Foraging behaviour and habitat use in the European Starling, *Sturnus vulgaris*, in an agricultural environment

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Suddenly hooligan baby starlings
Rain all round me squealing,
Shouting how it's tremendous and everybody
Has to join in and they're off this minute!

.....

Sizzling bodies, snaky black necks craning
For a fresh thrill - Where next? Where now?
                                        Where? - they're off
All rushing after it
Leaving me fevered, and addled.

Where I sit writing my letter
Ted Hughes 1986

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Abstract

Recent changes in agricultural practice have reduced the diversity of habitats for a number of bird species, including the European Starling *Sturnus vulgaris*. I investigated the distribution of a starling population on farmland, and related this distribution to the availability of suitable habitats by studying the foraging behaviour of individual birds.

I observed a preference of the overwintering flock for established pasture fields, particularly those which were closer to the central roost, which had shorter grass and which provided feeding areas further from hedges. I also demonstrated the role of leatherjacket *Tipula paludosa* availabilities in influencing the starlings' choice of feeding site. These prey were shown experimentally to be preferred over earthworms *Lumbricus* spp. which were the other main type of invertebrate prey available. I was unable to detect any systematic temporal pattern of habitat use which could have been linked to an appropriate theoretical framework (e.g. Ideal Free Distribution).

I investigated the impact of starling foraging on prey availability by observing the behaviour of captive starlings allowed to forage in small enclosures. These experiments indicated that, at the level of foraging pressure expected in natural flocks, there was no significant resource depression during a single flock feeding visit to any one site. Furthermore I proposed that the extent of resource depression during the winter was insufficient to cause a shift in the birds' choice of foraging habitat over this period.

The apparent lack of effects of resource depression raised the question of why starlings did not feed in the most preferred fields all the time. Further enclosure experiments investigated how an individual's foraging success might be affected by feeding with conspecifics. I found no evidence for enhancement or depression of foraging success as a result of feeding where another bird had just previously foraged, and little evidence for an effect of feeding in the presence of two other birds, despite changes in vigilance and time spent fighting. A possibly greater heterogeneity of these effects when in the natural flock situation was considered in relation to the observed flock departures. These and other effects (e.g. sampling the environment) were discussed as possible causes for the observed flock movements between fields.

A final enclosure experiment investigated the impact of starling foraging on prey availability during the breeding season and demonstrated significant resource depression in a preferred field over the chick-feeding period. I then discussed starling foraging and the availability of suitable habitats in relation to the documented population decline of this species.

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Chapter 1

General Introduction

1.1 Introduction

The characteristically patchy landscape of traditional British farmland is important to a large number of bird species, providing them with a diverse range of habitats. Recent changes in agricultural practice have, however, challenged this diversity, with deleterious consequences for many species (Potts 1991). In the light of these current agricultural trends, we need to explore whether bird populations can continue to survive on farmland, and to consider the implications of land-use changes for those species concerned.

The European Starling (hereafter referred to as the starling) is a particularly abundant species on pastoral farmland, and its utilisation of such an environment might be expected to be strongly influenced by patterns of agricultural land-use. Despite a population decline recorded in recent years (Feare 1987), the starling is still regionally a very abundant species. Its general biology and ecology have been widely studied (for review see Feare 1984), thus it provides us with a suitable model species which can be used to examine some of the issues important in relating population distributions to land-use changes.

1.2 The study species

In the light of Feare's (1984) extensive review I shall restrict my own description of the starling to a summary of those areas pertinent to this research.

1.2.1 Distribution

The starling is widespread throughout the British Isles and Europe, as well as extending into western Asia. It has also been successfully introduced into North America, South Africa, southern Australia and New Zealand. However, despite the apparent success of this species in a diverse range of habitats, a number of studies have recorded a declining starling population, which was first reported in northern

Europe in the early 1960s (Coulson 1960; von Haartman 1978; Heggberget & Myrberget 1980; Ojanen *et al.* 1978, 1979; Tianen *et al.* 1989) and which has become increasingly apparent in Britain in more recent years (Feare 1987; 1994). Some reductions in the numbers of starlings were once thought to have been as a result of persecution of the species as a pest, but direct attempts at reducing populations (e.g. exploding the nocturnal roosts) were largely ineffectual due to the size of the source population which was able to replace very rapidly those birds which had been removed (Tahon 1980). More effective measures were those which prevented pest damage by denying the starlings access to the targeted food sources, such as cherry orchards and cattle sheds, from which economically significant losses have been reported (Feare 1980, 1989; Feare & Wadsworth 1981; Feare *et al.* 1981; Wright 1973).

The population decline can instead be attributed almost exclusively to changes in land-use and in agricultural practices. von Haartman (1978) cited agricultural biocides as a possible cause of reduced fecundity; the effects of biocides were also implicated by Ojanen *et al.* (1978, 1979), but they regarded changes in land-use, particularly afforestation, as a prime cause of the population decline. Tianen *et al.* (1989) discussed the effects of changes in farming on Finnish starling populations, describing the increasing areas of cereal and root crop monoculture which had replaced pasture and reduced the area of suitable foraging habitat for the starlings, thus causing a decline in the population.

In Britain, areas such as Norfolk, where vast areas of monoculture have replaced traditional mixed pasture and arable land, have also proved to be less favourable habitats for starlings (Summers & Cross 1987). These changes in land-use have restricted dramatically the amount of suitable feeding habitat, resulting in the documented population declines (Feare 1987; 1994).

1.2.2 Diet and foraging behaviour

One reason for the starlings' success in invading new habitats may be the flexibility of its diet. Although it relies for much of the time on soil invertebrates, it will feed on invertebrates picked from the surface of the ground or of leaves, and will also 'hawk' aerial insects. It captures prey from the upper soil layers by using a characteristic bill action. The combined stabbing and gaping action, termed 'Zirkeln' by Lorenz (1949), serves to push apart soil and dense vegetation, while the low positioning of the starling's eye-sockets in its skull allows it to focus its gaze between the opened mandibles so it can search the hole for prey. Such exploratory probes are made frequently by starlings, as they walk over a feeding patch, with the bird relying largely on visual cues to locate its prey.

A very diverse range of invertebrates has been documented in the starlings' diet (Kluyver 1933). During late summer, when insects are less abundant, fruit may become an important part of their diet, particularly for the recently fledged birds; grain found in harvested fields at this time of year will also be taken. Starlings will readily exploit 'artificial' sources of food, taking food scraps put out by people, and barley or commercial feed pellets found in cattle, pig and sheep barns. This observed flexibility in the starling's diet permits it to eat different food items at different times of the year, taking advantage of those sources of food which are most abundant in the different seasons, and reducing the risk of starvation.

In common with a number of other species (A. Gosler, pers. comm.) this foraging flexibility is further enhanced by the adaptability of the digestive physiology. The starling's gut shows seasonal changes in its length (Al-Joborae 1979) in response to seasonal changes in the proportion of vegetable matter in its diet; thus its intestine length increases during the winter, during which time a greater proportion of vegetable matter has been found in the starling's diet.

1.2.3 Annual cycle

For non-migratory populations territorial defence of nest sites begins in late January or February, when the male sings to attract a mate. Nest-building, mate guarding and copulations lead up to the first clutches being laid in early to mid April, although this is subject to climatic variation. The normal brood size is five eggs, with a maximum of eight. Incubation lasts for 12 days, so that the first chicks usually hatch near the beginning of May. Up to two broods may be raised by a pair of adults in any one year.

After fledging, the young birds remain close to their parents for the first few days, begging for and receiving food, but within a couple of weeks they gain independence and join other fledglings to feed in flocks. These flocks remain around the colony for a few more weeks, exploiting any readily available sources of food. It is these juvenile flocks that are considered to be the main culprits of losses to fruit orchards. During August and September the young, inexperienced birds will exploit the abundant soft fruits which may be a nutritionally important food source for them rather than competing with adults for scarce soil invertebrates (Herrera & Jordane 1981; Stevens 1985).

By late summer and early autumn the large flocks of juveniles disperse. Although British populations are largely non-migratory, some local movements do occur, as evidenced by the appearance of unmarked individuals in the winter population at Wytham, and the relatively stable size of the resident population.

1.2.4 Flocking behaviour

The starling is a gregarious species and its semi-colonial, synchronous breeding is another contributory factor to its success. Apart from breeding pairs, which often roost in their nest cavities, starlings roost communally at night. These roosts may afford the starlings better protection against predation, and may even serve as 'information centres' for the location of food resources (Ward & Zahavi 1973). Feare (1984) reviewed a number of studies which examined the possible energetic benefits to starlings of communal roosting. Yom-Tov *et al.* (1977) found that the temperature within a starling roost was 5.0 - 8.5°C higher than the surrounding area, but this was attributed to features of the roosting site, rather than to metabolic heat production by the starlings. They concluded that, for many individuals, the cost of flying from daytime feeding areas to communal night-time roosts was not compensated for by any energetic gains of communal roosting. Therefore, roosting must confer other advantages.

Aggregations of over 1,000,000 birds have been recorded at pre-roost assemblies by Feare (1984). At Wytham, the usual number of 300 birds was, on occasion, seen to rise to approximately 1,500 birds roosting at the study site. Such large numbers are never seen during the day, in feeding flocks, for which a few hundred is a more usual maximum; thus, daytime flocks may fly many miles to assemble at the night-time roosts. Wynne-Edwards (1929) documented a feeding area to roost site distance of 38 km, while a North American study observed distances of up to 80 km (Hamilton & Gilbert 1969).

In addition to the night-time roosts, starlings will also utilise day-time roosting areas, closer to the feeding sites, where any non-foraging time is spent resting, preening or singing. The relationship between these 'diurnal activity centres' (DAC's) and night time communal roosting sites was examined by Morrison & Caccamise (1985), who found that birds were more faithful to their DAC's than to the communal roosting areas. This pattern is particularly applicable to regions in which suitable feeding areas are sparsely scattered. For a site such as Wytham, where many of the birds are resident throughout the year, and which provides both suitable feeding and roosting areas, a largely consistent aggregation of birds tend to feed and roost at the same site.

During the non-breeding season starlings feed almost exclusively in flocks, the advantages of which will be discussed in detail in Chapters 7 & 8. When visiting a feeding site the whole flock shows movement across the area as each bird walks over the ground, generally in the same direction, in search of food items. Additional movement occurs via a 'rolling' mechanism whereby those birds towards the rear of the flock may fly up and move closer to the front, where they continue to feed.

1.3 The prey species

Despite the apparent flexibility of the starlings' diet, their most important food source for much of the year is soil invertebrates. For the Wytham birds the most abundant of these invertebrates are leatherjackets, which are the larvae of the common cranefly *Tipula paludosa*, and earthworms *Lumbricus* spp.

1.3.1 *Tipula paludosa*

The larval stage of this species has been documented as an important constituent of the starling's diet in a number of studies (e.g. Dunnet 1955; Tinbergen 1981). The smooth, grey grubs are found in upper soil and dense vegetation layers, particularly in limestone and alluvial grasslands (Coulson 1959). The life cycle is completed once a year with the imago stage emerging in late summer. Coulson (1962) recorded an emergence peak during mid July in Westmorland (Northern England), but he observed that emergence times from late August to mid October, with a peak in mid September, recorded at Rothamsted (Southern England) were more representative of English populations.

After emerging, the adults live for only a few days. They copulate and lay eggs almost immediately, so that eggs are usually located close to the place of emergence. Larvae emerge from the eggs approximately 14 days later, and they subsequently pass through the first two instars very rapidly, before reaching the third instar in which they overwinter for the next 25 weeks. During this time the larvae remain near the surface, only retreating deeper during periods of extreme weather, but never going below a depth of 150 mm (Rennie 1917). Rennie (1917) also observed the larvae forming compact earthen cells, which were believed to allow a period of quiescence under adverse conditions. For much of the life cycle, the larvae appear to be resistant to desiccation, only the newly laid eggs and first instar larvae being susceptible (Coulson 1962). Although the larvae tend to remain in the same areas, if their food supply becomes limiting they will show some surface migration (Rennie 1917), particularly on mild spring nights (Tinbergen 1981). A greater insight into the nature of vertical movements of the larvae, within the soil column, would provide a greater understanding of the starlings' patterns of habitat use, particularly in relation to renewal of prey availabilities once a patch has been foraged and depleted.

In spring the larvae pass through to the final instar and, as ambient temperatures increase, they show a rapid increase in biomass, reaching a maximum length of 40 - 50 mm. At this time, they start living in small J-shaped burrows (de Jong 1922) which, by the middle of June, are up to 50 mm deep. Pupation occurs in

July, the exact timing of which is determined by environmental conditions (e.g. dryness of the ground), followed by emergence in the late summer or early autumn.

1.3.2 Lumbricids

Earthworms are the other major type of soil invertebrate found at Wytham, and they form a part of the starlings' diet both during the winter and in the summer when the parent birds are rearing young. The commonest species in British grassland are *Lumbricus terrestris, Allolobophora longa, Allolobophora caliginosa* and *Octolasium cyaneum.* Of these, *L. terrestris* was the most commonly found species at Wytham.

In contrast to leatherjackets, the earthworm lifecycle can start at any time in the year (Edwards & Lofty 1972), although it is a temperature-dependent process and so shows some seasonal variation. Fewer cocoons, in which the ova are laid, are produced in wetter and colder conditions and there is a threshold at 3°C, below which none are produced. The number of cocoons peaks during spring and autumn.

Earthworms can continue to grow throughout the year but this is also a process that is dependent on environmental conditions; hence most growth generally occurs during the spring and autumn. During the summer, many species enter a period of diapause during which they coil up into a knot and encase themselves with mucus. They can respond to other periods of adverse conditions by going into temporary quiescence. This is a more frequent occurrence during the summer than in the winter, due to a greater tolerance of cold and wet conditions, than of hot and dry conditions.

The vertical distribution of earthworms is species-dependent. Further variation, within species, is determined by temperature and moisture of the ground. All of the species common in pasture go down to a depth of at least 100 mm. *L. terrestris* can reach depths of 2.5 m, although it is more commonly found at a depth of approximately 1 m. During January and February most earthworms retreat to below 75 mm but as the soil temperature increases some species rise to the top 75 mm layer, retreating down again during the summer as temperatures rise further and the soil dries out.

1.4 The study site

The University Farm, Wytham, Oxfordshire (OS grid reference SP 4708) is a mixed pasture and arable farm, situated on part of the river Thames flood-plain, to the west of Oxford. The northern edge of the farm is bordered by the Thames, a tributary of which also forms the eastern boundary. The western edge of the farm rises up to Wytham Great Wood, while the southern boundary extends to Wytham village. A soil survey of the study area, conducted by the Soil Survey and Land Research Centre, for the Environmental Change Network (M. Morecroft, pers. comm.), showed that many of the fields bordering the river are based on alluvial clay. A large area of this ground comprises grey stoneless clay (Fladbury series) which is frequently waterlogged by fluctuating groundwater levels, while a smaller area of the same region is better drained (Linnet series) but also susceptible to seasonal inundation by rising groundwater. The fields around the farm buildings are of well drained calcareous clay loam (Badsey series), which contrasts with the moderately well drained clay (Folksworth series) of those fields which lie between the farm and the woods, and are subject to some seasonal waterlogging.

The total study area of 226.4 hectares comprised 39 fields and a range of types of cultivation which included winter wheat, winter barley, oil seed rape as well as temporarily uncultivated fields assigned under the Common Agricultural Policy (Arable Area Payments). Other fields of permanent pasture or grass-ley were grazed by sheep and cattle and / or used for silage cultivation.

A nest-box colony was established around the farm buildings in 1977 (Evans 1980). This was added to in 1985 (Wright 1990) to give 61 boxes, which were still present at the time of the present study (October 1991 - March 1994). Two further nest-box colonies, of 40 boxes each, were established in 1990 at adjacent sites, each approximately 1 km from University Farm. Evergreen trees at the University Farm site were used by the starlings during the non-breeding season as a night time roost site, while much non-foraging time during the day was spent resting on overhead wires at the north-east edge of the farm buildings.

The farm buildings themselves were visited frequently by the wintering starlings. Previous studies (for review see Feare 1984) have demonstrated the extent to which starlings may feed at such sites. Although I was unable to obtain data on the amount of food taken by the starlings from the barns and cattle sheds, the potential importance of such supplementary food sources to the starlings' daily energy requirements should not be overlooked (e.g. Feare & McGinnity 1986).

During the breeding season all breeding adults were colour-ringed. Additional birds were caught and colour-ringed during the winter by baiting a modified crow-trap which attracted birds during much of the winter. This ringing effort meant that at least 70% of the study population were marked and could be individually identified.

1.5 Research objectives

A knowledge of how individuals respond to variables in their environment is fundamental to an understanding of the behaviour and distribution of populations. More specifically, in order to explain how a population is distributed in response to the availability of food, it is necessary to examine foraging behaviour at the individual level.

Despite the value of such an approach, it has only been developed relatively recently, and the extent to which it can be used to examine the distribution of bird populations has yet to be realised to its full potential. Goss-Custard (1970a) demonstrated the usefulness of this kind of approach in his study of redshanks (*Tringa totanus*) in which he related the densities of feeding redshank to those areas of their estuarine habitat in which their feeding efficiency was highest. Extensive studies of oystercatchers (*Haematopus ostralegus*) have demonstrated the effect of differences in competitive ability on the distribution of individuals across a range of feeding sites (Goss-Custard *et al.* 1982a).

In parallel with these studies of the distribution of wader flocks in relation to the availabilities of estuarine invertebrates, I hoped to be able to explain some aspects of the starlings' utilisation of their agricultural environment by considering the availability of soil invertebrates to these birds. However, a more complete understanding of how individuals respond to the availability of resources may be achieved by having a theoretical framework from which to work. One such approach is that of the Ideal Free Distribution (IFD) theory, the application of which may be useful for understanding the important factors in the management of bird populations (Bernstein *et al.* 1991a).

The original IFD theory (Fretwell & Lucas 1970; Fretwell 1972; for review see Kacelnik *et al.* 1992) predicted how individuals were distributed within their environment in relation to the availability of resources. The model by Fretwell & Lucas (1970) made simple predictions based upon a small number of assumptions (i.e. individuals have perfect knowledge of their environment, there is no cost of moving between patches and all individuals are equal), but more recent refinements have taken into account competitive differences between individuals (Houston & McNamara 1988; Parker & Sutherland 1986; Sutherland & Parker 1985; 1992; Sutherland *et al.* 1988), the imperfect knowledge that individuals have, and the intrinsic need for learning about their environment (Bernstein *et al.* 1988), the cost of travelling between sites (Bernstein *et al.* 1991b), and the effect of the state of individuals, as represented by their energy reserves (McNamara & Houston 1990). The increasing complexity of these models creates a clearer theoretical understanding of how various factors contribute towards the distribution of individuals in relation to their resources. The importance of taking into consideration these modifications of the IFD was underlined by Kennedy & Gray (1993), who reviewed a number of empirical tests of the theoretical predictions. They found a systematic deviation from the theoretical IFD such that the distribution of organisms was consistently less extreme than the distribution of resources; thus they recommended that future tests of the IFD should take into account the consequences of factors such as competitive asymmetries and travel between sites.

With this kind of theoretical background in mind, I hoped to be able to relate my empirical observations of the starlings' use of their habitat to a theoretical framework, from which it might be possible to predict the consequences of future habitat changes on the starling population. This approach has recently been taken in other theoretical studies (Sutherland & Anderson 1993; Sutherland & Dolman 1994), and has been applied to populations of Bean Geese (*Anser fabalis*) and Wigeon (*Anas penelope*) by Sutherland & Allport (1994).

The majority of my work was conducted in the winter, during which time the starlings feed exclusively in flocks. The feeding ecology and behaviour of starlings during the breeding season has received considerable attention (Tinbergen 1981; Tinbergen & Drent 1980), the result of which has been a far greater understanding of the starlings' foraging strategies at this time of year. Far less is known, however, about the foraging strategies of starlings during the winter, and it is on these that I will concentrate for the majority of the study.

The first step to understanding how populations interact with their environment is to gain a clear picture of how that population is distributed; thus the initial objective of this study, which I deal with in Chapter 2, was to establish which parts of the available habitat the study population used the most. By quantifying the feeding site preferences of the resident starlings, I then hoped to establish some correlates for these preferences, both in terms of physical features of the birds' foraging habitats, and in terms of the availabilities of prey. The role of these invertebrate availabilities in influencing habitat choice are considered in Chapter 3, in which I also introduce the experimental technique which allowed me to obtain more detailed data on the foraging behaviour of individuals than can be obtained from merely observing individuals in the flock. A brief diversion from this technique is presented in Chapter 4, where I describe a laboratory experiment which explored a possible preference for leatherjackets over earthworms as an additional factor which may influence the starlings' habitat preferences.

In addition to ascertaining these preferences and the factors with which they may be correlated, I was also interested in examining temporal patterns of habitat use and the role of changes in prey availability in influencing the starlings' distribution. For much of the time the starlings fed as a single flock, which meant that I was effectively dealing with the movement of one unit between a number of habitats. This kind of situation is comparable to the study by Davies & Houston (1981) who described temporal movements of individual pied wagtails (*Motacilla alba*) around their habitat and related these movements to a 'temporal' Ideal Free Distribution. In a similar way, I might have expected the starling flock to show some kind of temporal pattern of habitat use which could be predicted on the basis of prey availabilities, and it was to this aspect of the starlings' habitat use that I was most interested in applying a theoretical framework.

In Chapter 5 I return to field experiments and address the effects of changes in the availability of prey on the starling's habitat use by examining the role of depletion of prey as a result of foraging by the starlings. Measuring the availabilities of prey and how these may change would not only relate to the patterns of starling habitat use, but would also provide an indication of the extent of the impact the overwintering population was having. In other words, given the amount of suitable habitat that was available, were the resident birds having a significant impact on those prey populations, and was resource abundance a limiting factor for the overwintering population at the present level of resource availability? This question is pursued in Chapter 6, in which I also take into account some of the implications of feeding in a flock rather than as a solitary individual. A further experiment is described in Chapter 7, in which I examine some additional effects of feeding in the presence of other birds, and ask whether this is likely to affect the starlings' distribution within their habitat. The experiment described in Chapter 8 represents a switch to the breeding season, in which I examine the impact of parental foraging by the starlings on the prey that remain in the environment, after overwinter depletion has already occurred.

The findings of all these chapters are reviewed in Chapter 9, in which I relate the results of the experiments to the original objectives, and address any new questions which may have arisen in the light of this research.

Chapter 2

The distribution of starlings in their environment

2.1 Introduction

In studying a species' distribution in relation to resource availability, it is necessary to establish how individuals use the available habitat. For starlings, most information on how they use farmland during the winter is, at present, based upon studies of large-scale flock movements (e.g. Summers & Cross 1987; Tucker 1992), as well as upon general observations of resident flocks (Feare 1980; 1981a). Information on how individual flocks use their habitat on a finer scale is lacking. East & Pottinger (1975) conducted a detailed study of the impact of New Zealand starlings on grass grub (*Costelytra zealandica*) populations and, although their study encompassed many of the pertinent questions I would like to consider in this work, they dealt with a system which comprised different invertebrate populations than those encountered by British populations of starlings. Tinbergen (1981) provided rigorous data for the distribution of parental starling foraging visits in relation to distributions of their prey. The question of how starlings apportion their visits during the breeding season is, however, very different from the question of how the overwintering flock is distributed between available habitats, and it is this latter question I wish to address in this chapter.

In addition to establishing overall preferences for particular habitat types, it is of interest to know how starlings use different fields on a temporal basis. Prey availability might be expected to change in time and space, with starlings causing local resource depression, which can then be restored while the flock feeds elsewhere. By utilising preferred fields in a systematic pattern, the starlings may be able to maximise prey capture rates so as to 'harvest' invertebrates from the soil (e.g. Brent Geese *Branta bernicla*, feeding on Sea Plantain *Plantago maritima*, Prins *et al.* 1980). However, complex interactions with prey densities may be unimportant to starlings and differences between fields arising through soil structure, crop height or local predation threat may dictate where starling flocks feed at any one time.

The influence of prey availability on the starlings' habitat preferences will be addressed in subsequent chapters. This chapter is restricted to a more descriptive study, in which I aim to explore how physical features of the birds' environment influence their choice of feeding habitat. I intend to quantify the feeding site preferences of the resident population throughout the winter, and to relate these preferences to field type, characterised by crop type and crop height, field area, distance to the nearest hedge, and the distance of the field from the central roost. Associations with other bird species are also investigated. Having established any feeding site preferences, a further objective was to determine whether these preferred sites were exploited systematically, thus enabling me to build a clearer picture of any spatio-temporal patterns of habitat use.

2.2 Methods

2.2.1 Study site

The study was carried out from November 1991 to March 1992 at the University Farm, and encompassed a total study area of 226.4 ha. This area comprised 39 fields which were classified into 9 different types of cultivation: 1) permanent pasture, 2) rough pasture, 3) new grass ley - re-seeded in the last year, 4) old grass ley - re-seeded more than a year ago, 5) bare ploughed ground, 6) winter wheat, 7) winter barley, 8) oil seed rape, and 9) maize. Information on these crop types, as well as the area of each field were obtained from farm records. The distances of fields from the farm buildings were calculated to the nearest 10 m using 1:5,000 scale maps, distances being taken from the estimated centre-point of each field. In order to estimate the mean distance to the nearest hedge within each field the distance was measured from the centre-point of each map grid-square (1 grid-sqare represented 1 ha) to the nearest hedgeline. All the values within each field were then averaged to give a mean distance to the nearest hedge for that field. Rainfall, and maximum and minimum temperature records for the preceding 24 hours were obtained from daily records collected at the adjacent University Field Station.

2.2.2 The census method

I selected a route which allowed me to census all parts of the study area. Although much of this route was taken in a vehicle, it was necessary to census some areas on foot. The order in which sites were visited was randomised to control for the effect of time of day, and I conducted a full census twice a week from 1st November 1991 to 17th March 1992. By mid-March, the height of many crops made estimation of starling numbers difficult. This time of year also signalled the break-up of winter feeding flocks prior to breeding; therefore the census was terminated then.

The census was carried out a total of 32 times and was conducted during mid morning (start 09:15 - 11:00 hrs; ranging from 2.5 to 4.5 hours after dawn), taking approximately 90 min. The total number of starlings seen during any one census was not affected by the time it took to complete the census (r^2=0.041, n=32, P=0.267), or by start time relative to dawn (r^2=0.021, n=32, P=0.428). I observed each site once during each census by scanning with 8x40 binoculars, and recorded the number of starlings seen on the ground (any birds in flight were excluded). If, during the census, the birds moved from a field which I had already visited, to a field not yet visited, I did not record the flock on the second occasion. Starlings resting or preening were only seen in the vicinity of the farm buildings. Hence, I took the number of birds in each field to represent the number actively feeding. I also recorded the numbers of other insectivorous birds, including Golden Plover *Pluvialis apricaria*, Lapwing *Vanellus vanellus*, Black-Headed Gull *Larus ridibundus*, Fieldfare *Turdus pilaris*, Redwing *Turdus iliacus*, Magpie *Pica pica*, Rook *Corvus frugilegus*, Crow *Corvus corone*, and Jackdaw *Corvus monedula*. The presence and number of Greylag Goose *Anser anser* and Canada Goose *Branta canadensis* was also recorded. Although these geese are not insectivorous, they fed in flocks and grazed the grass in some of the pasture fields, both factors possibly influencing the distribution of the starlings. Few birds smaller than Redwing were seen, and these species were ignored owing to the difficulty of censusing them accurately.

The numbers of cows and sheep were scored for each field, but as the cows spent much of the winter inside cow sheds and were only grazed in the fields for short periods at the beginning and end of the census period, their presence was not included in any analyses.

Once a week, the height of the crop was measured using a ruler placed on end in the sward. From this, fields were ranked into five sward height categories: 1) <2 cm, 2) 2-4 cm, 3) 4-6 cm, 4) 6-8 cm, and 5) 8-10 cm.

2.2.3 Intensive flock observations

In addition to this census data, further information on how the flock apportioned its time between different parts of the farm was collected during a total of nine all-day watches, between 29th November and 23rd January 1992. On each of these days I made observations of location and number of any feeding starlings at 0.5 h intervals throughout the day (approximately 08:00 - 16:30 hrs). For analyses of flock residence times I categorised a flock arrival as when a minimum of 10 birds had landed in a field. Subsequent additions to this group were not classed as further flock arrivals. I recorded a flock departure once the number of birds feeding at any one site fell below 10. I collected most of this data from the top of a grain silo, which provided a clear view of the majority of the fields used by the starlings. Those parts of the farm which I could not see from the silo were viewed from alternative sites at regular intervals. In order to avoid any disturbance to the birds I conducted all my observations at some distance from where the birds were feeding using binoculars or a telescope.

2.2.4 Data collection and analyses

In comparing the utilisation of different feeding sites and movements between them, it is not possible to say whether the starlings perceive these as distinct foraging patches. However, by treating each field as a separate and independent feeding site, I was at least able to deal with a spatial scale on which agricultural management and associated changes in land use occur. Therefore, the field represents the unit for all statistical analyses in this part of the study. The amount of foraging by the starlings was calculated as the number of starlings seen per hectare, thus controlling for the size of fields and availability of each field type, and was expressed as 'foraging density'.

These values were calculated for each field on each census and an overall mean for each field then obtained. Certain bird species were nearly always seen together and so for the purpose of analyses these were grouped: Rooks, Carrion Crows and Jackdaws were grouped as 'corvids' and Redwings and Fieldfares were grouped as 'thrushes'. The low number of observations of waders and geese precluded their inclusion in any further analyses. The large number of non-pasture fields with very low starling densities meant that the data were not normally distributed and the skew could not be corrected using transformations. In these cases non-parametric statistics were used in the analyses.

2.3 Results

2.3.1 Starling numbers

There were approximately 300 (range 90 to 480) starlings present over the duration of the study. At least 70% of these were colour-ringed and the continued presence of the majority of these individually marked birds indicated that they were resident on the farm for the whole study period. During each census, the birds were usually seen feeding together at one site in a single large flock. On some occasions, however, the flock fragmented into two, or three sub-flocks which fed at different sites around the farm.

2.3.2 The effect of season and weather

The dependence of the starlings on natural or artificial sources of food may have been linked to temperature or to time of year, but a multiple regression of temperature, date and rainfall on the numbers of starlings seen feeding in the fields did not reveal any significant effects overall (r^2=0.170, n=32, P=0.151). Within this regression, there was an almost significant negative trend with mean temperature (P=0.055) but no effect of date (P=0.301) or rainfall (P=0.631). The overall effect of these factors on numbers of birds in the farm buildings was also non-significant (r^2=0.147, n=32, P=0.209);

rainfall and mean temperature had no effect (*P*=0.591 and *P*=0.594, respectively) but there was a non-significant positive trend with date (*P*=0.071).

2.3.3 The utilisation of different fields

Pasture fields, more specifically old grass ley and permanent pasture, were used far more than arable field types (Fig. 2.1), and grouping fields into the 9 different field types shows these differences to be significant (Kruskal-Wallis, *H*=17.868, d.f.=8, *P*=0.022). In order to explore this preference in more detail, it was necessary to look at just the field types that were used by the flock; hence further analyses were performed only on data from pasture field types (i.e. permanent and rough pasture and new and old grass ley, *n*=24).

As the starling flocks returned to the farm buildings during the day between foraging bouts, one might expect that fields closer to the farm buildings would be utilised the most, an effect confirmed by Fig. 2.2a. The starlings were also seen to prefer those fields in which the mean distance to the nearest hedge was greater (Fig. 2.2b). These effects, together with field area, were examined in a multiple regression, which produced an overall significant effect (Table 2.1), and within which both distance to the nearest hedge and distance to the farm buildings were significant. As might be expected, field area was found to be correlated with the distance within each field to the nearest hedge (*r*=0.632). The lack of effect of field area on starling foraging densities may therefore have been due to fields of a similar area having differing amounts of hedgline around them and the starlings preferring to feed in square fields bordered by fencing than in long thin fields enclosed by hedgerows, despite both field types being of a similar area.

The foraging density of the starlings was also significantly negatively correlated with sward height (Spearman rank R_S=-0.251, *n*=24, *P*=0.029). This correlation could not be attributed to starlings being more visible in fields with shorter grass since the height of the sward (mean=33.4 mm, SE=0.31, *n*=24) was sufficiently low for the starlings to have been visible in all of the pasture fields.

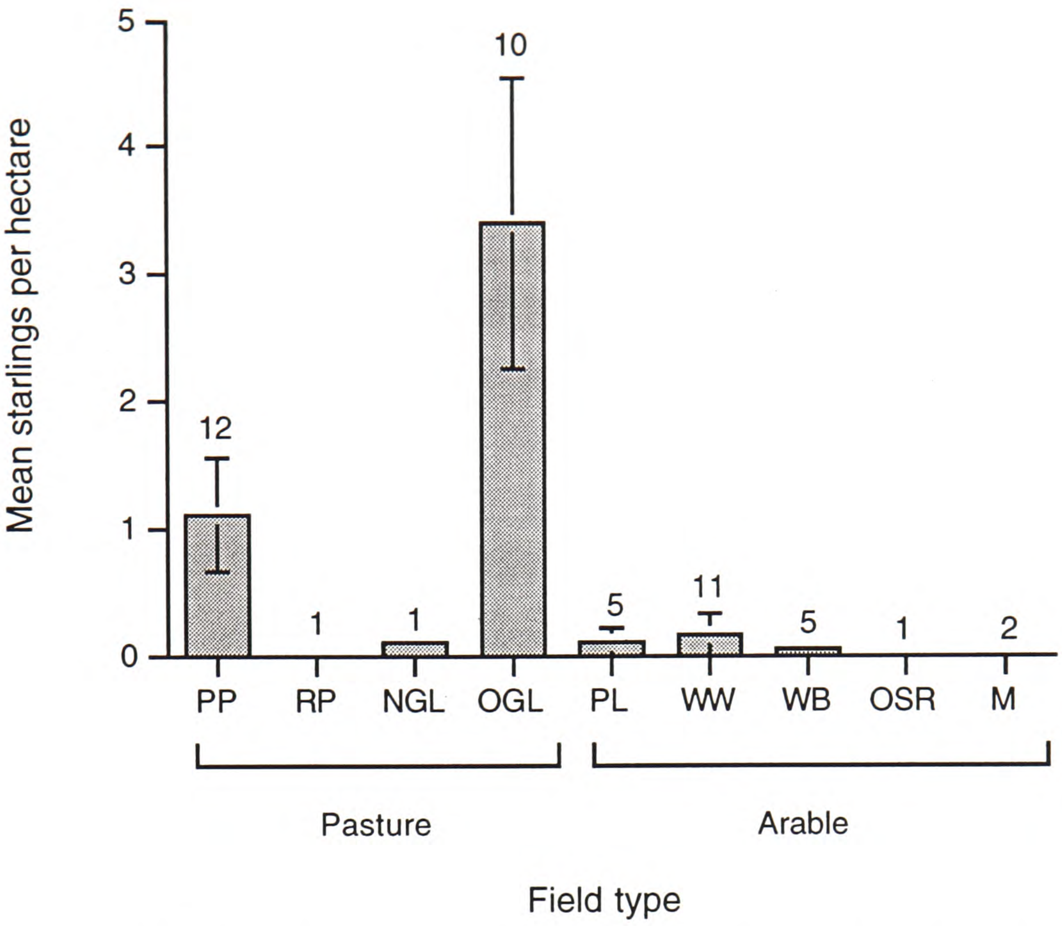


Figure 2.1. Mean (±SE) starling foraging densities (mean number of starlings per hectare) for fields (sample sizes given above bars) of each crop type (PP=permanent pasture, RP=rough pasture, NGL=new grass ley, OGL=old grass ley, PL=ploughed, WW=winter wheat, WB=winter barley, OSR=oilseed rape and M=maize (stubble)). Values are means of 32 independent transects taken over a five-month period (November '91 to March '92) at University Farm, Wytham.

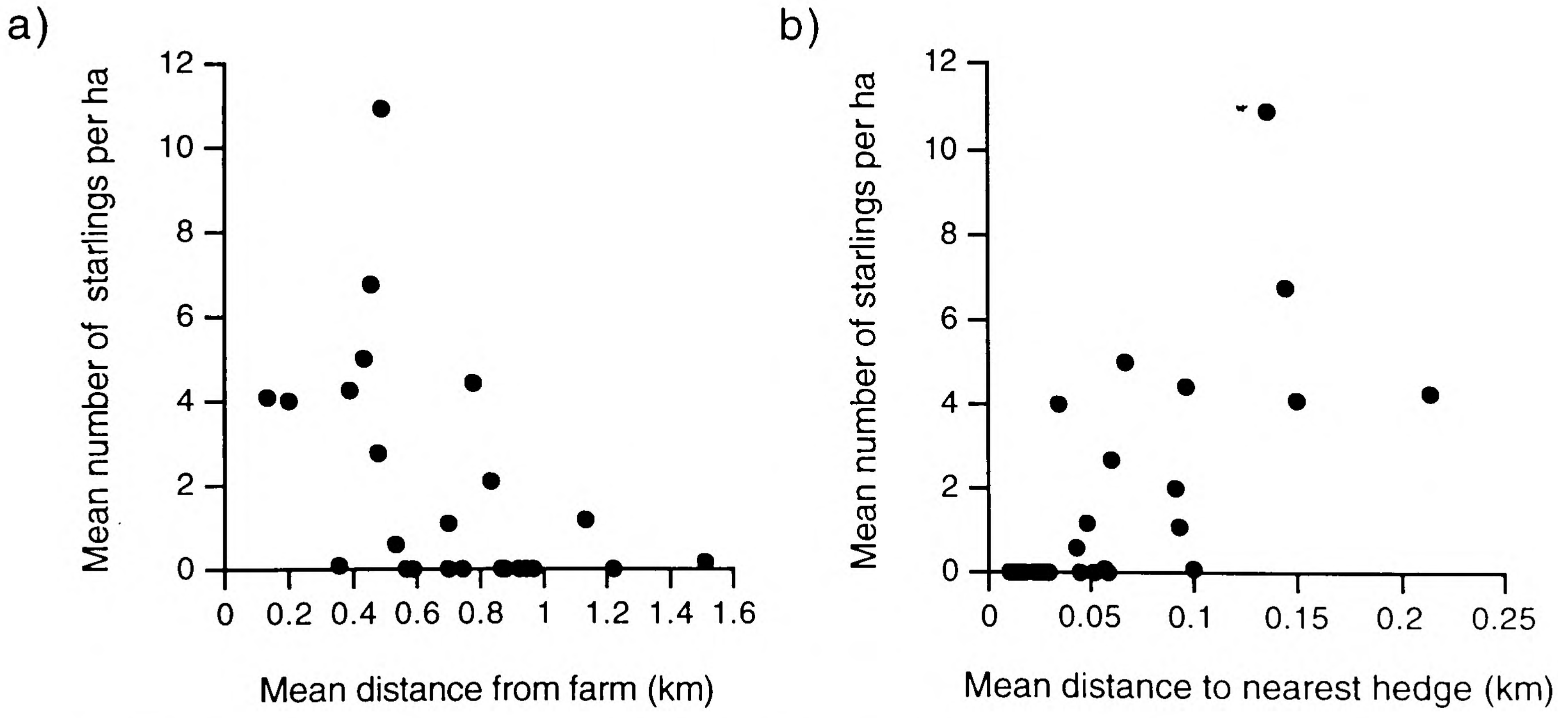


Figure 2.2. The effect on the starling foraging densities (mean number of starlings per hectare) in grass fields (permanent, temporary and scrub pasture and new and old grass ley) of: **a)** distance of each field from the farm buildings (km); and **b)** mean distance within each field to the nearest hedge (km). Both variables were significant factors in multiple regression analysis (Table 2).

Table 2.1: The effect on starling foraging densities (square root + 0.1 transformed) of mean distance from the farm buildings (ln transformed), area of the field (ln transformed) and mean distance to the nearest hedge (ln transformed). Regression coefficients (slopes), r^2 values, and *P*-values are shown for: **a)** each factor tested separately; and **b)** as part of a multiple regression including every factor (multiple-r^2=0.596, *P*=0.001).

	a)			b)	
Factor	**Slope**	r^2	***P*-value**	**Slope**	***P*-value**
Ln(Distance)	-0.817	0.274	0.009	-0.724	0.033
Ln(Area)	0.178	0.025	0.408	-	-
Ln(Hedge)	0.805	0.475	<0.001	0.609	0.026
Degrees of Freedom		1,22		2,21	

2.3.4 Distribution of other species

Calculation of thrush and gull foraging densities showed that they shared similar field-type preferences with starlings, associations being significant between both starlings and thrushes (Pearson Correlation, r=0.618, n=24, P<0.001) and starlings and gulls (r=0.465, n=24, P=0.021). There was no significant association between starlings and corvids (r=0.078, n=24, P=0.721).

2.3.5 The effect of sheep

In order to see whether there was any relation between the numbers of starlings and the presence of sheep, a contingency table was constructed which compared the number of times starlings were present or absent in a field in which sheep were grazing with the expected number of observations of starlings if the presence of sheep had no effect on the starlings' choice of field (i.e. starlings would be observed in field as many times when sheep were there as when sheep were absent). There was no apparent preference or avoidance of sheep (χ^2=2.55, d.f.=1, P=0.110).

2.3.6 Patterns of field utilisation in the all-day observations

There were 156 separate observations of the flock, at 11 different sites, during the all-day watches. As with the census observations, the starlings spent most of their time feeding in a single, large flock, but were also seen to separate into smaller sub-flocks for some of the time. Using these observations it was possible to calculate additional values of foraging densities for all those fields seen to be used by the starlings on those days. Again, permanent pasture and old grass ley were used most intensively, the 9 different field types experiencing significantly different foraging densities (Kruskal-Wallis, H=19.593, d.f.=8, P=0.012). The values obtained for each field from these observations were significantly correlated with those calculated from the census data (R_s=0.808, n=50, P<0.001), indicating that the same patterns of field utilisation were operating during the all-day observations as have already been demonstrated from the census data.

A one-way ANOVA of the mean residence times (to the nearest 0.5 h) of the starlings at each site showed a significant difference between the sites ($F_{10,155}$=3.050, P=0.002), and there was a positive, significant trend between these residence times and the observed foraging densities (Fig. 2.3: R_s=0.645, n=11, P=0.041). In contrast, there were no significant differences between return times to each site ($F_{9,133}$=1.762, P=0.082) and no significant correlation between starling foraging densities and these return times (R_s=0.382, n=11, P=0.252).

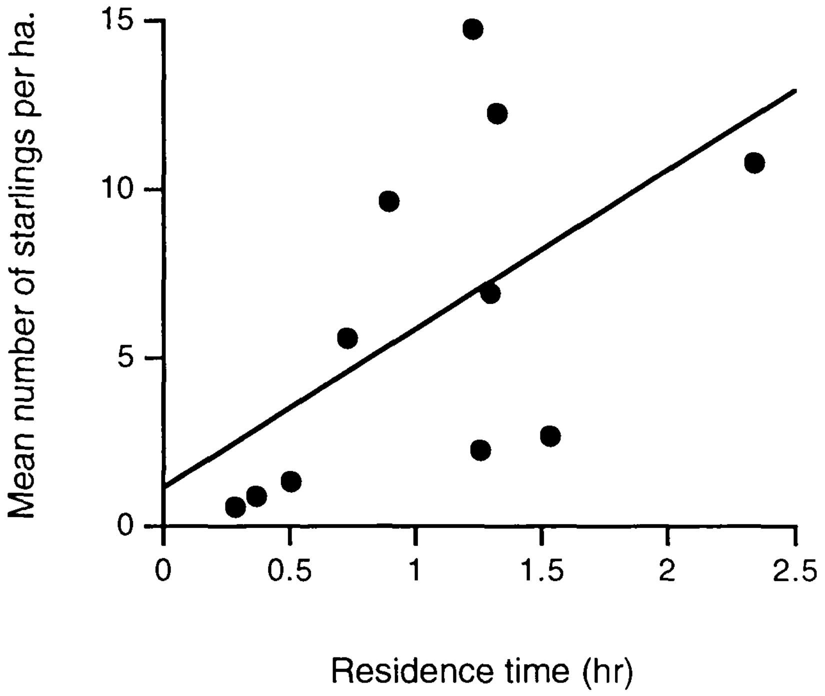


Figure 2.3. Starling foraging density (mean number of starlings per ha) in relation to mean residence time of the flock (recorded to the nearest 0.5 h), at each site. Line represents best fit through the data.

To address the question of whether the starlings showed any spatial organisation in the way in which they moved between fields, I examined the distance that the flock moved. For every move made by the flock from one field to another, the distance between the centre points of these two sites was measured. A frequency distribution of these distances was then plotted and compared with two separate expected distributions. Figure 2.4 shows a distribution of distances moved calculated on the assumption that when leaving a feeding site the flock was equally likely to visit any other feeding site. It is apparent that the flock moved significantly shorter distances than expected (χ^2=48.946, P<0.001). However, a more realistic null hypothesis is one which takes into account the flock's preferences for certain fields. Figure 2.4 also compares the observed distribution with an expected distribution based upon the different foraging densities at each site i.e. the number of moves to each feeding site were apportioned according to the observed foraging densities at these sites. Although this produced closer agreement between observed and expected distributions, the starlings still showed significantly more moves over shorter distances than expected (χ^2=21.727, P<0.005).

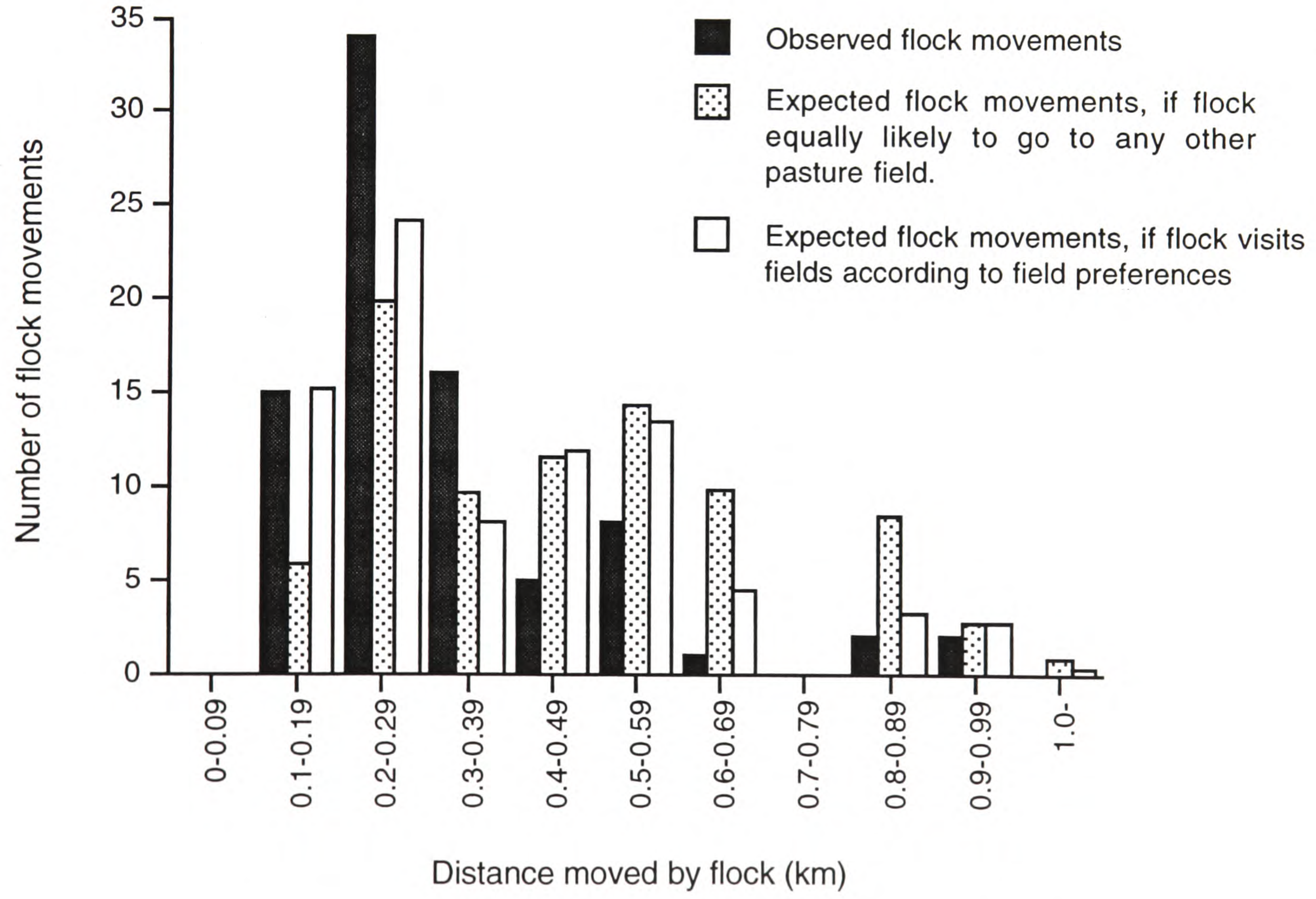


Figure 2.4: Observed frequency distribution of distances travelled by the flock when moving between feeding sites, compared with expected distributions. One expected distribution was calculated on the basis that the flock was equally likely to move to any other field; the other distribution was calculated on the basis that the flock would visit each field according to the observed starling foraging densities of those fields.

The distance moved by the flock can also be related to the number of moves to feeding sites in adjacent and non-adjacent fields. For each field used by the flock, the observed number of moves to adjacent fields was compared with the expected number of moves to these fields if the flock had shown an equal distribution of moves between all fields normally visited. A paired t-test of these values showed that there was a significant tendency to move to adjacent fields (t=2.712, d.f.=9, P=0.023).

2.4. Discussion

2.4.1 Numbers of foraging starlings

The general observation that the study population of starlings remained resident around one farm for most of the winter supports findings described by Feare (1981b) for starlings in Hampshire, and contrasts with the wider ranging populations described for Norfolk by Summers & Cross (1987). Although this winter flock is small relative to other known starling populations (Feare 1984), it appears to represent a locally important winter roost and feeding site, as indicated by the presence of known colour-ringed individuals throughout the winter. The availability of pasture fields, and a reliable source of animal feed from cattle and sheep barns, all adjacent to a suitable night roost site, also served to attract additional, unmarked birds to the larger foraging flocks throughout the winter.

The total number of starlings seen using the farm buildings as a food source decreased slightly, but not significantly, towards the end of the census period. Such a trend may have been related to changes in ambient temperature and the start of breeding. Although artificial sources of food were available throughout the study period, they would only have been important when the preferred natural prey were scarce and the birds' energy demands were high during earlier colder periods (Bailey 1966; Dunnet 1956; Feare & McGinnity 1986; Taitt 1973). In addition, greater numbers of larger invertebrate prey become available in the soil at the end of the winter, representing the start of the peak in biomass which coincides with breeding (Dunnet

1955; Tinbergen 1981). This greater prey availability may be linked to increasing prey size and higher activity levels, as warmer temperatures encourage movement of the invertebrates nearer the surface.

In this study the weak effect of low temperatures on the numbers of starlings feeding around the farm buildings may be explained by an absence of any particularly cold spells during the study period. This suggests there is a temperature threshold above which the starlings do not have to depend on artificial food sources, a possibility demonstrated by Feare (1981a) who concluded that the numbers of starlings feeding on pasture were reduced significantly only when the soil became frozen.

2.4.2 Field preferences of starlings

The starling flocks showed a clear preference for grass fields, both permanent pasture and established grass leys, with all arable crop types experiencing far lower foraging densities. These results agree with general observations reported in Feare (1984), and more specific data on unmarked populations by Gromadzki (1980) and Tucker (1992), who both found a strong preference of starlings for permanent grass fields. A similar preference of invertebrate-feeding corvids for grassland has been shown by Waite (1984), who linked this preference to higher invertebrate densities. Tucker (1992) also showed that the preferred pasture fields contained greater densities of soil macro-invertebrates, and concluded that this explained the preference of birds for these fields. In arable fields, regular disturbance of the ground and application of insecticides may have depleted the densities of invertebrates in the soil. Unlike in Tucker's (1992) study, arable fields in the present study did not receive any farmyard manure during the census period and consequently did not even attract birds on a temporary basis.

The starlings in the present study could have used the farm buildings exclusively to obtain high-energy foods, such as barley, from animal feeds thereby avoiding the cost of travelling to feed in the fields. The use of fields by these birds may therefore reflect the importance of soil invertebrates to starlings; Feare & McGinnity (1986) proposed that at least 60% of a starling's diet has to consist of invertebrates for all the bird's nutritional requirements to be met. Despite the Wytham birds being able to take pig pellets, which may have been a more balanced nutritional source than the barley taken by birds in Feare & McGinnity's study, their continued use of pasture fields suggests they may have been compensating for some nutritional inadequacy of the pellets by foraging for invertebrate prey.

The role of predation in determining the starlings' choice of feeding site should also be taken into account. Flying to and from the fields may have had an associated cost of predation but once in the fields the birds would have been afforded relatively clear visibility of any approaching predator. When feeding in the more confined environment of the farm buildings the starlings might have been more vulnerable to 'ambush' attacks but this cost may have been countered by a reduced risk of predation from aerial predators. The optimal trade-off between food and predation is given detailed theoretical consideration by Houston *et al.* (1993) who generate general models to predict the optimal behaviour for both short (e.g. vigilance level) and long-term (e.g. growth decisions and associated choice of habitat) situations, using parameters which include the animal's state and the danger of predation.

2.4.3 Field area and the proximity of hedges

No flock preference was shown for feeding in larger fields, but the starlings did feed significantly more in those fields which provided feeding areas further away from hedges. An effect of field area was recorded by Tucker (1992), but this could have been due to the larger range of field sizes in his study area compared with the Wytham site. Predator avoidance provides the best functional explanation for both these effects, with larger fields allowing birds to detect and avoid predators while the predator is still some distance away. By avoiding those fields with hedges close to feeding sites, starlings would not only have had greater all-round visibility, but would also have been able to reduce the risk of ambush attacks from predators, such as Sparrowhawks (*Accipiter nisus*). These were to seen on rare occasions to successfully predate starlings from the study population. A similar predator avoidance argument was used by Barnard and Stephens (1981) in their explanation of why Fieldfares (*Turdus pilaris*) preferred to feed away from hedges.

2.4.4 The effect of distance

There was a clear effect of distance from the farm buildings on the preference displayed by the starling flock. This was due to the farm buildings being used as a central resting and feeding site in between feeding excursions to the fields. This use of a central place is less apparent in more open environments where starlings have to travel much further to feed, such as in areas of intensive arable farming (e.g. Norfolk; Summers & Cross 1987). Although Wytham provides foraging on a much smaller and more concentrated scale, the birds still chose to feed in fields closest to their central roost, thus meeting their foraging requirements with the minimum energy expenditure from flight. Such an argument also explains why the starlings moved to adjacent fields more often than would be expected from the availability of different feeding sites.

2.4.5 The effect of sward height

Sward height of the grass fields was shown to have a strong effect on the starlings' choice of foraging site, a finding supported by Williamson and Gray (1975). Shorter grass probably facilitated probing and mobility and increased visibility, both to search for food and to see potential predators approaching, thus allowing greater foraging rates (Brownsmith 1977; Eiserer 1980). One factor which will influence sward height is the presence of sheep, but the lack of any association between starlings and sheep may be explained by effects such as cropped grass and dung deposition appearing gradually while sheep were present and lasting after the sheep had been removed from a particular field.

2.4.6 Associations with other bird species

Starlings foraging in the fields were often part of mixed-species flocks and a particularly strong association was observed with Fieldfares and Redwings, which also preferred established pasture fields over arable fields. These thrushes often increased the size of the starling flocks by two or three hundred to give mixed flocks of substantial sizes. In their study of single and mixed-species flocks of Fieldfares and Redwings, Barnard & Stephens (1981) concluded that mixed flocks were always formed by Fieldfares joining the Redwings, and it was largely the Fieldfares which benefited from being in a mixed rather than a single-species flock. Clergeau (1990) tested the attractiveness of starlings to a range of other species and found that only species smaller than starlings were attracted to models of starlings placed on a lawn. Based on this finding he suggested that it is starlings which are attracted to redwings rather than the other way round, given the difference in size between the two species. It cannot be determined from the data presented here whether it was the starlings which responded to the presence of the thrushes or whether the thrushes were choosing to feed in those fields in which the starlings were present, but it is likely that the starlings were gaining some benefit from the presence of other species. In an aviary study, Powell (1974) showed that starlings will spend less time being vigilant when in larger flocks containing either other starlings or Tri-colored Blackbirds (*Agelaius tricolor*). The costs and benefits of feeding within a group will be considered in more detail in Chapters 6 & 7.

2.4.7 Temporal distribution of the starlings

From data collected during the all-day watches I demonstrated that the starlings tended to move to adjacent fields and over shorter distances than expected, but I was not able to detect any regular temporal pattern of movement between these fields. I might have expected the flock to leave feeding sites as prey availability was temporarily depleted (Barnard & Stephens 1981) but, although the flock was seen to apportion significantly different amounts of time to each of its preferred sites, these residence times did not exhibit any obvious diurnal pattern (pers. obs.). Feare (1980) observed similar difficulties in predicting the number of starlings which would be feeding at cattle feedlots at any one time. Many short-term changes of feeding site probably resulted from random disturbance or from the presence of predators. This role of disturbance in influencing where the starlings fed may have explained the correlation between habitat preferences and residence times, with the starlings preferring to feed at those sites where their feeding bouts were least likely to be halted prematurely through the arrival of predators or other disturbing factors.

So far then, I have been unable to provide evidence for the starlings employing a systematic temporal pattern of field usage in order to 'harvest' their invertebrate prey. A more rigorous test of the existence of such a pattern would be one which showed whether or not the probability of return to a field was related to how long ago the flock last visited the field. With return and residence times recorded only to the nearest 0.5 h the extent to which such an analysis of the present data could be interpreted is limited. In addition, movement of birds to and from the main flock during feeding visits may have resulted in the time that the flock was recorded as resident being greater than the residence times of particular individuals. Collection of accurate return and residence times of individual birds within the feeding flock would have required a marking technique other than colour leg rings (e.g. wing tags).

2.5 Summary

A standard census route, used to describe the pattern of winter field utilisation by a population of starlings at University farm, Wytham, showed that the flock preferred to use established pasture and grass ley fields, particularly those which were closer to the farm buildings, had shorter swards and provided feeding sites which were further from hedges.

A more detailed distribution of the starlings in the fields and around the farm was mapped during all-day watches, revealing no regular temporal pattern in flock movements or residence times at different feeding sites. The flock did, however, move significantly more times than expected to nearby feeding sites in adjacent fields.

Some aspects of the starlings' habitat use (e.g. movement to nearby feeding sites) may be explained by established theoretical expectations (e.g. minimisation of energetic costs), but the apparent unpredictability of the order in which particular fields were visited makes it difficult to explain these movements using a suitable theoretical framework.

Chapter 3

Relating starling habitat preferences to prey availability

3.1 Introduction

In the last chapter I showed how the starlings' choice of feeding site could be related to physical features of their environment. The distribution of individuals within their environment will, however, also be influenced by the response of each bird to spatial and temporal variations in the distributions of their prey (e.g. Sutherland 1982a & b), and it is this role of prey availabilities that I will discuss in this chapter.

A major prey item of starlings is the leatherjacket (*Tipula paludosa*) (Dunnet 1956; Feare 1984; Tinbergen 1981). Despite extensive mapping of this prey species (Barbash *et al.* 1991; McCracken 1992), levels of its local availability have yet to be assessed in conjunction with temporal and spatial patterns of starling flock movements. Tinbergen (1981) obtained detailed measurements of the distribution of leatherjackets in relation to the sites visited by parental foraging starlings, but the interaction between predator and prey distributions will be very different during the non-breeding season when the birds feed in a flock.

In order to understand such predator-prey interactions it is necessary to establish how prey are distributed. Previous measures of such distributions have been based largely on direct measurements of prey densities, obtained from soil cores (e.g. Tucker 1992). Such measurements can provide an accurate picture of the numbers and types of invertebrates present in the soil, but they give no indication of the proportion of these invertebrates that are actually available to the birds. Hence, measurements of absolute prey densities on their own are of restricted value for gaining a better understanding of how predators respond to the distribution of their prey (Goss-Custard 1984). I will refer to absolute prey densities as prey 'abundance'. This contrasts with prey 'availability', which I define as that proportion of total prey which can be obtained by foraging birds.

I obtained measurements of prey availability by recording the foraging behaviour of individual starlings. Such observations cannot be made easily on individuals feeding in a flock (see Chapter 5), but close observations can be made of captive birds, held in small cage enclosures (1m x 1m x 0.5m). Such a technique has already been used successfully by Tinbergen (1981), and my own experience with this experiment showed that the starlings soon adapted to feeding in such enclosures. By using the birds themselves as a bioassay, it was therefore possible to get an accurate measure of the prey that was available to the starlings in a range of habitats. Furthermore, not only did the enclosures allow me to sample prey availability in those habitats preferred by the starlings, but also in fields not normally visited by the flock.

3.2 Methods

3.2.1 Flock census

Although data were already available for the flock's habitat preferences (Chapter 2), this experiment was conducted in the winter (1992/93) following that in which the original census data had been collected (1991/92). Therefore to control for any changes in the flock's pattern of habitat use, which may have been affected by year-to-year differences in environmental conditions or changes in land use, the census was repeated using a similar technique as in the previous year. The census was conducted twice a day for seven days prior to the experiment (described below), at approximately 90 minutes after the flock emerged from its night time roost (09:30 hrs) and again at 14:30 hrs (approximately 90 minutes before the flock returned to the roost). No census data were collected during the experimental phase, but after this time the censuses were continued for a further seven days, in order to check for any effect of date on the availability of prey which may, in turn, have influenced the observed foraging densities of the starling flock. The resulting foraging densities (mean number of starlings per hectare) were calculated in the same way as those calculated in the previous chapter.

The flock used the same fields in the winter of 1992/93 as in that of 1991/92 as well as using a grass ley field that had been resown in November 1991 and only became established in the second winter of this study. The absence of starlings from arable fields meant that year-to-year changes in the cropping regimes of these fields did not affect the observed habitat preferences. Table 3.1 shows which fields were selected, on the basis of their observed flock foraging intensities and similar distances from the farm buildings, for the measurement of prey availability.

Table 3.1: Mean flock foraging densities (starlings per hectare) in the six fields chosen for experimental measurements of prey availability.

Field	Field type	Mean foraging density (starlings per hectare)	Mean distance from farm buildings (km)
12c	Winter wheat	0	0.302
16	Old grass ley	0	0.195
23	Old grass ley	0.25	0.479
13	New grass ley	6.35	0.347
2b	Old grass ley	7.29	0.484
3	Old grass ley	7.53	0.450

3.2.2 Measurement of prey availability using enclosures

a) Experimental technique

Six adult starlings (five males and one female) were caught from the resident population and held in outdoor enclosures (2 m long x 2 m wide x 1 m high) for the duration of the experimental period. As with all later exclosure experiments, each individual was used in only one experiment before being released back into the wild. Food (Turkey starter crumbs, Orlux softbill pellets and mealworms *Tenebrio molitor*) and water were available *ad lib.* throughout this period, and a nest box in one corner of the enclosure provided shelter and a means of catching the birds from the enclosure.

For test sessions, the birds were transferred to test enclosures (1 m long x 1 m wide x 0.5 m high). Once the birds were settled and feeding freely in these enclosures (usually after a maximum of 10 - 15 min) I started the test sessions. The birds were food-deprived from 16:00 hrs on the day prior to testing, and trials were started at 08:00 hrs the following morning. Each bird experienced only one 10-minute trial on any day. Once the trial had been completed the birds were returned to the holding enclosures and given *ad lib.* food until 16:00 hrs. Training was started on 28th October 1992 and all testing was completed by 16th November 1992.

b) Experimental design

Each of the six fields to be tested was divided into nine regions of approximately equal area, of which six were then chosen at random. Within each of these regions one site was randomly allocated, allowing each bird to be tested once in each of the six fields. In allocating these experimental sites I assumed that those areas of the fields I would be sampling were representative of those areas actually visited by the wild flock. Although the flock may have actually favoured certain areas of each field over other areas (pers. obs.), for the purpose of this, and subsequent enclosure experiments, I was interested in dealing with differences between fields rather than within fields.

All six birds were tested on each day and so to minimise any effect of time of day on prey availability, the birds were split into two groups of three, which were tested simultaneously by two observers. Birds and fields were allocated randomly between the two observers on each of the six days.

3.2.3 Data collection and analyses

The birds' foraging behaviour in the enclosures was recorded on video-tape, from a hide positioned a few metres from the enclosure. Data on number of surface pecks, number of exploratory probes (these were distinguished from deeper probes, which were directed repeatedly at the same site when the bird had located a prey item and was attempting to extract it from the ground), time and prey type for each prey capture were collected from the video-tapes at a later date using an event-recording programme. Due to the resolution of the videos and the size of prey types, these were categorised only as earthworms (Lumbricidae) or arthropod larvae (mostly leatherjackets). The behavioural data were then used to calculate prey capture rate (slope of cumulative number of prey captures divided by time in trial), search effort (slope of cumulative number of probes divided by time in trial) and reward rate (slope of cumulative number of prey captures divided by cumulative number of probes).

Comparisons of these variables were made between fields using repeated-measures ANOVA, with bird (n=6) as the subject. These prey availability measurements per field were related to flock foraging densities using Spearman Rank Correlations.

3.3 Results

Within individual foraging trials I observed no effect of satiation, as shown by the linear relationship between number of probes made by each bird and time during the trial (Fig. 3.1a). Any non-linearity in rates of prey capture would therefore have reflected changes in the availability of prey, rather than changes in the birds' motivational state, but the significantly linear relationship between the number of prey caught with time (Fig. 3.1b) indicated that any depletion of prey could be considered to be negligible.

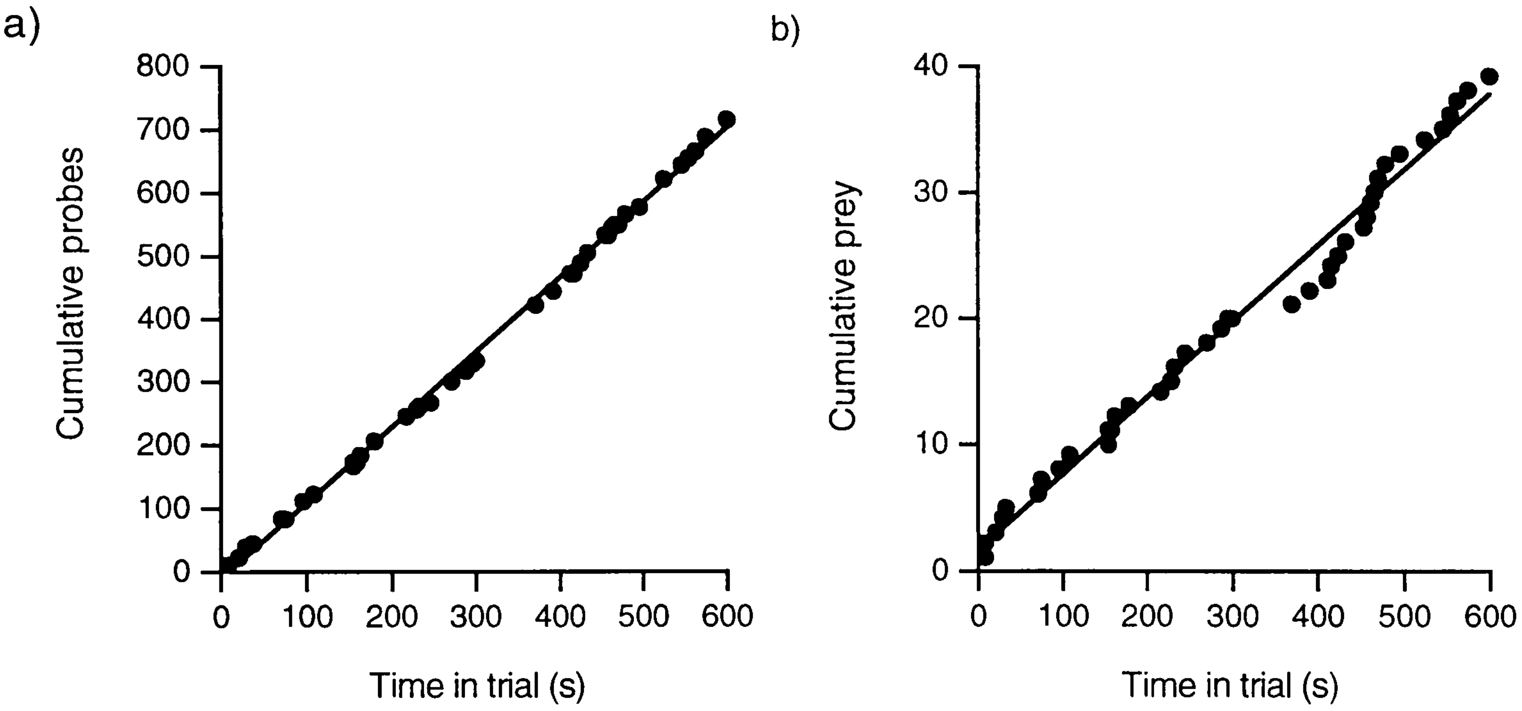


Figure 3.1. Example plots for one bird of **a)** rate of searching, expressed as the cumulative number of probes made with time, within a single representative feeding trial (y=-8.812+1.187x, r^2=0.998, P<0.001); **b)** rate of prey capture, expressed as the number of cumulative prey captures with time, within a single representative feeding trial (y=1.648+0.06x, r^2=0.986, P<0.001).

Prey capture rates were significantly different in each of the six fields ($F_{5,25}$=3.365, P=0.019) and were correlated with the mean flock foraging densities in each of those fields (Spearman rank R_S=0.928, n=6, P=0.038). However, there was also a significant difference in search effort between the fields ($F_{5,25}$=4.534,

P=0.004), which showed an almost significant correlation with the ranked foraging densities of the six fields (R_S=0.870, n=6, P=0.052). A re-analysis of the capture rates controlled for these differences in search efforts by expressing the prey captures as a rate per probe rather than a rate per second of foraging, to give reward rates. There was no significant difference between the resulting reward rates in the six fields ($F_{5,25}$=1.414, P=0.254) and there was a positive but non-significant trend between flock foraging density and reward rate (R_S=0.754, n=6, P=0.092). Therefore, it seems that much of the difference in prey capture rates between fields could be explained by higher search rates in the preferred fields. For analyses presented below I return to expressing the birds' foraging success in terms of capture rate (captures per unit time) rather than reward rate (captures per probe), so that I may then estimate how many prey the wild birds can capture from each of the fields during a day's foraging.

Separating the total prey into the two main prey types revealed highly significant differences in the numbers of each type captured in the six fields. The capture rate for larvae differed between fields (Fig. 3.2: $F_{5,25}$=3.78, P=0.011) and was found to be correlated with the observed flock foraging densities in those fields (R_S=0.928, n=6, P=0.038). In contrast, although there were significant differences in the numbers of worms captured per unit time between the six fields (Fig. 3.2: $F_{5,25}$=6.495, P<0.001), there was no correlation with the foraging densities in those fields (R_S=-0.116, n=6, P=0.795).

Plotting the experimental capture rates against the actual flock foraging intensities in each field, rather than their ranked values, revealed a marked dichotomy in their distribution, with fields either being very rarely visited or visited frequently (Fig. 3.3a). To explore this apparent 'foraging threshold', the amount of energy obtainable from invertebrates in each of the fields was calculated. The energy provided by each of the two main prey types was estimated by nutritional analyses (Appendix I: earthworms = 24.63 kJ/g dry weight; leatherjackets = 23.76 kJ/g dry weight). These values of energy per gram of dry weight were converted to energetic values per prey item using mean dry weights of each of the two prey types, collected from soil core sampling (Chapter 5 & 6: Earthworms = 41.0×10^{-3}g ± 1.3×10^{-3}; Leatherjackets = 6.9×10^{-3}g ±

0.6×10^{-3}). A loose estimation of the number of prey caught over the duration of a day's foraging (e.g. a maximum of 8 hours) can be extrapolated from the number caught during the 10 minute experimental enclosure sessions and from this it is possible to calculate the daily energy obtainable from leatherjackets and from earthworms, in each of the six fields. Relating these estimates of energy availability to the observed flock foraging densities (Figure 3.3b) shows that the starlings did not necessarily feed in those fields which offered the highest gross energy intake. Although the starlings could meet the total estimated daily energy requirement (DER) of an adult starling (230 kJ, Gromadzki 1979) by feeding on a mixture of earthworms and leatherjackets in any of the pasture fields, they preferred to feed in those fields in which they were able to maximise the amount of energy obtainable from leatherjackets rather than from earthworms.

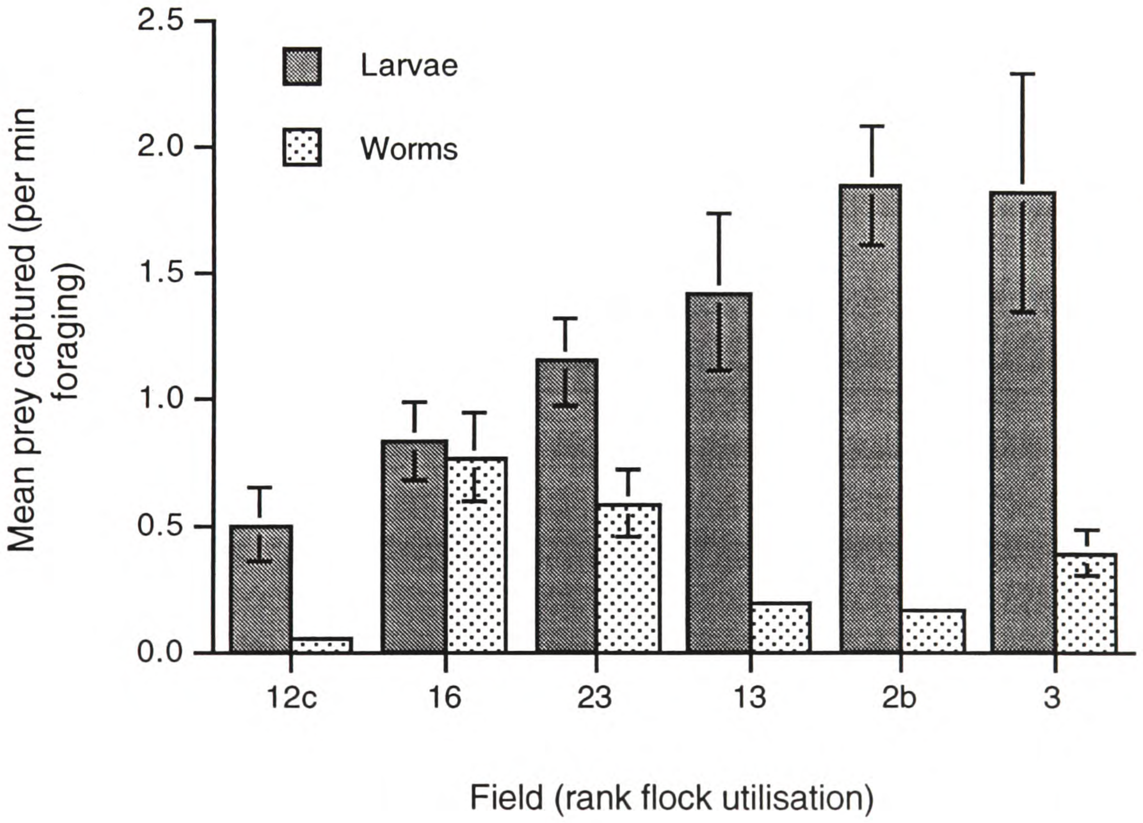


Figure 3.2. Mean prey capture rates (mean number of prey captured per minute of foraging) of captive starlings allowed to forage in experimental enclosures in each of 6 fields. The fields are ranked according to the observed foraging densities (starlings per hectare) of the wild flock, with increasing flock utilisation moving from left to right (i.e. field 12c = lowest rank flock utilisation).

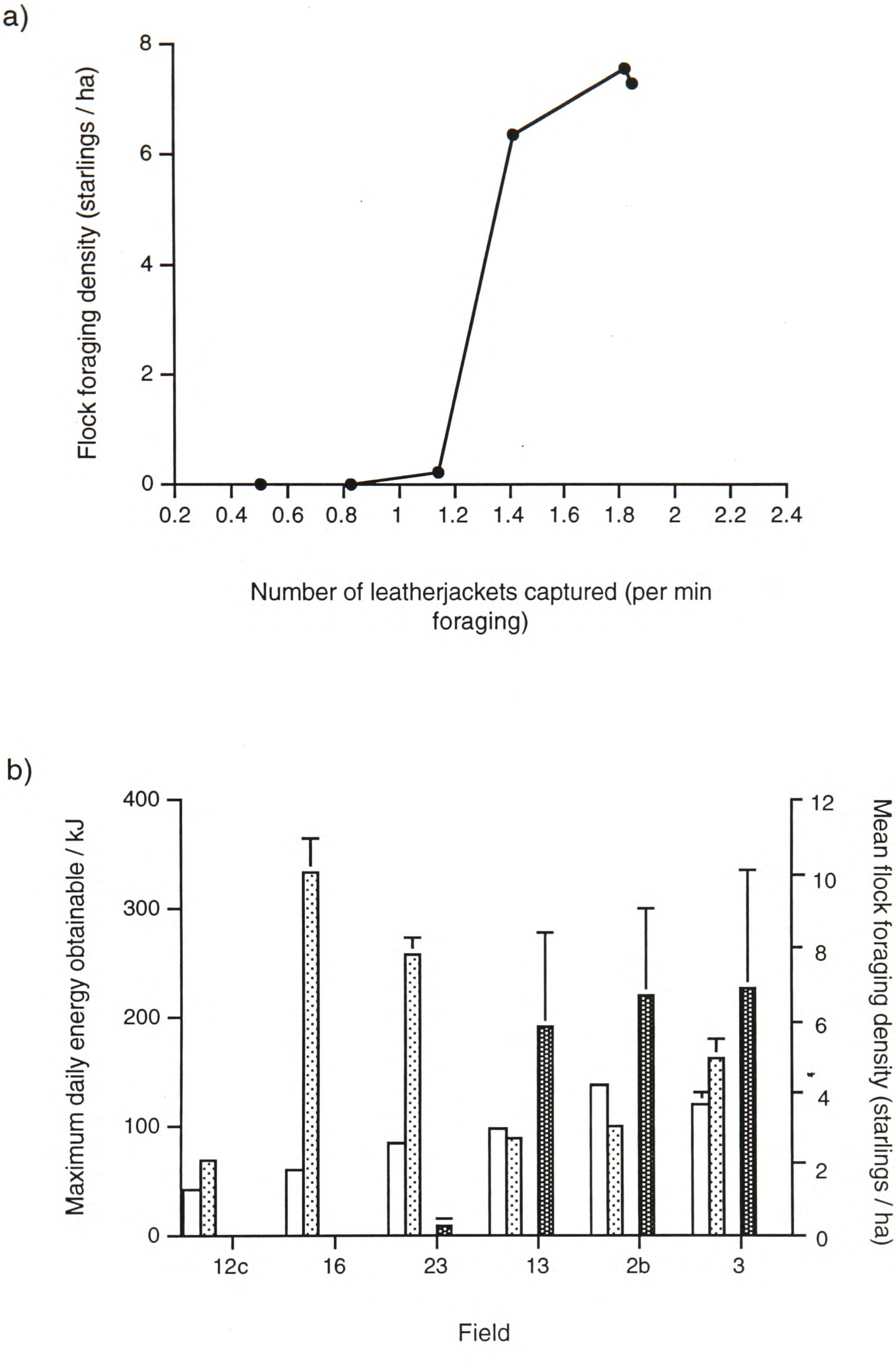


Figure 3.3. Observed flock foraging densities (mean number of starlings per hectare) in each of the six fields **a**) plotted against capture rates (mean number captured per minute foraging) of larval prey types for captive birds allowed to forage in the experimental enclosures and; **b**) in relation to the mean estimated energy (± SE) obtainable by a single bird, from earthworms and leatherjackets, captured from each of the fields in one day's foraging. Open bars represent energy obtainable from leatherjackets; light bars represent energy obtainable from earthworms; and dark bars represent mean foraging densities of the wild flock.

3.4 Discussion

Analyses of the foraging data support previous studies (Tucker 1992; Waite 1984) which have shown that pasture fields contain higher levels of invertebrate prey than arable fields. More importantly, the results presented here demonstrate that not only is a starling's choice of field linked to the amount of prey available, (e.g. Barnard 1980a; Goss-Custard 1970a; Waite 1984), but that is the availability of arthropod prey which influences this choice. Earthworm availabilities apparently had little effect on a starling's field preferences.

This conclusion assumes that the types and proportions of prey captured by my experimental birds were a representative measure of the prey captured by starlings feeding in the natural flock. As a result of being held in captivity the experimental birds' feeding behaviour and prey selection might have changed (e.g. regular provision of an artificial diet might have changed the birds' energetic and nutritional requirements). As I pointed out at the beginning of this chapter (and see Chapter 5) it is not possible to get sufficiently close to the wild birds to get accurate measures of their feeding behaviour. Hence, had sufficient time been available, an alternative comparison of 'natural' and 'experimental' prey captures would have required faecal analyses (e.g. Chough *Pyrrhocorax pyrrhocorax*, McCracken *et al.* 1992).

Relating the field preferences to estimates of energy availability showed an apparent 'foraging threshold' such that the starlings would only visit those fields from which they could obtain a certain amount of their DER from leatherjackets, rather than earthworms. Starlings devote a considerable amount of time each day resting or preening (C. Feare pers. comm.), but even if they had fed for the maximum possible of eight hours, none of the fields would have been able to meet all the birds' DER from leatherjackets. An examination of the diet of starlings (Feare & McGinnity 1986) found that they required 60% of their diet to comprise invertebrates, and the rest could be made up from other, high-energy, sources of food, such as barley. My own observations showed that the flock did not stay in the same field all the time (Chapter 2), but spent some time feeding in the farm buildings, or on flood meadows over the river and beyond the range of my study site. Thus, although they concentrated the majority of their feeding effort in the preferred fields, the starlings gained further contributions to their daily energy requirements from less preferred sites. Feeding on high-energy animal feeds for some of the time may reduce the time necessary for foraging and permit the starlings time for other behaviours, as well as reducing the time they have to spend in areas where they may be at a higher risk of predation (Barnard 1980b).

Investigating the starlings' apparent preference for leatherjackets over earthworms as a source of energy requires more controlled experiments. Nutritional analyses (Appendix I) do not show any marked differences in the nutritional or energetic quality of the two prey types. However, these analyses are based upon invertebrate samples collected during the summer. The nutritional quality of the prey may change at different times of year, and so the possibility of such nutritional differences being an underlying cause of winter feeding preferences cannot be ruled out. Goss-Custard (1977a) described a similar prey-type preference in redshank *Tringa totanus*, in which the preferred prey were of less energetic value than other, less-preferred prey. Although several mechanisms for this preference are discussed, Goss-Custard concluded that the basis for it had yet to be determined. Further consideration will be given to a preference by starlings for leatherjackets over earthworms in the next chapter, in which other possible reasons for such a preference will also be discussed.

In addition to the availability of invertebrates and their contribution to the starlings' DER, an additional factor influencing where the starlings preferred to feed became apparent during experimental trials in the arable field. The high clay content of the soil, combined with heavy rainfall during the experimental period, meant that the starlings' beaks rapidly became clogged with wet soil which also stuck to their feet and belly feathers. Foraging trials in this field were very fragmented as the birds allocated time to attempts to preen themselves. I concluded that this would deter the starlings from feeding in arable fields, particularly during wet periods, and in newly ploughed or recently sown fields in which the soil structure is loose. In contrast, the more compact, vegetated soil of pasture fields would seem to provide a more favourable foraging substrate.

3.5 Summary

I provided evidence in Chapter 2 that the starlings' field preferences could be linked to physical features of the fields, but in this chapter I have also explained the observed habitat preferences in terms of the availability of prey. This was quantified by studying the foraging behaviour of individual birds allowed to forage in small cage enclosures which were erected in a sub-sample of the fields available to the flock. The experimental birds' capture rates in each of the fields were found to be significantly correlated with the observed flock foraging densities. This correlation was a prey-specific effect, the flock showing higher foraging densities in those pasture fields where the availability of larval prey types rather than earthworms was higher. This field preference was also compared to the amount of energy obtainable from the two major types of invertebrate prey. How changes in these prey availabilities might influence the starlings' movements between feeding areas will be considered in Chapters 5 & 6.

Chapter 4

Do starlings have a prey-type preference?

4.1 Introduction

In the last chapter I demonstrated a correlation between the fields used by the foraging flock, and the availability of larval prey in those fields. The invertebrate larvae were predominantly leatherjackets (*Tipula paludosa*), and although large numbers of earthworms (*Lumbricus* spp.) were also available in some of the fields, there was no correlation between their availability and the starlings' habitat preferences.

The observed correlation between prey type availability and field preference may have been due to a common preference of starlings and their prey for particular soil types, which provide both a favourable environment for the larvae, and an easy substrate for the starlings to probe. Alternatively the starlings may have had a dietary preference for larvae, a possibility which can be explored more easily (e.g. Tinbergen 1981) than the more complex question of interactions between prey types and their environment.

Prey choice can be influenced by a number of parameters which include energetic and nutrient constraints (Goss Custard 1977b), handling time (Elner & Hughes 1978) and encounter rate (Krebs *et al.* 1977). All these factors may explain an observed prey preference, and will influence an individual's foraging strategy (Stephens & Krebs 1986). However, before examining their role in diet selection it is necessary to address the simpler question of whether a diet preference actually exists.

I decided to explore diet preference in the laboratory where birds, which had experienced both prey types in their natural situation, could be brought into a more controlled environment. A classic technique of examining diet selection and diet composition has been stomach or gizzard-contents analysis (e.g. Al-Joborae 1979; Dunnet 1956), but in measuring seed selection by pigeons Brown (1969) instead advocated the use of controlled preference tests. He observed that indirect measures of food-choice behaviour reflected limitations of the environment as much as the birds' preferences; thus, although Tinbergen (1960) was able to establish diet preferences of tits *Parus* spp. by recording the prey items brought by adults to their nestlings, the observed food preferences were still influenced by the availability and abundance of particular food types. By exploring diet preference in the laboratory, I was therefore able to eliminate all other correlates of prey type (e.g. availability in the environment; soil penetrability), control the amount of recent experience of each prey type received by the birds, and attribute any preference for one prey type over the other to characteristics of the prey themselves (e.g. palatability, digestibility).

4.2 Methods

4.2.1 Subjects

Eight adult starlings were trapped from the Wytham population immediately prior to the experiment. During the experimental period the birds were housed individually in cages (0.78 m long x 0.55 m wide x 0.53 m high), in which they were in visual but not auditory isolation from one another. Apart from during experimental sessions and during preceding food deprivation periods the birds had free access to food (turkey starter crumbs, Orlux softbill pellets and mealworms *Tenebrio molitor*) and water. The same mixture of food was used as reinforcements during training sessions. The reinforcements used in the experiment were natural prey types (Earthworms, *Lumbricus* sp., and Leatherjackets, *Tipula paludosa*), collected from the field and presented to the birds individually.

4.2.2 Prey

Live prey were collected from a permanent pasture field at the University Farm, Wytham. Turves of soil 0.3 m x 0.3 m were cut to a depth of approximately 50 mm. These were then inverted onto large Tulgren funnels, constructed from sheets of 15 mm gauge chicken wire placed over the end of sheet-metal funnels (diameter 0.5 m). These were positioned beneath 400 W greenhouse lights as a source of low intensity heating. As invertebrates emerged from the turves they were collected in plastic pots, lined with damp paper, placed beneath the funnels. Each turve was left in place for 24 - 48 h and the collecting pots were checked daily for invertebrates. The invertebrates were then maintained in soil cultures at 4°C until needed for the experiment. Immediately prior to being used in an experimental session wet weights of each prey item were taken.

4.2.3 Apparatus

Experiments were conducted in the house cages. The end panel of each of these cages could be replaced with an operant panel (Fig. 4.1a), which was put into place for training and experimental sessions. At the centre of the panel was a transluscent perspex pecking key (35 mm diameter, Campden Instruments) that could be illuminated with white light from behind. A magazine for delivery of food was positioned on either side of the key, at a distance of 28 mm. Each magazine (Fig. 4.1b) had a small rectangular dish for holding the reinforcements, access to which was gained via a transparent perspex door through which the starlings were able to see the prey. The door was hinged from the top and could be locked in the closed, vertical position by an electromagnet, thus denying the birds access to the dishes. A light bulb above each dish could be illuminated to indicate when the magazine door was unlocked.

The operant panel was linked to an Acorn Archimedes microcomputer running the Arachnid experimental control language (Paul Fray, Ltd.). The computer controlled the presentation of stimuli and the reward contingencies, as well as recording the birds' performances on training and test sessions.

4.2.4 Procedure

a) Magazine training

Prior to the start of training, the birds were given two days to settle in the experimental cages, after which they were taught to feed from the magazines. Initially the magazine doors were propped open, giving the birds free access to food in the

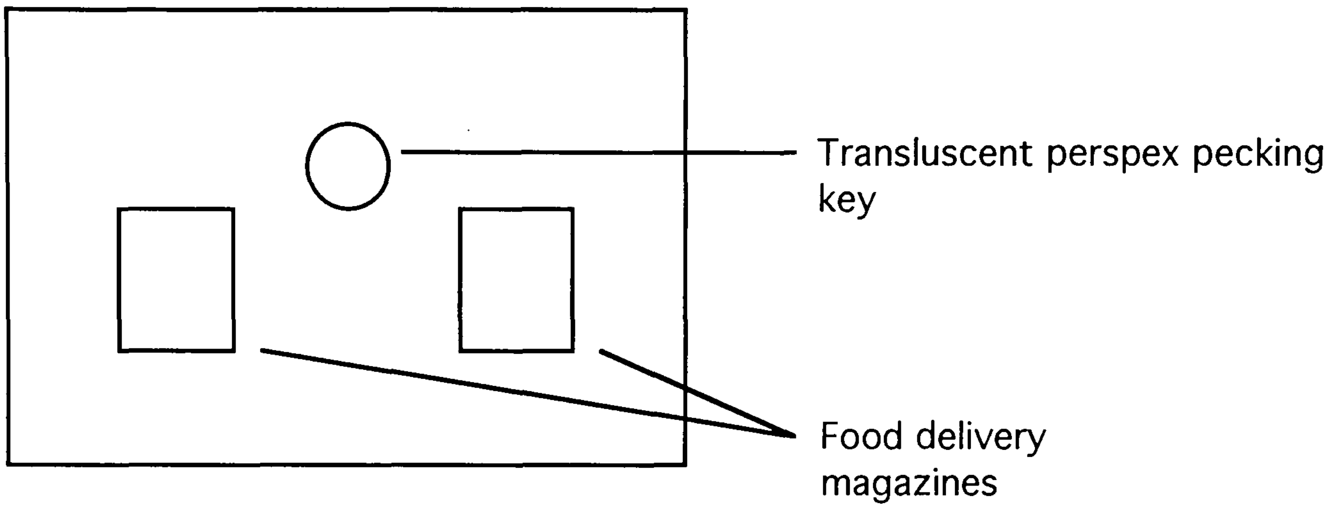


Figure 4.1a: Diagram of operant panel, showing relative positions of pecking key and food delivery magazines.

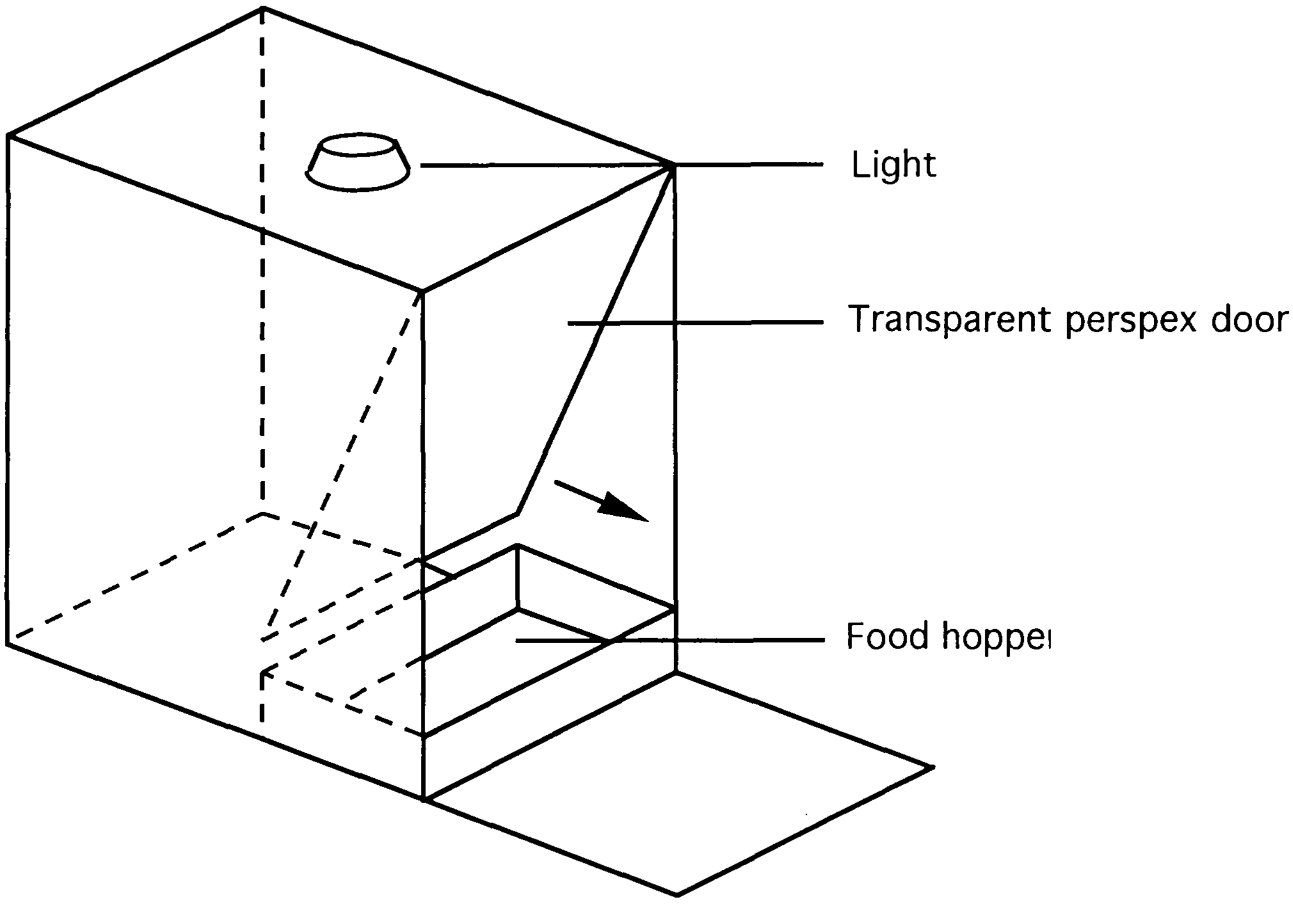


Figure 4.1b: Magazine for delivery of food.

dishes. Once they were feeding from the open magazines (usually after several hours) the doors were gradually lowered so that the birds had to use their beaks and heads to open them fully. By the end of Day 2 of training most of the birds could open the doors and feed from the magazines, although some required an additional day of training to become completely adept at this.

Once the birds had learnt to feed from the magazines, they were exposed to the association between the magazines being lit and the doors being unlocked. Each bird received three sessions of 40 trials each day for two days (Days 3 & 4). Before the first session of the day, the birds were food-deprived for approximately five hours. The birds were deprived again for about 45 minutes between each session. After the third session the birds were given free access to food and water until the following morning, when they were deprived again.

During trials the light in one of the two magazines came on for a reward time, and the door was unlocked accordingly, giving the bird access to the reinforcement. At the end of the reward time, the light extinguished and the door re-locked, denying the bird further access to the food. After an inter-trial interval (ITI) one of the magazines was illuminated again and the door unlocked. The order in which the magazines were lit was randomised. Initially the length of access to the magazine was 10 s and the ITI was 10 s. Over the course of the 6 sessions the period of access to the magazine was reduced gradually to only 4 s and the ITI increased to 30 s. As the birds learnt the schedule they became progressively quicker at gaining access to the magazines and tended to feed for the maximum time allowed, therefore it was necessary to reduce the reward time to prevent the birds becoming satiated too quickly.

b) Conditioning

For the next three days (Days 5-7) each bird received two sessions of 30 conditioning trials each day. As before, the birds were food deprived for approximately five hours prior to the start of the day's sessions, and were further deprived for about one hour between each session. Again they were given *ad lib.* food and water once the day's sessions had been completed.

The schedule for each trial was programmed as follows. A trial began with presentation of the stimulus (a white light) on the pecking key. A fixed interval (FI) schedule was programmed on the key such that the first peck made by the bird on the key, after the FI had timed out, extinguished the stimulus. There was also a maximum time limit after which the light extinguished independently of the behaviour of the bird. After this maximum time limit, or earlier if the bird had pecked the key, the light was extinguished and the light in one of the two magazines lit to indicate that the magazine was unlocked and therefore available to the bird. After a programmed time interval this light was extinguished and the magazine door re-locked. This was followed by an ITI during which no stimuli were presented. In summary, if the bird did not peck the key, as was the case at the beginning of training, it experienced the full period of the stimulus followed by reinforcement. Once the bird pecked the key this pecking behaviour was reinforced by the food being made available sooner.

For these trials the FI was 0.5 s and the maximum time limit 11.5 s (i.e. the schedule would expire after a total of 12 s unless the bird pecked before this time), the length of access to the magazine was 4 s and the ITI was 60 s. All the birds autoshaped to pecking the key and learnt the schedule of reinforcement.

4.2.5 Experimental design

The last two days (Days 8 & 9) were test days. One prey type was allocated to each magazine such that half of the birds received leatherjackets on the right and earthworms on the left, and the remaining four birds received them on the opposite sides. Each bird received one test session per day, and was food-deprived for five hours prior to testing. Each session comprised 12 blocks of three trials. The schedule for these trials was the same as for the conditioning trials, except that there was no maximum time limit. Hence the bird did not receive any reinforcement until it had pecked the central key. The first two trials of each block were forced choice trials so that by pecking the key the bird gained access to only one of the magazines. On the first trial it was able to open the magazine on one side of the pecking key, and on the second trial the reinforcement on the other side of the key was made available. On the third trial the birds were given a simultaneous choice, such that pecking the central key illuminated and unlocked both magazines simultaneously. However, as soon as they opened one magazine, the light in the other one was extinguished and the door locked. If the bird had failed to open either door by the end of the four second reward time, both lights were extinguished and the doors relocked. The order of presentation of forced trials was alternated between blocks, and after the sixth block the side on which each prey type was presented was swapped in order to control for any side preference the birds may have had.

On Day 8 the birds were given a choice between whole leatherjackets (mean weight = 0.058g, C.V. = 57.5%) and whole earthworms (mean weight = 0.651g, C.V. = 72.9%), but on Day 9 the earthworms were cut into pieces (mean weight = 0.048g, C.V. = 53.1%) of a similar size to leatherjackets.

4.2.6 Data analyses

Prey type preference was quantified in two ways:

1) For each bird, the number of times the leatherjacket magazine was opened during each choice trial was expressed as a proportion of the total number of choice trials. These proportions were then compared in a one-sample t-test with an expected proportion of 0.5, which would have been observed if the birds had shown no preference for either of the prey types.

In conducting the above analysis, I assumed that the birds had learnt immediately the position of each of the prey types. However, it is more realistic to assume that they required some time to learn these positions, and so I repeated the above analysis , using data only from blocks 4, 5 & 6, and blocks 10, 11 & 12, i.e. the last three blocks in which leatherjackets were presented on the left and earthworms on the right, and the last three blocks in which leatherjackets were presented on the right and earthworms on the left.

2) For each bird, the number of trials (forced and choice) on which it ate a prey item was expressed as a proportion of the number of times it had an opportunity to do so (i.e. the number of times it gained access to the reward by opening the magazine door). These proportions were compared for leatherjackets and earthworms in a paired t-test.

In both cases, separate analyses were done for the two types of choice (whole leatherjackets versus whole earthworms, and whole leatherjackets versus pieces of earthworms). Arcsine square-root transformations of the data were performed where necessary to normalise the data.

4.3 Results

Of the eight experimental birds, only seven completed testing. Although the eighth bird was successfully trained, it failed to respond during test sessions and was excluded from the experiment. Therefore, for statistical analyses the number of subjects was seven.

4.3.1 Proportion of choices as a measure of prey preference

When presented with a choice between leatherjackets and whole earthworms, analyses of all the trials did not demonstrate any significant difference between the proportion of times leatherjackets were chosen (53.6%) and the proportion expected (50%) if the birds had been choosing at random (t=0.743, n=7, P=0.484). Similarly, the birds showed no choice preference (leatherjacket choices = 56%) for either prey type when presented with leatherjackets, and pieces of earthworm of a comparable size (t=0.975, n=7, P=0.367).

In contrast, restricting the analysis to the last three blocks of each of the two arrangements of prey revealed a significant preference for leatherjackets (73.9%) over whole earthworms (Fig. 4.2: t=2.985, n=7, P=0.025). When presented with leatherjackets and pieces of earthworms, the birds showed no preference (leatherjacket choices = 52.3%; Fig. 4.2: t=0.217, n=7, P=0.835).

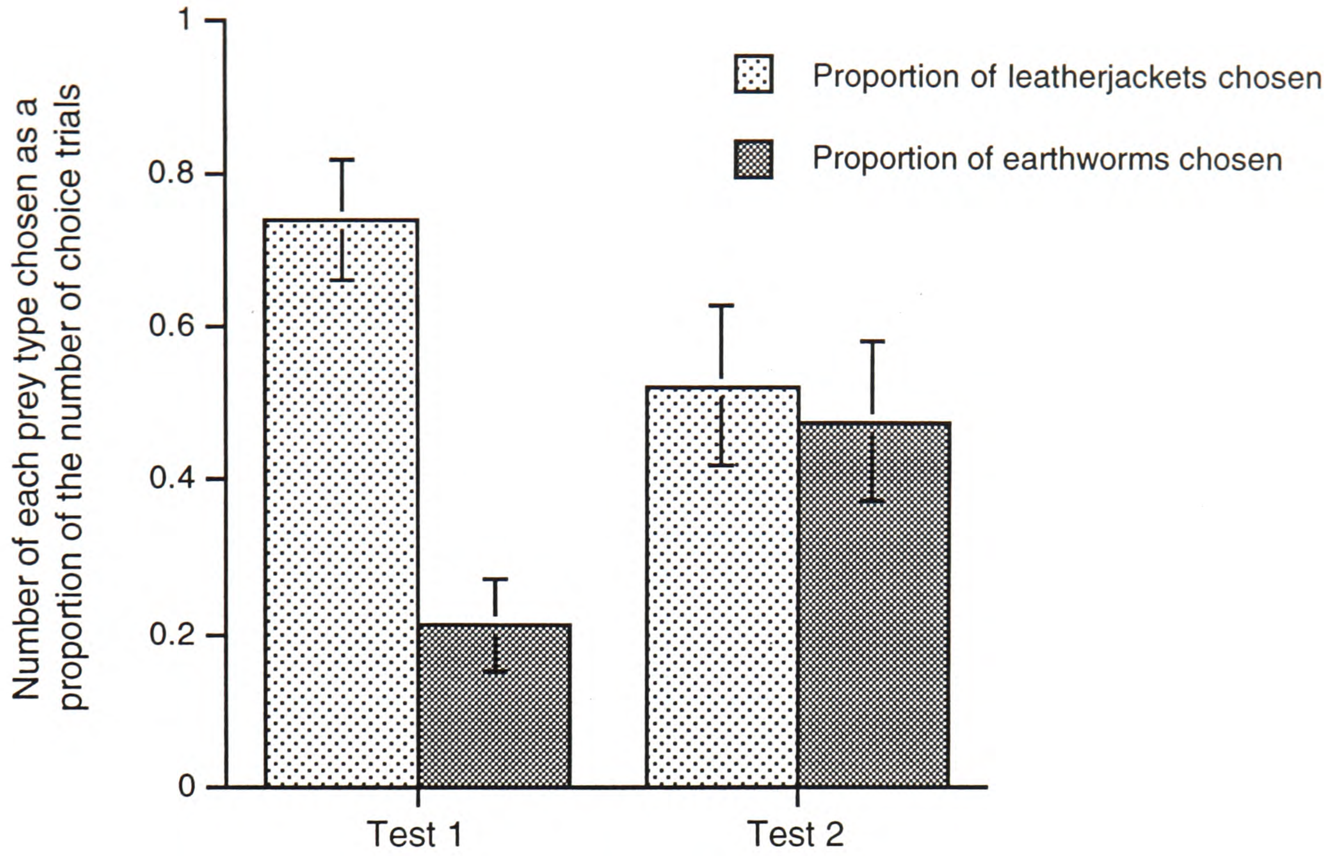


Figure 4.2. Number of times each prey type was chosen by starlings in a laboratory prey choice experiment as a proportion of the number of choice trials (using data only from the last three blocks of each prey arrangement, therefore total number of choice trials = 6). Data is shown for presentation of whole earthworms and leatherjackets (Test 1), and for presentation of pieces of earthworms and leatherjackets (Test 2).

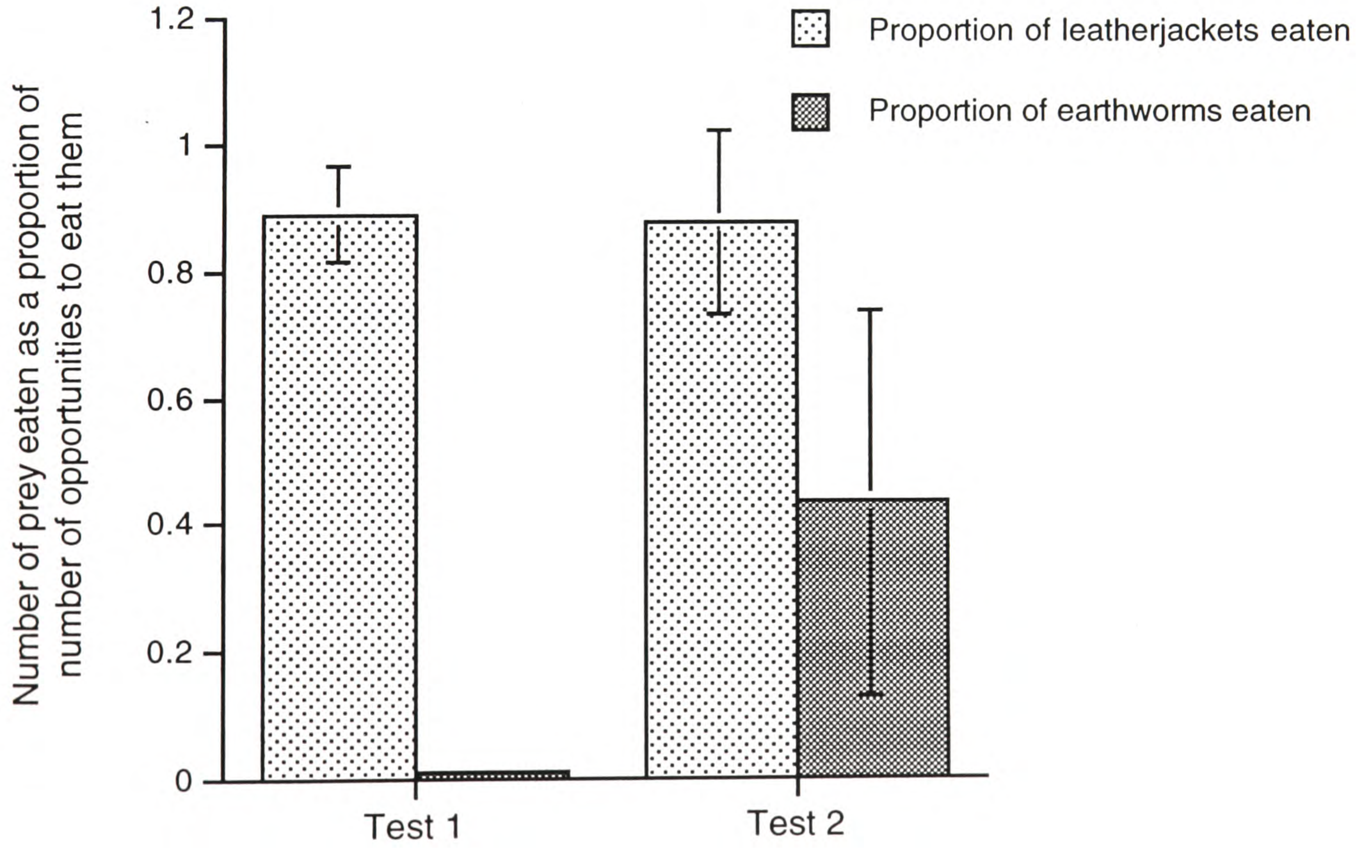


Figure 4.3. Number of times each prey type was eaten by starlings in a laboratory prey choice experiment as a proportion of the number of times the magazine door was opened to obtain a prey item. Data is shown for presentation of whole earthworms and leatherjackets (Test 1), and for presentation of pieces of earthworms and leatherjackets (Test 2).

4.3.2 Number of prey eaten as a measure of prey preference

Analyses of the number of trials on which the birds actually ate each of the two prey types revealed a highly significant preference for leatherjackets over whole earthworms (Fig. 4.3: t=18.715, n=7, P<0.001). Indeed, observations showed that only one earthworm was ever actually consumed. When presented with leatherjacket-sized pieces of earthworms, the birds ate more of these than they had of whole earthworms, but they still ate significantly more leatherjackets (Fig. 4.3: t=3.513, n=7, P=0.013).

4.4 Discussion

Initial analyses of the proportions of leatherjackets chosen during the simultaneous choice trials did not provide evidence for a prey-type preference, but restricting analyses to later choice trials did reveal a preference for leatherjackets. A lack of preference during early trials may have been due to it being over-ridden by the birds' hunger, such that the larger earthworms were chosen until the birds were sufficiently satiated to be able to exhibit their preference. However, the very small number of earthworms eaten provides weak evidence for this as an explanation and it is more likely that the initial lack of preference was due to the birds having to learn about the positions of the prey.

Despite the evidence for this preference, elucidating the cause of it is beyond the scope of the experimental data, although certain possible causes can be discussed.

4.4.1 The size of prey

The increase in the number of earthworms which were chosen and eaten when presented as pieces, rather than as whole items, suggests that the size of prey item may be a factor contributing to the starlings' choice of prey. Larger prey will be more profitable, but this may be counteracted by the extra handling time required. My own observations of birds feeding in the field have shown that they may spend several minutes wiping a worm on the grass, possibly to break it up into a more manageable size. Larger prey items may also create a 'digestive bottleneck', a possibility which is discussed in more detail below.

A more controlled test for this effect of size would have been achieved by also cutting up the leatherjackets, but the small size of many of these prey made it difficult to do so effectively. A more direct test of the effect of size would have been to present the birds with different sizes of the same type of prey. However, despite some natural variation, the range of sizes of leatherjackets was too small to provide a suitable sample with which the birds could be tested, necessitating the use of earthworms instead. From observations made during the experiment, it seemed that the birds were very reluctant to feed on earthworms, despite being food-deprived for a considerable length of time, and it is doubtful whether the birds could be encouraged to feed on them sufficiently in order to obtain the necessary observations. Although artificial food could have been used it would have been very difficult to mimic the characteristics of natural prey which make the handling of larger prey items more awkward.

4.4.2 The quality of prey

Prey preference may have been due to nutritional factors, but analyses of samples collected from soil cores during the winter showed both prey types to have water contents of approximately 80% (Appendix I), and specimens collected during the summer breeding season did not show any significant differences in the energetic or nutritional content between the two prey types (Appendix I). Despite this lack of differences, Wright *et al.* (unpublished data) found that starling chicks which received a greater proportion of earthworms in their diet fledged at lower body weights than those achieved by chicks fed on a similar biomass of larval prey. Therefore, it appears that earthworms are in some way an inferior quality food item, possibly owing to the relatively large quantities of soil in their gut, or to their mucus coating, both of which may also make them less palatable. Tinbergen (1981) showed a similar result of feeding inferior quality food to chicks, but in his study it was the leatherjackets which were the less preferred prey, the starlings preferring to take caterpillars of the Antler Moth *Cerapteryx graminis*.

One possible consequence of these nutritional differences is a difference in digestibility. Kenward & Sibly (1977) explained a feeding preference in woodpigeon, *Columba palumbus*, by a digestive bottleneck when the birds fed on brassicas. However, an analysis of breakdown rates of food ingested by starlings (Coleman 1974a) showed that earthworms disappeared from the gut more rapidly than the other food items in the experimental diet, which included adult and larval beetles, spiders, weevils, Lepidopteran larvae, and wheat grains, but not leatherjackets.

4.4.3 Previous experience of prey types.

Given that the individuals used in this experiment were wild-caught, their choice in the laboratory may have been a reflection of the amount of experience of each prey type they had received in the field. If, for example, they had had more experience at handling leatherjackets, they may have learned to deal with them more efficiently than they could earthworms. Such specialisation for particular prey types was shown by Goss-Custard *et al.* (1988) who demonstrated that oystercatchers (*Haematopus ostralegus*) either became 'hammerers' or 'stabbers' of mussels and selected an appropriate size class of prey type accordingly.

It is possible that encounter rates for earthworms are lower than for leatherjackets. Soil core analyses have shown that leatherjackets are more abundant than earthworms in one of the most preferred pasture fields, and this field certainly yields higher capture rates for larval prey types. McCracken (pers. comm.) observed that leatherjackets in his study area (Islay, Scotland) always stayed in the top 20 - 30 mm of soil whereas earthworms migrated up and down the soil profile. He proposed that these behavioural differences may make leatherjackets easier to locate and more consistently available to foraging birds than earthworms. These behavioural differences may be particularly marked when the invertebrate prey are disturbed; earthworms can retreat very rapidly down the soil column when attempts are made to extract them from the ground (pers. obs.).

Observations of the birds during experimental sessions showed that some individuals were initially extremely wary of approaching the earthworms. Relating this to the field situation, it is unlikely that the starlings encounter many whole live earthworms above the surface of the soil. Those that do occur above the surface during the day are likely to be moribund, and probably an unsuitable prey for the birds. Individuals allowed to forage in experimental enclosures occasionally failed to eat worms that they had extracted from the soil, although they usually spent some time wiping them on the ground. This was also observed by East & Pottinger (1975), who attributed this behaviour to attempts to remove the earthworms' mucus coating, which may be a deterrent for the starlings. Although starlings may spend some time also wiping leatherjackets on the ground, possibly in order to break the skin (Tinbergen 1981), these prey were always eaten once they had been extracted from the ground.

4.5 Summary

A choice experiment, conducted in the laboratory, provided strong evidence that the starlings had a prey-type preference for leatherjackets over earthworms. Owing to the controlled conditions of the experiment, it was possible to attribute at least some of this preference to features of the prey themselves, rather than being representative of the availability of each prey type in the starlings' natural foraging environment. There was some evidence that part of this preference could be attributed to the effects of size. Other explanations for the preference may lie in differences in nutritional quality, palatability or digestibility of the two prey types, but investigating these possibilities would require further research.

Chapter 5

Do starlings have a significant impact on prey availabilities?

5.1 Introduction

In Chapter 2 I established the habitat preferences of the overwintering starlings, and presented some correlates for these preferences. The correlations were based upon measurements of physical features of the birds' environment (e.g. rainfall, temperature, and land use), all of which could have influenced foraging conditions and the availability of prey. These factors were monitored throughout the census period, and thus they provided a measure of how they may have affected the starlings' choice of habitat throughout the winter. Here I examine how prey availability itself might be expected to change.

In their study of wintering wildfowl, Goss-Custard & Charman (1976) took into account the effects of such spatial and temporal factors on the availability of prey, but they also highlighted the need to consider the effect of the birds' behaviour on resource availability. Although in Chapter 3 I used the starlings' foraging behaviour to obtain measurements of prey availability, those correlations were based upon data collected over a short time period. They provided no indication as to how these prey availabilities might have changed over a longer time period, as a result of the birds' foraging.

A brief review of the role of predation on invertebrate densities by shorebirds has been given by Puttick (1984), and examples of the subsequent effects this depletion may have on the birds' own foraging behaviour are outlined by O'Connor & Brown (1977), and Zwarts & Drent (1981). Empirical data from similar studies are starting to be incorporated in a theoretical framework which allows predictions of the distributions of individuals resulting from the effects of long-term prey depletion (Sutherland & Anderson 1993; Sutherland & Allport 1994). A possible response by birds to resource depletion is best exemplified by Prins *et al.* (1980) who described the movements of Brent Geese *Branta bernicla* between winter foraging areas, as they grazed down Sea Plantain *Plantago maritima*. Similar changes in feeding area have also been shown for Barnacle geese *Branta leucopsis* (Ebbinge *et al.* 1975), which were seen to use a number of areas in succession, abandoning an area when approximately 2600 goose-days had accumulated per hectare; Barnard & Thompson (1985) observed that food availability was the main factor influencing the distribution and movement of plovers (*Charadrii*) within and between fields, with the birds allowing sufficient time for the food to renew before returning to a feeding site.

Although there was no obvious temporal pattern in how the starlings used the available habitats (Chapter 2), it was apparent that the birds did not remain in the most preferred sites all the time, but showed frequent movements between fields. These shifts may have been instigated by disturbance (Chapter 2), or by the need to acquire energy at a higher rate, attained by feeding on different prey types in other fields (Chapter 3). A third possibility is that the birds may have been depleting prey in their preferred habitats, only returning to feeding areas once the levels of invertebrates had been replenished. Although this is a similar idea to that demonstrated by Prins *et al.* (1980), who showed how Brent Geese revisited feeding areas every four days in order to harvest Sea Plantain, an important difference with the starlings is that soil invertebrates are a non-renewable food source during the winter months; thus any renewal of invertebrate availabilites can only be as a result of movement of invertebrates within the soil column.

The objective of the experiment described here is to investigate whether or not starlings cause significant depletion of their prey. If such an effect of depletion is observed then it also becomes necessary to address the question of whether this depletion is permanent, or whether it is renewable over a period of time. The repeated returns by the flock to the same feeding sites may have been due to a lack of any permanent effects of prey depletion; departures from sites may have instead resulted from temporary depletion or from factors unrelated to foraging. If there were any effects of depletion, a preference for particular sites may be explained by less depletion and/or more rapid renewal in these fields (e.g. Barnard & Thompson 1985).

To address the question of prey depletion, I used the enclosures technique described in Chapter 3. In addition to the previously described advantages of observing captive, rather than flock-feeding, individuals, these enclosures also allowed control over the length of time for which an experimental patch was foraged. In order to assess the relevance of these experimental measurements of foraging rates to the rates of prey capture that occur in natural flocks, I also attempted to obtain data on the foraging rates of individuals within the flock.

5.2 Methods

5.2.1 Experimental measurements of foraging rates

5.2.1.1 Subjects

Eight adult starlings (four males and four females) were caught from the resident population at University Farm, Wytham. For the birds' feeding and maintenance see Chapter 3.

Throughout the experimental period the birds were held in outdoor enclosures (described in Chapter 3), but for test sessions they were transferred to test enclosures (2 m long x 2 m wide x 1 m high; Fig. 5.1). All the birds were given several training sessions in these test cages, and once they were settled and feeding freely I began test sessions. Trials were started at approximately 08:00 hrs and the birds were food deprived from 17:00 hrs the previous evening. Each bird was given only one experimental trial on any one day and once the day's trials had been completed I returned the birds to the holding enclosures and gave them *ad lib.* food until the next period of deprivation.

5.2.1.2 Experimental design

From within the range of fields used by the starlings, I selected two permanent pasture fields. The field census data (Chapter 2) showed that one of these fields (Field 2b) was used extensively by the starling flock (the 'preferred field') and the other (Field 16) was very rarely visited (the 'non-preferred' field). I divided each field into eight regions (on a 2 x 4 grid) of approximately equal area, and within each of these regions selected one experimental site at random.

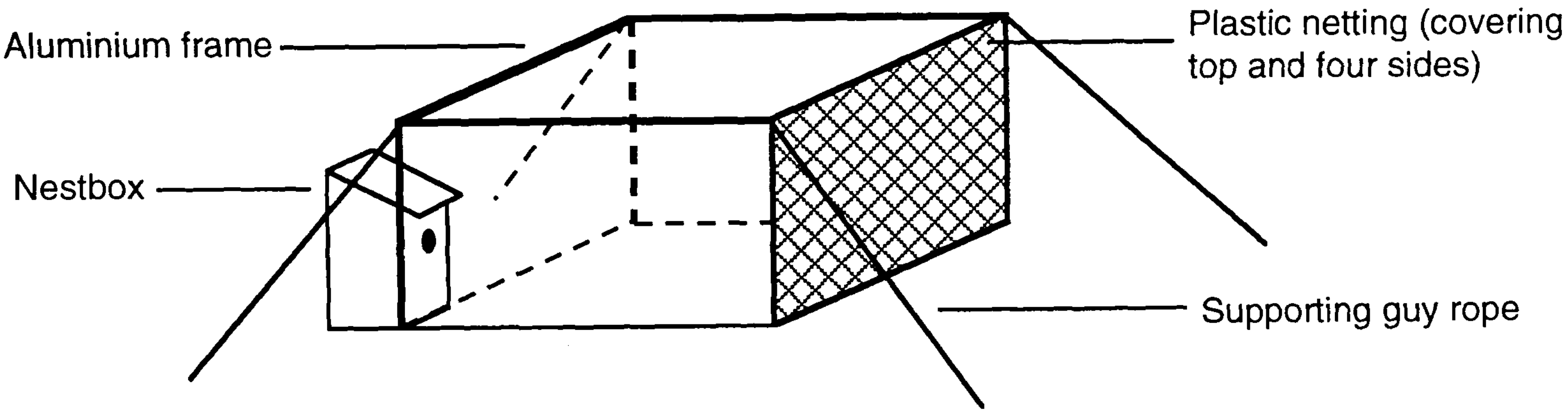


Figure 5.1: Experimental enclosure, measuring 2 m x 2 m x 1 m.

Each bird experienced three foraging treatments in each of the two experimental fields. The treatments were categorised in terms of the level of foraging the experimental site had received: 1) no recent previous foraging (the test enclosures were erected the day before testing to protect the area from foraging by wild birds); 2) foraged on by one bird for 20 minutes immediately prior to the present foraging trial; and 3) foraged on for two successive 20 minute sessions 24 hours previously. This third treatment was designed to test for any renewal of prey availabilities, should resource depression have occurred during the first part of the experiment. Apart from on the first day of testing, on which there was no Treatment 3, the third treatment was actually carried out first on any day, prior to treatments 1 and 2 at a new site (see Table 5.1).

Training was started on 25/2/92 and all testing had been completed by 27/3/92. In order to equalise any temporal changes in prey availability, I alternated testing in the two fields on a daily basis, rather than completing all testing in one field before the other. Each foraging trial was halted once the bird had foraged for a specified length of time; therefore total trial duration varied according to how long the birds took to settle at the start of each session.

Table 5.1: Experimental design: allocation of birds (A-H) to experimental sites and treatments. Treatment 1 (T1) = 20 minutes of foraging on a site which has received no previous foraging; Treatment 2 (T2) = 20 minutes of foraging on a site which has already been foraged on for 20 minutes; and Treatment 3 (T3) = 20 minutes of foraging on a site which has been foraged on for two 20-minute consecutive sessions 24 hours previously. P= preferred field; NP = non-preferred field.

Day	Field	Site	Bird for T1	Bird for T2	Field	Site	Bird for T3
1	P	1	A	B			
2	NP	1	B	A	P	1	C
3	P	2	C	D	NP	1	B
4	NP	2	D	C	P	2	A
5	P	3	B	A	NP	2	D
6	NP	3	A	B	P	3	D
7	P	4	D	C	NP	3	A
8	NP	4	C	D	P	4	B
9	P	5	E	F	NP	4	C
10	NP	5	F	E	P	5	G
11	P	6	G	H	NP	5	F
12	NP	6	H	G	P	6	E
13	P	7	F	E	NP	6	H
14	NP	7	E	F	P	7	H
15	P	8	H	G	NP	7	E
16	NP	8	G	H	P	8	F
17					NP	8	G

I obtained additional information on prey types and invertebrate densities from soil cores, taking six (50 mm diameter and 50 mm depth) from each experimental site as soon as all foraging trials had been completed at that site. Another six cores were taken in conjunction with these, but from a control site placed randomly in any one of the eight regions. Invertebrates were extracted from the cores, using a similar technique to Tucker (1992), as soon after the cores had been collected as possible (usually on the same day). Each core was placed in a 0.2 m diameter, 1 mm gauge mesh seive underneath a spray funnel which delivered water. The cores were gently oscillated backwards and forwards, exposing all of the soil sample to the water spray. Once the majority of the soil had been broken up and washed away (after 1-2 h) the debris was hand-sorted and given further washing under a tap. Any excess water was removed from the specimens by placing them on filter paper, and they were then weighed to obtain wet weights. All the invertebrates were sorted into broad taxonomic groups, and then heated at 50°C in a drying oven to a constant dry weight.

5.2.1.3 Data collection and analyses

The birds' foraging behaviour in the enclosures was recorded on video-tape (Panasonic M10 camera) from a hide positioned a few metres from the enclosure. This allowed me to collect data on number of exploratory probes into the soil (see Chapter 3), time and prey type for each prey capture, from the video-tapes at a later date using an event-recording programme. The resolution of the videos and size of prey types restricted categorisation of these prey to earthworms (Lumbricidae) or arthropod larvae. From these behavioural data, I calculated prey capture rate (slope of cumulative number of prey caught divided by time in trial), search effort (slope of cumulative number of probes divided by time in trial) and reward rate (slope of cumulative number of prey caught divided by cumulative number of probes). Comparisons of these variables were made between fields using repeated-measures ANOVA, with bird (n=8) as the subject.

5.2.2 Measurements of flock foraging rates

These data were collected during November and December 1992, using a similar method to that which was used during the all-day flock observations of the previous season (Chapter 2). For these observations data collection was restricted to the first two hours of the morning, commencing when the starlings emerged from their night-time roost, at approximately 08:00 hrs. I recorded the number and location of any starlings feeding in the fields every five minutes. Each field had been divided into 9 approximately equal regions (on a 3 x 3 grid), which were marked onto a map, allowing the flock's approximate position within each field to be noted. For each flock observation, the inter-bird distances, measured in bird lengths, were estimated for those birds at the front, back, each side and centre of the flock. These distances were then converted to mm by multiplying them by the average bird length of 150 mm, and could be used to calculate the mean bird densities of each flock.

I selected randomly one bird at each of the five positions in the flock and recorded its foraging behaviour for approximately one minute, making a continuous commentary of its foraging behaviour into a tape recorder. I used behavioural categories of 'probe' (exploratory probes into the ground), 'prey capture', 'head-up' (when the bird raised its head to look around - for scans lasting longer than three seconds the bird was classed as having stopped feeding), 'step' and 'fight' (any attack or defence of a site or prey item, involving another individual). These behaviours were then transcribed onto computer using an event-recording programme.

5.3 Results

5.3.1 Enclosures

5.3.1.1 Behavioural data

The linear relationship between number of probes made by each bird and time during the trial (Fig. 5.2a) indicated no observable effect of satiation within individual foraging trials. Any non-linearity would therefore have represented changes in the availability of prey rather than in the birds' motivational state. However, the significant linear relationship between the cumulative number of prey captures and time in trial indicated that any reduction in the availability of prey to the birds during these periods could be considered to be negligible (Fig. 5.2b).

Despite this significantly linear relationship between cumulative number of prey captures and time in trial, examination of Figure 5.2b suggests that capture rates may have been greater during the first 100 seconds of the feeding trial. A similar effect is suggested by Figures 3.1b (Chapter 3), 6.3b (Chapter 6) and 8.2b (Chapter 8). The existence of such an effect might provide evidence for a 'creaming-off' effect of the most available prey (e.g. Tinbergen & Drent 1980) and may affect the interpretation of foraging data from the enclosure experiments. To investigate this possible non-linearity in individual capture rates, the mean time between prey captures during the first 300 s (shorter time periods encompassed an insufficiently small number of prey captures) was compared with the mean time between prey captures during the third 300 s of each 20 min trial. A repeated measures ANOVA, with bird (n=8) as the subject, revealed no significant difference betweeen these time periods ($F_{1,7}$=1.004, P=0.350) and showed similar non-significance when also taking into account any differences between foraging treatment ($F_{2,7}$=0.071, P=0.932). For further analyses I therefore assumed the capture rates to be linear during each recorded foraging bout.

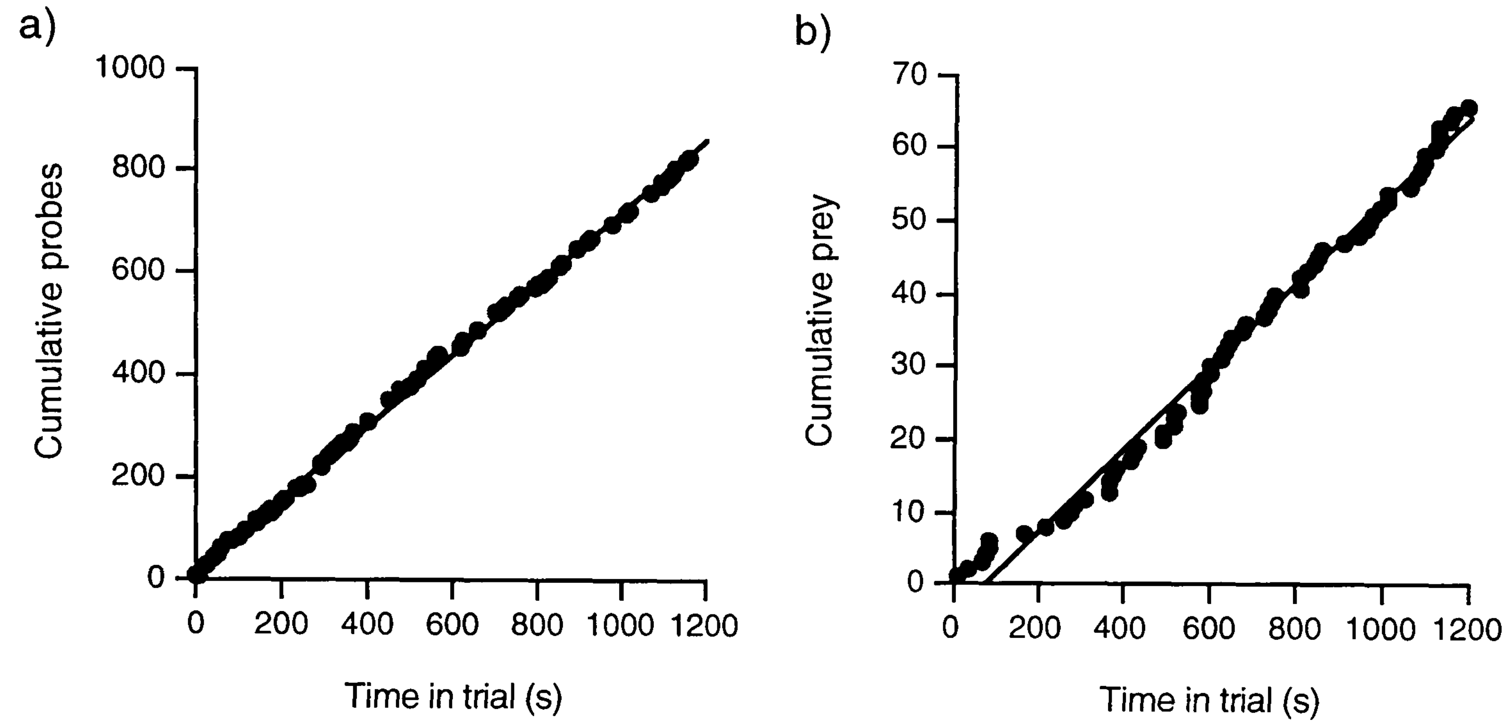


Figure 5.2. Example plots for one bird of **a)** rate of searching, expressed as the cumulative number of probes made with time, within a single representative feeding trial (y=14.598+0.709x, r^2=0.999, P<0.001); **b)** rate of prey capture, expressed as the cumulative number of prey captures with time, within a single representative feeding trial (y=-4.505+0.057x, r^2=0.988 P<0.001).

Over all foraging trials, the total number of prey captured by the birds was significantly greater in the preferred field than in the non-preferred field-($F_{1,7}$=7.825, P=0.027). Expressing these prey captures as a rate per unit foraging time reduced this difference, such that it was marginally significant (Fig. 3; $F_{1,7}$=5.45, P=0.052), and there was no change in these capture rates across the three treatments (Fig. 5.3; $F_{2,7}$=0.831, P=0.456).

Search effort (cumulative number of probes with time) also showed no differences between the three treatments ($F_{2,7}$=2.336, P=0.130), and although the birds made more probes per unit time in the preferred field, this search effort was not significantly greater than in the non-preferred field ($F_{1,7}$=3.627, P=0.099). Capture rates were re-analysed, to take into account any slight differences in search effort, by expressing them as a rate per probe rather than a rate per second of foraging. The resulting reward rates (cumulative number of prey caught divided by cumulative number of probes) were similar in the two fields ($F_{1,7}$=1.203, P=0.309), and there was no difference between treatments ($F_{2,7}$ =0.373, P = 0.695).

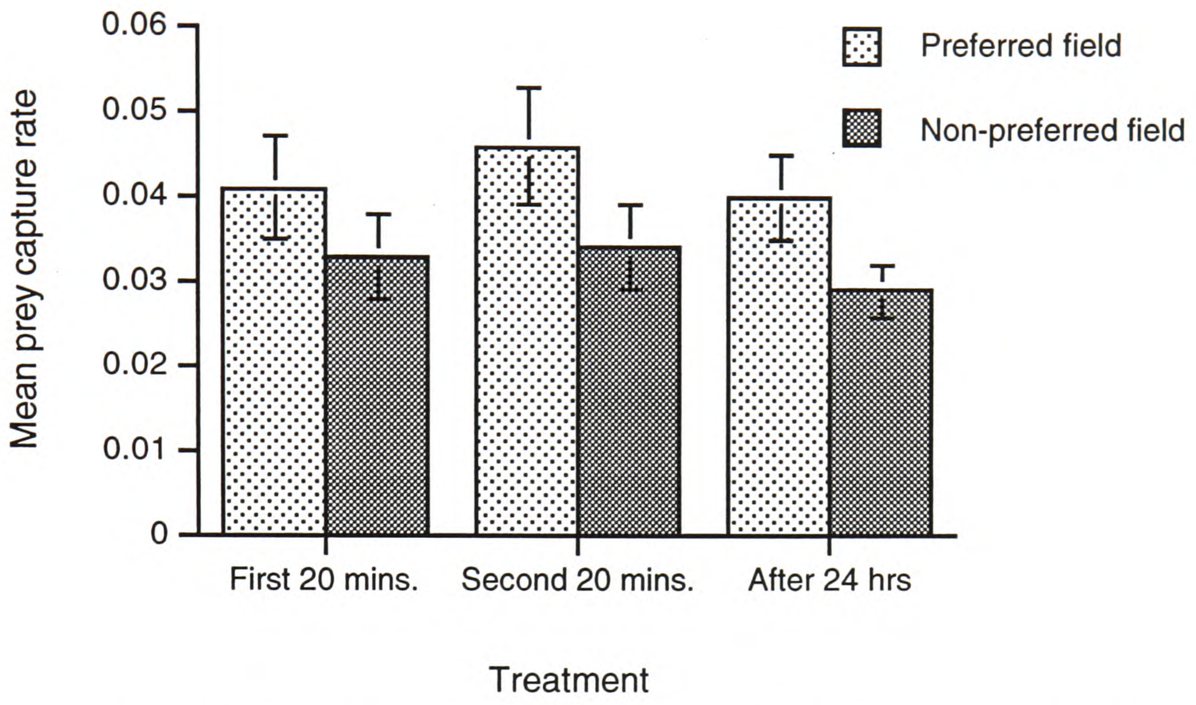


Figure 5.3. Mean (±SE) prey capture rate (number of prey captured per second of foraging) of captive birds allowed to forage in experimental enclosures in two pasture fields (one preferred by the wild flock, and the other non-preferred), for each of the three foraging treatments: Treatment 1 = 20 minutes foraging on a site previously unforaged; Treatment 2 = 20 minutes foraging on a site previously foraged for a 20 minute period and; Treatment 3 = 20 minutes foraging on a site which had been foraged on for two consecutive 20-minute sessions 24 hours previously.

5.3.1.2 Prey-type differences

The main prey types present in the two fields were shown from the soil cores (see next section) to be leatherjackets (*Tipula paludosa*) and earthworms (*Lumbricus* sp.), although small numbers of larval and adult beetles (Coleoptera) and fly larvae (Diptera) were also present. A comparison of reward rates for earthworms and larvae showed significantly higher reward rates for larval prey (Fig. 5.4; $F_{1,7}$=52.447, P<0.001). This difference was particularly marked in the preferred field; hence there was a significant interaction between field and prey type (Fig. 5.4; $F_{1,7}$=15.343, P=0.006). A lack of treatment effect ($F_{2,14}$=0.724, P=0.502) was consistent for both prey types, as indicated by a non-significant interaction between prey type and treatment ($F_{1,7}$=1.128, P=0.351).

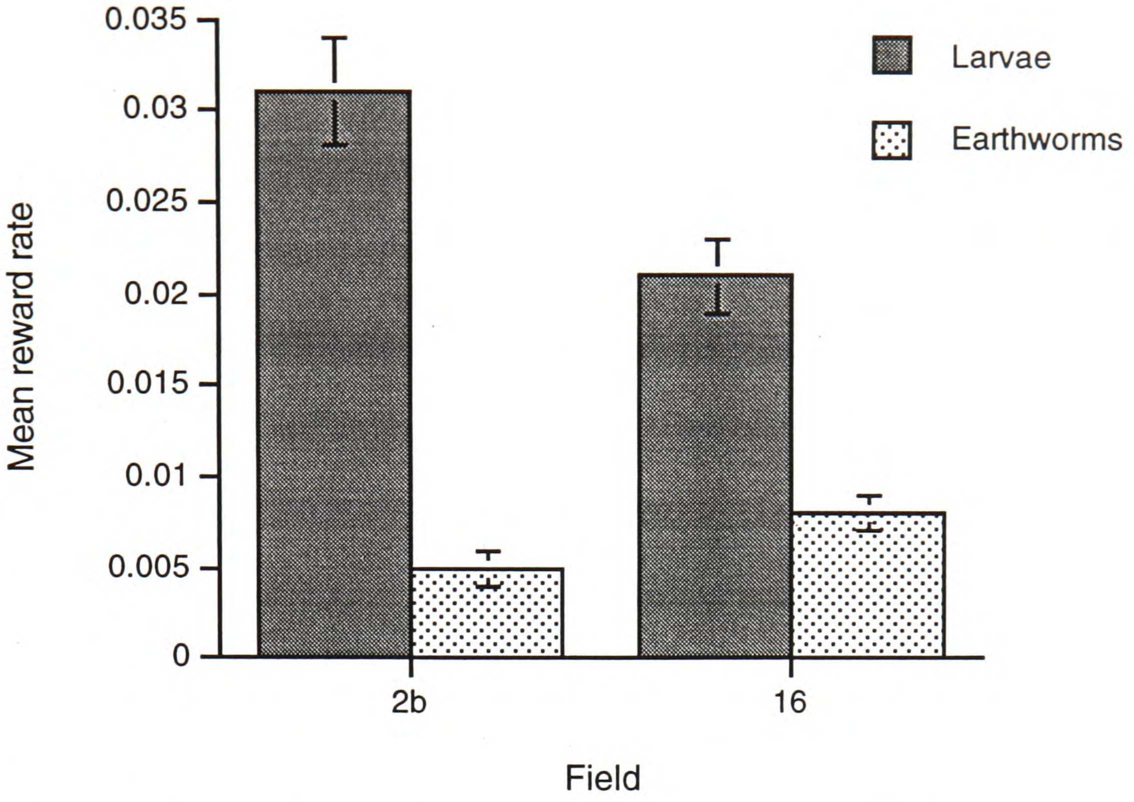


Figure 5.4. Mean (±SE) earthworm and larvae reward rates (number of prey captures per probe) for captive birds allowed to forage in experimental enclosures, in a field preferred by the wild flock (Field 2b) and in a field not preferred by the wild flock (Field 16).

A better measure of reward rate would incorporate biomass differences of each prey type. Hence biomass reward rates were calculated using the mean wet weights of earthworms and larvae collected from the soil cores (mean worm wet weight = 0.131g, s.e. = 0.018g; mean larvae wet weight = 0.034g, s.e. = 0.013g). Controlling for these differences in biomass showed similar biomass reward rates in both fields ($F_{1,7}$=0.288, P=0.608), and no overall difference between the two prey types ($F_{1,7}$=0.002, P=0.969). However, within each field the prey-type difference persisted ($F_{1,7}$=14.678, P=0.006), with larvae predominating over earthworms in the preferred field and earthworms yielding a greater biomass per foraging effort than larvae in the non-preferred field.

5.3.2 Soil cores

The types of prey collected in the soil cores reflected those captured by the birds, with earthworms and leatherjackets predominating. In terms of numbers of prey items there was no significant difference between fields ($F_{1,56}$=0.109, P=0.742) but a significantly greater biomass was collected from the non-preferred field ($F_{1,56}$=8.679, P=0.005). The total numbers of each of the two prey types were very similar

($F_{1,56}$=0.984, P=0.325) but the biomass of earthworms was greater than of larvae ($F_{1,56}$= 7.323, P=0.001).

The within-field difference in prey types captured by the birds was reflected in the soil cores, with more larvae occuring in the preferred field and earthworms being the most abundant type in the non-preferred field (Fig. 5.5a; $F_{1,56}$=11.379, P=0.001). This difference persisted when controlling for the differences in biomass (Fig. 5.5b; $F_{1,56}$=7.718, P=0.007). The lack of any apparent depletion of prey by the birds was reflected in a lack of difference between soil cores extracted from the experimental sites and those from the control sites (prey numbers: Fig. 5.5a; $F_{1,56}$=0.039, P=0.843; prey biomass: Fig. 5.5b; $F_{1,56}$=0.236, P=0.629).

5.3.3 Flock observations

Owing to the frequent movements of the birds, both within the flock and between feeding sites, it was difficult to get a close enough view of individuals to distuinguish their feeding behaviours. This problem was exacerbated by target birds often being obscured by vegetation or by other birds. These factors combined to severely restrict the quantity of data that could be collected. Thus attention was instead concentrated on collecting data on flock densities and movements, from which estimates of flock foraging pressures could be calculated and compared with those exerted by the experimental birds.

Using mean values of the inter-bird distance, flock size, flock residence time, area of regions within each field, and number of these regions covered by the flock in any one visit (Table 5.2), the mean, minimum and maximum foraging pressures exerted by the flock were calculated (Appendix II). These calculations made certain assumptions: i) when at a feeding site all individuals were engaged in feeding to the exclusion of other behaviours (e.g. preening or resting); ii) the mean inter-bird distance was representative of the whole flock (i.e. there was an even rather than an aggregated distribution); iii) any movement of the flock over a feeding area was at a constant rate; iv) the flock foraged on the whole area of each region visited; and v) the flock did not revisit any part of the feeding area during a single visit. The mean flock

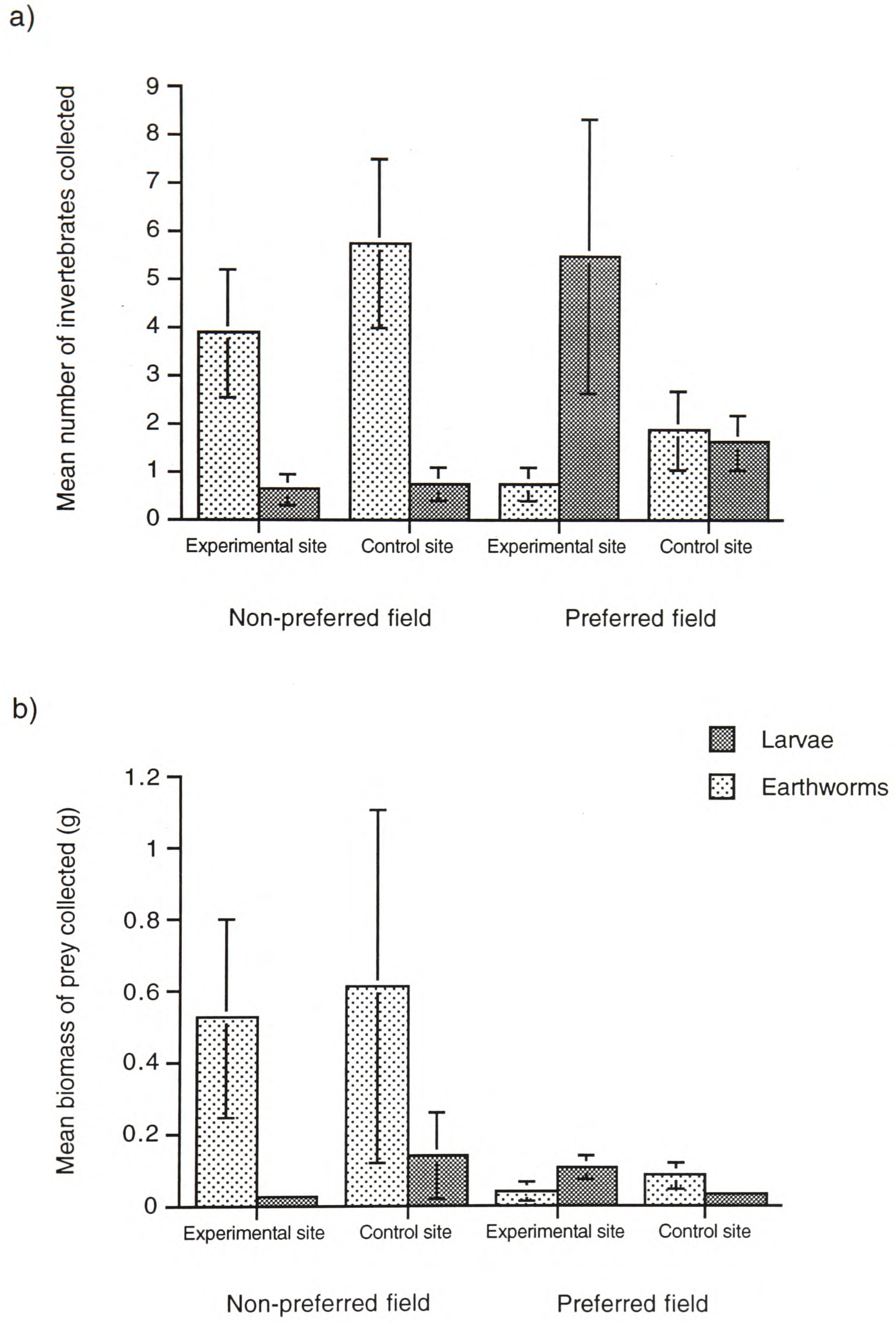


Figure 5.5. a) Mean (±SE) number and **b)** mean wet weight of earthworms and larvae in soil cores extracted from experimental sites, which had previously been foraged by captive birds in experimental enclosures, and control sites, which had not been experimentally foraged. Sites were sampled in a field preferred by the wild flock, and in a field not preferred by the wild flock.

foraging pressure (Appendix IIa) was therefore calculated to be 0.346 bird-minutes/m^2. The maximum flock foraging pressure per visit (Appendix IIb), which assumed that the flock remained resident on the same area of ground throughout the duration of its feeding visit, was estimated at 63.72 bird-minutes/m^2, while at the other extreme, the minimum foraging pressure (Appendix IIc) was 0.227 bird-minutes/m^2.

Table 5.2: Flock measurements, collected during a series of intensive flock observations, on which estimates of flock foraging pressures (Appendix II) are based.

	Mean	S.E.
Flock size (number of birds)	146.76	10.79
Flock residence time (minutes)	24.39	2.19
Interbird distance (bird lengths) (1 bird length = 150 mm)	5.10	0.32
Field area (ha)	5.32	1.01
Number of regions covered during one feeding visit	1.75	0.12

5.4 Discussion

5.4.1 Field and prey-type differences

The greater availability of larvae (predominantly leatherjackets) in the preferred field, shown by both behavioural and soil-core data, supported the findings of Chapter 2. The slightly greater search efforts (probes per time) of the birds when feeding in this field may have been an expression of their preference for these larval prey, demonstrated in Chapter 4. The higher probe and capture rates in the preferred field may also have been a reflection of differences in handling times for the two prey types. Observations of experimental birds suggested that the negligible handling time of larvae (also observed by East & Pottinger (1975)) contrasted with one which was very variable for earthworms, with individuals spending as long as a minute or more manipulating larger worms.

5.4.2 Depletion of prey

Any depletion of prey at the experimental levels of foraging intensity was not evident from the analyses of prey capture rates or reward rates. Obviously, in the absence of any observable resource depression, it is not possible to say anything about renewal of prey, once a patch has been foraged. Although measurements of flock foraging rates with which to compare these experimental rates could not be obtained, it was possible to compare the experimental and flock foraging pressures. Thus the experimental foraging pressure of 2 birds feeding consecutively on 4 m^2 for 20 minutes per bird created a foraging pressure of 5 bird-minutes/m^2 for each bird, and 10 bird-minutes/m^2 after both birds had fed. In contrast with these foraging pressures, which yielded no depletion of prey, the mean flock foraging pressure, at 0.346 bird-minutes/m^2, was almost thirty times less than that of the experiment. Although the maximum calculated flock foraging pressure was six times greater than the experimental value, this maximum value was calculated on the basis of there being continued foraging on the same area of ground without any movement by the flock, which is probably an unrealistic scenario; thus the experimental foraging pressure appears to be towards the upper limit of what might be expected to occur in the flock. The implication of this is that any one visit by the flock to a field will not cause a detectable reduction in the availability of prey.

The above conclusion assumes that the foraging success of individuals is homogeneous throughout the flock. In reality, those birds at the back will be feeding on areas which have already been partially depleted a few minutes earlier by those at the front of the flock (Evans & Dugan 1986; Prins *et al.* 1980). Foraging rate will also be influenced by the presence of other birds in the flock (Goss-Custard 1980). The implications of flock feeding rather than solitary feeding are discussed in more detail in Chapters 6 and 7 but, despite these differences in foraging success within the flock, the expected mean flock foraging pressure calculated from the present experiment is such that any movements between feeding sites is likely to have been due to factors other than depletion of prey.

Such a lack of effect of depletion on foraging rates means that the flock will be able to return repeatedly to a particular site in order to feed, a finding which I described in Chapter 2. However, there will be a limit to the number of visits that can be made, because of the finite numbers of invertebrates in the soil. Thus, for the flock to be able to use the same habitats continually throughout the year, the levels of prey availability at the start of the winter must be far greater than that needed by the birds at that time. Evans & Dugan (1986) discuss how shorebirds may be able to assess the quality of a potential feeding area when they first arrive in the autumn, and only utilise the area if the density of prey is sufficiently abundant to sustain the population in mid-winter. The experiment I have described in this chapter was conducted in February, by which time some depletion of prey will already have occurred, but the continued use of the same fields for the rest of the winter and into the breeding season (see Chapter 8) suggested that there were still sufficient prey left to support the starlings over this time period, hence the lack of impact on prey availabilities during a single flock visit.

Although studies of overwintering waders have demonstrated significant depletion of the invertebrate food stocks (e.g. Goss-Custard 1969, 1980; O'Connor & Brown 1977; Székely & Bamberger 1992), Goss-Custard & Charman (1976) found that the daily food intake rate of an individual Brent Goose was only reduced once approximately 75% of food had been removed from its foraging area. Thus, although the proportion of prey available to the foraging waders may decrease, prey densities may still be sufficient to maintain the birds' intake rates (Goss-Custard 1984). Goss-Custard & Charman (1976) also pointed out that the waders in their studies tended to spread out over the food gradient before any single area became seriously depleted, thus allowing them to continue exploiting the same area throughout the winter.

A similar lack of prey depletion was demonstrated in starlings feeding on grass grubs *Costelytra zealandica*, in New Zealand (East & Pottinger 1975). Although they demonstrated localised depletion of this pest species in areas of very high starling densities, those areas supporting average starling numbers (0-152.1 starling hours per ha per day) did not experience significant grass grub mortality.

5.4.3 Increased foraging success by the second bird?

Although there was no significant effect of treatment on the foraging success of individuals, Figure 5.2 suggests a slight increase in prey capture rates during treatment 2, rather than any decrease. This pattern may have been due merely to a small sample size, but there is also the possibility that the second bird was in some way increasing its foraging success as a result of following the previous bird. The prominent probe marks left in the soil by the first bird may well have been used by the second bird as an indication that the area already been foraged, and therefore depleted, in a similar way that oystercatchers *Haematopus ostralegus* use the accumulation of empty shells at 'anvil' sites as an indication of previous depletion of that feeding area (O'Connor & Brown 1977). Alternatively, the starlings could have used probe marks as an indication of an area of particularly high prey abundance on which it was worth foraging, and this will be explored further in Chapter 6.

5.5 Summary

The extent to which foraging starlings depress the availability of resources was investigated by allowing captive birds to forage in experimental enclosures for an extended period of time. Observations of the wild flock provided me with estimates of the natural level of foraging. The experimental foraging pressures, which I estimated to be greater than those expected in the flock, produced no observable effect of depletion. I therefore concluded that any depletion imposed by a single flock visit had a negligible impact on the total availability of prey in any one area. The reasons for feeding site departures must be more subtle than absolute prey depletion by the foraging flock, and will be discussed in more detail in subsequent chapters.

Chapter 6

Flock feeding and resource depression

6.1 Introduction

At the levels of foraging intensity imposed in the last experiment there was no depletion of prey observed. I estimated that those levels of foraging probably lay towards the upper end of the range expected within the wild foraging flock, from which I concluded that the natural flock was not causing significant prey depletion during one foraging visit to a site.

However, the last chapter also drew attention to the non-renewable nature of the starlings' invertebrate food source during winter. This means that some depletion, however slight, must be occurring each time a site is visited by the feeding flock. The level of foraging pressure at which this depletion becomes significant is an important consideration for the overwintering starlings. Are prey sufficiently abundant for the flock to continue using the same sites throughout the winter, or will the availability of prey be depleted after just a few visits, such that the flock then has to move to other, less-preferred sites?

This chapter also addresses the question of a possible effect of increased foraging success by feeding where another individual has just fed, an effect alluded to in the last chapter. As a flock-feeding species, a starling's feeding rate can be influenced by the presence of other individuals. The lower levels of vigilance per individual will increase foraging rate (Pulliam 1973). Foraging success can be further increased through social learning, whereby a bird attends to the foraging behaviour of other flock members (e.g. Turner 1965). In contrast with these benefits of flock feeding, there will also be costs associated with feeding in the company of others. There are many studies illustrating the response of individuals to a reduction in feeding rate resulting from interference from other birds (e.g. waders: Goss-Custard 1977c,1980; Goss-Custard & Charman 1976; Puttick 1984). How these factors interact to determine the spacing behaviour of flocking individuals is discussed by Myers

(1984), and the costs and benefits of flocking are given theoretical consideration by Pulliam & Curaco (1984), and Székely *et al.* (1991).

The above effects are attributable to behavioural interactions between individuals, and will be discussed in more detail in the next chapter. However, a starling will also be subject to indirect or 'exploitation' interference of its feeding behaviour, through the effects of conspecifics on its invertebrate food source. An obvious cost of feeding with other individuals is that local food availability will be depleted more rapidly than when feeding alone. This 'exploitation depression' (Charnov *et al.* 1976) may be in the form of non-renewable depletion as a result of other birds eating the prey (Goss-Custard 1980). Alternatively, a predator avoidance response of the invertebrates will invoke a temporary reduction in their availability to the birds (Charnov *et al.* 1976; Feare 1984; Goss-Custard 1980; Zwarts & Drent 1981), the extent of such an effect being influenced by the spacing of individuals within the flock (Goss-Custard 1970b, 1976). In contrast, individuals may increase their feeding rate by attending to cues left by other birds. As was suggested in Chapter 5, starlings may use probe marks left by others as an indication that a particular area has already been foraged and depleted, an effect shown by tits (*Parus* spp.) feeding on pine cones (Gibb 1962). Alternatively, the foraging marks may represent an area of high prey density which is worth foraging (East & Pottinger 1975).

This chapter addresses the question of how one starling's foraging success is affected by feeding on a patch that has already been foraged by another starling a few minutes previously. This is pertinent to the flock-feeding situation in which the majority of individuals will be positioned behind at least one, if not several, other individuals (Evans & Dugan 1986), and thus be susceptible to the indirect interference from these other flock members. This question has already been given some attention in Chapter 5, although that experiment was primarily concerned with looking for effects of depletion of prey. This experiment provides a further test for an effect of resource depression, as well as providing a more controlled test for the indirect effect of feeding with conspecifics.

I used the experimental enclosures once more and, by comparing the foraging success of an individual allowed to forage on a piece of ground not foraged during the previous 24 hours with a similar area of ground which had been foraged a few minutes beforehand, I was able to look for any effects of indirect interference . The same bird was then left to forage in the test enclosure for several hours to see whether this level of foraging pressure was sufficient to cause significant depletion of invertebrate availability.

6.2 Methods

6.2.1 Subjects

Eight adult starlings (four males and four females) were trapped from the resident population at University Farm, Wytham. The feeding and maintenance for these birds was the same as for those used in Chapter 3.

6.2.2 Experimental design

Testing was carried out in the 'preferred' and 'non-preferred' pasture fields used in the last experiment (Chapter 5). Within each field, I selected randomly one experimental site from each of the eight regions previously assigned to the fields, such that all the birds could be tested in both fields.

The test enclosures measured 2 m wide x 2 m long x 1 m high, and I divided the ground area within each enclosure into four quadrats, each measuring 1 m x 1 m (Fig. 6.1). The boundaries of these areas were delineated by 50 mm high strips of wire mesh which formed a cross in the centre of the enclosed area and extended to each of the four sides. For the manipulation phase of the experiment, I covered two diagonally opposing quadrats with 1 m^2 sheets of 5 x 10 mm gauge wire mesh. These sheets were raised off the ground by 50 mm, so that the substrate below was beyond the starlings' probing range.

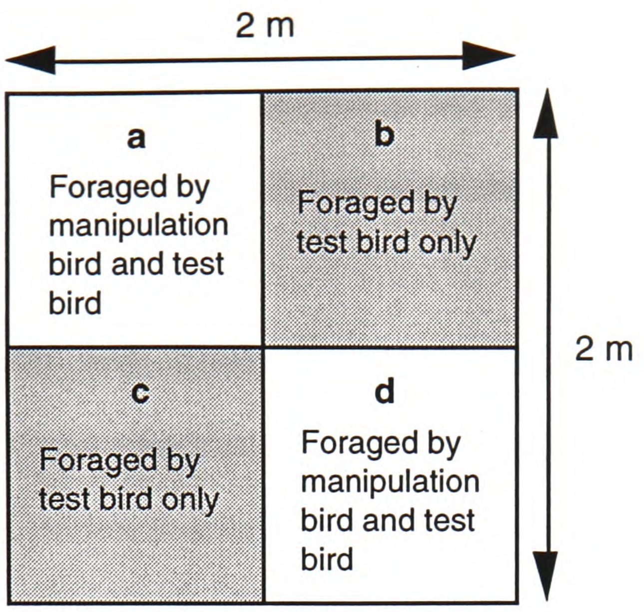


Figure 6.1: Allocation of experimental foraging treatments to ground area of test enclosure. Quadrats **a** and **d** were foraged on by one ('manipulation') bird for 10 minutes. All four quadrats were then foraged on by a second ('test') bird for four hours.

Each experimental session began with a manipulation phase, during which I allowed one of the birds to forage in the enclosure for 10 minutes. This amount of foraging (10 min on 2m ^{2}) imposed the same foraging pressure as in the first treatment of the experiment described in Chapter 5, in which the first bird foraged for 20 min on 4 m^2; thus I was able to test for the possible enhancement effect seen in that experiment. After the manipulation phase of this experiment, the bird was removed from the enclosure and the protective sheets of mesh taken up, thus exposing the whole area of the enclosure to the next foraging bird. I then released a second bird into the enclosure and allowed it to forage for four hours. The first twenty minutes of this session were recorded, as well as a further 10 minutes once the bird had been in the enclosure for an hour. A final 10 minutes were recorded at the end of the four-hour period. The bird was then returned to the holding enclosure and given *ad lib.* food for the rest of the day.

Training was started on 6/2/93 and all testing had been completed by 27/2/93. As with the previous experiment, testing in the two fields was alternated on a daily basis in order to control for any effects of date or weather on prey availability.

Additional information regarding prey types and densities was obtained from soil cores. At each of the experimental sites, six soil cores (80 mm diameter and 150 mm depth) were taken from random positions within the site immediately after the test session at that site had been completed. Another six were taken from a randomly chosen control site, positioned in any one of the eight allocated regions of the field. Invertebrates were extracted from the cores using the technique described in Chapter 5.

6.2.3 Data collection and analyses

As in the previous experiment, I recorded the birds' foraging behaviour on video to allow data collection at a later date. The behavioural data was used to calculate prey capture rate (slope of cumulative number of prey captures divided by time in trial), search effort (slope of cumulative number of exploratory probes divided by time in trial) and reward rate (slope of cumulative number of prey captures divided by cumulative number of exploratory probes). Comparisons of these variables were made between fields and treatments using repeated-measures ANOVA. A full set of data was collected from only 7 of the birds, hence the number of subjects was reduced to 7 for all analyses.

6.3 Results

6.3.1 Field and prey-type differences

It has already been established in previous experiments (Chapters 3 and 5) that the main types of prey captured by the foraging starlings are earthworms and arthropod larvae (particularly leatherjackets, *Tipula paludosa*). The predominance of these two soil invertebrate types in the birds' prey captures was again apparent in this experiment. Analyses of prey-type reward rates (prey per probe) (Table 6.1a) showed that larval reward rates were greater in total than those for earthworms. As before, a significant interaction between field and prey type effects was explained by more larvae than earthworms in the preferred field but no difference between prey types in the non-preferred field (Fig. 6.2).

Differences in biomass were accounted for by multiplying reward rates by the mean wet weights of the two prey types (mean worm wet weight = 0.185g, S.E.= 47.0

mg; mean larval wet weight = 0.030 g, S.E.= 4.7 mg). Subsequent analyses (Table 6.1b) showed no significant difference between the total biomass reward rates of each prey type, and a slight, but non-significant, difference between the fields. However the significant interaction between field and prey type persisted, with larvae predominating over earthworms in the preferred field and earthworms yielding a greater biomass than larvae in the non-preferred field.

Table 6.1: Two-way repeated-measures ANOVA with reward rate of captive birds allowed to forage in experimental enclosures as dependent variable. Reward rate is expressed as **a)** mean number of prey captured per probe made by the bird, and **b)** mean biomass of prey captured per probe made by the bird. Factors were prey type (earthworms or larvae) and field (preferred or non-preferred by the wild flock). Error d.f. = 6.

		a) numbers		**b) biomass**	
Factor	**d.f.**	***F*-ratio**	***P*-value**	***F*-ratio**	***P*-value**
Prey type	1	25.613	0.002	1.933	0.214
Field	1	6.265	0.046	4.340	0.082
Prey type * Field	1	24.711	0.003	43.298	<0.001

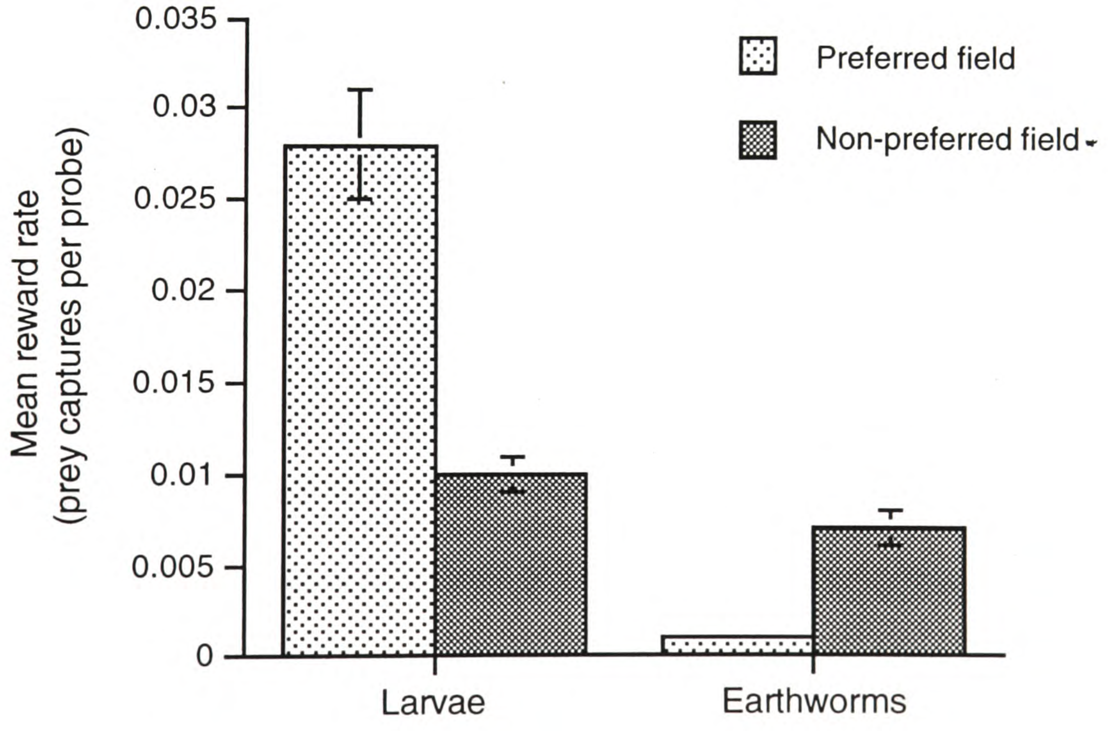


Figure 6.2. Mean (±SE) reward rate (mean number of prey captures per probe) of captive birds allowed to forage in experimental enclosures in a field preferred by the wild flock, and in a field not preferred by the wild flock. Reward rates are separated into those for larval prey captures, and those for earthworm captures.

6.3.2 Measuring depletion of prey availability

Consistent with both earlier enclosure experiments (Chapters 3 and 5) linear relationships were found within individual trials both for the number of probes made with time (Fig. 6.3a) and the number of prey captures made with time (Fig. 6.3b). Therefore any effects of satiation or depletion were considered to be negligible.

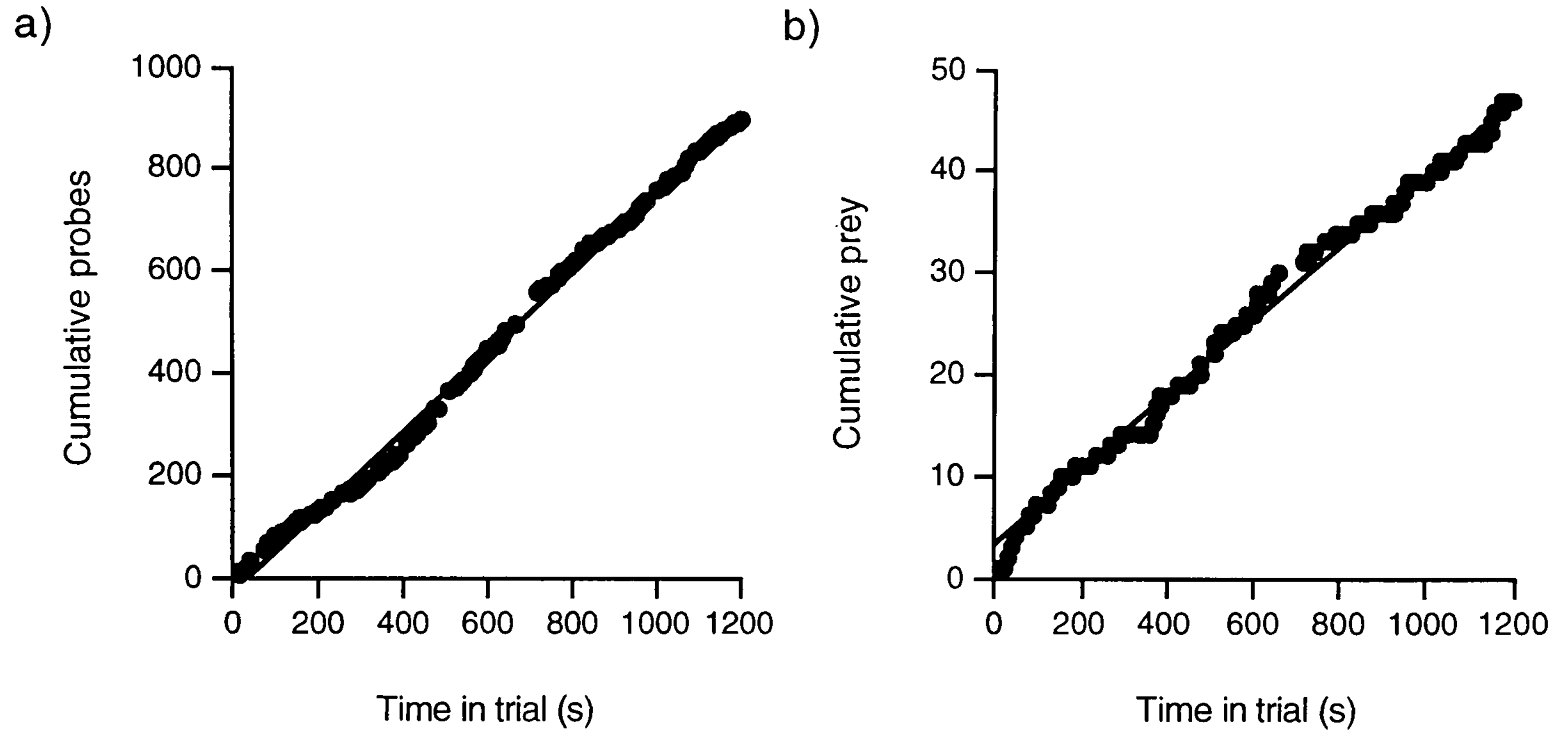


Figure 6.3. Example plots for one bird of **a)** rate of searching, expressed as the cumulative number of probes made with time, within a single representative feeding trial (y=-26.25+0.782x, r^2=0.997, P<0.001); **b)** rate of prey capture, expressed as the cumulative number of prey captures with time, within a single representative feeding trial (y=3.148+0.037x, r^2=0.994, P<0.001).

In contrast, analyses of capture rates (Table 6.2a) over the duration of the whole experimental session showed a significant decrease over the four-hour test period. However, prey capture success rate will also have been affected by the number of foraging probes each bird made (Table 6.2b). Although search efforts did not differ between the two fields, there was a significant change in search efforts over the duration of the experimental session, showing an increase over the first hour of foraging, but declining again by the end of four hours.

To take account of these differences in search effort, prey capture was expressed as a rate per probe, rather than per unit time (Table 6.2c). These reward rates were greater in the preferred field than in the non-preferred field, but both fields showed a significant decrease over the four hours of foraging (Fig. 6.4). *Post-hoc* contrasts of the means showed that prey availability was significantly lower at the end of the first hour than at the beginning of the session ($F_{1,12}$=8.012, P=0.015). The difference between reward rates at the start and after four hours was even more significant ($F_{1,12}$=26.743, P<0.001).

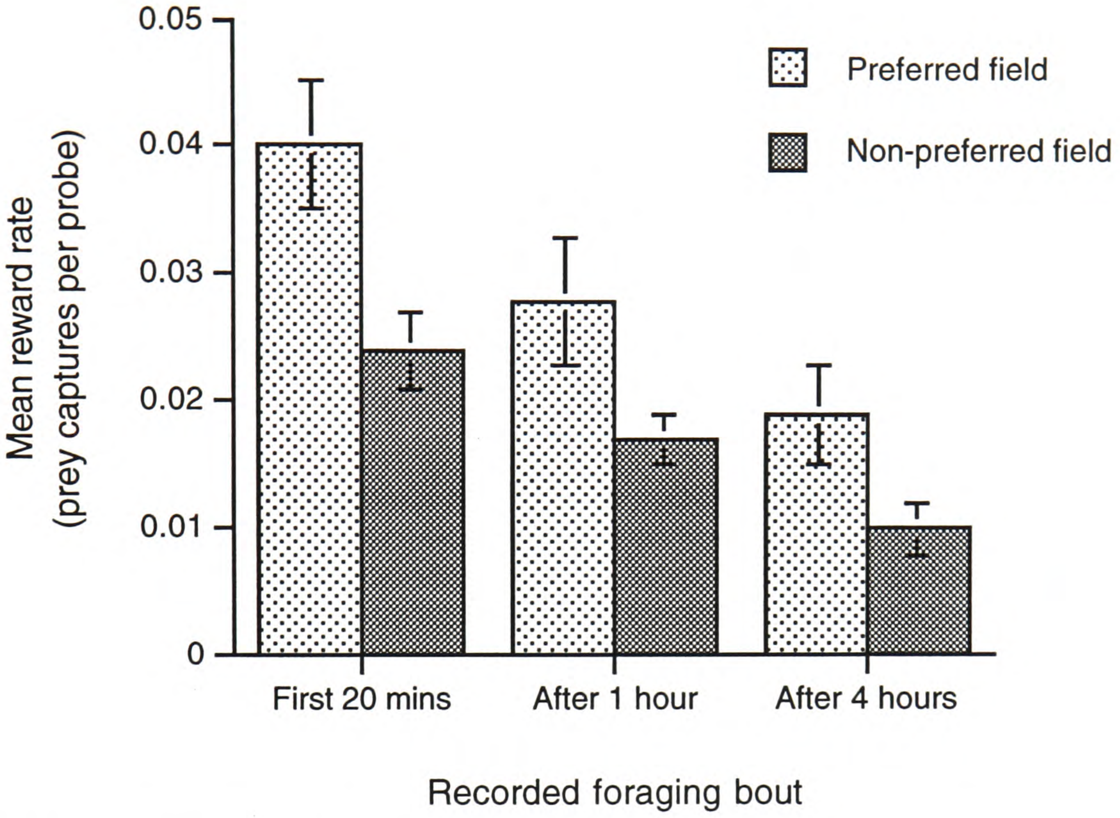


Figure 6.4. Mean (±SE) reward rate (number of prey captures per probe) in the two experimental fields (one of which was seen to be 'preferred' by the wild flock, and the other 'non-preferred'), sampled for three recorded foraging bouts during the four-hour period that captive birds were allowed to forage in experimental enclosures. Foraging bouts were recorded during the first twenty minutes of the test session, for ten minutes once the bird had been in the enclosure for an hour, and for a final ten minutes at the end of the four-hour period.

6.3.3 Measuring the indirect effects of foraging by conspecifics?

There was no difference in the amount of searching (Table 6.2b) by the experimental birds in the two parts of the enclosure (previously foraged, and previously unforaged), and this lack of difference persisted throughout the four-hour period of foraging. In contrast, although overall capture rates (Table 6.2a) were similar in both parts of the enclosure, how capture rates changed over the duration of the experimental period was different in each of the two parts. This difference will be described below in terms of reward rates (i.e. prey captures per probe, rather than per time).

Combining search efforts and prey capture rates showed there to be no significant difference between the resulting reward rates (Table 6.2c) in each part of the enclosure (Fig. 6.5). However the pattern of change in reward rates over the four-hour period was significantly different between the two parts of the enclosure (Fig. 6.5). A comparison of the first two time periods only showed a significant interaction between the effects of treatment and time ($F_{1,7}$=12.396, P=0.010). It is clear from Figure 6.5 that this effect was due to a reduction in the reward rate in that part of the enclosure which had not previously been foraged, with no such decrease in that part which had been foraged. In contrast with this result, a comparison of the second and third treatments only showed no significant interaction between the effects of time and treatment ($F_{1,7}$=3.170, P=0.125).

Table 6.2: Three-way repeated-measures ANOVA with **a)** capture rate (mean number of prey captures per minute foraging); **b)** search effort (mean number of probes per minute foraging); and **c)** reward rate (mean number of prey captures per probe), of captive 'test' birds allowed to forage in experimental enclosures as dependent variables. Factors were field (preferred or non-preferred by the wild flock), length of time foraging on the whole enclosure area, and treatment (part of enclosure previously foraged by another ('manipulation') bird for 10 minutes prior to the test session, and part of enclosure not previously foraged by another bird) Data for 'manipulation' bird is not included in this analysis. Error d.f. = 6.

		a) Capture rate		b) Search effort		c) Reward rate	
Factor	**d.f.**	***F*-ratio**	***P*-value**	***F*-ratio**	***P*-value**	***F*-ratio**	***P*-value**
Field	1	13.159	0.011	1.690	0.241	6.293	0.046
Time (foraging)	2	5.999	0.016	10.703	0.002	13.412	0.001
Treatment	1	2.118	0.196	1.588	0.254	0.116	0.745
Field * Time	2	0.615	0.560	0.466	0.639	0.517	0.609
Field * Treatment	1	0.071	0.780	2.034	0.204	0.744	0.423
Time * Treatment	2	5.100	0.025	0.020	0.980	6.234	0.014
Field * Time * Treatment	2	1.220	0.330	0.187	0.832	0.584	0.573

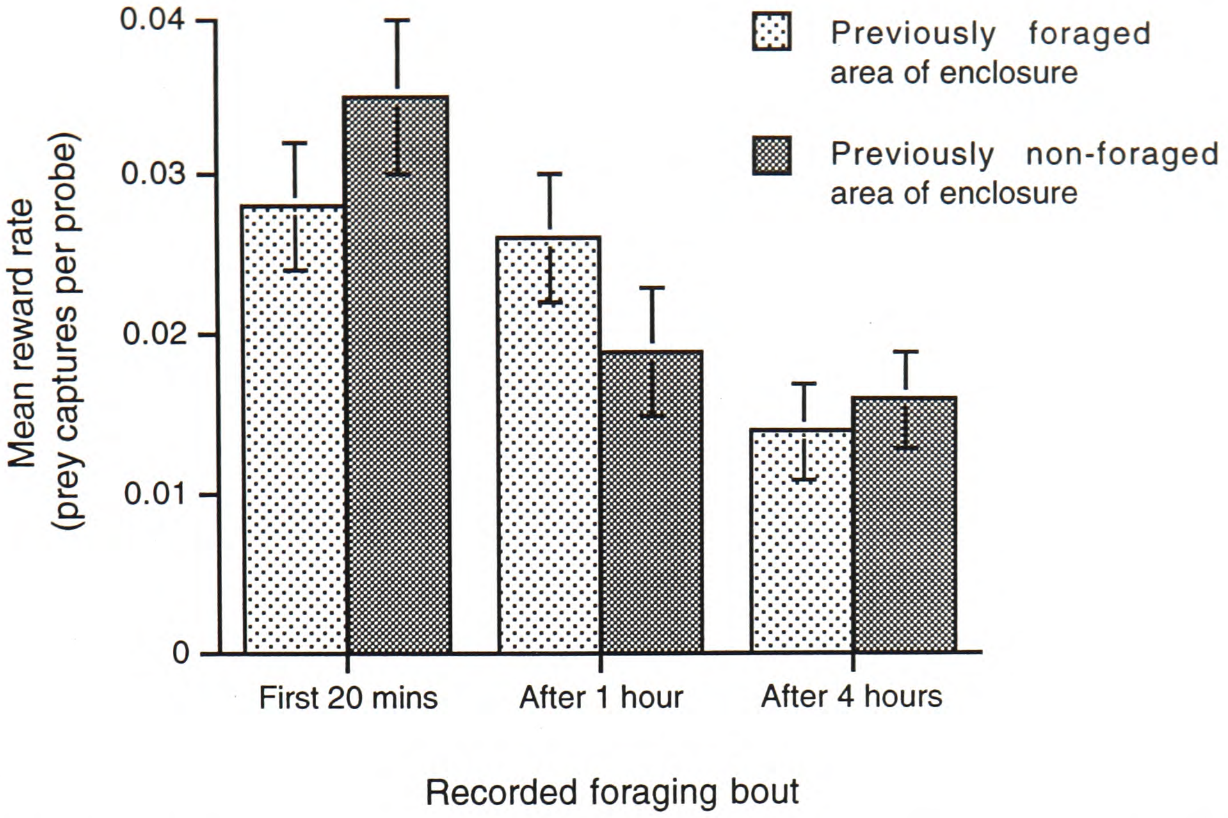


Figure 6.5: Mean (±SE) reward rate (number of prey captures per probe) of captive birds allowed to forage in the experimental enclosures. Half of the enclosed area had previously been foraged on by another bird, immediately prior to foraging by the test bird; the other half of the enclosed area had received no such foraging. Reward rates are shown for each of the three recorded foraging bouts (20 minutes at the start of the four-hour period, 10 minutes after an hour of foraging, and 10 minutes at the end of the four-hour test session).

Any indirect effects of conspecific foraging were also examined by comparing foraging success during the manipulation phase with that attained during the first twenty minutes of the test period, the latter on both previously foraged and previously unforaged areas of the enclosure. Search efforts attained during the manipulation phase were not significantly different to those in each part of the enclosure during the first twenty minutes of testing (Table 6.3a). Despite these similarities in search efforts, analyses of reward rates (Table 6.3b) showed a significant difference between the three treatments and between fields (Fig. 6.6a). *Post-hoc* contrasts of the means of combined data for both fields showed that reward rates on that part of the enclosure not foraged prior to the test period (i.e. not foraged by the manipulation bird) were significantly greater than reward rates on the remaining part of the enclosure, both when it was foraged during the manipulation period ($F_{1,12}$=22.653, P<0.001) and when it was foraged during the test period ($F_{1,12}$=7.982, P=0.016). Comparison of these latter two treatments showed similar reward rates on the same area of enclosure during manipulation and testing. ($F_{1,12}$=3.471, P=0.074).

Table 6.3: Two-way repeated-measures ANOVA with **a)** search effort (mean number of probes per minute foraging); and **b)** reward rate (mean number of prey captures per probe), of captive birds allowed to forage in the experimental enclosures as dependent variable. Factors were field (preferred or non-preferred by the wild flock), and foraging treatment (quadrats a & d [see Fig. 1] after foraging by manipulation bird; quadrats a & d after foraging by manipulation and test bird; quadrats b & c, foraged by test bird only). Error d.f. = 6.

		a) search effort		**b) reward rate**	
Factor	**d.f.**	***F*-ratio**	***P*-value**	***F*-ratio**	***P*-value**
Field	1	33.000	<0.001	6.399	0.039
Treatment	2	0.687	0.519	11.459	0.001
Field * Treatment	2	0.500	0.617	0.034	0.967

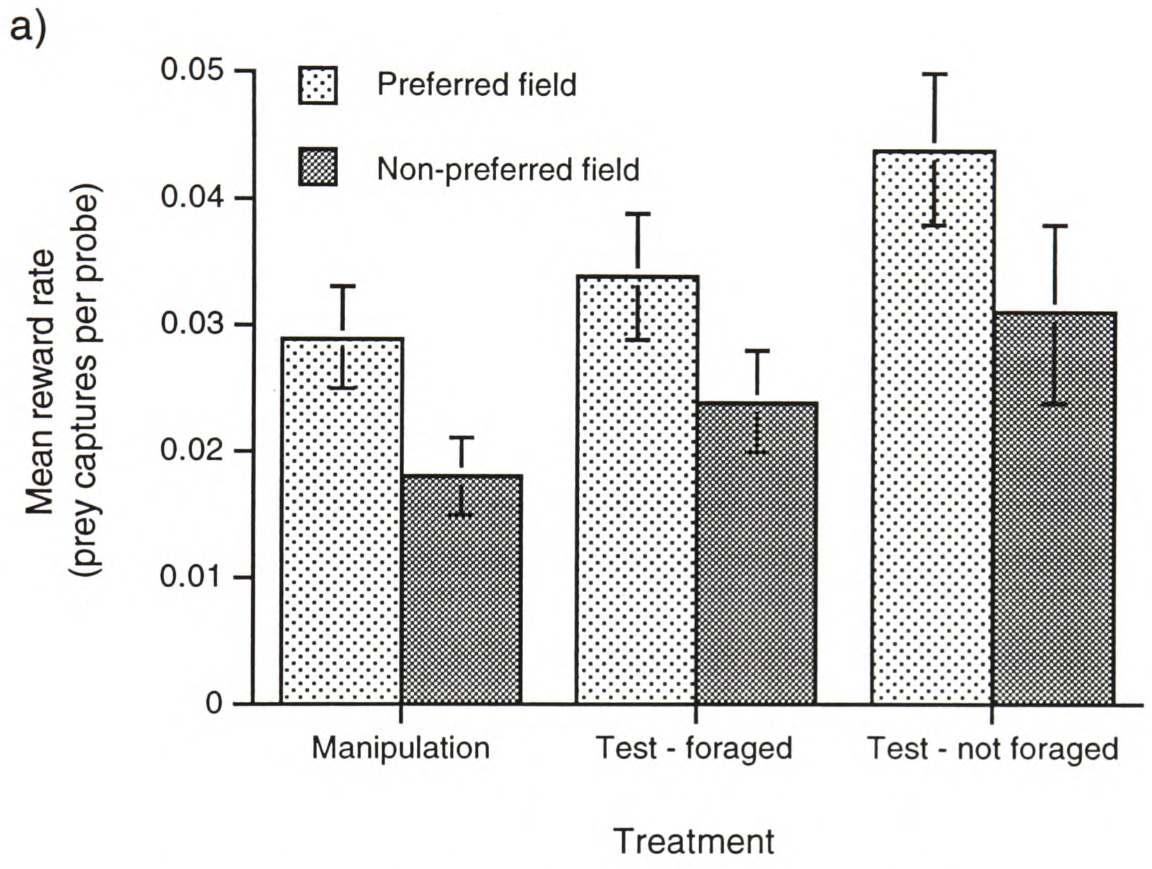


Figure 6.6. Mean (±SE) reward rate (number of prey captures per probe) attained by captive birds allowed to forage on one half of the experimental enclosure area, for 10 minutes ('manipulation'), compared with the first 20 minutes of foraging by a second bird then allowed to forage on both parts of the enclosure - that which had previously been foraged by the manipulation bird ('test - foraged'), and that which had not previously been foraged by manipulation bird ('test - not foraged). Results are shown for a pasture field preferred by the wild flock compared with a pasture field not preferred by the wild flock.

6.3.4 Soil cores

As previously stated, the invertebrates collected from the soil cores were predominantly earthworms (*Lumbricus* spp.) and leatherjackets (*Tipula paludosa*). Although small numbers of beetle larvae and adults (Coleoptera), and fly larvae (Diptera) were also extracted from the cores, their sample sizes were too small for them to be included in any analyses.

Analyses of the numbers of invertebrates collected from the soil cores (Table 6.4a) showed no difference between the two fields, but found there to be significantly more leatherjackets than earthworms. Despite a significant reduction over the duration of experimental sessions in the availability of prey to the experimental birds there appeared to be no such reduction in the abundance of prey, as shown by the lack of significant difference between the number of invertebrates collected from experimental sites and the number from non-foraged, control sites.

In terms of biomass (Table 6.4b), there was an almost significant difference in the amount of invertebrates collected in each of the two fields, but no difference between control and experimental sites. There was a significantly greater biomass of earthworms than of larvae, much of which was collected from the non-preferred field.

Table 6.4: Three-way ANOVA with **a)** numbers of each invertebrate prey type; and **b)** wet weights of each invertebrate prey type, collected from soil cores (150 mm deep and 80 mm diameter) at each site, as dependent variables. Factors were field (preferred or non-preferred by the wild starling flock), prey type (larvae or earthworms) and treatment (sites previously foraged, for four hours, by captive starlings in experimental enclosures, or sites not foraged). (Error d.f. = 56).

		a) numbers		b) wet weights	
Factor	**d.f.**	***F*-ratio**	***P*-value**	***F*-ratio**	***P*-value**
Field	1	0.654	0.422	3.870	0.054
Prey type	1	9.244	0.004	7.490	0.008
Treatment	1	0.063	0.802	0.575	0.451
Field * Prey type	1	0.040	0.841	1.806	0.184
Field * Treatment	1	0.563	0.456	0.001	0.977
Prey type * Treatment	1	0.011	0.915	0.208	0.650
Field * Prey type * Treatment	1	0.841	0.363	0.987	0.325

6.4 Discussion

6.4.1 Field and prey-type differences

Although not the central question of this experiment, the consistency of the observed differences in the availabilities of prey type to the birds should be noted. The experimental measures of prey availability made so far (Chapters 3, 5 and the present experiment) spanned a period of twelve months, throughout which the pattern of prey availabilities between the two experimental fields remained constant. This stability may be attributed largely to the unchanging management of these two permanent pasture fields. In contrast, many of the other fields, including those sown with grass ley, underwent frequent year to year changes in their management. Although observations have shown that the starlings are quick to respond to favourable changes in management (e.g. grass cutting, Tinbergen 1981) the consistency of other parts of their environment should be important in contributing to the birds' successful exploitation of the available habitats. The importance of a stable habitat has been discussed in relation to shorebirds (Evans & Dugan 1986) which may assess the quality of a feeding area in autumn in order to predict invertebrate densities and potential intake rates later in the winter. Such assessments, however, are only valid in stable environments and are of no value in unstable habitats prone to disturbance.

6.4.2 Depletion of prey availability

By increasing the duration of foraging it was possible to see a significant depression in prey availabilities after one hour (15 bird-minutes/m^2), and an even greater reduction after four hours (60 bird-minutes/m^2). How do these levels of prey depletion relate to the foraging intensity exerted by the flock? At the mean estimated flock foraging pressure (Appendix II: 0.346 bird-minutes/m^2) the flock would have to have visited any particular feeding area 15 / 0.346 = 43 times to cause the depletion seen after one hour of experimental foraging (assuming that the levels of prey availability are not renewed between each visit), and would have to have visited the same site 173 times (= 60 / 0.346) to deplete prey availabilities down to the level seen at the end of the experimental session. Obviously, there may have been a significant reduction in the availability of prey in less than an hour. However, I demonstrated in Chapter 5 that at a foraging pressure of 10 bird minutes/m^2 (40 minutes of foraging on the same area ($4m^2$) of enclosure as in this experiment) there was no significant depression; hence I have at least been able to identify the range of foraging pressures between which I estimate that flock foraging first has a significant impact on the availability of prey.

These estimates are consistent with my earlier prediction (Chapter 5) that a single flock feeding visit to an area is unlikely to be causing significant depletion of prey. Although evidence is also presented that prey will be depleted over many visits, these trips will be interspersed by visits to many other similar sized feeding sites. Hence, I would expect the extent of depletion at any one site to be a gradual process over an extended period of time (Goss-Custard & Charman 1976), which is more likely to be in terms of weeks or even months rather than days.

Although this experiment produced a significant reduction in the availability of prey to the birds, even at the end of four hours the birds were still obtaining some prey. These final capture rates may have been insufficient to sustain the wild birds during the middle of the winter, but it has already been indicated that these low levels of prey availability will not be reached until later on in the season. By this time, depletion will be compensated for, at least in part, by an increase in invertebrate biomass (Dunnet 1955; Tinbergen 1981). This will effectively constitute some renewal of invertebrate availabilities, and may reduce the impact of overwintering prey depletion on the flock.

Although it appears that any long term depletion of prey is unlikely to have a significant effect on the starlings' choice of feeding site during the winter, the consequences of any overwinter depletion may become more significant later on in the year. Chapter 8 will investigate whether there are still sufficient prey available during the breeding season, when the birds' energetic requirements escalate.

Despite the observed depression in the level of food available to the birds, as a consequence of the experimental birds' foraging, analyses of soil core data revealed no significant reduction in the abundance of prey. This then provides further support for the suggestion that the starlings are only removing a subset of the invertebrates which could potentially be available to them, as well as underlying the need to distinguish between the issues of prey abundance and prey availability. Although we can address the question of prey abundance by taking soil cores, only by examining the foraging behaviour of the birds can we begin to understand the more pertinent issue of the availability of prey.

6.4.3 Is an individual's feeding rate subject to exploitation interference?

The test birds' reward rates in that part of the enclosure which had also been fed on by manipulation birds equalled the reward rates achieved by the manipulation birds, and were even higher on that part of the enclosure which had not been foraged by the manipulation birds. In accordance with this result the reduction in the test birds' reward rates over the first hour of forging was only significant in that part of the enclosure which had not previously been foraged (i.e. where their reward rates were initially higher).

Any difference between the test birds' search efforts in the two parts of the enclosure was not detected, but the observed pattern in the reward rates may have reflected differences in the foraging efficiency of test birds compared with manipulation birds. The test birds, perhaps due to greater hunger levels as a result of slightly longer deprivation, may have been better at capturing prey, but this increased efficiency was only manifested in those areas of the enclosure where prey was still sufficiently abundant (i.e. where no previous foraging had occurred). Once the most accessible prey had been removed any differences between the two parts of the enclosure may have equilibrated, this being compatible with the observed equilibration of reward rates.

Had the test birds been using physical cues left by the manipulation birds to direct their own foraging effort I would have expected to see differences in search effort between the two parts of the enclosure. The apparent absence of any such adjustment is consistent with East & Pottinger's (1975) studies in which they observed that, instead of attending to probe marks left by other birds, their starlings appeared to be probing at random and used their own foraging success as a cue to the most profitable foraging area (Charnov 1976).

The results of this experiment do not provide evidence for exploitation depression. Comparison of the experimental foraging pressures with those calculated for the flock (Appendix II) shows that the foraging pressure of 5 bird-minutes per m^2

imposed during the manipulation phase was approximately 15 times the mean expected flock foraging pressure per visit, suggesting that any effects of exploitation depression would also be absent from the flock. However, this takes no account of the heterogeneity of flock foraging pressures within the flock and although the above prediction may be true for those birds towards the front of the flock, those at the back are going to be feeding on areas previously foraged by many birds rather than just one bird (Evans & Dugan 1986; Prins *et al.* 1980). Any effects of feeding with conspecifics when at the back of the flock will therefore be magnified and the possibility of exploitation depression cannot be discounted.

The proposed heterogeneity of foraging pressures and associated effects across the flock may be a causal effect for the apparently premature departure of the flock from a feeding site, before prey depletion has occurred. Observations show 'rolling' movements of the flock across feeding areas, with birds from the middle or back of the flock flying up and moving to the front (East & Pottinger 1975). While those feeding at the front of the flock can attain sufficiently high feeding rates, it is likely that those at the rear will be experiencing lower foraging success and may be forced to move, either flying to the front of the flock or moving to a new feeding site (e.g. rock doves *Columba livia*, Perusse & Lefebvre 1985). If the latter is true, the remaining birds would then be expected to follow if the cost of moving to a new feeding site is outweighed by the cost of remaining where they are but in a much reduced flock.

The dynamics of flock size has been studied in detail by Barnard (1980c) and is reviewed by Barnard & Thompson (1985). In his study of house sparrows *Passer domesticus*, Barnard (1980c) found that as flock size increased, subdominant birds were ousted from the best feeding areas (i.e. areas of highest seed density). These birds then left the flock if the feeding rates they attained after being ousted were too low. However, Barnard also found that when feeding in areas of high predation risk (i.e. in open fields rather than in barns) the flock left a feeding area much sooner. In these cases some birds often remained and were seen to experience an increased intake rate once the majority of the flock had left, suggesting that in these cases the subdominants chose to remain on good feeding areas so that they could exploit them once the more dominant birds had left.

For the starlings, flock departures from feeding sites are often extremely fast and so it is very hard to determine which individuals are actually instigating a departure. However, establishing the details of such flock movements and relating them to individual reward rates at different positions within the flock would be necessary in order to explore this as a possible mechanism of flock movements between feeding sites.

6.5 Summary

The impact of intensive foraging on the availability of prey was investigated and the effects of following behind other foraging birds on an individual's foraging success were explored by observing the foraging behaviour of captive starlings feeding in experimental enclosures

In both a pasture field preferred by the wild flock and in pasture field not preferred there was a significant decrease in prey available to the experimental birds after one hour of foraging. I estimated that this level of resource depression would equate to approximately 43 separate flock visits to any one site, (assuming a mean estimated flock foraging pressure), thus a single flock feeding visit would be unlikely to significantly reduce the availability of prey to the birds.

When the birds were given access to ground which had already been foraged by another starling their foraging success was no lower than that achieved by the earlier bird, providing no evidence for exploitation depression of prey availabilities. At the levels of foraging expected in the flock I estimated that an individual's reward rate would not be decreased as a result of following behind one other bird. The effects of following behind many birds, as is the case in natural flocks, may be much greater. Consequent reductions of foraging success are proposed as one possible cause of within, and between, flock movements, but further research would be required to explore this.

Chapter 7

Foraging performance of individuals feeding in flocks

7.1 Introduction

The experiment described in the previous chapter was concerned with the impact of indirect interference by conspecifics on an individual's foraging success. The presence of other foraging birds may, in addition, have a direct influence on an individual's foraging rate, and it is these effects which I will address in this chapter.

An obvious advantage of feeding within a group is that each individual needs devote less time to vigilance, and can devote more time to searching for food (Pulliam 1973). A further advantage to being in a group is the so-called 'dilution' effect (Hamilton 1971), whereby the probability of an individual being predated decreases as the number of individuals in the flock increases. Predation risk may be further reduced by 'confusion' effects (e.g. Neill & Cullen 1974), which make it harder for a predator to single out a target when there are several possible targets grouped together. Although each individual therefore needs to devote less time to vigilance the overall level of vigilance may be maintained or even increased above that of the individual level (Cresswell 1994). Cresswell demonstrated that although larger flocks of redshanks *Tringa totanus* were preferentially attacked by raptors, an individual's probability of being killed in these larger flocks was lower than in smaller flocks. This reduction in predation risk, as a result of feeding in larger flocks, has also been demonstrated for starlings (Jennings & Evans 1980; Keys & Dugatkin 1990; Powell 1974).

Foraging rate may also be increased by various mechanisms encompassed under the broad term of social learning (e.g. Krebs 1973; for review see Heyes 1993). Social facilitation (Zajonc 1965), whereby an individual performs a behavioural repertoire in response to seeing the same behaviour being elicited by conspecifics, has been demonstrated in domestic chicks (McFarland 1985). Alternatively, individuals can benefit from local enhancement, using the location of other birds as an indication of suitable feeding sites (Krebs 1974; Waite 1981), as well as using the foraging success of conspecifics to assess patch quality, as has been demonstrated in starlings (Templeton & Giraldeau, pers. comm.)

Foraging success is, however, also dependent on an individual's dominance ranking within the group (Goss-Custard 1980). Thus, although a dominant individual can further enhance its feeding rate by displacing other individuals from the best sites, or by stealing food items from them, those that are less dominant will accordingly experience a reduced foraging success (Goss-Custard *et al.* 1982b). Furthermore, as shown by Pulliam & Curaco (1984), the overall feeding rate of a flock may show an inverse relationship with group size due to these competitive interactions. The implications of this competition on an individual's choice of feeding site has been demonstrated in oystercatchers, *Haematopus ostralegus* (Ens & Goss-Custard 1984; Goss-Custard & Durrell 1987a, b; Goss-Custard *et al.* 1984). The role of dominance hierarchies also influences the distribution of starlings at foraging sites (Feare & Inglis 1979; Inman 1990). Therefore, when examining the foraging success of starlings in their winter feeding flocks, it is essential that any effects of the presence of conspecifics are considered (for a review of these effects in gull and plover flocks see Barnard & Thompson 1985).

Such examination of the role of direct interference is necessary for validating the enclosure experiments described in Chapters 3, 5 and 6. These experiments used observations of captive birds feeding on their own to make inferences about the feeding behaviour of the wild flock. The necessity of these measurements was justified by the lack of detailed information which could be obtained from direct observations of flock-feeding individuals (Chapter 5). However, although the experimental foraging pressures have been shown to fall within the range of foraging pressures we would expect to find in the flock, what has not yet been shown is whether the rates of foraging attained by captive individuals are comparable to those within the wild flock.

The aims of this experiment were two-fold: i) to measure the effect direct interference may have on a starling's foraging success when feeding with conspecifics; and ii) to test whether or not the results from a single bird are comparable with those from a group of three birds, from which I hoped to gain some measure of how representative my previous experimental measures were of the rates of foraging occurring in the natural flock.

Using captive birds held in the enclosures, the foraging behaviour of an individual feeding alone was compared with that of an individual feeding in a 'flock'. Due to restrictions imposed by the size of enclosures, experimental design and aviary space for the birds, the flock size was limited to three birds. The effect of bird density within this 'flock' was manipulated such that the birds either had the same amount of space per bird as when foraging alone, or the flock density was three times greater than that for a solitary bird.

7.2 Methods

7.2.1 Subjects

Nine starlings were trapped from the resident population at University Farm, Wytham. When not being used in experimental trials, the birds were held in a large outdoor aviary (4 m long x 2.5 m high x 3 m wide). Their maintenance was the same as for those birds used in the experiment described in Chapter 3. All the birds were marked individually with colour leg rings, but to aid quick identification during feeding trials I also marked the birds with small strips of plastic, differing in shape and colour, which were glued to their crown feathers. I then divided the birds randomly between three groups, each of three birds, and kept these groupings the same for all experimental trials. All the birds were juvenile males and by having the same age and sex class I hoped to minimise any differences in dominance. However, I was not able to control for the number of competitive interactions, which may have been increased through escalations.

After a week's settling-in period, the birds were given several training sessions in the test enclosures. The enclosures were of two sizes: 'small' measured 1 m x 1 m x 0.5 m (i.e. ground area of 1 m^2), and large, which measured 1.75 m x 1.75 m x 0.5 m (i.e. ground area of 3 m^2). Once the birds were settled and feeding freely in the test situation (after five days), I began the experimental sessions. The first trial was started at 08:00 hrs each day and the birds were food-deprived from 16:00 hrs the previous evening. Each bird was given only one trial on any day. Once the day's trials had been completed the birds were returned to the holding aviary and given *ad lib.* food for the rest of the day.

Training was started on 8/11/93 and all testing was completed by 1/12/93.

7.2.2 Experimental design

The 'preferred' field used in the last two experiments (Chapters 5 & 6) served as the experimental field in this experiment. The field was divided into 27 approximately equal regions (on a 3 x 9 grid), and within each of these regions I allocated one experimental site at random, such that there was one site for each of the feeding trials. There were three experimental treatments: 1) one starling feeding alone in a small cage; 2) one starling feeding with two others in a small cage; and 3) one starling feeding with two others in a large cage. Every bird experienced all three treatments, and for those trials in which the bird was feeding with the rest of its group, the trial was repeated three times on three separate days, so that I could obtain an independent measure of each bird's foraging behaviour. Trials were halted once the focal bird had foraged for fifteen minutes, hence total trial duration varied depending upon how long it took to settle down at the start of each session.

7.2.3 Data collection and analyses

As in the experiments described previously, I recorded the birds' foraging behaviour on video-tape, from a hide. In addition to the same data collection as in previous experiments (number of surface pecks, number of probes into the soil, time and prey type for each prey capture), the number of times the bird lifted its head was also recorded. I did not include 'scans' lasting longer than approximately three seconds, and on these occasions regarded the bird as having stopped feeding.

For group feeding trials I recorded data on the number of agonistic interactions. These were classed as any occasion on which the focal bird either attacked or defended itself from another bird, for a feeding site or prey item. A successful encounter by the focal bird indicated dominance, and an unsuccessful encounter was regarded as sub-dominance.

As before, the resolution of the videos restricted categorisation of the prey types to either earthworms or arthropod larvae. I then used the behavioural data to calculate prey capture rate (slope of cumulative number of prey captures divided by time in trial), search effort (slope of cumulative number of probes divided by time in trial), reward rate (slope of cumulative number of prey captures divided by cumulative number of probes), and 'vigilance' (slope of cumulative number of head-ups divided by time in trial). For this final category of behaviour I have assumed a functional explanation of vigilance, although it is possible that the birds were raising their heads between feeding for some other purpose. Comparisons of the above variables were made between treatments using repeated-measures ANOVA with bird (n=9) as the subject.

7.3 Results

The number of prey obtained per unit time by individual birds was similar in all three treatments ($F_{2,8}$=1.298, P=0.300) as were search efforts ($F_{2,8}$=0.143, P=0.868). There was also no overall difference in reward rates (Fig. 7.1; $F_{2,8}$=2.096, P=0.155) but in view of the apparent difference between reward rates for one bird alone and a bird feeding in a group in a large cage I conducted a *post-hoc* contrast of the means. This showed the difference to be almost significant ($F_{1,8}$=4.152, P=0.059).

Analyses of the number of head-ups per unit time showed there to be no significant effect of treatment (Fig. 7.2; $F_{2,8}$=2.864, P=0.086). However, I was only interested in the difference between the head-up rate of a bird feeding alone and its head-up rate when feeding in a group, and was less interested in the effect of the density of the birds for this analysis. Therefore I contrasted the mean head-up rate for one bird alone with the pooled data for both group treatments. This showed the difference between the head-up rate in the two treatments ('alone' or 'group') to be significant ($F_{1,8}$=5.162, P=0.037) which was compatible with individuals being less vigilant when feeding in a group than when feeding alone.

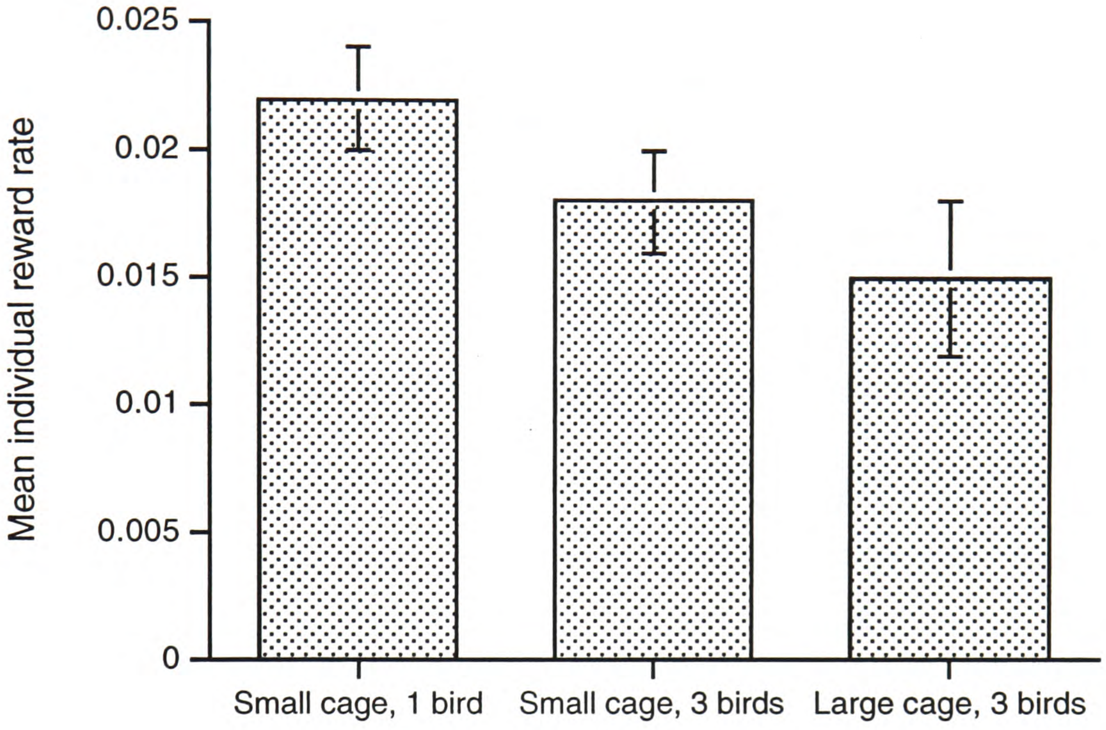


Figure 7.1. Mean (±SE) individual reward rates (number of prey captures per probe) in each of the three treatments: one bird feeding alone in a small cage (area $1m^2$); one bird feeding with two others in a small cage ($1m^2$); and one bird feeding with two others in a large cage ($3m^2$).

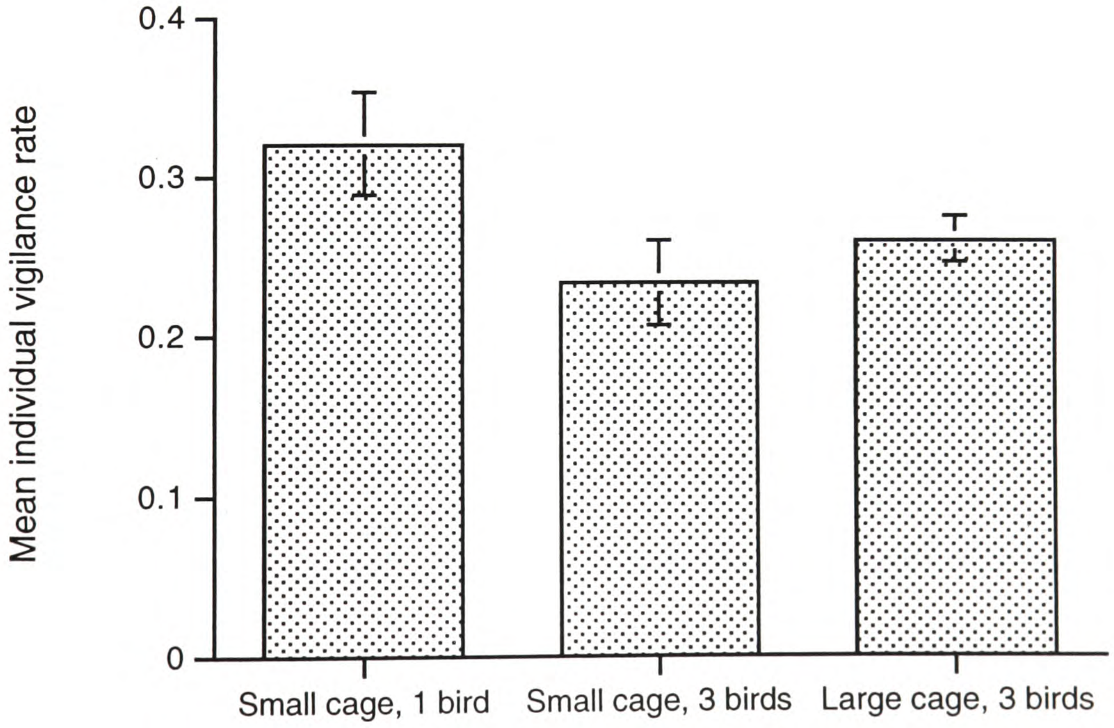


Figure 7.2. Mean (±SE) individual vigilance rate ('head-ups' per second) in each of the three treatments: one bird feeding alone in a small cage (area $1m^2$); one bird feeding with two others in a small cage ($1m^2$); and one bird feeding with two others in a large cage ($3m^2$).

For group feeding trials the number of successful encounters by the focal bird in the small and large cage was recorded per unit time. A paired t-test of these dominance scores showed no significant differences (t=0.465, n=9, P=0.655) between the two cage sizes and associated bird densities, and there was a similar lack of difference in the scores for subdominance (t=0.001, n=9, P=0.776). Regression analyses were performed to examine the effect of dominance on reward rate. These analyses revealed no significant correlation either in the large cage (r^2=0.002, n=9, P=0.902) or the small cage (r^2=0.185, n=9, P=0.247). Similarly, the number of unsuccessful encounters per unit time, representative of subdominance, had no significant effect on reward rate in the large cage (r^2=0.215, n=9, P=0.208) or in the small cage (r^2= 0.283, n=9, P=0.140). Hence dominance ranking could not be considered to have any significant effect on individual foraging success, as recorded here, in either of the group foraging trials.

7.4 Discussion

The conditions imposed in this experiment showed no detectable effects on an individual's reward rate of feeding in the presence of conspecifics. The lack of effects observed in these experimental flocks (which were necessarily small to allow collection of accurate data on individual foraging behaviour) may have been representative of the strength of effects seen in natural flocks, but it does not rule out the possibility that the greater number of birds in wild flocks may produce stronger effects.

There was a weak indication that birds feeding alone may attain a slightly higher reward rate than when feeding in their groups in the large enclosures. There was also evidence, however, that the solitary birds spent more time with their heads up (suggesting greater vigilance), a finding which was in accordance with Pulliam's (1973) prediction and with empirical data presented by Powell (1974). Any reduction in the solitary birds' foraging rate through time allocated to vigilance may have been compensated for by the absence of time spent interacting with other birds, hence the slightly higher reward observed for these solitary birds. This finding contradicts a previous study of captive starlings (Feare & Inglis 1979) in which all birds fed faster in a flock situation than when alone, probably as result of social facilitation. In their study, however, the experimental birds had been held in an outdoor aviary for nearly a year prior to the experiment, and were fed artificial food (turkey starter crumbs) presented in a trough, which minimised any food searching time; thus the observed contradiction in the two results may be due to the differences in the experimental techniques.

As suggested above, the slightly lower reward rates of birds feeding in a group could have resulted from time allocated to fighting with other group members, which I calculated to occupy approximately 6% of their foraging time. In their study of oystercatchers, Zwarts & Drent (1981) demonstrated a reduction in intake rate with increasing bird densities. Greater depletion of mussels contributed to this reduction in intake rate, but interference between individuals also played a role. Similar reductions in oystercatcher intake rates, when under direct competitive pressure, have been demonstrated by Goss-Custard *et al.* (1982b, 1984). While dominant birds actually increased their intake rates by stealing food items from other birds, the intake rates of lower ranking birds suffered as a consequence, largely because these less dominant birds allocated more time to watching out for potential attacks.

Contrary to other evidence (Feare & Inglis 1979; Goss-Custard 1977c), but consistent with Keys & Dugatkin's (1990) study of foraging flocks of starlings, an increase in flock density in this experiment did not increase the level of aggression. Furthermore, there was no correlation between each bird's foraging success and the number of aggressive encounters it won. This lack of correlation between dominance and intake rate has also been observed in oystercatchers (Goss-Custard *et al.* 1984). Although their study demonstrated a significant correlation between dominance and intake on the preferred mussel beds, where high densities of dominant birds created a lot of aggression, there was no such correlation on less preferred beds where lower ranking birds fed at lower densities. An absence of any effect of aggression in this experiment may have therefore resulted from low densities, or from a lack of heterogeneities in dominance ranking. All the birds were juvenile males and so, although aggression occurred, it may have arisen through escalations between the birds rather than from an established dominance hierarchy. The picture may be very different in larger flocks in which a range of age and sex classes might be expected to yield a greater dominance effect (e.g. Feare & Inglis 1979; Inman 1990), although in those studies, as with the present experiment, the birds were forced to feed in their experimental groups. In natural flocks the birds will be able to choose with which other birds they feed, thus minimising the potential for any detrimental effects of fighting.

This experiment has provided little evidence for any effects on an individual's foraging success of feeding within a group. Although some foraging time was lost through fighting with others, it did not appear to significantly reduce reward rate, and may have been compensated for by the reduced time necessary for vigilance. I might expect the magnitude of these effects to be influenced by the dominance ranking of each bird and by its physical position in the flock. Such an effect was demonstrated for Barnacle Geese, *Branta leucopsis* (Black *et al.* 1992), in which dominant males and their family groups actively monopolised the best food availability, at the edge of the flock. Testing for these effects with the starlings is, however, beyond the scope of this experiment.

More pertinent to the present research is whether the extent of these effects are sufficient to invalidate any conclusions about flock-feeding that have so far been drawn from the previous enclosures experiments. The differences in feeding rates observed between solitary birds and those in groups were slight. Although at the outset it was commented that the observed differences may have been strengthened by a larger experimental flock size, consideration of foraging pressures (1 bird alone = 15 bird-minutes per m^2; 3 birds on $1m^2$= 45 bird-minutes per m^2; and 3 birds on $3m^2$ = 15 bird-minutes per m^2) indicates that these are far greater than the mean value expected in the flock (Appendix II). Hence any variations in flock reward rates resulting from changes in the density of birds are likely to be of a similar or even reduced magnitude relative to the variations in reward rates induced by the experimental treatments. It seems reasonable to conclude, therefore, that the foraging rates exhibited by solitary birds in previous experiments will have fallen within the range of those occurring in the flock and may be used as a representative measure of within-flock foraging performance.

7.5 Summary

The foraging success of starlings allowed to forage alone, in an experimental enclosure, was compared with their foraging success when feeding in the presence of two other birds. No significant effect on an individual's reward rate of feeding in a group was detected. When alone, birds allocated more time with their heads raised, a behaviour which is compatible with increased vigilance, but an associated loss of feeding time was compensated for by the absence of any interactions with other birds, to which birds feeding in groups allocated a proportion of their time. There was no evidence for any effect of dominance on an individual's foraging success. I conclude that the foraging rates of solitary birds fall within the range of foraging rates expected within the natural flock, but a more accurate quantification of individual feeding rates within wild flocks would require a different experimental approach which can deal with a more realistic natural flock size.

Chapter 8

The impact of parental starling foraging on prey availability

8.1 Introduction

In preceding chapters I have considered the starlings' overwinter response to spatial and temporal variations in the availability of their prey. I concluded that, over the winter period, absolute prey depletion or 'exploitation depression' (Charnov *et al.* 1976) caused by the birds was not sufficient to influence their choice of feeding site. Such depletion of prey may, however, have more long-term implications, as any impact on resource availability during the winter will also deplete resources for later in the year. The breeding season is a particularly sensitive time, during which the availability of food is a critical factor underlying brood size and nestling survival of birds (Lack 1954, 1966); the influence of food availability on breeding success has been demonstrated for starlings, both in terms of the availability of potential foraging sites (Tiainen *et al.* 1989), and of suitable prey (Tinbergen 1981; Dunnet 1955). Although an overwinter reduction in the number of invertebrates is partly compensated by a spring increase in their biomass (Tinbergen 1981; Dunnet 1955), there is no further input of numbers until later on in the year. Leatherjackets only emerge as adults in late August and September (Coulson 1962); hence the summer can often be a period of resource limitation, at least in terms of soil invertebrates, for the starlings (Feare 1984). It is the extent of any such limitation, as a result of 'exploitation depression', that I wish to address in this chapter.

Changes in food availability are partly influenced by environmental variations (for review see Wiens 1989) but, as I have already discussed in Chapter 5, spatial and temporal distributions of resources are also influenced by the foraging behaviour of the predators themselves. The consequences of summer prey depletion on subsequent patterns of foraging behaviour have been demonstrated by Tinbergen & Drent (1980) who observed a shift in the sites visited by parent starlings as areas previously visited by the birds were depleted of prey. Such impact of bird populations on their invertebrate food sources has been quantified in a number of studies (e.g. Atlegrim

1989; Bock *et al.* 1992; Churchfield *et al.* 1991; East & Pottinger 1975; Holmes *et al.* 1979; Joern 1986) in which prey populations were compared between predated and non-predated sites, the latter protected from predation by the use of exclosures.

In this chapter a similar approach is taken to quantify the impact of starling parental foraging on the availability of their invertebrate prey. By excluding the breeding starlings from parts of their usual feeding areas, the reduction in resource density can be measured. However, although the question of how absolute numbers of prey may be affected is of interest, a fuller understanding of predator-prey interactions can be gained by knowing what changes are occurring in the amount of prey available to the birds. The importance of distinguishing between prey abundance and the proportion of those prey that are actually available to the birds was underlined by Goss-Custard (1984).

This chapter, therefore, addresses both questions of prey abundance and of prey availability, the latter measured by using the enclosures technique once more. By allowing experimental birds to forage both in areas foraged by the wild birds and in areas from which the wild birds had been excluded it was possible to measure any changes in the amount of prey available to the birds, both in the short term, after a few hours of foraging, and in the long term, over the time in which broods were being raised at the colony. The underlying prey abundances were then measured by extracting soil cores from the experimental sites, and from control sites which had not been foraged, thus allowing the impact of foraging by starlings on the total prey populations to be quantified.

8.2 General Methods

8.2.1 Experimental design

I carried out this experiment in the two permanent pasture fields ('preferred' and 'non-preferred') that were also used for the experiments described in Chapters 5 and 6. Each field was divided into nine regions (on a 3 x 3 grid), of which six were chosen at random. Within each of these regions one experimental site was selected, also at random. Each bird was then allocated to one site in each field, and received all treatments, in each field, at that same site.

Sites were divided into exclosure and non-exclosure regions and within these regions I allocated individual 1 m x 1 m plots for each foraging trial. I also took soil cores from these plots, as described below. Tests for short-term depletion at the start of chick-feeding were restricted to the non-exclosure regions (Fig. 8.1a), while tests for long and short-term depletion at the end of chick-feeding were conducted in both parts of the experimental site (Fig. 8.1b). The exclosure regions measured 2 m x 2 m and were covered by sheets of 10 mm gauge plastic-netting stretched over four wooden posts and secured to the ground with metal pegs. The posts were 0.5 m high and positioned at each corner of the exclosure site. Each exclosure was surrounded by single strand barbed wire fencing to protect it from the cattle present in both fields. Although it was not possible to selectively exclude starlings from the exclosure sites whilst maintaining access to other species, starlings are the only bird species to feed on soil invertebrates to any extent at the Wytham study site during the summer.

In order to equalise date and weather effects between fields and between treatments I alternated testing in the two fields daily, thus controlling for any long-term temporal changes in prey availability.

8.2.2 Maintenance of the exclosures

As I wanted to be able to attribute any variation in levels of prey availability to the effect of the wild birds' feeding, it was desirable for conditions inside and outside the exclosures to be as similar as possible. However, the lack of grazing in the exclosures meant that the grass had to be cut. This was done weekly, using a Stihl strimmer, and I then raked the cut vegetation from the surface of each site. I took measurements of sward height; soil (30 mm depth), surface and sward temperature; and soil moisture, from all exclosure and control sites 72 hours after the weekly cut. Sward height was measured using a modified point quadrat which served as a sward stick. I took the height where the tip of the tillers touched the horizontal slide.

Temperature was measured to the nearest 0.5°C with an electronic probe, and a garden moisture meter was used to record soil moisture on a relative scale of 1-10. Taking into account the effects of field and day, a three-way ANOVA showed no significant differences between exclosure and non-exclosure sites for all measures (all P-values > 0.131).

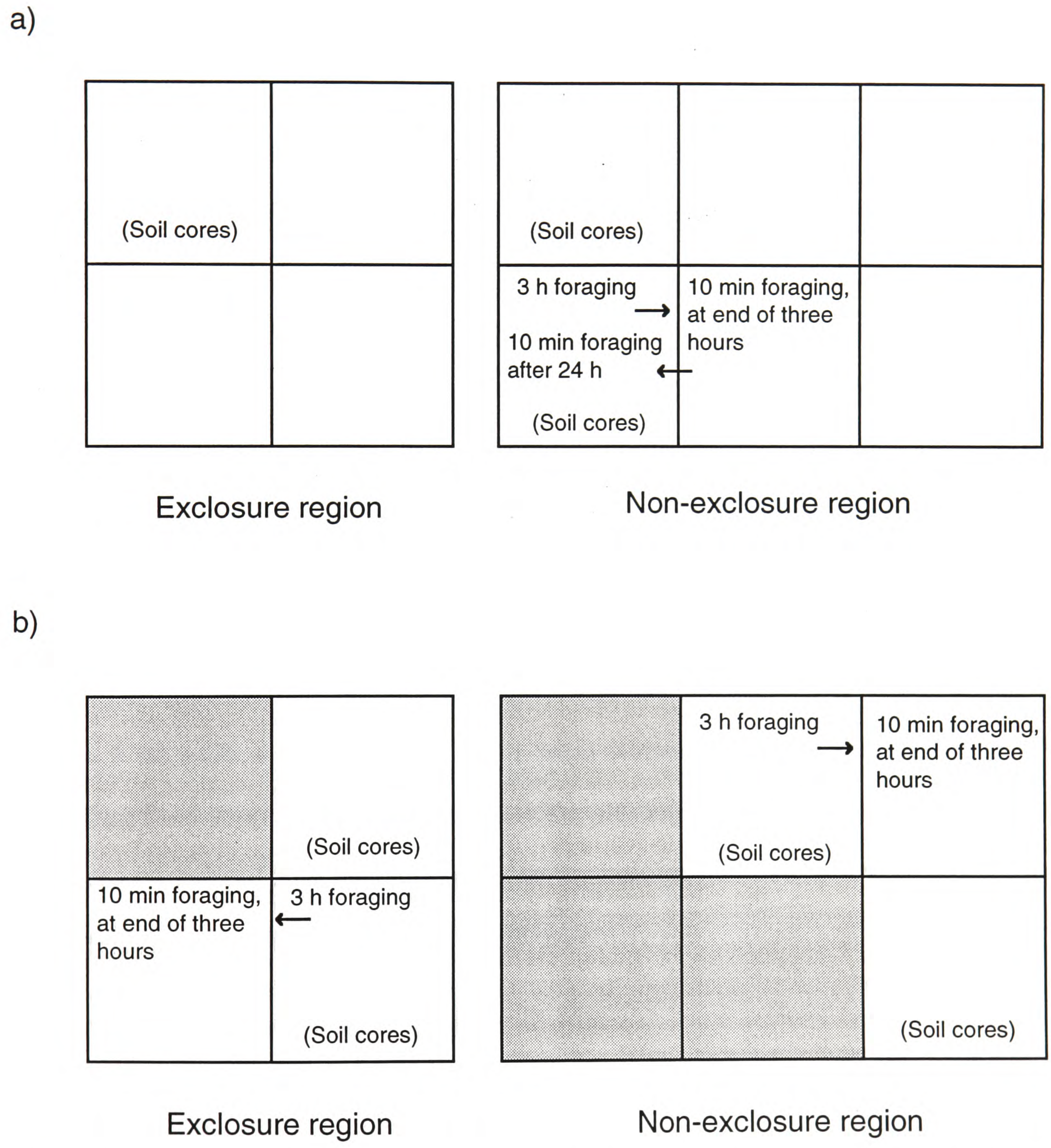


Figure 8.1. Example of allocation of experimental foraging trials for captive birds, and soil core extraction plots to an experimental site for **a)** pre-chick feeding experimental phase and **b)** post-chick-feeding experimental phase (shaded areas represent plots already used during pre-chick-feeding phase).

Although micro-climatic conditions did not appear to be affected by the change in management imposed by the exclosures, cutting rather than grazing produced a visible change in the structure of the sward (Parsons *et al.* 1984). This change could be quantified by obtaining measures of tiller density of the vegetation (Hodgson *et al.* 1981) collected with the soil cores (see below). I compared the tiller densities and wet biomass of vegetation in a three-way ANOVA, which took into account any effects of field or experimental site. Although the wet biomass of vegetation was not significantly altered by experimental manipulation ($F_{1,120}$=1.147, P=0.286), tiller densities were significantly lower inside the exclosures ($F_{1,120}$=11.505, P<0.001).

8.3 Measurements of prey availability using foraging behaviour of captive birds

8.3.1 Subjects

Six adult starlings (three males and three females) were caught from the resident population immediately prior to the breeding season. The birds were held in outdoor enclosures (2 m long x 2 m wide x 1 m high) during both experimental phases, and were transferred to an outdoor aviary for the intervening period. Their feeding and maintenance was the same as for the birds used in the experiment described in Chapter 3.

For experimental sessions the birds were transferred to test enclosures (1 m long x 1 m wide x 0.5 m high). Trials were started at approximately 08:00 hrs, following food deprivation from 20:00 hrs the previous evening. Once the day's trials had been completed I returned the birds to the holding enclosures and gave them *ad lib.* food until the next period of food deprivation.

8.3.2 Measuring short-term depletion

I conducted this phase of the experiment on seven consecutive days, starting from when the first nestling starlings hatched at the colony on May 1st. For each experimental trial I released the subject into the test enclosure for a three-hour period, and recorded 10-minute foraging bouts at the start and end of this period. After this three-hour foraging session the bird was transferred to an adjacent experimental control enclosure in which it was allowed to forage for a further 10 minutes. This showed whether any prey depletion in the test enclosure was due to removal of prey by the bird (indicated by higher capture rates in the control enclosure), or to diurnal movements of the soil invertebrates taking them out of the starling's probing range (indicated by equal capture rates in test and control enclosures). I left the test enclosure in place until the following morning, when the bird was given a final 10-minute foraging bout to test for any effect of prey 'renewal' in the experimentally foraged patch.

8.3.3 Measuring long-term depletion

The measures of prey availability obtained during the short-term depletion phase were also used as initial measures of prey availability for the long term-depletion phase. I started this part of the experiment on 15th June (7 weeks after the start of the first experiment) for 6 consecutive days, by which time all successful starling broods within the Wytham colony had fledged. This second experimental phase was also timed to occur before emergence of the adult tipulids, the larvae of which are a major source of prey for the Wytham population. Analyses of soil cores collected during the first experimental phase (see below) showed the predominant species to be *Tipula paludosa*, which emerges in late summer (late August - September) in the South of England (Coulson 1962).

During this second experimental phase each experimental bird was given two foraging sessions in each of the two fields, one within the excluded region, and the other in the adjacent non-exclosure region on which wild birds had been able to forage throughout the preceding two months. The protocol for each foraging session was the same as that used in the first experimental phase, except that I omitted the foraging trial after 24 h, having already addressed the question of prey renewal during the earlier experiment.

8.3.4 Data collection and analyses

As in previous enclosure experiments, I recorded the birds' foraging behaviour onto video-tape. Data collection was the same as described in Chapter 3. Comparisons of the variables of prey capture rate (slope of cumulative number of prey captures divided by time in trial), search effort (slope of cumulative number of probes divided by time in trial), and reward rate (slope of cumulative number of prey captures divided by cumulative number of probes) were made between fields using repeated-measures ANOVA, with bird (n=6) as the subject.

8.3.5 Results

8.3.5.1 Behavioural data

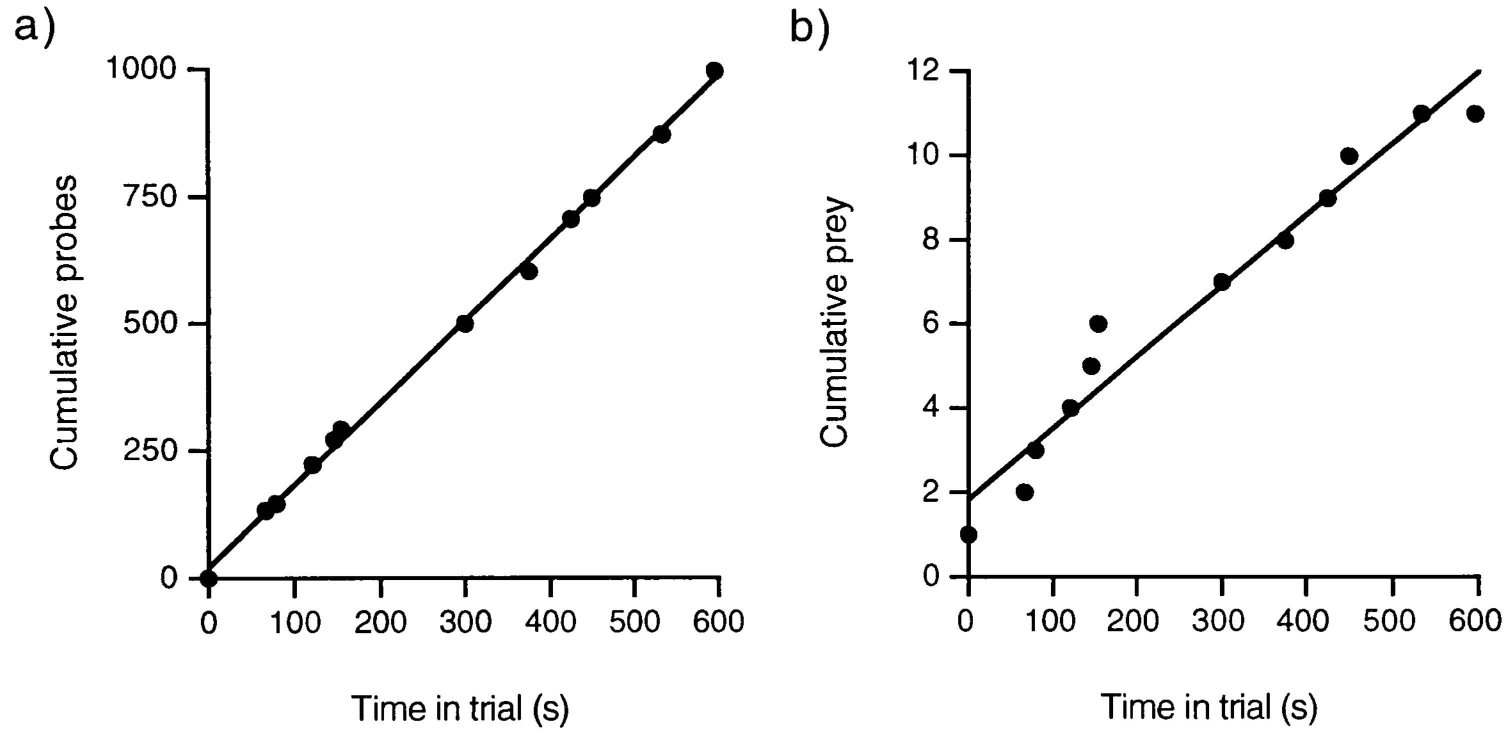


Figure 8.2. Example plots for one bird of **a**) rate of searching (cumulative number of probes made with time) within a single feeding trial (y=20.185+1.620x, r^2=0.999, P<0.001); **b**) Rate of prey capture (cumulative number of prey captures with time), within a single feeding trial (y=1.838+0.017x, r^2=0.957, P<0.001).

As with previous foraging data, the number of probes made by each bird and time during individual trials showed a linear relationship (Figure 8.2a). The number of prey caught with time was also linear (Figure 8.2b). Therefore any effects of satiation or depletion within individual recorded foraging bouts were considered to be negligible. Comparing these graphs with similar graphs for earlier enclosure experiments shows there to be fewer probes and fewer prey captures made per time in this experiment. This effect may have resulted from the ground being drier and harder than during previous winter experiments. This appeared to discourage the starlings from probing, and also reduced the number of prey they were able to capture per unit time.

8.3.5.2 Measuring short-term depletion: pre-chick-feeding period

There was a significant difference in prey capture rates (number of prey captured per unit foraging time) between the two fields, and between the recorded foraging bouts at different times during individual foraging sessions (Table 8.1a). However, the number of prey caught by the birds will also depend upon the number of probes made during the foraging sessions. Search efforts (number of probes per minute of foraging) were similar in both fields, but showed a significant difference between recorded foraging bouts (Table 8.1a). The effects of these differences in search efforts, on the birds capture rates, were controlled for by expressing the number of captures as a rate per probe, rather than per unit time. The resulting reward rates were not significantly different in the two fields, but were still significantly different between recorded foraging bouts (Table 8.1a; Fig. 8.3). *Post-hoc* contrasts, within the ANOVA, of the means for each recorded foraging bout showed a significant reduction in reward rate from the start of the foraging session to the end of the three-hour period ($F_{1,15}$= 9.724, P<0.001). There was, however, no significant difference between reward rates attained at the end of the three hours, and those the following day ($F_{1,15}$=0.070, P=0.795). Also, there was no significant difference between reward rates at the start of the experimental trial and those in control plots at the end of the three-hour period ($F_{1,15}$=0.988, P=0.336).

Separating the total prey into the two main prey types (earthworms and leatherjackets) showed that, in both fields, leatherjackets yielded far higher reward rates than earthworms (Fig. 8.4; $F_{1,15}$= 13.715, P<0.001). The greater abundance of leatherjackets meant that reward rates for this prey type influenced greatly the total prey reward rates in each of the foraging bouts, while the very low numbers of earthworms showed little variance.

Table 8.1: Results of a two-way repeated-measures ANOVA with **i)** prey capture rate (mean number of prey captured per minute foraging); **ii)** search effort (mean number of probes per minute foraging); and **iii)** reward rate (mean number of prey captures per probe) of captive birds foraging in experimental enclosures as dependent variables. Factors were field (preferred by the wild birds, and not preferred) and treatment (individual foraging bouts recorded at start and end of three hours of foraging, in experimental enclosure; at end of three hours in control enclosure; and 24 hours later in experimental enclosure*). Measurements were of short-term depletion at **a)** the start of chick-feeding and **b)** the end of chick-feeding. Number of subjects = 6 (error d.f. = 5).

* At the end of chick-feeding (**b**) the last foraging bout after 24 h was not recorded, but whether the trials were conducted inside or outside the exclosures were included as treatments.

			i) Capture rate		**ii) Search effort**		**iii) Reward rate**	
	Factor	**d.f.**	***F*-ratio**	***P*-value**	***F*-ratio**	***P*-value**	***F*-ratio**	***P*-value**
	Field	1	9.457	0.028	1.338	0.300	4.739	0.081
a)	**Treatment**	3	37.145	<0.001	3.785	0.033	28.996	<0.001
	Field * Treatment	3	1.336	0.300	2.639	0.088	2.029	0.153
	Field	1	3.270	0.130	0.214	0.663	0.042	0.845
b)	**Treatment**	5	36.209	<0.001	6.937	<0.001	4.496	0.005
	Field * Treatment	5	0.953	0.465	2.008	0.112	0.710	0.500

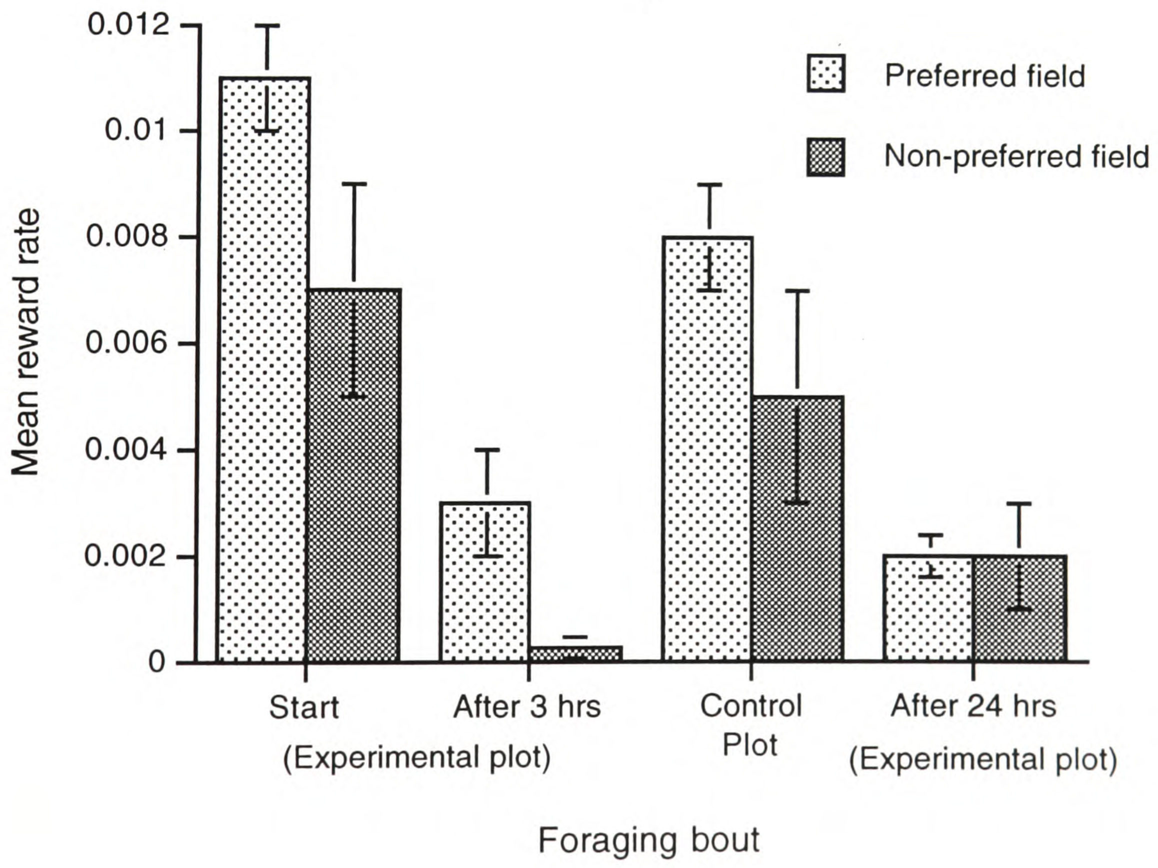


Figure 8.3. Mean (±SE) reward rate (prey captures per probe) of captive birds foraging in experimental enclosures, in a field preferred by the wild birds and in a field not preferred, during pre-chick-feeding short-term depletion experimental phase. Measurements were taken in each of the 10-minute foraging bouts, recorded at the start and end of a three-hour foraging period in the test enclosure, at the end of three hours in a control enclosure, and 24 hours later, in the test enclosure.

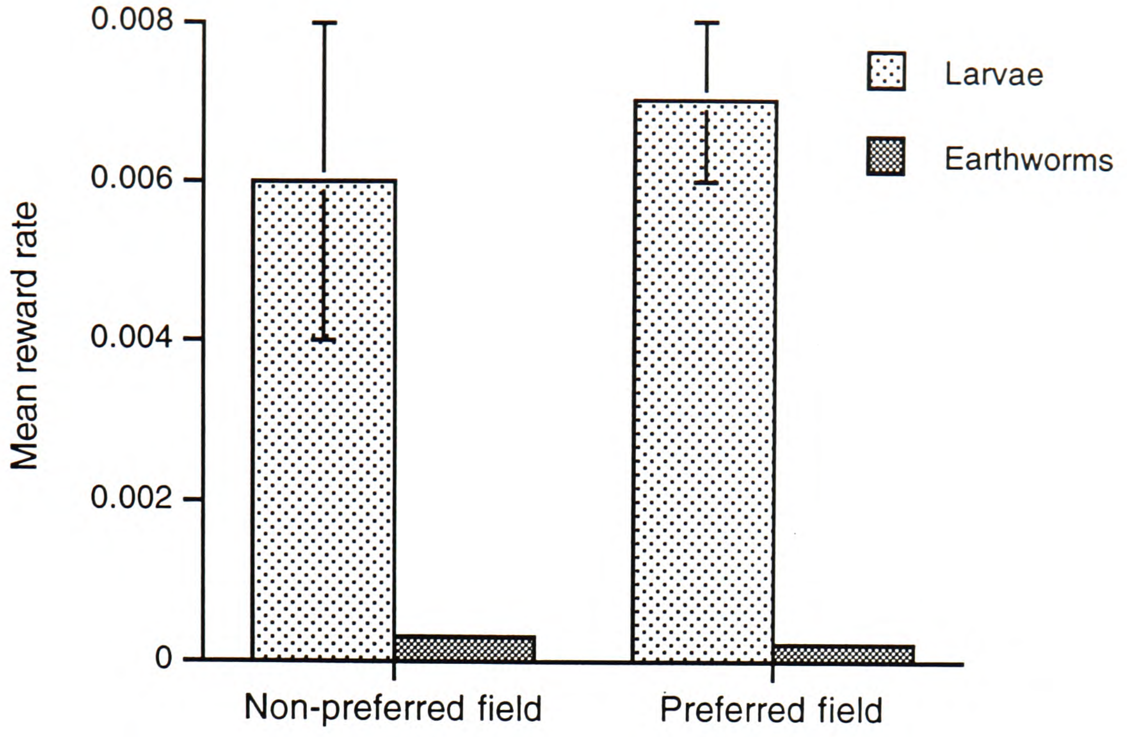


Figure 8.4: Mean (±SE) total reward rates (prey captures per probe) for captive birds foraging in experimental enclosures in a field preferred by the wild birds, and a field not preferred. Reward rates are shown for earthworms and larvae.

Reward rates were also calculated in terms of biomass of the two prey types, using mean wet weights of prey items obtained from soil cores (leatherjackets = 0.36g±0.05; earthworms = 0.56g±0.21), which were then multiplied by the numbers of each prey type captured. Although earthworms had a much greater biomass per individual item, the birds captured greater numbers of leatherjackets, resulting in significantly greater biomass reward rates for leatherjackets ($F_{1,15}$=112.513, P<0.001).

8.3.5.3 Measuring short-term depletion: post-chick-feeding period

At the end of the chick-feeding period there was no significant difference in prey capture rates between the two fields, but there was still a significant reduction over the three-hour experimental period (Table 8.1b). There were also changes in search effort (Table 8.1b) as fewer probes per unit time were made during the latter part of the test period, before increasing again when the birds were transferred to the control cage. Controlling for search effort produced very similar reward rates in both fields, but showed significant differences between foraging bouts (Table 8.1b). These differences showed a similar pattern to those seen at the start of the chick-feeding period, but *post-hoc* contrasts of the means produced no significant effects.

8.3.5.4 Long-term depletion

In order to establish the extent of prey depletion over the duration of the chick-feeding period, comparisons were made between reward rates at the start and at the end of this period. In addition reward rates inside and outside the enclosures were compared at the end of the chick-feeding period. Comparisons were made only between the first 10-minute foraging bout of each session.

There was no difference in overall reward rate between the two fields. However there was a significant effect of treatment (Table 8.2; Figure 8.5) and *post-hoc* contrasts of the means showed that much of this effect was due to foraging by the wild birds in the preferred field such that reward rates were significantly lower at the end of chick-feeding than at the start (Figure 8.5; $F_{1,10}$=9.708, P=0.011); thus by the end of this period reward rates outside the exclosures were lower than those inside the exclosures, although not quite significantly so ($F_{1,10}$=4.500, P=0.060). In contrast, reward rates within the exclosures were the same at the start and end of the chick-feeding period ($F_{1,10}$=0.989, P=0.344). There was no significant long term depletion in the non-preferred field ($F_{1,10}$=0.861, P=0.375).

Table 8.2: Results of a three-way repeated-measures ANOVA with reward rate (prey captures per probe) for captive birds foraging in experimental enclosures as dependent variable, and field (preferred by the wild birds / not preferred by the wild birds), exclusion ('foraged / not foraged by wild birds') and prey type (earthworms / larvae) as factors. Results are from measurements of long-term depletion over the chick-feeding period.

Factor	d.f.	*F*-ratio	*P*-value
Field	1	0.008	0.931
Exclusion	2	5.261	0.028
Prey type	1	62.688	<0.001
Field * Exclusion	2	2.829	0.106
Field * Prey type	1	0.589	0.478
Prey type * Exclusion	2	11.218	0.003
Field * Exclusion * Prey type	2	1.414	0.288

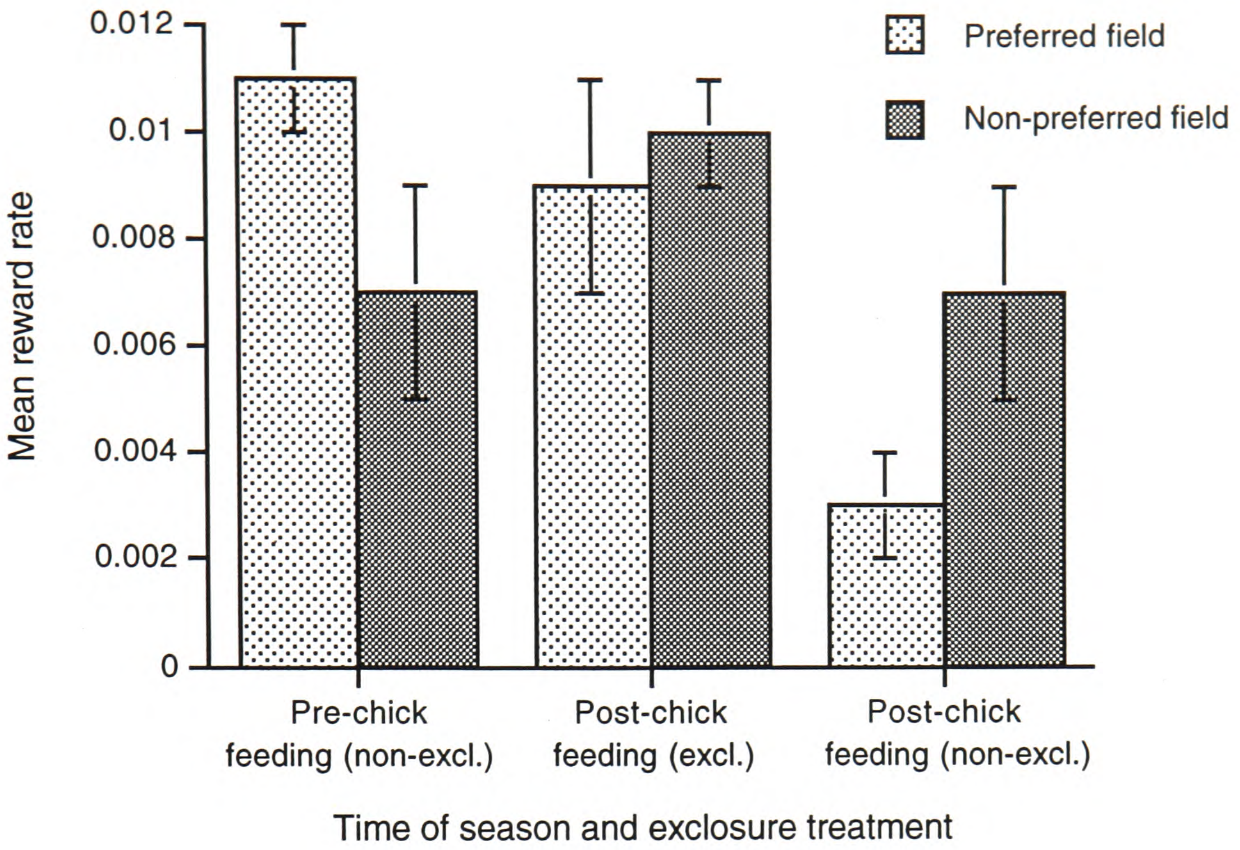


Figure 8.5. Mean (±SE) reward rate (prey captures per probe) for captive birds foraging in experimental enclosures, in a pasture field preferred by the wild birds and in a pasture field not preferred by the wild birds. Results shown for first recorded 10-minute foraging bout of three-hour experimental session, for three different treatments: non-exclosure ('non-excl.) sites (to which wild birds had access) at start of chick feeding; same sites at the end of chick feeding; and exclosure (excl.) sites (to which wild birds denied access) at the end of chick feeding.

The depletion of prey seen in the preferred field over the duration of the chick-feeding period was attributable to changes in the availability of larval prey (Figure 8.6a). Although overall larval reward rates were similar in both fields ($F_{1,5}$=0.084, P=0.784), the significant reduction in these rates ($F_{2,10}$=9.269, P=0.005) was largely due to removal of larvae by the wild birds from the preferred field; thus *post-hoc* contrasts of means in the preferred field showed a significant decrease in the availability of larval prey at non-exclosure sites ($F_{1,10}$=8.342, P=0.016). This effect was absent from the non-preferred field ($F_{1,10}$=0.012, P=0.914). In both fields the absence of foraging by the wild birds at the exclosure sites was reflected in a lack of reduction in prey available to the experimental birds (preferred field: $F_{1,10}$=0.133, P=0.723; non-preferred field: $F_{1,10}$=3.207, P=0.104).

No difference was detected in the availability of earthworms between the two fields ($F_{1,5}$=3.382, P=0.125), nor was their availability affected by the presence or absence of feeding by the wild birds ($F_{2,10}$=1.46, P=0.278). This lack of change in reward rates may be attributed to the very low availability of this prey type (Figure 8.6b), or to a lack of preference by the experimentally foraging birds for earthworms (Chapter 4). In either case, the low sample sizes of earthworms meant that any effect was not detected.

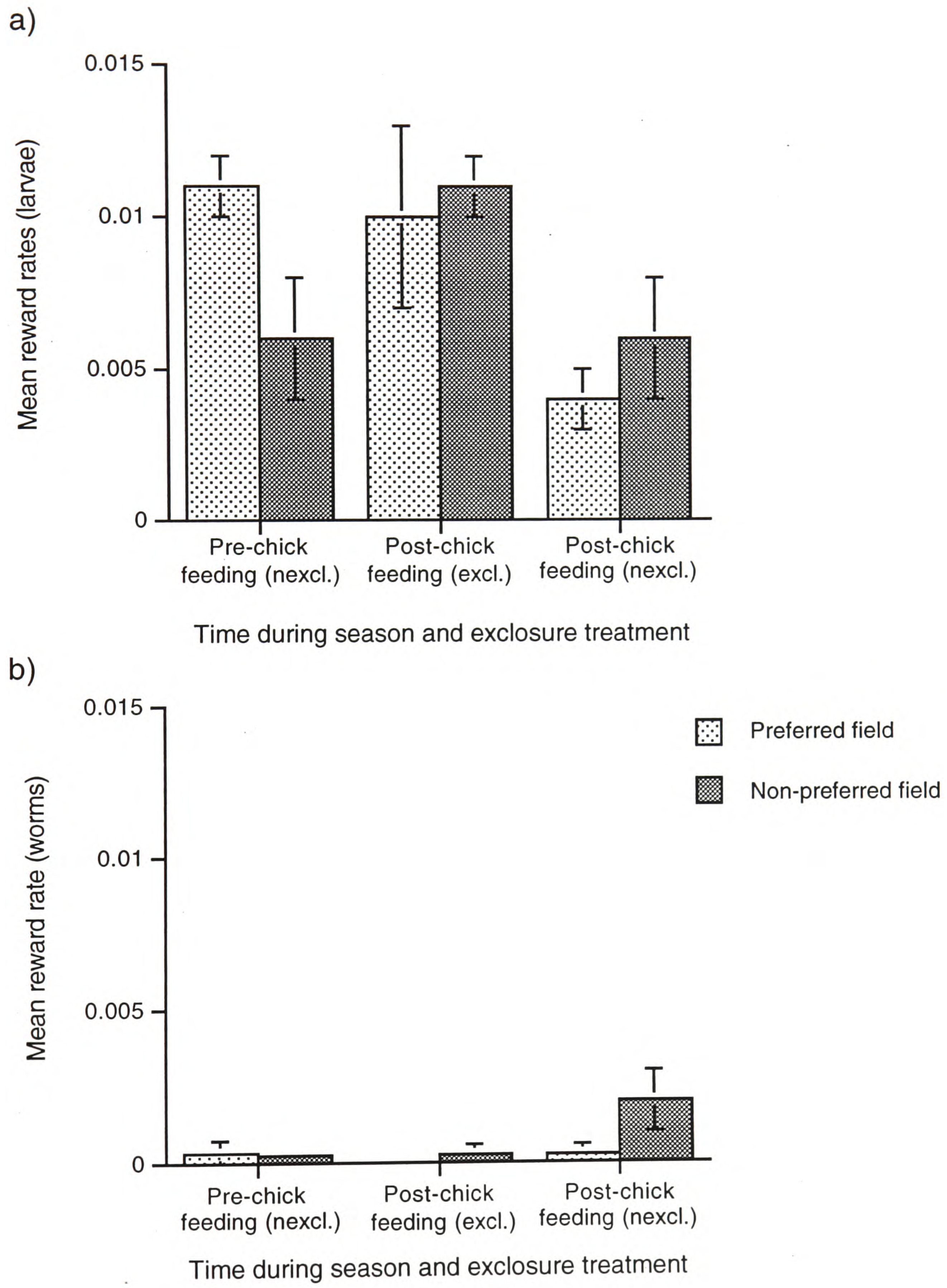


Figure 8.6: Mean (±SE) prey type reward rate (prey captures per probe) for captive birds foraging in experimental enclosures in a field preferred by the wild birds, and in a field not preferred. Results are shown for first 10-minute recorded foraging bouts of three-hour experimental session. Measurements taken at non-exclosure ('nexcl.') sites (to which wild birds had access) at start of chick feeding; at the same sites at the end of chick feeding; and at exclosure ('excl.') sites (to which wild birds were denied access) at the end of chick feeding. Reward rates shown for **a)** larval prey, and **b)** earthworms.

8.4 Measurements of prey abundance using soil cores

8.4.1 Methods

During the first experimental phase, I extracted six cores (80 mm diameter and 150 mm depth) from each experimentally foraged plot, six from an adjacent non-experimentally foraged plot and six from a 1 m x 1 m plot within the exclosure (Fig 8.1a). I sampled sites once foraging trials at those sites had been completed.

During the second experimental phase, I again took six cores from each experimentally foraged plot and an adjacent non-experimentally foraged plot, both inside and outside the exclosures (Fig. 8.1b). As with the previous cores, experimental sites were sampled once each day's foraging trials had been completed at those sites. The cores were washed and hand-sorted using the technique described in Chapter 5, and invertebrates retained for nutritional analyses (Appendix I)

8.4.2 Results

8.4.2.1 Prey types

In addition to leatherjackets and earthworms, which were the predominant prey available to the birds, the soil cores also yielded small numbers of beetles (*Scarabus* spp., *Staphylinus* spp., and *Carabus* spp.), fly larvae (Stratiomyidae and Bibionidae), moth larvae (Noctuidae), centipedes (Chilopoda), and millipedes (Diplopoda), although the numbers of all these were considered to be negligible and were excluded from any analyses.

8.4.2.2 Invertebrate numbers

There was a great deal of variation in the low numbers of invertebrates found in the cores, and this tended to mask any effect of treatment. The core means of individual prey item wet-weights were taken for each treatment at each site and the values from each of the six sites then analysed in a three-way ANOVA which looked for an effect of field, treatment and prey type.

8.4.2.3 Pre-chick-feeding soil cores

The total wet weight of invertebrates in cores taken at the start of the chick-feeding period did not differ significantly between the two fields, and there was no effect of foraging by the experimental birds on prey density (Table 8.3). A greater total biomass of earthworms could be attributed to the predominance of this prey type in the non-preferred field. The majority of invertebrates extracted from the preferred field comprised leatherjackets, and the total biomass of prey in this field was slightly smaller than in the non-preferred field.

Table 8.3: Results of a three-way ANOVA with wet weight of each prey type collected in soil cores as dependent variable. Factors were field (preferred by wild birds / not preferred by wild birds), treatment (site foraged by experimental bird, adjacent control site not foraged by experimental bird, and control site within exclosure area) and prey type (earthworms / larvae). Results are from cores extracted at the start of chick-feeding period.

Factor	d.f.	*F*-ratio	*P*-value
Field	1	0.001	0.991
Treatment	2	0.483	0.620
Prey type	1	5.669	0.021
Field * Treatment	2	2.923	0.061
Field * Prey type	1	0.549	0.462
Prey type * Treatment	2	0.844	0.435
Field * Treatment * Prey type	2	3.411	0.040

8.4.2.4 Post-chick-feeding soil cores

At the end of chick-feeding, the total biomass of earthworms was still significantly greater overall than that of leatherjackets (Table 8.4). Many of these earthworms were found in the non-preferred field, which had a significantly greater biomass of invertebrates than the preferred field; invertebrates collected from the preferred field comprised mostly leatherjackets.

Table 8.4: Results of a three-way ANOVA with wet weight of each prey type in soil cores as dependent variable. Factors were field (preferred by wild birds / not preferred), treatment (site foraged / site not foraged by experimental bird, and foraged / not foraged by wild birds) and prey type (earthworms / larvae). Results are from cores extracted at the end of the chick-feeding period.

Factor	**d.f.**	***F*-ratio**	***P*-value**
Field	1	5.761	0.019
Exclosure treatment	3	5.156	0.003
Prey type	1	26.290	<0.001
Field * Exclosure treatment	3	2.377	0.076
Field * Prey type	1	24.417	<0.001
Prey type * Exclosure treatment	3	3.133	0.030
Field * Excl. treatment * Prey type	3	3.631	0.016

There was a significant effect of foraging by birds (experimental and / or wild) (Table 8.4), but Figure 8.7 clearly demonstrates that this difference was due to the exclosures preventing foraging by the wild birds, rather than removal of prey by the experimental birds; i.e. there was a difference between exclosure and non-exclosure sites, but no difference between experimentally foraged and non-experimentally foraged sites. A greater biomass in the exclosure sites than in the non-exclosure sites could be seen in both fields, but *post-hoc* contrasts of means showed that this effect was significant only in the non-preferred field (comparison of sites on which experimental birds foraged: $F_{1,80}$=11.09, P=0.001; non-experimentally foraged sites: $F_{1,80}$=8.442, P=0.005). In the preferred field, the foraged sites within the exclosures did not yield a significantly greater biomass than those outside the exclosures ($F_{1,80}$=0.593, P=0.444), and there was a similar lack of effect between non-experimentally foraged sites ($F_{1,80}$=0.64, P=0.609).

The wet weights of invertebrates extracted from cores taken at non-exclosure, non-experimentally foraged sites (i.e. those sites which had been foraged by wild birds but not by experimental birds) were significantly lower at the end of the chick-feeding period, than at the start (Table 8.5a; Fig. 8.8). Much of this change was due to a reduced density of earthworm biomass in the non-preferred field. In contrast, the almost significant reduction in numbers, rather than biomass, of invertebrates collected was due to a decrease in numbers of leatherjackets (Table 8.5b).

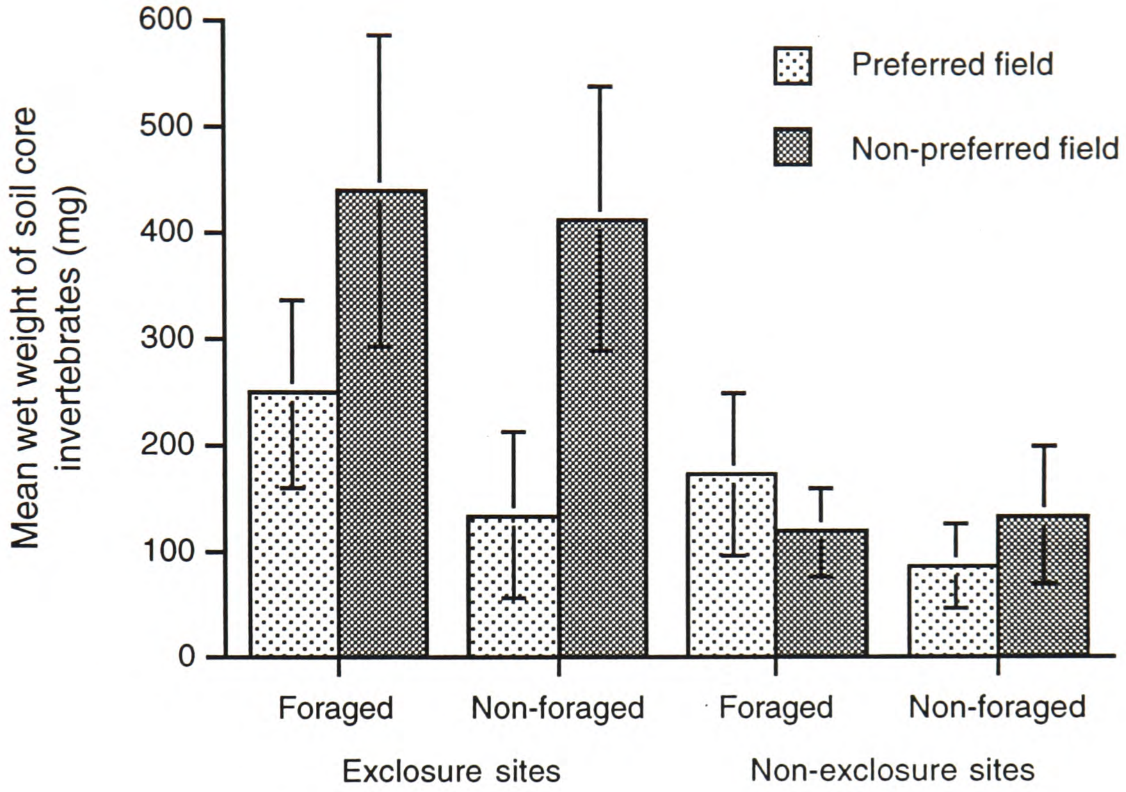


Figure 8.7. Mean (±SE) wet weight of invertebrates collected in soil cores taken from experimentally foraged ('foraged') and non-experimentally foraged ('non-foraged') sites in both exclosure (not foraged by wild birds) and non-exclosure (foraged by wild birds) regions. Results are shown for a field preferred by the wild birds and a field not preferred by the wild birds.

Table 8.5: Results of a three-way ANOVA with field (preferred by wild birds / not preferred), date (start of chick-feeding period / end of chick-feeding period) and prey type (earthworms / larvae) as factors, and **a)** wet weight of invertebrates in soil cores as dependent variable, and **b)** number of invertebrates as dependent variable.

		a) Wet weights		b) Numbers	
Factor	**df**	***F*-ratio**	***P*-value**	***F*-ratio**	***P*-value**
Field	1	4.234	0.046	1.525	0.224
Date	1	5.016	0.031	3.846	0.057
Prey type	1	3.892	0.055	7.322	0.010
Field * Date	1	2.517	0.121	0.214	0.646
Field *Prey type	1	9.880	0.003	1.634	0.208
Prey type * Date	1	0.297	0.589	3.853	0.056
Field * Date * Prey type	1	3.979	0.053	0.233	0.632

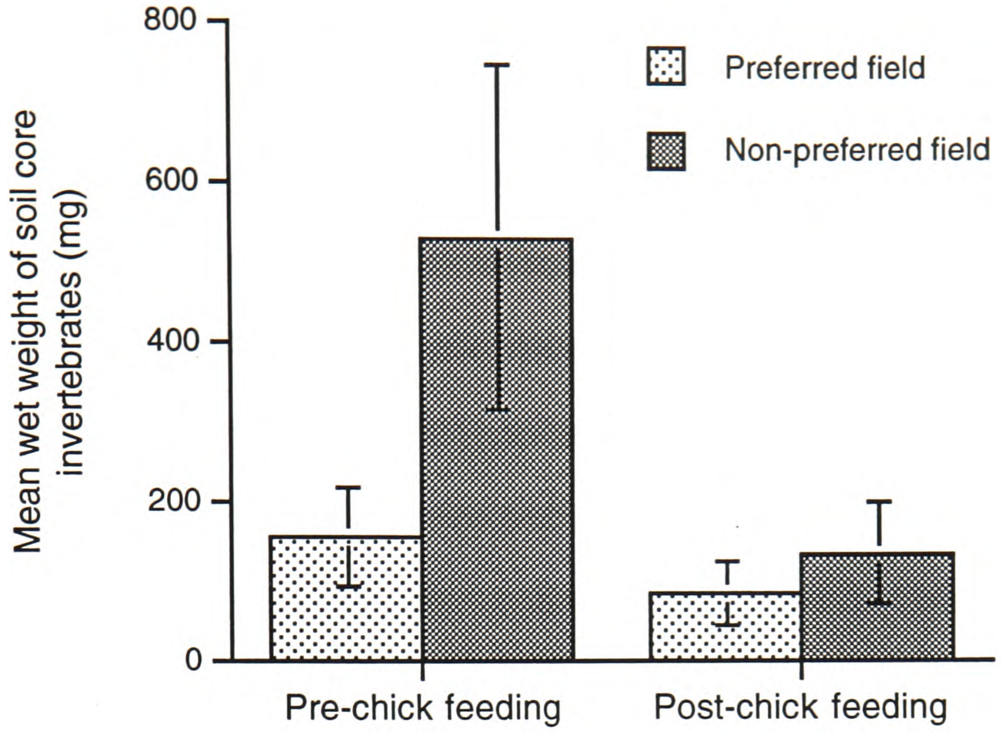


Figure 8.8. Mean (± SE) wet weight of invertebrates collected in soil cores taken from non-exclosure, non-experimentally foraged sites (i.e. sites to which wild birds had access, but which were not foraged by experimental birds) at start and end of chick-feeding period.

8.5 Discussion

8.5.1 Short-term depletion of prey availabilities

Short-term depletion of the starlings' invertebrate prey, when individuals foraged on the same patch for several hours, was considerable, particularly at the start of the season. The recovery of prey capture rates when the birds were transferred to the control enclosures at the end of three hours confirmed that the apparent depletion in the experimental sites did not result from the birds becoming satiated, and was not due to diurnal movements of the invertebrates, which may have taken them out of the probing range of the starlings. This is supported by other data for intake rates when feeding on leatherjackets (Tinbergen 1981), in which starlings were seen to attain a peak in intake rates during the middle of the day.

Long-term depletion of leatherjackets at any one site may have been counteracted by nocturnal overground movements sometimes made by this species (Tinbergen 1981). However, the low capture rates attained when the birds were returned to the experimental sites 24 h after initial foraging trials suggests that, if any such movements were occurring, they were insufficient to compensate for the removal of prey by the starlings.

Despite this evidence for short term depletion of prey, foraging individuals in the wild are unlikely to have such a dramatic impact on prey availability at one site over such a short time period. Although previous enclosure experiments have shown that foraging rates of birds held in enclosures are comparable to those expected of birds feeding in a wild flock, the 'natural' foraging rates will be maintained for much shorter time periods. Tinbergen's (1981) intensive observations of a single breeding female showed that, over seven days, the maximum duration of a single feeding visit to any 1 m^2 plot was 150 s. Thus the observed short term depletion is unlikely to occur in non-captive situations, when the bird is not forced to continue feeding on the same piece of ground.

This measure of short term depletion may, however, provide a useful prediction of the impact of long term predation. The Wytham colony of 60 boxes supports approximately 120 breeding adults, thus the maximum number of birds which could feed on any $1m^2$ plot would be 120. Using Tinbergen's (1981) observed maximum site residence time of 150 s as a guideline, the maximum amount of foraging on a single plot over 7 days would therefore equate to $18x10^3$ s (= 5 h) of foraging by a single bird. My data shows that after three hours of foraging by a single bird on 1 m^2 there was significant depletion of the available invertebrates, such that prey capture rates were much lower than the threshold intake rates predicted by Tinbergen (1981). Below these threshold intake rates, Tinbergen observed an increased probability that birds would leave a site to feed elsewhere. Obviously, it is very unlikely, given the total area of foraging habitat available to the starlings (c. 250 ha), that all the birds would visit the same small area. It is more realistic, however, to expect a subset of these birds to make a number of visits to the same site. Hence over the duration of the chick-feeding period (in this year there was chick-feeding activity for approximately 7 weeks), during which time each bird will have made several thousand feeding visits (Feare 1984), we might expect to see significant depletion of prey availabilities occurring at individual sites.

8.5.2 Long-term depletion of prey availabilities

The results of the long term depletion study support the prediction made from the results of the short term depletion study. Although prey availabilities will be affected by factors additional to predation by birds (e.g. leatherjackets may be susceptible to a viral infection, J. Coulson pers. comm.), it is apparent that the starlings exerted a considerable impact on the availabilities of their prey. This was particularly noticeable in the 'preferred' field, from which the starlings were able to extract higher numbers of leatherjackets, a preferred prey (Chapter 4). Such a prediction of prey depletion is in accordance with numerous studies, reviewed by Wiens (1989), in which significant depletion of prey was attributed to removal by birds.

Wiens (1989) also pointed out, however, that although the birds may be depleting their prey, this does not necessarily mean that they are limited by the supply of their food. For the present study, comparison of total prey availabilities at the start and end of the chick-feeding period showed a 40% reduction overall, but much of this reduction was concentrated in the 'preferred' field (73%). In contrast, there was no reduction in the non-preferred field. The impact of such a reduction in prey availability was consistent with the observed patterns of habitat use by the starlings (Wright *et al.* unpublished data). Although the adult starlings continued to use the preferred field throughout the chick-feeding period, its intensity of use declined slightly towards the end of the period, and the number of visits to other sites, including the non-preferred field, increased. One contributory factor to this shift in habitat use may have been the observed decline in prey availabilities in the preferred fields over the period of study.

Reasons for the starlings' preference for the preferred field were addressed in Chapter 4, in which a preference for leatherjackets over earthworms was demonstrated. Wright *et al.* (unpublished data) observed that when given larger broods to feed parent starlings maintained the biomass of food brought to each chick by increasing the number of earthworms in the chicks' diet. The cost of this adjustment was lower fledging weights of these chicks. Thus, in ideal conditions, the parent starlings chose to feed in those habitats from which they could obtain their preferred prey. Tinbergen (1981) reported a similar finding, except that in his study his birds had an alternative preferred prey. Although they still fed leatherjackets to their chicks, Tinbergen proposed that an excess of this prey may make the chicks' droppings very wet and loose, as was originally observed by Kluyver (1933).

8.5.3 Measuring prey abundance with soil cores

The densities of earthworms extracted in soil cores appeared to contradict the measures of earthworm availability indicated by the behavioural data. The birds were unable to extract as many earthworms as in previous, winter-time experiments, particularly in the non-preferred field. However, over the summer experimental period there was very little rain and the ground in all the fields was rather hard. Hence it is quite likely that the earthworms had retreated deeper into the soil column, out of the probing range of the birds, but still within the sampling range of the soil cores. Such a finding provides support for the distinction between prey abundance and prey availability, and demonstrates that measurement of prey density alone is an inadequate measure of potential intake rate (Tinbergen 1981). This observation is supported by a comparison of my estimates of percentage reductions in total prey availability (40%) and total prey abundance (68%).

The foraging pressure exerted by the parent starlings during chick-feeding had a significant impact on the availability and abundance of invertebrate prey. Indeed, what is regarded as an agricultural pest species (Feare 1980, 1989; Feare *et al.* 1992) in orchards and cattle feeding lots may be an important biological controlling agent of larval pest species on pasture (Coleman 1974b; East & Pottinger 1975). Although I have already shown in Chapter 6 that short term depletion also occurred during the winter, the soil invertebrates were sufficiently abundant to support the resident population throughout this period. In contrast, depletion of prey during the breeding season is such that prey availability to the birds may become limited in those preferred habitats used most extensively by the starlings. The starlings were able to respond to this depletion, caused by their own foraging, by switching to other feeding sites and associated prey types.

A decline in numbers of starlings over the past twenty or so years (Feare 1987; Orell & Ojanen 1980) has been attributed to changes in land-use practices. However, in areas of pastoral farming the starling is still locally abundant, and the continued success of the starling in such areas may be attributed to the flexibility in its choice of diet (Feare 1984). This adaptability allows starlings to accommodate changes in the availability of particular prey types, although they may experience slightly reduced breeding success when forced to feed on less preferred prey or habitats (e.g. as when forced to feed larger broods, or when breeding towards the end of the season). Wiens (1989) reviews a number of studies which demonstrate the impact of predation by birds on prey availability. For some of the studies discussed there is no indication that such depletion has any repercussions on the species concerned (e.g. Holmes *et al.* 1979), while for others it can impose severe restrictions (e.g. Högstedt 1980). Despite the starlings' ability to adapt to some changes in the availability of their prey, the extent to which they can accommodate these changes is dependent on the availability of a range of feeding habitats. In the absence of such diversity, they will become increasingly restricted by depression of their prey.

8.6 Summary

The impact of foraging by parent starlings during the chick-feeding period on the availability of soil invertebrate prey was investigated by studying the foraging behaviour of individual captive birds foraging in cage enclosures. Measures were obtained in a pasture field 'preferred' by the wild starlings, and in a pasture field 'not preferred'. In each of these fields prey availability in areas to which the wild birds had been allowed to forage was compared with that of areas from which the wild birds had been excluded.

Both at the start and end of the chick-feeding period, significant depletion of soil invertebrate availability occurred after just a few hours of feeding by captive birds. This depletion was attributed to removal of prey by the foraging birds, rather than to movements of the prey in the soil column, or to satiation of the birds. There was also evidence for long-term depletion, largely as a result of the removal of leatherjackets from the preferred field.

In addition to examining prey availability, prey abundance was measured from soil cores. Cores were taken from experimentally foraged and non-experimentally foraged ('control') sites, both inside and outside the exclosures, in each of the two fields. Foraging by the wild birds during the chick-feeding period caused a long-term depletion in prey abundance. There was no short-term depletion of prey abundance as a result of foraging by the experimental birds. The densities of earthworms in the soil cores were greater than the availabilities indicated from the behavioural data, suggesting that soil core analysis alone is insufficient to predict starling foraging rates on particular prey types.

The observed level of depletion was compared with patterns of foraging visits made by the wild starlings to the two experimental fields, and the interaction between starling foraging and prey availability was discussed at the population level.

Table 8.6: Summary of results, showing whether or not there was depletion of prey available to experimental birds (using measures of reward rate [number of prey captures per probe]), and whether or not there was depletion of invertebrate abundance (using soil core data), in the short term at the start and end of the chick-feeding period, and in the long term over the duration of the chick-feeding period. Results are shown separately for the two main types of invertebrate (earthworms and larvae), and for the two experimental fields, one of which was preferred by the wild birds, and the other of which was not preferred.

Field	Measurement	Short term depletion (pre-chick feeding)		Short term depletion (post-chick feeding)		Long term depletion	
		Larvae	Earthworms	Larvae	Earthworms	Larvae	Earthworms
Preferred:	Prey availability (experimental birds)	Yes	No*	Yes	No*	Yes	No
	Prey abundance (soil cores)	No	No	No	No	Yes	No
Non-preferred:	Prey availability (experimental birds)	Yes	No*	Some	No*	No	No
	Prey abundance (soil cores)	No	No	No	No	Some	Yes

* Few prey items captured by the birds

Chapter 9

General Discussion

The objectives of this thesis, as outlined in Chapter 1, were to establish the habitat preferences of the resident starling population at Wytham, to look for any patterns of use of these preferred habitats, and to provide some explanations, both theoretical and empirical, for the observed distributions of the overwintering flock. By gaining a more detailed understanding of how the starlings were distributed within their agricultural environment I hoped to gain a greater insight into the implications of land-use changes for starling populations.

9.1 Review of results

I began in Chapter 2 by describing the starlings' distribution in their environment. The observed flock habitat preferences were shown to be correlated with physical features of the birds' environment (e.g. distance of the fields from the central roost, and sward height), but in Chapter 3 I also revealed a relation between prey type availabilities and the starlings' choice of feeding habitat.

A preference for fields in which the availabilities of larval prey were greater may have been due to characteristics of those fields (e.g. soil types), but it was also possible that the birds were selecting fields according to the types of prey available. A laboratory test of this, described in Chapter 4, showed a preference by starlings for leatherjackets over earthworms, for which a difference in size between the two prey types was partly responsible. Further possible causes of the preference were discussed, but additional research is required to establish the extent to which other factors may contribute to this preference.

I then went on to address how the starlings' distribution within the available habitats may have been influenced by temporal variation in the availability of prey. Some of this variation could be attributed to environmental effects (e.g. soil temperature), but I also expected the distribution and availability of prey to be affected by the foraging of the birds themselves. In Chapter 1 I suggested a temporal

Ideal Free Distribution as a possible theoretical framework for describing the starlings' distribution in response to such changes in the availability of prey. Observations of the flock's movements described in Chapter 2 demonstrated some predictability in the starlings' pattern of habitat use, with the birds tending to move to adjacent fields, but I was unable to detect any obvious temporal pattern which I could have gone on to test in terms of an Ideal Free Distribution or similar theoretical framework. In generating their model of optimal searching strategies of predators, Comins & Hassell (1979) pointed out that any real foraging strategy is likely to deviate from an expected theoretical pattern, with the final strategy being influenced by a number of factors other than just maximising prey encounter rate. The apparent absence of any temporal pattern shown by the Wytham starlings may have resulted from their impact on prey availabilities being insufficient to demand any systematic 'harvesting' of their prey. Alternatively a number of unquantified effects (e.g. disturbance) may have masked any underlying pattern which the starlings could have followed under ideal conditions.

In order to explore the possibility that depletion of prey was insufficient to demand systematic prey 'harvesting' I was interested in quantifying the extent to which prey availabilities were actually being reduced by flock foraging visits to any one site. The observations made in Chapter 2, that the flock was not remaining in the most preferred habitats all the time, suggested that the starlings may have been causing some resource depression in these areas. Greater depression of resources in some fields or less renewal of these prey may have been a further factor influencing the starlings' habitat preferences, in addition to the physical features of their environment which have already been discussed.

The experiment described in Chapter 5 was designed to test for such an effect of resource depression by allowing two birds to feed consecutively on the same area of ground. In contrast to Tinbergen's (1981) study, in which he used a similar experimental approach to demonstrate depletion of prey during the summer, there was no reduction in the availability of prey in my winter experiment. This apparent lack of depletion was true for both a field preferred by the wild flock, and a non-preferred field.

The lack of depletion caused by two birds feeding consecutively on the same piece of ground, particularly the lack of a reduction in the second bird's foraging success was explored further in Chapter 6. That experiment examined in more detail how an individual's foraging success was affected by feeding on a piece of ground which had previously been exploited by another bird, as is the case in feeding flocks. The experiment also provided a further opportunity to look for the level of foraging pressure at which depletion of prey occurred.

From the results of this experiment I was unable to detect any detrimental effects on the second bird's foraging success as a result of feeding on an area previously exploited by another bird, despite the level of foraging imposed by the first bird being comparable to that estimated to occur in the flock. There was however a significant reduction in the amount of prey available to the experimental birds over the duration of the whole experimental session. I estimated that the level of experimental foraging pressure at which depletion was first observed (after one hour of foraging) equated to 43 flock feeding visits, and that a single feeding visit by the flock would be insufficient to cause a significant reduction in the availability of prey. The estimated lack of impact during a single flock visit was such that I concluded prey were sufficiently abundant during the winter for any reduction in their numbers during a single flock feeding visit to be negligible compared to the total numbers present. The starlings' continued use of the same pasture fields throughout the winter (pers. obs.) also suggested that even after many flock feeding visits the preferred fields still had adequate prey available for the birds to feed there.

I gave further attention to the effects on an individual's foraging success of feeding with conspecifics in Chapter 7, in which I quantified some of these effects experimentally. Contrary to expectations based on other studies (e.g. Feare & Inglis 1979), I found no evidence for any significant effects on the target bird's foraging success as a result of feeding within a 'flock' of three birds.

This lack of an effect within my experimental flock may have been because such effects only become apparent in more natural flock sizes, a possibility which would require further investigation. If, however, my experimental measures were representative of the feeding behaviour shown by individuals when feeding within natural flocks, they would have supported my earlier estimates of the level of flock foraging pressure at which depletion of prey becomes significant, these estimates being based upon observations of individual birds foraging alone in their enclosures.

The experiments discussed so far have not provided any evidence that prey depletion was enough to significantly affect the starlings' foraging success and subsequent choice of feeding site during the winter. However the effects of this overwinter depletion did become important during the breeding season, when further depletion occurred. The extent of this depletion was investigated in Chapter 8 in which I observed a significant reduction in the availability of soil invertebrate prey over the duration of the chick-feeding period. It seems therefore that although the availability of soil invertebrates appeared to be relatively unaffected by overwinter depletion, the non-renewable nature of these prey meant that further feeding by the birds during the chick-feeding period was sufficient to depress resources to a significantly lower level (Fig 9.1). This depletion may have been the cause of the observed switch to less preferred fields shown by the parent starlings later on in the breeding season.

9.2 Can flock departures from the preferred habitats be explained?

The estimated lack of depletion of prey imposed by a single flock visit, during the winter, raised the question of why the flock was leaving the preferred habitats. Some of these departures were as a result of disturbance, and others coincided with a return by the flock to the farm, where the birds rested between feeding bouts. Other movements, however, involved the flock shifting to a less preferred field and it is these movements for which an explanation is sought.

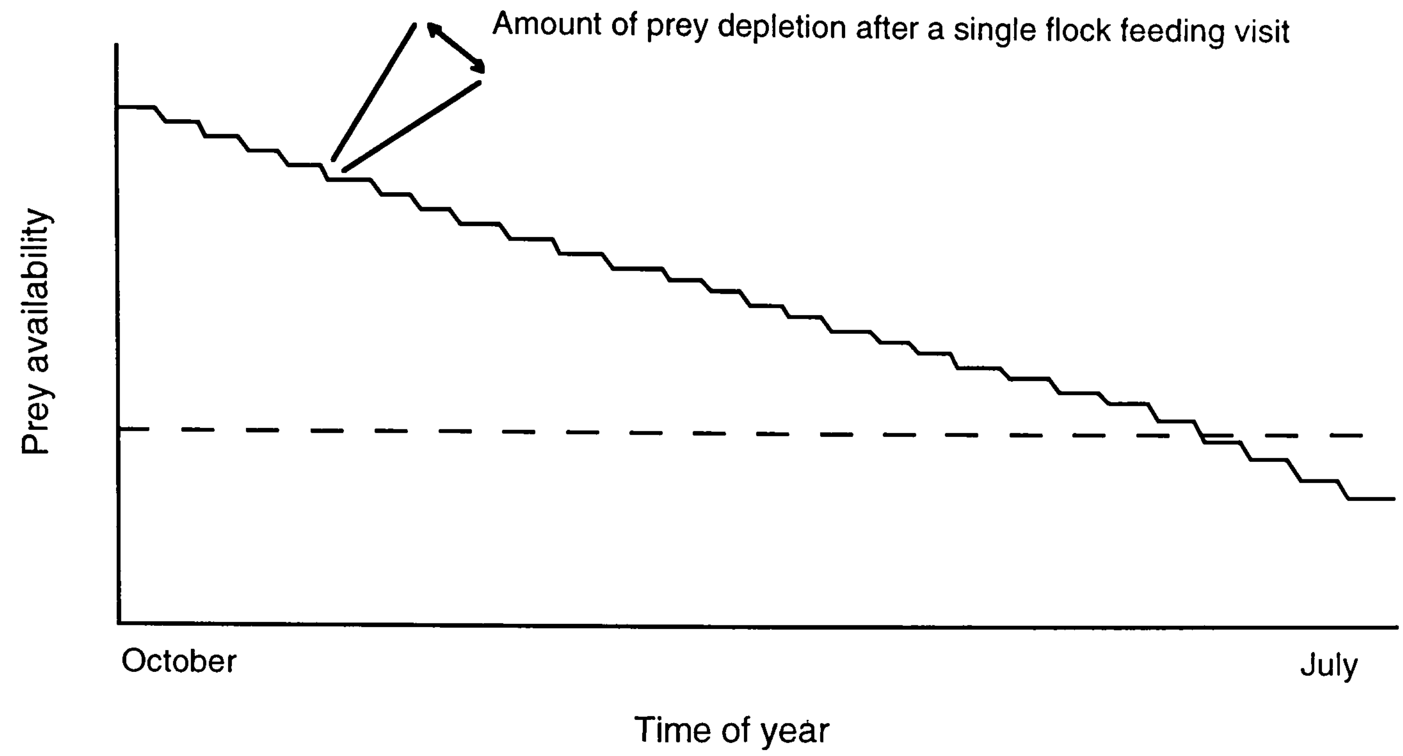


Fig 9.1 Schematic diagram showing how prey availability might be depleted by starling foraging from the start of winter through to the end of the chick-feeding period in a preferred pasture field. Individual flock visits cause a small reduction in the availability of prey (represented by each step down in the curve) but repeated visits to the same field cause a far greater long term reduction. Towards the end of the chick-feeding period prey availability falls below the 'threshold' level (represented by dashed line) below which it is no longer profitable for the birds to feed in the field, resulting in a shift to less preferred fields. The linear rate of decline in prey availability shown here is not assumed to be representative of the actual rate in decline.

9.2.1 Selection of most profitable prey

The observed movements to less preferred fields could have been a response to subtle changes in the availabilities of prey. Tinbergen & Drent (1980) described how starlings first remove the most accessible prey, 'creaming-off' items from the most profitable areas. In a similar way, although the Wytham birds could have met their daily energy requirements by feeding in the most preferred fields for the whole day (Chapter 3), they might have been able to meet their energetic requirements more quickly by first removing, from a number of fields, those prey which were easiest to capture. If such an effect was true I might expect individuals feeding within the flock to show higher foraging success during the first visits of the day to particular fields. A lower foraging success when returning to those fields later in the day may result from the most accessible prey having already been removed during earlier visits.

9.2.2 Sampling the environment

Transient increases in prey availabilities may have resulted from events such as slurry spraying, silage cutting or, in those fields closest to the river, waterlogging. In order to exploit these short term abundances of prey, the starlings would need to sample their environment, so that they can update their assessment of 'preferred' and 'non-preferred' fields, and learn about any changes in the availability of prey. Hence movements which were apparently 'unnecessary' might have had an information-gathering function. Such a possibility could have been tested for by 'seeding' non-preferred pasture fields with prey (e.g. by scattering mealworms) and observing the subsequent field visits made by the starlings. Had the birds been gathering information about the profitability of these less preferred fields, I would have expected to see an increase in starling foraging densities in these fields once they had been 'seeded'.

9.2.3 Influence of conspecifics on individual foraging success

A further source of movements to less preferred habitats may have been a heterogeneity of effects between individuals within the flock. The implications of aggression and interference on the choice of foraging site have been studied extensively in oystercatchers (Goss-Custard 1980; Goss-Custard et al. 1982a; 1984) in which it was shown that the dominant, aggressive birds fed most successfully on the most profitable mussel beds. As the density of birds increased, less dominant individuals had to spend more time avoiding attacks from the dominant birds, and so could achieve a higher rate of feeding by moving to poorer feeding areas in which a lower availability of prey was compensated for by fewer birds. Similarly, Barnard (1980c) observed how those sparrows which experienced low feeding rates within the flock either left to feed elsewhere, or attempted to move to a better position within the flock. In both cases, changes in the availability of prey to the birds were determined not by prey distributions, but by predator distributions and interactions between those predators.

Contrary to those observations, my own experimental manipulations did not provide evidence for any such effects between individuals. Such a lack of observable effects may have been because they do not occur within starling flocks. Given the previously discussed evidence to the contrary from other species, such an outcome would be rather unexpected and would warrant further investigation. Alternatively, a lack of effect may have been due to limitations of the experimental technique. I have already demonstrated how the enclosures can provide information about the foraging behaviour of individual birds that is more accurate and detailed than can be obtained from observations of the flock. However, when extending the question from individual feeding behaviour to that which occurs in a flock, the enclosures are limited by the group size they can deal with.

To explore more rigorously the possible heterogeneities of effects within the flock, and resulting flock dynamics, therefore requires a different approach which can access detailed data from the flocks themselves. In order to confirm whether or not there are any effects between individuals which influence their choice of feeding strategy, we need to measure the feeding rates of birds at different positions within the flock, establish which individuals are instigating departures and, in the event of flock fragmentation, what age and sex classes are found in the resulting sub-flocks. Such an approach would then complement the detailed data on individual foraging behaviour obtained experimentally in enclosures. It would also confirm whether or not the enclosures are a useful way of exploring the feeding behaviour of groups of starlings, in the same way that the enclosures technique has provided a valuable insight into the feeding behaviour of starlings feeding individually.

9.3 The implications of land-use changes on starling populations

In the light of the findings presented here, what can be said about the distribution of starlings in relation to land-use changes? The detrimental effects of intensification of agriculture on starling populations have been documented extensively (for review see Feare 1984). These effects were discussed in Chapter 1, in which I concluded that declining populations are largely as a result of the loss of suitable habitats. What is less clear is the time of year at which these land-use changes have the greatest impact on starling populations.

9.3.1 The impact of resource limitation on overwintering starlings

There is some evidence that starlings are most vulnerable during the winter, although Coulson (1960) cautioned against the biased nature of the data upon which this proposition was based, observing that winter is the time at which starlings are found nearer to human habitations, hence leg rings are more likely to be recovered. Furthermore, Feare (1984) reviewed a number of studies which indicated that, in Britain at least, starlings carry sufficient fat and protein reserves for them to survive the short periods of severe weather and associated food shortage experienced in this country (Taitt 1973; Ward 1977). It is likely, therefore, that starling populations will only experience significant overwinter mortality rates during very severe winters (Dobinson & Richards 1964).

More recently, however, Feare (1994) has documented a decline in the numbers of overwintering starlings in Lincolnshire. He attributed this decline to a number of changes in farming practice, which have not only reduced the amount of grassland and fallow land available to the birds, but have also denied the birds access to alternative feeding sites such as poultry and pig units, and silage clamps. These are all important sources of food for the starlings when availabilities of their natural invertebrate prey are low (Dunnet 1956; Feare & McGinnity 1986; Taitt 1973). Feare concluded that removal of these supplementary feeding sites have added to the effects of habitat loss, thus reducing the starlings' overwinter survival, and exacerbating any detrimental effects during the summer.

In contrast to Feare's (1994) findings the Wytham data presented here suggest that under the present agricultural regime, which maintains a mixture of arable and pasture fields and continues to provide access to supplementary feeding sites, the starlings are unlikely to experience reduced winter survival. Although I have demonstrated the starlings' dependence on particular types of grassland, the invertebrates in these habitats were found to be sufficiently abundant to support the resident population throughout the winter. Any reduction in the availability of established pasture would be unlikely to have a dramatic impact on the overwintering starlings, largely due to the availability of other feeding areas. The extensive flood meadows that form the south-west boundary of the farm were beyond the range of my study area, but were clearly within the starlings' range, with the flock sometimes flying over the river to feed on those areas. The flock only visited those parts of the flood meadows closest to the farm, but the majority of the meadows, as well as other pasture fields at the periphery of the study area, were well within the range of distances which starlings have been documented to travel in order to reach suitable feeding areas (Wynne-Edwards 1929). The worst consequence, therefore, of a modest reduction in the availability of pasture would be that the starlings would have to work harder to obtain food, spending more of their time travelling to feeding sites and capturing less accessible prey.

The overwintering conditions for the Wytham starlings were further improved by the availability of alternative sources of food. In contrast to Feare's (1994) study population, the Wytham starlings had access to silage and to cow, sheep and pig sheds. The pig sheds provided a particularly abundant source of food but the intensive exploitation of this source was of economic significance, as has been in the case in other agricultural areas (e.g. Feare & Wadsworth 1981; Feare 1980). The farm manager's plans to net off the sheds, to prevent further losses, may have some influence on the starlings' future overwinter survival.

9.3.2 The impact of resource limitation during the breeding season

In contrast to the apparently low rates of winter mortality, previous studies have provided evidence that mortality rates, both of adult and juvenile starlings, are greater in the summer, particularly just after the breeding season. Part of this effect may be a result of the behaviour of the invertebrate prey which I described in Chapter 1. Aestivation by earthworms reduces their accessibility to the birds, and summer pupation and emergence of leatherjackets adds to the depletion already caused by foraging birds. Feare (1984) described the increased vulnerability of parent birds at this time of year, which was as a result of low reserves and greater energetic demands imposed by moulting.

My own data suggest some resource limitation in the summer for the Wytham starlings. In Chapter 8, I showed a significant reduction in the availability of prey over the duration of the chick-feeding period particularly in the preferred field. This depletion of prey coincided with an observed switch by the parent birds to less preferred feeding sites. The experimental birds' reward rates were reduced by approximately 44% by the end of chick-feeding. Given that prey availabilities had already been reduced overwinter by over 50%, the final availabilities of prey would have not been more than a quarter of those originally available. Alternative foods, such as pig pellets, may have been nutritionally adequate but the low water content of this food source could have resulted in a number of the chicks dying from dehydration or heat exhaustion (Cotton, pers. comm.), particularly during periods of hot, dry weather when the availability of soil invertebrates would have been very limited.

Although the study population does not appear to be in decline at present, it is less obvious whether or not further changes in farming practice will be detrimental to the breeding birds. A reduction in the availability of suitable feeding sites and foraging opportunities will be more deleterious at this time of year when increased foraging demands on the parent starlings will restrict the adjustments that they can make to their foraging strategies. Thus any further reduction in the availability of suitable pasture to the birds may be sufficient to restrict the starlings' feeding opportunities, such that the size and number of broods that can be successfully raised falls below the present level. Obviously this current breeding success may also be limited by other factors such as the availability of suitable breeding sites, a possibility supported by the presence of a number of non-breeding 'floater' starlings at Wytham each year (Wright, pers. comm.). The future size of the resident population following the addition of approximately twenty nest-boxes to the colony prior to the 1994 breeding season will also indicate the extent of previous nest-site limitation.

In summary, despite the potential limitations during the summer, it appears that at present any changes in land-use have not been sufficient to cause a significant local population decline. The Wytham population is not isolated, as evidenced by the immigration of unmarked individuals during the winter, but the extent to which it is a source or a sink population cannot be determined without more data on dispersal of the Wytham-bred individuals. Although it is not possible, therefore, to quantify the mortality rates of the Wytham birds, the continued stability in overall numbers suggests that any such mortality is unlikely to be a result of increasing resource limitation.

The University farm is representative of many farms of the region, which employ a mixture of pasture and arable practices. The management of pasture fields may actually be beneficial to the starlings, as has already been documented for a number of bird species in upland areas (Bignal & McCracken 1993). Ungrazed fields which are cut sporadically for silage may provide the starlings with an abundance of invertebrate prey for a limited period, but fields which are grazed regularly provide a far more suitable long-term foraging habitat. The pastoral farming of this region contrasts markedly with the intensive monoculture in other parts of the country (e.g. Norfolk, Summers & Cross 1987) in which the far more extreme changes in agricultural practices have had a very evident, damaging effect on starling populations.

Appendix I :

Nutritional and energetic analyses of earthworms (*Lumbricus* spp.) and leatherjackets (*Tipula paludosa*).

All analyses presented here are based upon invertebrate samples collected from soil cores (Chapter 8) and are according to M. Townsend (pers. comm.).

I.i Estimation of protein content

Individual dried samples were boiled in concentrated sulphuric acid, with a Selenium tablet catalyst. Once the solution had become colourless, after a maximum of five hours, the solution was allowed to cool. An automated calorimeter provided a measure of ammonium content, from which it was possible to calculate the percentage of organic nitrogen. This value was multiplied by 6.25 to give an estimate of % protein. The values for each prey type are presented in Appendix I.vi.

I.ii Estimation of lipid content

Individual dried samples were steeped in petroleum ether (b.p. 60-80c) in plastic-stoppered specimen tubes for 48 hr. Approximately 90% of the solvent was pippetted off and the remainder allowed to evaporate. The samples were ground up, and steeped in a solution of 75% methanol and 25% chloroform for 96 hr, after which most of the solvent was removed. This was repeated for a further 48 hr, the majority of the solvent then removed, and any remaining allowed to evaporate. Samples were oven dried at 50°C for 24 hr to remove any traces of solvent. The samples were then weighed and the difference between these values and initial dry weight values used to calculate the percentage of lipid.

The procedure for lipid extraction also removed some protein. This loss was quantified by conducting protein extraction on the same sample, after lipid extraction had been performed. The value for lipid content was then corrected for the loss of weight attributable to protein having been removed from the sample. The values for each prey type are presented in Appendix I.vi.

I.iii Estimation of ash content

Dried samples were burned in a muffle furnace at 500°C for 5 hr, and the residue weighed to obtain ash content. The values for each prey type are presented in Appendix I.vi.

I.iv Estimation of carbohydrate content

The values of protein, lipid and ash were extracted from the initial dry weight values, and the remaining difference was attributed to carbohydrate content. The values for each prey type are presented in Appendix I.vi.

I.v Estimation of energy content

Mean calorific values for protein (5100 cal/ash-free g), lipid (9500 cal/ash-free g) and carbohydrate (4100 cal/ash-free g) (Cummins & Wuycheck 1971) were used to calculate mean energy values for each taxonomic group of invertebrates collected from the cores. The final values were converted to kJ/ash-free g, and are presented in Appendix I.vi.

I.vi Dry and wet weights, and nutritional data for invertebrate samples.

	Leatherjackets		Earthworms	
	Mean	**SE**	**Mean**	**SE**
Wet weight (mg)	439.07	32.87	284.00	103.65
Dry weight (mg)	54.60	4.70	132.30	72.70
Protein (%)	51.87	1.30	54.08	2.91
Lipid (%)	26.40	2.30	29.50	1.84
Ash (%)	9.80	1.30	10.43	6.90
Carbohydrate (%)	11.93	-	5.99	-
Energy (kJ/g dry weight)	23.76	-	24.63	-

Appendix II:

Calculation of estimated mean, minimum and maximum flock foraging pressures.

These calculations are based on measures obtained from the flock observations described in Chapter 5:

	Mean	SE
Flock size (number of birds)	146.76	10.79
Flock residence time (number of minutes)	24.39	2.19
Interbird distance (bird-lengths [1 bird length = 0.15 m])	5.10	0.32
Field area (ha)	5.32	1.01
Number of regions covered by flock in one feeding visit (each field divided into 9 regions of approximately equal area).	1.75	0.12

IIa) Mean flock foraging pressure

Mean interbird distance = mean number of bird lengths between birds x length of one bird

$= 5.1 \times 0.15$

$= 0.765$ m

Mean bird density = (number of birds per m)^2

$= (1 / 0.765)^2$

$= 1.709$ birds / m^2 (see footnote)

Mean flock area = mean number of birds in flock / mean bird density

$$= \frac{146.762}{1.709}$$

$= 85.89$ m^2

Mean area of one field region = mean field area / number of regions per field

$= 5.32 / 9$

$= 5.911 \times 10^3$ m^2

Therefore, mean area visited during one flock visit = mean number of regions visited x mean area of one region

$= 1.75 \times 5.911 \times 10^3$

$= 10.34 \times 10^3\ m^2$

Number of moves the flock must make to cover whole area = mean area visited during a single flock visit / mean area of flock

$= \frac{10.34 \times 10^3}{85.89}$

= 120.44 times (i.e. a flock of area 85.89 m^2 must feed in 120.44 different areas, if it is to cover the whole of a feeding region of area $10.34 \times 10^3\ m^2$, during a single feeding visit.

Thus, mean foraging intensity during a single flock visit = mean number of birds per m^2 / number of different areas the flock must visit

$= \frac{1.709}{120.44}$

= 0.014 birds / m^2

Mean foraging pressure = mean foraging intensity x mean flock residence time

= 0.014 x 24.39

= **0.346 bird-minutes / m^2**

IIb) Maximum flock foraging pressure (= mean foraging pressure + 95% CL)

Calculation of maximum flock foraging pressure assumes that a flock of maximum density and maximum size remains feeding on the same area of ground (i.e. no movement across the field) for the maximum flock residence time.

Minimum interbird distance = (mean number of bird lengths between birds - 95% CL) x length of one bird

$= (5.1 - (1.96 \times 0.32)) \times 0.15$

= 0.671 m

Maximum bird density = (number of birds per m)^2 $= (1 / 0.671)^2$

= 2.22 birds / m^2

Therefore, maximum foraging intensity = 2.22 birds / m^2

Maximum flock residence time = Mean flock residence time + 95% CL

$= 24.39 + (1.96 \times 2.191)$

= 28.682 min

Maximum flock foraging pressure = Maximum foraging intensity x maximum residence time

= 2.22 x 28.682

= **63.72 bird-minutes per m^2**

IIc) Minimum flock foraging pressure (= mean foraging pressure - 95% CL)

Calculation of minimum flock foraging pressure assumes that a flock of minimum density and minimum size feeds on the maximum area of ground (i.e. moves across the maximum number of regions) in the minimum residence time.

Maximum interbird distance = (mean number of bird lengths between birds + 95% CL) x length of one bird

= (5.1 + (1.96 x 0.32)) x 0.15

= 0.859 m

Minimum bird density = (number of birds per m)^2 = (1 / 0.859)^2

= 1.35 birds / m^2

Minimum number of birds in a flock = 146.762 - (1.96 x 10.79)

= 125.614

Therefore minimum flock area $= \frac{125.614}{1.35}$

= 93.05 m^2

Maximum area of one region = maximum field area / number of regions in each field

$= \frac{5.32 + (1.96 \times 1.01)}{9}$

= 0.811 ha

= 8.11 x 10^3 m^2

Maximum number of regions visited = 1.75 + (1.96 x 0.12)

= 1.985

Therefore, maximum area visited = maximum number of regions visited x maximum area of one region

$$= 1.985 \times 8.11 \times 10^3 \text{ m}^2$$

$$= 16.10 \times 10^3 \text{ m}^2$$

Maximum number of times flock must move to forage whole area during one feeding visit = maximum area visited / minimum area of flock

$$= \frac{16.10 \times 10^3}{93.05}$$

$$= 173.02$$

Thus, minimum foraging intensity = minimum number of birds per m^2 / maximum number of different areas the flock must visit

$$= 1.35 / 173.02$$

$$= 0.008 \text{ birds / m}^2$$

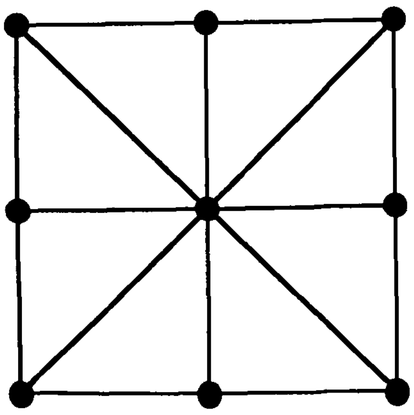
Minimum foraging pressure = minimum foraging intensity x minimum flock residence time

$$= 0.008 \times (24.39 - (1.96 \times 2.19))$$

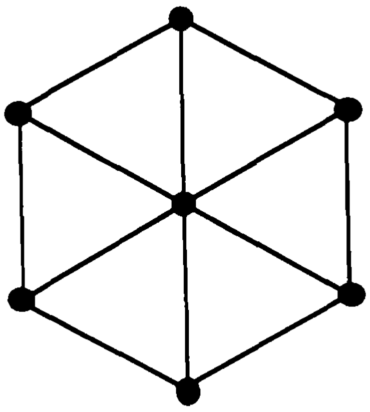
= **0.157 bird-minutes / m^2**

Footnote: A frequency distribution of the actual inter-bird distances showed a negatively skewed (i.e. greater frequency of shorter distances) normal distribution of inter-bird distances within the flock, indicating an aggregated or random distribution. However, in the above calculations I have assumed that the birds were arranged on a regular square grid (Fig. 1a) with an interbird distance, which was the mean of the observed flock values. A more rigorous assumption of an even distribution is one which assumes a regular hexagonal arrangement (Fig. 1b), such that all birds are equidistant from one another. However, I estimated that the increased accuracy afforded by assuming a hexagonal configuration had a negligible effect on the final calculated values of mean, minimum and maximum flock foraging pressures, due to greater variation of other parameters of flock observations. Hence, for the purpose of these calculations, I assumed a simpler 'square' arrangement of birds within the flock.

a)



b)



Appendix III :
Soil core and capture rate data - Chapter 5

Appendix IIIa: Soil core data (core dimensions were 50 mm diameter and 50 mm deep. Field 16 = 'non-preferred' field and Field 2b = 'preferred' field).

			Experimentally foraged sites				Control sites			
			Earthworms		Larvae		Earthworms		Larvae	
Field	Site	Core	Numbers	Wet weight (g)	Numbers	Wet weight (g)	Numbers	Wet weight (g)	Numbers	Wet weight (g)
16	1	1	0	0.00	0	0.00	1	0.27	0	0.00
16	1	2	1	0.27	0	0.00	0	0.00	0	0.00
16	1	3	2	0.27	2	0.13	0	0.00	0	0.00
16	1	4	1	0.02	0	0.00	0	0.00	0	0.00
16	1	5	1	0.12	0	0.00	0	0.00	0	0.00
16	1	6	1	0.18	0	0.00	0	0.00	0	0.00
16	2	1	4	0.33	1	0.03	4	0.41	0	0.00
16	2	2	1	0.14	1	0.04	2	0.09	0	0.00
16	2	3	0	0.00	0	0.00	2	0.28	0	0.00
16	2	4	0	0.00	0	0.00	0	0.00	0	0.00
16	2	5	0	0.00	0	0.00	0	0.00	0	0.00
16	2	6	0	0.00	0	0.00	0	0.00	0	0.00
16	3	1	2	0.03	0	0.00	3	0.17	0	0.00
16	3	2	0	0.00	0	0.00	3	0.26	2	0.08
16	3	3	0	0.00	0	0.00	6	0.42	1	0.28
16	3	4	0	0.00	0	0.00	3	0.36	0	0.00
16	3	5	0	0.00	0	0.00	2	0.47	0	0.00
16	3	6	0	0.00	0	0.00	0	0.00	0	0.00
16	4	1	0	0.00	0	0.00	1	0.16	0	0.00
16	4	2	0	0.00	0	0.00	1	0.02	0	0.00
16	4	3	0	0.00	0	0.00	1	0.04	0	0.00
16	4	4	0	0.00	0	0.00	1	0.13	0	0.00
16	4	5	0	0.00	0	0.00	1	0.02	0	0.00
16	4	6	0	0.00	0	0.00	0	0.00	0	0.00

			Experimentally foraged sites				Control sites			
			Earthworms		Larvae		Earthworms		Larvae	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
16	**5**	**1**	1	0.07	0	0.00	1	0.03	0	0.00
16	**5**	**2**	0	0.00	1	0.01	2	0.18	0	0.00
16	**5**	**3**	1	0.02	0	0.00	0	0.00	1	0.04
16	**5**	**4**	0	0.00	0	0.00	0	0.00	0	0.00
16	**5**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
16	**5**	**6**	0	0.00	0	0.00	0	0.00	0	0.00
16	**6**	**1**	1	0.03	0	0.00	1	0.04	0	0.00
16	**6**	**2**	1	0.01	0	0.00	1	0.07	1	0.03
16	**6**	**3**	2	0.25	0	0.00	1	0.34	0	0.00
16	**6**	**4**	1	0.15	0	0.00	1	0.08	0	0.00
16	**6**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
16	**6**	**6**	0	0.00	0	0.00	0	0.00	0	0.00
16	**7**	**1**	0	0.00	0	0.00	2	0.08	0	0.00
16	**7**	**2**	0	0.00	0	0.00	1	0.06	0	0.00
16	**7**	**3**	0	0.00	0	0.00	2	0.12	0	0.00
16	**7**	**4**	0	0.00	0	0.00	0	0.00	0	0.00
16	**7**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
16	**7**	**6**	0	0.00	0	0.00	0	0.00	0	0.00
16	**8**	**1**	2	0.66	0	0.00	0	0.00	1	0.03
16	**8**	**2**	3	1.25	0	0.00	2	0.55	0	0.00
16	**8**	**3**	3	0.21	0	0.00	1	0.28	0	0.00
16	**8**	**4**	3	0.20	0	0.00	0	0.00	0	0.00
16	**8**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
16	**8**	**6**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**1**	**1**	1	0.17	0	0.00	1	0.08	0	0.00
2b	**1**	**2**	0	0.00	0	0.00	2	0.94	0	0.00
2b	**1**	**3**	0	0.00	0	0.00	2	0.15	1	0.04
2b	**1**	**4**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**1**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**1**	**6**	0	0.00	0	0.00	0	0.00	0	0.00

			Experimentally foraged sites				Control sites			
			Earthworms		Larvae		Earthworms		Larvae	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
2b	**2**	**1**	1	0.01	0	0.00	0	0.00	1	0.03
2b	**2**	**2**	0	0.00	0	0.00	0	0.00	2	0.04
2b	**2**	**3**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**2**	**4**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**2**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**2**	**6**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**3**	**1**	0	0.00	2	0.03	0	0.00	1	0.02
2b	**3**	**2**	0	0.00	2	0.07	0	0.00	0	0.00
2b	**3**	**3**	0	0.00	1	0.01	0	0.00	0	0.00
2b	**3**	**4**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**3**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**3**	**6**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**4**	**1**	0	0.00	1	0.02	0	0.00	1	0.03
2b	**4**	**2**	0	0.00	1	0.01	0	0.00	0	0.00
2b	**4**	**3**	1	0.02	2	0.01	0	0.00	0	0.00
2b	**4**	**4**	0	0.00	2	0.02	0	0.00	0	0.00
2b	**4**	**5**	2	0.03	1	0.04	0	0.00	0	0.00
2b	**4**	**6**	0	0.00	1	0.01	0	0.00	0	0.00
2b	**5**	**1**	0	0.00	1	0.12	1	0.16	0	0.00
2b	**5**	**2**	0	0.00	1	0.02	0	0.00	0	0.00
2b	**5**	**3**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**5**	**4**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**5**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**5**	**6**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**6**	**1**	0	0.00	0	0.00	0	0.00	2	0.1
2b	**6**	**2**	0	0.00	0	0.00	1	0.25	0	0.00
2b	**6**	**3**	0	0.00	0	0.00	0	0.00	1	0.03
2b	**6**	**4**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**6**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**6**	**6**	0	0.00	0	0.00	0	0.00	0	0.00

			Experimentally foraged sites				Control sites			
			Earthworms		Larvae		Earthworms		Larvae	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
2b	**7**	**1**	0	0.00	1	0.02	1	0.04	0	0.00
2b	**7**	**2**	0	0.00	2	0.03	0	0.00	1	0.01
2b	**7**	**3**	1	0.23	22	0.16	0	0.00	1	0.04
2b	**7**	**4**	0	0.00	0	0.00	1	0.05	0	0.00
2b	**7**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**7**	**6**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**8**	**1**	0	0.00	1	0.01	0	0.00	0	0.00
2b	**8**	**2**	0	0.00	2	0.10	0	0.00	0	0.00
2b	**8**	**3**	0	0.00	1	0.12	0	0.00	0	0.00
2b	**8**	**4**	0	0.00	1	0.01	0	0.00	0	0.00
2b	**8**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**8**	**6**	0	0.00	0	0.00	0	0.00	0	0.00

Appendix IIIb: foraging data from enclosures (prey captures per second of foraging by captive birds).

		First 20 min		Second 20 min		20 min after 24 h	
Field	**Site**	**Earthworms**	**Larvae**	**Earthworms**	**Larvae**	**Earthworms**	**Larvae**
16	**1**	0.004	0.014	0.007	0.030	0.008	0.033
16	**2**	0.008	0.024	0.013	0.012	0.004	0.018
16	**3**	0.008	0.022	0.005	0.005	0.005	0.018
16	**4**	0.018	0.004	0.013	0.018	0.027	0.011
16	**5**	0.008	0.016	0.002	0.015	0.006	0.025
16	**6**	0.011	0.036	0.008	0.046	0.014	0.015
16	**7**	0.010	0.020	0.004	0.035	0.010	0.010
16	**8**	0.007	0.057	0.009	0.025	0.007	0.010
2b	**1**	0.006	0.021	0.003	0.020	0.006	0.030
2b	**2**	0.005	0.025	0.004	0.052	0.004	0.035
2b	**3**	0.004	0.061	0.003	0.069	0.004	0.039
2b	**4**	0.007	0.020	0.002	0.036	0.008	0.044
2b	**5**	0.005	0.041	0.008	0.051	0.004	0.046
2b	**6**	0.003	0.035	0.002	0.029	0.003	0.014
2b	**7**	0.014	0.023	0.001	0.020	0.013	0.019
2b	**8**	0.006	0.055	0.008	0.049	0.010	0.037

Appendix IV:
Soil core and capture rate data - Chapter 6

Appendix IVa: Soil core data (Core dimensions were 80mm diameter and 150 mm deep Field 16 = 'non-preferred' field and Field 2b = 'preferred' field).

			Experimentally foraged sites				Control sites			
			Earthworms		Larvae		Earthworms		Larvae	
Field	**Site**	**Core**	**Numbers**	**Wet weight (mg)**	**Numbers**	**Wet weight (mg)**	**Numbers**	**Wet weight (mg)**	**Numbers**	**Wet weight (mg)**
16	**1**	**1**	1	0.08	41	0.45	2	0.37	0	0.00
16	**1**	**2**	3	0.45	105	1.05	2	0.35	0	0.00
16	**1**	**3**	4	0.49	10	0.11	2	0.27	0	0.00
16	**1**	**4**	2	0.18	1	0.01	8	1.15	0	0.00
16	**1**	**5**	1	0.09	15	0.19	5	0.36	0	0.00
16	**1**	**6**	3	0.04	0	0.00	5	0.74	0	0.00
16	**2**	**1**	1	0.14	0	0.00	0	0.00	1	0.01
16	**2**	**2**	0	0.00	1	0.01	0	0.00	1	0.02
16	**2**	**3**	0	0.00	1	0.03	0	0.00	1	0.01
16	**2**	**4**	0	0.00	0	0.00	5	1.74	0	0.00
16	**2**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
16	**2**	**6**	0	0.00	0	0.00	0	0.00	0	0.00
16	**3**	**1**	9	0.85	3	0.07	0	0.00	38	0.48
16	**3**	**2**	9	1.22	1	0.01	2	0.38	72	0.92
16	**3**	**3**	3	0.82	0	0.00	2	0.38	0	0.00
16	**3**	**4**	3	0.78	41	0.55	8	1.53	85	1.14
16	**3**	**5**	2	0.18	13	0.11	1	0.33	0	0.00
16	**3**	**6**	0	0.00	0	0.00	3	0.32	248	3.94
16	**4**	**1**	2	0.48	0	0.00	6	1.35	0	0.00
16	**4**	**2**	1	0.15	0	0.00	3	0.74	0	0.00
16	**4**	**3**	0	0.00	0	0.00	5	0.32	0	0.00
16	**4**	**4**	0	0.00	0	0.00	3	0.34	1	0.09
16	**4**	**5**	0	0.00	0	0.00	4	0.85	0	0.00
16	**4**	**6**	0	0.00	0	0.00	14	2.85	0	0.00

			Experimentally foraged sites				Control sites			
			Earthworms		Larvae		Earthworms		Larvae	
Field	**Site**	**Core**	**Numbers**	**Wet weight (mg)**	**Numbers**	**Wet weight (mg)**	**Numbers**	**Wet weight (mg)**	**Numbers**	**Wet weight (mg)**
16	5	1	3	1.19	18	0.25	1	0.32	1	0.02
16	5	2	6	0.96	161	2.59	5	1.84	0	0.00
16	5	3	3	0.51	5	0.06	2	0.25	0	0.00
16	5	4	8	0.66	0	0.00	7	1.40	9	0.09
16	5	5	3	0.47	0	0.00	2	0.34	0	0.00
16	5	6	7	0.86	0	0.00	0	0.00	0	0.00
16	6	1	0	0.00	4	0.06	3	0.61	0	0.00
16	6	2	0	0.00	22	0.38	4	1.05	0	0.00
16	6	3	2	0.23	0	0.00	4	0.23	1	0.01
16	6	4	2	0.55	103	2.03	7	2.93	0	0.00
16	6	5	3	1.51	0	0.00	5	0.91	1	0.01
16	6	6	1	0.29	0	0.00	2	0.27	0	0.00
16	7	1	4	0.34	0	0.00	6	0.82	19	0.27
16	7	2	6	0.47	15	0.16	1	0.26	0	0.00
16	7	3	8	0.81	0	0.00	2	0.30	0	0.00
16	7	4	2	0.11	0	0.00	8	1.28	6	0.07
16	7	5	2	0.17	0	0.00	4	0.28	0	0.00
16	7	6	8	0.90	1	0.01	0	0.00	0	0.00
16	8	1	1	0.11	0	0.00	2	0.12	0	0.00
16	8	2	2	0.28	0	0.00	3	0.42	1	0.01
16	8	3	4	0.53	0	0.00	3	0.83	0	0.00
16	8	4	15	1.55	105	1.68	3	0.28	0	0.00
16	8	5	0	0.00	0	0.00	0	0.00	0	0.00
16	8	6	0	0.00	0	0.00	0	0.00	0	0.00
2b	1	1	1	0.03	11	0.12	2	0.30	10	0.15
2b	1	2	3	0.9	0	0.00	0	0.00	3	0.14
2b	1	3	4	0.38	1	0.01	1	0.01	7	0.07
2b	1	4	6	2.0	0	0.00	1	0.01	0	0.00
2b	1	5	2	0.72	2	0.02	0	0.00	1	0.01
2b	1	6	3	0.26	0	0.00	0	0.00	2	0.02

			Experimentally foraged sites				Control sites			
			Earthworms		Larvae		Earthworms		Larvae	
Field	**Site**	**Core**	**Numbers**	**Wet weight (mg)**	**Numbers**	**Wet weight (mg)**	**Numbers**	**Wet weight (mg)**	**Numbers**	**Wet weight (mg)**
2b	2	1	1	0.16	26	0.41	0	0.00	1	0.02
2b	2	2	1	0.02	1	0.03	2	0.84	2	0.02
2b	2	3	0	0.00	11	0.16	3	0.35	1	0.03
2b	2	4	0	0.00	5	0.07	8	1.67	1	0.06
2b	2	5	1	0.06	2	0.03	8	5.38	5	0.06
2b	2	6	1	0.02	2	0.05	0	0.00	0	0.00
2b	3	1	3	1.31	16	0.18	0	0.00	1	0.02
2b	3	2	3	0.75	0	0.00	0	0.00	74	1.19
2b	3	3	3	0.34	0	0.00	0	0.00	0	0.00
2b	3	4	0	0.00	0	0.00	0	0.00	0	0.00
2b	3	5	0	0.00	0	0.00	0	0.00	0	0.00
2b	3	6	0	0.00	0	0.00	0	0.00	0	0.00
2b	4	1	1	0.03	0	0.00	0	0.00	24	0.45
2b	4	2	0	0.00	6	0.06	0	0.00	1	0.02
2b	4	3	0	0.00	1	0.01	0	0.00	1	0.04
2b	4	4	2	0.75	30	0.43	0	0.00	3	0.09
2b	4	5	0	0.00	0	0.00	0	0.00	2	0.06
2b	4	6	0	0.00	0	0.00	0	0.00	33	0.41
2b	5	1	0	0.00	5	0.14	2	0.12	39	0.61
2b	5	2	1	0.04	1	0.04	0	0.00	2	0.15
2b	5	3	0	0.00	0	0.00	3	0.06	0	0.00
2b	5	4	0	0.00	0	0.00	0	0.00	18	0.30
2b	5	5	0	0.00	0	0.00	0	0.00	4	0.04
2b	5	6	0	0.00	0	0.00	0	0.00	0	0.00
2b	6	1	1	0.15	0	0.00	0	0.00	1	0.01
2b	6	2	0	0.00	46	0.71	0	0.00	11	0.17
2b	6	3	0	0.00	0	0.00	2	0.72	15	0.26
2b	6	4	0	0.00	0	0.00	0	0.00	0	0.00
2b	6	5	0	0.00	0	0.00	0	0.00	0	0.00
2b	6	6	0	0.00	0	0.00	0	0.00	0	0.00

			Experimentally foraged sites				Control sites			
			Earthworms		Larvae		Earthworms		Larvae	
Field	**Site**	**Core**	**Numbers**	**Wet weight (mg)**	**Numbers**	**Wet weight (mg)**	**Numbers**	**Wet weight (mg)**	**Numbers**	**Wet weight (mg)**
2b	**7**	**1**	0	0.00	1	0.02	1	0.22	0	0.00
2b	**7**	**2**	0	0.00	3	0.15	1	0.02	0	0.00
2b	**7**	**3**	0	0.00	0	0.00	0	0.00	1	0.01
2b	**7**	**4**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**7**	**5**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**7**	**6**	0	0.00	0	0.00	0	0.00	0	0.00
2b	**8**	**1**	1	1.07	1	0.06	0	0.00	235	3.48
2b	**8**	**2**	0	0.00	6	0.06	2	0.70	2	0.02
2b	**8**	**3**	0	0.00	2	0.02	3	0.25	22	0.34
2b	**8**	**4**	1	0.03	66	0.77	0	0.00	0	0.00
2b	**8**	**5**	2	0.22	49	0.53	3	1.06	0	0.00
2b	**8**	**6**	1	0.27	1	0.04	0	0.00	3	0.12

Appendix IVb: Foraging data from enclosures (Qa&d shows capture rates on that part of the enclosure foraged by both manipulation and test birds; Qb&c show capture rates on that part of the enclosure foraged only by test birds).

Earthworm captures per second of foraging by captive birds:

		Manipulation	Test: 1st 20 min		Test: 10 min after 1 h		Test: 10 min after 4 h	
Field	**Site**	**Qa&d**	**Qa&d**	**Qb&c**	**Qa&d**	**Qb&c**	**Qa&d**	**Qb&c**
16	**1**	0.005	0.002	0.007	0.006	0.012	no data	no data
16	**2**	0.008	0.015	0.025	0.016	0.004	0.000	0.003
16	**3**	0.011	0.003	0.037	0.017	0.008	0.003	0.006
16	**4**	0.005	0.007	0.002	0.003	0.003	0.000	0.006
16	**5**	0.003	0.007	0.005	0.007	0.006	0.007	0.006
16	**6**	0.016	0.013	0.012	0.013	0.005	0.003	0.003
16	**7**	0.011	0.010	0.011	0.013	0.014	0.003	0.014
16	**8**	0.021	0.011	0.013	0.010	0.003	0.013	0.003
2b	**1**	0.007	0.000	0.004	0.000	0.007	0.006	0.008
2b	**2**	0.001	0.006	0.000	0.003	0.000	0.000	0.007
2b	**3**	0.001	0.002	0.000	0.005	0.003	0.000	0.000
2b	**4**	0.007	0.000	0.005	0.000	0.002	0.000	0.003
2b	**5**	0.001	0.002	0.004	0.000	0.000	0.000	0.000
2b	**6**	0.000	0.004	0.005	0.007	0.003	0.002	0.011
2b	**7**	0.002	0.002	0.000	0.003	0.000	0.000	0.000
2b	**8**	0.005	0.002	0.001	0.000	0.000	0.000	0.000

Larvae captures per second of foraging by captive birds:

		Manipulation	Test: 1st 20 min		Test: 10 min after 1 h		Test: 10 min after 4 h	
Field	**Site**	**Qa&d**	**Qa&d**	**Qb&c**	**Qa&d**	**Qb&c**	**Qa&d**	**Qb&c**
16	**1**	0.008	0.032	0.052	0.028	0.018	no data	no data
16	**2**	0.020	0.011	0.009	0.016	0.025	0.018	0.003
16	**3**	0.011	0.023	0.015	0.017	0.008	0.008	0.003
16	**4**	0.010	0.013	0.021	0.020	0.009	0.005	0.003
16	**5**	0.008	0.04	0.005	0.034	0.028	0.017	0.019
16	**6**	0.014	0.00	0.005	0.011	0.005	0.010	0.005
16	**7**	0.009	0.023	0.023	0.013	0.011	0.009	0.019
16	**8**	0.005	0.011	0.021	0.003	0.012	0.010	0.003
2b	**1**	0.035	0.042	0.036	0.039	0.053	0.012	0.013
2b	**2**	0.064	0.024	0.048	0.039	0.013	0.019	0.015
2b	**3**	0.077	0.051	0.025	0.053	0.020	0.024	0.034
2b	**4**	0.019	0.047	0.048	0.036	0.009	0.066	0.052
2b	**5**	0.048	0.036	0.056	0.083	0.071	0.018	0.007
2b	**6**	0.032	0.017	0.038	0.063	0.019	0.014	0.030
2b	**7**	0.048	0.091	0.100	0.114	0.072	0.034	0.030
2b	**8**	0.041	0.046	0.068	0.000	0.038	0.011	0.006

Appendix V :
Soil core and foraging data - Chapter 8

Appendix Va: Soil core data (Core dimensions were 80mm diameter and 150 mm deep. Field 16 = 'non-preferred' field and Field 2b = 'preferred' field).

Pre-chick-feeding cores - earthworms

			Exclosure sites		Non-exclosure sites			
					Experimentally foraged		Control	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
16	1	1	3	0.557	3	0.197	3	0.328
16	1	2	0	0.000	0	0.000	2	0.327
16	1	3	0	0.000	0	0.000	0	0.000
16	1	4	0	0.000	0	0.000	0	0.000
16	1	5	0	0.000	0	0.000	0	0.000
16	1	6	0	0.000	0	0.000	0	0.000
16	2	1	1	0.048	2	0.213	2	0.521
16	2	2	1	0.145	2	0.480	1	1.466
16	2	3	1	0.196	0	0.000	2	0.123
16	2	4	0	0.000	0	0.000	0	0.000
16	2	5	0	0.000	0	0.000	0	0.000
16	2	6	0	0.000	0	0.000	0	0.000
16	3	1	0	0.000	1	0.435	1	0.848
16	3	2	0	0.000	0	0.000	2	0.151
16	3	3	0	0.000	0	0.000	2	0.400
16	3	4	0	0.000	0	0.000	1	0.181
16	3	5	0	0.000	0	0.000	0	0.000
16	3	6	0	0.000	0	0.000	0	0.000
16	4	1	1	0.104	1	0.055	2	1.038
16	4	2	1	0.187	1	0.114	1	0.126
16	4	3	1	0.960	1	0.065	0	0.000
16	4	4	0	0.000	0	0.000	0	0.000
16	4	5	0	0.000	0	0.000	0	0.000
16	4	6	0	0.000	0	0.000	0	0.000

			Exclosure sites		Non-exclosure sites			
					Experimentally foraged		Control	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
16	5	1	0	0.000	0	0.000	0	0.000
16	5	2	0	0.000	0	0.000	0	0.000
16	5	3	0	0.000	0	0.000	0	0.000
16	5	4	0	0.000	0	0.000	0	0.000
16	5	5	0	0.000	0	0.000	0	0.000
16	5	6	0	0.000	0	0.000	0	0.000
16	6	1	0	0.000	0	0.000	0	0.000
16	6	2	0	0.000	0	0.000	0	0.000
16	6	3	0	0.000	0	0.000	0	0.000
16	6	4	0	0.000	0	0.000	0	0.000
16	6	5	0	0.000	0	0.000	0	0.000
16	6	6	0	0.000	0	0.000	0	0.000
2b	1	1	1	1.456	0	0.000	0	0.000
2b	1	2	0	0.000	0	0.000	0	0.000
2b	1	3	0	0.000	0	0.000	0	0.000
2b	1	4	0	0.000	0	0.000	0	0.000
2b	1	5	0	0.000	0	0.000	0	0.000
2b	1	6	0	0.000	0	0.000	0	0.000
2b	2	1	0	0.000	1	0.925	0	0.000
2b	2	2	0	0.000	0	0.000	0	0.000
2b	2	3	0	0.000	0	0.000	0	0.000
2b	2	4	0	0.000	0	0.000	0	0.000
2b	2	5	0	0.000	0	0.000	0	0.000
2b	2	6	0	0.000	0	0.000	0	0.000
2b	3	1	0	0.000	0	0.000	0	0.000
2b	3	2	0	0.000	0	0.000	0	0.000
2b	3	3	0	0.000	0	0.000	0	0.000
2b	3	4	0	0.000	0	0.000	0	0.000
2b	3	5	0	0.000	0	0.000	0	0.000
2b	3	6	0	0.000	0	0.000	0	0.000
2b	4	1	1	0.354	0	0.000	0	0.000
2b	4	2	1	0.098	0	0.000	0	0.000
2b	4	3	0	0.000	0	0.000	0	0.000
2b	4	4	0	0.000	0	0.000	0	0.000
2b	4	5	0	0.000	0	0.000	0	0.000
2b	4	6	0	0.000	0	0.000	0	0.000

			Exclosure sites		Non-exclosure sites			
					Experimentally foraged		Control	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
2b	5	1	1	0.070	1	0.040	1	0.047
2b	5	2	0	0.000	0	0.000	1	0.052
2b	5	3	0	0.000	0	0.000	0	0.000
2b	5	4	0	0.000	0	0.000	0	0.000
2b	5	5	0	0.000	0	0.000	0	0.000
2b	5	6	0	0.000	0	0.000	0	0.000
2b	6	1	1	0.435	2	0.138	0	0.000
2b	6	2	1	0.064	0	0.000	0	0.000
2b	6	3	1	3.697	0	0.000	0	0.000
2b	6	4	0	0.000	0	0.000	0	0.000
2b	6	5	0	0.000	0	0.000	0	0.000
2b	6	6	0	0.000	0	0.000	0	0.000

Pre-chick-feeding cores - larvae

			Exclosure sites		Non-exclosure sites			
					Experimentally foraged		Control	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
16	**1**	**1**	0	0.000	0	0.000	0	0.000
16	**1**	**2**	0	0.000	0	0.000	0	0.000
16	**1**	**3**	0	0.000	0	0.000	0	0.000
16	**1**	**4**	0	0.000	0	0.000	0	0.000
16	**1**	**5**	0	0.000	0	0.000	0	0.000
16	**1**	**6**	0	0.000	0	0.000	0	0.000
16	**2**	**1**	0	0.000	0	0.000	0	0.000
16	**2**	**2**	0	0.000	0	0.000	0	0.000
16	**2**	**3**	0	0.000	1	0.515	0	0.000
16	**2**	**4**	0	0.000	0	0.000	0	0.000
16	**2**	**5**	0	0.000	0	0.000	0	0.000
16	**2**	**6**	0	0.000	0	0.000	0	0.000
16	**3**	**1**	0	0.000	0	0.000	0	0.000
16	**3**	**2**	0	0.000	0	0.000	0	0.000
16	**3**	**3**	0	0.000	0	0.000	0	0.000
16	**3**	**4**	0	0.000	0	0.000	0	0.000
16	**3**	**5**	0	0.000	0	0.000	0	0.000
16	**3**	**6**	0	0.000	0	0.000	0	0.000

			Exclosure sites		Non-exclosure sites			
					Experimentally foraged		Control	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
16	**4**	**1**	0	0.000	0	0.000	1	0.080
16	**4**	**2**	0	0.000	0	0.000	0	0.000
16	**4**	**3**	0	0.000	0	0.000	0	0.000
16	**4**	**4**	0	0.000	0	0.000	0	0.000
16	**4**	**5**	0	0.000	0	0.000	0	0.000
16	**4**	**6**	0	0.000	0	0.000	0	0.000
16	**5**	**1**	0	0.000	0	0.000	2	0.796
16	**5**	**2**	0	0.000	0	0.000	0	0.000
16	**5**	**3**	0	0.000	0	0.000	0	0.000
16	**5**	**4**	0	0.000	0	0.000	0	0.000
16	**5**	**5**	0	0.000	0	0.000	0	0.000
16	**5**	**6**	0	0.000	0	0.000	0	0.000
16	**6**	**1**	0	0.000	0	0.000	0	0.000
16	**6**	**2**	0	0.000	0	0.000	0	0.000
16	**6**	**3**	0	0.000	0	0.000	0	0.000
16	**6**	**4**	0	0.000	0	0.000	0	0.000
16	**6**	**5**	0	0.000	0	0.000	0	0.000
16	**6**	**6**	0	0.000	0	0.000	0	0.000
2b	**1**	**1**	2	0.266	0	0.000	3	0.407
2b	**1**	**2**	2	0.000	0	0.000	2	0.671
2b	**1**	**3**	0	0.489	0	0.000	0	0.000
2b	**1**	**4**	0	0.000	0	0.000	0	0.000
2b	**1**	**5**	0	0.000	0	0.000	0	0.000
2b	**1**	**6**	0	0.000	0	0.000	0	0.000
2b	**2**	**1**	1	0.409	2	0.883	1	0.409
2b	**2**	**2**	0	0.000	0	0.000	0	0.000
2b	**2**	**3**	0	0.000	0	0.000	0	0.000
2b	**2**	**4**	0	0.000	0	0.000	0	0.000
2b	**2**	**5**	0	0.000	0	0.000	0	0.000
2b	**2**	**6**	0	0.000	0	0.000	0	0.000
2b	**3**	**1**	0	0.000	0	0.000	1	0.398
2b	**3**	**2**	0	0.000	0	0.000	0	0.000
2b	**3**	**3**	0	0.000	0	0.000	0	0.000
2b	**3**	**4**	0	0.000	0	0.000	0	0.000
2b	**3**	**5**	0	0.000	0	0.000	0	0.000
2b	**3**	**6**	0	0.000	0	0.000	0	0.000

			Exclosure sites		Non-exclosure sites			
					Experimentally foraged		Control	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
2b	4	1	0	0.000	0	0.000	0	0.000
2b	4	2	0	0.000	0	0.000	0	0.000
2b	4	3	1	0.307	0	0.000	0	0.000
2b	4	4	0	0.000	0	0.000	0	0.000
2b	4	5	0	0.000	0	0.000	0	0.000
2b	4	6	0	0.000	0	0.000	0	0.000
2b	5	1	0	0.000	0	0.000	0	0.000
2b	5	2	0	0.000	4	0.182	1	0.338
2b	5	3	0	0.000	3	0.171	0	0.000
2b	5	4	0	0.000	0	0.000	0	0.000
2b	5	5	0	0.000	0	0.000	0	0.000
2b	5	6	0	0.000	0	0.000	0	0.000
2b	6	1	0	0.000	0	0.000	0	0.000
2b	6	2	0	0.000	0	0.000	0	0.000
2b	6	3	3	0.407	0	0.000	0	0.000
2b	6	4	0	0.000	0	0.000	0	0.000
2b	6	5	0	0.000	0	0.000	0	0.000
2b	6	6	0	0.000	0	0.000	0	0.000

Post-chick-feeding cores - earthworms

			Exclosure sites				Non-exclosure sites			
			Experimentally foraged		Control		Experimentally foraged		Control	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
16	1	1	4	0.504	3	0.405	1	0.037	0	0.000
16	1	2	1	0.035	1	0.038	1	0.065	0	0.000
16	1	3	2	0.066	1	0.036	0	0.000	0	0.000
16	1	4	0	0.000	2	0.282	0	0.000	0	0.000
16	1	5	0	0.000	2	0.058	0	0.000	0	0.000
16	1	6	0	0.000	0	0.000	0	0.000	0	0.000
16	2	1	2	0.328	2	0.363	2	0.246	1	0.272
16	2	2	4	0.254	1	0.153	0	0.000	1	0.135
16	2	3	1	0.099	3	0.160	0	0.000	2	0.245
16	2	4	1	0.070	1	0.032	0	0.000	1	0.034
16	2	5	2	0.075	2	0.276	0	0.000	0	0.000
16	2	6	0	0.000	0	0.000	0	0.000	0	0.000

			Exclosure sites				Non-exclosure sites			
			Experimentally foraged		Control		Experimentally foraged		Control	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
16	3	1	1	0.014	5	0.335	1	0.299	1	0.158
16	3	2	2	0.154	2	0.050	3	0.577	2	0.167
16	3	3	1	0.070	0	0.000	1	0.036	0	0.000
16	3	4	0	0.000	0	0.000	0	0.000	0	0.000
16	3	5	0	0.000	0	0.000	0	0.000	0	0.000
16	3	6	0	0.000	0	0.000	0	0.000	0	0.000
16	4	1	2	0.507	3	0.306	1	0.028	2	0.242
16	4	2	1	0.228	5	0.287	1	0.082	2	0.191
16	4	3	3	0.448	2	0.209	4	0.289	0	0.000
16	4	4	1	0.053	4	0.226	0	0.000	0	0.000
16	4	5	1	0.016	1	0.019	0	0.000	0	0.000
16	4	6	0	0.000	2	0.071	0	0.000	0	0.000
16	5	1	3	0.721	1	0.076	1	0.068	1	0.070
16	5	2	2	0.233	1	0.097	1	0.096	0	0.000
16	5	3	0	0.000	1	0.222	0	0.000	0	0.000
16	5	4	0	0.000	0	0.000	0	0.000	0	0.000
16	5	5	0	0.000	0	0.000	0	0.000	0	0.000
16	5	6	0	0.000	0	0.000	0	0.000	0	0.000
16	6	1	3	0.238	1	0.083	3	0.224	1	0.080
16	6	2	1	0.059	2	0.329	0	0.000	0	0.000
16	6	3	4	0.214	0	0.000	0	0.000	0	0.000
16	6	4	0	0.000	0	0.000	0	0.000	0	0.000
16	6	5	0	0.000	0	0.000	0	0.000	0	0.000
16	6	6	0	0.000	0	0.000	0	0.000	0	0.000
2b	1	1	2	0.085	2	0.133	1	0.085	0	0.000
2b	1	2	0	0.000	4	0.540	2	0.272	0	0.000
2b	1	3	0	0.000	3	0.158	0	0.000	0	0.000
2b	1	4	0	0.000	1	0.056	0	0.000	0	0.000
2b	1	5	0	0.000	1	0.021	0	0.000	0	0.000
2b	1	6	0	0.000	0	0.000	0	0.000	0	0.000
2b	2	1	1	0.062	0	0.000	1	0.047	0	0.000
2b	2	2	0	0.000	0	0.000	0	0.000	0	0.000
2b	2	3	0	0.000	0	0.000	0	0.000	0	0.000
2b	2	4	0	0.000	0	0.000	0	0.000	0	0.000
2b	2	5	0	0.000	0	0.000	0	0.000	0	0.000
2b	2	6	0	0.000	0	0.000	0	0.000	0	0.000

			Exclosure sites				Non-exclosure sites			
			Experimentally foraged		Control		Experimentally foraged		Control	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
2b	3	**1**	1	0.068	2	0.130	1	0.069	1	0.091
2b	3	**2**	4	0.251	1	0.057	0	0.000	1	0.097
2b	3	**3**	0	0.000	0	0.000	0	0.000	1	0.028
2b	3	**4**	0	0.000	0	0.000	0	0.000	0	0.000
2b	3	**5**	0	0.000	0	0.000	0	0.000	0	0.000
2b	3	**6**	0	0.000	0	0.000	0	0.000	0	0.000
2b	4	**1**	2	0.056	0	0.000	1	0.080	1	0.196
2b	4	**2**	0	0.000	0	0.000	1	0.043	1	0.029
2b	4	**3**	0	0.000	0	0.000	2	0.065	0	0.000
2b	4	**4**	0	0.000	0	0.000	0	0.000	0	0.000
2b	4	**5**	0	0.000	0	0.000	0	0.000	0	0.000
2b	4	**6**	0	0.000	0	0.000	0	0.000	0	0.000
2b	5	**1**	1	0.046	1	0.068	1	0.040	2	0.141
2b	5	**2**	0	0.000	1	0.031	0	0.000	1	0.010
2b	5	**3**	0	0.000	1	0.024	0	0.000	0	0.000
2b	5	**4**	0	0.000	0	0.000	0	0.000	0	0.000
2b	5	**5**	0	0.000	0	0.000	0	0.000	0	0.000
2b	5	**6**	0	0.000	0	0.000	0	0.000	0	0.000
2b	6	**1**	2	0.280	3	0.389	0	0.000	0	0.000
2b	6	**2**	1	0.048	0	0.000	0	0.000	0	0.000
2b	6	**3**	2	0.149	0	0.000	0	0.000	0	0.000
2b	6	**4**	0	0.000	0	0.000	0	0.000	0	0.000
2b	6	**5**	0	0.000	0	0.000	0	0.000	0	0.000
2b	6	**6**	0	0.000	0	0.000	0	0.000	0	0.000

Post-chick-feeding cores - larvae

			Exclosure sites				Non-exclosure sites			
			Experimentally foraged		Control		Experimentally foraged		Control	
Field	Site	Core	Numbers	Wet weight (g)	Numbers	Wet weight (g)	Numbers	Wet weight (g)	Numbers	Wet weight (g)
16	1	1	0	0.000	0	0.000	0	0.000	0	0.000
16	1	2	0	0.000	0	0.000	0	0.000	0	0.000
16	1	3	0	0.000	0	0.000	0	0.000	0	0.000
16	1	4	0	0.000	0	0.000	0	0.000	0	0.000
16	1	5	0	0.000	0	0.000	0	0.000	0	0.000
16	1	6	0	0.000	0	0.000	0	0.000	0	0.000
16	2	1	0	0.000	1	0.394	0	0.000	0	0.000
16	2	2	0	0.000	0	0.000	0	0.000	0	0.000
16	2	3	0	0.000	0	0.000	0	0.000	0	0.000
16	2	4	0	0.000	0	0.000	0	0.000	0	0.000
16	2	5	0	0.000	0	0.000	0	0.000	0	0.000
16	2	6	0	0.000	0	0.000	0	0.000	0	0.000
16	3	1	0	0.000	0	0.000	0	0.000	0	0.000
16	3	2	0	0.000	0	0.000	0	0.000	0	0.000
16	3	3	0	0.000	0	0.000	0	0.000	0	0.000
16	3	4	0	0.000	0	0.000	0	0.000	0	0.000
16	3	5	0	0.000	0	0.000	0	0.000	0	0.000
16	3	6	0	0.000	0	0.000	0	0.000	0	0.000
16	4	1	0	0.000	0	0.000	0	0.000	0	0.000
16	4	2	0	0.000	0	0.000	0	0.000	0	0.000
16	4	3	0	0.000	1	0.385	0	0.000	0	0.000
16	4	4	0	0.000	0	0.000	0	0.000	0	0.000
16	4	5	0	0.000	0	0.000	0	0.000	0	0.000
16	4	6	0	0.000	0	0.000	0	0.000	0	0.000
16	5	1	0	0.000	0	0.000	0	0.000	0	0.000
16	5	2	0	0.000	0	0.000	0	0.000	0	0.000
16	5	3	0	0.000	0	0.000	0	0.000	0	0.000
16	5	4	0	0.000	0	0.000	0	0.000	0	0.000
16	5	5	0	0.000	0	0.000	0	0.000	0	0.000
16	5	6	0	0.000	0	0.000	0	0.000	0	0.000

			Exclosure sites				Non-exclosure sites			
			Experimentally foraged		Control		Experimentally foraged		Control	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
16	6	1	0	0.000	0	0.000	0	0.000	0	0.000
16	6	2	0	0.000	0	0.000	0	0.000	0	0.000
16	6	3	0	0.000	0	0.000	0	0.000	0	0.000
16	6	4	0	0.000	0	0.000	0	0.000	0	0.000
16	6	5	0	0.000	0	0.000	0	0.000	0	0.000
16	6	6	0	0.000	0	0.000	0	0.000	0	0.000
2b	1	1	2	0.278	0	0.000	0	0.000	0	0.000
2b	1	2	1	0.232	0	0.000	1	0.414	0	0.000
2b	1	3	0	0.000	0	0.000	1	0.254	0	0.000
2b	1	4	0	0.000	0	0.000	0	0.000	0	0.000
2b	1	5	0	0.000	0	0.000	0	0.000	0	0.000
2b	1	6	0	0.000	0	0.000	0	0.000	0	0.000
2b	2	1	1	0.080	1	0.160	2	0.712	1	0.149
2b	2	2	0	0.000	2	0.130	0	0.000	0	0.000
2b	2	3	0	0.000	1	0.026	0	0.000	0	0.000
2b	2	4	0	0.000	0	0.000	0	0.000	0	0.000
2b	2	5	0	0.000	0	0.000	0	0.000	0	0.000
2b	2	6	0	0.000	0	0.000	0	0.000	0	0.000
2b	3	1	2	0.108	1	0.030	0	0.000	0	0.000
2b	3	2	0	0.000	0	0.000	0	0.000	0	0.000
2b	3	3	0	0.000	0	0.000	0	0.000	0	0.000
2b	3	4	0	0.000	0	0.000	0	0.000	0	0.000
2b	3	5	0	0.000	0	0.000	0	0.000	0	0.000
2b	3	6	0	0.000	0	0.000	0	0.000	0	0.000
2b	4	1	0	0.000	0	0.000	0	0.000	0	0.000
2b	4	2	1	0.679	0	0.000	0	0.000	0	0.000
2b	4	3	0	0.000	0	0.000	0	0.000	0	0.000
2b	4	4	0	0.000	0	0.000	0	0.000	0	0.000
2b	4	5	0	0.000	0	0.000	0	0.000	0	0.000
2b	4	6	0	0.000	0	0.000	0	0.000	0	0.000
2b	5	1	0	0.000	1	0.128	4	0.182	0	0.000
2b	5	2	2	0.937	0	0.000	3	0.171	0	0.000
2b	5	3	0	0.000	0	0.000	0	0.000	0	0.000
2b	5	4	0	0.000	0	0.000	0	0.000	0	0.000
2b	5	5	0	0.000	0	0.000	0	0.000	0	0.000
2b	5	6	0	0.000	0	0.000	0	0.000	0	0.000

			Exclosure sites				Non-exclosure sites			
			Experimentally foraged		Control		Experimentally foraged		Control	
Field	**Site**	**Core**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**	**Numbers**	**Wet weight (g)**
2b	**6**	**1**	0	0.000	0	0.000	0	0.000	2	0.259
2b	**6**	**2**	0	0.000	0	0.000	0	0.000	1	0.171
2b	**6**	**3**	1	0.314	0	0.000	0	0.000	0	0.000
2b	**6**	**4**	0	0.000	0	0.000	0	0.000	0	0.000
2b	**6**	**5**	0	0.000	0	0.000	0	0.000	0	0.000
2b	**6**	**6**	0	0.000	0	0.000	0	0.000	0	0.000

Appendix Vb: Foraging data from enclosures

Pre-chick-feeding prey captures per second of foraging by captive birds (non-exclosure sites)

		Test 1: 1st 10 min		Test 2: 10 min after 2h		Test 3: 10 min after 24 h		Control (10 mins after T2)	
Field	**Site**	**Ew**	**Larvae**	**Ew**	**Larvae**	**Ew**	**Larvae**	**Ew**	**Larvae**
16	**1**	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.004
16	**2**	0.000	0.008	0.000	0.000	0.000	0.002	0.000	0.010
16	**3**	0.002	0.062	0.000	0.000	0.002	0.002	0.000	0.010
16	**4**	0.001	0.020	0.000	0.002	0.000	0.009	0.003	0.020
16	**5**	0.000	0.015	0.002	0.000	0.000	0.002	0.000	0.006
16	**6**	0.000	0.007	0.002	0.000	0.000	0.001	0.002	0.042
2b	**1**	0.000	0.014	0.000	0.006	0.000	0.009	0.000	0.017
2b	**2**	0.002	0.018	0.000	0.009	0.000	0.007	0.000	0.017
2b	**3**	0.000	0.013	0.000	0.000	0.004	0.004	0.000	0.009
2b	**4**	0.000	0.020	0.000	0.007	0.000	0.008	0.000	0.020
2b	**5**	0.000	0.019	0.000	0.006	0.000	0.004	0.002	0.014
2b	**6**	0.000	0.015	0.002	0.002	0.000	0.007	0.000	0.015

Post-chick-feeding prey captures per second of foraging by captive birds (earthworm capture rates shown only for first 10 minutes of foraging session. Thereafter captures of earthworms found to be negligible)

		Exclosure sites				Non-exclosure sites			
		Test 1:First 10 min		Test 2: 10 min after 1 h	Control (10 min after T2)	Test 1:First 10 min		Test 2: 10 min after 1 h	Control (10 min after T2)
Field	**Site**	**Ew**	**Larvae**	**Larvae**	**Larvae**	**Ew**	**Larvae**	**Larvae**	**Larvae**
16	**1**	0.000	0.017	0.000	0.022	0.007	0.100	0.000	0.017
16	**2**	0.000	0.014	0.003	0.008	0.002	0.009	0.000	0.002
16	**3**	0.002	0.009	0.000	0.018	0.001	0.005	0.000	0.004
16	**4**	0.000	0.009	0.000	0.021	0.000	0.009	0.000	0.009
16	**5**	0.000	0.009	0.008	0.013	0.001	0.012	0.000	0.014
16	**6**	0.000	0.011	0.000	0.015	0.000	0.000	0.000	0.010
2b	**1**	0.000	0.006	0.002	0.002	0.003	0.005	0.000	0.005
2b	**2**	0.000	0.006	0.000	0.011	0.000	0.001	0.002	0.008
2b	**3**	0.000	0.003	0.002	0.007	0.000	0.001	0.001	0.008
2b	**4**	0.000	0.017	0.000	0.014	0.000	0.002	0000	0.008
2b	**5**	0.000	0.009	0.004	0.014	0.000	0.009	0.004	0.009
2b	**6**	0.000	0.017	0.000	0.014	0.000	0.002	0.000	0.008

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