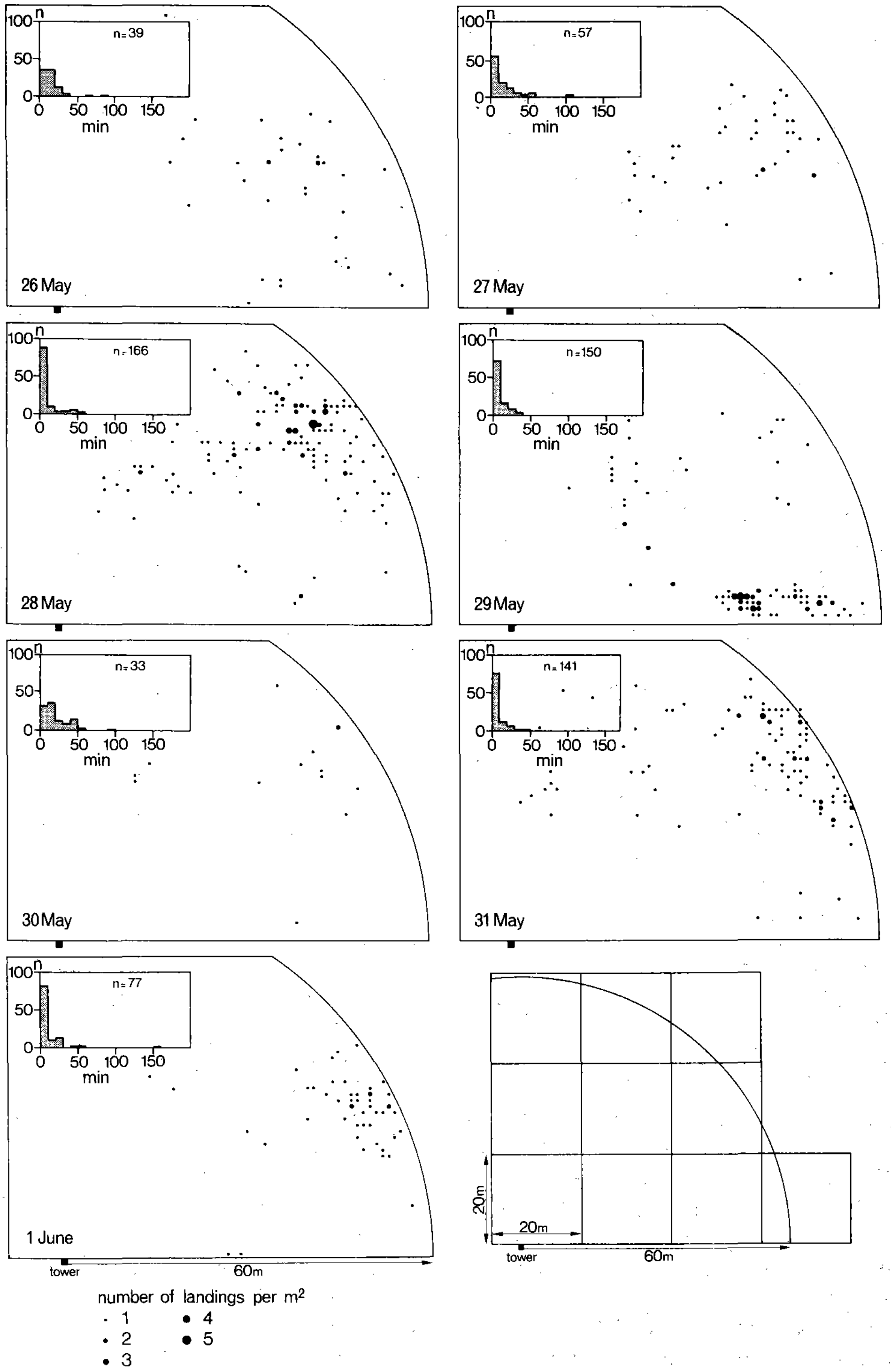


Fig. 27. Record of landing sites of female 39 on seven consecutive dates in 1979. Insets show frequency histograms of time intervals between visits (time scale in minutes). All visits fell within the area depicted at lower right, the majority within the sweep of the rangefinder.

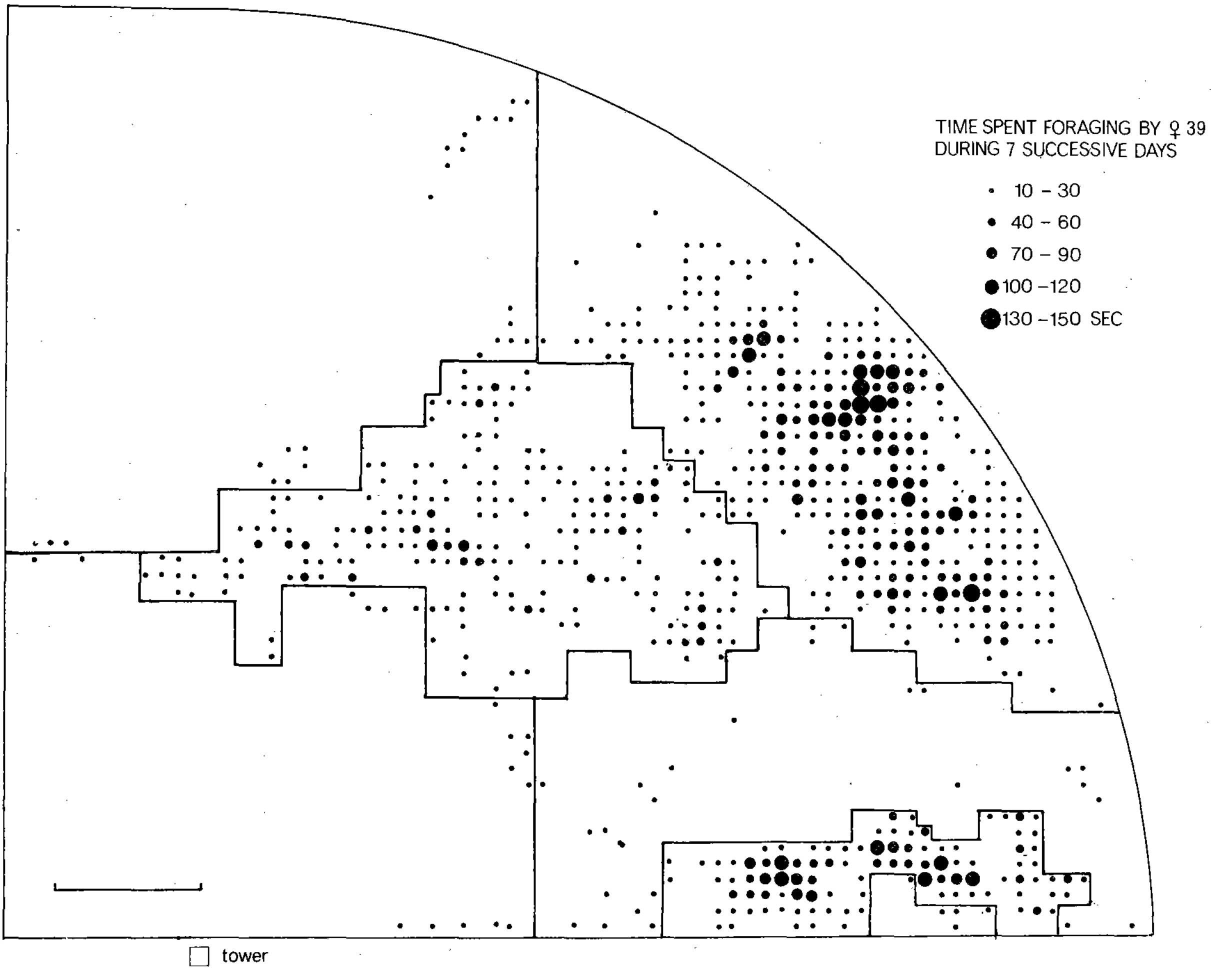


Fig. 28. Delineation of exploitation centres as revealed by summation of search patch measurements of female 39 over seven dates in 1979 (search seconds per m^2). The area remaining, after the three centres were recognized, has been divided arbitrarily into marginal zones (areas least visited, see text).

mazing precision, possibly on different scales. The fine scale on which foraging takes place stresses the importance of having detailed data on search path, to unravel the factors governing foraging decisions. For instance, the use of only 20 × 20 m plots in the analysis cannot solve the problem.

To evaluate the correspondence between prey density and female's landing sites, as shown in Fig. 24, we have to chose an arbitrary unit to compare the two. On basis of the distribution of the search effort we selected three unbroken areas of high search effort. The rest of the observation area was divided into areas of roughly the same size (Fig. 28). In Fig. 29 we plotted the number of visits per square meter against the average density of Leatherjackets in these areas.

The positive relationship found suggests a threshold density at approximately 70 Leatherjackets per square meter. Below this level, hardly any exploitation occurs. The female thus strongly concentrates her search effort on high density areas. One of the possible cues for the foraging Starling could be the intake rate. Therefore, the average intake rates for different areas are given in the same figure. A clear relation between prey density and intake rate indeed exists, thus it is not unlikely that intake rate is a potential cue for the birds in allocating search time.

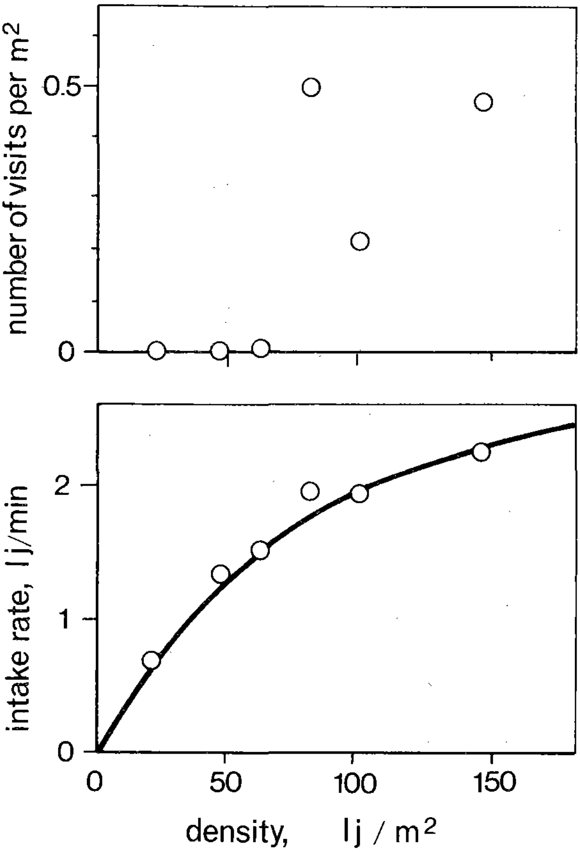


Fig. 29. Data summary for female 39 feeding on Leatherjacket. Visitation rate (top panel) and mean intake rates (lower panel) are shown for each of the units distinguished in the search effort map (Fig. 28) of this individual.

In conclusion, we can say that there is a close correspondence between prey density and the site on which a Starling decides to land. This confirms the hypothesis of caloric maximization within one prey species. Since intake rate correlates well with prey distribution it could provide a possible cue for the Starling. To pursue the effect of intake rate on foraging decisions we have to analyse the behavioural data we have in more detail. The aim will be to say more about the mechanism involved.

4.2.3. Intake rate as a causal factor

To understand how such a relationship between prey density and landing sites develops we have to look in more detail at the behaviour of the birds. The way we approached this was to determine experimentally whether intake rate is a causal factor in site choice and than examine the correlations between site choice and intake rate to explain the pattern observed. This enables us to say something more about how Starlings use the information they gather on distribution of the prey species.

Optimal foraging theory is based upon a few parameters only. Of these intake rate is a central one and presumed to be maximized as a foraging goal. This implies that the bird should be able to measure either intake rate or some related parameter directly or, indirectly via some habitat character related to intake. Since this last possibility is far from hypothetical in the field situation, we designed an experiment to test the causality between intake and probability of a visit. If wild Starlings can measure intake rate and use this to make decisions, we would expect that the probability of their visiting an area would increase with increasing intake rate. There are some predictions in the literature about the form this curve should follow. Royama (1970) expected the function to be increasing but did not specify the form. Krebs (1978) expected a sudden switch from little attention to all attention at the decision point. In data taken from Herrnstein (1975) and in his own data he found that this was only so when the birds had time to find out about the different intake rates in different places. Thus time is necessary to measure intake rate (sampling). Field experiments, where food density was increased (Tinbergen 1976), have shown that a causal relationship exists. In the experiment, a feeding table as described on p.28 was set up 10 m from a nestbox so that the table could be seen from our observation point. One free-living male with nestlings was trained to visit the table as described previously. Intake rate could be manipulated from the observation point. After a training period of 5 days we started to vary intake rate and measured the total number of feeding trips our male made and the proportion of these spent on the table. The prediction was that if the bird could measure intake rate and used it in allocating its visits, the proportion of the visits made to the table would be positively related to the intake rate. The intake rate was changed every three hours, but within this period was kept as constant as possible. Experiments were done for 7 successive days. In total 12 different intake rates were offered, approximately straddling average intake rate in the Leatherjacket grid.

The results give a clear positive relationship between the number of visits to the table and the intake rate offered there. No stepwise change in preference could be detected, but the duration of the test could have affected this (Fig. 30).

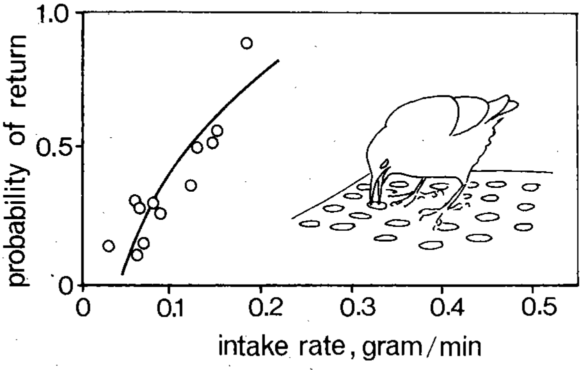


Fig. 30. Response of male GH3 to variation in reward rate of mealworms offered at a feeding table stationed near the nestbox. Each point represents a test of around 3 hours at a given reward rate, held constant by the observer for that period. Results have been expressed as probability of returning to the table within the test period.

In concluding, we may say that Starlings can use intake rate in deciding where to land. In the following section we will see what role this ability plays in their allocation of time over the foraging area.

4.2.4. Short term effects of intake rate

As described previously, in 1979 we collected data on the search path and intake rate of an individual Starling, female 39. Her average intake rate per visit showed considerable variation (Fig. 31). This variation originates mainly from the prey distribution relative to the search path of the bird, and thus contains information on the prey distribution over the area searched through.

Since we have shown that Starlings can estimate intake rate for a certain site we would predict that the decision where to land would be dependent on this estimate. More specifically, we would predict that the intake rate of any visit would be negatively correlated with the landing distance. The landing distance is defined as the distance between the site of take off on visit n and the site of landing on visit n + 1.

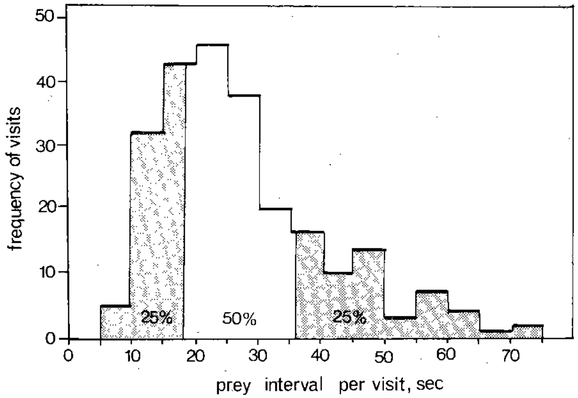


Fig. 31. Frequency distribution of Leatherjackets intake rates of female 39 within the sweep of rangefinder on seven consecutive days in 1979. This summation allows classification of visits as belonging to the upper 25%, central 50%, or lower 25%, as far as intake rate is concerned.

To answer this question we analysed the landing distances for successive visits. We plotted a frequency distribution of these landing distances for two different cases: when the preceding visit had a high intake rate (> 3.15Lj/min and when the preceding visit had a low intake rate (< 1.88Lj/min).

The frequency distribution of landing distances following a high intake rate differs significantly form those following a low intake rate (Fig. 32). Landings within five meters of the preceding visit occur significantly more frequently following a high intake rate, (chi-square 9.46, d.f. = 1 $p < 0.01$), and landings beyond 20 m occur less frequently. The first effect is even more pronounced when we concentrate only on the first five meters with a meter scale (Fig. 33).

If intake rate was high the female concentrates around the same spot, and is reluctant to go far away (> 20 m). If intake rate was low, this area (∅ 4.5 m) is avoided on the next visit and the chance of leaving the area altogether (> 20 m) is much higher. These data mean that Starlings can remember sites on the foraging area with extremely high precision after only one visit, within a meter, i.e. the precision of the data. This amazing ability must be an important weapon in optimizing search effort relative to prey distribution.

Starlings can build up a map of intake rates of a foraging area at least over a short period, and use this for exploitation of the Leatherjackets. If this behaviour is adaptive we would expect a relatively high intake rate in the visit following a visit with a high intake rate. Fig. 34 gives a plot of the average intake in following visits against landing distance from preceding visits. When the bird lands within one meter there is a clear effect, intake rate is higher than in the other two categories. This fits in with the earlier result that aggregation of landing sites is on a scale of 1 m or smaller!

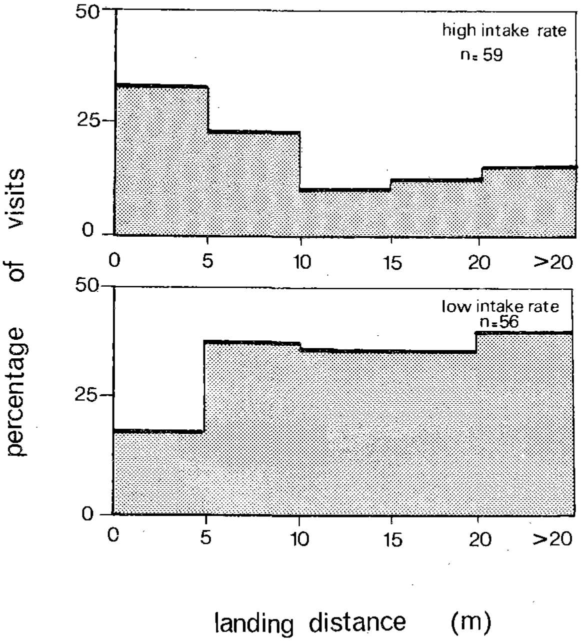


Fig. 32. Tendency to land close to the previous take-off site depending on whether a high (upper panel) or low (bottom panel) intake rate had been experienced there (for definition of high and low see fig. 31). Data for the nearest five meters in more detail in fig. 33.

Does the ability of the female to use this detailed information decay over time? Since Starlings alternate visits to the polder area with visits to the saltmarsh, and the latter take a long time, we are in the position to say something about the effect of time away on subsequent decisions on landing site. To evaluate this point we compared the frequency distributions of the landing distances for visits preceded by polder visits with

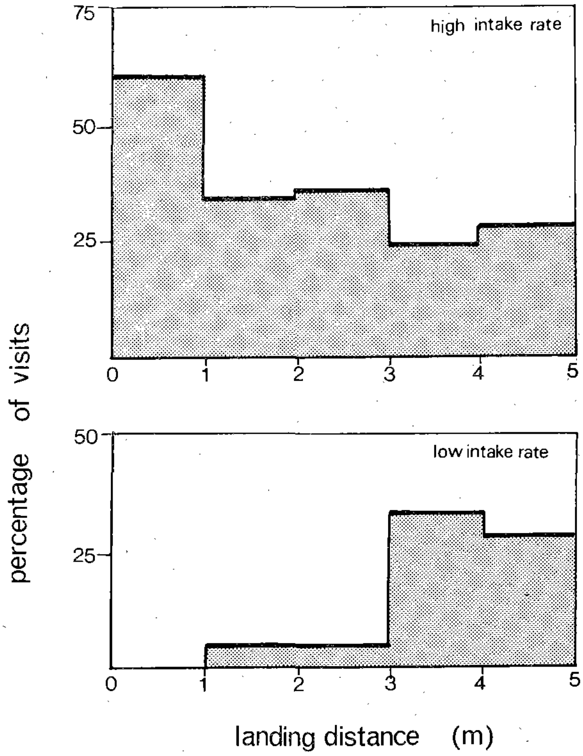


Fig. 33. Further detail on tendency to land close to previous take-off site depending on intake experienced there (dissection of nearest five meters, see Fig. 32, and Fig. 31 for distinction of "high" and "low" intake rates).

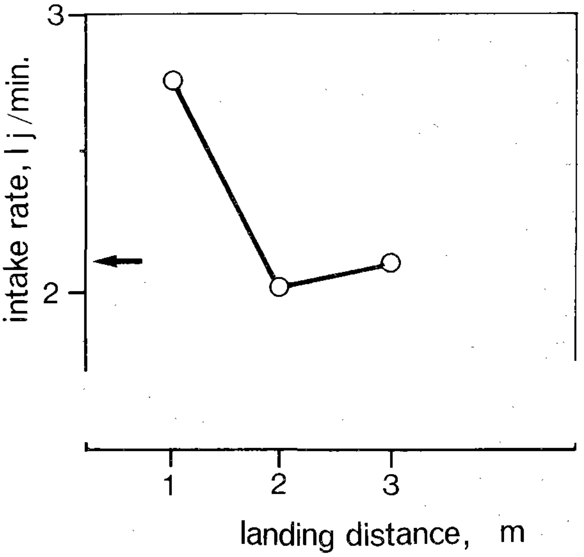


Fig. 34. Intake rate (Leatherjackets caught per minute) experienced during a follow-up visit in relation to the distance from previous take-off point. Data concern visits following a *high intake* visit. Mean level of intake for the general area shown by arrow.

those interrupted by a single saltmarsh visit.

There is a significant difference (Fig. 35a, b) between the two (Kolmogorov-Smirnov, $p < 0.001$). Shifts over distances of more than 20 meters occur much more frequently and shifts over short ranges less frequently after a saltmarsh visit. This effect can not be explained by differences in intake rates in the preceding polder visits.

This difference in site choice could be adaptive to short term changes in prey availability, which would cause the information to quickly become out of date. If this were the case we would expect the change in distribution of landing sites to be a function of the time that the bird is away. Therefore, we selected a new category of pairs of visits where inter-visit time to the nestbox was roughly as long as a saltmarsh visit. In these cases, time away from the Leatherjacket area was equal. The results show (Fig. 35c) that the birds seem to use more information after returning from the nestbox, although the sample size is small. Thus the bird probably does not react to short term change in availability of the prey. It is not clear what the causal factor for this effect could be. Since a visit to the saltmarsh generally takes place only when the young are relatively satiated, the subsequent transition to Leatherjacket hunting may trigger a different hunting tactic. For instance, when hunger of the young is low parents might more readily sample unknown areas to gather information, thus causing a shift in landing distances. Experiments have been planned to pursue this possibility.

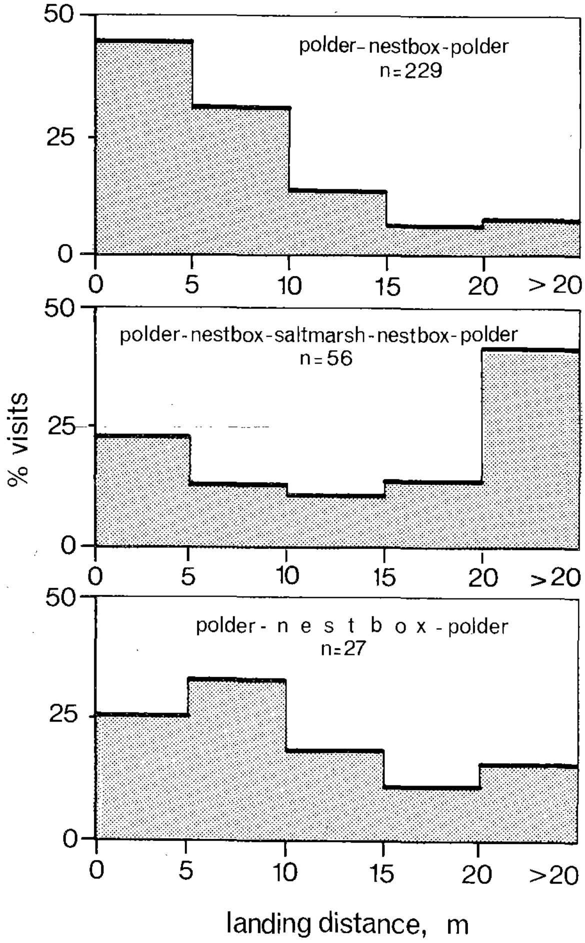


Fig. 35. Tendency of female 39 to land close to previous landing site in the polder, depending on whether (top) a short nest box visit intervenes, (centre) a saltmarsh visit intervenes or (bottom) a brooding bout in the nestbox, which is as long as a saltmarsh visit intervenes.

DISCUSSION

The effects described in this last chapter are very short term. What is the information the Starling used over a longer term? Part of the answer to this question lies in the distribution of the landing sites we found. It is striking that some areas are almost never visited by the Starlings. Because visits in these areas are so sparse it appears as if they generalise low intake rates to a large area. This generalization could be based on vegetation type since small differences in vegetation do occur. Moreover, the mere position of such poor areas could also be important. It is known from prey sampling that Leatherjacket areas which are good in some years are intermediate or poor in others.

This is an argument against the use of only vegetation although this could be associated with information on intake rates by learning within years. Although the role of the vegetation has not been studied in great detail, I want to stress that vegetation type alone cannot be sufficient as a cue.

How birds generalize is a point of importance. Work is planned in a restricted laboratory situation to evaluate this point. Possibly the different levels of aggregation of landing sites we suggested earlier, relates to this. The smallest scale (below 1 square meter) is most likely to be caused by short term learning via intake rates. The larger scale possibly has more to do with generalization on vegetation type. In general we can conclude that decisions on landing sites are affected by intake rate and, probably in a more generalized way, by vegetation type.

An important point is that average Leatherjacket density differs between years. Do the decisions of individual Starlings adapt to these differences or do Starlings use a fixed decision point? This is the subject of the next section.

4.2.5. The effect of the average prey density

Foraging environments fluctuate considerably from year to year. The question is whether Starlings adapt their foraging decisions to these different situations. As the data on exploitation of the foraging area point to a threshold density below which no exploitation occurs, we use a model where a Starling decides to come back to an area only if its intake rate is above a particular threshold.

Now imagine that we have a single prey system with different average densities each year. Predictions for the response to prey density each year can then be based on the mechanism by which the threshold is arrived at. Three alternative mechanisms might exist.

a) Site choice is not affected by intake rate. This possibility can be ruled out since we have already shown an effect exists.

b) Site choice depends on a *fixed* threshold, which does not vary between years. If intake is below the threshold the probability of a visit is 0. There is no discrimination between the sites above the threshold.

c) The threshold is tuned to the average yearly density or some related parameter. With this *adjustable* threshold, exploitation can be limited to the best areas only.

Since we collected data in different years with different prey densities we can test these predictions with our data. Fig. 36 gives the percentage of visits as a function of the intake rate per 20 x 20 meter plot for the different years. For two years, direct data on the number of visits and the intake rate of an individual bird were known (1978 and

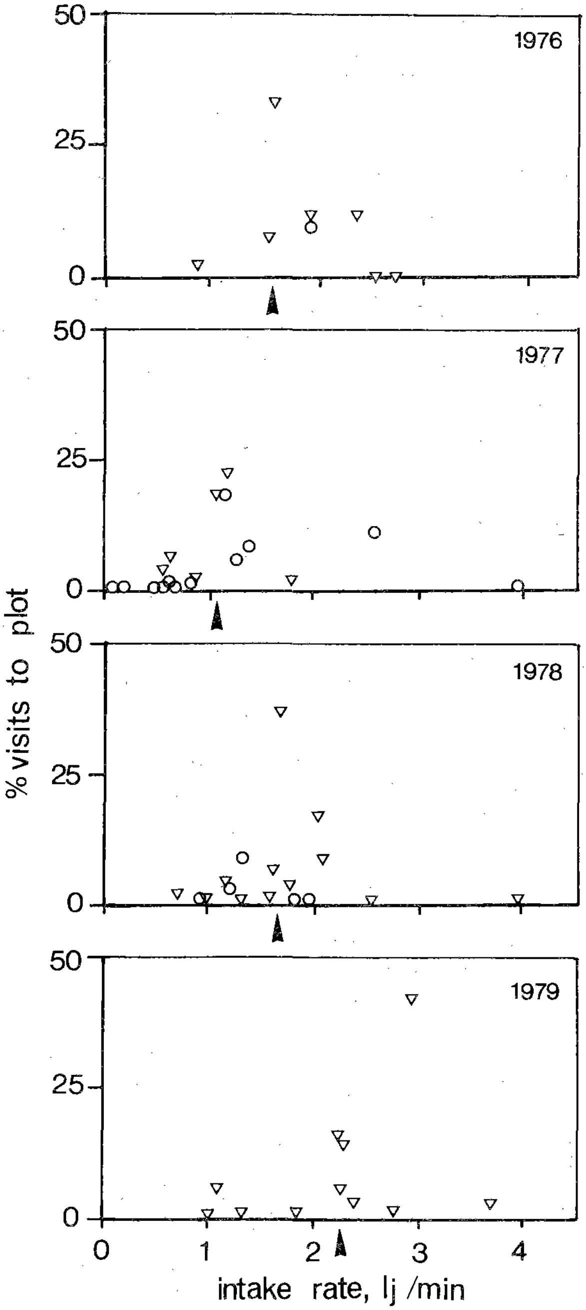


Fig. 36. Visitation in relation to intake rate: data for a different individual in each of four seasons, each point representing data for a 20 x 20 m grid plot (triangles denote plots where Leatherjacket density was also measured by core samples, circles are plots with unknown density). For each season a rejection threshold level is shown by the arrow (see text for derivation).

1979). For 1976, the number of visits of one individual were known but, to obtain enough data on intake rates, I had to include values measured from other individuals using the same plot. For 1977, the intake rate could only be estimated by using the data from photographs. The number of Leatherjackets brought to the young per time of absence gives a minimum estimate of the intake rate. Since time budgets are known we can subtract the flight time to arrive at foraging time. A more serious problem in these data is that we do not know how many Leatherjackets were taken by the female for her own consumption. Since we have data on this point for three other seasons however, we could therefore estimate this by averaging. In this way we were able to transform the photo intake rate to "real" intake rate.

Although there is a positive trend in the data for all years the correlation is not so well established for different reasons. Undoubtedly the choice of a 20 x 20 meter plot was not particularly good, since, in 1979 at least, the search effort was aggregated on an much smaller scale. Moreover, there are some plots that gave a high intake but were not visited frequently. The latter could not be explained by any effect of distance from the nest.

The approximate decision levels were estimated by selecting the visits with the lowest intake rate from those plots that had more than 10% of the total visits. This intake rate was taken to be the threshold value for the bird. We include a threshold value for the 1976 data despite the fact that only few points are available. Clear differences occur between years which indicates that the birds do not use a fixed threshold. Apparently the Starlings use an adjustable threshold and modify their decision dependent on the environment. The rule in all years seems to be that a low intake predicts low frequencies of visits, but a high intake rate can have either a high or a low frequency of visits.

The next question is what does the bird use as a reference? The simplest possibility, as suggested by Charnov (1973) is that the bird uses its own mean intake rate over a certain period as a reference. This is plotted in Fig. 37 and seems to be a likely candidate. The birds tend not to visit a certain area when the intake is lower than the average intake of the bird over the period investigated. There is a problem of circularity: If a bird spends most of its time in a certain area its average intake rate will approach the value of that area. Small fluctuations of intake might cause the bird to leave the area although other areas may be even less good. In this way we would not expect the bird to stay too long on a particular area. This might enhance sampling.

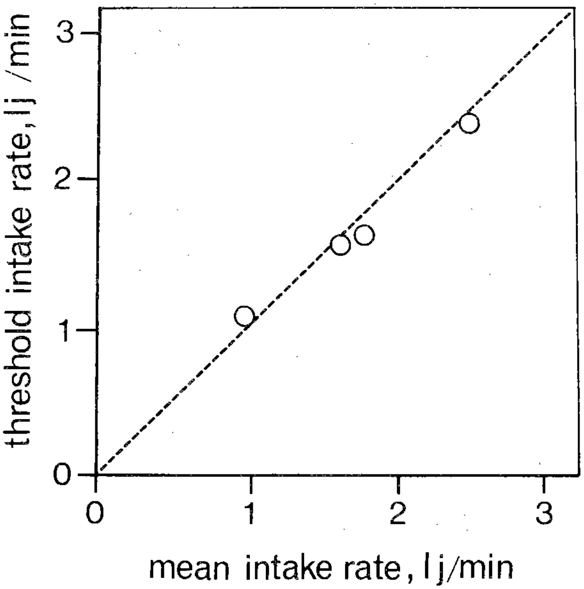


Fig. 37. Rejection threshold intake rates (as determined each season, see Fig. 36) in relation to the mean intake rate experienced by an individual foraging in the Leatherjacket grid. Each year a colour-ringed female was observed intensively, allowing a realistic approximation of the actual mean intake rate (MIR) experienced by the bird (see text). The figure implies that rejection thresholds may be determined by MIR.

To see whether this adjustability of threshold could be verified in the laboratory we did an experiment in which the preference of foraging Starlings was measured in situations with different average prey densities. The birds were individually tested on two or three feeding tables. Each test had a different average density. The prediction was that if a fixed threshold was used, only tables with a density above this threshold would be visited. If the threshold was adjustable the best table should always be chosen.

Each bird was tested for five minutes each day and the time spent on the different tables was recorded. Only data after preference stabilized (± 4 tests) were used. The results are given in Fig. 38. All the birds show a clear preference for the best areas. What was a poor table in one situation was judged to be the best in another. Also in the laboratory the decision criteria adjust to the environment, a feature that will have great survival value in an environment that changes as much as the natural foraging habitat does.

These laboratory experiments demonstrate that Starlings have the potential of learning where the best areas are, although they may not always use this.

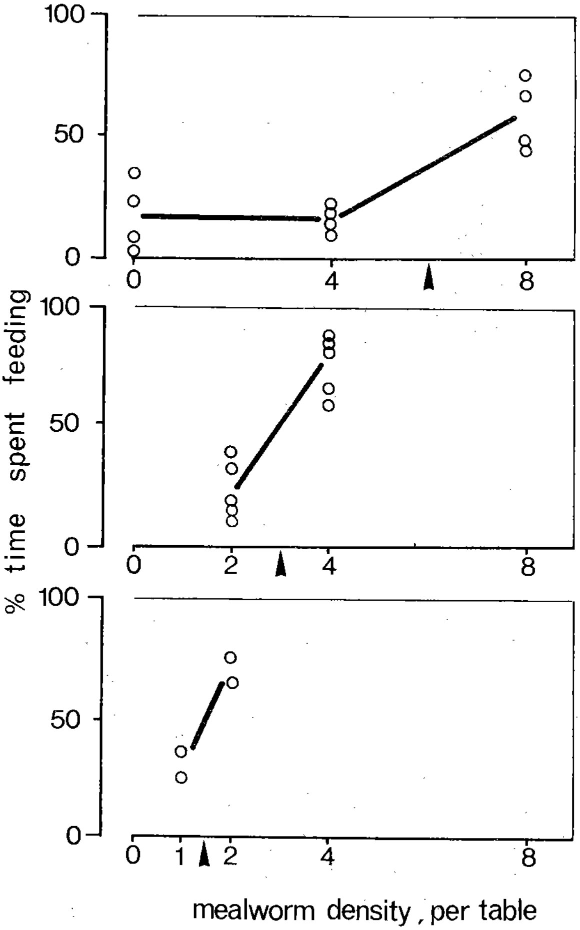


Fig. 38. Rejection threshold as determined in laboratory trials. Each point, expressed as the per cent of test time devoted to feeding on one table in a choice situation, refers to results from one individual for one test week (see text for test schedule). Density of mealworms on each table (table area 0.9 m²) was held approximately constant during each trial by the observer who used a event recorder to score position and behaviour of the bird. Trial A concerns a hand-raised bird with simultaneous choice of three tables, trials B and C, wild caught birds each choosing between 2 tables.

4.3. THE DECISION WHEN TO LEAVE

4.3.1. How long to stay

Once a Starling has landed on the foraging area it has to decide whether to stay or leave. To see whether caloric maximization is the foraging goal in these decisions we will first analyse the relation between prey density and duration of the visits. To do this we computed in Fig. 39 the average duration of the visits for the areas described in section 4.2.2. for which prey density was known. The durations show no clear trend with increasing density. Normally, less prey are taken from the low density areas.

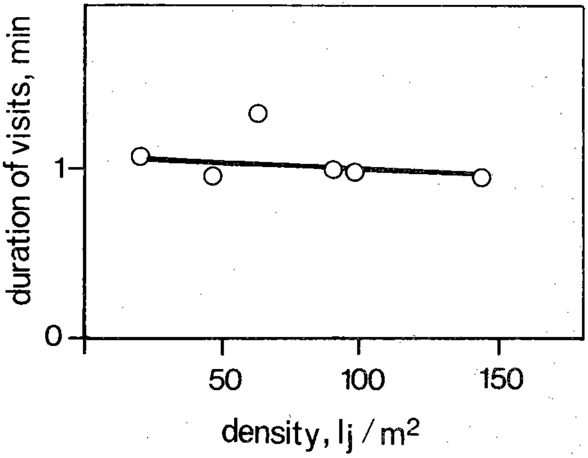


Fig. 39. Duration of visit to Leatherjacket grid by female 39 in relation to prey density, means for seven consecutive days in 1979. Each point refers to one of the units distinguished in Fig. 28 (three exploitation centres and three marginal zones).

This can be explained partly by the dependence of the decision of leave an area on intake rate. Normally, a Starling only leaves the foraging area to go to the nestbox and feed its young. However, in 17% of the visits (n = 341) our female decided to take off and land on another site in the Leatherjacket area before returning. The average duration of visits preceding site shifts was 49 sec (SD = 46.2, n= 58). This is shorter than the average duration for all visits to the foraging area ($\bar{x}$ = 60.2 sec, see section 4.2.2.). The intake rate for these visits is clearly lower than in normal visits (1.07 versus 2.00 Leatherjackets per min). It is very likely that this low intake rate causes the female to leave, and this contributes to the "independence" of visit duration from prey density.

4.3.2. Load size

Once a bird has decided to exploit a certain site it has to decide how many prey items it should take back to the nest (load size). Intuitively, one would think, the more the better, but this is not the general rule. Charnov and Orians (1973) and Orians and Pearson (1979) developed a model for this kind of situation which we shall use here.

As stated already, they call a bird that has to return regularly to some central place (such as the nest) a "central place forager". A trip that is made to collect food for the young for instance, is called a roundtrip, and consists of a flight to the foraging area, the actual foraging bout and the flight back. They state that to harvest efficiently, the bird should maximize the intake rate over the total roundtrip.

The authors expect that birds who bring more than one prey item to the young (multi-prey loaders) will be hindered in catching the next prey once they already have one in the bill. This would result in a progressively diminishing capture rate. With their model it is possible to predict the optimal time spent at the site and the load size.

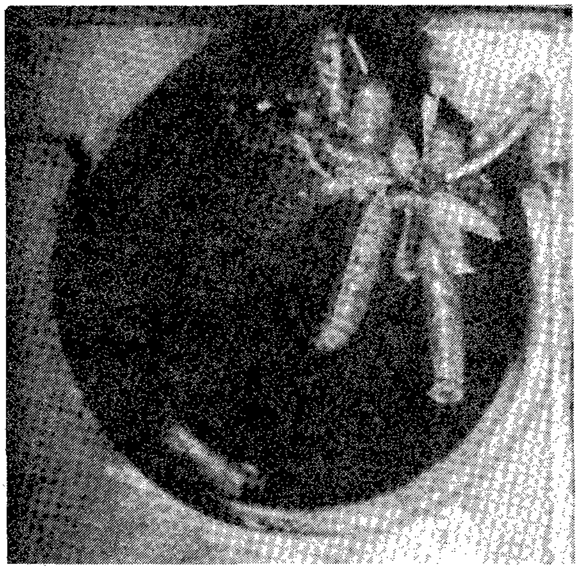


Fig. 40 gives their solution to this problem. The curve shows the cumulative intake over the time the bird spends foraging (T) in a roundtrip. If Tf is the time spent flying in the roundtrip we can predict the optimal number of prey (Lopt) that should be brought back to maximize intake rate. The optimal solution is given by the tangent a from time for roundtrip (Tf + T) to the cumulative intake curve. From this model, we can predict the foraging bout length (Topt) and the load size (Lopt) for different flight times and loading curves.

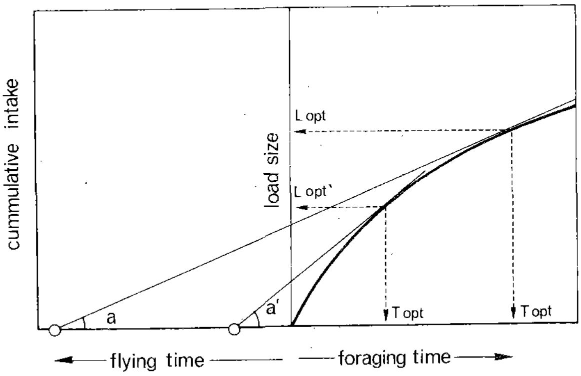


Fig. 40. Charnov & Orians' (1973) graphical solution of optimal foraging bout length and load size. This is derived from the loading curve (= cumulative intake curve) in combination with the required round-trip flight time. As explained in the text, given the form of the loading curve (diminishing rate of return over time, applicable to many situations), a shortening of the round-trip flying time will result in a decrease in the optimal duration of stay in the foraging area (from Topt to Topt') as well as in the load size (from Lopt to Lopt').

To evaluate whether the Starlings do solve the problem in this way we measured loading curves for different sites. Starlings indeed seem to be hindered since the time to collect the second prey for their young is on average longer than the time to collect the first prey (Table 12). This hindering is related to the behaviour of the bird. A feeding Starling has to dig in the ground. When it has a prey item in the bill, it must lay this aside before it can dig. After digging, it picks up the prey item again before resuming search. Since it takes time to find the Leatherjackets again this certainly accounts for some of the time loss ob-

Table 12. Data required for load size computations, parent Starlings collecting Leatherjackets

Date	Prey interval (sec)			Round trip flight time		Number of Tipula consumed	Number of Tipula in bill		
	First	Second	n	(sec)	n	by parent per round trip	*observed*	n	*predicted*
28.05.79	16.4	30.7	11	15	35	0.9	1.12	200	1
29.05.79	13.7	24.2	9	14	23	1.2	1.12	126	1
31.05.79	19.5	21.2	11	15	47	0.9	1.19	139	3
02.06.78	23.4	28.5	23	25	20	0.5	1.36	85	1
02.06.78	13.7	25.6	14	60	11	0.9	2.17	14	2

first prey interval: parent not carrying prey
second prey interval: parent encumbered by Tipula in bill

served. Whether having prey items in the beak also leads to less efficient searching is not known. Again there is a complicating factor since Starlings usually start a foraging bout by feeding for themselves and only collect prey for the young during the last phase of the visit. When Starlings are searching for themselves the intervals between successive prey are relatively constant, resulting in the first part of the loading curve being linear.

The loading curves were constructed as follows: It was assumed that when parents were collecting for themselves there was a constant interval between prey catches, when parents switched to collecting food for the young it was assumed that keeping prey in the beak resulted in each subsequent prey interval being a constant fraction longer than the preceding one. Since the mean moment that parents switch to collecting for the young is known from direct observations (Table 12) we use a linear function for the first part of the loading curve, where the tangent of the line is 1: prey interval up to the moment the parent would switch to collecting for the young. From that moment on the loading curve was constructed as a stepwise function as follows: Starting with the first uninfluenced interval, each subsequent interval was lengthened by a constant fraction. After each step the cummulative intake was raised by one prey unit.

Since flying time was measured we can now construct the optimal solution for the curves and predict the number of prey that should be taken back to the nest from areas at various distances. Fig. 41 gives a plot of both predicted and measured values. Although there are few observations they all (but one) fit the trend.

A stronger suggestion that the theory fits comes from a case where flight distance does not vary but loading curve is radically different. This occurred when fertiliser was applied to a field that had previously had a normal loading curve. The fertiliser had the following effect on the Leatherjackets. Normally, Leatherjackets are in their burrows in daytime, but, after fertiliser application some were lying between the grass the next morning. This had an enormous effect on the efficiency of the Starlings. Instead of walking at their normal speed they ran over the meadow without digging for Leatherjackets. They selec-

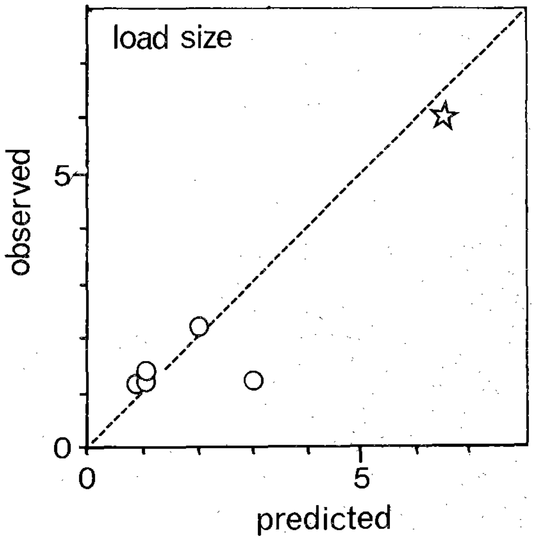


Fig. 41. The relation between observed load size and that predicted by Charnov & Orian's model (see Fig. 40). Observed load sizes were taken from the photo data of one individual on a particular day. Predicted load sizes are based on the mean loading curves for a number of individuals as measured on a particular area and roundtrip flight times for the individual for which load sizes were estimated. Aside from the variations caused by shifts in roundtrip flight times in the main body of the data (circles) a major change in loading curve followed application of fertiliser (star, see Fig. 42).

tively searched for the Leatherjackets that occurred between the grass, picking them up one after the other without putting down those already in the bill. The hindering effect was therefore nil, causing our prediction to jump to 5 to 8 Leatherjackets per visit (Fig. 42).

The average number of Leatherjackets actually brought back was 5.8 per feed, as compared to 1.12 in the normal situation. This is probably very close to the maximum number they can physically collect.

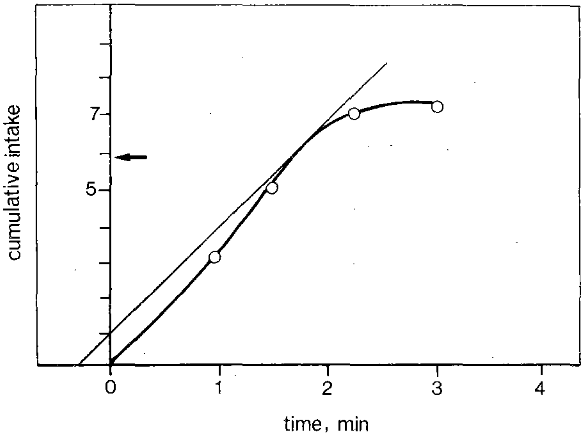


Fig. 42. Observations on total number of prey captured in relation to time elapsed on the foraging site for Starlings collecting moribund Leatherjackets driven to the surface by application of fertilizer. Roundtrip flight time was measured at 17 seconds. Moreover, according to the Charnov-Orians model the tangent to the loading curve yields an optimal load size between six and seven. The observed load size was in fact 5.9 (arrow).

In the polder of Schiermonnikoog the fields are mowed in a sequence from west to east. As a result, fields far from the colony are mowed first, while those close to the colony are mowed later. Once a field is mowed, the Starlings react very promptly by visiting it, probably responding to the mowing machine. Fields are mostly visited for some time before a new area becomes available. In this situation we found a very clear cut effect of distance on load size (Fig. 43). A sixfold increase in flight time gives a twofold increase in load size, for both male and female birds. Thus, there is an effect of flying time and form of the loading curve on load size. The model does predict trends in the data.

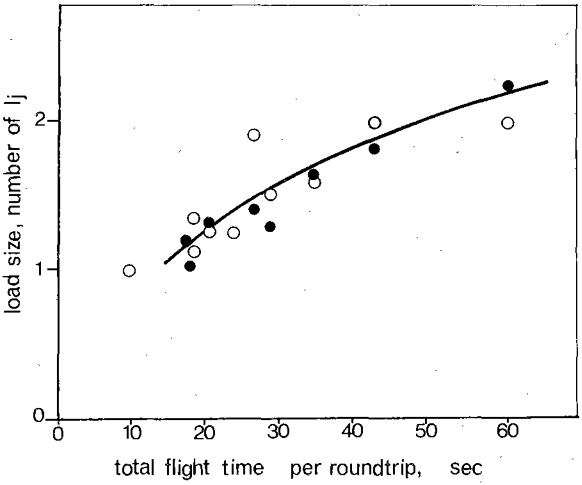


Fig. 43. Load size (number of Leatherjackets in the bill) in relation to total flight time per roundtrip for Starlings collecting food for their young in the polder (black dots = ♂, open circles = ♀). The line is drawn by eye.

However, the foraging goal need not necessarily be maximizing intake rate. Two factors can be suggested that might be important in this respect. Firstly energetics may play a role because flying back with prey in the bill may be extremely costly. Secondly, by putting down prey, birds run a risk of not finding them again or of being robbed. The latter would be more of a risk near the colony in view of the greater concentration of birds here. All these factors could explain the trends also predicted by using such a goal as maximizing intake rate. Further experiments and observations are needed here.

5. IMPACT ON THE PREY AND REPERCUSSIONS FOR THE STARLING

As was stated at the outset, one of the long term goals of foraging work is to evaluate the impact of the predator on the population dynamics of its prey. As far as the Starling is concerned, at least one study has been devoted to this problem. In this, East and Pottinger (1975) looked at the predation of birds on beetle grubs living in pastureland in New Zealand. In my own study, some information on this problem has already been published and will not be repeated in detail here (see Tinbergen and Drent, 1980).

The removal of prey is also of paramount importance for the predator, since his own intake rate is bound to suffer from this impact on the population. Local prey depletion is assigned a key role in foraging theory, where the resultant fall in intake rate is considered a governing influence in the decision when to leave the site. As we shall see, predator impact is a complex issue since not all prey are, in fact, available at any one moment in time. From this it follows that measurement of prey density alone, even though completely accurate, is inadequate and will not yield sufficient information to predict either impact or potential intake rate.

Since my primary interest was the interpretation of foraging decisions, foraging histories of individual Starlings were emphasized, i.e. I chose to devote my time to increasing the detail known about one individual bird rather than collecting generalized data on the whole colony. The following discussion therefore revolves about the question at what rate do prey densities change in the field situation as a result of predation by the individual and how sensitive is intake rate to these changes of density in prey. Where relevant, I will point out what types of observation we now need to fill in the picture for the interaction of predator and prey on a colony-wide scale.

We collected data with the rangefinder on the search effort (time spent searching per m^2) of female 39 by plotting the position of the foraging bird every 10 seconds as described in section 4.2.2. The pooled data for a week period is given in Fig. 44. It is striking that the distribution of search effort is almost identical with the distribution of landing sites (Fig. 24). This is caused by the fact that once a bird has landed, it will only stay for a short period.

It will be recalled that foraging visits were recorded by two teams of observers in the tower, one concentrating on measuring intake rate directly, the other on measuring the search path and location of prey capture by means of the rangefinder. The total time spent feeding in the area was thus known exactly, but for various reasons exact locations of prey capture were not

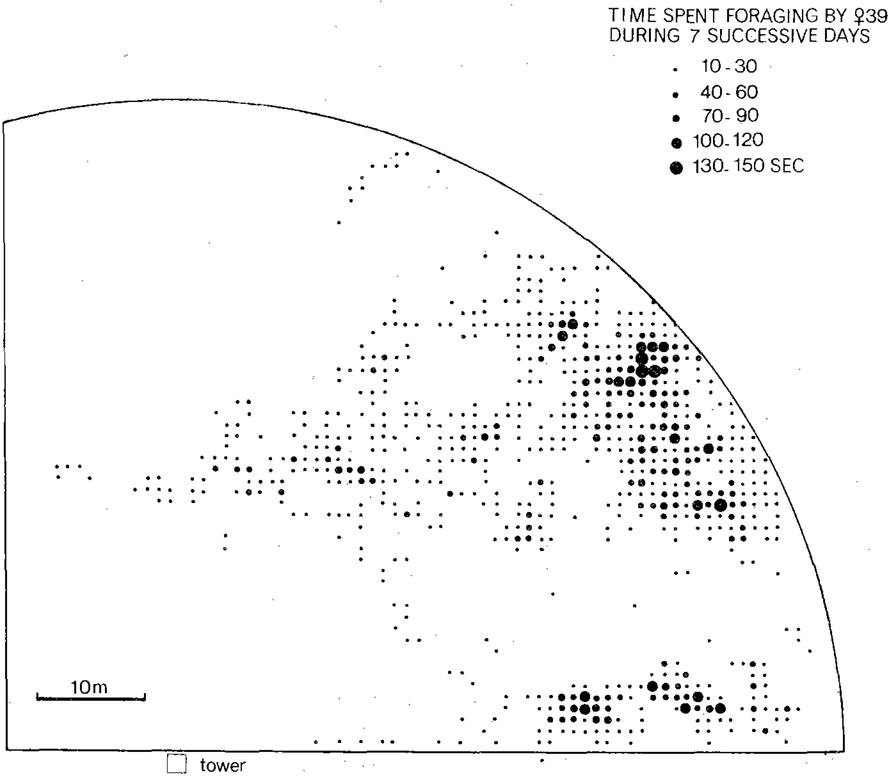


Fig. 44. Map showing accumulated search time per square meter plot of female 39 searching for Leatherjackets within the sweep of the rangefinder on seven consecutive days in 1979 (see also Fig. 24 ff).

always obtained. To correct for missed locations we assumed that the percentage missed by the observers was constant between areas.

By collating the time spent searching in each area with the intake rate, this gives us the number of prey taken. We computed the percentage of prey taken from each area by female 39 for that week in Fig. 45.

Surprisingly enough, in one week of "intensive" exploitation, the female hardly has any effect on the prey population. We have to remember, however, that other Starlings also exploit the area. We assume that their site choice is similar to our female's. This is not far from the truth as the general impression and occasional counts support this view. Since eight pairs foraged on this area their impact on the most intensively exploited sites could amount to a depletion of 24.5% of its prey population. This figure for impact is only reached very close to the colony and can be regarded as very high in comparison to that over a larger area. For instance, the impact over the whole area covered by the rangefinder was a depletion of 0.58% for our female, thus 9.27% for all eight pairs. Since there is a strong effect of distance from the colony on the total number of visits we can expect impact to decrease with distance. Further away from the colony values will be much lower, except in good localities.

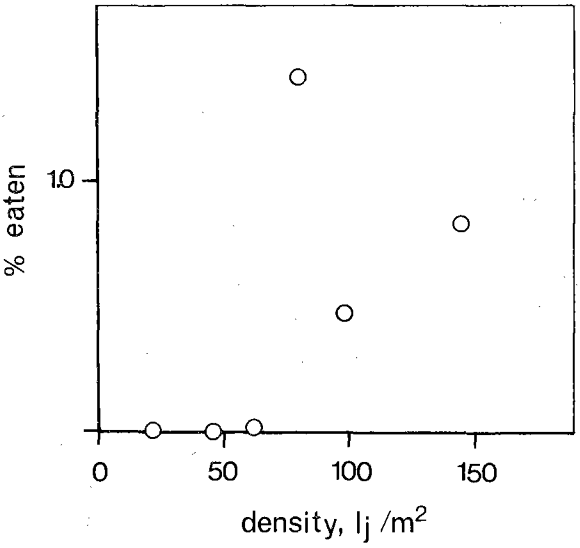


Fig. 45. Prey removed from Leatherjacket grid by female 39 during seven consecutive days in 1979. Basic data concern total search time (see Fig. 28) and observed intake rates (see Fig. 29) on each of the six units determined in Fig. 28.

The question now arises whether this depletion can explain shifts in the site choice of our female. To do this we have to analyse the cycle of exploitation of an area. Earlier work (Tinbergen and Drent, 1980) suggests that intake rate on a site under exploitation increases before it decreases. Their explanation was that the bird has to learn about the aggregation of the prey in the first phase, and depletes the prey population locally in the second phase. Because we now have detailed data on site choice it is worthwhile following this idea up.

Firstly, the pattern of the landing sites between days (Fig. 27) shows clearly that landing site distribution is less aggregated at first, although this is not statistically significant. Gradually three sites of major exploitation emerge. When we look at intake rates on a plot of 20 x 20 m these increase in time to an exploition peak and then decrease (day 1—5, resp. 1.8, 1.9, 2.6, 2.4, 1.0 Leatherjackets per min). This indicates that Tinbergen and Drent's suggestion that a learning process involving the building up of a map of intake rates is indeed present, at least at first.

We shall now consider whether the exploitation centres the individual bird has learned to distinguish are abandoned when the intake rate in these specific localities begins to fall, which is in line with the theoretical expectation. As we shall see, the problem then is to decide if the observed decline in intake rates is a repercussion of prey depletion. In selecting the data for this test we have to choose an exploitation centre of such small dimensions that the whole cycle of exploitation is covered. This is only the case for the smallest of the centres, which as mentioned before, was used heavily on one rainy day.

I plotted the intake rate and the number of visits on this rather small (160 m^2) exploitation center as a function of time (Fig. 46). Before this day of heavy use intake rates were relatively high, they dropped over this day and stayed low thereafter. Charnov's expectation that prey depletion causes intake rate to go down, causing the bird not to revisit the area, might be a reasonable interpretation for this.

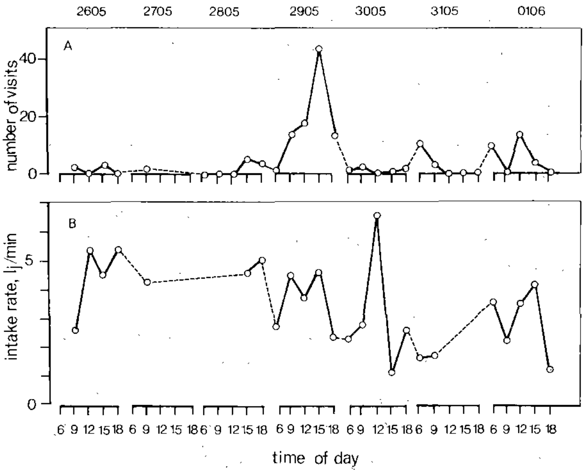


Fig. 46. Record of visitation rate (A) and intake rates (B, Leatherjackets per minute foraging time) in one of the three centres exploited by female 39. Local depletion causing declining intake rates may be the reason the female lost interest in this area.

To be able to estimate the prey depletion we measured prey density before exploitation occurred. In total 12800 Leatherjackets were available in the area (surface times density) of which 198 were eaten by our female. This means that she removed only one Leatherjacket per square meter. Again assuming that a maximum of 8 pairs were using the same area, roughly 20% of the prey were eaten. According to our density-intake rate relationship (Fig. 32b) this would cause a decrease in the intake rate of less than 20%. In fact the intake rate decreases by 60%! This steep decrease in intake rate might be caused by the fact that exploitation starts at the very best areas and gradually spreads over areas with lower prey density. Therefore, we compared the actual intake rate at the end of exploitation with the intake rate at onset, computed from average prey density over the whole area. Intake rates at the end of exploitation would correspond with an area having a prey density of 20 Leatherjackets per square meter (Fig. 46). Since average prey density at the onset was 80 per m^2, this would mean that 60 Leatherjackets have been taken per square meter.

One possible explanation for the bad correspondence between the actual number of Leatherjackets eaten by our female (1 per square meter) and the estimated number of Leatherjackets taken (60 per square meter) is that there is only a certain fraction of the prey population available to the Starlings. Even if all 16 birds were feeding on the area this could still not account for such a large discrepancy. The fast decrease in intake rate could be caused by the Starling itself (depletion or depression), or by other factors which influence availability (for instance, the rain).

Therefore we need a more direct way of answering the problem: does intake rate decline as a direct result of the removal of prey by the Starling? To do this, experiments were done with wild-caught individuals confined in small cages (2 × 2 m) that could be moved about on the field (Leatherjacket grid). Observation of the intake was made from a hide placed against the cage, which minimized the effect of these experiments on the colony birds. To eliminate the effect of hunger on intake rate we used two test birds for the same experimental area. The experience of these wild-caught birds is unknown. Changes in intake rate between first and second birds of a test set are presented here. The first Starling was allowed to forage on this small Leatherjacket area for some 11 minutes and we recorded intake rate and total foraging time. After this the bird was removed and the second Starling was allowed to forage for a similar time of the same area. The sod (top 5 cm) was then taken out and final prey density was measured. Prey density prior to the experiment could be computed since the number of Leatherjackets taken by the Starlings was known. Fig. 47 shows the intake rate as a function of the prey density at the moment that the bird started its experiment. The pairs of test results are connected with a dashed line, and show clearly that the decrease in intake rate by far exceeds the decrease in prey density. This strongly suggests that the Starlings only prey on a small available fraction of the Leatherjackets actually present.

An estimate can be made of what fraction of prey is minimally available when we assume that for a particular test, intake rate would fall with prey density during exploitation, as can be deduced from the intake rate density curve for the first birds. Both the measured decrease in intake rate and the density drop are known. The intake

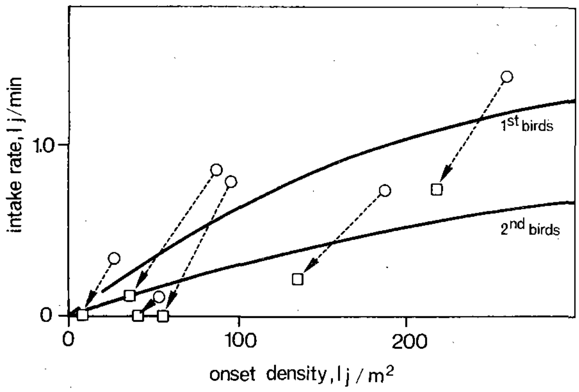


Fig. 47. Indirect evidence for selective predation by Starlings on Leatherjackets hiding in the soil. Experiments with wild-caught individuals allowed to forage for 11.7 (SD 3.96) minutes in an enclosure (0.15 m^2) placed on the Leatherjacket grid utilized by the wild birds. Total prey caught was directly observed and, as remaining prey were extracted from the soil at the end of each experiment, the density at onset could be determined exactly (abscissa). Each experiment involved a pair of birds. The second bird was allowed to feed alone in the enclosure directly after the first. Each pair of data points is here connected by an arrow. Curves show mean intake rates for first and second birds (data from M. P. Gerkema, pers. comm.).

rate of the second bird is much lower than the density decrease would predict. According to the intake rate/density curve of the first birds it would correspond to a much lower prey density. The actual density drop between the first and the second bird divided by the expected density drop (as estimated above) gives us an estimate of the available fraction which amounts to 44% available.

The fact that the experimental birds have a lower intake rate than female 39 over the whole density range (Fig. 29) has yet to be explained. It is very likely that there is a gradient in availability in the prey population. In the experiment, we left one Starling on a very small area for a long period which was around 30 times as long as female 39 stayed during a week of observation in a comparable sized area. Normally, the Starlings must only take the very easy to get prey, but in our experiment they were forced to forage for a long period and thus might also have take the less easy to get prey. This may explain the differences between the intake rate density curves. We think that it is very likely that wild Starlings "cream-off" the easiest to get prey, depleting only those locations where prey are within reach. Alternatively the fact that the experimental birds lacked long term knowledge about the area might have influenced the level of intake rate.

It is not yet sure why only a particular fraction of the prey should be more available than the remainder. Possibly the structure of the vegetation has something to do with it. For instance, detectability might be higher in those parts where the vegetation is short or open. Alternatively, the depth at which the Leatherjackets occur might be important. Tinbergen and Drent (1980) showed that groups of Starlings foraging on a population of *Cerapteryx graminis*, almost totally depleted the caterpillars that were in the surface of the sod, but hardly touched the caterpillars and pupae lower down, probably resulting in a higher survival in the pupae that are normally located deeper.

It is suggestive that, when Starlings return to the same spot more often in a run of visits their intake rate lowers. Coming back to the same spot was defined as the female landing within three meters of the take off point of the previous visit. Clearly, this is related to the high intake rate of the first visit. After two or three visits in a row to the same spot there is a significant decrease in intake rate (Fig. 48). This could be caused by depletion, but alternatively the bird could lose contact with small areas of high density. The latter could result from a combination of the systematic search of our female and the size of local high density areas. The level of intake rate at which she leaves a spot corresponds with the average level of intake rate of a single visit.

In conclusion we can state that Leatherjackets are differentially available to a foraging Starling. Starlings "cream-off" those that are easy to get and thus deplete the potential best foraging sites. It is very likely that this depletion causes the bird to undertake shifts in foraging sites.

Our impression regarding the search tactic is that Starlings tend to land next to, but not on, the site previously searched if the intake rate was high there, implying systematic search.

As a result of the differential availability of the Leatherjackets, impact will be limited. Starlings would only influence Leatherjacket populations if they select those Leatherjackets that produce the highest number of offspring. Our impression

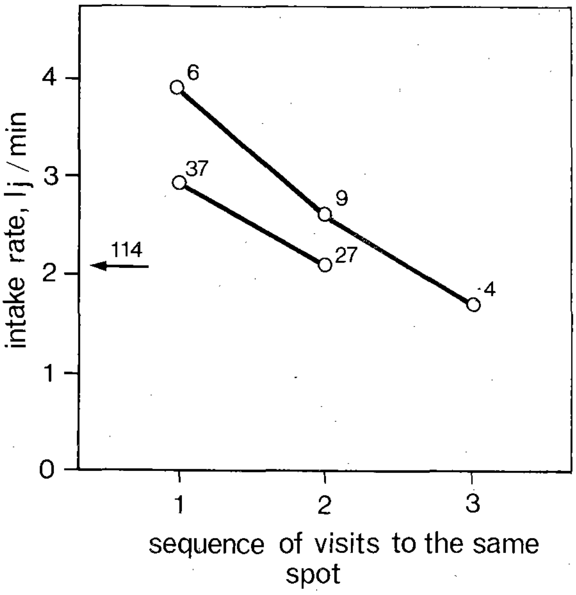


Fig. 48. Decline of intake rate of female 39 when revisiting sites on the Leatherjacket grid within the sweep of the range finder, A "foraging spot" is considered to extend to a maximum of three meters from the take-off point. Some of these spots are visited twice (37 cases, for which intake rate on the second visit was measured in 27) and sometimes even three times (9 cases) again the data are not complete). Arrow indicates level of intake where there was only one visit.

is that the *Cerapteryx* population might suffer a significant loss from Starlings, since large flocks do aggregate on the caterpillar areas when young have fledged.

To bring the question of impact further we have to have records of specific sites instead of specific individuals. Depletion for the predator is always relative in the sense that it must be related to some dimensions of area, and we are now faced with the problem of which units the Starling itself uses in exploiting an area, and how intake rates are collated to provide decisions. We will try to unravel these elements in the discussion.

6. THE STARLING IN THE CONTEXT OF GENERAL FORAGING THEORY

6.1. THE SPATIAL COMPONENT: THE PATCH

Every ecologist will agree with MacArthur (1966, 1972) that the resources of foraging birds are "distributed in a patchwork in three dimensions of the environment". To model foraging behaviour, MacArthur chose to simplify nature by introducing the minimal assumption of "repeatability", a postulate providing the searching bird with "a fairly clear statistical expectation of the resources it will come upon". To put these notions in a concrete framework of environmental structure, MacArthur defined the *patch* as a distinct spatial unit within which prey distribution is random. Patches are separated by corridors lacking prey items, consequently the time budget of the predator can be considered in two components, foraging time within the patch, and travel time between patches. He made a further assumption on patch hunting stating that the predator itself has an effect on the prey supply (or more precisely on the segment of "available prey") such that the intake rate experienced drops during the timespan of a single visit to the patch (Charnov & Orians 1973, Krebs et al. 1974). As we shall see, this last feature of the theory has repercussions on the expected sequence of decisions of the predator, in that, providing some reference intake value exists, intake rate can be seen as the variable controlling patch visit duration.

Laboratory work is commonly designed to provide discrete feeding opportunities — "patches" — in order to meet the assumptions underlying theoretical predictions of foraging theory, but the field worker keen on recognizing the extent of "patches" in the real world has little to go on. Any kind of prey aggregation can be termed a "patch", and Krebs (1978) has aptly straddled the possibilities by stating "Patches might be discrete natural units . . . or statistical heterogeneities in a superficially uniform habitat".

The aim here is to discover whether patches exist in the world of the Starling and whether it uses them as a unit in reaching decisions, as was visualized by MacArthur. Small scale, systematic irregularities in prey distribution probably owe their origin to vegetation differences that influence the quality of the microhabitat for a particular prey. Mosaic patterning in vegetation is possibly the most common causative factor for patches in prey distribution.

Turning now to the world of the Starling, I will first consider the saltmarsh which has often been characterized by botanists as the epitome of mozaic patterning. Fig. 49A gives a map of an area on the Schiermonnikoog saltmarsh predominated by two vegetation types and includes the positions of individual *Cerapteryx* caterpillars as determined by sampling. In this case, clearly segregated, high density pockets of caterpillars coincide with the vegetation type, a situation where patches in the prey distribution indeed occur. For the polder situation (Fig. 49B) the distribution of Leatherjackets over a small part of the study area is compared with a relief map. Here also, there is some correspondence between habitat character and the prey distribution. The distribution of prey species thus depends very much on patterns in vegetation or elevation in the Starling's habitat. Since these characters can vary unlimitedly in space we can expect any size of patch in the natural environment. Regarding the Leatherjackets on Schiermonnikoog we know patches of around 200 m² and for *Cerapteryx*, pockets vary between 20 m² and several hectares on the saltmarsh.

Whether these patches are exploited by the Starlings in the way MacArthur sketched is our next question. The correspondence between prey distribution and landing sites shows that the bird

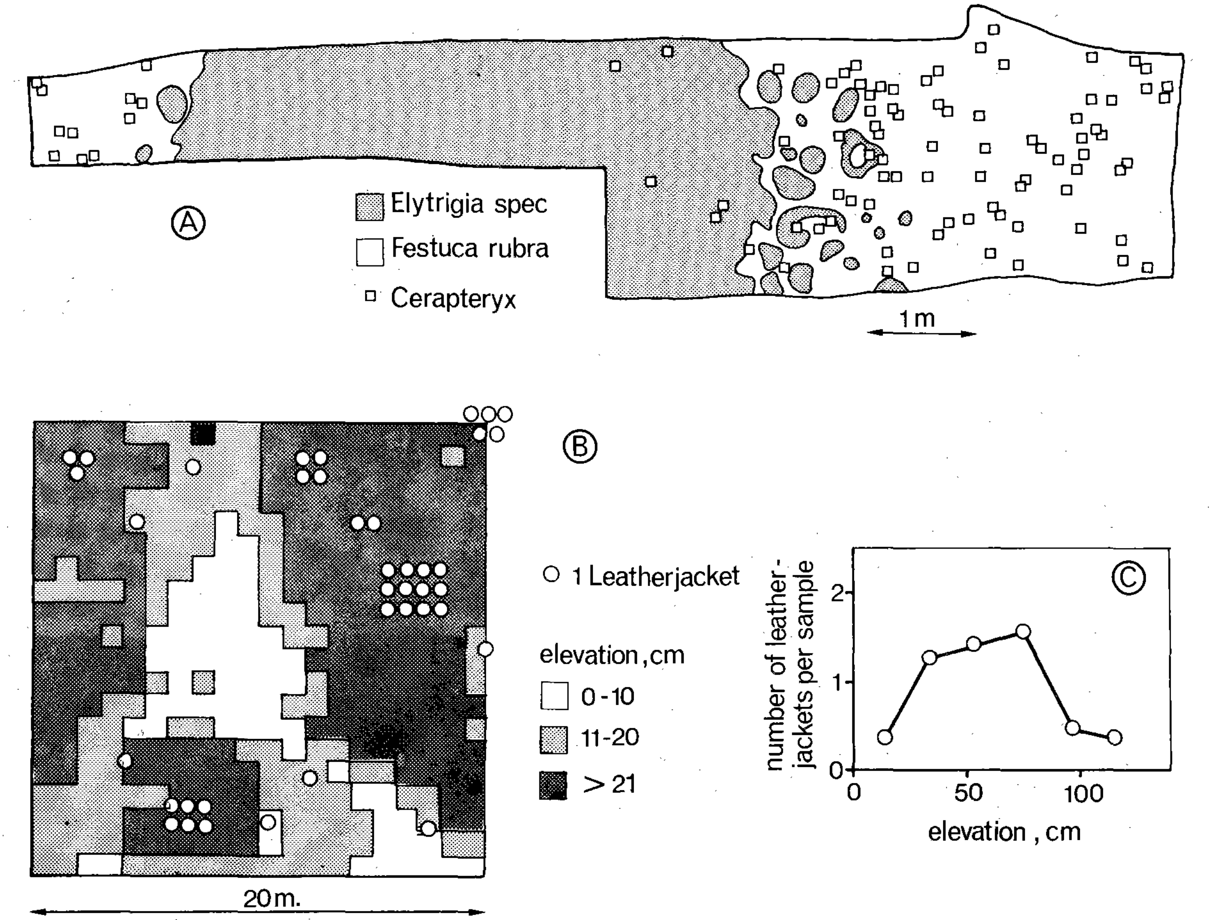


Fig. 49. Relation between prey distribution and habitat characters. Panel A shows a small part of the saltmarsh containing two vegetation types. The distribution of *Cerapteryx graminis* is almost entirely confined to the *Festuca rubra* plants, which therefore could be used as a cue for the Starling.
Panel B shows a relief map of a small part of the Leatherjacket grid. Each block of circles represents one sample. Samples were taken in a regular pattern. Panel C shows the relation between elevation and the number of Leatherjackets caught per sample over twelve 20 x 20 m plots.

does indeed exploit the prey patches, areas we earlier called exploitation centers. However, when we try to fit the Starlings way of exploiting these patches into the theory two important deviations show up. Firstly, as only three exploitation centers are in use by an individual Starling over the period of a week, the repeatability of patches, at least on this scale, cannot be as important as theory assumes. Secondly, both prey distribution and landing sites are far from randomly dispersed within such a patch.

To get around this problem, and to fit the data to the theory I will introduce here a two level concept of patchiness, the *macro-patch* and the *micro-patch* (Fig. 50). The macro-patch consists of a center of exploitation that corresponds with a large area which is exploited over a relatively long term: in the Starling case, some hours of foraging time spread over a period of several days within an area of around 200 m². Within these macro-patch areas, search and prey distribution are far from random as landing sites are most highly aggregated in plots smaller than one square meter. I shall call this very small scale aggregation the micro-patch. These micro-patches probably consist of potential living sites for the prey, where they are liable to be attacked by the predator as suggested by observations of the detailed foraging behaviour during a visit. Two arguments suggest that these micro-patches have much in common with MacArthur's patches. They are very small and must be so abundant that, if the predator can recognize them, it will be possible for the bird to build up a theoretical expectation for yield, since repeatability is very high. The second point is that it is very likely de-

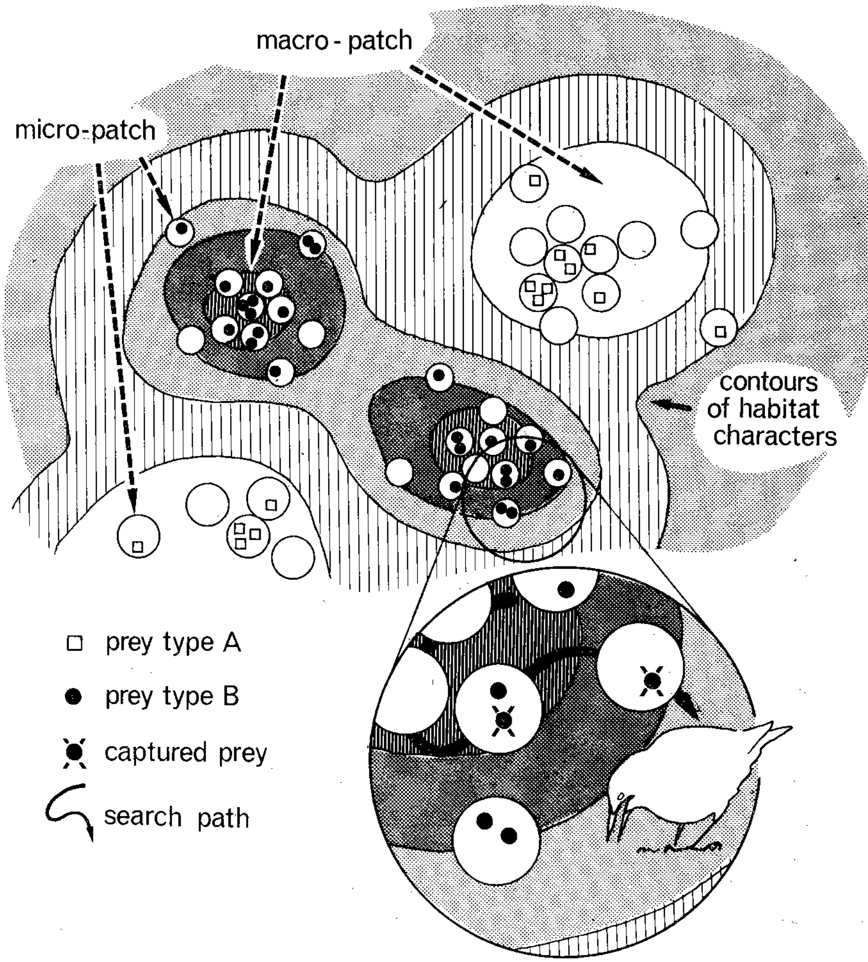


Fig. 50. The Starling foraging world as we see it now. Different prey types occur in different habitats or habitat types, here distinguished by the contours of habitat characters. The very small "units", micro-patches, are the potential living sites of the prey and can be occupied by more than one prey item, but they always contain the same species. The position of the micro-patch is dependent on habitat characters, and a spatially segregated group of micro-patches makes up a macro-patch. Within a micro-patch the prey distribution is thought to be random, but any distribution can occur within a macro-patch. As indicated in the enlarged circle Starlings search for micro-patches partially depleting them as they move through. The position of micro-patches is important information in defining macro-patches. Further details in text.

pletion does take place after one visit within such a micro-patch, as suggested by the depletion experiment.

In my opinion, the micro-patch is the one studied so much in laboratory work while only a few experiments have been devoted to macro-patches. Zach & Falls (1979) have struggled with this problem in their fieldwork on foraging in Ovenbirds (*Seiurus aurocapillus*) and caution that in nature the food supply is likely to be "a complex mozaic of patches of different sizes, shapes and densities . . . distances between patches must be highly variable and boundaries ill defined". The way out of this dilemma is to distinguish clearly between the patch as currently employed in foraging theory (my "micro-patches") and the patch as it can be distinguished purely from the spatial irregularities or discontuities of the prey (the units Zach & Falls tried to uncover by quadrat sampling, my "macro-patches"). This may be a good point to reconsider Royama's view of environmental organization. He assumed (Royama, 1970) that "different species occupy different niches", defining niche as "the place where the prey species mainly occurs". His basic argument is that different prey species are segregated in space. Thus, a predator looking for prey will only encounter one prey species within a niche. In view of the usage of "patch" in the contemporary literature, I will here consider Royama's niches as "patch types" to avoid an unnecessarily complex vocabulary.

The next problem is which type of information a foraging Starling uses to maximize its intake rate. The units of information are in the first place the micro-patches, where we expect that the bird has a good statistical expectation derived from a long period, possibly even a span of several years. Within the search path of a single visit the Starling will encounter more than one of these micro-patches. A second type of information must also be used, the specific location. If a certain visit was good in terms of intake rate, the Starling tends to generalize this information over a slightly larger part of the macro-patch, including some new micro-patches. On the next visit there is an increased chance that the bird will land very close to, but in our opinion not overlapping with, the last search path.

A bad experience on a visit induces avoidance of the area over which generalizations occurs, in our data this is around 6 meter in diameter (see Fig. 33). Thus in exploiting a macro-patch the Starling uses measurements of its position in combination with intake rate.

To underline this aspect I will present data on an experiment where Starlings in the laboratory were offered two feeding tables. Each feeding table had a fixed intake schedule so that the bird received a mealworm on every fiftieth peck, independent of the position of the bird on the table. When the bird changed tables after a certain number of pecks it would have to go on and do the additional pecks to make up fifty when returning again before it got a new mealworm. The birds were tested one hour daily for two weeks. At the end of this period a peculiar effect was seen for some birds which I shall exemplify by giving the data for one individual. All the prey captures occurred on a particular corner of the feeding table, although the reward was independent of the position of the bird (Fig. 51). Apparently the bird thought that particular sites on the table were good, presumably because first prey catches took place in this corner.

When we look at the location of pecks the bird delivered between prey catches we see that the bird alotted its time over the whole table, leaving the area of expected prey captures, but returning before it could expect the next prey. Thus, the bird used an expectation in time or number of pecks for the moment that the next prey was to be caught but, in addition, remembered a location where it had to be to find prey. This result stresses the importance of the location of single prey catches even when no other cues such as vegetation, are available. Why the bird bothered to walk around on the table at all between prey catches, and did not deliver all the pecks in the corner where prey catch was expected, cannot be explained. Possibly this may have something to do with sampling, where the bird keeps track of reward rates on the rest of the table.

Thus the general conclusion here is that we visualize the Starling foraging environment as being built up of habitats with macro- and micro-patches. Micro-patches are depleted within a single visit, and the bird pools information in ex-

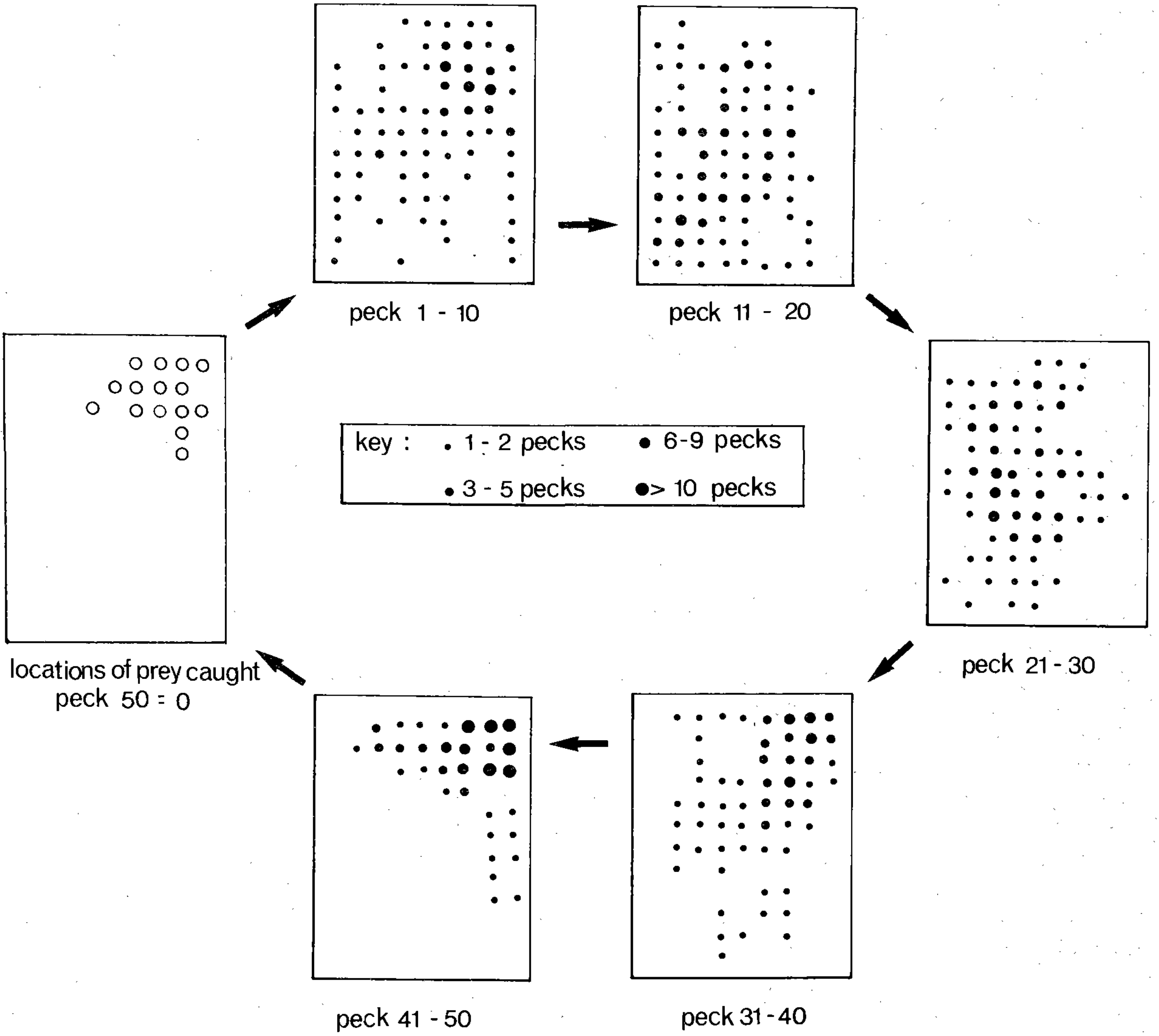


Fig. 51. The importance of the location of the prey caught. One Starling was allowed to forage on two feeding tables in the laboratory, and was rewarded with a mealworm on every 50th peck. In the course of two weeks prey catches became more and more confined to one corner of the table (panel upper left) although reward had been independent of the position of the bird on the table. The figure shows what happened on one of these tables in one experiment, two weeks from starting the series. The fifty pecks the bird has to do in between prey catches are spread over the table in such a way that we conclude that the bird expected to catch a prey item in the corner after some 40 pecks or a certain time span. This could not be due to the normal way of searching as, before learning, the bird took around 100 pecks to cover the table.

ploiting them. For exploitation of the macro-patch the birds use, in addition, information on the location of intake rates experienced in the past. They build up, as it were, a map of intake rates from which they select their landing sites within the macro-patch. This information can also provide clues on the boundaries of the macro-patch, since prey distribution and thus intake rate will not always correspond with vegetation boundaries. Depletion of a macro-patch will be made up of the depletion of the available micro-patches, and therefore it will be less predictable. The term over which information should be used is dependent on the renewal rate of the prey (see also Kamil 1978). We do not know anything about this rate for specific prey such as the Leatherjackets but would not be surprised if it corresponds to a time period of a day or even shorter. Possibly the grazing of cattle has an influence on the availability of prey on a micro-patch level (a bite of a cow) and, if this is the case, new micro-patches might be created in a fashion totally dependent upon grazing activity, an hypothesis that deserves to be followed up.

6.2. PREY CHOICE

Having considered how the foraging bird organizes hunting to exploit the natural discontinuities in prey distribution, the next step is to review ideas on the decision which prey species should be hunted.

Royama's (1970) assumptions on the spatial segregation between prey species, as described above, fit the Starling case, although we cannot confirm this for the fine scale. Furthermore, theoretical reasons also make it very likely that his assumption is valid, especially when we narrow down his niche concept. Royama's "niche" corresponds to my macro-patch concept for Leatherjackets and caterpillars, but with my micro-patch concept for bibionid flies.

Royama argued that the decision on prey choice would be solely dependent on the relative profitabilities of the prey species in their niches. This is clearly not true for the Starling situation. Profitability of caterpillars is much lower than that of Leatherjackets, but still caterpillars are taken in large quantities. The table experiment (Fig. 18) illustrates this very nicely.

Our data are also at variance with MacArthur's model. He reckons that patch choice precedes prey choice, since different prey species are assumed to occur within patches. Since this is not true for the main prey species of the Starlings they have to decide on prey choice before they decide on macro-patch choice. Furthermore, we can test one aspect of MacArthur's compression hypothesis. MacArthur predicts that in an unproductive environment the bird will tend to take a broader prey spectrum. In our experiments on enlarged brood sizes (comparable to making the environment less productive) the opposite is the case. Parents tend to concentrate on the prey species that yields the highest amount of energy per unit time devoted to searching.

Since I think that the spatial segregation of different prey species is a very common feature in nature, I expect that this sequence of prey choice preceding macro-patch choice is common in predators.

6.3. NESTLINGS DEFINE THE FORAGING GOAL

Prey choice during the breeding season is governed by the information the nestlings pass to the parent. The hunger of the young influences the foraging goal the parents use. Very hungry young change the foraging goal of the parents towards maximizing energy over time, while satiated young make the parent shift its foraging goal towards "quality" maximization. The term over which these foraging goals are switched can be very short as seen in the results of the experiments where the hunger state of the young was manipulated.

Ultimately, the interplay between these different foraging goals are facets of the general long-term foraging goal of maximizing fitness since the quality of the food has an effect on the survival of the nestlings.

When variations in food resources or in nest demand occur, the combination of these two factors will force the parent to bring a certain diet. With high nest demand and low resources the parent may maximize energy, consequently bringing too monotonous a diet. Eventually this will lead to mortality among the nestlings, thus decreasing nest demands and allowing the parents to increase the quality of the diet up to the point that some young survive.

The reason that parents do not bring a fixed diet must originate in the fluctuations normally existing in the resources. It is very likely that quality aspects of the diet are critical only after a long period of deficiency (days?) while energy is always needed and has strong effects on the survival of the young on a shorter time base. Hence the reason that parents bring poor quality food may be to see the young through until resources become richer again, and high quality can be met with once more.

With this mechanism we can expect that when energy rich prey is very abundant, its percentage in the diet may even decrease with increasing density of this prey. In fact the data in Fig. 8 suggest that this might have been the case in 1979, since the parents had to spend less time finding the energy source, thus leaving more time to spend on the quality source.

Our general impression is that the survival of the young is a smooth function of the diet composition. A dietary system involving absolutely defined minimal rations as employed in Pulliam's (1975) model does not seem to exist.

However, in terms of McFarland's model (described in Krebs, 1978) the crucial thing now is to describe the benefit curves for the diet of both parents and young. Probably some conflicts will show up between the optimal solution for parents and that for the young.

6.4. FORAGING DECISIONS AND RESEARCH PERSPECTIVES

As we view it now, foraging decisions are organized in a hierarchy, in the sense that there is an invariate sequence of decisions leading eventually to the capture of prey and return of the foraging bird. For the Starling, this hierarchy is illustrated in Fig. 52 in a form used as a focus of discussion in our group for the past couple of years. Each level of drawing represents a decision level, the time sequence starting at the nestbox (top panel) and working downwards to the moment of prey capture, each level narrowing down the units of the food resource over which decisions are taken. This hierarchy, most likely of the "branching" type, (see Dawkins 1976) is imposed by the structure of the resources as seen through the eyes of the predator. For example, the units of prey distribution recognized by the Starling may conceivably be more schematic than that revealed by actual measurement of prey location, since the Starling must work from incomplete information and is bound to simplify nature by utilizing some threshold or combination of threshold values in distinguishing units for exploitation.

Although our hierarchical scheme is, in the first place, intended to apply specifically for the Starling foraging situation on Schiermonnikoog, we are convinced that the basic features of this hierarchy apply widely to foraging birds. We hope that critical analysis of the sequence of decisions in other birds will be undertaken to support or disprove this line of thought, rather than accepting any pattern beforehand. Before considering the various decisions in the light of previous ideas, it may be useful to emphasize the main line of evidence behind the concept presented here.

The experiments whereby the state of hunger of the brood was manipulated (see section 4.1.) demonstrated conclusively that signals from the nestlings play a decisive role in forming the decision of the parent over the species of prey to be taken next. For simplicity, the choice faced by the parent is here narrowed to two prey species, each living in an altogether different habitat, as is the case covered by our experiments. As will be mentioned later, we consider this idea the key towards unravelling the complex problem of how the diet comes to be assembled. Once the prey species has been settled upon, the hunting locale must be decided, and this second level of decision is guided by previous experience of the parent. Our measurement of consecutive landings, making use of the rangefinder, has shown that the distance between consecutive visits when the same prey is being exploited is strongly influenced by the intake rate achieved on the first. Hunting trips with high reward thus lead to follow-up visits in the same area, underlining the significance of location in the exploitation system of the Starling. Measurements of search effort (foraging time per square meter) expended by one individual Starling over a period of seven consecutive days suggests that at any one moment in time the parent utilizes two to three such zones of high intake, which we have distinguished as "exploitation centres" and classified as "macro-patches" in the previous section.

The final level distinguished here concerns the micro-distribution of the prey, and the way in which the actively searching predator examines a series of potential prey sites in succession (in our case probing the vegetation-soil interface). As we know from our observations on tame birds restricted to enclosures on the Leatherjacket grid two phenomena are involved: *detection* of the prey, and the effect of even a single foraging visit

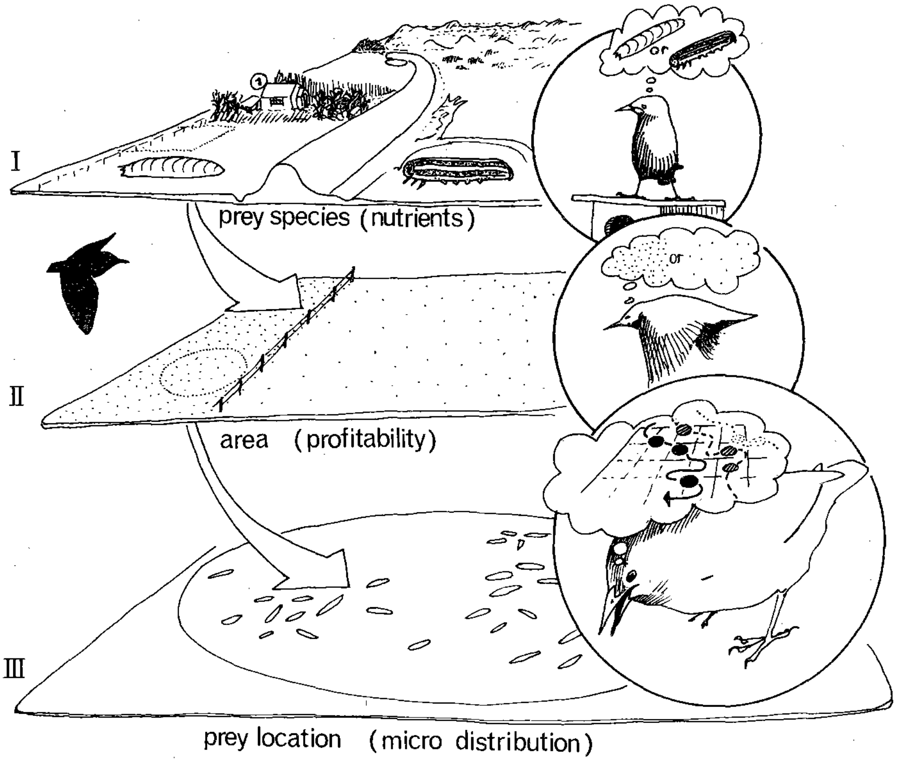


Fig. 52. A hierarchy of foraging decisions for the Starling on Schiermonnikoog. The bird on the nestbox has first to choose the prey species, since they occur in different habitat types. This choice is probably governed by nutrients. In this diagram the bird chose the prey type on the left (Leatherjacket). The second level of decision is which area to land on which is reached by using relatively long term information on profitability of the area. The third level of decision is that on exact landing site, and the development of the search path. The micro-distribution plays an important role here. This diagram was earlier published by Drent (1978).

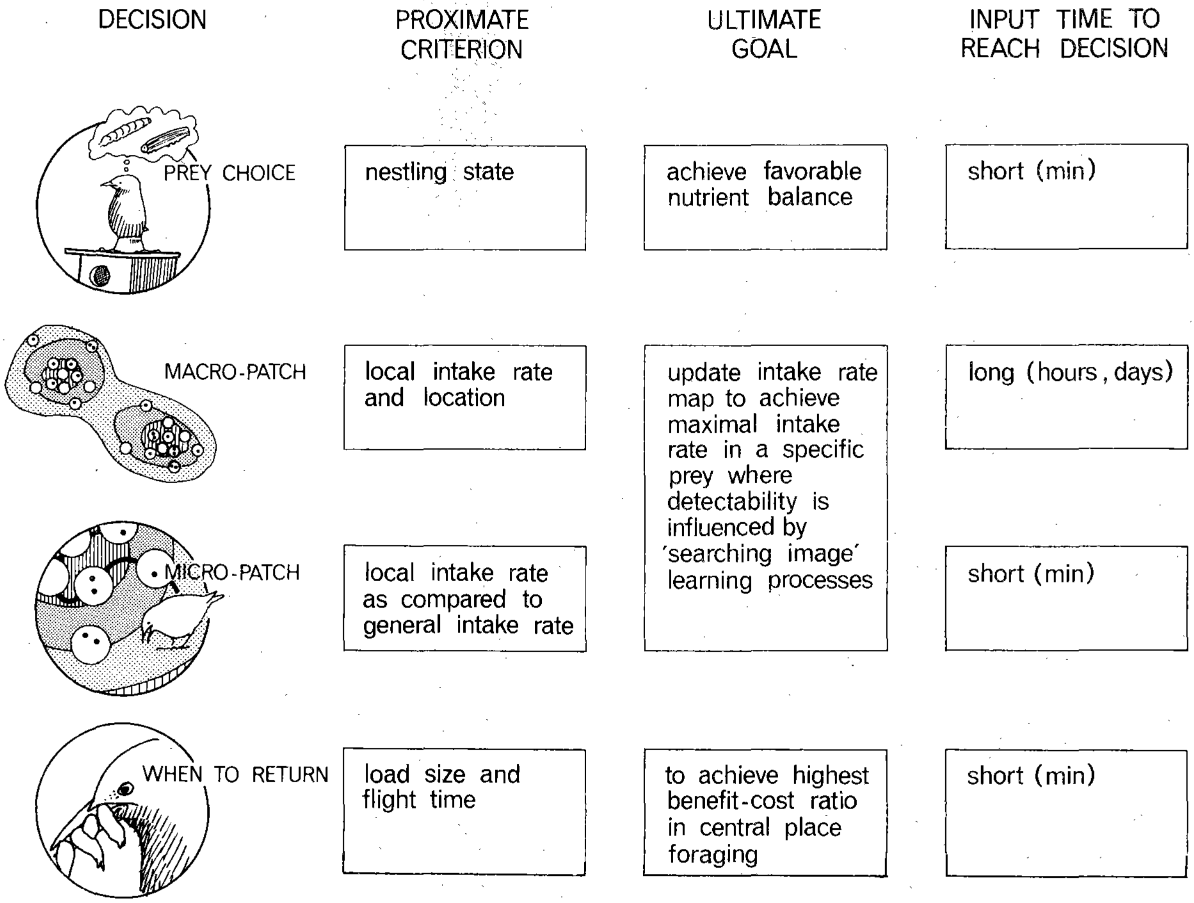
in *depleting* the resource. Our measurements on free-ranging birds indicate that subsequent search paths may converge with, but will not overlap preceding ones, implying that depletion is a regular event in a single visit to a particular spot. These facts in combination have led to the suggestion that these potential prey sites be distinguished as "micro-patches".

In Fig. 53 I have attempted a flow diagram of the principal foraging decisions, distinguishing the primary criterion relied upon, the input time required to reach the decision, and the goals served (providing at the same time, a catalogue of topics for continuing research in this field as I see it at the moment).

For the decision on prey choice, the analysis of the nutrient content of prey species and its relation to nestling survival is a primary goal for future work, and can be couched in terms of the benefit curves employed by McFarland (1978). A fascinating ethological subsidiary to this problem is unravelling the communication code employed by the nestlings in making clear their demands to the parents.

The choice of macro-patches must be based on information on intake rates achieved in different locations in the foraging area. Before understanding this we have to discover how information on intake rate experienced in different micro-patches is stored and collated and, over what size of area this is generalized. The second question is of primary importance in understanding foraging behaviour in the field and hence in predicting the diet, but I must confess that it is not at all clear at the moment what chain of steps in fieldwork is needed to bring us further.

Decisions at the level of the micro-patch are probably the ones we know most about. Krebs et al. (1974), Charnhov (1973), Hubbard & Cook (1978), Cowie (1977) analyzed foraging behaviour in a laboratory setting involving patches in MacArthur's usage of the term, whereas Beukema (1968), Smith (1974a, b) and Thomas (1974) were occupied with area restriction, behavioural responses that probably have to do with exploitation of less well defined micro-patches. A lot of effort has to be directed towards the problem of differential availability, a problem with roots at



DECISION	PROXIMATE CRITERION	ULTIMATE GOAL	INPUT TIME TO REACH DECISION
PREY CHOICE	nestling state	achieve favorable nutrient balance	short (min)
MACRO-PATCH	local intake rate and location	update intake rate map to achieve maximal intake rate in a specific prey where detectability is influenced by 'searching image' learning processes	long (hours, days)
MICRO-PATCH	local intake rate as compared to general intake rate		short (min)
WHEN TO RETURN	load size and flight time	to achieve highest benefit-cost ratio in central place foraging	short (min)

Fig. 53. The chain of decisions a Starling has to make in foraging.

this level, as is true of the rate of depletion which must follow from this. These two inextricable problems (availability and depletion) are the theoretical backbone of the micro-patch.

Finally the decision on when to return to the nest has to be tackled. The main problem here is to see whether load size, visit duration, or some combination of both, is the crucial parameter. Since Starlings tend to leave the foraging area just after they have captured a prey load size must be important. Predictions for load size taken from Charnov & Orians' central place foraging theory differ depending on the goal (maximizing intake rate over time as distinct from minimizing energy input over time) thus opening the way to interesting field tests, especially if manipulation of brood size is included.

Looking back on the main stream of research on foraging, it is pertinent to ask whether basic concepts introduced by others have disappeared from view in the general scheme presented here. Tinbergen (1960) assumed that birds encountered their prey in a *random* fashion (order and interval), a view reappearing in the assumption of random encounter experienced by the predator within the patch as formulated by MacArthur (e.g. 1972), Charnov (1973) and others.

MacArthur's major premise on *repeatability* of the environment can be found in our scheme at the level of the micro-patch. Work descended from MacArthur's original theory and later extended to decision making in all sorts of animals ties in with the micro-patch level. *Area restriction* (Tinbergen *et al.* 1967, Beukema 1968, Smith

1974a, b) can be viewed as a behavioural response at the micro-patch level, although in these cases the boundaries are less well defined. Thomas (1976) discovered that in addition to showing area restricted search after eating a prey, Sticklebacks (*Gasterosteus aculeatus*) show *area avoidance* following the rejection of a prey. This rejection might foreshadow the intention to change prey species as suggested by Thomas and therefore would, perforce, involve a large scale shift in hunting location corresponding with the expected segregation in space of different goal is the finding that area avoidance lasts much longer than area restriction.

Aside from the laboratory approach pioneered by Smith and Dawkins (1971) work on the macro-patch level has received little attention so far, perhaps because the importance of the topographic component in foraging has not been emphasized until now.

Although the ideas advanced by Tinbergen (1960) and Royama (1970) concerning the basis for prey choice decisions can be experienced as contradictory, this is a misconception as Royama himself has been at pains to point out. The searching image hypothesis and the profitability concept are of a different order (proximal versus ultimate in evolutionary terms) and have been inserted at different levels in our flow diagram accordingly.

Tinbergen's ideas on searching image as a proximate mechanism involved in prey detection remains a challenge to those studying the basis of selective "learning to see" (Dawkins 1971, Croze 1970) at the level of prey encounter. Royama was interested in the ultimate achievements of the animal resulting from a long pedigree of evolution, and not in the mechanism by which proximate decisions are shaped. In our diagram his profitability concept can best be implemented at the level of both macro- and micro-patch choice, provided each contains different prey species. Direct field evidence that profitability is the criterion governing prey choice has not been forthcoming in my study (and field evidence collected by others on this point is at best ambiguous) but the profitability concept is undoubtedly of central significance in choice between localities where exploitation of one prey species is concerned.

The second major concept advanced by Tinbergen, the thought that variation in the diet reflected some basic physiological needs of the nestlings, is a theme recurring here at the first order decision level. Royama found that specific food was brought to the nestling Great Tit in the first few days of life and concluded "spiders have special nutritive value, important for growth of nestlings in an early stage, which is not found in other types of food" (Royama, 1970) but in the perspective of his model he sees this as an unimportant irregularity. However, the data we collected shows that for Starlings, this nutrient argument holds for the whole nestling period. This implies that different prey species have different values for the nestlings, quite distinct from their profitability scaling as evaluated by the foraging parent. Possibly certain prey species are functionally interchangeable as concerns their acceptability to the young. Our impression is that this is so, and it is this hope that makes further experimentation particularly urgent.

Often foraging systems involving herbivores are contrasted with insectivores in that herbivores are expected to have a quality aspect in their decisions and insectivorous birds are not. According to our work this distinction is not valid for the Starling, and we would not be surprised if the wedge so driven into this dichotomy will prove more general, fitting other insectivorous species as well.

I introduced this study as contributing to the evaluation of fitness, and therefore brood-size manipulations were introduced in an attempt to grapple with this problem. The entirely unexpected realignment of goals by the parents beset by supernormal broods brought home to me that an optimal diet set is absent, what does exist is a strategy to assemble the "best diet under the circumstances" whereby quality benefits and time(energy) costs are evaluated. Systematic study of reactions of the parents when under pressure to perform, while monitoring energy expenditure, is in my opinion an appealing line of work and owes its inspiration to the thinking of Lack (as summarized in his 1954 and 1966 books). I am pleased to acknowledge my debt to his thinking and was stimulated by both of his books particularly by the frontispieces illustrating nestling diet.

7. ACKNOWLEDGEMENTS

First of all I want to express my deep gratitude to Dr. R. H. Drent for giving me the possibility to do this work. His keen field interest and broad knowledge helped me a great deal in formulating the questions. Discussions while working in the field and criticism on the manuscript until deep into the night were especially important for improving my own thinking. I must mention here Mrs. Drent, since she gave us the time, space and climate necessary for this kind of work. Professor Dr. H. N. Klomp criticized the manuscript, although I only allowed him little time to do this. Further I want to thank him for his alacrity in facilitating acceptance of the manuscript for publication.

I want to thank Mr. R. Nieuwenhuis, opzichter der Domeinen on Schiermonnikoog, for his permission to work on the saltmarsh and the adjoining pastureland. Mr. F. Visser, chairman of the "Boeren belang", kindly allowed us to work on their land.

Discussion with different colleagues have set the stage to develop my own work. I want to mention especially Dr. S. Daan, Dr. J. G. van Rhijn, Dr. H. Biebach, Drs. J. Prop, Drs. L. Zwarts, Dr. K. Westerterp and Drs. J. Tinbergen. Prof. Dr. G. P. Baerends kindly discussed the more behavioural problems with me. In an early stage of my education I had the pleasure of working under Prof. N. Tinbergen on Walney Island and he stimulated me very much to take up a field project. Later visits to Oxford were very valuable, especially the discussions with Dr. J. R. Krebs and Dr. R. J. Cowie. A visit of Dr. E. L. Charnov to Groningen was also very valuable. Discussing some data his comment was: Gee man, does this really happen in nature? Dr. Gethin Thomas needs special mentioning since discussion with him in both the first and the last stages of the work smoothed my way into theory, in addition he carefully corrected the manuscript in content and English. Mrs. T. P. J. Tinbergen-Frensdorf criticized and thereby substantially improved the Dutch summary.

Since nowadays fieldwork uses complex techniques this study was very dependent on our technical staff. J. van der Laan and J. W. Koenes and his staff built the nestboxes for the Starling colony and the feeding tables among numerous other things. W. J. Beukema and his staff developed the photocell system to trigger the automatic camera, allowing us to have high quality material. J. H. Nijboer was our handy man, putting together bits and pieces of materials to make valuable equipment for us. J. J. H. Suurd provided glasswork and funnels for extracting insects from the soil and alcohol to preserve them.

R. Vodegel kindly put aside his own work to help me recompute some data. Mrs. H. Lochorn-Hulsebos typed and retyped the manuscript with an amazing speed, encouraging me to write faster. Drs. G. Blokzijl helped with technical aspects, such as cameras and hides and H. Visscher was always organizing the administration in an optimal fashion. I also thank D. Visser for preparing Figs. 24, 27 and 53 and L. Hoekstra for preparing Figs. 1, 2, 5 and 44. Drs. J. Ebbinge from the T.H. in Delft arranged for me to borrow the Zeiss Jena rangefinder, and designed extra prisms to improve the range.

I want to express my thanks to all the students that have assisted me, without whom such an extensive study would have been impossible. All participated as a part of their study and kindly allowed me to use their data. The ongoing discussion with those that identified themselves with the project provided the right background. I want to mention especially here J. Prop, J. Smakman, G. Damsma, M. P. Gerkema, T. Meijer, T. Griede and G. Gänshirt, who helped in the fieldwork and A. Verkaik, J. Wiemans-Kneepkens, H. Leever, H. Smit, J. de Heer and J. Wanink who did this in the laboratory experiments. In addition numerous 3rd year students helped by their work in the yearly field course on Schiermonnikoog.

Finally I want to express my gratitude to Riekje Fijlstra who apart from drawing most of the figures, provided a pleasant background enabling me to work so intensively during a long period of her and my own life.

8. SUMMARY

1) Six seasons of field work on the Dutch island Schiermonnikoog were devoted to testing the hypothesis that parent Starlings conform to the principle of caloric maximization in their choice of prey and hunting site as would be predicted by the profitability concept introduced by Royama.

2) The study is based on direct observations of intake rate of the Starlings coupled with automatic photographic records of prey delivered to the nest (Fig. 7). The latter allow subsequent measurement of prey length and hence estimate of weight of the prey. Since the parents were individually colour-marked, detailed time-budget observations were possible (Fig. 5) and in the final season search paths and prey captures were measured synchronously.

3) The menu of the nestling Starlings is dominated by only a few species in all years. These were collected from the pastureland surrounding the colony ("polder") or from the adjoining saltmarsh (Fig. 10). The chief prey collected from the polder is the Leatherjacket *Tipula paludosa*, whereas the saltmarsh provides the caterpillar *Cerapteryx graminis*, the beetle *Telephorus fuscus* and in some years other important prey (Table 4).

4) After each feeding the parent Starling must decide which prey to collect next and since *Tipula* and *Cerapteryx* occur in quite distinct habitats, it is possible for the observer to quantify parental choice in this particular dichotomy. In the course of the day the time required to collect one prey varies in a characteristic fashion, showing a clear mid-day peak in apparent availability of the Leatherjacket (Fig. 13) but the rate of delivery of prey to the nest does not follow these trends (Fig.

12). The governing influence of nestling hunger revealed by manipulations of the nestlings (see point 5) helps to explain these discrepancies particularly as nestling hunger state has an obvious and deep-seated relation to time of day.

5) Time required to collect one *Cerapteryx* from the saltmarsh is far in excess of time needed for one *Tipula* from the nearby polder, and from the viewpoint of caloric return on time or energy expended by the parent it is not clear why *Cerapteryx* is brought at all. Field experiments on choice (either with prey fully visible, Table 6, or with prey concealed under flaps in feeding tables, Fig.18) confirm the preference of the parent Starling for *Cerapteryx*. Apparently other criteria have priority, and manipulation of the state of hunger of the brood provide a strong case that the *quality* of the prey (i.e. nutrient composition) is the reason for including *Cerapteryx* in the diet. When the level of nestling demand is not too high, the parents persist in collecting caterpillars, but when demand is high (nestlings deprived and/or supernormal broods, see Figs. 19, 20, 21) parents revert to the easier-to-collect Leatherjacket. There is some evidence (Fig. 23) that Leatherjackets are detrimental to the health of the nestlings if fed in large quantities over long periods of time, so we are dealing here with a compromise situation. An indirect assessment of parental diet (Fig. 22) shows that the female parent reduces her own caterpillar consumption when stressed by the large broods, she then delivers all caterpillars captured to the young at the cost of a pure Leatherjacket diet for herself to ensure them of a varied diet.

6) Having decided which prey to collect, the next decision facing the parent Starling is where to land. This problem is considered for the Leatherjacket area where detailed observation of landing sites and subsequent search paths were collected using an optical rangefinder (Fig. 25). The main body of data refer to hunting by one female Starling on seven consecutive days in the 1979 season (Fig. 27). Summation of search path measurements in this period (Fig. 28) reveal a concentration of hunting in three exploitation centres, which can be contrasted with three marginal zones. Direct observation showed that the bird spent most of its time in the areas yielding the highest intake rates (Fig. 29) and an extensive sampling programme indicated that these coincide with the areas with highest prey density, allowing the conclusion that the threshold for exploitation at this time was about 70 Leatherjackets/m² (Fig. 29 top). By mounting a feeding table near one nest and measuring usage by the local male (Fig. 30) in relation to reward rate (manipulated by the observer) the causal link between intake rate and site choice was verified.

7) The history of exploitation of Leatherjackets, particularly the pattern of landings in time, strongly argues for the use of topographic memory. Analysis of landings in relation to the previous take-off point, depending on whether a high or a low intake rate had been experienced there, showed that landings tended to be close if intake had been high, and farther away if previous intake had been low (Fig. 32). This negative correlation between landing distance and prior intake rate persists even on the finest scale achieved (Fig. 33, data grouped in meter classes). That this fine-scale topographic memory may be overruled in some situations is apparent when switches to other prey habitats intervene (Fig. 35). Use of topographic cues on a meter by meter scale, implies at the very least, a clumping in prey distribution, a pattern which has been verified by absolute sampling at the smallest plot-size considered (25 cm², see Table 11).

8) Is the threshold intake rate for Leatherjacket exploitation discovered for the individual Starling observed in 1979 always the same? By considering visits to 400 m² plots in the Leatherjacket grid in relation to directly observed intake rates (Fig. 36) thresholds were found to vary from year to year. The simplest criterion for the individual bird is to rely on its accumulated experience on intake rates, and set the threshold equal to the mean for that period (Fig. 37). Laboratory tests confirm the adjustability of the rejection threshold (Fig. 38).

9) The simplest form of foraging trip consists of a flight out, collection of prey at the hunting site, and flight back to the nest with prey. Depending on the roundtrip flight time as well as the cumulative intake, Charnov & Orians' model (Fig. 40) can be used to predict the optimal loadsize, i.e. how many prey should the Starling collect for its

nestlings in one trip. Since the fit to the empirical data is a reasonable one (Figs. 41 and 42) further analysis of the mechanisms the parent relies on in deciding on load size should be undertaken.

10) Does the parent Starling deplete the prey stock to such an extent that its intake rate suffers, hence leading to abandonment of the site? Our best data on the short-term influence of prey removal on subsequent hunting success results from experiments with small enclosures on the Leatherjacket grid where two captive birds were introduced, one after the other. The second bird always suffers a depressed intake rate (Fig. 47), an effect much stronger than can be explained by the absolute number of prey removed by the first bird. The most likely explanation for this is that the prey are differentially available for capture. This finding leads one to expect that birds will tend to abandon a site after only a small proportion of the prey stock has been removed, since even at modest levels of depletion intake rate will decline sharply. The 7-day Leatherjacket exploitation cycle watched in detail yields the estimate, that only twenty percent of the prey were removed from the best areas by all the Starlings together (Fig. 45). It follows that prey sampling alone, even though completely accurate, is inadequate to predict impact and/or potential intake rate of the predator. The problem of differential availability and the related phenomenon of depleting the catchable fraction, i.e. creaming-off the prey, is an unwelcome reality that must be faced in any field study.

11) In the final synthesis, it is argued that two facets from the Starling work deserve incorporation in general foraging theory. Discontinuities in the distribution of the prey cannot be adequately described by employing a one-level concept of patch. Instead, it is argued that patches exist at two levels (Fig. 50): At one level micro-patches can be distinguished; these are the indivisible units of prey distribution characterized by MacArthur's repeatability concept within which prey encounter is random; due to these features and their very small scale, exploitation is short-term. At the other level we have the macro-patch. This consists of a cluster of micro-patches and prey distribution is of low repeatability or even unique: the bird exploits these centres by relying on long term spatial memory. It is at this level that intake rate has decisive influence. Although it can be argued that the habitat characters causing discontinuities in prey distribution do in fact form a continuum we prefer to distinguish two discrete levels of organization because we feel these are entities in the decision structure of the predator.

12) The second facet deemed widely applicable is the hypothesis that the decision on prey species precedes the decision on where to go (Fig. 52). We argue that current profitability theory offers a reasonable basis for interpreting the decisions governing choice of site within one prey species, but we wish to emphasize that the decision on which prey species to collect next is of a higher order in the hierarchy of decisions: in the nestling situation this is influenced by the compromise between the physiological demands of the brood and the foraging limits of the parent. Although we do not yet understand how these limits are set, both a limit on hunting time as well as energy expended are liable to be involved. Athough there is concrete evidence for the existence of the fine-scale spatial level in the decision hierarchy (level III corresponding with the macro-patch) we have inserted an undefined abstraction at the level of a conglomeration of macro-patches ("area") to cover the possibility that there is some generalization (for example in "remembering" intake rates) above level III.

9. REFERENCES

Beukema, J. J. 1968. Predation by the three-spined stickleback (Gasterosteus aculeatus L.), the influence of hunger and experience. Behaviour 31: 1—126.

Biebach, H. 1979. Energetik des Brütens beim Star (Sturnus vulgaris). J. Orn. 120: 121—138.

Charnov, E. L. 1973. Optimal foraging: some theoretical explorations. Ph. D. thesis, University of Washington.

Charnov, E. L. & G. H. Orians. 1973. Optimal foraging: some theoretical explorations. Publ. of Biol. Dept. University of Utah, S.L.C.

Cowie, R. J. 1977. Optimal foraging in Great Tits (Parus major). Nature 268: 137—139.

Croze, H. J. 1970. Searching image in carrion crows. Z. Tierpsychol. Beiheft 5: 1—85.

Davies, N. B. 1977. Prey selection and social behaviour in wagtails (Aves: Motacillidae). J. Anim. Ecol. 46: 37—57.

Dawkins, R. 1976. Hierarchical organisation: a candidate principle for ethology. In: P. P. G. Bateson & R. A.

Hinde (eds.). Growing points in ethology. Cambridge University Press.

Dawkins, M. 1971. Perceptual changes in chicks, another look at the "search image" concept. Anim. Behav. 19: 566—574.

Drent, R. H. 1978. Investeren in nakomelingschap (Investment in offspring). Inaugural lecture, Groningen: 1—36

Drent, R. H. & S. Daan. The prudent parent: Energetic adjustments in avian breeding. Ardea (in press).

Dunnet, G. M. 1955. The breeding of the Starling (Sturnus vulgaris) in relation to its food supply. Ibis 97: 619—622.

East, R. & R. P. Pottinger. 1975. Starling (Sturnus vulgaris L.) predation on grass grub (Costelytra zealandica (White), Melolonthinae) populations in Canterbury. N. Z. J. Agric. Res. 18: 417—452.

Goss-Custard, J. D. 1977. Predator response and prey mortality in the redshank (Tringa totanus L.) and a preferred prey (Corophium volutator Pallas). J. Anim. Ecol. 46: 21—36.

Hairston, N. J., R. W. Hill & U. Ritte. 1971. The interpretation of aggregation patterns. In: G. P. Patil, E. C. Pielou & W. E. Waters (eds.). Statistical Ecology 1: Spatial Patterns and Statistical Distributions. Penn. State University Press, Philadelphia.

Herrnstein, R. J. & D. H. Loveland. 1975. Maximising and matching on concurrent ratio schedules. J. Exp. Anal. Behav. 24: 107—116.

Hubbard, S. F. & R. M. Cook. 1978. Optimal foraging by parasitoid wasps. J. Anim. Ecol. 47: 593—604.

Jong, W. H. de. 1922. Over Emelten. Pub. Plantenziektenk. Dienst Wageningen 28.

Kacelnik, A. 1979. Studies on foraging behaviour and time budgeting in Great Tits (Parus major). Ph. D. thesis, University of Oxford.

Kamil, A. C. 1978. Systematic foraging by a nectar-feeding bird, the Amakihi (Loxops virens). J. Comp. Phys. Psych. 92: 388—396.

Kendeigh, S. C., V. R. Dolnik & V. M. Gavrilov. 1977. Avian Energetics. In: J. Pinowski & S. C. Kendeigh (eds.). Granivorous birds in ecosystems. Cambridge Univ. Press: 127—204.

King, J. R. 1974. Seasonal allocation of time and energy resources in birds. In: R. A. Paynter (ed.). Avian Energetics, Publ. Nuttall Orn. Club, No. 15: 4—85.

Kluyver, H. N. 1933. Bijdrage tot de biologie en de ecologie van de Spreeuw (Sturnus vulgaris vulgaris L.) gedurende zijn voortplantingstijd. Pub. Plantenziektenk. Dienst Wageningen.

Krebs, J. R. 1978. Optimal foraging: decision rules for predators. In: J. R. Krebs & N. B. Davies (eds.). Behavioural ecology, an evolutionary approach, Blackwell Scientific Publications, Oxford, London, Edinburgh, Melbourne.

Krebs, J. R., J. C. Ryan & E. L. Charnov. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. Anim. Behav. 22: 953—964.

Krebs, J. R., J. T. Erichsen, M. I. Webber & E. L. Charnov. 1977. Optimal prey selection in the Great Tit (Parus major). Anim. Behav. 25: 30—38.

Krebs, J. R., A. Kacelnik & P. J. Taylor. 1978. Optimal sampling by foraging birds: an experiment with Great Tits (Parus major). Nature 275: 27—31.

Lack, D. 1948. Natural selection and family size in the Starling. Evolution 2: 95—110.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Clarendon Press, Oxford.

Lack, D. 1966. Population studies of birds. Clarendon Press, Oxford.

Lind, H. 1965. Parental feeding in the Oystercatcher (Haematopus o. ostralegus (L.)) Dansk. orn. Foren. Tidsskr. 59: 1—31.

Lorenz, K. Z. 1949. Ueber die Beziehungen zwischen Kopfform und Zirkelbewegung bei Sturniden und Ikteriden. In: E. Mayr & E. Schütz (eds.). Ornitologie als biologische Wissenschaft.

MacArthur, R. H. 1972. Geographical Ecology. Harper & Row.

MacArthur, R. H. & E. R. Pianka. 1966. The optimal use of a patchy environment. Amer. Natur. 100: 603—609.

McFarland, D. J. 1977. Decision making in animals. Nature 269: 15—21.

McFarland, D. J. 1978. The assessment of priorities by animals. In: Dempster, M. & D. J. McFarland (eds.). Animal Economics. London, Academic Press.

Moss, R., G. R. Miller & S. E. Allen. 1972. Selection of heather by captive red grouse in relation to age of the plant. J. Appl. Ecol. 9: 771—781.

Orians, G. H. & H. S. Horn. 1969. Overlap in foods and foraging of four species of blackbirds in the Potholes of central Washington. Ecology 50: 930—938.

Orians, G. H. & N. E. Pearson. 1979. On the theory of central place foraging. In: D. F. Horn (ed.). Analysis of Ecological Systems. Ohio State University Press: 155—177.

Perrins, C. M. 1965. Population fluctuations and clutch-size in the Great Tit (Parus major L.). J. Anim. Ecol. 34: 601—647.

Pfeifer, S. & W. Keil. 1958. Versuche zur Steigerung der Siedlungsdichte höhlen- und freibrütender Vogelarten und ernährungsbiologische Untersuchungen Nestlingen einiger Singvogelarten in einem Schadgebiet des Eichenwicklers (Tortrix viridana L.) im Osten von Frankfurt am Main. Biol. Abh. 15/16: 1—52.

Pulliam, H. R. 1975. Diet optimisation with nutrient constraints. Amer. Nat. 109: 765—768.

Pulliam, H. R. 1980. Do chipping sparrows forage optimally? Ardea (in press).

Pyke, G. H., H. R. Pulliam & E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52: 137—154.

Royama, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits (Parus major L.). Ibis 108: 313—347.

Royama, T. 1970. Factors governing the hunting behaviour and the selection of food by the Great Tit (Parus major L.). J. Anim. Ecol. 30: 619—668.

Royama, T. 1971. Evolutionary significance of predators response to local differences in prey density: a theoretical study. In: P. J. den Boer & G. R. Gradwell (eds.). Dynamics of populations, Proc. Adv. Study Inst. Oosterbeek 1970, Pudoc, Wageningen.

Schneider, W. 1972. Der Star (Sturnus vulgaris). Die Neue Brehm. Bücherei, A. Ziemsen Verlag, Wittenberg Lutherstadt.

Schoener, T. W. 1971. Theory of feeding strategies. A. Rev. Ecol. Syst. 2: 359—404.

Smith, J. N. M. 1974a. The food searching behaviour of two European thrushes. I. Description and analysis of search paths. Behaviour 48: 276—302.

Smith, J. N. M. 1974b. The food searching behaviour of two European thrushes. II. The adaptiveness of the search patterns. Behaviour 49: 1—61.

Smith, J. N. M. & R. Dawkins. 1971 The hunting behaviour of individual Great Tits in relation to spatial variations in their food density. Anim. Behav. 19: 695—706.

Smith, J. N. M. & H. P. A. Sweatman. 1974. Food searching behaviour of titmice in patchy environments. Ecology 55: 1216—1232.

Southwood, T. R. E. 1978. Ecological methods. Chapman & Hall, London.

Thomas, G. 1974. The influences of encountering a food object on subsequent searching behaviour in Gasterosteus aculeatus L. Anim. Behav. 22: 941—952.

Thomas, G. 1976. Gust and Disgust or the causes of Alliesthesia: Motivational changes upon exposure to food stimuli in Gasterosteus aculeatus (L.). Ph. D. thesis, University of Groningen.

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. & R. H. Drent. 1980. The Starling as a successful forager. In: C. J. Feare & E. N. Wright (eds.). Understanding Agricultural bird problems (in press).

Tinbergen, L. 1960. The natural control of insects in pine woods. I. Factors influencing the intensity of predation in song birds. Arch. Néerl. Zool. 13: 265—343.

Tinbergen, N., M. Impekoven & D. Franck. 1967. An experiment on spacing out as defence against predators. Behaviour 28: 307—321.

Torre-Bueno, J. R. & J. Larochelle. 1978. The metabolic cost of flight in unrestrained birds. J. Exp. Biol. 75: 223—229.

Westerterp, K. R. Nestling energy balance in relation to brood size in the Starling, Sturnus vulgaris. Ardea (in press).

Zach, R. & J. B. Falls. 1978. Prey selection by captive ovenbirds (Aves: Aprulidae). J. Anim. Ecol. 47: 929—943.

Zach, R. & J. B. Falls. 1979. Foraging and territoriality of male ovenbirds (Aves: Parulidae) in a heterogeneous habitat. J. Anim. Ecol. 48: 33—52.

10. SAMENVATTING

Op het Waddeneiland Schiermonnikoog werden zes seizoenen veldwerk besteed aan het toetsen van de huidige voedselzoektheorie. Als centrale vraag werd gesteld of Spreeuwen beslissingen over de keuze van prooisoort en landingsplaats nemen met het doel een zo hoog mogelijk energetisch rendement te behalen. De kernvraag is of dit door de theorie (Royama, MacArthur) geformuleerde doel ook werkelijk voor de dieren geldt.

Om deze hypothese in het veld te toetsen werden met behulp van automatische camera's gegevens over het dieet van de jongen van een bepaald nest verzameld (Fig. 7). De vogel zelf bediende de sluiter door met de kop een fotocelgordijn te onderbreken. Tegelijkertijd werd het gekleurringde vrouwtje van hetzelfde nest continu gevolgd om gegevens over haar tijdsbesteding (Fig. 5), plaatskeuze en vangsnelheid te verkrijgen. Om gegevens over de rol die ruimtelijke leerprocessen spelen te verzamelen werden in het laatste seizoen bovendien synchroon gegevens verzameld over de exacte positie van landingsplaatsen met behulp van een optische afstandsmeter. Ter ondersteuning van de veldgegevens werden veld- en laboratoriumexperimenten gedaan, waarbij een voedertafel gebruikt werd. Deze voedertafel bestaat uit een blad met gaten, afgedekt met rubber flappen. Onder de flappen kan al of niet een prooi zitten. De Spreeuw is in staat om met een sperrende beweging de flappen te openen en de prooi eronder te vangen. Door een ladensysteem is het zelfs mogelijk de beloning precies in te stellen.

Het menu van de jonge spreeuwen bestaat in hoofdzaak uit enkele prooisoorten; dit geldt voor alle jaren (Tabel 4). De belangrijkste prooisoorten zijn *Tipula paludosa* M (Emelt), *Cerapteryx graminis* L. (rups), *Hadena monoglypha* (rups) en *Telephorus fuscus* (zachtschildkever). Deze worden op verschillende plekken verzameld, de Emelt in de polder dichtbij het nest, de rupsen en de kevers in de kwelder verderop (Fig. 10).

De ouderspreeuw staat bij het verlaten van de nestkast voor de beslissing welke prooi ze moet halen. Omdat de belangrijkste prooisoorten in verschillende gebieden voorkomen is het voor de waarnemer mogelijk om de keuze van de ouder te kwalificeren als een "*Tipula*-" of een "*Cerapteryx*"-keuze, te meer daar de dieren zeer gericht òf naar de polder òf naar de kwelder vliegen.

Uit de directe waarnemingen van de vangsnelheid van Emelten blijkt dat deze een dagritme heeft, met een piek in het midden van de dag (Fig. 13). Uit het fotomateriaal blijkt echter dat de Emelten niet volgens deze trend naar de jongen gebracht worden (Fig. 12). Hoewel we niet beschikken over directe gegevens van de vangsnelheid van rupsen door de dag, wijzen berekeningen aan de hand van het fotomateriaal erop dat er bij de rupsen ook een dergelijke discrepantie is. Experimenten waarbij de honger van de jongen werd gemanipuleerd en het effect op de prooikeus van de ouders werd gemeten (zie verderop) maken het aannemelijk dat dit een effect is dat door de dagelijkse variatie in de honger van de jongen wordt bepaald, en dus niet door het rendement alleen. Daar rupsen van de verre kwelder komen is de tijd nodig om een rups te verzamelen veel langer (7×) dan voor een Emelt. Vanuit dit gegeven is het ook niet mogelijk binnen het raamwerk van de theorie (zo hoog mogelijk rendement) te begrijpen waarom Spreeuwen wel rupsen halen. Veldexperimenten waarbij beide prooitypen werden aangeboden, tonen aan dat de ouders inderdaad een sterke voorkeur voor de rupsen hebben.

De eerdergenoemde experimenten waarbij de honger van de jongen gemanipuleerd werd maken het zeer aannemelijk dat we met een kwaliteitsaspect te maken hebben (Tabel 6, Fig. 18). Wanneer de vraag van het nest sterk toeneemt beslist de ouder de makkelijk te halen prooi te nemen, waarbij de jongen, door honger gedwongen, de bruine bonen maar zoet moeten vinden. Loopt door de "injectie" aan energie de honger van de jongen weer terug, dan zal de oudervogel geleidelijk meer voedsel van hoge kwaliteit in het dieet opnemen (rupsen) (Figs. 19, 20, 21). We weten nog erg weinig van de fysiologische aard van het kwaliteitsverschil tussen deze prooisoorten. Wel heeft Kluyver aannemelijk gemaakt dat Emelten indien lang en in grote hoeveelheden gevoerd, nadelige gevolgen voor de jongen opleveren (Fig 23). Dit komt tot uiting in een sterke vervuiling van het nest doordat de waterig geworden faeces van de jongen niet door de ouders kunnen worden verwijderd. Indirecte schattingen van het dieet van het vrouwtje maken aannemelijk dat zij ook haar eigen menu sterk verandert, afhankelijk van de vraag van het nest. Bij een grote vraag eet ze zelf nauwelijks rupsen, maar gebruikt die tijd voor het zoeken van voedsel voor de jongen (Fig. 22). Dit doet vermoeden dat het vrouwtje zelf in staat is de nadelige gevolgen van een tijdelijk rupsenarm dieet te ondervangen.

Het is van groot belang dat meer werk wordt verricht aan de fysiologische aspecten van dit soort prooikeuzes om uiteindelijk tot een goed begrip van predatie te komen. Omdat dergelijke aspecten minder belangrijk zullen zijn bij de keuzes tussen individuen van één prooisoort hebben we ons er in de rest van het verhaal op toegelegd om dezelfde principes te toetsen binnen één prooisoort.

Wanneer een oudervogel besloten heeft om een bepaalde prooisoort te nemen is de volgende beslissing waar te landen. Dit probleem hebben we in de polder bekeken, waar door de schaal van het terrein en de positie van landingsplaatsen de meest nauwkeurige analyse mogelijk was. Omdat we met leerprocessen te maken hebben concentreren we ons op een individu, het vrouwtje in dit geval, met de hoop de belangrijkste factoren op te sporen, om later gerichte vragen te kunnen stellen voor een analyse op populatieniveau. Met behulp van een optische afstandsmeter werden de posities van de landingsplaatsen en opeenvolgende zoekpaden ingemeten op een tijdsbasis van 10 sec. voor een individueel vrouwtje gedurende zeven dagen continu waarnemen (Fig. 25).

Summatie van de zoekpadmetingen laten zien dat er in de waarnemingsweek van drie exploitatiecentra kan worden gesproken, die zijn gescheiden door gebieden met weinig bezoek (Fig. 28). Uit synchrone, direkte, waarnemingen van de vangsnelheid bleek dat de meest bezochte gebieden ook de hoogste vangsnelheid opleverden. Een uitgebreid monsterprogramma laat zien dat dit ook de gebieden met de grootste Emeltendichtheid zijn. In 1979 blijkt de grens van het exploiteerbare gebied voor de Spreeuw bij een dichtheid van ongeveer 70 Emelten per m² te liggen (Fig. 29). Uit experimenten met voedertafels, waarbij de vangsnelheid voor een wilde Spreeuw kon worden ingesteld, bleek dat de veranderingen daarin ook inderdaad veranderingen in bezoek-frequentie tot gevolg hebben (Fig. 30).

Het verloop in de tijd van de exploitatie van Emeltengebieden, speciaal de keuze van de landingsplaatsen, wijst sterk op het belang van een topografisch geheugen. De afstand tussen een landingsplaats en het opvliegpunt van het vorig bezoek is sterk afhankelijk van de vangsnelheid bij dat vorige bezoek. Een hoge vangsnelheid vergroot de kans dat een volgende landing dichtbij is, terwijl een lage vangsnelheid juist het tegenovergestelde effect veroorzaakt. (Fig. 32). Op welk een fijne schaal dit een rol speelt wordt duidelijk als de gegevens worden opgesplitst in de kleinst mogelijke klassen van 1 m. Het gebied dat een Spreeuw selectief kan kiezen of mijden heeft een straal van rond de drie meter (Fig. 33).

We wisten al dat de honger van de jongen invloed op de prooikeuze heeft, maar door opsplitsing van de gegevens (Fig. 35) kunnen we suggereren dat de honger van de jongen ook invloed op de plaatskeuze van de oudervogel kan hebben. Als de jongen minder honger hebben, en de ouders toch naar de polder gaan, spenderen ze waarschijnlijk hun tijd meer op onbekende gebieden. Experimenteel kan dit gebied makkelijk ontsloten worden door tegelijkertijd de honger van de jongen op korte termijn te manipuleren en de plaatskeuze van de ouders te meten.

Het gebruik van een zo fijn topografisch geheugen moet zijn overlevingswaarde aan het karakter van de prooiverspreiding ontlenen. Inderdaad blijkt dat de prooiverspreiding zelfs op de kleinst gemeten eenheden (25 m²) geklusterd is. De volgende vraag is of de dichtheid waarbeneden een Spreeuw een voedselzoekgebied verwerpt altijd dezelfde is als in 1979. Voor vier waarnemingsjaren werden bezoeken aan twaalf 400 m² vakken geregistreerd en opnamesnelheden gemeten (Fig. 36). Het blijkt dat de verwerpingsdrempel van jaar tot jaar verschilt. Het meest eenvoudige criterium voor het individu lijkt een drempel, die afgeleid is van de eigen gemiddelde opname over de periode (Fig. 37). In laboratoriumexperimenten bleek de verwerpingsdrempel inderdaad aanpasbaar aan de situatie (Fig. 38).

Het basiselement in de dag van een Spreeuw die voedsel voor zijn jongen zoekt is de voedselvlucht, waaronder we de vlucht naar het fourageergebied, het fourageren ter plekke en de vlucht terug verstaan. Charnov & Orians formuleerden een model (Fig. 40) op basis waarvan de vliegtijd van een voedselvlucht en de cumulatieve opname tijdens het voedselzoeken de optimale lading aan terug te brengen prooien konden bepalen. De voorspellingen passen aardig bij de door ons gevonden waarden (Figs. 41, 42) en het lijkt dan ook zeer de moeite waard om de achterliggende mechanismen verder te analyseren.

We komen nu aan de vraag toe in hoeverre het vrouwtje haar eigen fourageermogelijkheden beïnvloedt door het wegeten van prooien. We verwachten dat terwijl zij prooien wegeet, ze haar eigen vangsnelheid ziet verminderen en uiteindelijk het gebied moet verlaten. De beste gegevens betreffende dit punt komen van een experiment over de korte-termijneffecten van het wegeten van prooien op de opnamesnelheid van de Spreeuw. Paren in de winter gevangen Spreeuwen werden, de één na de ander, in een kleine kooi op het Emeltengebied los gelaten. Van beide dieren werd de opnamesnelheid gemeten, en daar ook het aantal prooien dat tijdens de proef gegeten werd bekend was, kon door uitgraving van alle Emelten na de proef de aanvangsdichtheid voor beide experimenten berekend worden. Het blijkt dat de tweede vogel ten opzichte van de aanwezige dichtheid van Emelten een sterk verlaagde opname heeft (Fig. 47). De meest plausibele uitleg voor dit effect is dat individuele Emelten verschillen in vangbaarheid, waarbij het eerste beest zich concentreert op de makkelijkst vangbare fractie. Uit deze resultaten verwachten we dat de wilde Spreeuwen een gebied zullen verlaten lang voordat absolute uitputting duidelijk wordt. Dit is in overeenstemming met de gegevens, daar één van de gebieden die werd geëxploiteerd reeds verlaten werd toen slechts 10% van de prooien was weggegeten (Fig. 45). In overeenstemming met onze kooiexperimenten bleek opnieuw dat er een scherpe teruggang in vangsnelheid werd geconstateerd. In studies over voedselzoeken is dit "afromen" door de predator een essentieel gegeven voor elk veldwerk.

Uiteindelijk beargumenteren we dat twee facetten van het Spreeuwenwerk in de huidige voedselzoektheorie moeten worden opgenomen. Het blijkt niet mogelijk om onregelmatigheden in de prooiverspreiding te vangen in een model met slechts één niveau van "gegroepeerdheid", in de Engelse literatuur als "patch" aangeduid. Vanuit de gegevens zoals wij die verzameld hebben maken we duidelijk dat deze "patches" op zijn minst op twee niveaus bestaan (Fig. 50).

De "micro-patch" is het kleinste ondeelbare element in de prooiverspreiding waarvoor de aanname van MacArthur geldt. Deze houdt in dat eenheden zich vaak herhalen, zodat de vogel een duidelijke statistische voorspelling over hun eigenschappen kan opbouwen en dat binnen de eenheden de ontmoetingskans met een prooi lukraak is. Door de schaal van de "micro-patches' is de exploitatie een zaak van korte termijn.

Op een ander niveau hebben we de "macro-patch", bestaande uit een cluster van "micro-patches" waarvan de rangschikking nauwelijks herhaald wordt in de omgeving of zelfs uniek is. De vogel moet daarom tijdens het exploiteren van deze eenheden een lange termijn ruimtelijk geheugen gebruiken. Op dit niveau heeft de vangsnelheid een beslissende invloed op de plaatskeuze.

Hoewel het mogelijk is om de omgeving van een predator in plaats van verdeeld in discrete niveaus als continuum te beschouwen, hebben wij de voorkeur aan het eerste gegeven omdat we verwachten dat de predator bij zijn beslissingen met dergelijke eenheden werkt. Het tweede facet dat wij in de theorie ingebouwd willen zien is de hypothese dat prooikeuze vooraf gaat aan gebiedskeuze van de predator (Fig. 52). Wij beargumenteren dat de beslissingen van een vogel ten opzichte van één prooisoort door de profitability-theorie (Royama) gedekt worden, maar leggen er tegelijkertijd de nadruk op dat de beslissing, welke prooisoort te halen van een hogere orde is, die niet alleen door het rendements-concept kan worden verklaard.

Naast de belangrijke rol die de fysiologische behoeften van de jongen in de prooikeuze spelen bestaan er concrete feiten om het bestaan van een fijnmazige ruimtelijke component in de plaatskeuze binnen een prooisoort in de hiërarchie van beslissingen te beargumenteren (niveau III). Tussen deze twee beslissingsniveaus hebben wij een veel minder onderbouwd niveau ingevoegd, dat van een conglomeratie van micro-patches (niveau II), om de mogelijkheid open te houden dat de vogel ook op dat niveau generaliseert, bijvoorbeeld bij het onthouden van de vangsnelheid.

Op het moment zijn wij bezig om met laboratoriumexperimenten meer vat te krijgen op de eenheden die een vogel gebruikt en hopen daar later op terug te komen.