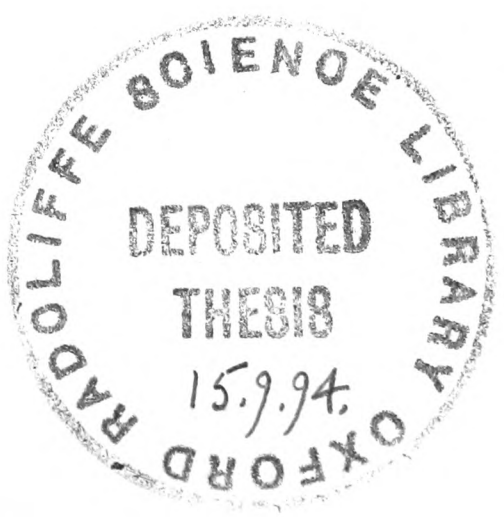
The factors affecting reproductive success and breeding density in a rural population of blackbirds, *Turdus merula* L.

Dan Chamberlain

Wolfson College

A thesis submitted for the degree of Doctor of Philosophy, Hilary Term, 1994.



Abstract

The aim of this thesis was to identify the factors determining reproductive success and breeding density in a rural population of blackbirds occupying contiguous woodland and farmland habitats. Once these factors were identified, an attempt was made to assess the quality of the two habitats in terms of reproductive success.

Predation was the major factor affecting reproductive success. There were no significant effects of habitat on predation when habitat was defined as farmland, woodland and woodland edge. When defined in terms of nesting density, high density 'hot-spot' areas had significantly greater nesting cover and lower predation rates than territories in farmland or in the rest of the wood.

Parents could adjust their provisioning rates according to chick demand. Consequently chicks in larger broods were not significantly different in weight to chicks in smaller broods. The seasonal change in clutch size is therefore well adapted to conditions for raising nestlings, although there was indirect evidence that female condition may limit clutch size early in the season. The nestlings were fed two main diet types, earthworms and caterpillars, the availability of the former being related to rainfall and temperature and the latter occurring in a seasonal peak. Nestlings fed on predominantly earthworm diets were significantly heavier, thus caterpillars are probably a lower quality prey. Starvation was a minor cause of nestling mortality. There was some evidence that farmland birds were more dependent on earthworms than woodland birds, and consequently only farmland broods showed a significant relationship between weight and rainfall. This conferred no disadvantage to farmland broods, although this may have implications for reproductive success in very dry years.

Farmland breeders showed some characteristics of a population in a sub-optimal habitat. Breeding density was low on farmland compared with woodland. This in part may have been due to lack of suitable nesting cover. An experiment with artificial nests indicated that predation would be proportionately higher on farmland if nesting density was increased. Year-to-year variations in density across the whole study site paralleled the relative harshness of the preceding winter. Food supplementation prior to the breeding season had no effect on subsequent breeding density or clutch size.

It is concluded that farmland is potentially a sub-optimal habitat if subject to different conditions of weather or breeding density than those observed during the three years of this study.

Acknowledgements

I would first like to thank Ben Hatchwell for supervision above and beyond the call of duty, and for showing me what dedication to field work really means. I would also like to thank Chris Perrins for allowing me to tap into his vast ornithological knowledge, particularly in the later stages of the project. A special thanks should also go to Thais Martins for being such a conscientious field assistant (and for doing what I told her).

Moral support, advice and general abuse was provided by my C22 colleagues, José Arévalo, Bea Arroyo, Marc Cellier, Jon King, Dave Max, John Muddeman, Jim Ramos and Rick Woodburn. Beers and respect were provided by Glen Spraggon, Rich Ladle and Gareth Morgan. Finally I am most grateful to Vian Bakir for emotional support during my years in Oxford.

Contents

Chapter 1

Introduction and General Methods

General Introduction: The components affecting avian reproductive success

There are four fundamental components that determine lifetime reproductive success in individuals: longevity, mating success, fecundity and offspring survival (Clutton-Brock, 1988). Of these, longevity is perhaps the hardest to determine when dealing with animals in which dispersal and mortality are difficult to distinguish, as in many bird species (Newton, 1989). Truly accurate determinations of lifetime reproductive success may only be possible in long term studies when an individual's reproductive success can be monitored throughout its life.

Mating success is also a hard component to measure. Observation can only predict the real mating success of individuals by comparing the relative number or duration of copulations (Smith, 1984). Recent advances in molecular techniques have enabled a precise measure of mating success (e.g. Burke et al., 1989), showing that the common assumption, that a putative parent is also the biological parent, does not always hold true (Birkhead and Møller, 1992).

Both fecundity (e.g. clutch size, number of young hatched) and the subsequent survival of the offspring are the more commonly studied components of reproductive success in birds (Clutton-Brock, 1988; Newton, 1989). Whilst fecundity and offspring survival are in general readily determinable, in terms of either clutch size, number of young hatched, number of breeding attempts and number of young fledged, a problem often exists in obtaining accurate information on survival of offspring after fledging due to difficulties in observation or relocation of the young. This problem may be amplified given that some studies have suggested that the post-fledging period of parental care is the most critical for offspring survival (Smith, 1978; Sullivan, 1989). However, the weight of older nestlings has been shown to be closely correlated with the probability of survival to the next breeding season in some species, including the blackbird (Magrath, 1991) which largely overcomes this problem.

In this study, estimates of reproductive success were made in a rural population of blackbirds *Turdus merula*, taking measurements associated with fecundity (clutch size, number of breeding attempts per season and brood size) and offspring survival (nest predation rates, number of young fledged and nestling weight) in order to ascertain the main factors affecting reproductive success. As much of the study involved correlational and comparative evidence of groups of territories, particularly in relation to habitat, rather than a comparison of life histories of individuals, it was assumed that the longevity of individuals would have no effect on reproductive success. It was also assumed that blackbirds were typical of most solitary monogamous breeders in that in the majority of cases the putative parents were the biological parents (Birkhead and Møller, 1992).

In this chapter, I briefly review the factors affecting fecundity and offspring survival, both in terms of ultimate (i.e. evolutionary) and proximate (i.e. affecting physiological condition) factors, paying particular attention to food supply and habitat. Whilst many life-history studies have been performed on insects, and to a lesser extent, mammals (Clutton-Brock, 1988), the examples used in this study will be largely restricted to studies on birds. The aims of the project and general methods used in the majority of chapters of this thesis are also presented.

1 Clutch size

The central tenet of studies of reproductive rates in birds over the last forty years has been Lack's hypothesis (Lack, 1947). This predicts that a female will lay that clutch from which the maximum number of young can be raised and recruited into the breeding population. Therefore each individual should adjust its own clutch size to that which is most productive, and any (artificial) manipulation of the clutch size should result in a decrease in potential fitness.

Whilst Lack's hypothesis has received general support (e.g. Klomp, 1970; Lessels, 1992; Stearns, 1992), a major discrepancy in many studies (Stearns, 1992, reports 40/53 studies) has been that brood enlargements have resulted in more offspring

surviving to fledge than would have been raised from the natural clutch size. Thus birds are apparently laying a 'conservative' clutch in many cases. A number of theories have been put forward to explain this discrepancy (Lessels, 1992; Stearns, 1992), but most of the work has concentrated on trade-offs between clutch size and chick quality or parental survival.

An implicit assumption of Lack's hypothesis is that as brood size increases, parents will not be able to increase parental effort accordingly, thus individual nestling quality is reduced and brood reduction occurs. Although some studies have found no evidence for an upper limit to provisioning effort of parents (Nur, 1984; 1987), the majority of studies have found that individual chick weight was lower in experimentally enlarged broods (27/40 studies; Stearns, 1992), and in no cases has it been higher. As chick weight is generally a good measure of the probability of survival to breed (Perrins, 1965; Magrath, 1991), then Lack's hypothesis cannot necessarily be rejected if studies take into account only the number of young fledged.

If a trade-off exists between parental effort and subsequent survival or fecundity, then this may have to be taken into account as an additional or alternative cost to raising an enlarged brood, and may therefore explain the lower than expected clutch size of many species. A number of studies have reported increased weight loss of parents with an increase in brood size (Nur, 1984; 1988; Smith et al., 1988) or subsequent lowered survival or fecundity of further breeding attempts (Askenmo, 1979; Slagsvold, 1984; Roskaft, 1985; Gustaffson and Sutherland, 1988). However, effects on parental survival are probably rare relative to the effects on offspring survival (Stearns, 1992).

A further explanation for the discrepancy between the commonest and most productive clutch size is that the effects of nest predation keep the clutch size lower than the size that would produce the most young. This effect would occur if the probability of nest predation increased with increasing brood size (Slagsvold, 1982), either due to increased activity at the nest making it more detectable, or more noise from hungrier nestlings. This effect is particularly striking in many tropical passerines which lay

unusually small clutches and are subject to high predation rates (Skutch, 1949; Snow, 1962).

(i) Variation in clutch size

Clutch size often varies from year to year in a population. This may be due to food availability (Perrins, 1979; Järvinen, 1982) or ambient temperature prior to the breeding season (Järvinen and Väisänen, 1984), or to population density (Perrins, 1979; Arcese and Smith, 1988). These variations are linked to the condition of the female prior to laying , but they may also be seen as an adaptation to future food availability. The timing of laying is also an important factor, as most bird species lay larger clutches earlier in the season (see below).

Different populations of birds also differ. This may be an effect of habitat, clutch size typically being higher in habitats with greater food supplies (e.g. Newton, 1976; see below). Latitude also affects clutch size, with clutch size increasing at higher latitudes (Lack, 1947). This may be an indirect adaptation to food supply, the longer hours of daylight in more northerly regions enabling birds to provision nestlings for longer and thus raise more offspring (Lack, 1947). There are, however, a number of exceptions to this pattern in clutch size which have led to alternative explanations. Royama (1969) suggested that at lower (warmer) latitudes, large broods may expend more energy due to hyperthermia than an equivalently sized brood experiencing lower temperatures. Ricklefs (1969) suggested that predation pressure increased at lower latitudes, thus it would pay to have smaller clutches as they could be raised more quickly and are less likely to attract predators. None of these hypotheses are mutually exclusive and all may have had some influence on geographical variation in clutch size.

Variation also typically occurs between individuals within any given year. This may be related to individual quality, with the birds who are better at raising a brood (e.g. due to more efficient foraging) laying a larger clutch. Defining what constitutes 'quality' in adult birds is difficult, but in many species individuals making their first breeding attempt tend to lay a smaller clutch (Lack, 1954). These birds tend to be

subordinate to older birds, and typically will be less efficient foragers (Marchetti and Price, 1989).

2 The timing of breeding seasons

Lack (1954) suggested that birds time their breeding seasons so that the period of maximum nestling demand coincides with the period of greatest food abundance. For example, the timing of laying in the great tit *Parus major* is very closely related to the peak in caterpillar abundance in the environment (Gibb, 1950). The great tit, in common with many other passerines, shows a seasonal decline in clutch size which is considered to be an adaptive response to a decrease in reproductive success as the season progresses. However, certain other species (including the blackbird) show a peaked seasonal pattern in clutch size. Species such as these are typically resident and multi-brooded, so may start breeding as early as possible, and they tend to be generalist feeders thus timing is not linked to the abundance of a particular prey type (Crick et al., 1993).

Most supplemental feeding experiments prior to laying do not have any effect on clutch size (Boutin, 1990). Instead the effect tends to be to advance laying date (Desrochers, 1992; Nilsson and Svensson, 1993), which implies that timing of the first breeding attempt may be related to female condition. The common observation that breeding starts earlier in milder springs (e.g. Snow, 1958; Perrins, 1965) supports this idea.

3 Reproductive success

(i) Food supply

It is widely accepted that animal populations are ultimately limited by food supply (Martin, 1987). Outside the breeding season, milder winters, lower population and an increased food supply tends to result in increased survival rates and subsequent breeding densities (Ekman et al., 1981; Janssen et al., 1981; Kallander, 1981). Within the breeding season, food is usually of crucial importance to reproductive success, as is

demonstrated by the close link between food supply and the timing of laying (see Section 2). Whilst there are a few species which are probably not limited by the abundance of prey species within a breeding season (Perrins, 1979; Rosenberg et al., 1982), many experiments providing supplemental food during the breeding season have increased fledging success and chick quality (Crossner, 1977; Högstedt, 1981; Reyer and Westerterp, 1985; Arcese and Smith, 1988). A factor to be taken into consideration in these studies is that prey abundance is not necessarily the same as prey availability, and the efficiency at which an animal can forage will also be important. Supplemental feeding experiments tend to involve readily available food at fixed locations, so little or no searching effort by the parents will be involved.

(ii) Predation

Predation is the most important proximate component of reproductive success in most, if not all, open nesting passerines (Lack, 1954). Many factors may affect the degree of predation. Tinbergen et al., (1967) showed that predators exhibit 'area-restricted searching' after successfully locating a prey item. Tinbergen argued that cryptic prey items (such as birds' nests) should be over dispersed in such a way as to exceed the distance from which predators detect them directly. Some studies have shown that predation rate increases with increasing nesting density (e.g. Krebs, 1971; Dunn, 1977) thus apparently supporting the ideas of Tinbergen.

Andersson and Wiklund (1978), in experiments with fieldfares *Turdus pilaris*, showed that predation was greater in clumped than in solitary replica nests, as expected by Tinbergen's work. However, measurements on real colonies showed that predation was in fact lower in colonial nests. This was due to communal anti-predator attacks. This demonstrates that there can be advantages to nesting colonially. These may arise not only through communal defence, but also by a 'dilution effect' (Hamilton, 1971) in large colonies.

The quality of nesting cover on a territory may also affect predation rates (Holm, 1973; Osborne and Osborne, 1980). For example, Edwards (1983) found that

the degree of cover on a blackbird territory was negatively related to the predation rate . This may have important implications for habitat quality (see Section 4).

4 Habitat as a factor in reproductive success

Habitat quality is here defined in relation to the relative reproductive success of individuals across habitat types. Separation of habitat quality and territory quality is not a clear-cut issue. On a micro-scale, all territories are likely to differ in some characteristics, and if taken to an extreme definition, could be classified as different habitats. In this thesis, habitat is defined on a macro-scale, where there are clear-cut differences in habitat structure (e.g. woodland and farmland).

Habitat quality is often related to food abundance (e.g. Greenlaw, 1978; Lundberg et al., 1981; Hussell and Quinney, 1986). Newton (1976), found that sparrowhawks *Accipiter nisus* which nested in habitats with greater prey abundance laid larger clutches and raised more young. Long-term survival of nestlings was also greater in these habitats as a significantly greater proportion survived to breed.

The effects of the quality of available nest sites within a habitat have been well studied (e.g. Holm, 1973; Pleszczynska, 1978; Edwards, 1983), although little has been done on between-habitat differences. Birds nesting in farmland tend to suffer lower predation rates than birds nesting in woodland habitats, which is probably due to a greater predator density in woodland (Snow and Mayer-Gross, 1967). However, in some species whose natural (i.e. pre-*Homo sapiens*) habitat is woodland, the farmland population shows characteristics of being in a sub-optimal habitat in terms of breeding age structure, survival and population stability (Krebs, 1971; Williamson, 1971; Murton and Westwood, 1974; O'Connor and Fuller, 1986), thus factors other than predation may need to be taken into account.

Often, less productive habitats have subordinate, typically younger, birds than better quality habitats (e.g. Krebs, 1971; Møller, 1982). This can be seen in certain species in the British farmland bird community, where younger breeders and non-

breeding 'floaters' are more common than in the woodland habitat (e.g. Krebs, 1971; Williamson, 1971; Murton and Westwood, 1974; O'Connor, 1986).

Younger, subordinate birds may be forced into sub-optimal habitats by more vigorous competitors who will then monopolise a greater share of resources (an Ideal Despotic Distribution; Fretwell, 1972). In this case differential success would be expected in habitats of differing resource quality. Alternatively, when competitive abilities of individuals do not differ, a similar distribution could occur without competitive exclusion, if habitat quality (related to resource availability in this case) decreases with an increasing number of competitors (e.g. Brown, 1969). The first habitat could then be occupied up to a certain threshold density, when it would become just as profitable to occupy the next best habitat (Ideal Free Distribution; Fretwell and Lucas, 1969; Fretwell, 1972). Therefore success should be equal across habitat types, but density will be lower in habitats of lower quality.

A further characteristic of populations in sub-optimal habitats is that they are less stable over time, as a consequence of greater mortality and younger birds moving into better habitats in later years (e.g. Krebs, 1971). Returning again to the farmland habitat as an example, woodland passerines tend to show smaller year-to-year fluctuations in population size compared with conspecifics in farmland (O'Connor and Fuller, 1985).

Exactly why populations breeding on farmland show sub-optimal characteristics is not known; from what is known of relative predation rates across habitat types, predation seems an unlikely factor, although no thorough studies have been done to date. Differing food supply across habitats, either affecting reproductive success, or possibly even winter survival, seems to be a likely factor, but again no detailed information on differences in food availability between woodland and farmland habitats is available in the scientific literature.

Farmland is the predominant habitat type in lowland Britain, and it supports many bird species whose origins were the deciduous forests which once covered most of Britain. Whilst there has been some work dealing with populations of birds on

farmland (O'Connor and Shrubb, 1986), and on the effects of management practices on the farmland bird community (Lack, 1992), there have been no detailed studies on factors affecting distribution or reproductive success of woodland birds nesting on farmland. The interactions between contiguous woodland and farmland habitats are also largely unknown, with the exception of the work of Krebs (1971), but this work concentrates more on population structure and movements than on specific factors affecting reproductive success.

Aims

The aim of this thesis is to determine the factors affecting reproductive success and breeding density in a rural population of blackbirds, particularly in terms of predation and feeding ecology, and to use this information to ascertain the quality of the farmland habitat compared with the bird's natural habitat, woodland. The blackbird is used as the study animal as it is perhaps the commonest bird occurring in both woodland and farmland habitats (O'Connor and Shrubb, 1986); whilst its breeding ecology is well studied in urban populations (e.g. Snow, 1958; Edwards, 1983; Magrath, 1989), no detailed studies have been carried out in woodland and no studies at all on farmland populations.

In the first part of this thesis the question of habitat effects are ignored, and a general account of reproductive success (Chapter 2), parental provisioning (Chapter 3) and prey availability and its effect on chick quality (Chapter 4) is presented. The aims of these early chapter are two fold: firstly, an attempt is made to identify the major factors affecting reproductive success, and consequently the factors affecting the evolution of clutch size and the timing of breeding in blackbirds; the findings are then used as a framework to analyse differences between habitat types, in terms of reproductive success, diet, breeding density and the age structure and between-year movements of the adult population (Chapter 5).

Chapters 6 and 7 are experimental chapters which aim to test hypotheses suggested by the results of the previous chapters. In Chapter 6, an experiment on nest

predation using artificial nests is described in order to determine differing effects of nest density on the degree of predation in different habitat types. Chapter 7 begins with a comparison between urban and rural populations of blackbirds. An experiment is then presented which aims to test the effects of increased pre-breeding season food supply on clutch size and breeding density. Finally, conclusions are presented in Chapter 8.

General Methods

The methods used in Chapters 2, 3, 4 and 5 of this study are essentially the same, only the analyses differ. Therefore the methods common to these chapters are presented as one section. Methods specific to a particular chapter are presented where necessary.

1 The Study Site

The study took place in the Spring and Summer of 1991, 1992 and 1993 on the Wytham Estate, Oxford. The study area covered approximately 340 hectares of contiguous woodland and farmland habitat. The woodland (95 ha.) was predominantly oak *Quercus robur* and sycamore *Acer pseudoplatanus* with a generally sparse understorey, though there were a few localised patches of dense scrub (see Gosler, 1990 for a full habitat description).

The farmland (245 ha.) consisted of a variety of arable crops (34% of area used for cereals and 13% for oilseed rape), grazed pasture and grass leys (41%), and set-aside areas (12%). Fields were typically bordered by low hawthorn *Crataegus monogyna* hedgerows, although many fields were bordered only by fences, with some 40% of all fields having no hedge border.

2 Meteorological Data

Daily rainfall and temperature data were obtained from the University Field Laboratory, Wytham. In the following analyses two measures of rainfall are used. Total rainfall over a stated period (in millimetres) is used in the analysis of diet and

chick weight (Chapter 3). However, this method does not take into account the effects of rainfall on soil moisture conditions over a long period, which may reflect prey (earthworm) abundance. Desrochers (1991) described soil moisture conditions using a rainfall index calculated thus:

rf index = (100% rainfall in last 24 hours) + (50% rainfall 24 to 48 hours) + (25% rainfall 48 to 72 hours) + (12.5% rainfall 72 to 96 hours).

Temperature is measured by considering the mean morning (0800-1200) temperature, as most observations were carried out in this period.

3 Reproductive Success

The whole study site was covered regularly by observers from late February onwards. Territories were located (usually by noting the presence of singing males) and nests were searched for at likely locations within a territory. After a nest had been discovered it was visited periodically to check its progress. When a clutch successfully hatched (day 0) it was visited regularly and each chick was weighed and measured (tibia length), sometimes daily up to day 9 (1991 only), but usually only on day 8. Magrath (1991) showed that the probability of a blackbird's survival to independence, and also the probability of it's recapture as an adult, was related to day 8 weight of nestlings. Therefore day 8 weight will be assumed to be an accurate measure of chick 'quality' throughout this study.

In order to be able to identify individual birds, all chicks were ringed with a unique colour ring combination on day 8. Also an attempt was made to catch and colour ring all breeding adults within the study area. In addition, adults were aged when possible (Svensson, 1992) and weighed and measured (wing length, bill length, and tarsus length).

4 Diet and Provisioning

Observations of feeding visits were made at certain nests where the habitat allowed. Nests containing chicks up to six days old were watched for one or two hour observation periods per day (1991 n=22 nests; 1992 n=11 nests; 1993 n=17 nests). In 1991 and 1993 certain nests were observed for 12 hour observation periods (0600-1800) on either day 8 (n=6) or day 9 (n=11), though one nest was watched on day 7 and one on day 10. During these periods the observers would position themselves thirty to fifty metres away from the nest (or closer when observing from a hide) and, with the aid of a telescope and binoculars, record: (i) the time of nest visits for each parent; (ii) the time of departure; and (iii) the prey load delivered. It was not always possible to record prey loads, but the number of prey, prey type and prey size were recorded per visit where possible.

The size of earthworms, caterpillars and slugs brought to the nest were recorded in relation to the bird's bill length, and then converted to calorific equivalents, taking the 'standard' bill length as approximately 25mm. Additionally, earthworms were also classed as 'thin' (smaller in diameter than the base of the bill) and 'fat' (larger than the base of the bill). The loads were converted to energy equivalents, taking data from earlier studies (Mason, 1970; Bryant, 1973; Rogers et. al., 1977; Edwards, 1983; Snow and Snow, 1988).

All one and two hour observations took place between 0800 and 1200. All twelve hour observation periods took place between 0600 and 1800.

5 Analysis

Statistical procedures were taken from Zar (1984). Statistical analyses were performed using Statview and Minitab statistical packages. All means are presented $\pm$ standard deviation, apart from some figures where standard errors are used (typically when standard deviations are large).

Although the data were gathered over three breeding seasons, analyses usually deal with the combined data set, as most effects should be independent of year, even

though certain independent variables may differ between years. For example, one year may have consistently lower temperatures than the other two, but when considering the effect of temperature on individual chick weight, the actual year that the temperature occurred in should be unimportant.

A problem that occurs throughout the analysis in this thesis is that of independence. Data were often gathered from the same parent(s) on more than one occasion, such as when a pair makes two or more attempts in a season, or in successive seasons. These appear in the analyses as independent events. Generally the analyses in this thesis assume that environmental effects (e.g. food supply, temperature) will have a far greater effect on provisioning and reproductive success than individual parental ability. This is likely to have little effect on trends which are the same at an individual and population level, such as the general analyses presented in Chapter 2 (for example, the seasonal pattern to clutch size). For analyses dealing with reproductive success per territory across habitats (Chapter 5), the problem can be avoided by analysing the data from separate years. The major problem comes when dealing with chick weights and provisioning rates of parents, when sample sizes are small (so it is desirable to have as large a sample size as possible), and the number of non-independent data points is fairly large. For each of these cases, the specific problems are discussed in the relevant chapters, and some conservative analyses of truly independent data are performed to test the effect of repeated sampling from the same individuals.

Chapter 2

The Breeding Season and Reproductive Success.

Introduction

Lack (1954) proposed that birds will be adapted to time their breeding seasons so that the period of maximum chick demand coincides with the period of optimal conditions (usually food supply) for raising the maximum number of young. This central tenet has received general support, most convincingly from studies on great tits (Gibb, 1950; Perrins, 1979), which time their breeding seasons to coincide with the period that caterpillars are most abundant in the environment. There is still often much variation within a given year, which may be related to parental quality and the food supply available to the female prior to laying (Perrins, 1970).

In multi-brooded species such as the blackbird, annual reproductive success is determined in part by the number of broods raised in a season, rather than on the success of a single brood. Crick et al. (1993) proposed that multi-brooded species should start breeding as early as possible, before the optimal time (i.e. the time when most young can be raised from a brood). Blackbirds are apparently very plastic in their timing of breeding, showing much year-to-year variation (Snow, 1958), broods having been recorded in January and October.

Lack (1947) suggested that birds lay a clutch which will produce the maximum number of young which will survive to fledge. The seasonal rise and fall in the clutch size of the blackbird (Snow, 1958) is therefore likely to reflect a rise and fall in conditions for raising nestlings. Snow (1958) suggested that this was largely due to variations in the food supply, the peak in clutch size coinciding with a period when both the main prey types, caterpillars and earthworms, are plentiful. The mean nestling weight, which reflects the chances of a chick's survival to breed (Magrath, 1991), was highest at this time of year, even though there would have been greater competition for food within the nest. In the earlier part of the season, caterpillars and other insect larvae are unavailable, and the lower temperatures also probably have an effect on chick energy expenditure. In the later part of the breeding season earthworms tend to be less available due to the drier conditions (Edwards and Lofty, 1972). This is supported by the fact that blackbirds prolong their breeding season in wet summers (Snow, 1958).

In addition to food supply, a major determinant of reproductive success in the blackbird, and other open nesting passerines is nest predation (Snow, 1958; Best, 1977; Knupp et al., 1977). Snow (1958) reported a predation rate of 50% on urban blackbird nests and 86% in woodland. Differential predation within a habitat is dependent on the amount of nesting cover within a territory (Edwards, 1983).

In this chapter, I describe the reproductive success, both within and between years, for the whole study population, concentrating particularly on nestling quality (chick weight) and predation.

Methods

The methods used for the determination of reproductive success used in this chapter are detailed in Chapter 1. All data are from nests where either a nest was actually found in a territory, or where fledglings were seen on a territory, even if no nest was found. Nests were often found which had already been predated or abandoned. In these cases it was usually obvious what the fate of the nest had been, either from direct evidence, or in relation to the timing of other nesting attempts. Predated nests often had some sign of physical damage, such as the lining being pulled up (indicative of corvid predation- Groom, 1993), or they contained fragments of broken egg shell. Nests which were suspected of being abandoned before laying, or which had an unknown fate were left out of the subsequent analyses.

Results

1. Weather

The mean morning temperature and total rainfall per five day period throughout each breeding season are shown in figures 2.1 and 2.2. Not surprisingly, there is a steady increase in temperature in all years as the season progresses, although 1991 was consistently colder than the other two years. A two factor analysis of variance (which takes account of the seasonal trend) revealed a significant difference in temperature between breeding seasons ($F_{2,20}$=5.88, P=0.0001; 1991 mean=10.22$\pm$2.69.°C., 1992 mean=12.63$\pm$4.15°C., 1993 mean =11.65$\pm$3.39°C).

As winter temperature may affect population density (Karlsson and Kallander, 1977) and possibly the onset of breeding (Snow, 1958) this is also considered. There was a significant difference in mean morning temperature in January and February between years, 1991 being significantly colder than the other two years (ANOVA $F_{2,174}$=5.78, P=0.004; 1991 mean = 2.91$\pm$3.60°C, 1992 mean = 4.67$\pm$3.69°C, 1993 mean = 4.85$\pm$2.95°C). There was also a significant difference in the number of days experiencing freezing temperatures between years (χ^2=9.54, df=2, P<0.01; figure 2.3).

There was no particular seasonal pattern of rainfall common to all years. Overall differences between years were not significant ($F_{2,20}$=1.01, P=0.47; 1991 mean=7.19$\pm$8.08mm, 1992 mean=7.85$\pm$9.01mm, 1993 mean =9.34$\pm$9.43), although there were some points of difference that are worth noting, especially that the end of the 1991 breeding season was relatively wet.

2. Reproductive Success

(i) Length of Season

The start of the breeding season was similar in all years; in 1991 the first egg was laid on 20th March, in 1992 the first egg was laid on the 24th March and in 1993, on 17th March. There was more variation in the finish of the breeding season, the respective dates for final clutches being 9th July, 2nd July, and 21st June for 1991,

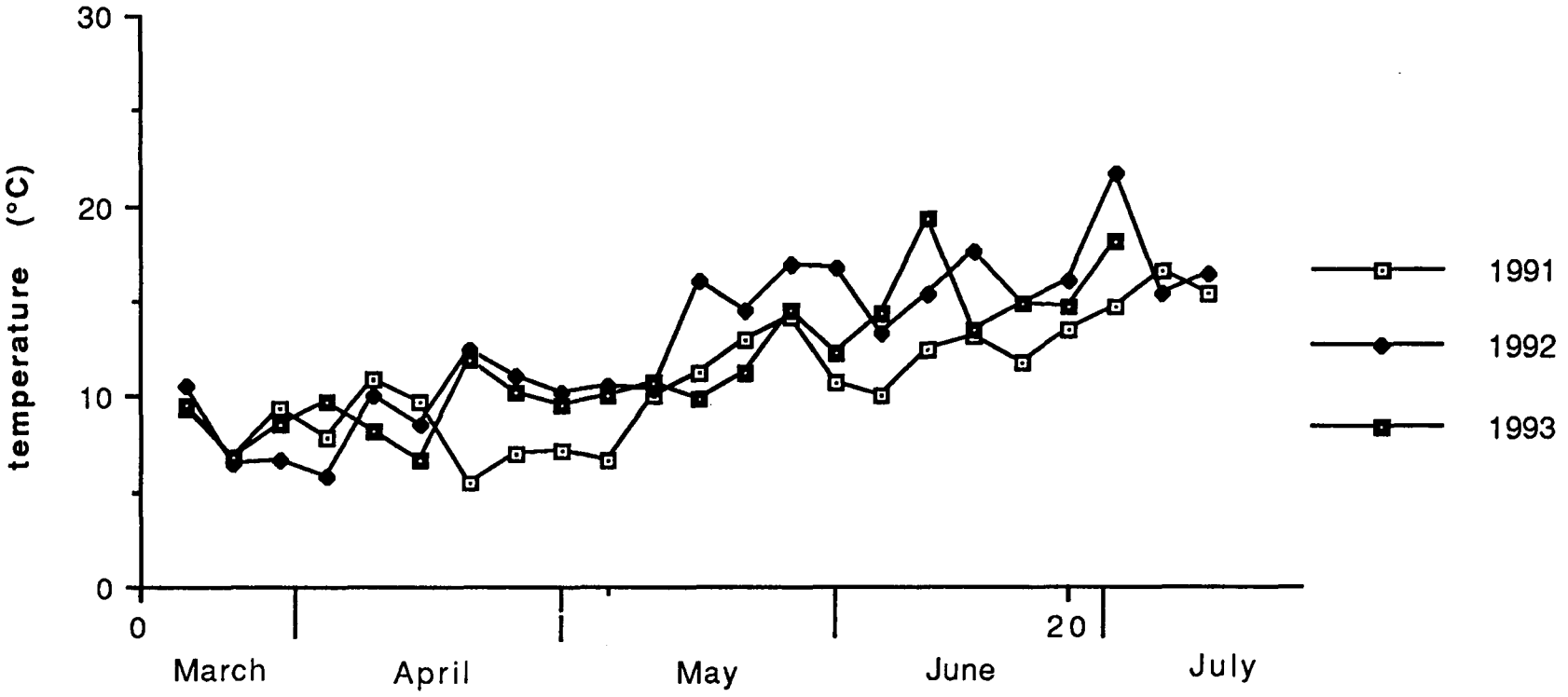
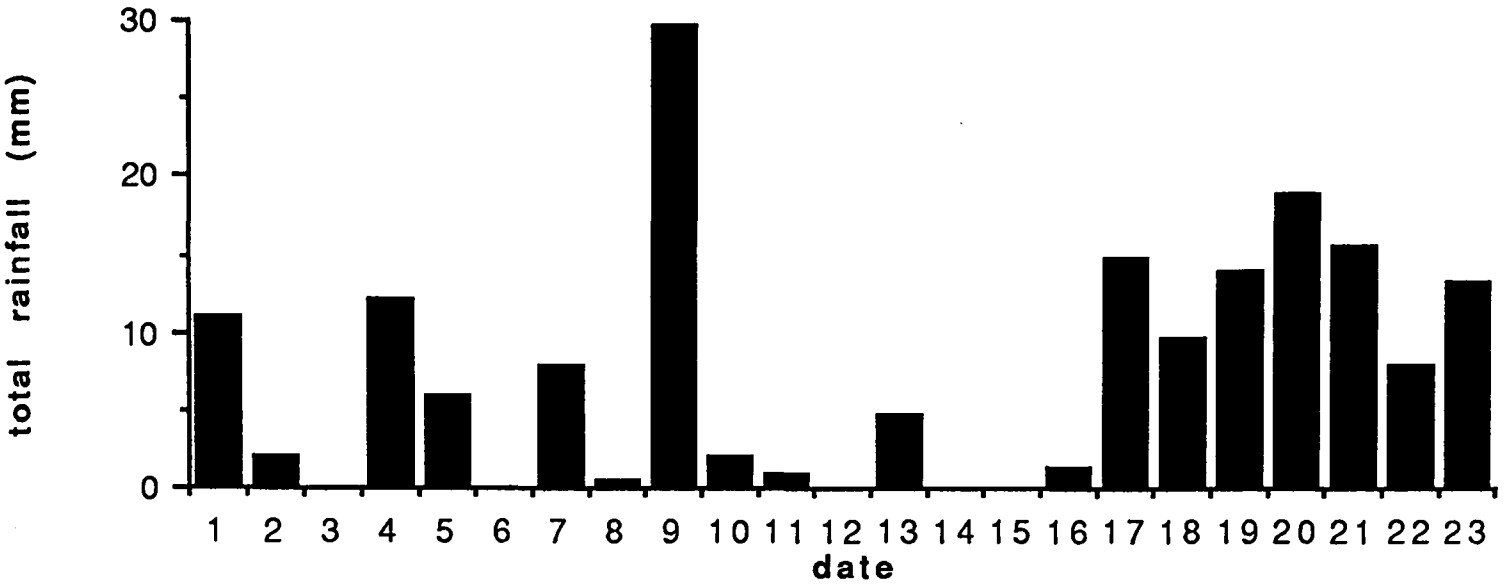
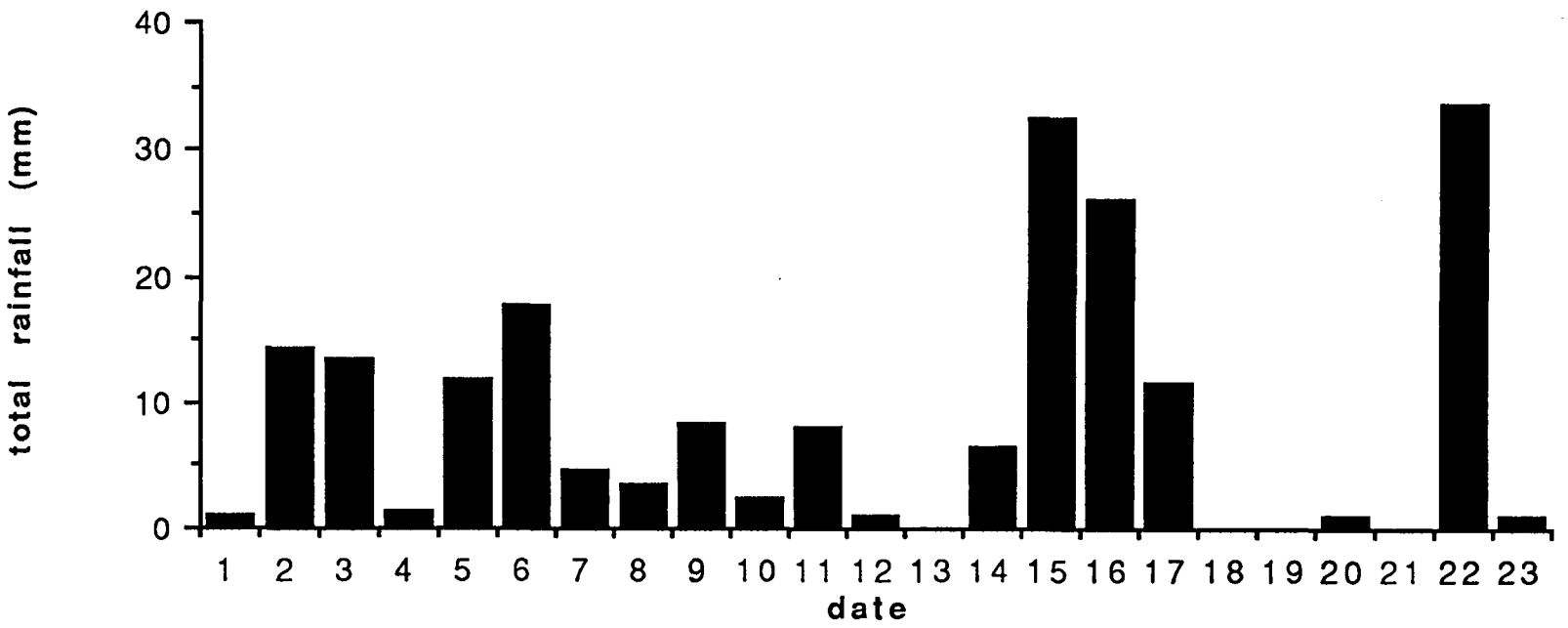


Figure 2.1: Seasonal variation in mean temperature per five day period. Period 1=18-22/3; period 2=23-28/3 etc. The range of dates is based on the earliest and latest completed clutches.

(A) 1991



(B) 1992



(C) 1993

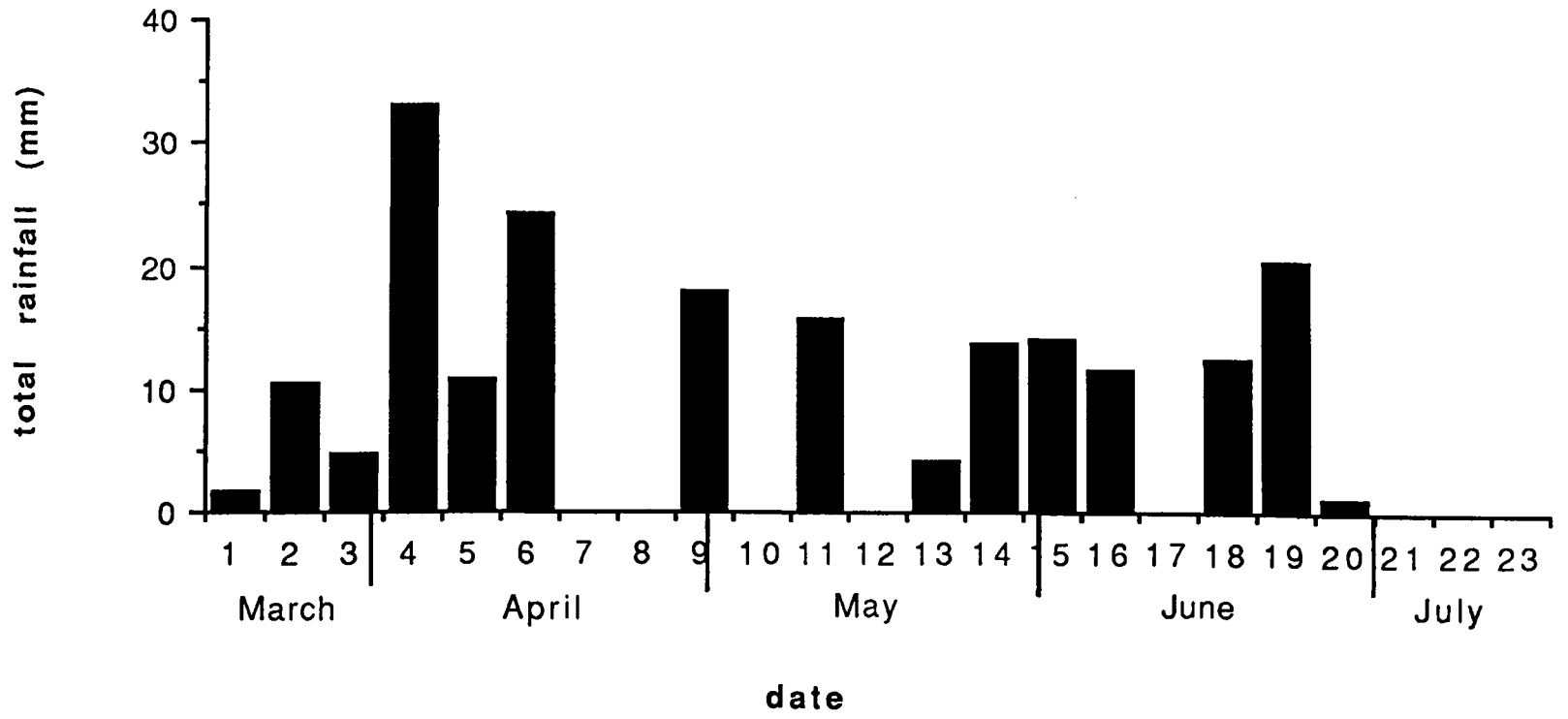


Figure 2.2: Seasonal variation in total rainfall for five day periods throughout the breeding season. Period 1=18/3-22/3; period 2=23/3-27/3 etc. The range of dates is based on the earliest and latest completed clutches.

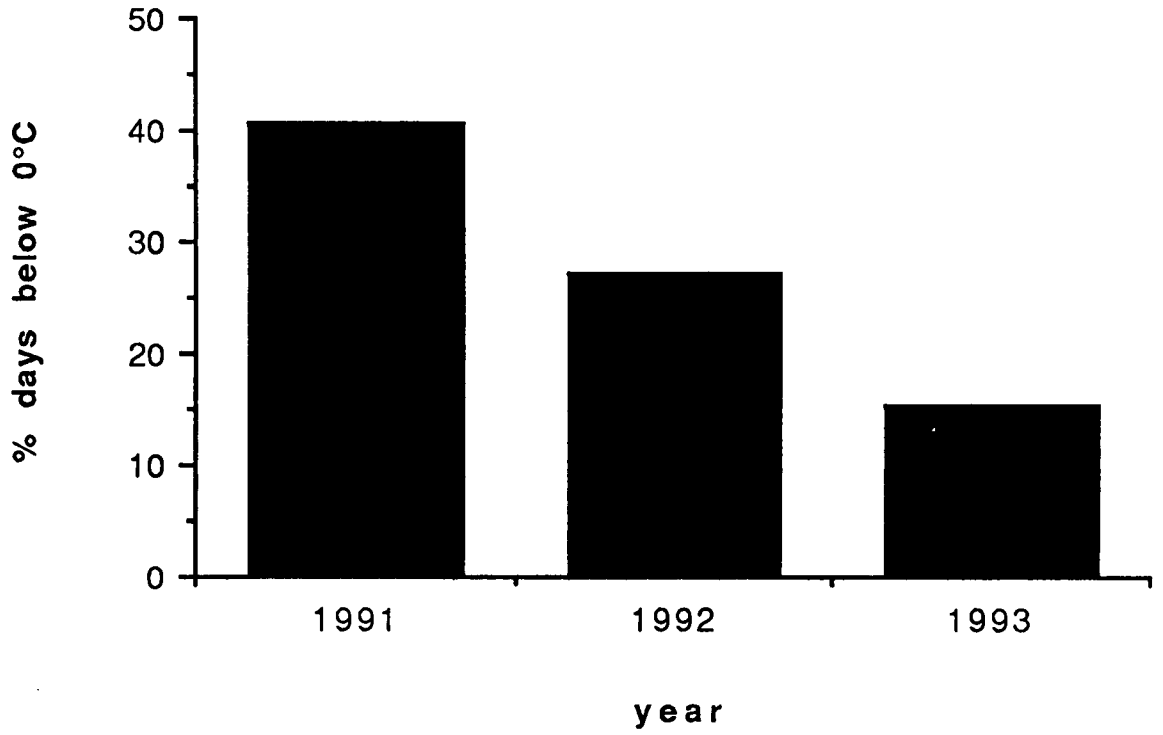


Figure 2.3: The proportion of days experiencing temperatures below 0°C in January and February. Sample size=59 in each year.

1992 and 1993. The mean number of known nesting attempts per pair was 2.28±1.18 (n=53) in 1991, 2.59±1.12 (n=64) in 1992, and 2.96±1.37 (n=76) in 1993. The difference between years was significant (ANOVA $F_{2,192}$=4.75, P=0.01), although this is almost certainly due to an increase in nest finding ability rather than a result of any biological significance. Indeed, a reverse trend in the mean number of nesting attempts would be expected based on the length of each breeding season.

(ii) Clutch Size

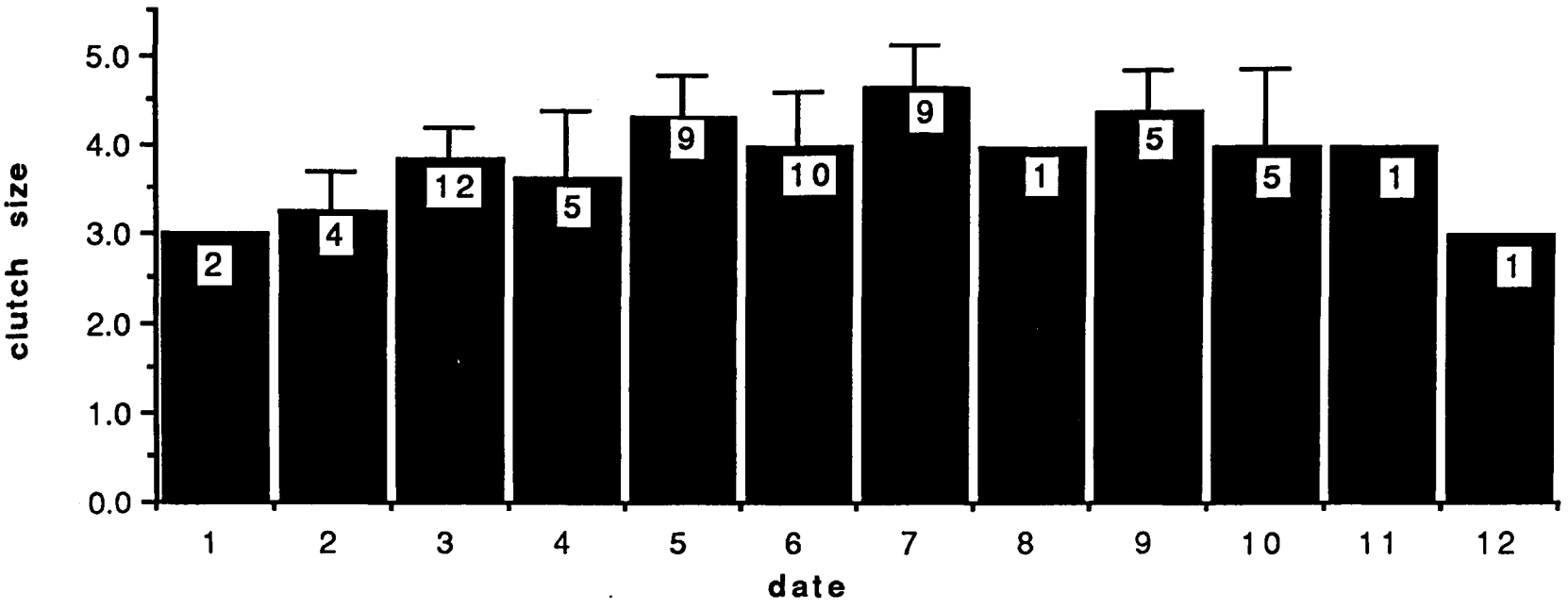
The clutch size of blackbirds varies through the breeding season, typically increasing to a maximum of five eggs in late May (three clutches of six were found, one in 1992 and two in 1993) and thereafter showing a decrease (fig. 2.4). Although 1992 had the highest mean peak clutch size, overall 1993 had consistently higher clutch sizes than the other two years, particularly in the early part of the breeding season, the respective dates for the first five egg clutch being 20th April, 28th April and 12th April. When comparing clutch size between years, the effect of date was controlled for by considering mean clutch size per ten day period. This revealed that the difference between years was significant (two factor ANOVA $F_{2,232}$=3.51, P=0.032; total mean 1991 = 4.03±0.70, n=62; mean 1992 = 4.00±0.79, n=97; 1993 mean = 4.17±0.72, n=103).

The above analyses use each clutch laid as an independent event. Strictly speaking, this is invalid as each individual bird will lay a number of clutches throughout the season. However, although there will be some variation in the clutch size between individuals, the general seasonal trend and year/habitat effects are likely to be stronger, individual variation with temperature or date following the population trend (Snow, 1958)

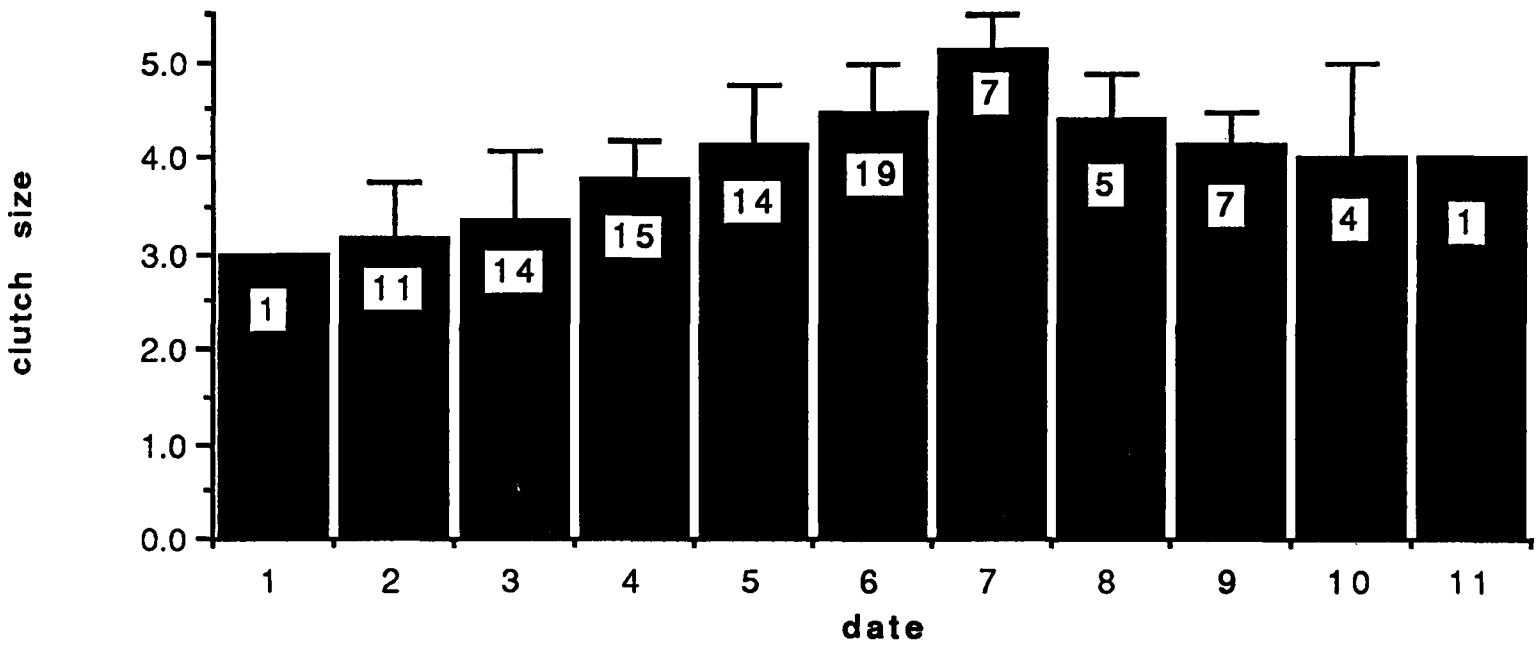
(iii) Predation

Nest failure rates were high, predation accounting for over 95% of all failure. In 1991, 73% (88/121) of nests which reached the egg laying stage were predated, in

(A) 1991



(B) 1992



(C) 1993

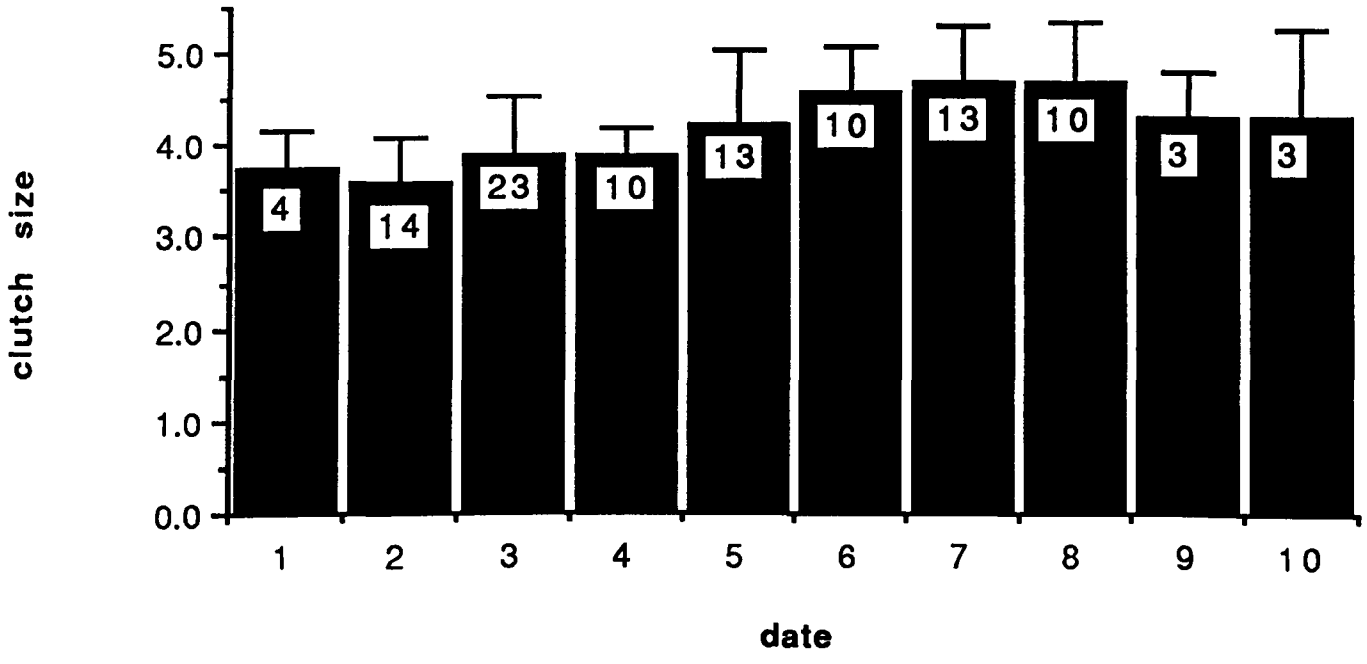


Figure 2.4: Mean clutch size per ten day period throughout the three breeding seasons. Error bars represent standard deviations. Numbers on columns represent sample sizes. Date 1=18-28/3; date 2=29/3-8/4 etc.

1992, 80% (133/166) were predated, and in 1993, 84% (188/223) were predated. The difference in the proportion of nests predated between years was significant (χ^2=6.62, df=2, P<0.05). This result could have been due to an increase in observers' abilities to find nests before the chicks had hatched. Nests were sometimes found by locating provisioning adults, so finding nests containing chicks was relatively easy. Other nests which never reached the chick stage may have been found with greater frequency as the study progressed. This may also explain the significant difference in the number of known attempts per year. An alternative explanation for the differences in predation between years may be predator density. Unfortunately there are no data available on predator densities at Wytham.

Although actually witnessing a predation was very rare (only five instances in three years), some attempt could often be made to identify the type of predator responsible (203/510). Avian predators (probably mostly jays *Garrulus glandarius* and magpies *Pica pica*) cause little damage to the nest structure, except that the nest lining is often pulled up during removal of the eggs (Groom, 1993). This was the commonest type of identified predation, making up 65.5% (133/203) of the total . Nests which had been pulled apart, often accompanied by broken egg shells or blood, were assumed to have been predated by foxes or badgers, which occurred in 29.6% of nests (60/203). Complete nests with large pieces of the egg intact were assumed to be due to weasel *Mustela nivalis* predation, a conclusion which was reached after a weasel was actually seen predating a nest, although these were rare, accounting for a mere 3.4% of predations (7/203). Additionally, a further three nests (1.5%) were probably predated by cats.

The above figures give some idea of the relative importance of different predators, but they will be biased towards predators that leave more obvious signs. Avian predation was probably a lot more common than these figures suggest, given that the majority of predators left no clue as to their identity.

There was no particular seasonal pattern to nest predation, but the differences between months were significant (χ^2=8.59, df=3, P<0.05; fig. 2.5), April having the

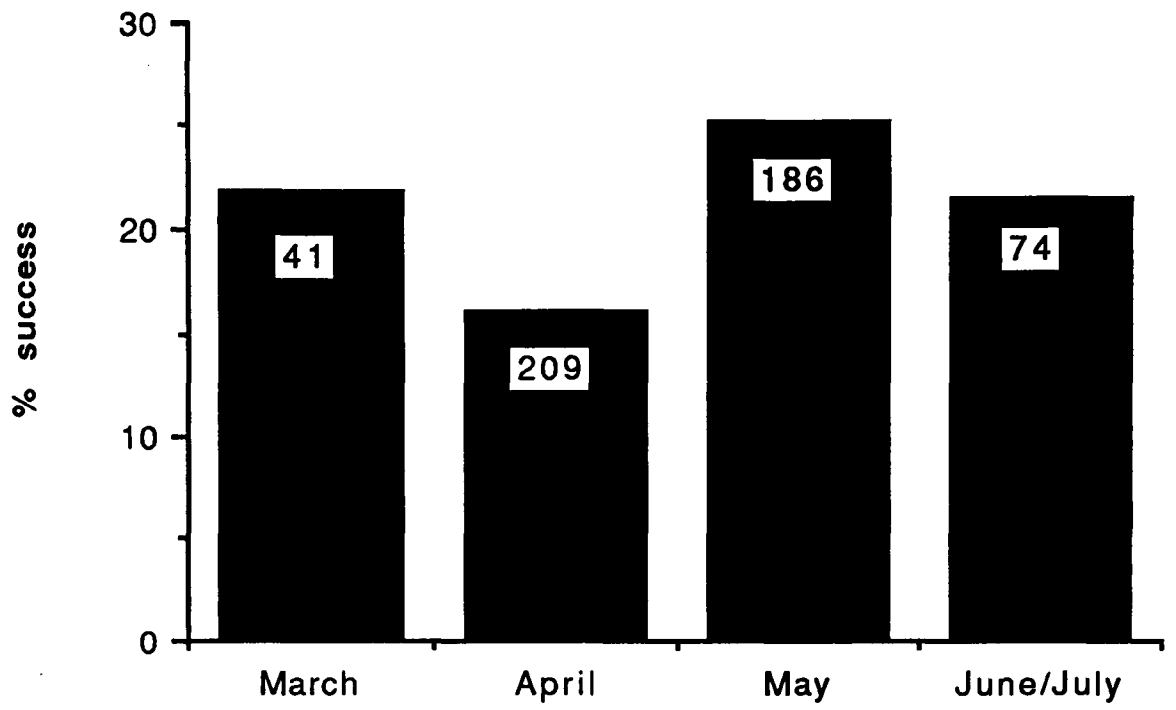


Figure 2.5: The seasonal variation in nesting success.
The date is the date of clutch completion.

lowest success rate. Note that this analysis uses the date of clutch initiation, thus a clutch layed in May would have the best chance of survival.

The chances of a nest being predated may to some extent be dependent on the stage of the breeding cycle. For example, if the nest is being visited at a high rate by the parents, then this may increase the likelihood of a predator detecting the nest. Begging calls may also increase the risk. In order to analyse this the nesting cycle was divided into four parts: the laying period, the incubation period, the early nestling phase, and the late nestling phase when provisioning rate has reached a maximum. If it is assumed that predation is random with respect to the stage of the nesting cycle, then there should be no significant difference in the daily predation rates of each part of the nesting cycle.

Table 2.1 shows a χ^2 analysis on the rate of predation at each nesting phase, where expected values are calculated by multiplying the proportion of total nesting cycle time taken up by each phase (based on the modal periods; 4, 12, 7 and 6 days respectively) by the total number of predations.

There were significant differences in the amount of predation at each nesting stage. The differences were greatest at the incubation stage (higher than expected) and the early nestling phase (lower than expected). Therefore, although significant differences were detected, the original hypothesis, that predation should increase with increasing activity at the nest, is not supported.

(iv) Starvation

The starvation rate was fairly low in all years, occurring in 4 out of 31 (12.90%) nests of known history which successfully hatched in 1991 and survived to at least day 8, in 7 out of 46 (15.21%) nests in 1992 and 3 out of 50 (6.0%) nests in 1993. The difference in the number of nests experiencing starvation between years was not significant (df=2, χ^2=1.61, P>0.50), nor was there any significant difference in the number of fledglings raised per pair ($F_{2,190}$=2.22, P=0.11; 1991 mean = 2.19$\pm$2.27; 1992 mean = 1.56$\pm$1.89; 1993 mean = 1.45$\pm$2.02) or the number of fledglings raised per successful nest between years ($F_{2,79}$=1.87, P=0.16; 1991 mean = 3.53$\pm$0.87;

Table 2.1: A χ^2 analysis of the effect of nesting cycle stage on predation rates. Expected predation rates are based on the proportion of time occupied by each nesting stage. ***P<0.001, df=3.

STAGE	TOTAL PREDATION	PROPORTION OF TIME OF EACH STAGE	EXPECTED PREDATION	χ^2
laying	46	0.138	35.60	3.04
incubation	147	0.414	106.81	15.12***
age 0-6	30	0.241	62.18	16.65***
age 7-12	35	0.207	53.41	6.35**
total	258	1.0	258	41.16***

1992 mean = 3.02±0.85; 1993 mean = 3.35±1.22). Two nests were left out of the analysis due to the disappearance of the male parent. In one case this was almost certainly due to disturbance, and resulted in the eventual starvation of the whole brood. The second instance involved a nest where the male disappeared, probably having been taken by a predator. In this case the lone female was able to successfully raise two of the original four chicks.

It is interesting to note that all starvation occurred in a short period from late May to late June in 1992, a period which had some very high temperatures and which also contained the caterpillar peak (although rainfall was still fairly high, only one nest having a rainfall index of 0 on the day of starvation), whereas starvation in 1991 and 1993 was much more evenly spaced throughout the season (fig. 2.6).

Starvation was significantly higher at higher brood sizes (G-test=12.71, df=5, 0.05>P>0.025 - figure 2.7). This implies that nestling dominance hierarchies are more common in larger broods due to an increase in hatching asynchrony with brood size (Magrath, 1989). According to Snow (1958) skeletal growth follows a relatively constant pattern which is independent of the weight of the chick, and is therefore a better predictor of chick age. This also seems to be the case in this study as tibia length was a much less variable measure than chick weight (weight variance=16.60, tibia variance=1.00; variance ratio test $F_{85,85}$=16.60, P<0.0001). There was a significant relationship between the variability (standard deviation) of tibia length per brood and brood size (linear regression r=0.37, df=84, P=0.001), therefore larger broods tended to have greater hatching asynchrony and consequently a greater age range of chick size.

3 Chick growth

Blackbird nestlings show sigmoidal growth curves for both weight gain and, to a lesser extent, skeletal growth as measured by tibia length (fig. 2.8), a pattern common to most bird species (O'Connor, 1984). The period of maximum growth is between day 3 and 7, before a levelling off at days 8 and 9, at approximately 2/3 adult weight.

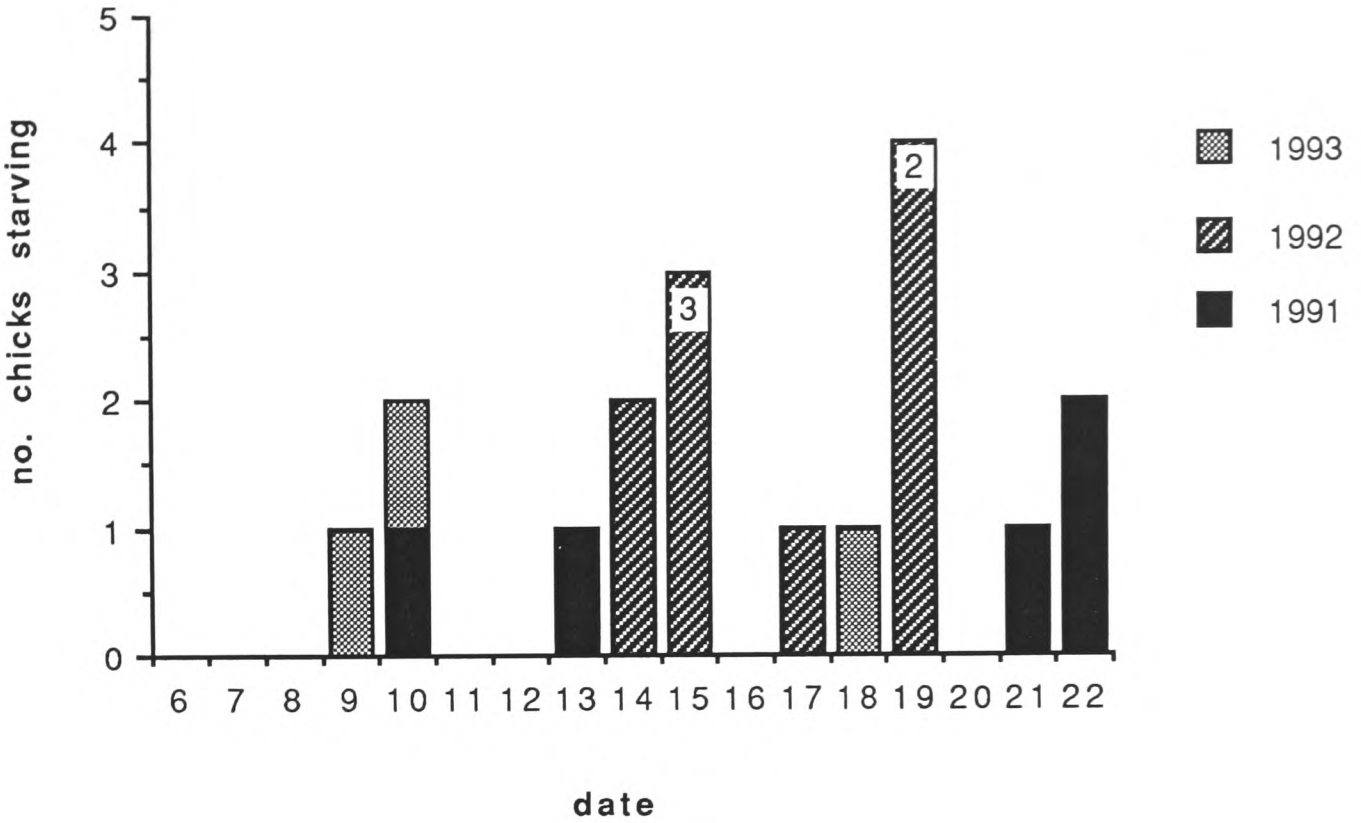


Figure 2.6: The seasonal variation in the numbers of chicks starving per five day period, where period 6=13-17/4; period 2=18-22/4 etc. The number of nests involved is stated on the columns except when n=1.

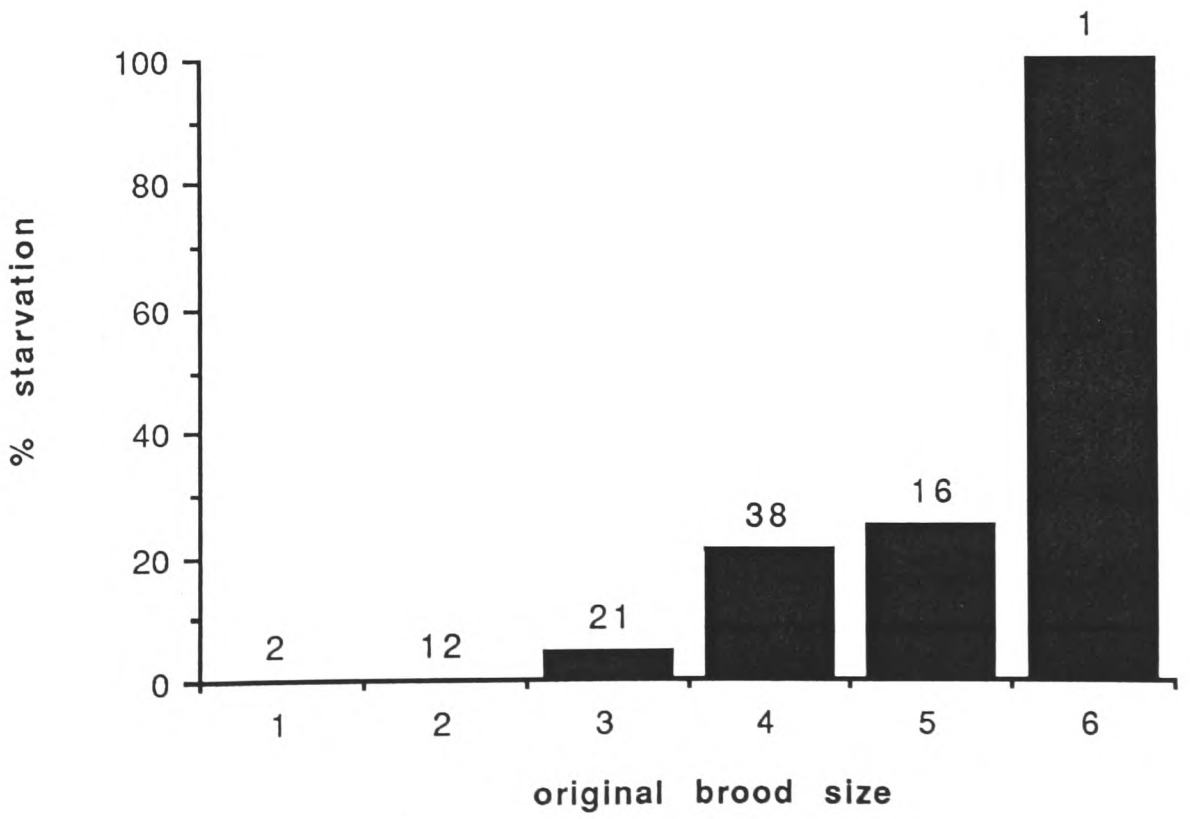
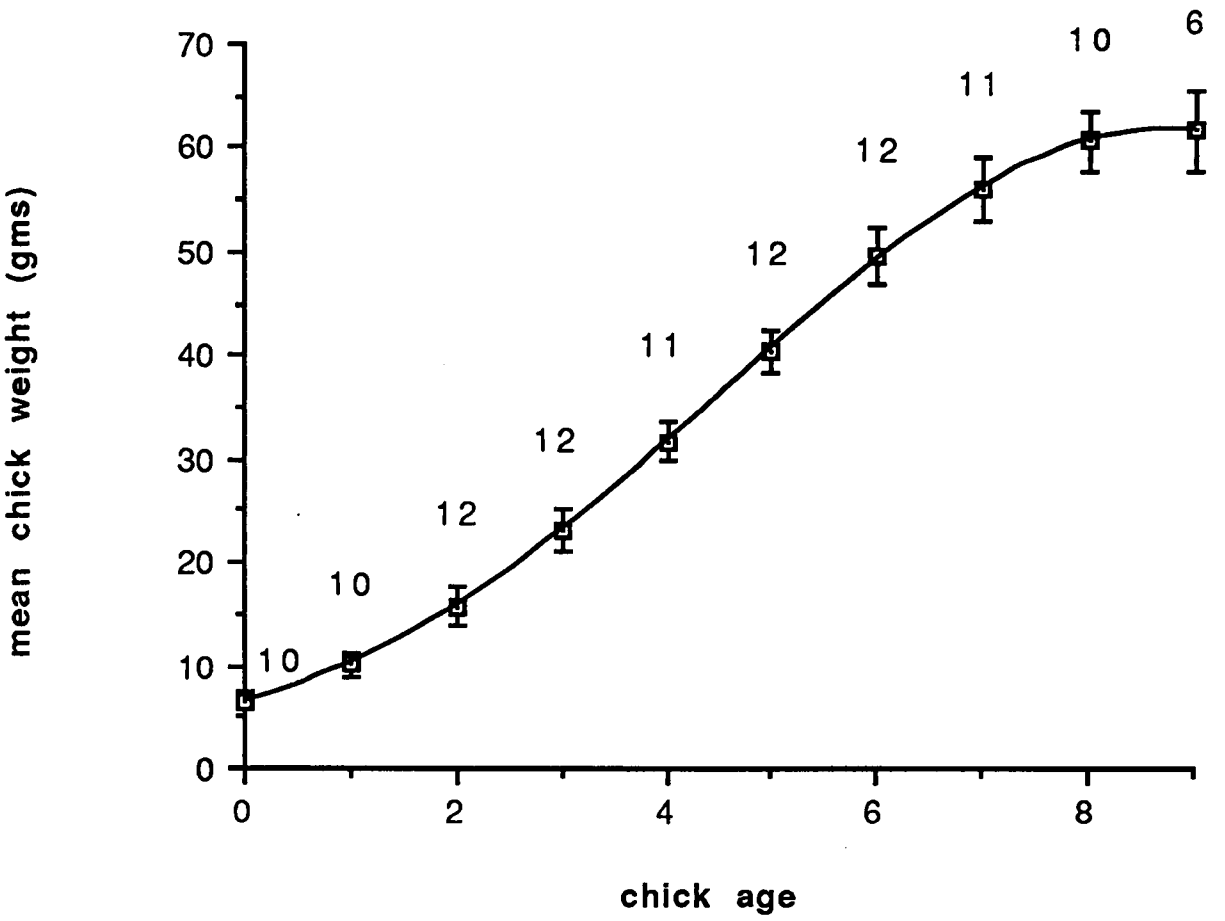


Figure 2.7: The proportion of nests surviving to day 8 which experienced brood reduction, where numbers above columns represent total sample sizes.

(A)



(B)

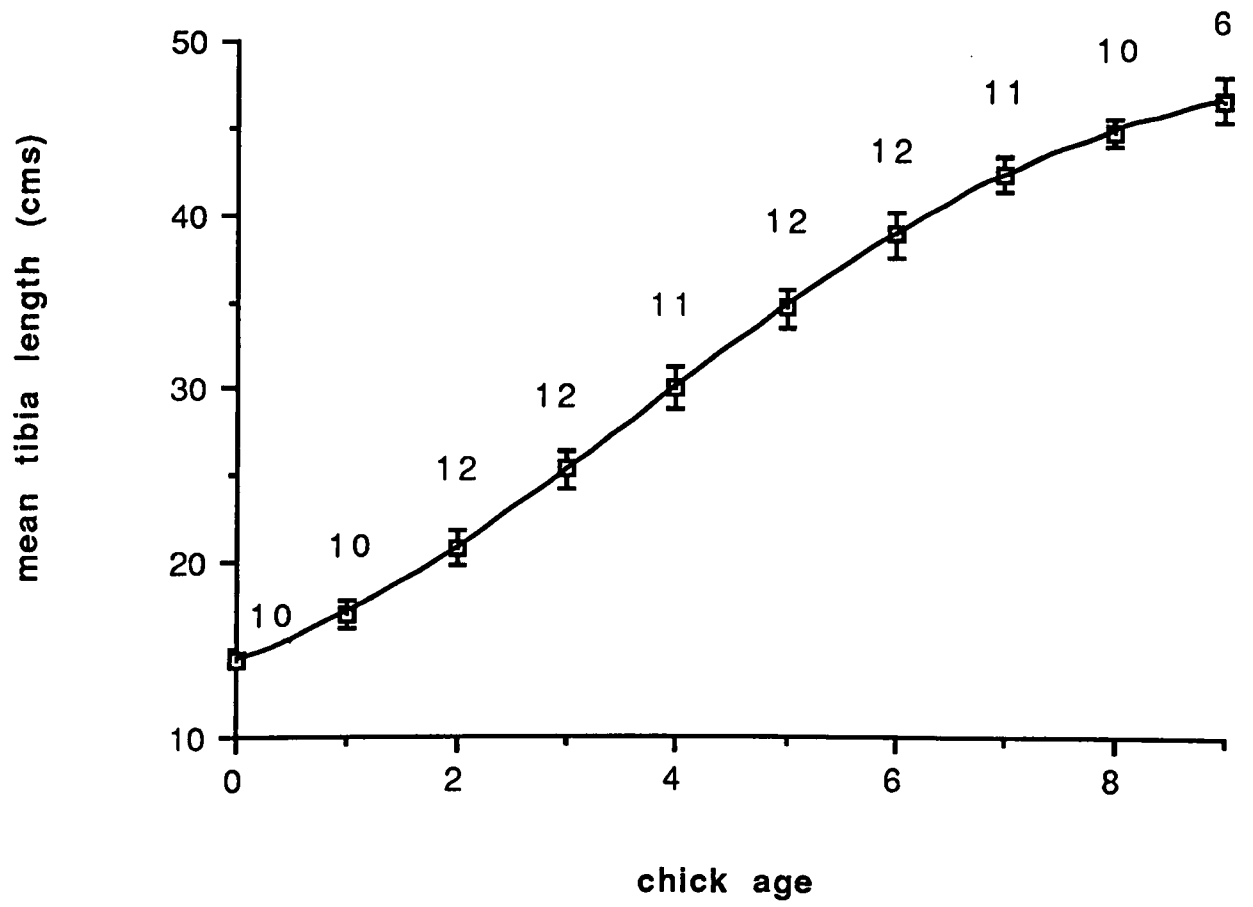


Figure 2.8: Daily chick growth in 1991. (A) chick weight, (B) tibia length. Sample sizes are given above means. Curves were fitted by eye.

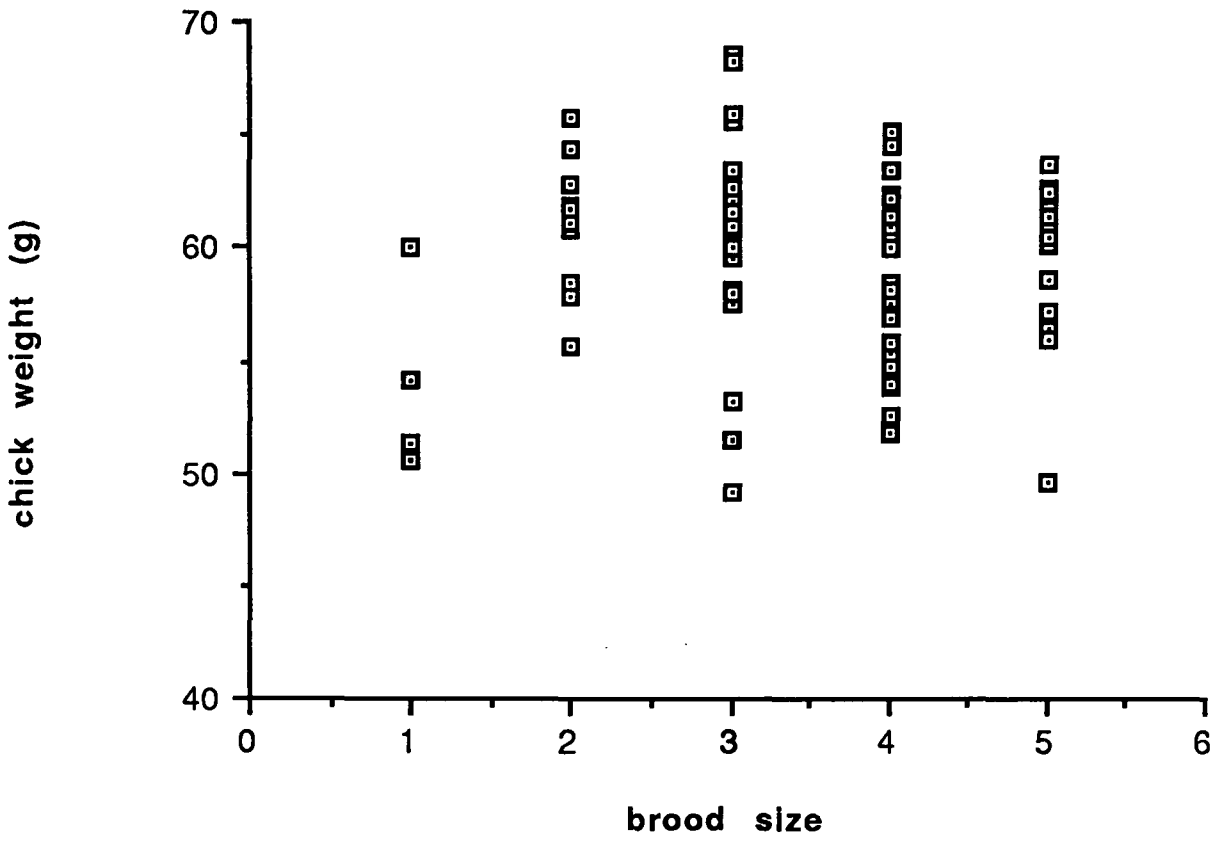
In this study no weights were taken after day nine to avoid the risk of broods 'exploding' out of the nest (Snow, 1958).

There was no significant effect of brood size on mean chick weight (linear regression r=-0.03, df=84, P=0.82), or mean tibia length (r=-0.02, df=84, P=0.86; fig. 2.9) using results from all years combined.

There was a significant seasonal increase in mean chick weight in 1993 (linear regression r=0.40, df=31, P=0.02; a quadratic function was not a significantly better fit than a linear function: $F_{1,30}$=2.73, P>0.20), but not in the other two years (1991 r=0.01, df=25, P=0.97; 1992 r=0.11, df=24, P=0.59; see figure 2.10). There was a positive trend when years were combined (linear regression r=0.18, df=84, P=0.09), although these results, particularly the latter, are probably meaningless given the large amount of scatter. In a species such as the blackbird, it is unlikely that food supply, the most likely factor affecting chick weight, will be highly dependent on seasonal changes. Rather, short term changes in environmental conditions are more likely to have an effect, thus chick quality is more likely to be related to measures of rainfall and temperature rather than date (see Chapter 4). There were no significant differences in mean day eight chick weight between years (ANOVA $F_{2,83}$=1.08, P=0.35; 1991 mean = 60.0$\pm$4.45 g; 1992 mean = 58.37$\pm$3.85 g; 1993 mean = 59.09$\pm$3.92 g)

One problem with this data set is that some weights come from broods fed by the same parents and are therefore not independent. In total 10 females and 10 males were parents at two or more nests from which brood weights were recorded. As the weight of chicks is likely to depend on the contribution of both parents, only repeated nests with the same pair of parents are wholly non-independent. Between years, this occurred in only two instances, the divorce rate being high in this sample. Repetition within years was more of a problem, with eight pairs in total having two weighed broods per season, and one pair with three weighed broods. If within-individual effects are the same or less than between-individual effects, then effectively each nest can be considered as an independent event. To examine this, a conservative analysis was performed in which a single brood's weight was selected at random from those broods

(A)



(B)

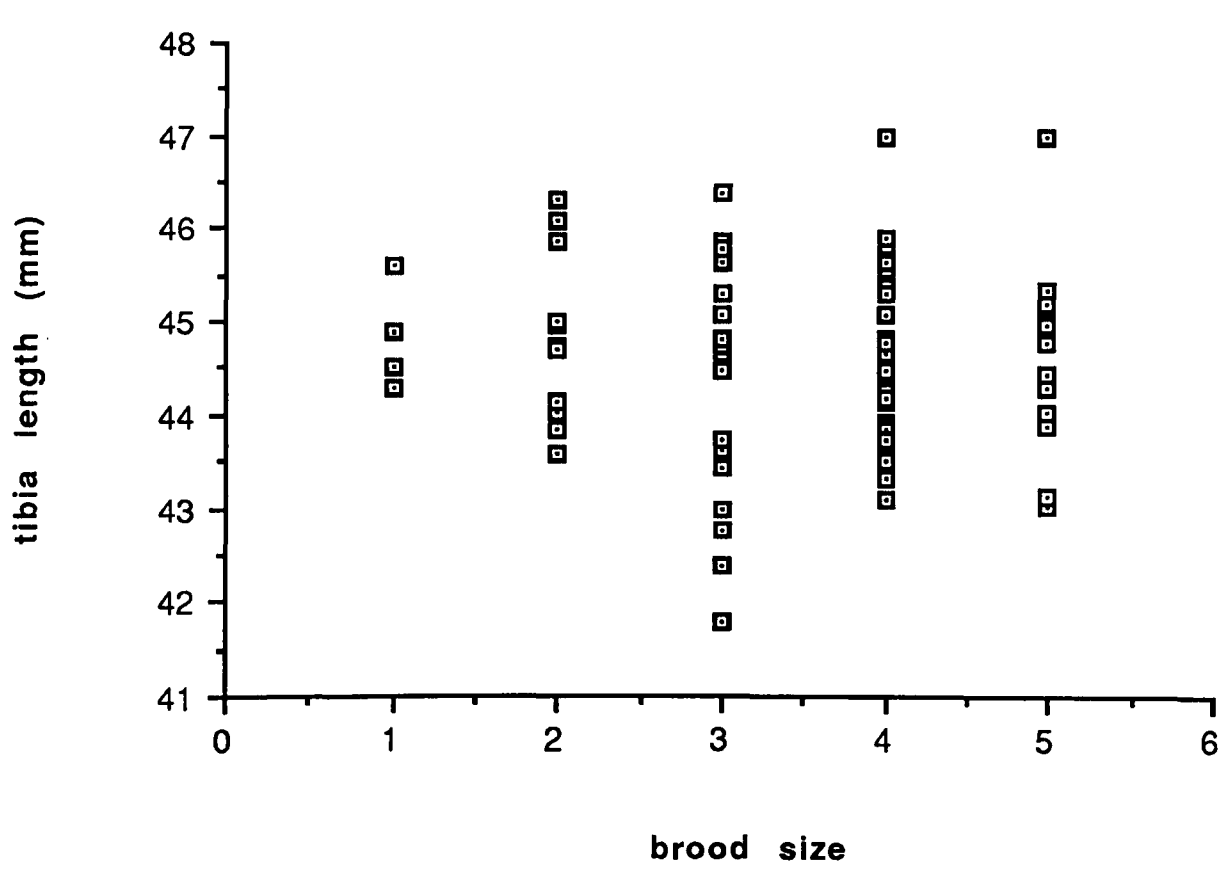
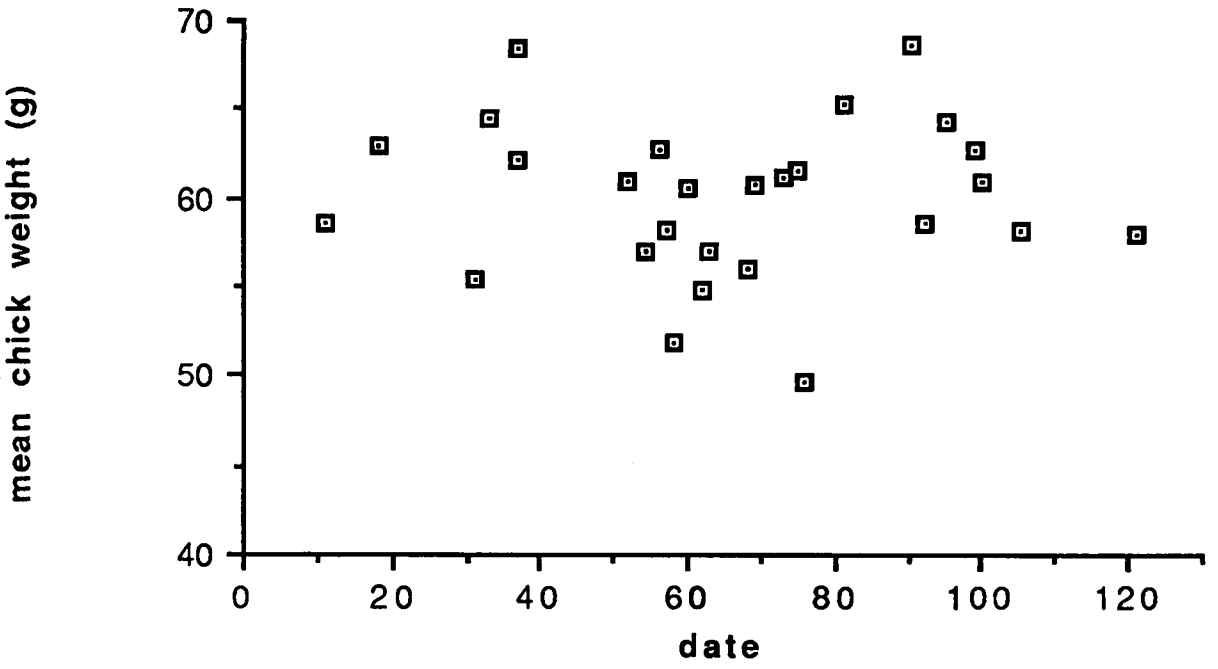
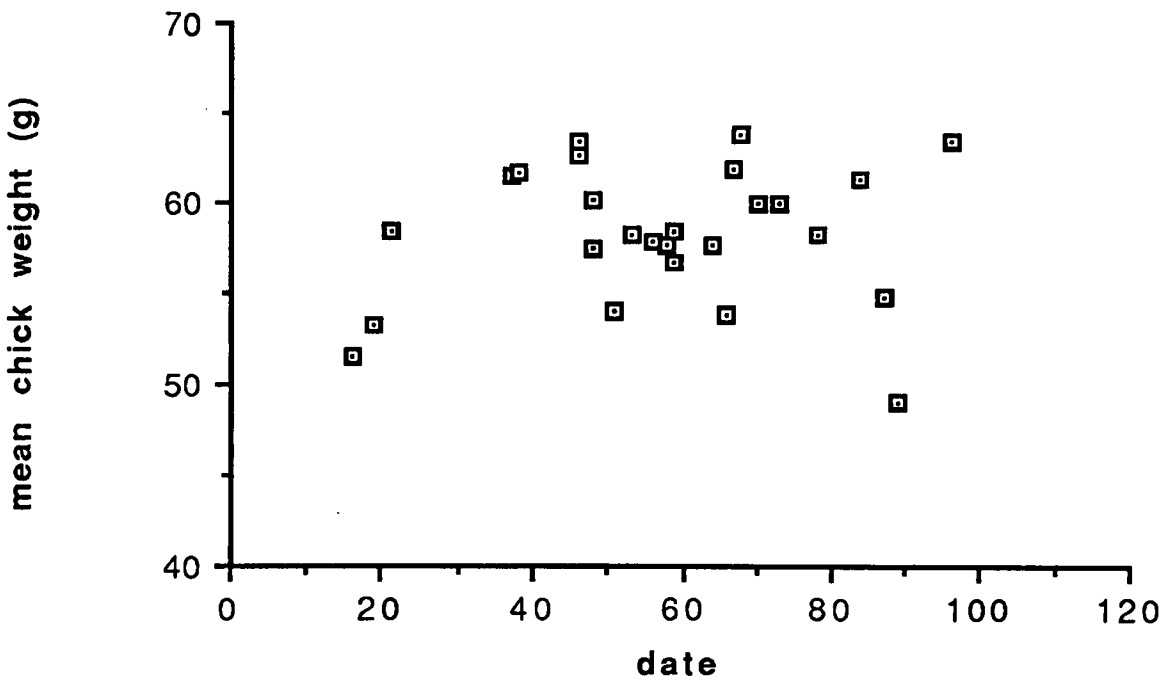


Figure 2.9: The effects of brood size on (A) mean chick weight per brood, and (B) mean tibia length per brood. No relationships had slopes significantly different from 0.

(A) 1991



(B) 1992



(C) 1993

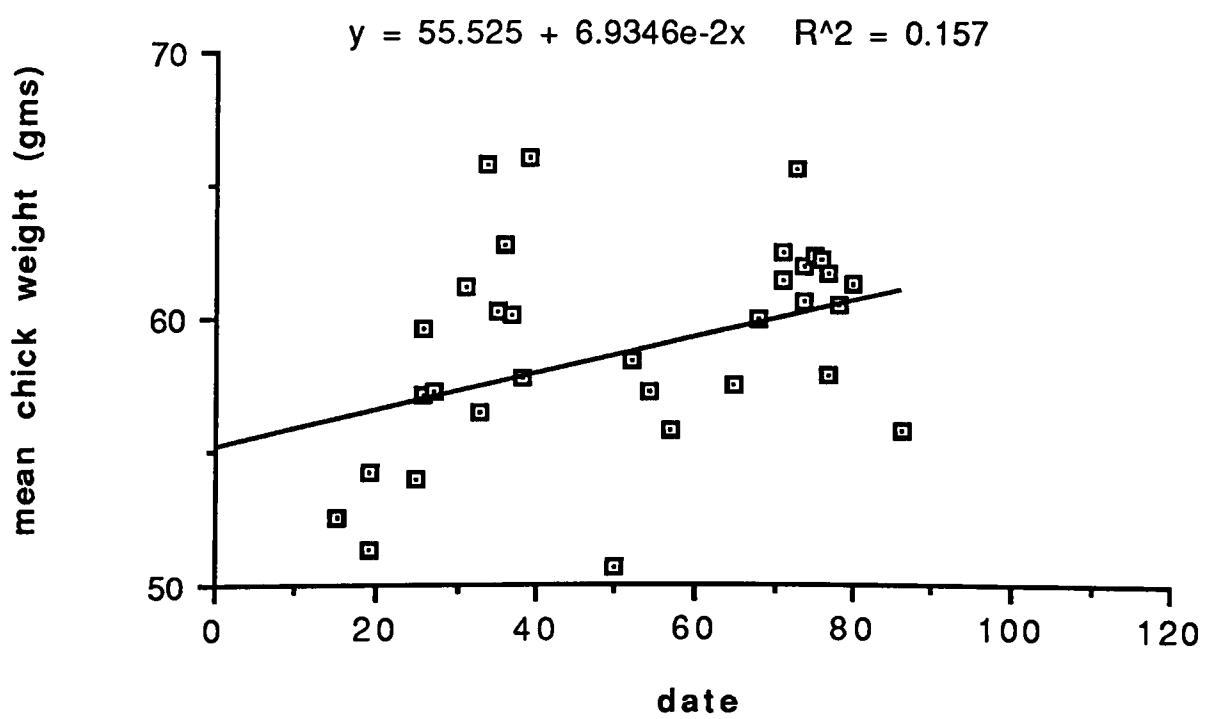


Figure 2.10: The effect of date on mean chick weight, where date 1 = 1/4.

which were fed by the same individuals. Table 2.2 showed that this analysis made no differences to the relationships with brood size or to differences between years. Therefore, in subsequent analyses, each nesting attempt was treated as an independent event.

Discussion

The variation in the length of breeding season between years was due more to variation in the timing of the final breeding attempt, rather than the onset of breeding. To some extent , this was probably due to the effects of rainfall on earthworm availability, particularly in 1991 when there was steady rainfall throughout June, a factor known to prolong breeding in blackbirds (Snow, 1958; Magrath, 1989).

The mean clutch size showed significant variation between years when the seasonal effect was controlled for, 1993 having consistently higher clutch size than the other two years. According to Lack's hypothesis, clutch size is adapted to be at its highest during the period of optimal conditions for raising young (usually food supply). Although 1991 had significantly lower mean temperatures than the other two years, there was no significant difference between 1992 and 1993 in measures of either rainfall or temperature. As these two measures are linked to earthworm availability (Desrochers, 1992; this study, Chapter 4), it seems unlikely that the difference in clutch size between 1993 and the other years was in any way linked to food supplies during the breeding season.

Högstedt (1981) showed that the clutch size of magpies *Pica pica* was significantly increased by the addition of food to territories before the start of the breeding season. Therefore, the condition of the laying female may influence early clutch size (although this has not been supported in the majority of species; Boutin, 1990). The harsher winter of 1991 may have meant that less food was available in the pre-laying period so that the energy demands of the female would have been greater. The greatest difference in clutch size was between 1993 and the other two years, so

Table 2.2: The effect of brood size and year on day eight nestling weight, comparing analyses using an 'independent' data set and a data set containing some repeated observations from the same parents.

Pearsons r given for brood size, F statistic from ANOVA given for year.

	BROOD SIZE	YEAR	n
independent	r=-0.12, P=0.32	$F_{2,71}$=0.61, P=0.55	74
non-independent	r=-0.03, P=0.82	$F_{2,83}$=1.08, P=0.35	86

minimum pre-season temperature (measured by the number of freezing days), rather than the average temperature, may be a better indicator of the harshness of the preceding winter (see Chapter 7 for the effects of a supplemental food supply).

As expected on the basis of other studies (Snow, 1958), predation was high. As cover has been shown to be an important component of reproductive success in blackbirds (Edwards, 1983), the seasonal increase in nesting cover throughout the breeding season due to the development of foliage would be expected to be accompanied by a concomitant increase in nesting success. The higher than expected success rate at the beginning of the season may have been due to the fact that early nests were at a low density (there was always a large variation between the date of first attempts), and would therefore be unprofitable prey for predators to search for. As the number of nests increases, they will become a more profitable prey item, and predators will develop a 'search-image' (Tinbergen et al., 1960) for them. By April when the majority of pairs have started nesting, but nesting cover is still not fully developed (pers. obs.), many predators may be actively searching for nests, which may explain the significantly lower success rate in this month.

Although there was significant variation in the amount of predation at different stages of the nesting cycle, the incidence of predation did not increase at later nesting stages as predicted. One problem with the analysis is that the degree of exposure that each nest was subject to could not be controlled for. There was a high variance in the amount of cover that each nest was exposed to, so it is possible that only well hidden nests survived up to hatching. If the results are considered as two separate groups, egg stage and nestling stage (i.e. 'good' and 'bad' nests), then predation does increase with an increase in activity at the nest.

Starvation was very rare compared to other studies (Snow, 1958; Magrath, 1989). This is probably a reflection of the greater overall abundance of prey in rural habitats, most studies having previously concentrated on urban populations. When starvation did occur, it tended to be higher in larger broods. This is probably due to the inability of the parents to provide enough food to eliminate sibling competition, and

brood reduction is facilitated by the establishment of hatching hierarchies due to hatching asynchrony, the degree of which is greater at higher brood sizes (Howe, 1976; Magrath, 1989). However, the incidence of starvation was very low, so in most cases it is probable that enough food was available.

Nestling weight did not vary significantly with brood size. Therefore it would appear that parents are able to adjust their effort according to brood demand. This may be linked with food supply, the adjustment only being possible when food is most abundant, a period that may coincide with the period of highest mean brood size (Snow, 1958; see also Chapters 3 and 4).

There was no evidence of higher weights in the middle of the season, as reported by Snow (1958). There was a significant effect of date in one year only (1993), which was due to low weights at the beginning of the season. The lack of significant variation across the season may be indicative of the interacting factors of clutch size and diet, which produce chicks of similar quality throughout the season. These factors will be discussed further in subsequent chapters.

Chapter 3

Nestling Provisioning I: Effects of Brood Size, Chick Age and Brooding.

Introduction

Von Haartman (1953) showed that parent pied flycatchers *Ficedula hypoleuca* adjusted their feeding rate according to the hunger level of the chicks, demand level being communicated by vocal cues. Larger broods and older chicks are likely to have greater feeding demands, thus parental provisioning should increase accordingly. But in many species there is either no increase in provisioning with brood size, or there is a small increase which is not proportionate to brood size (see review in Klomp, 1970). Lack (1954) suggested that this was due to parental effort reaching a maximum at average brood sizes (fig. 3.1).

If at higher brood sizes the demands of the nestlings exceed the parents' provisioning abilities, then an inverse relationship between measures of individual chick quality and brood size will be expected. This has been shown to be the case in some species e.g starling *Sturnus vulgaris* (Lack, 1948), house wren *Troglodytes aedon* (Arnold, 1993) and Paridae (Lack, 1950). However other studies have shown that the existence of a relationship may depend on factors such as food abundance (e.g. Lack et al., 1957; Dunnet, 1955), or whether broods are above average in size (e.g. Royama, 1966). Additionally, some authors have not detected an upper limit to parental feeding frequency within the natural range of brood sizes (e.g. Nur, 1984).

Royama (1966) suggested that provisioning did not increase in proportion to brood size due to decreased energy expenditure per individual nestling in larger broods, rather than a limit to parental ability. A large brood will effectively have a lower surface area to volume ratio than a small brood, thus the heat loss per unit of mass will be less, and consequently chick demand for food will be lower than that expected on the basis of the numbers alone. This idea has received experimental support (Mertens, 1969; O'Connor, 1975), although Nur (1984) suggested that, in the blue tit *Parus caeruleus* at least, the effect may only be apparent at smaller than average brood sizes.

Provisioning typically increases with chick age up to a point, usually close to fledging, and then either levels off or decreases (e.g. Royama, 1966; Seel, 1969; Westerterp, 1973; Hails and Bryant, 1979; Tinbergen, 1981). The reason for this

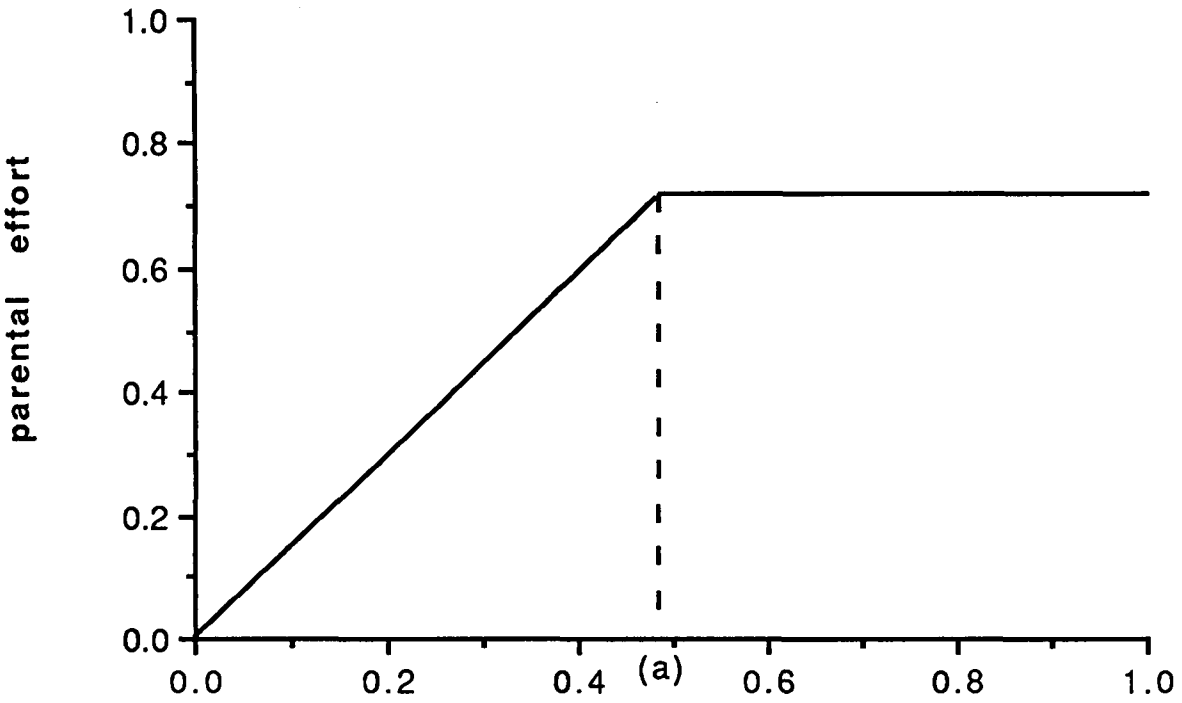


Figure 3.1: Parental effort reaches a maximum at a certain level of nestling demand (a), where demand may be brood size or chick age. Units are arbitrary.

common observation has been put down to the development of full homiothermy, as the levelling-off period tends to coincide with the development of the feathers, in addition to other physiological changes (O'Connor, 1975). Chick growth curves show a similar pattern, being sigmoidal in most species of bird (O'Connor, 1984; this study, Chapter 2), the decrease in the rate of chick growth paralleling the decrease in feeding rate.

The amount of brooding done by the female tends to show a negative linear relationship with the age of the chick (Skutch, 1976). This is probably related both to the greater degree of thermoregulation in older chicks, but also the greater foraging demands on the parents. Similarly a negative relationship between brooding and brood size may be expected, though this may not be apparent at early ages when demand is low and chicks are almost wholly ectothermic (O'Connor, 1975).

This chapter analyses both provisioning and brooding in parent blackbirds in relation to brood size and the age of the chicks. As ambient temperature can affect the age at which homoiothermy is possible (O'Connor, 1975), this is also considered.

Methods

The methods used for the determination of reproductive success and nestling provisioning used in this chapter are detailed in Chapter 1.

Results

1. Nestling Provisioning

For the majority of nest watches, the size and composition of individual loads could be determined (1966 out of 2300 deliveries). The size of a further 311 loads was estimated based on averages of known load sizes. In 23 cases only a rough estimation of load size could be made. These were classified into small, medium and large loads. The calculation of these values was based on dividing the distribution of all load sizes from twelve hour samples into approximately equal thirds (fig. 3.2). Any load that was classified as small, medium or large had a mean value calculated for it based on all

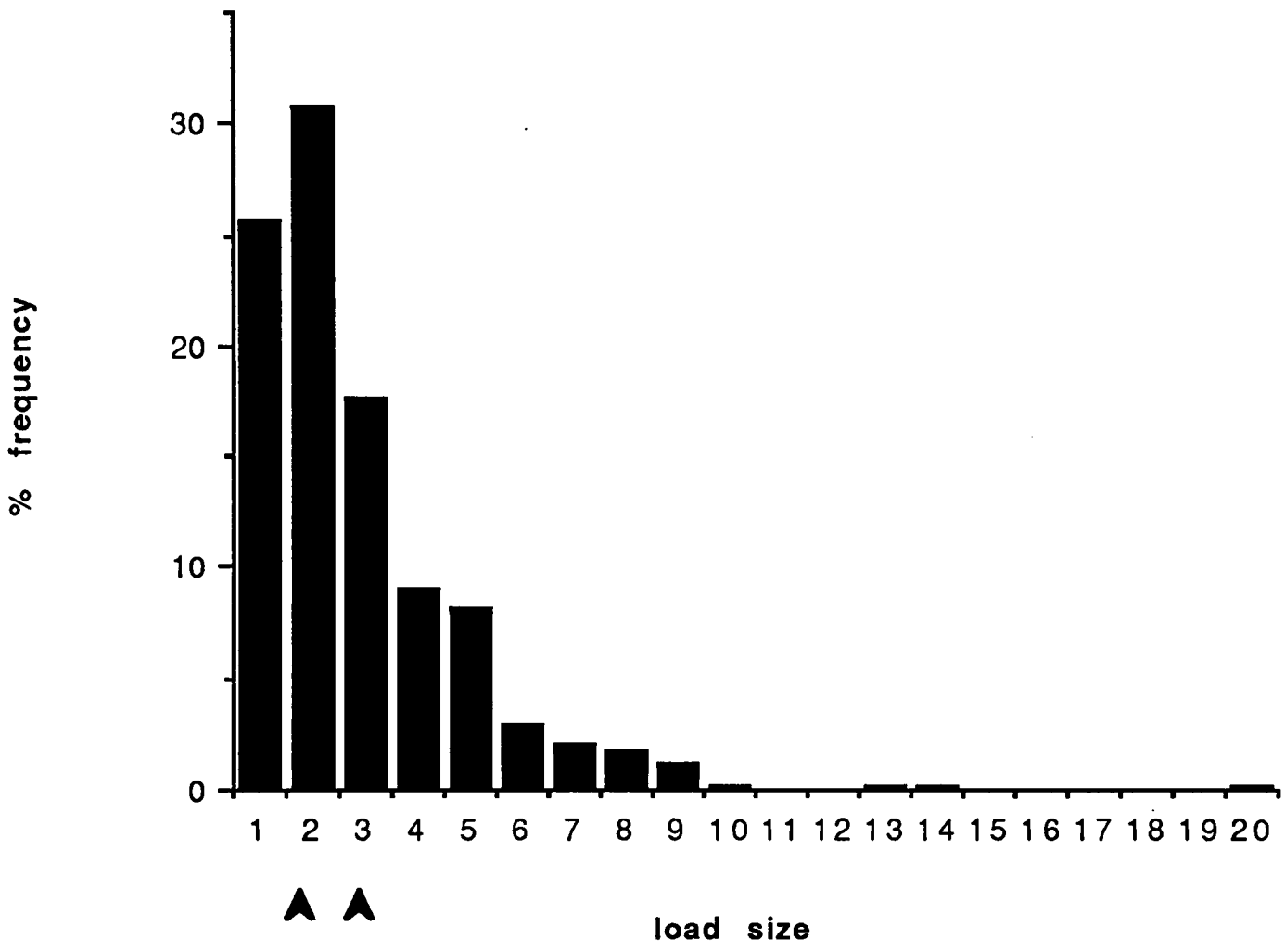


Figure 3.2: The frequency distribution of load sizes taken from twelve hour watches. Each interval = 350 calories. Total sample size = 847. Arrows represent approximately 33% of the data.

observations (for that particular nest) which fell within the appropriate third in figure 3.2.

In some cases a very small load was delivered, the exact composition of which could not be determined (n=73), even though a good view of the parent was obtained. In these cases the average value of all identified deliveries of under 100 calories was used (mean = 61±26, n=42).

Sometimes it was impossible to determine load size (for example, because a parent delivered with its back to the observer). This occurred in 238 out of a total of 2300 deliveries (years combined). When analysing total calories delivered per 12 hour watch period, mean values were used in place of missing observations. These were calculated by taking the mean of the previous ten deliveries and the subsequent ten deliveries from the missing value (totals were only calculated in this way if missing values made up less than 10% of the total). Otherwise data from shorter watch periods with missing values were not used for the analyses in this chapter.

(i) Sex Differences

Over all chick ages, males tended to have a higher energy delivery rate to the nest than females (paired t-test: t=4.71, df=87, P=0.0001; male mean=4134±3274 cal/hr; female mean=2625 ±2936 cal/hr). As the relative contributions of the parents may differ with the age of the chick (for example, females brood more when chicks are younger; this study, see Section 3.3) it is more accurate to consider sex differences in relation to chick age. This shows that males tended to deliver significantly more energy to the nest at all but the most extreme ages, when differences were not significant (Table 3.1). The pattern is similar for two hour sample times, although oddly, little or no significant differences were detected at ages 7 and 8 (Table 3.2).

There was also a highly significant difference between male and female energy delivery rates for twelve hour sample periods (paired t-test: df=16, t=2.62, P<0.001). Given the above differences and the fact that females may be more constrained in their

Table 3.1: Paired t-tests between male and female provisioning rates (cal/hr±standard deviation) at different chick ages for 1 hour sample times. Negative t-values represent higher female mean provisioning rates, and positive values indicate higher male mean provisioning rates. Years are combined.
(*)0.10>P>0.05, **0.05>P>0.01, ***P<0.01.

CHICK AGE	MALE	FEMALE	PAIRED t	NO. PAIRS
1	143±191	468±1035	-0.76	6
2	427±387	145±197	2.22(*)	9
3	1291±1756	406±690	1.72	11
4	1526±2134	264±264	3.23***	15
5	1602±1830	491±571	2.97***	20
6	2382±1984	1339±1310	2.59**	17
7	2100±1298	1343±1673	4.72***	18
8	1894±1230	885±1026	3.09***	18
9	1995±1899	1064±1310	3.59***	17
10	2353±1964	1206±725	2.24**	12
11	1274±1453	612±449	1.11	6

Table 3.2: Paired t-tests between male and female provisioning rates (cal/2hr±standard deviation) at different chick ages for 2 hour sample times. Negative t-values represent higher female mean provisioning rates, and positive values indicate higher male mean provisioning rates. Years are combined.
(*)0.10>P>0.05, **0.05>P>0.01, ***P<0.01.

CHICK AGE	MALE	FEMALE	PAIRED t	NO. PAIRS
3	1256±1309	369±253	1.50	3
4	2134±1763	1169±1152	0.94	6
5	3832±26470	1191±767	2.96**	10
6	4612±3315	1852±1840	4.22***	9
7	4509±2744	2680±1937	2.08(*)	9
8	4124±1848	2144±2177	1.61	8
9	4833±2492	2027±1447	4.30***	12
10	4819±1592	1450±764	4.33***	6

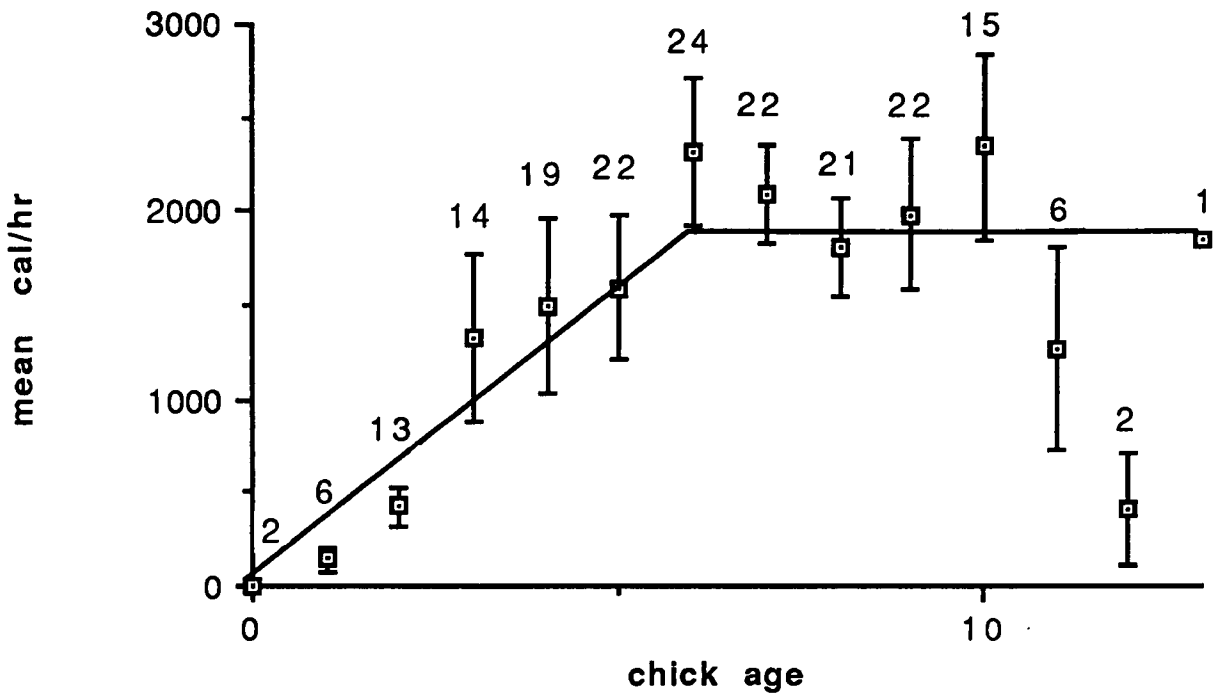
provisioning, all further analyses will consider sexes separately, in addition to considering total (sexes combined) provisioning.

(ii) The Effects of Chick Age

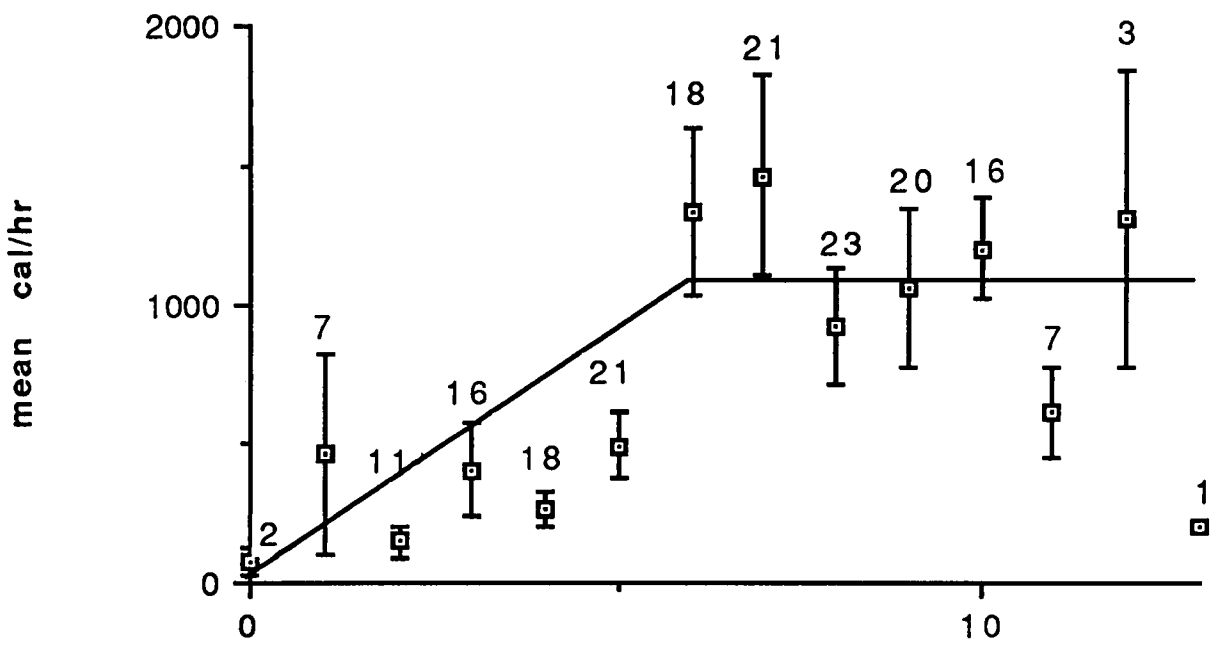
Male, female and total energy delivery rates were significantly correlated with chick age at both one hour (correlation: male r=0.32, df=187, P<0.0001; female r=0.27, df=182, P<0.001; total r=0.40, df=151, P<0.0001) and two hour sample times (regression: male r=0.30, df=79, P<0.006; female r=0.31, df=81, P=0.02; total r=0.31, df=61, P=0.01). F-tests revealed that in the one hour samples, a quadratic expression was a significantly better fit than a linear one for male and total delivery rates, but in females, delivery rates were more accurately described by a linear function (male $F_{1,188}$=10.54, P<0.01; female $F_{1,183}$=3.31, P>0.10; total $F_{1,153}$=10.10, P<0.01). Conversely, for two hour sample periods, male and total delivery rates were best described by linear functions and female delivery rates were best described by a quadratic function (male $F_{1,80}$=2.99, P>0.10; female $F_{1,82}$=5.50, 0.05>P>0.01; total $F_{1,62}$=3.73, P>0.10). Whether a relationship is linear or not seems to depend on whether there were high or low values at the older age groups. As there were fewer data gathered at these ages (10 and 11 especially), it is probably more accurate to say that there tends to be a levelling-off in feeding rate, which occurs at around day 6 (compare fig. 3.1).

To test this further, regression analysis was carried out on delivery rates divided into two age groups, 0-6 and 7-13. As suspected, there was a significant linear increase in feeding rate with age in the younger age group for one hour samples (male r=0.37, df=97, P<0.001; female r=0.34, df=91, P=0.001; total 0.46, df=77, P<0.001- fig. 3.3), and in all but one of the two hour samples (male r=0.47, df=35, P=0.003; female r=0.31, df=34, P=0.07; total r=0.52, df=27, P=0.004- fig. 3.4). In the older age group there was no significant relationship between delivery rate and age in either one hour (male r=0.01, df=90, P=0.91; female r=-0.08, df=89, P=0.44; total r=-0.10, df=72, P=0.41- fig. 3.3) or two hour sample times (male r=0.08, df=44, P=0.58;

(A) male



(B) female



(C) total

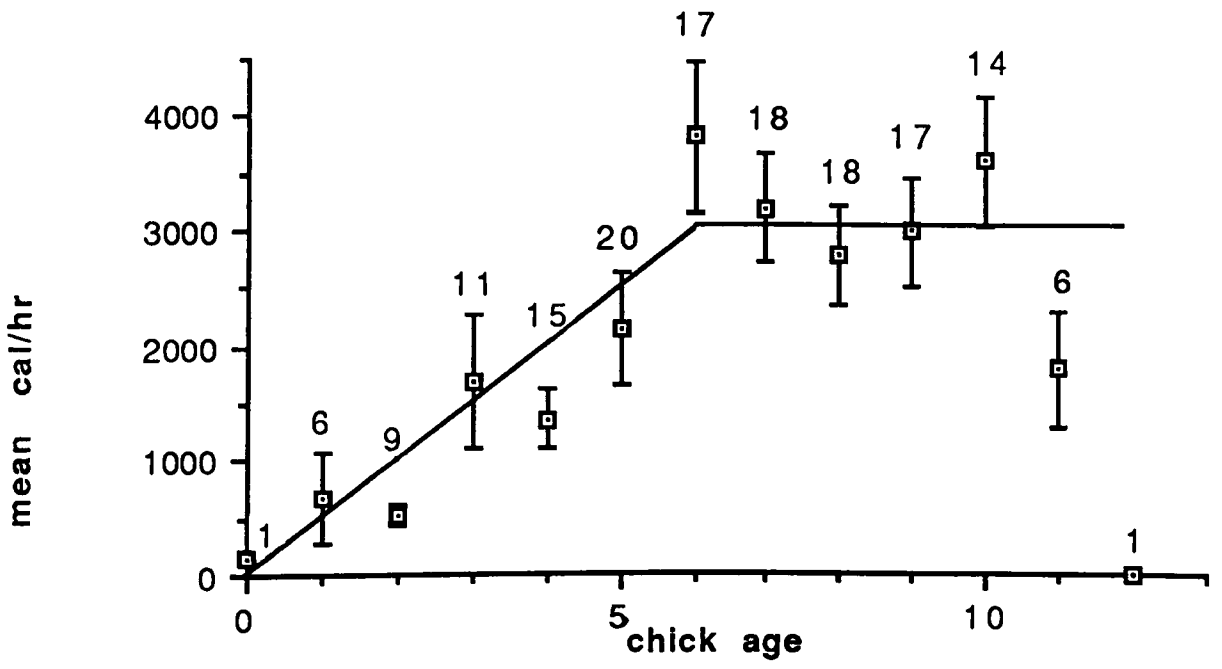
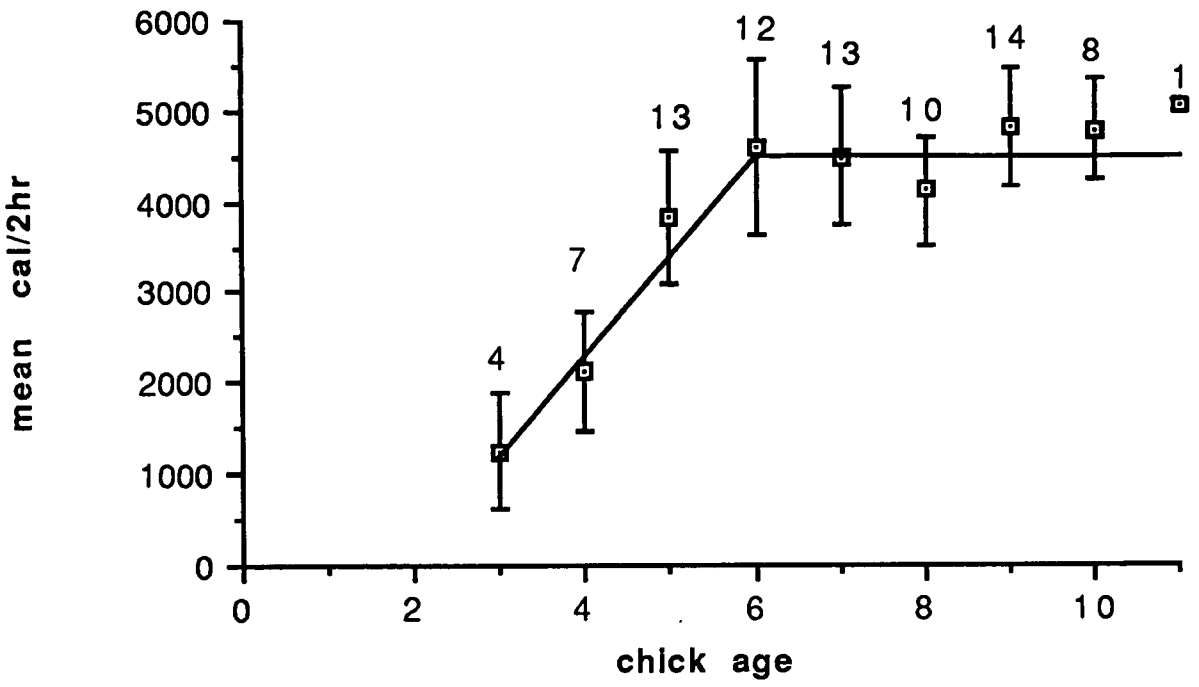
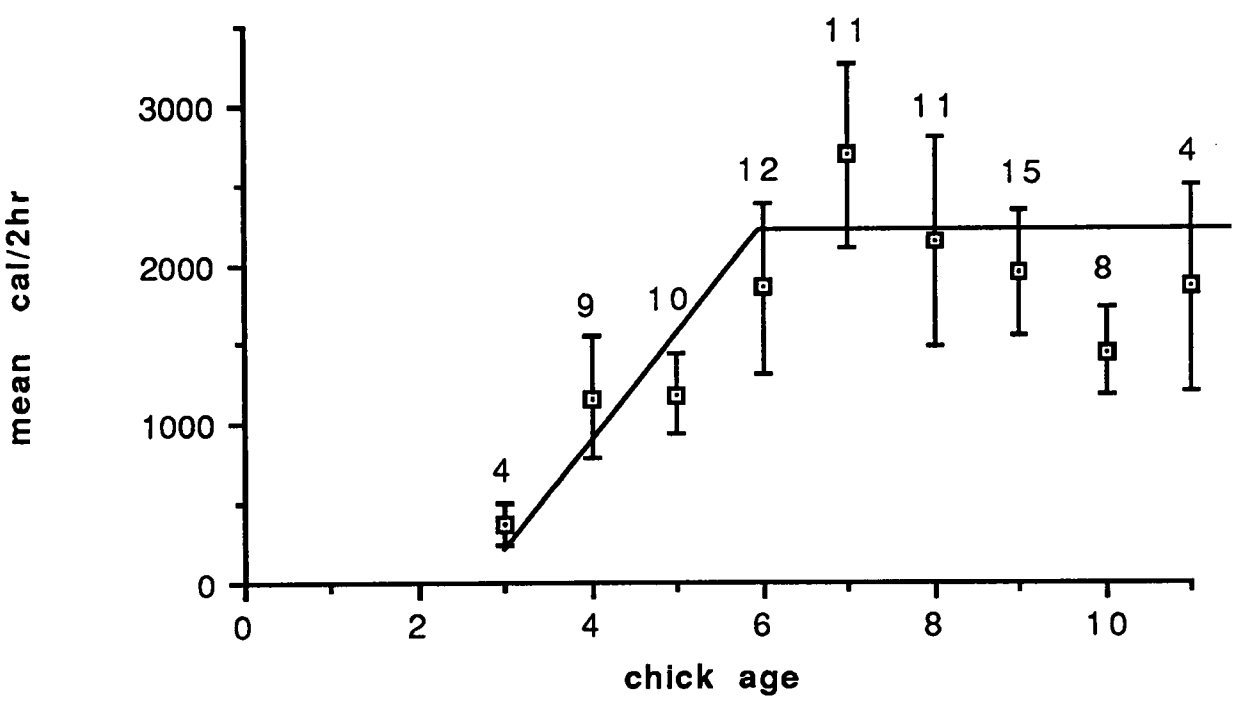


Figure 3.3: The effect of chick age on hourly nestling provisioning. Means and standard error bars are given. Numbers above means represent sample sizes. Lines were fitted by eye.

(A) Male



(B) Female



(C) Total

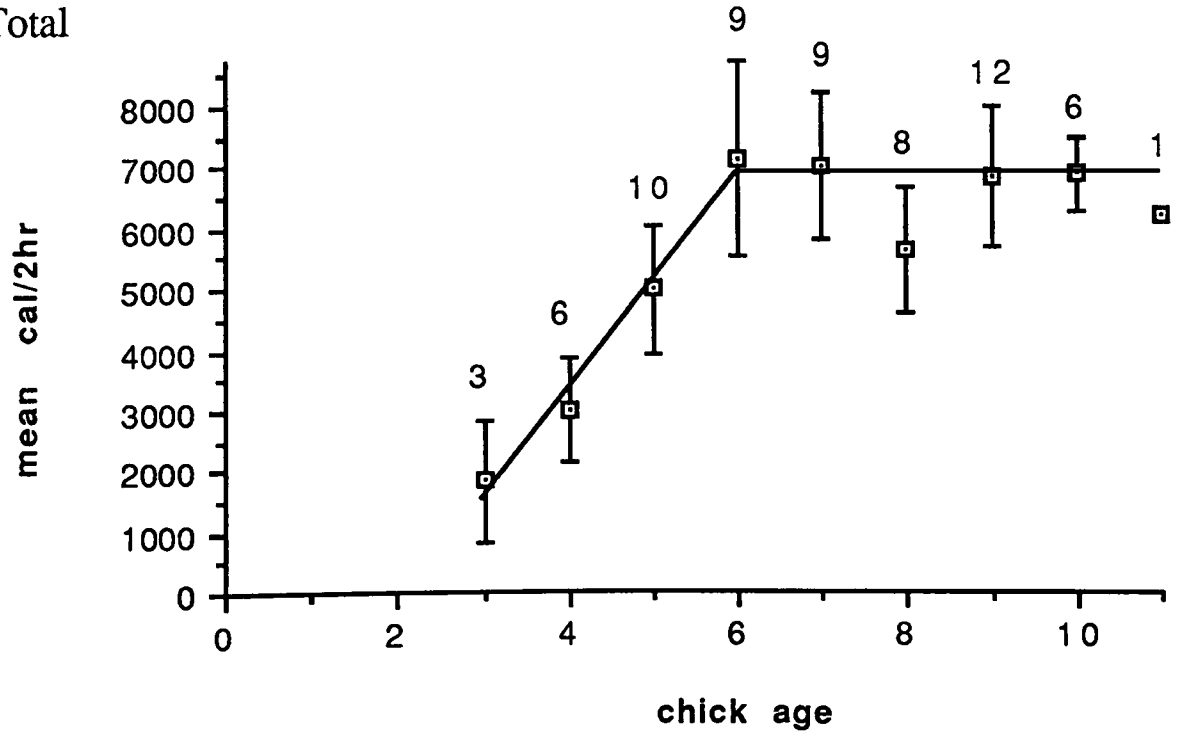


Figure 3.4: The effect of chick age on two-hourly nestling provisioning. Means and standard error bars are presented. Numbers above means represent sample sizes. Lines were fitted by eye.

female r=-0.21, df=47, P=0.14; total r=0.01, df=34, P=0.96- fig. 3.4). These results therefore indicate that provisioning does indeed reach an asymptote at day six.

Further analyses will not control for age when considering energy delivery rates from beyond the point of inflection (day 6) onwards. Instead, mean rates from day 7 onwards will be used, giving a single value for each nest. This will of course entail losing some information, but handling the data in this way enables easier analysis and avoids potential statistical problems such as pseudoreplication (Hurlbert, 1984). However, when considering individual loads (Section 1(iv)), there were often large differences in the sample sizes that the means were calculated from. In order to reduce the influence of means from small samples, only means calculated from at least ten observations are used.

(iii) The Effect of Brood Size

The effect of brood size on calorific delivery rate was analysed at each age group for both sexes separately, and for total delivery rates. Note that total delivery rate was calculated as male + female delivery rate from the same watch period. It was uncommon to record adequate provisioning data from both male and female per nest, thus sample sizes for total delivery rate will be *at most* equal to the smallest individual sample size for a given age.

Significant effects of brood size were found on both female and total mean delivery rate between ages 7 and 12, but not earlier at the one hour sample period (Table 3.3). At the two hour sample period, more significant results were obtained at different ages, but again the age period 7-12 showed the most significant results, male, female and total delivery rates being significantly correlated with age (Table 3.4). (Note that in addition to smaller sample sizes, two hour watches had no data available at chick ages 1 and 2).

For twelve hour watch periods there was a significant positive relationship in males (linear regression: r=0.56, df=12, P=0.04) and a positive, although non-significant, trend in females (r=0.51, df=11, P=0.07). As in two-hour sample periods,

Table 3.3: The effect of brood size on hourly provisioning rates (cal/hr). Pearson's correlation coefficients (r) and sample sizes are given. Note that mean cal/hr from day 7-12 is used. (*)0.10>P>0.05, **0.05>P>0.01, ***P<0.01.

CHICK AGE	MALE r	n	FEMALE r	n	TOTAL r	n
1	0.31	6	0.05	7	0.10	6
2	-0.21	13	0.40	11	-0.10	9
3	0.27	14	0.11	16	0.24	11
4	0.36	18	0.38	18	0.50(*)	15
5	0.30	22	0.07	21	0.31	20
6	0.23	24	0.01	18	0.17	17
7-12	0.27	34	0.47***	33	0.38**	29

Table 3.4: The effect of brood size on two-hourly provisioning rates (cal/2hr). Pearson's correlation coefficients (r) and sample sizes given. Note that mean cal/2hr from day 7-12 is used. (*)0.10>P>0.05, **0.05>P>0.01, ***P<0.01.

CHICK AGE	MALE r	n	FEMALE r	n	TOTAL r	n
3	0.67	4	0.98**	4	0.70	3
4	0.15	7	0.24	9	0.17	6
5	0.70***	13	0.11	10	0.67**	10
6	-0.08	12	-0.15	12	-0.05	9
7-12	0.60***	27	0.54***	25	0.73***	24

brood size had the most significant effect on combined delivery rates (r=0.80, df=11, P=0.002). Note that no adjustment for chick age is made in the above analysis as previous analyses indicated that there was no effect of age on provisioning rates at ages 7-12, when all day watches were carried out.

The results therefore indicate that provisioning is adjusted to the size of the brood at older ages, when feeding has reached its highest rate. This relationship was particularly strong when considering the total calories delivered by both parents within a given watch period. In subsequent analyses the effect of brood size on delivery rate will be corrected to brood size four (the mean brood size - see Chapter 2) by using the slopes of the significant regressions presented above.

(iv) Provisioning Efficiency

In certain cases it may be more appropriate to consider nestling provisioning in terms of the delivery efficiency (energy delivered per unit time spent away from the nest) of individual loads. Generally, mean delivery efficiencies should produce similar results to using total calories per hour. However, they are more appropriate if we wish to compare the efficiencies of different prey types, particularly for data from the same nest. Therefore in this section, the effects of brood size on delivery efficiency are considered, mainly in order to make the necessary corrections for the more detailed analyses presented in Chapters 4 and 5.

Figure 3.5 shows the frequency distribution of all intervisit times recorded from 12 hour watches. The vast majority (97.6% in both males and females) of intervisit times are below an hour. However, it was considered that too few inter-visit times could be recorded from one hour samples (for example, a bird delivering twice in an hour would only have one inter-visit time recorded). Therefore, for the analysis of inter-visit times and delivery efficiencies, only data from two and twelve hour samples are used. As the amount of calories delivered per load is unlikely to be affected by sampling period, this analysis uses data from all watch periods.

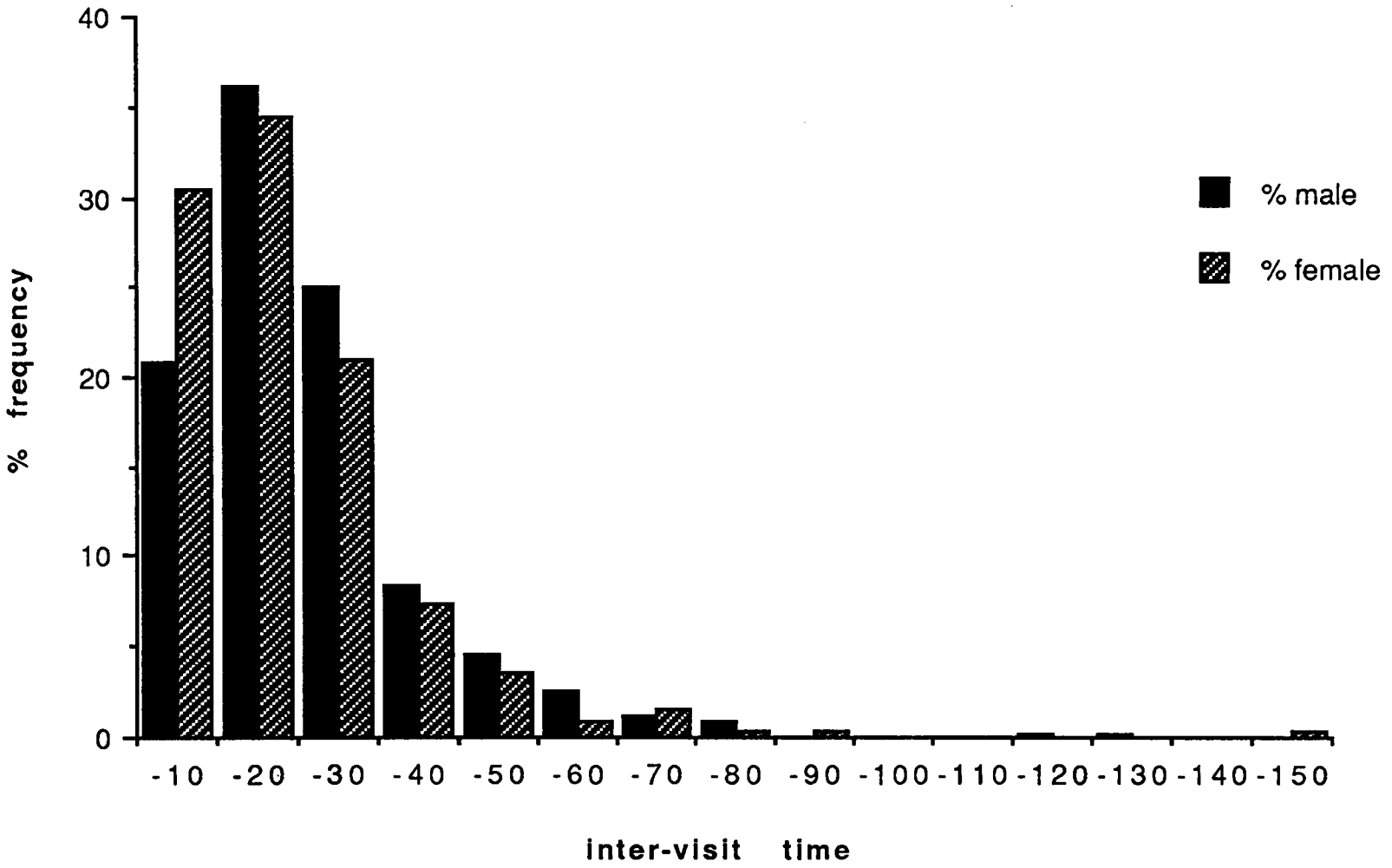


Figure 3.5: The frequency distribution of inter-feed intervals from twelve hour sample periods. Sample sizes: male n=561, female n=391.

There was no significant effect of brood size on inter-visit times in either males or females between ages 7-12, although males did show quite a strong positive trend (linear regression: male r=0.36, df=26, P=0.06; female r=-0.04, df=23, P=0.87). This contrasts with the results for calories per watch period where highly significant relationships were found. This shows that measures of visit rate (i.e. inter-visit period) are not necessarily good measures of true energy delivery rate.

Considering mean calories per load, there was a significant positive effect of brood size in females (r=0.43, df=20, P=0.03) but not males (r=0.16, df=24, P=0.43). Combining the two measures of load size and inter-visit time produces a measure of delivery efficiency, calculated by dividing the calories delivered by the preceding inter-visit time. Mean delivery efficiency was not significantly affected by brood size, although a positive trend was shown in females (male r=0.25, df=24, P=0.23; female r=0.38, df=21, P=0.07).

As before, all significant (P<0.05) results will be used to correct to a standard brood size of four in subsequent analyses.

(v) Non-independent data

A total of 48 nests were watched for at least one hour during the three years. One problem with analysis of the data collected is that some observed nests had the same parents, either within a season, or between years. In 1991 this was the case in four pairs of nests, in 1992, one pair, and in 1993, one pair and one trio (i.e. three nests from the same pair were watched). Between years, there were eight individuals which had nests observed in two of the three years, and two individuals which had nests watched in all three years.

Strictly speaking, data gathered from different nests but from the same individual bird(s) should not be used in the same data set as they are not independent. However, this problem will be minimised if variation between individuals is no greater than variation within individuals (i.e. the effects of independent variables are the same

within and between individuals; see Davies and Hatchwell, 1992 for treatment of a similar problem).

One effect non-independent data may have on an analysis is an increase in the likelihood of type I errors. If this is occurring, then omitting non-independent data points should decrease significance. Table 3.5 shows a repeat analysis of the effect of brood size on provisioning variables at ages 7-12, but only one value was allowed from each individual bird, rejected values being chosen at random. Comparison with results from the full data set shows that the non-independent data had very little effect on the significance of relationships. Inclusion of this type of data is therefore unlikely to markedly affect the outcome of analyses. All future analyses will consider each individual nest as an independent event.

2. Brooding

There were significant negative relationships between the proportion of time spent brooding per watch period (expressed as an arcsine squareroute function to normalise the data, Zar, 1984) and brood size at ages 5 and 7-10 for 1 hour samples (Table 3.6). Similarly, there were significant effects at age 7, 9 and 10 in two hour samples (Table 3.7), and a significant effect with twelve hour samples ($r=-0.65$, $df=14$, $P=0.006$). All subsequent analyses involving the proportion of time spent brooding will be corrected to brood size 4 (the total mean brood size- see Chapter 2) using regression equations from the significant results presented.

As females tended to brood less with higher brood sizes, a negative relationship between inter-visit time and brood size may be expected, but this was not observed. However, when at the nest, a female would sometimes either just sit at the nest rim or spend periods apparently either repairing or adjusting the nest lining rather than actually brooding. The effect of this may have been enough to make female inter-visit times and time spent brooding effectively independent of one-another.

There was a significant decrease in brooding per hour with chick age (fig. 3.6) for both one hour (linear regression: $r=-0.62$, $df=47$, $P<0.0001$) and two hour (linear

Table 3.5: The effects of brood size on provisioning parameters at chick ages 7-12, comparing the full data set with a data set where repeated observations (i.e from the same individual birds) have been removed.

Pearsons correlation coefficients and sample sizes are given.

(*)0.10>P>0.05, **0.05>P>0.01, ***P<0.01.

		REPEATS OMITTED		FULL DATA SET	
		Pearsons r	n	Pearsons r	n
cal/hr	m	0.19	29	0.27	34
	f	0.44**	24	0.47***	33
cal/2hr	m	0.58***	22	0.60***	27
	f	0.50***	19	0.54***	25
cal/load	m	0.10	23	0.16	26
	f	0.47**	21	0.43**	25
inter-visit	m	-0.39(*)	24	-0.36(*)	28
time	f	0.03	21	-0.04	25
cal/inter- visit	m	0.23	25	0.25	26
time	f	0.37	19	0.38(*)	23

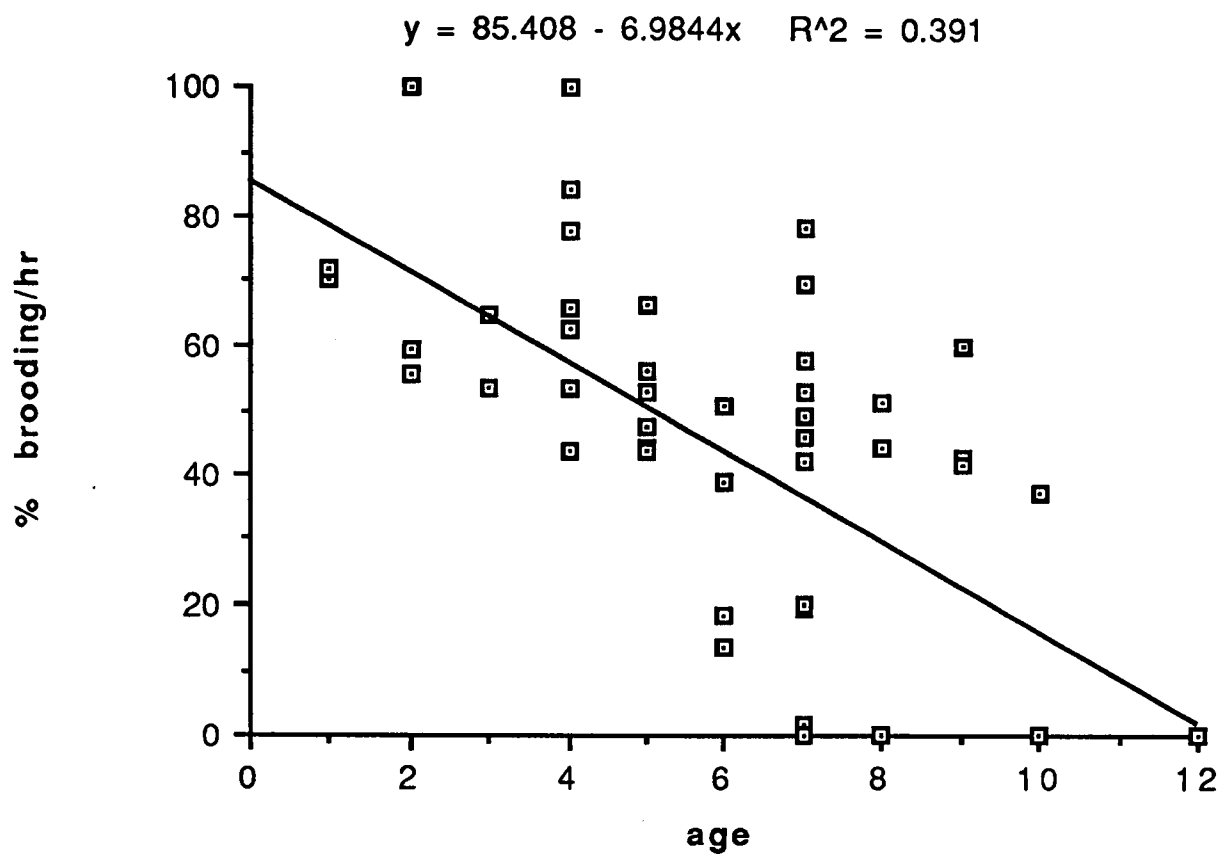
Table 3.6: The effects of brood size on brooding (arcsine (sqrt. min./hr)). Pearson's correlation coefficients (r) and sample sizes given. Brooding/hr transformed to arcsine (brooding/hr). **0.05>P>0.01, ***P<0.01.

CHICK AGE	BROODING r	n
2	0.04	14
3	0.22	21
4	0.24	27
5	-0.46**	28
6	-0.10	29
7	-0.36**	31
8	-0.60**	30
9	-0.66***	27
10	-0.56**	21
11	-0.38	14

Table 3.7: The effects of brood size on brooding (arcsine (sqrt. min./2hr)). Pearson's correlation coefficients (r) and sample sizes given. Brooding/hr transformed to arcsine (brooding/2hr). **0.05>P>0.01, ***P<0.01.

CHICK AGE	BROODING r	n
3	-0.62	5
4	0.12	10
5	-0.28	12
6	-0.39	17
7	-0.47**	18
8	-0.31	20
9	-0.69***	16
10	-0.75**	8

(A) One hour samples



(B) Two hour samples

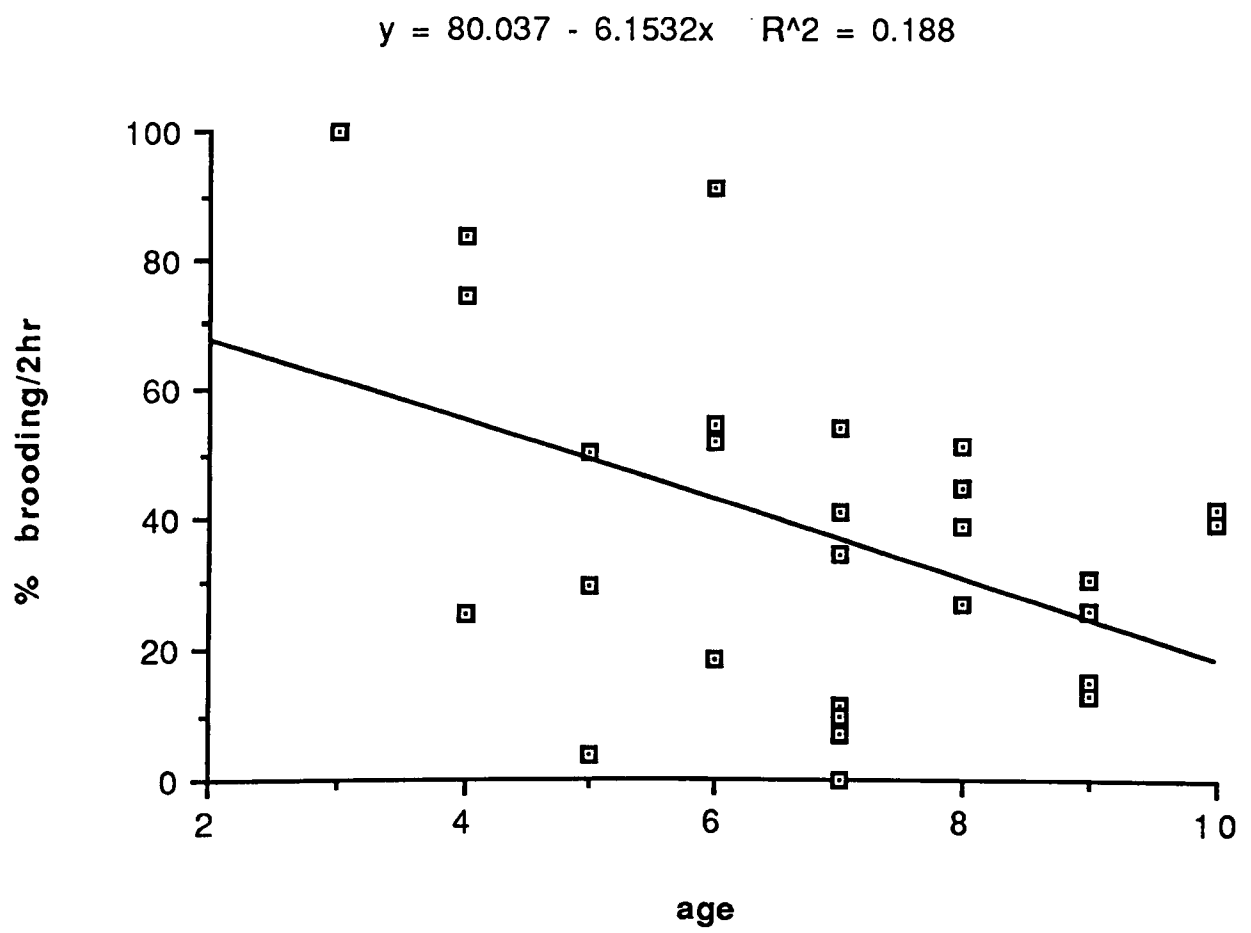


Figure 3.6: The effect of chick age on brooding at (A) one hour, and (B) two hour sample times. Note that only one data point per nest (chosen at random) appears in each analysis.

regression: r=-0.42, df=29, P=0.02) sample times, where percentages were transformed with the arcsine function for the analysis. Note that in figure 3.6 only one data point (chosen at random) was used per nest in each analysis in order to avoid pseudoreplication.

3. Effects of Ambient Temperature

At lower temperatures the energy requirements of the chicks are likely to be high in order to maintain body heat. As young chicks are unable to maintain their body temperature, the female may have to do more brooding at lower ambient air temperatures. When chicks are older, greater energy demands of the nestlings at low temperatures may lead to a higher provisioning rate by the parents.

Only at a few age groups were there significant relationships between hourly provisioning rates and mean morning temperature (Table 3.8). The lack of consistent trends in the results, and the fact that the directions of the significant relationships are different in males and females, means that these results should be viewed with some caution. No significant effects of temperature on two-hourly provisioning rates were found (Table 3.9).

Temperature tended to have a negative effect on the proportion of time spent brooding per hour when the effect of brood size was controlled for, although the effect was significant only at chick ages 2, 6, 7 and 11 (Table 3.10). There were similar negative relationships between temperature and the proportion of time brooding from two hour samples, although significance was observed only at ages 5 and 6 (Table 3.11).

Discussion

The observed increase in energy delivery rate up to day 6 could either be indicative of an upper limit to parental provisioning ability, or of chick demand reaching a constant level. As parents were able to vary provisioning rate with brood size from

Table 3.8: The effects of mean morning air temperature on hourly provisioning rates (cal./hr). Pearson's correlation coefficients (r) and sample sizes given. Note that mean cal/hr between day 7-12 is used, adjusted for the effects of brood size where appropriate (see 3.2). (*)0.10>P>0.05, **0.05>P>0.01, ***P<0.01.

CHICK AGE	MALE r	n	FEMALE r	n	TOTAL r	n
1	0.56	6	-0.29	7	-0.17	6
2	-0.11	13	-0.04	11	-0.10	9
3	0.61**	14	-0.51**	16	0.58(*)	11
4	-0.01	18	-0.29	18	-0.21	15
5	-0.21	22	-0.03	21	-0.21	20
6	0.03	24	-0.19	18	0.04	17
7-12	-0.08	34	0.01	33	-0.10	29

Table 3.9: The effects of mean morning air temperature on two-hourly provisioning rates (cal./2hr). Pearson's correlation coefficients (r) and sample sizes given. Mean cal/hr between day 7-12 is used, adjusted for brood size where appropriate (see 3.2). Note that there were too few data to carry out regression of total provisioning rate at age 3. **0.05>P>0.01, ***P<0.01.

CHICK AGE	MALE r	n	FEMALE r	n	TOTAL r	n
3	0.44	4	-0.46	4	n/a	
4	0.32	7	0.37	9	0.49	6
5	-0.33	13	-0.15	10	-0.30	10
6	-0.30	12	-0.08	12	-0.19	9
7-12	-0.22	27	-0.02	25	-0.31	24

Table 3.10: The effects of ambient air temperature on brooding (arcsine min./hr). Pearson's correlation coefficients (r) and sample sizes given. Brooding/hr transformed to arcsine (brooding/hr).**0.05>P>0.01, ***P<0.01.

CHICK AGE	BROODING r	n
2	-0.58**	14
3	0.29	21
4	-0.19	27
5	-0.17	28
6	-0.37**	29
7	-0.40**	31
8	-0.08	30
9	0.10	27
10	-0.16	21
11	-0.60**	14

Table 3.11: The effects of ambient air temperature on brooding (arcsine min./2hr). Pearsons correlation coefficients (r) and sample sizes given. Brooding/2hr transformed to arcsine (brooding/2hr).**0.05>P>0.01, ***P<0.01.

CHICK AGE	BROODING r	n
3	-0.07	5
4	-0.12	10
5	-0.61**	12
6	-0.59**	17
7	-0.21	18
8	-0.12	20
9	-0.08	16
10	-0.32	8

day 7 onwards, the former hypothesis can be rejected. The developement of homoiothermy, through physiological changes or feather growth (O'Connor, 1975) could be a factor in the occurrence of this provisioning 'plateau', although an additional factor may be that chick growth is relatively slow after day 6 (Chapter 2). This alone would lead to a prediction of a decrease in chick demand, which there was some evidence for, although the trend was not statistically significant. It is possible that larger body size leads to higher metabolic costs, for example, due to increased chick mobility, thus demand is maintained at a constant level, even though weight increases only slowly.

After day 6, brood size rather than chick age is the important component affecting parental provisioning. Both males and females delivered more energy to the nest per unit time at higher brood sizes, although this was achieved differently in each sex, the males increasing visit rate (i.e. decreasing inter-visit time), and the females increasing load size. These observations were supported by the fact that there was no relationship between chick weight and brood size (Chapter 2), showing the effect of increased parental effort on chick quality.

In common with provisioning, brooding was only affected by brood size at older age groups. The negative effect observed may have been due to an increase in female provisioning rates, although this seems unlikely as female inter-visit time was not affected by brood size, this surprising result being due to the female often attending the nest rather than actually brooding. An alternative, although not mutually exclusive explanation is that chicks in a larger brood expend less energy as the brood has a lower surface area to volume ratio (Royama, 1966), so brooding is not needed. Indeed, there may even be a risk of hyperthermia at high brood sizes (Mertens, 1969) in warmer temperatures. Quite why a female should sometimes spend long periods tending the nest rather than foraging is unclear.

When brood size was controlled for, there tended to be a negative effect of temperature on brooding, although this showed no consistent pattern with age. There was no relationship observed at ages 8, 9 and 10, peak feeding ages, but there were

significant effects at ages 5, 6 (1 and 2 hour samples) and 7 (2 hour only). After day 7, either the increase in feeding rate, or the increase in the chicks capacity for thermoregulation (O'Connor, 1975) may have meant that the effect of temperature became negligible.

There was no effect of temperature on provisioning by either parent when brood size was controlled for. Energy expenditure of chicks increases with a decrease in temperature (Westerterp, 1973), so some increase in energy uptake by the chicks was expected. This appears to have been achieved through brooding rather than feeding, at least at ages 5, 6 and 7, which although involving some energy expenditure of the female, may be less expensive than foraging.

A further factor not considered in this chapter is the effect of diet. The increase in energy delivery rate with brood size may to some extent be linked to the abundance of food. Most birds will be adapted to time their breeding season so that the period of maximum food abundance coincides with the period of highest brood energy demands (Lack, 1954), or in the case of the blackbird, the largest brood size. If higher food supplies do coincide with the largest broods, then food abundance must also be considered as a factor in parental provisioning ability.

Previous studies have tended to concentrate on either single brooded species or species with high natural ranges of brood size (often experimentally manipulated), especially in the Paridae (e.g. Lack, 1950; Royama, 1966; Nur, 1984). The lack of any evidence for an upper limit to feeding rates in the blackbird may therefore only be apparent if the whole range of brood sizes were available for comparison within a short period with fairly constant conditions, a situation which does not arise naturally[1].

In conclusion, it appears that blackbirds do not have an upper limit to provisioning effort within the natural range of brood sizes. Instead, they are able to adjust their provisioning according to the level of chick demand, thus chicks are at no disadvantage from being in larger broods in terms of the effort supplied by the parents

---

[1]A brood manipulation experiment was planned to be carried out on first broods in 1993, whereby broods were to be artificially increased. However, the high predation rate in the chosen study area made this impossible.

(although there was evidence of a greater risk of starvation in higher broods, which is probably more closely associated with the establishment of nestling age hierarchies- see Chapter 2). Brooding is adjusted in relation to the thermoregulatory requirements of the chicks in a similar manner, with ambient temperature also having some effect. The available diet type and prey abundance may also have effects on the above relationships. These will be dealt with in the next chapter.

Chapter 4

Nestling Provisioning II: Prey Availability and Nestling Diet

Introduction

Blackbirds feed on a variety of prey, but earthworms (Lumbricidae) usually form by far the largest proportion of their diet, particularly in the breeding season (Snow, 1958). There is a close relationship between earthworm availability in the top layer of soil and soil moisture (Edwards and Lofty, 1972), so rainfall may have a strong effect on blackbird foraging efficiency (Desrochers, 1991), breeding success (Batten, 1973; Magrath, 1989) and length of breeding season (Edwards, 1983). Other prey items, particularly caterpillars, but also adult insects, slugs and berries tend to be taken in drier periods (Snow, 1958; Török and Ludvig, 1985).

Török and Ludvig (1985) showed that predominantly earthworm diets were delivered to nestlings at a more efficient rate than other prey types, and that foraging distances for these loads were shorter, although the actual energy content of loads did not differ significantly between diet types. Although no mention of chick quality was made in the paper, chicks fed on earthworms would be expected to be heavier and have lower starvation rates than those fed on other diets.

One of the problems with the majority of dietary studies on blackbirds is that they only consider birds from urban populations, which tend to differ from rural populations in a number of aspects, notably breeding density (Snow, 1958; see Chapter 7). It is likely that the availability of prey types other than earthworms, particularly caterpillars, will be higher in woodland than urban habitats. Snow (1958) showed that woodland birds were less dependent on earthworms, and consequently over the breeding season chicks tended to be heavier and have lower starvation rates in woodland.

In addition to environmental factors, the diet delivered to the nestlings may be affected by nestling age. This may be because certain prey types are too large or indigestible for very young chicks; for example, urban blackbird nestlings tend to be fed more large insects and berries when they are older, virtually all prey deliveries in the first few days being of soft-bodied prey (Török, 1981). Nutrient requirement may also affect the type of prey delivered. It is a common observation that young *Parus*

nestlings are fed a large proportion of spiders (Gibb and Betts, 1963; Royama, 1970); the function of this is unknown but it seems likely that spiders contain some trace nutrient essential for growth (Perrins, 1979).

In some cases the demand of the brood can affect the diet selected by the parents. By experimentally increasing brood size Tinbergen (1981) showed that starlings switched from *Cerapteryx* larvae to the relatively high-energy Tipulid larvae (leatherjackets) in response to increased chick demand. However under normal conditions *Cerapteryx* larvae were the preferred prey type, despite having a lower energy delivery rate, as a large proportion of leatherjackets in the diet resulted in a high incidence of nest fouling. This example not only illustrates how chick demand can affect the parents' choice of diet, but also that maximisation of energy delivery rates may not always be an appropriate 'currency' to use as nutrient content is not taken into account.

In this chapter the diet delivered to rural blackbird nestlings is studied in relation to season, rainfall, temperature and relative prey availabilities. The relationship between nestling diet and nestling quality is discussed.

Methods

Observational methods used in the determination of diet are outlined in Chapter 1. Data from watch periods of any duration are used, except when studying energy delivery rates per load (or energy gain) when data from two hour observation periods only are used (see Chapter 2).

Sampling of the blackbirds major prey, earthworms, was carried out using the formalin extraction technique (Raw, 1959). Two habitat types were chosen: woodland with a dog's mercury *Mercurialis perennis* ground layer, and grazed open pasture. A sampling point was chosen at random within each sampling area and all ground vegetation and litter was cleared at that point. Four litres of 5% formalin solution was then applied evenly over a $0.25m^2$ area. The number and size of worms emerging from the soil over a six minute time interval was recorded. Worm size was recorded by size

class taken at 25mm increments. The length of worms delivered to the nest was measured in the same way (25mm is approximately equal to mean bill length). Sampling was carried out every ten to fifteen days and on each day six to ten quadrats were sampled. All samples were taken between 1100 and 1400. The calorific equivalents of the worms emerging per quadrat were calculated using length-energy conversions (Edwards, 1983) as outlined in the general methods (Chapter 1).

Data on caterpillar abundance were taken from results collected by Prof. C.M Perrins, Dr. A. Gosler and Dr. L. Cole as part of the long term study on great tit population ecology in Wytham Woods (see Perrins, 1979). The method consists of placing mesh-covered water-filled trays ($0.5m^2$) beneath oak trees. Caterpillars dropping from the canopy to the soil to pupate were collected in the trays between mid-May and mid-June. The mean number of caterpillars per tray was recorded for each day. Trays were sometimes visited at more than a days interval. In these cases the number of caterpillars was divided by the number of days since the previous check. Thus for each date on which a count was made, a score of the number of caterpillars per day per tray was obtained.

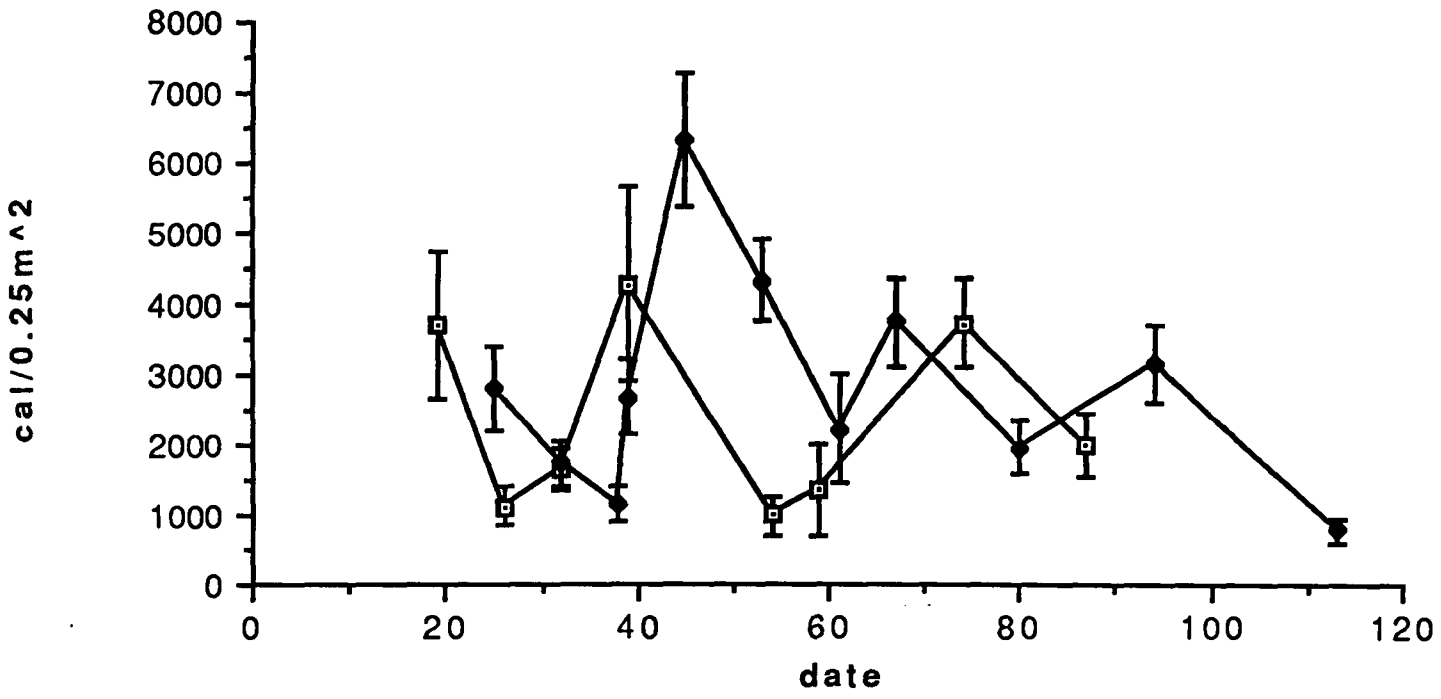
Results

1. Prey Availability

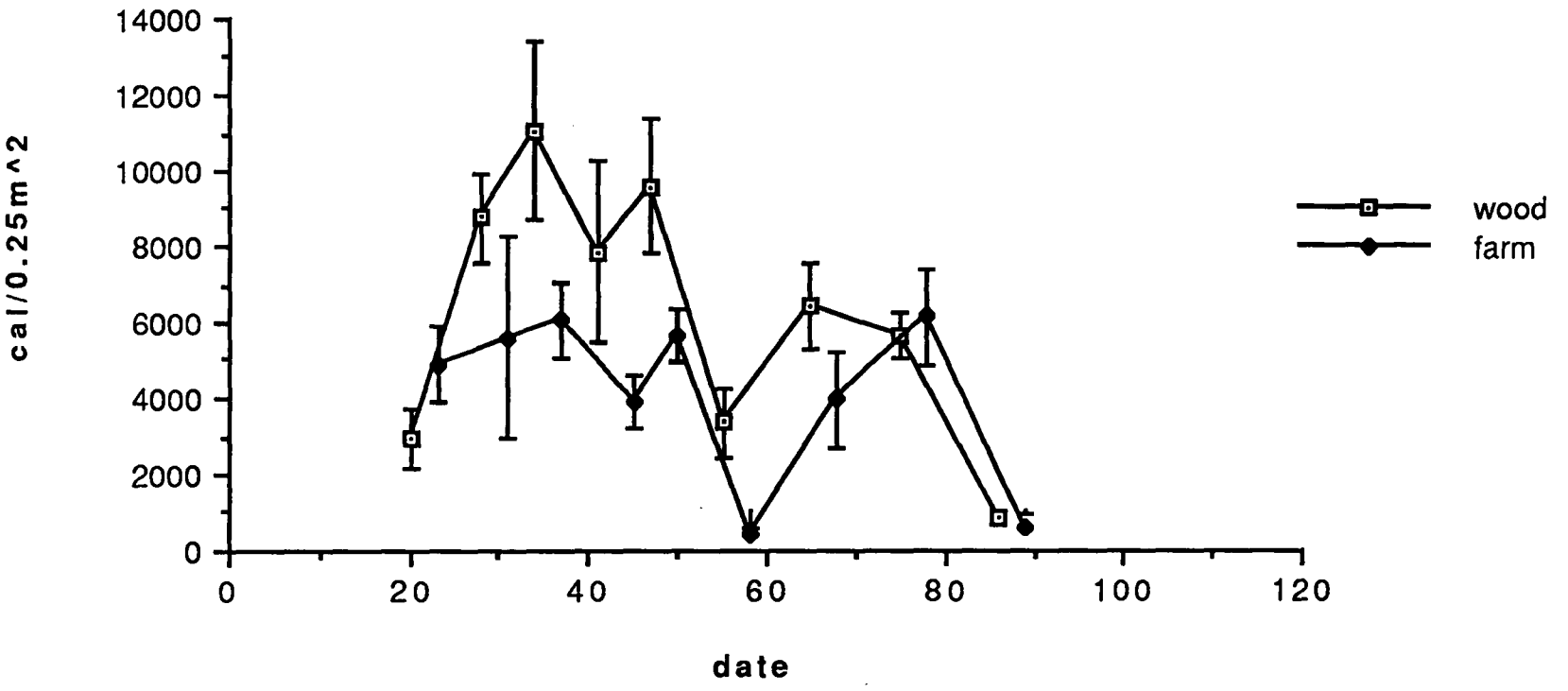
The seasonal variation in worm abundance, taken as the total calorific equivalent of earthworms emerging in a six minute period within a $0.25m^2$ quadrat, is shown in figure 4.1 Earthworm populations in the upper soil layers peak in April and show a decline throughout the summer (Edwards and Lofty, 1972). In all years the peak in earthworm abundance occurred at about the same time, between date 20 (20th April) and 35 (5th May), and showed a general decline thereafter.

The effects of rainfall and temperature on earthworm abundance are shown in Table 4.1. Earthworm abundance seemed to be more sensitive to rainfall in the farmland habitat, significant results occurring in 1991, 1992 and with combined years.

(A) 1991



(B) 1992



(C) 1993

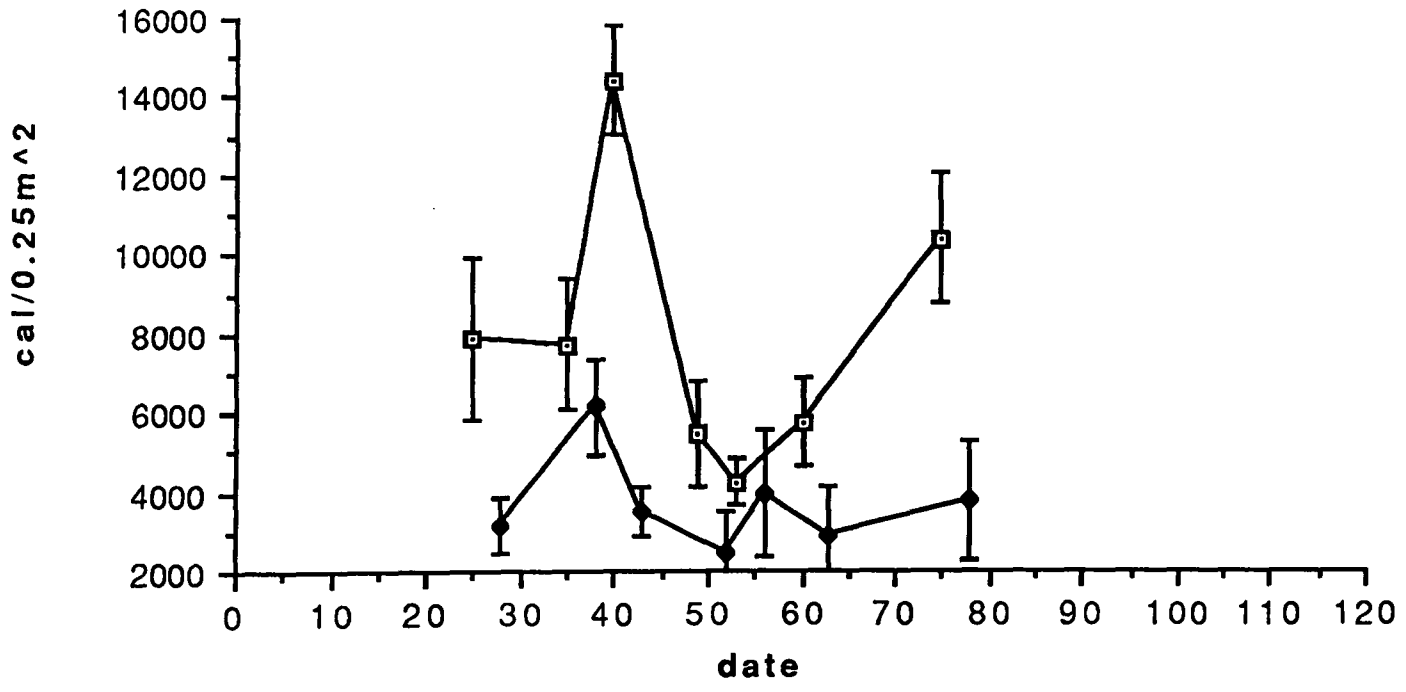


Figure 4.1: Seasonal variation in earthworm abundance in woodland and farmland. Error bars represent standard errors. Date 0=18/3. Sample sizes: n=10 for 1991; n=6 for 1992 and 1993.

Rainfall had a significant effect in woodland in 1992 only. There was also a significant negative effect of temperature in both habitats in 1992 (Table 4.1), and, when years were combined, there was a significant effect of temperature in woodland. There was some evidence of a correlation between rainfall and temperature on the sampling dates in 1992 (df=51, r=0.21, 0.10>P>0.05), so to control for this effect, a partial correlation was carried out in this year in order to separate the effects of rainfall and temperature (Table 4.2). This showed that only rainfall had a significant effect in woodland, and the effect of rainfall in farmland was also strong, but there was still some evidence of a slight (non-significant) effect of temperature.

The mean number of caterpillars found per tray per sampling day is shown in figure 4.2. The respective dates of peak abundance for the three years were 26/5, 23/5, and 31/5, the peak in 1992 being lower than in the other two years. There were no significant effects of rainfall or temperature on caterpillar abundance in any year (correlation coefficients: 1991 mean total rainfall r=0.25, df=16, P=0.30; mean temperature r=0.40, df=16, P=0.09; 1992 mean total rainfall r=0.18, df=11, P=0.55; mean temperature r=0.19, df=11, P=0.53; 1993 mean total rainfall r=0.06, df=7, P=0.88; mean temperature r=-0.52, df=7, P=0.15). This is as expected because environmental factors, particularly temperature, are more likely to affect long-term abundance and the timing of the caterpillar peak, rather than the immediate availability of the caterpillars (Perrins, 1979).

2 Nestling Diet

The observed percentage contribution of prey types to the diet, taken over five day periods during the breeding season, is shown in figure 4.3. All three years show similar patterns, with earthworms dominating the diet early in the season, followed by a caterpillar peak in late May-early June. The peak in caterpillars is about a week earlier in 1992, reflecting the earlier caterpillar peak in fig. 4.2.

The most noticeable differences occur at the end of the season when a much greater proportion of 'other' items appear in the diet in 1992. In 1992, items described

Table 4.1: The effect of rainfall and temperature on earthworm availability in woodland and farmland. Linear correlation coefficients and sample sizes (n) for total number of quadrats and the number of sampling days (in brackets) are given. (*)0.10>P>0.05, **0.05>P>0.01, ***P<0.01.

	WOOD			FARM		
	rf index	temp.	n	rf index	temp.	n
1991	0.08	0.04	100 (10)	0.45***	0.07	71 (8)
1992	0.35**	-0.27**	53 (9)	0.35**	-0.28**	52 (9)
1993	0.01	0.19	42 (7)	0.04	0.06	42 (7)
combined years	0.12(*)	-0.20**	189 (26)	0.32***	-0.07	165 (24)

Table 4.2: Partial correlation analyses of the effect of rainfall and temperature on earthworm availability in 1992. Partial correlation coefficients and sample sizes are given. (*).10>P>0.05, **0.05>P>0.01, ***P<0.01.

	WOOD			FARM		
	rf index	temp.	n	rf index	temp.	n
1992	0.33**	-0.22	53	0.32**	-0.25(*)	52

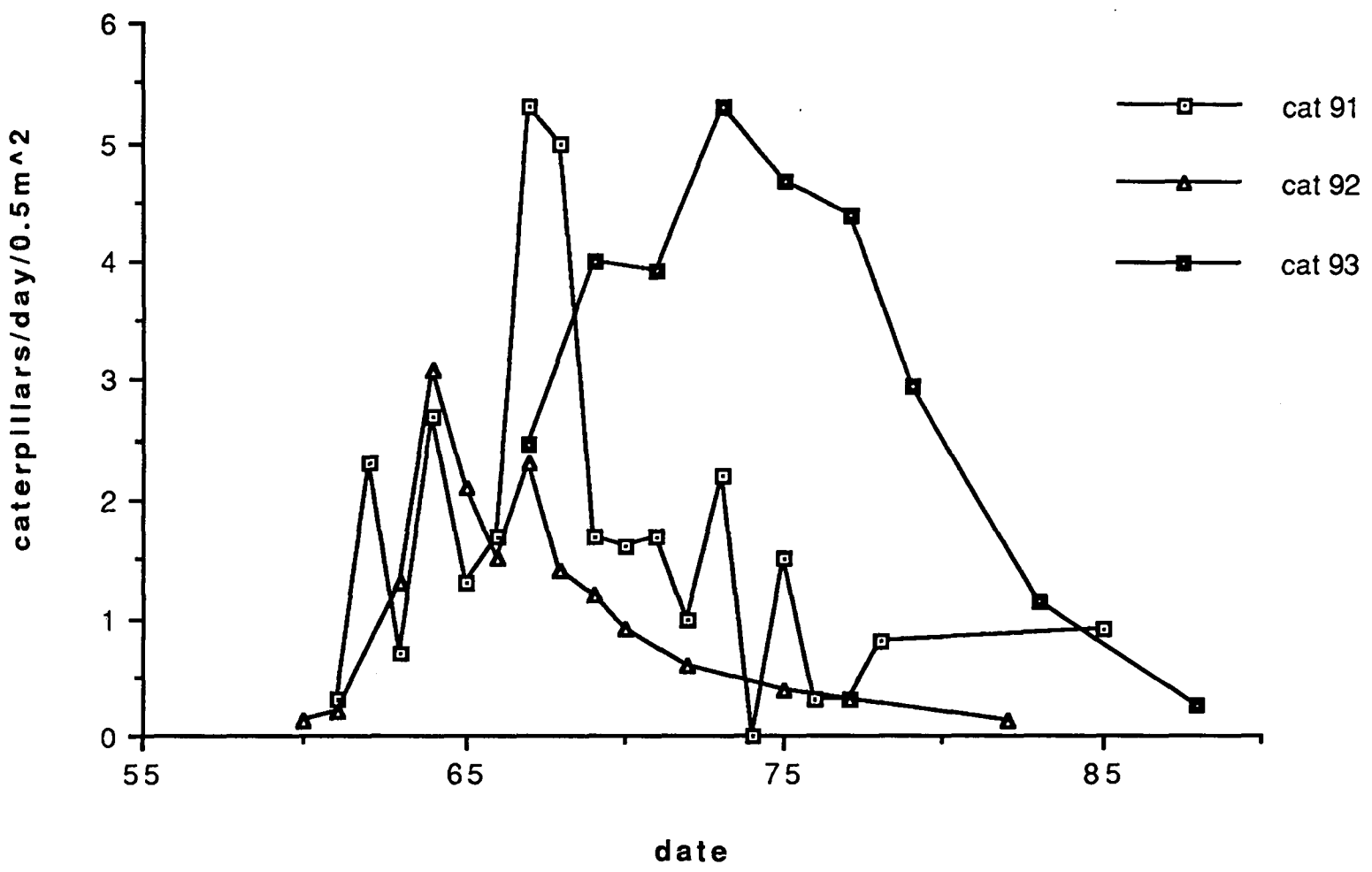
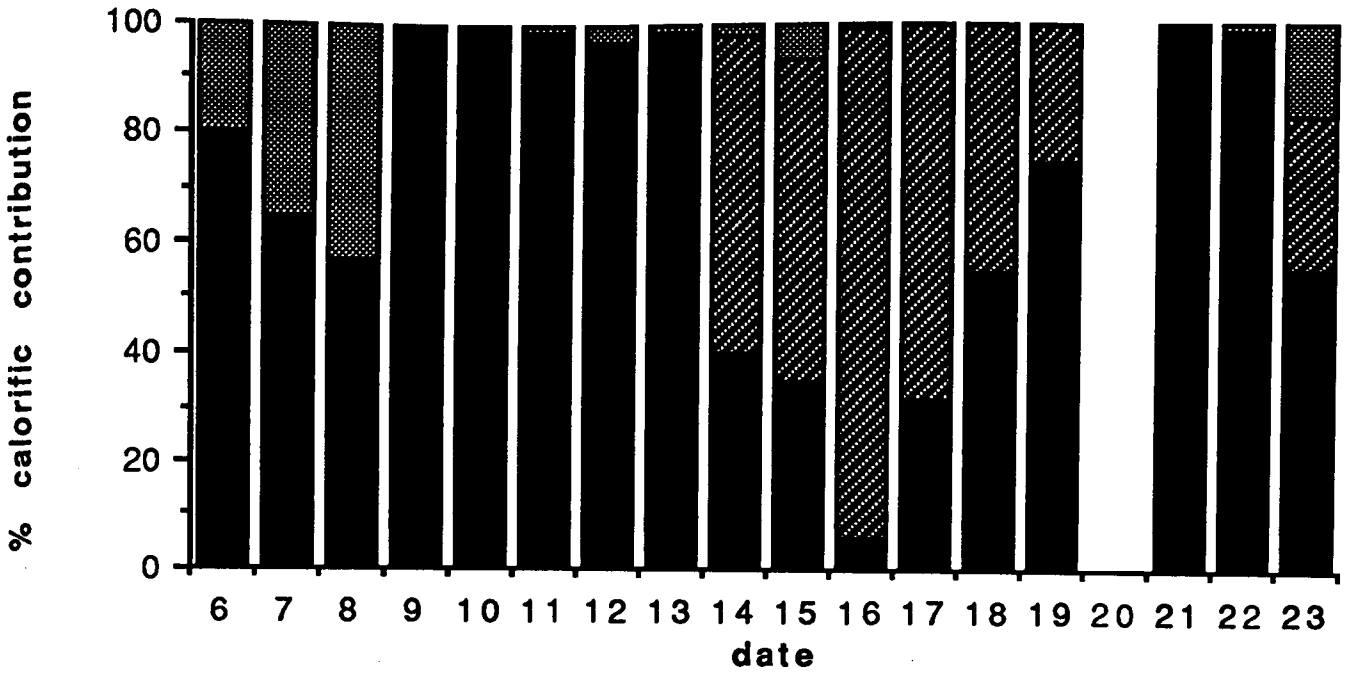
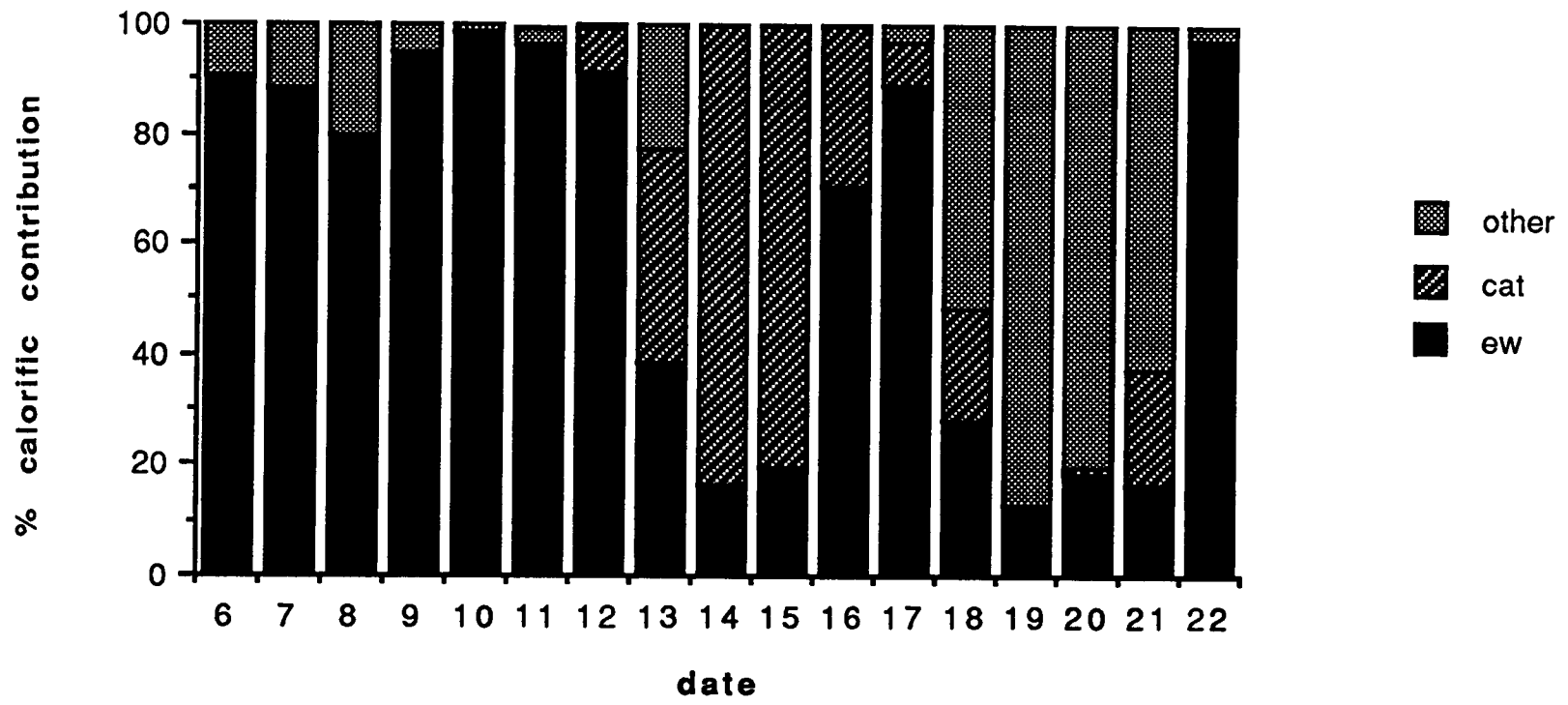


Figure 4.2: Seasonal variation in caterpillar abundance. Date 55=13/5. Sample sizes 1991 n=3-6 trays, 1992 n=15 trays, 1993 n=12 trays.

(A) 1991



(B) 1992



(C) 1993

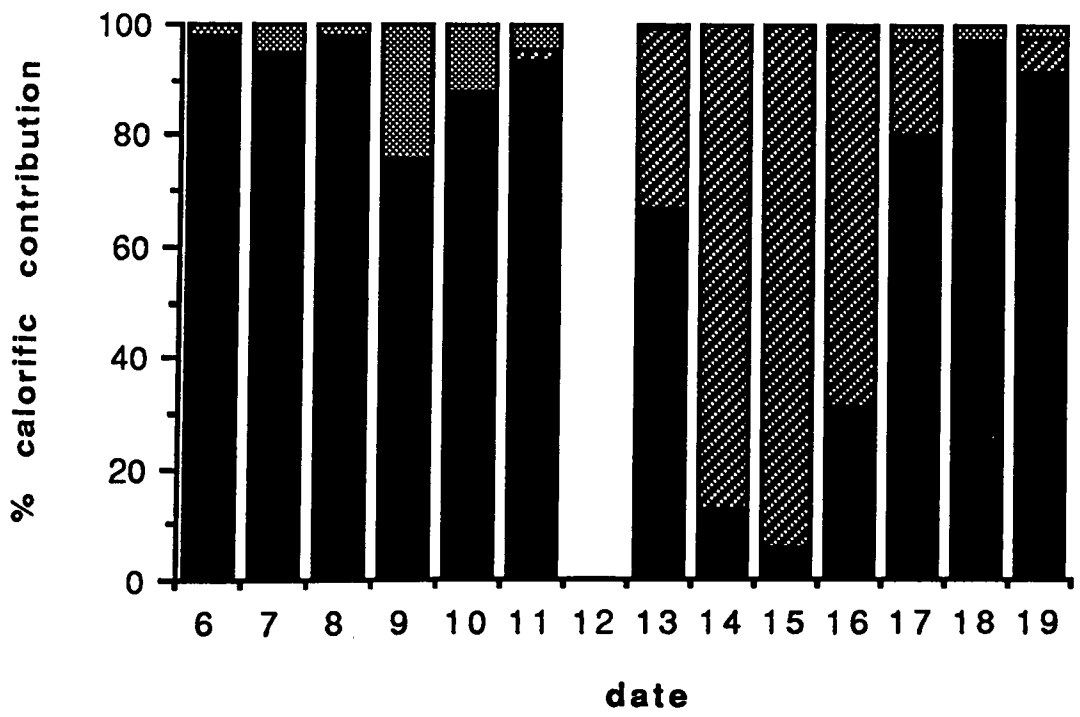


Figure 4.3: The percentage calorific contribution of prey types to the diet. Date is in 5 day periods where period 6=11-15/4.

as 'other' comprised mostly slugs and berries (mostly cherries *Prunus avium*). In 1991 berries (ivy *Hedera helix*) occurred only in early diets. In all years adult insects and larvae (mainly Diptera) were constantly present in the diet in small amounts.

It seems likely on the basis of other studies (Dyrcz, 1969; Török, 1981; Török and Ludvig, 1988) that the number of small prey items in the diet (such as insects and spiders) was underestimated. However, the calorific content of such prey is likely to be very small compared to earthworms or caterpillars (Edwards, 1983), so it is unlikely that a more accurate determination of diet would make any significant difference to estimates of energy contribution.

As earthworm abundance was related to rainfall and temperature in some years (Section 1), it may be expected that the proportion of earthworms in the diet is also related to these two variables if their occurrence in the diet is related to their abundance in the environment. Table 4.3 shows the results of a correlation carried out on the effect of total rainfall and temperature (mean morning temperature) per five day period on the proportion of each prey type in the diet per five day period.

According to some studies, rainfall should have a major effect on a blackbird's breeding success as this is related to earthworm abundance (see section 1). However, in this analysis rainfall had no significant effect on the occurrence of earthworms in the diet, or on the occurrence of caterpillars. There was a significant negative effect of rainfall on 'other' items in the diet. When the results from the caterpillar peaks are omitted, there was a stronger, though still non-significant effect of rainfall on the occurrence of earthworms ($r=0.27$, $df=25$, $P=0.18$), and a strong non-significant trend with mean temperature ($r=-0.36$, $df=25$, $P=0.06$). In other words, there was some evidence that the amount of 'other' items in the diet increased when temperatures were higher if caterpillars were not present in the environment, although this did not show as a significant relationship (Table 4.3).

The occurrence of earthworms in the diet was apparently more sensitive to temperature than rainfall. However, this may to some extent be an effect of date. Temperature increases throughout the season, but the caterpillar peak always falls at

Table 4.3: The effects of rainfall and temperature on the relative calorific contribution of different prey types to the diet per five day period (years combined). % data transformed to arcsine (sqrt.(x)). Pearsons correlation coefficients are given, sample sizes = 47 for all groups. **P<0.05.

DIET	RAINFALL mm	TEMPERATURE °C
earthworm	0.04	-0.37**
caterpillar	0.18	0.24
other	-0.30**	0.22

around the same time, in mid-May when temperatures will be warmer than the early earthworm-dominated part of the season. When only the latter part of the season was considered (from the first occurrence of caterpillars), there was no significant effect of temperature on the occurrence of earthworms in the diet (Pearson correlation r=0.001, df=25, P=0.99).

The occurrence of caterpillars in the diet was not related to either rainfall or temperature. It is unlikely that either measure would have a direct effect on caterpillar abundance, but there may have been an indirect effect if caterpillars were the less preferred prey type, and therefore only taken in conditions when earthworms were less available. There was no evidence for this, as caterpillars occurred in the diet during periods of high rainfall (compare figure 2.2). Additionally, in two out of three years, the proportion of caterpillars in the diet was significantly correlated with their abundance in the caterpillar trays (Spearman correlation: 1991 n=18, r=-0.01, P=0.98; 1992 n=13, r=0.76, P=0.01; 1993 n=7, r=0.89, P=0.02), implying that they are taken as prey items in direct relation to their own abundance, rather than their abundance relative to another prey type.

(i) Energy delivery rates

If it is assumed that the goal of parent blackbirds feeding young is to maximise energy delivery rates (which is not necessarily always the case- see Tinbergen, 1981), then during the 'caterpillar peak' (fig. 4.3) earthworms must be the less profitable prey. This may be because (i) caterpillars are always more profitable, whatever the conditions and are used to feed nestlings when available; or (ii) environmental conditions result in earthworms being less available and hence less profitable than caterpillars.

For this analysis, foraging efficiency was looked at in terms of the mean calories per watch period, mean calories per load, mean inter-visit time, and the 'energy gain' at the nest, calculated by dividing the energy delivered per visit (in calories) by the preceding inter-feeding interval (min.). As described in Chapter 3, all means are calculated from ages 7 to 12, and adjusted for the effects of brood size where

appropriate. Additionally, the nests are classified according to the predominant diet type of the loads, when a particular prey type made up over 50% of the calorific contribution to the diet.

There was no significant difference in mean delivery rates of calories per watch period between the two main diet types at either one hour (Table 4.4), two hour (Table 4.5), or twelve hour (Table 4.6) observation periods.

There was a tendency for calories per load delivered by males to be larger in nests fed predominantly on caterpillars (Table 4.7), but there were significantly longer inter-visit times for both parents (Table 4.8). As these two factors effectively cancel each other out in terms of delivery rate, it is perhaps not surprising to find no significant differences in provisioning efficiency (Table 4.9).

In the above analyses, mean values are grouped by predominant diet type, so although the majority of loads will be mainly from the stated diet, there will still be some loads which are entirely from the minority diet(s). A better way to analyse the efficiencies of prey types is to consider individual loads within nests. This requires that parents provision nestlings at a single nest with a mixture of earthworms and caterpillars. This only occurred at five nests (all-day watches). Table 4.10 shows the means for individual caterpillar-only and earthworm-only loads.

There was a significant, or nearly significant difference in energy gain between load types in two individuals (both females). Note, however, that trends in these, and in some of the other means are contradictory, and that small sample sizes and high variances occur in some of these samples.

(ii) Rainfall and temperature

As rainfall and temperature both have some effect on the blackbirds major prey type, earthworms, then these variables may be expected to have some effect on provisioning efficiency. Also, temperature may have an indirect effect on chick demand by affecting the chicks energy budget (see previous chapter). Table 4.11 shows the effect of mean rainfall and temperature on hourly, two-hourly, and twelve hourly

Table 4.4: Mean hourly energy delivery rates of the main diet types. Unpaired t- values, sample sizes (in brackets), and means ± standard deviations are given. No differences were significant.

	earthworm	caterpillar	unpaired t
male	2088±921 (23)	1503±127 (9)	1.45
female	1142±639 (23)	1028±460 (8)	0.46
total	3109±1259 (20)	2716±1112 (9)	0.73

Table 4.5: Mean two-hourly energy delivery rates of the main diet types. Unpaired t- values, sample sizes (in brackets), and means ± standard deviations are given. No differences were significant.

	earthworm	caterpillar	unpaired t
male	5448±1574 (19)	5058±1659 (6)	0.54
female	2845±1422 (18)	2285±1229 (5)	0.80
total	8287±2069 (17)	7722±3149 (5)	0.48

Table 4.6: Mean twelve-hourly energy delivery rates of the main diet types. Unpaired t- values, sample sizes (in brackets), and means ± standard deviations (actual values are $x10^3$) are given. No differences were significant.

	earthworm	caterpillar	unpaired t
male	29.85±8.34 (11)	31.44±11.65 (3)	0.27
female	16.95±17.56 (10)	15.25±1.98 (3)	0.16
total	44.60±10.63 (9)	46.68±10.44 (3)	0.30

Table 4.7: Mean calories per load of the two main diet types. Unpaired t-values, sample sizes (in brackets), and means ± standard deviations are given.

(*)0.10>P>0.05, **0.05>P>0.01, ***P<0.01

	earthworm	caterpillar	unpaired t
male	847±258 (18)	1127±395 (6)	2.02(*)
female	644±322 (17)	611±267 (6)	0.23

Table 4.8: Mean inter-visit times (min.) per load of the two main diet types. Unpaired t- values, sample sizes (in brackets), and means ± standard deviations are given. (*)0.10>P>0.05, **0.05>P>0.01, ***P<0.01

	earthworm	caterpillar	unpaired t
male	21.41±5.95 (19)	27.04±5.96 (7)	2.14**
female	16.66±4.76 (16)	23.11±7.44 (7)	2.52**

Table 4.9: Mean delivery efficiencies (cal/min.) per load of the two main diet types. Unpaired t- values, sample sizes (in brackets), and means ± standard deviations are given. (*)0.10>P>0.05, **0.05>P>0.01, ***P<0.01

	earthworm	caterpillar	unpaired t
male	61.98±22.20 (18)	59.46±20.67 (6)	0.25
female	48.91±44.38 (15)	32.93±9.26 (6)	0.86

Table 4.10: Mean energy gains (cal./min.) of earthworm and caterpillar loads in nests of joint diet occurrence. Unpaired t- values, sample sizes (in brackets), and means ± standard deviations are given. (*)0.10>P>0.05, **0.05>P>0.01, ***P<0.01

hatch date	sex	earthworms	caterpillars	unpaired t
25/5/91	male	53.5±47.9 (13)	30.1±21.9 (10)	1.64
31/5/91	female	75.52±86.91 (14)	28.33±17.10 (21)	2.38**
12/5/93	male	28.71±28.31 (10)	34.54±10.86 (5)	0.44
16/5/93	female	47.98±45.89 (10)	48.17±34.95 (24)	0.01
27/5/93	male	36.95±30.00 (4)	44.96±34.84 (6)	0.36
27/5/93	female	9.69±5.39 (4)	55.19±39.22 (7)	2.26(*)

Table 4.11: The effect of mean rainfall index (mm) and temperature (°C) on mean calories delivered per watch period between days 7-12.

Correlation coefficients and sample sizes are given, where r_s= Spearmans rank coefficient, r=Pearsons coefficient. (*)0.10>P>0.05.

		rainfall index		temperature	
watch period	sex	r_s	n	r	n
1 hour	m	0.23	34	-0.08	34
	f	0.24	33	0.01	33
	total	0.05	29	-0.10	29
2 hour	m	0.02	27	-0.22	27
	f	0.28	25	-0.03	25
	total	-0.04	24	-0.31	24
12 hour	m	-0.13	14	-0.44	14
	f	0.23	13	-0.49(*)	13
	total	-0.06	12	-0.28	12

provisioning rates, between days 7 and 12. In these analyses, rainfall is not distributed normally, so a non-parametric correlation is used.

Apart from a weak effect of temperature on female delivery rate per 12 hour period, no effects of either rainfall index or temperature were found. According to the prey sampling results (Section 1), meteorological factors had little effect on the immediate availability of caterpillars, thus when this diet predominates, delivery rates are unlikely to be affected by rainfall or temperature. Table 4.12 shows a repeat analysis of Table 4.11, but all nests with predominantly caterpillar diets are omitted.

In the absence of caterpillars in the diet, strong positive effects were shown between female delivery rates and mean rainfall index. The negative correlations between delivery rate and temperature tended to become stronger, particularly with longer sampling periods, although no correlations were significant.

(iii) Starvation

There was no significant difference in the number of nests experiencing nestling starvation between the two predominant diet types, with 10 out of 65 (15.38%) of earthworm-fed nests and 4 out of 25 (16.0%) caterpillar or other-fed nests experiencing some starvation (G-test: 1991 $G=0.27$, $df=1$, $P>0.75$; 1992 $G=0.05$, $df=1$, $P>0.90$; 1993 $G=0.64$, $df=1$, $P>0.50$).

(iv) Nestling weight

Magrath (1991) showed that the day 8 weight of ringed urban blackbird nestlings was directly related to their probability of re-capture, and from this inferred that survival to breeding was related to chick weight. Nestling weight may thus be used as a measure of nestling 'quality'.

In previous analyses there was little evidence to suggest that either main prey type was delivered to nestlings at a significantly higher rate than the other. If this were the case then no difference in the quality of chicks fed on different diets would be expected. However, when mean chick weights of earthworm-fed nests were compared

Table 4.12: The effect of mean rainfall index (mm) and temperature (°C) on mean calories delivered per watch period between days 7-12, in the absence of predominantly caterpillar-fed nests. Correlation coefficients and sample sizes are given, where r_s= Spearmans rank coefficient, r=Pearsons coefficient. (*)0.10>P>0.05, **P<0.05.

		rainfall index		temperature	
watch period	sex	r_s	n	r	n
1 hour	m	0.04	25	-0.05	25
	f	0.51**	25	0.09	25
	total	0.04	22	-0.07	22
2 hour	m	0.06	21	-0.39(*)	21
	f	0.40(*)	20	-0.01	20
	total	-0.04	19	-0.44(*)	19
12 hour	m	-0.45	11	-0.51	11
	f	0.30	10	-0.53	10
	total	-0.44	10	-0.40	10

with predominantly (over 50% calorific contribution) other diet types (mostly caterpillars, but three were fed 'other' diets consisting of berries, slugs, and adult insects) the predominantly earthworm-fed nests had significantly higher weights (unpaired t-test t=2.33, df=84, P=0.02; mean earthworm= 59.76±4.25 grams, n=63; mean other diets= 57.51±3.06 grams, n=23). These results classified the diet type of nests according to the seasonal diet profiles in figure 4.3, taking a predominant diet type as contributing over fifty percent of the total energy delivered. A further analysis considering observed nests with known diets did not reveal any significant differences, although the mean chick weights were very similar to the above result (t-test t=1.63, df=35, P=0.11; mean earthworm= 59.53±5.10 grams, n=24; mean other diets= 56.93±3.60 grams, n=13).

There was also a tendency for mean chick weights to be lower when caterpillars were present in the diet, regardless of their relative occurrence. A comparison of chick weight between nests falling within the caterpillar peak in each year, and all others revealed that broods in the caterpillar peak had significantly lower mean weights (unpaired t-test: t=2.01, df=84, P=0.05; mean non-caterpillar= 59.96±4.18 grams, n=47; mean caterpillar peak=58.21±3.78 grams, n=39).

According to Section 1, earthworm abundance is sensitive to both rainfall and temperature. Therefore an indirect effect of either rainfall or temperature may be expected on chick weight if alternative diets are less profitable, as the above results suggest. Neither measure had any effect on chick weight (linear regression: rainfall r=0.09, df=84, P=0.42; temperature r=0.08, df=84, P=0.48), where rainfall was measured as the total amount falling in the period since the brood hatched, and temperature as the mean morning temperature over the same period. Removing results from the caterpillar peaks did not affect the result (rainfall r=0.00, df=45, P=1.0; temperature r=0.13, df=45, P=0.39).

When analysing chick weight in terms of diet, it was assumed that other conditions (e.g. rainfall and temperature) did not differ significantly between periods of different predominant diet type (Table 4.3). This assumption was based on results

which considered rainfall and temperature per day over the whole season. However, the analysis of chick weight uses data from individual nests which may have been subject to short-term fluctuations in environmental conditions which differed from the general pattern. Considering the conditions that each individual nest was subject to may therefore yield different results.

There were significant differences between periods of different predominant (over 50% calorific contribution) diet type in the amount of rainfall (ANOVA: $F_{2,83}$=4.83, P=0.01 mean earthworm=17.12± 15.02mm, n=63; mean caterpillar= 8.35±8.60mm, n=20; mean other= 0.38±0.65mm, n=3), and large, but non-significant differences in mean temperature ($F_{2,52}$=2.69, P=0.07 mean earthworm=12.70± 3.48°C, n=63; mean caterpillar= 13.75±2.23°C, n=20; mean other=16.58±0.39°C, n=3) when considering only the conditions experienced by the nests used in the analysis of chick weight.

Further significant results were found when considering nests within the caterpillar peak for each year, regardless of the relative amounts of worms and caterpillars in the diet (i.e. simply whether caterpillars were present or absent). Rainfall was significantly lower during the caterpillar peak (unpaired t-test t=2.59, df=84, P=0.01 mean rainfall, caterpillars present =10.27+10.29mm, n=39; mean rainfall, caterpillars absent=18.01+16.07mm, n=47), and temperature was significantly higher (t=4.37, df=84, P=0.01, mean temperature, caterpillars present =14.61+2.56°C, n=39; mean temperature, caterpillars absent=11.82+3.24°C, n=47), again considering only the conditions experienced by the nests used in the analysis of chick weight.

One problem in the interpretation of the temperature data is that there is a steady increase in mean temperature as the season progresses (Chapter 2). The caterpillar peak will always occur at around the same time of the season, which will be relatively warm compared with the early earthworm-dominated diet, thus the significantly higher temperatures detected with caterpillar diets are likely to be associated with date rather than diet choice. In a further analysis, only nests from the start of the caterpillar peak onwards were used. This revealed significant differences in temperature between nests

of different predominant diet types (ANOVA $F_{2,79}$=4.24, P=0.02, mean temperature, earthworm nests= 15.37±2.30°C, n=32; mean temperature, caterpillar nests= 13.75±2.23°C, n=47; mean temperature, other nests=16.58±0.39°C, n=3), although predominantly earthworm-fed nests had a higher mean than caterpillar-fed nests, contradicting the earlier result. Thus the effect of temperature would indeed appear to have been an artefact of the increase with date.

Therefore the lower weight of caterpillar fed nests is probably a consequence of these nests occurring at times when there were low amounts of rainfall, and therefore earthworms were not readily available.

Discussion

1 Prey availability

The effects of rainfall index and temperature on earthworm abundance varied between years, but there was a tendency for woodland earthworm abundance to be more strongly related to temperature, and farmland earthworm abundance to be more strongly related to rainfall index. Differences in the effects of environmental variables between habitats are probably due to differences in habitat structure. Habitat differences in prey availability are considered more fully in Chapter 5.

A question that must be asked when considering these results is: how accurately do they reflect prey availability to the blackbird? Berg (1993), working on curlews *Numenius arquata*, found that they had a higher capture rate of earthworms on mown grass than on tillage, even though no significant difference in earthworm biomass was detected between habitats using a soil core sampling technique. The extent to which sampling techniques measure availability rather than abundance is therefore unclear. The formalin extraction technique used in this study may cause the emmergence of some worms which are much too deep in the soil for a blackbird to obtain. Further biases may also exist in that different species of earthworm vary in their response to formalin (Edwards and Lofty, 1972).

Despite the drawbacks with the formalin extraction technique, there is some evidence that it does provide some measure of availability. High temperatures or low soil moisture affect the efficiency of the method (Lakhani and Satchel, 1970), paralleling the effects of temperature and soil moisture on both the activity levels of earthworms, and the numbers found at the soil surface (Edwards and Lofty, 1972). Additionally, in this study some indirect evidence (some significant correlations between environmental variables and measures of provisioning) suggests that the sampling method truly reflects prey availability, although determination of actual intake rate in the sampling areas is needed before firmer conclusions are drawn.

As expected, caterpillars showed a peak in abundance in late May in all years. The sampling method, however, shows the peak in the numbers of caterpillars dropping to the soil to pupate. It will therefore not necessarily reveal the peak in abundance of all caterpillar species, as many do not pupate in this way. This could provide a major bias in the results. However in the three breeding seasons of this study, blackbirds were never seen to forage in trees, thus the only bias in the results will probably come from caterpillars that spend most of their larval life at or near ground level. The sampling method is therefore likely to be a reasonable reflection of prey availability in the woodland habitat.

2 Diet

When considering general seasonal trends in diet, there was no significant effect of rainfall on the occurrence of earthworms or caterpillars in the diet. Only the occurrence of 'other' items showed any effect, being negatively related to rainfall. Similarly, temperature had little effect, the only significant result detected being associated with the seasonal increase in temperature. As there was some evidence of earthworm availability being related to rainfall and temperature, this result may indicate that earthworms are not taken in relation to their abundance in the environment. However, as in the early part of the breeding season, the major alternative prey of

caterpillars is not available, a correlation between rainfall and the *proportion* of earthworms in the diet will not provide a meaningful result.

When the period of caterpillar availability was omitted from the analysis, there was a significant relationship between rainfall and energy delivery rate in females, which gives some indication that earthworms are taken by blackbirds in relation to their abundance in the environment.

In two out of three years, caterpillars appeared in the diet in proportion to their abundance in the environment. The occurrence of caterpillars in the diet was not apparently dictated by a lower availability of earthworms, therefore they may have been the preferred prey type. Many models of prey choice deal with a situation where a definite switch between prey types is involved (Stephens and Krebs, 1986). In the blackbird's case, both prey types occur on the ground so both may be encountered in a foraging bout, and a switch in search method or habitat/patch choice may not be necessary. Caterpillars are doubtless easier to collect than earthworms, which must be pulled from the soil, so a foraging blackbird may follow a simple rule of thumb, such as 'search for earthworms, but take any caterpillar which is found', assuming that both prey types are encountered in the same foraging site. Such an effect would explain the observed correlation between the occurrence of caterpillars in the diet and in the environment. There were no significant differences in energy delivery rates between the two diet types, which supports the above ideas, neither prey type being more profitable, and therefore preferred, over the other.

Why the observed relationship between caterpillar occurrence in the diet and in the environment did not occur in 1991 is unclear, but it is unlikely to be due to earthworms being more profitable than caterpillars (i.e. wetter conditions) during the peak in caterpillar abundance, as conditions were actually quite dry during this period in 1991 (Chapter 2, fig. 2.2). It may be that the low number of samples (n=3-6) in that year lead to inaccurate results.

(i) Sources of error

Throughout this chapter, the main foraging parameter used is energy delivery rate. The analyses therefore assume that: (i) calorific values taken from different studies are comparable; and (ii) energy delivery rate is the most important 'currency' (Stephens and Krebs, 1986) for the parents to maximise.

The calorific equivalents used in this thesis come from a number of different studies. Most importantly, the main prey types, earthworms and caterpillars, had calorific values taken from different works (Edwards, 1983; Rogers et al., 1977 respectively) which although both using calorimetry, had slightly different methods. The inaccuracy this may have produced must remain unknown.

Calorific energy (from carbohydrates and fats) is considered as the only measure of provisioning efficiency in this thesis. However, nutrient content or other compounds (such as digestion inhibitors- see below) per unit weight may differ between species. For example, protein is generally a more important nutrient for nestling growth (O'Connor, 1986) and hence nestling quality. If the protein contents of prey types were approximately equal, and increased with prey size in a manner similar to the energy content, then energy delivery rate would still be an adequate currency to use.

3 Nestling weight

As there was no significant difference between delivery rates of the main diet types, there was no expected difference between mean weight of chicks fed on different predominant diet types. However, earthworm-fed chicks were significantly heavier than chicks fed on other diets (i.e. predominantly caterpillars, and also fruit and insects). According to the general diet analysis, there was no significant difference in rainfall between periods of different predominant diet types. When the analysis was performed only on the data from individual nests used in the chick weight analysis, it was found that predominantly earthworm-fed broods occurred during periods with a significantly higher amount of rainfall than in the case of broods fed on caterpillar and

other diets. The results therefore indicate that a diet which is almost entirely dependent on caterpillars will be less profitable, in terms of chick quality, than a predominantly earthworm diet, or a diet where both prey types are available.

A further factor to consider may be the nutritional quality of the prey. Caterpillars are known to accumulate tannins from oak leaves which can inhibit digestion. Perrins (1976) showed that blue tit nestlings fed on a diet containing tannins grew more slowly than nestlings fed on an identical diet without additional tannins. Therefore, the presence of caterpillars in the nestling blackbirds' diet, especially those taken late in the season, may inhibit growth and lead to lower day-eight weights, despite the fact that there was no significant difference in the energy delivery rates of the two diet types.

4 Diet and clutch size

Lack (1954) proposed that birds are adapted to time their breeding attempts so that the period of maximum demand coincides with the period when conditions (usually food supply) are the most favourable for raising the maximum number of offspring. In blackbirds, parental effort (which is assumed to equal nestling demand) increases with brood size (Chapter 3), which is at its peak in the middle of the breeding season (Chapter 2).

Figure 4.4 shows the general seasonal trends in clutch size, earthworm abundance and caterpillar abundance, based on results for the three study years. Clutch size is at its maximum during the period when both prey types are fairly abundant and when there is unlikely to be over-reliance on a single prey type. However, the clutch size pattern is based on the date of clutch completion. Twelve days will elapse until the brood hatches, and a further seven days until the brood's demand for food reaches a maximum (Chapter 3). Therefore parent birds laying clutches of five eggs will face peak demand from their brood some three weeks after the period when the relative abundance of all prey types is at a maximum. Royama (1966) suggested the peak

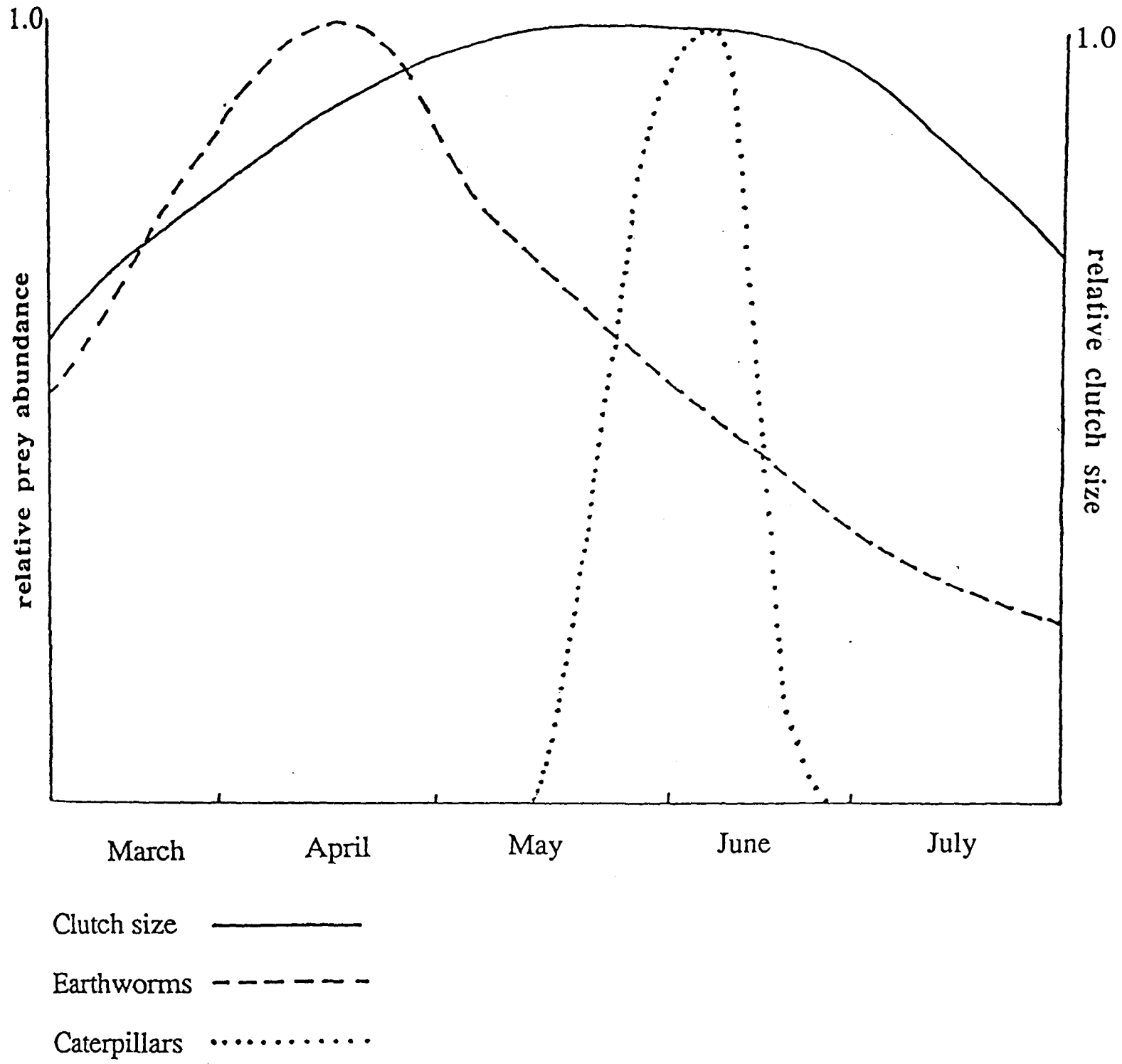


Figure 4.4: Seasonal variation in clutch size and abundance of earthworms and caterpillars throughout a typical breeding season. Relative abundance/clutch size of 1= the maximum observed value, based on the seasonal variation of means over the three years.

demand may in fact be reached after the chicks have fledged, in which case the clutch size would seem to be even less well adapted to the food supply.

Despite this, there was little apparent disadvantage of being in a larger brood, with the possible exception of an increased probability of starvation (Chapter 2), although the starvation rate was so low that the increase in probability would be very small. Therefore it would be difficult to conclude that clutch size in blackbirds, at least in some individuals, was non-adaptive.

Asynchrony increases as clutch size increases (Chapter 2), which may to some extent lessen the effects of having a large brood by spreading the peak demand of individual chicks (Hussell, 1972). Alternatively, it has been suggested that asynchronous hatching is a strategy adopted to cope with unpredictable food supplies, (Magrath, 1989, 1991), thus in good years the whole brood is raised, but in bad years brood reduction occurs. As starvation was very low in this study, it could be that none of the three years was 'bad'. One additional factor to consider is that of day length. The parents will have a few more hours of daylight in which to provision nestlings in the middle part of the season when the clutch size is at its peak.

Early clutch size was variable between years, the most noticeable difference being between 1993 and the other two years. As 1993 had the mildest winter (in terms of the number of freezing days), this may be linked to the conditions prior to egg laying. Therefore the lower early clutch size may be related to the condition of the laying female, rather than being an adaptive response to available food supplies. This idea is supported by the fact that the clutch size at laying is more closely related to better feeding conditions than brood size at periods of peak demand (fig. 4.4). This idea therefore predicts that raising a brood of five would be possible early in the season, but female condition acts as a constraint. This constraint could alternatively be viewed as an adaptive restraint if the female was physically able to lay a large clutch, but she chose not to, as stress early in the season may lead to reduced subsequent fecundity or increased risk of mortality. A feeding experiment testing this idea is presented in Chapter 7.

Chapter 5

Nesting Habitat as a Factor Affecting Reproductive Success

Introduction

The blackbird's original habitat was probably woodland edge, and it is still one of the commonest woodland birds (Marchant et al., 1990); but it has also been one of the most successful colonists of man-made habitats and is probably the commonest bird in both urban (Marchant et al., 1990) and farmland (O'Connor and Shrubb, 1986) habitats. Despite this, only urban populations have been subject to detailed studies (e.g. Snow, 1958; Edwards, 1983; Magrath, 1989), and little is known about populations in rural habitats, particularly the factors which determine their reproductive success.

Snow and Mayer-Gross (1967) found nest failure rates to be 88% in woodland blackbirds compared with 72% in farmland, failure being mainly due to predation. It is known from urban populations that cover is an important territorial resource (Osborne and Osborne, 1980; Edwards, 1983), thus the differences in the amount of available cover in each habitat could lead to differences in predation. However, as farmland tends to be a simpler and more open habitat, the opposite trend would seem intuitively more likely if differences in cover explained differences in predation across habitats. It is more likely that a higher number of predators in the woodland habitat causes the difference.

Woodland blackbirds are likely to be less dependent on worms than urban birds due to the abundance of caterpillars from late May until early June. During this period a prolonged dry spell should have less effect on food availability in woodland (Lack, 1968). Although little work has been done on woodland populations there is some evidence to suggest that this is the case; urban populations have a much higher incidence of nestling starvation than woodland populations and chick weight tends to be higher in woodland (Snow, 1958). Thus there is an indication that foraging in woodland is less constrained by weather conditions, although other factors (e.g higher nesting density and hence greater competition in gardens) cannot be ruled out.

The feeding conditions in farmland would be expected to be similar to those in gardens given the relatively small amount of cover and the large expanses of open substrate. Thus, on this basis a greater starvation rate and lighter chicks would be

expected on farmland in drier conditions. In wet conditions it is possible that farmland may provide the more efficient foraging since pasture (but probably not arable land) generally has a higher density of earthworms than woodland (Kruuk, 1978; Hofer, 1988).

There is no information available on the movements of adult blackbirds between woodland and farmland habitats or the age structure of the two populations from previous studies. However, there are certain characteristics common to many species which would indicate whether one habitat is sub-optimal. For example Krebs (1971) showed that great tits *Parus major* nesting in the less productive farmland habitat tended to be younger birds and therefore subordinate to the older birds nesting in woodland; also there was a 'floating' population of non-breeders which were mostly birds in their first breeding season. Removal of woodland territory holders was followed by a rapid colonisation of the vacated territories by farmland birds, thus it was concluded that farmland was the less-preferred, sub-optimal habitat.

If reproductive success does not differ significantly across habitat types, conclusions may not be drawn on the suitabilities of those habitats unless density is taken into account. If it is assumed that for species with multi-purpose territories (Hinde, 1956), territory quality declines with increasing density of competitors in the habitat, then there will reach a point when it is just as profitable to move into low density, less preferred habitats. In these situations an Ideal Free Distribution (Fretwell and Lucas, 1969) should be reached where gain rates (e.g. reproductive success) are equal across habitat types, but the more preferred habitat types will be occupied at a higher density than the less preferred habitats. However, this situation may be complicated if territory holders have unequal competitive abilities (Fretwell, 1972), as in the example of great tits, where individuals with a higher dominance status occupy the best habitat.

In this chapter, differences in reproductive success are considered in relation to habitat, focusing particularly on predation rates across habitat types, and differences in diet, nestling provisioning and prey availability. The age structure of populations in the

different habitats and movements from one breeding season to the next will also be described. In considering these habitat differences a third 'edge' habitat is defined where a nesting territory overlaps both woodland and farmland. In addition to presenting a ready choice of foraging between two habitats, there is some evidence that territories on woodland edge have different structural characteristics and consequently are subject to different levels of predation than territories wholly within the woodland habitat (Gates and Gysel, 1978).

Methods

Collection of provisioning, dietary and reproductive success data are detailed in Chapter 1. In addition to the normal nest observations, in 1992 and 1993 an attempt was made to determine the foraging destinations of parent birds provisioning nestlings. This was done by observing nests in edge habitats from a distance (c.50 metres) without a hide, and recording the destination of each foraging visit.

Territories were classified as either in wood, woodland edge (referred to as edge hereafter) and farmland. In most cases it was fairly obvious into which habitat a territory should be classed, the nesting attempts within that territory being some distance (100m+) from the habitat edge. Territories closer to the edge were more of a problem, but generally if all nesting attempts in a territory occurred in hedgerows, that territory was classed as farmland. If all nesting attempts were in woodland, they were only classified as woodland edge if (i) they were within 50m of the habitat edge, and (ii) if no territories lay between them and the habitat edge.

In Chapter 2, it was shown that measures of breeding success did not differ significantly between years. Therefore all analyses in this chapter will consider combined results, unless otherwise stated.

In 1993, a habitat survey was carried out in order to have some measure of the degree of nesting cover in each territory. An observer with little previous experience of the study site, and no knowledge of the distribution or breeding success of the blackbirds in the area, was asigned a number of sampling points in both woodland and

farmland. One sampling point was randomly asigned within each occupied territory. Additionally, other sampling points were spaced evenly around the study site, representing false territories. At each point, the observer would score the surrounding area (10m radius) from 1 to 5 on the basis of how difficult it would be to find a nest 1.5m above the ground, where 5 was very hard and 1 was very easy. This habitat survey was carried out once in early April, and an additional survey was carried out in early June in the woodland habitat. Although the survey was carried out in 1993, cover scores from this year were also analysed for occupied and unoccupied territories in the previous two years. These analyses assume that the cover per sampling point remains constant between years.

Results

1 Distribution of territories

The distribution of breeding and non-breeding territories in the study site for 1991, 1992 and 1993 are shown in figures 5.1, 5.2 and 5.3. It was not possible to accurately estimate territory boundaries, thus the territories shown are approximations based on the distribution of nesting attempts. In all years there was a relatively low number of territories on farmland compared with woodland or edge habitats, the respective numbers of pairs being 9, 26 and 19 in 1991, 10, 35 and 20 in 1992, and 14, 36 and 23 in 1993.

According to the early habitat survey, there were highly significant differences in cover between occupied and unoccupied territories in both woodland and farmland in all three years (Table 5.1). Late year woodland samples gave almost identical results (Table 5.2).

2. Clutch Size

Clutch size can vary in relation to territory quality (Newton, 1976; Lundberg et al., 1981; Högstedt, 1980), therefore differences in the quality of habitats may be reflected in differences in clutch size. The clutch size across habitat types was compared

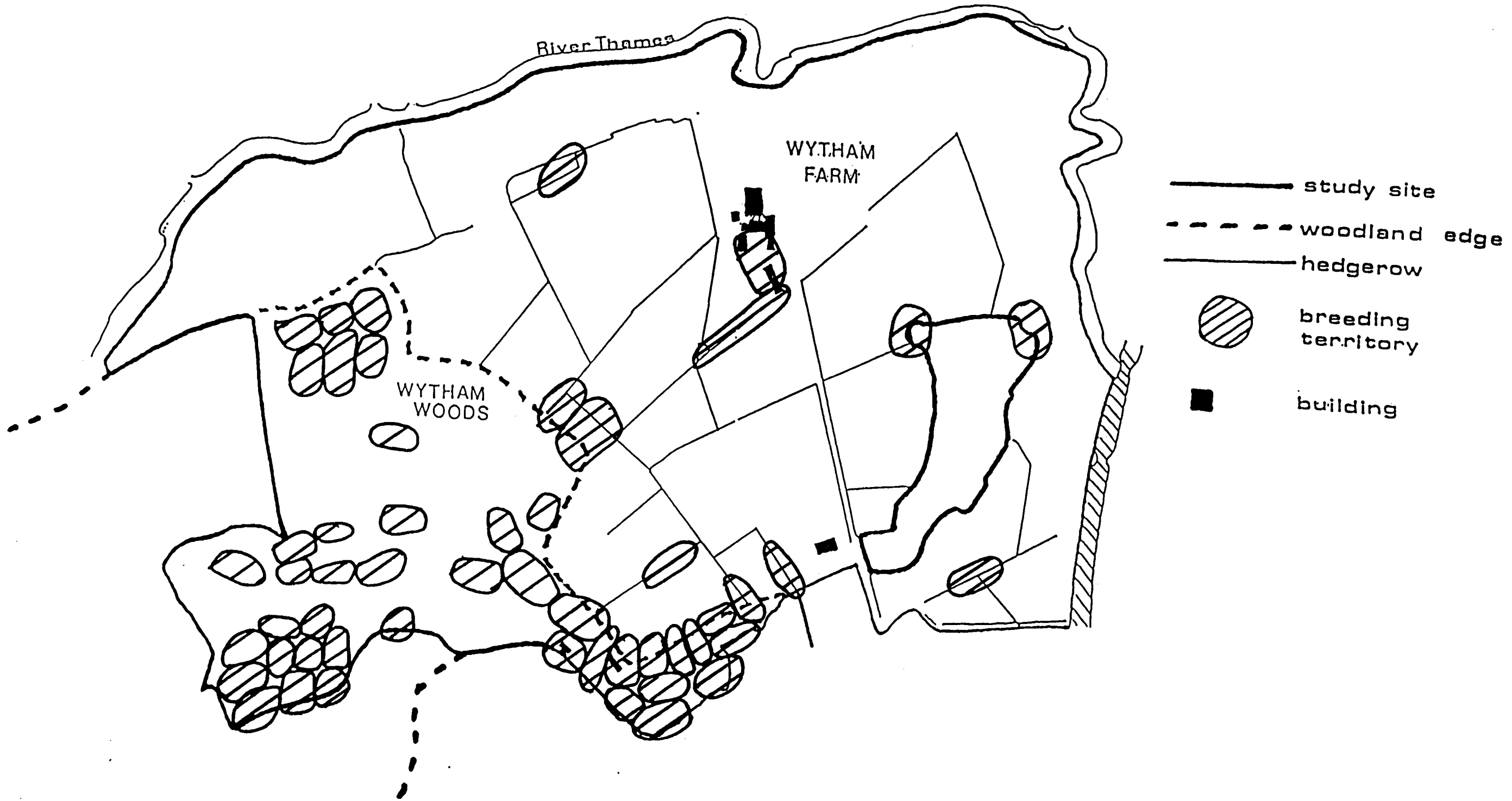


Figure 5.1: The distribution of breeding territories in 1991.

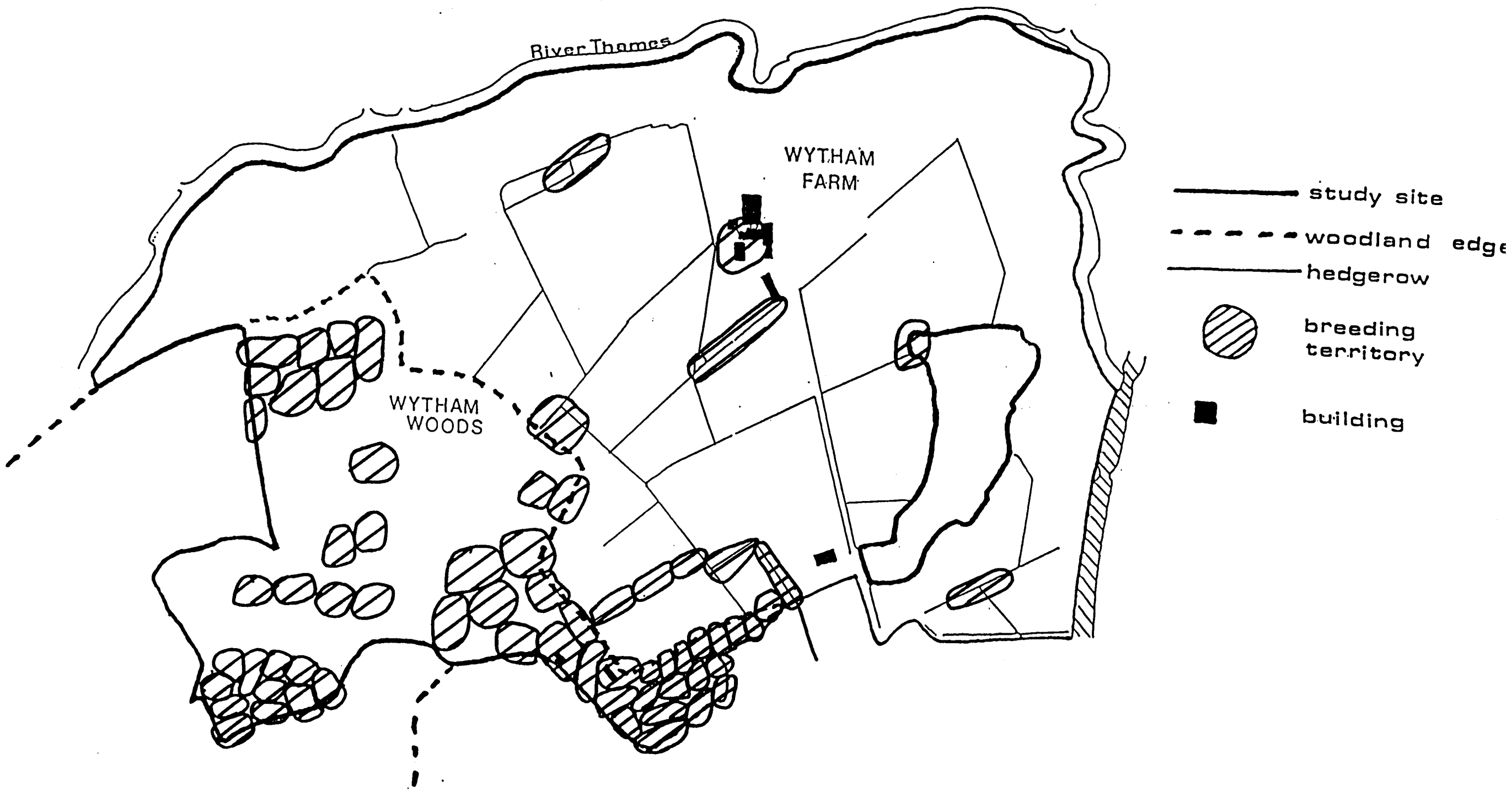


Figure 5.2: The distribution of breeding territories in 1992.

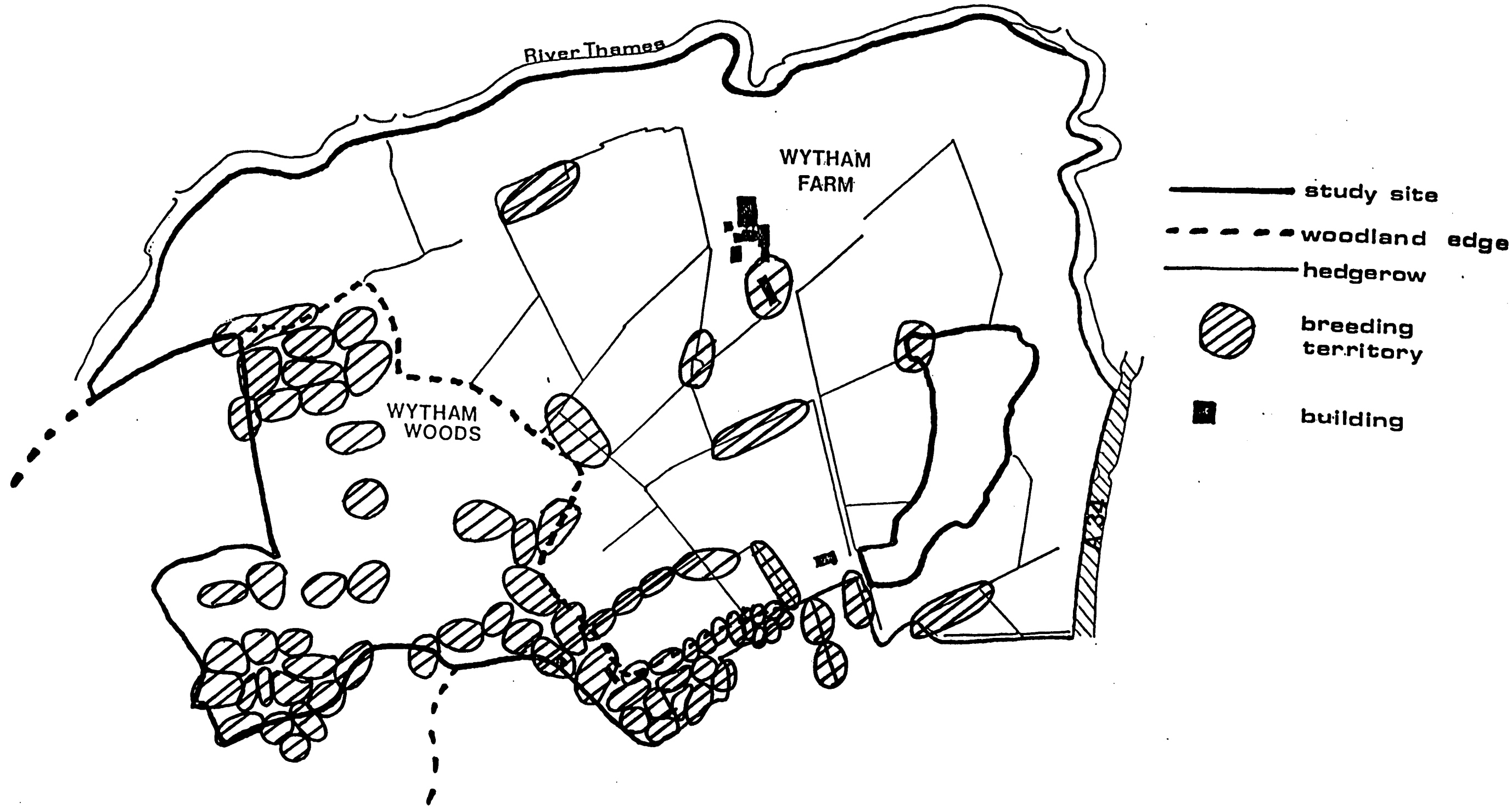


Figure 5.3: The distribution of breeding territories in 1993.

Table 5.1: Mean April cover scores for occupied and unoccupied sampling sites. z values calculated from the Mann-Whitney test are given where **0.05>p>0.01, ***p<0.01. Note that sample sizes only represent sampling points, and there was sometimes more than one sampling point within a territory.

YEAR	HABITAT	OCCUPIED	UNOCCUPIED	z
1991	wood	3.76±1.26	2.11±1.44	5.20***
		(48)	(52)	
	farm	3.47±0.99	2.72±0.99	2.52**
		(15)	(47)	
1992	wood	3.77±1.22	1.64±1.16	6.68***
		(57)	(43)	
	farm	3.78±1.06	2.52±0.82	4.02***
		(18)	(44)	
1993	wood	3.75±1.18	1.70±1.21	6.12***
		(57)	(43)	
	farm	3.64±1.09	2.51±0.79	4.05***
		(22)	(40)	

Table 5.2: Mean June cover scores for occupied and unoccupied sampling sites (woodland only). z values calculated from the Mann-Whitney test are given where **0.05>p>0.01, ***p<0.01. Note that sample sizes only represent sampling points, and there was sometimes more than one sampling point within a territory.

YEAR	OCCUPIED	UNOCCUPIED	z
1991	3.78±1.26	2.64±0.97	5.05***
	(48)	(52)	
1992	3.97±1.22	2.74±0.95	3.79***
	(57)	(43)	
1993	3.95±1.13	2.72±0.96	3.90***
	(57)	(43)	

using a two factor analysis of variance which considered the effects of date (Chapter 2) as well as habitat on clutch size. In order to create a more balanced design in the ANOVA, date was considered over twenty day periods, rather than ten day periods (as in fig. 2.1). In all years the effect of date was significant (1991 $F_{4,49}$=4.12, P=0.006; 1992 $F_{3,80}$=14.33, P=0.0001; $F_{4,88}$=4.58, P=0.0001; note that due to lack of data one twenty day period from 1992 is missing). There were no significant differences in clutch size between habitat types when years were considered individually (1991 $F_{2,49}$=0.11, P=0.89; 1992 $F_{2,80}$=2.02, P=0.14; 1993 $F_{2,88}$=0.43, P=0.65). There was, however, a significant difference in clutch size between habitats when years were combined, farmland clutches being significantly smaller than either wood or edge clutches ($F_{2,245}$=1.56, P=0.03; wood mean = 4.05$\pm$0.75, n=135; edge mean = 4.29$\pm$0.67, n=91; farm mean = 3.62$\pm$0.78, n=34)

3. Reproductive Success

There was no significant difference in the number of chicks raised to fledging per pair, the proportion of successful nests per pair, or the number of fledglings raised per successful nest between habitat types (Table 5.3). There was however a significant difference in nestling quality between habitats as measured by day eight weight, farmland birds tending to be heavier.

(Note that for the three columns sample sizes are not necessarily equal. % success is based on all nests where at least one fledgling was known to have fledged; fledglings/success was based on nests where the exact number of fledglings was known. This is not equal to the numbers for day eight weight as sometimes a nest was discovered after day eight, and also some nests which had weights taken on day eight did not necessarily survive to fledge.)

The greater mean weight of farmland broods could possibly have been due to taking a sample of nests which happened to be slightly older (albeit by less than a day). As age is more closely related to skeletal growth than weight (Magrath, 1991; this study, Chapter 2), slight differences in the ages of samples taken from different habitats

Table 5.3: Differences in measures of reproductive success between habitat types. ANOVA statistic given, with the exception of % success where a χ^2 test of association was performed (df=1). **0.05>p>0.01.

	WOOD	EDGE	FARM	TEST
fledglings	1.66±2.07	1.77±2.20	1.61±1.78	F=0.09
/pair	(87)	(73)	(33)	
% success	41.23	53.23	51.52	χ^2=2.53
	(97)	(62)	(33)	
fledglings	3.34±1.08	3.32±0.96	2.94±0.90	F=1.37
/success	(40)	(28)	(14)	
d.8 weight	58.32±3.72	58.99±4.48	61.63±3.57	F=4.44**
	(45)	(24)	(17)	

should show up in measures of tibia length. There was, however, no significant difference in mean tibia length between habitats (ANOVA F=0.31, P=0.73: mean wood = 44.61±1.03mm, n=45; mean edge = 44.50±1.10mm, n=24; mean farm = 44.57± 0.81, n=17).

The differences in weight could also have been brought about if the samples from one habitat happened to be taken from periods of significantly different prey abundance, reflected by rainfall and temperature (Chapter 4). There was no significant difference in either total rainfall in the previous eight days per nest (Kruskal-Wallis n=86, H=0.62, P=0.74), or mean temperature per nest (ANOVA $F_{1,85}$=0.37, P=0.69) between habitats. Therefore the difference in nestling weight between habitats would appear to be a genuine difference, rather than one brought about by chance due to other differences in the samples.

There was no significant difference in the cover scores between successful (at least one nestling known to have fledged) and unsuccessful territories in the early survey (Table 5.4). In the later survey (woodland only) there was a highly significant difference in one year only (Table 5.5). Note that these values are based on the cover scores of each sampling site, when they were within a territory. In some years a territory would overlap more than one sampling site, and in other years some territories were not in areas covered in the sample. Therefore some discrepancies exist between sample sizes in this and previous analyses of cover scores.

If figures 5.1, 5.2 and 5.3 are consulted it can be seen that territories are not distributed evenly across habitat types, some areas being occupied at a very high density. Areas with a density greater than twice the mean (0.5 pairs/ha) for the woodland/edge habitat were considered to be 'hot-spots' (fig. 5.4). There were significant differences in the mean number of fledglings produced per pair in 1991 and 1992 when comparing hot-spot territories with farmland and other woodland territories, hot-spots having the highest mean, and the rest of the woodland territories, the lowest (Table 5.6). Similarly, the proportion of successful nests differed across habitats, high success being associated with hot-spot territories and low success being associated with

Table 5.4: Mean cover scores for successful and unsuccessful territories in early April. z values calculated from the Mann-Whitney test are given. No results are significant.

YEAR	HABITAT	SUCCESSFUL	UNSUCCESSFUL	z
1991	wood	3.54±1.25 (24)	3.69±1.27 (18)	0.42
	farm	3.50±0.58 (4)	3.75±1.50 (4)	0.30
1992	wood	3.80±1.35 (25)	3.69±1.32 (32)	0.65
	farm	3.96±0.97 (5)	4.25±0.50 (4)	0.76
1993	wood	4.04±0.87 (23)	3.74±1.23 (36)	0.80
	farm	3.75±0.96 (4)	3.75±0.68 (6)	0.11

Table 5.5: Mean cover scores for successful and unsuccessful territories in early June. z values calculated from the Mann-Whitney test are given.
***P<0.001.

YEAR	SUCCESSFUL	UNSUCCESSFUL	z
1991	3.65±0.98 (24)	3.64±0.90 (18)	0.43
1992	4.29±1.00 (24)	3.22±0.87 (32)	4.11***
1993	3.60±1.03 (24)	3.99±0.87 (31)	1.40

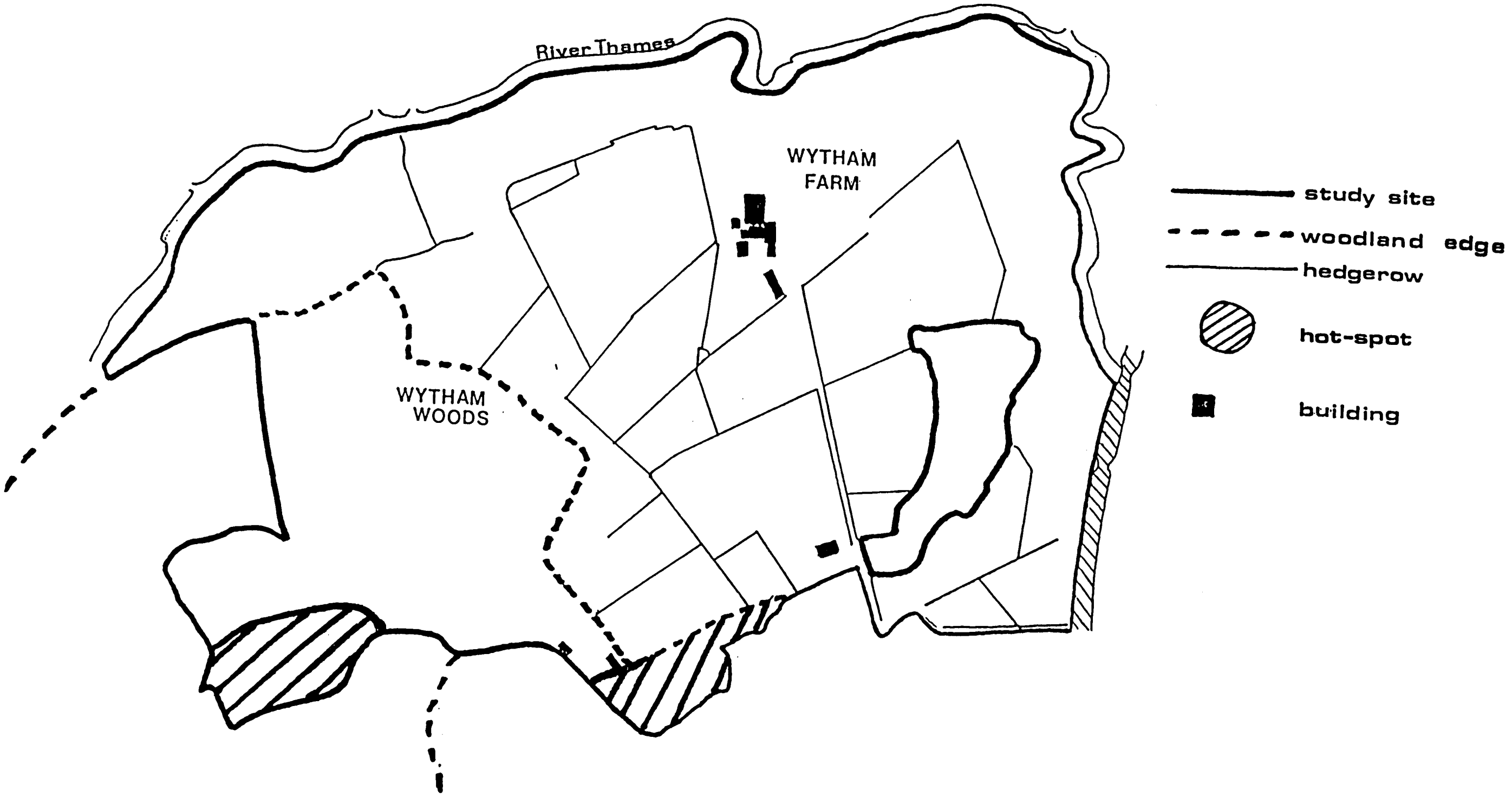


Figure 5.4: The distribution of 'hot-spots'.

Table 5.6: Breeding success of pairs in hot-spot territories and of pairs breeding outside hot-spots. ANOVA statistic given, with the exception of % success where a G– test or χ^2 test of association was performed (df=1).
(*)0.10>p>0.05, **0.05>p>0.01, ***p<0.01.

(A) 1991

	HOT-SPOT	FARM	THE REST	TEST
fledglings	3.42±2.39	1.57±1.59	1.00±1.59	F=8.51***
/pair	(24)	(9)	(20)	
% success	79.17	55.56	30.00	G=11.22***
/territory	(24)	(9)	(20)	
fledglings	3.81±0.86	2.80±0.84	3.50±0.58	F=2.92(*)
/success	(18)	(4)	(5)	
d.8 weight	59.21±4.17	63.28±3.84	57.81±4.29	F=3.22(*)
	(15)	(7)	(5)	

(B) 1992

	HOT-SPOT	FARM	THE REST	TEST
fledglings	2.18±1.91	1.90±1.85	0.77±1.66	F=4.34**
/pair	(28)	(10)	(26)	
% success	64.29	60.00	23.08	G=10.43***
/territory	(28)	(10)	(26)	
fledglings	3.00±1.03	3.20±1.30	2.38±0.48	F=0.77
/success	(17)	(5)	(4)	
d.8 weight	58.45±4.04	59.35±3.43	56.27±4.80	F=0.60
	(18)	(5)	(3)	

(C) 1993

	HOT-SPOT	FARM	THE REST	TEST
fledglings	1.27±1.94	1.43±1.95	1.67±2.18	F=0.27
/pair	(33)	(14)	(29)	
% success	33.33	28.57	41.38	χ^2=2.20
/territory	(33)	(14)	(29)	
fledglings	3.59±1.16	2.75±0.96	3.33±1.37	F=0.68
/success	(11)	(4)	(12)	
d.8 weight	58.79±3.44	61.59±2.39	58.50±4.61	F=1.23
	(14)	(5)	(14)	

the rest of the woodland territories. This was due to lower predation rates, rather than measures reflecting starvation (fledglings per success) or chick quality (although in one year there was a tendency for chick weight to be higher in farmland). Only in 1993 was there no significant difference between hot-spots and other habitats in terms of reproductive success.

There was no significant difference in the mean cover score between hot-spot and non-hot spot territories (Table 5.7) in the early habitat survey. However, when the later habitat survey was carried out, hot-spot territories had significantly higher cover scores than non-hot-spot territories (Table 5.8). Note that farmland was not included in this analysis as the scoring method used was probably not applicable between habitats.

4. Prey availability

In the previous chapter, it was shown that there was a significant effect of rainfall on earthworm abundance in both woodland and farmland, with some evidence of farmland being more sensitive, but that the effects differed between years. In 1991 there was no significant difference in the mean number of calories emerging per quadrat between habitats (unpaired t-test: t=1.09, df=169, P=0.28; mean wood = 2874$\pm$2260 calories, n=100; mean farm = 2470$\pm$2553 calories, n=71). In 1992 and 1993 most samples were carried out on the same day in each habitat, thus a more accurate two factor analysis of variance between habitats could be used which also takes into account seasonal variation. This produced a different result, woodland having a significantly higher earthworm abundance in both 1992 ($F_{1,76}$=11.2, P=0.001; mean wood = 7001$\pm$4410 calories, n=46; mean farm = 4561$\pm$3218 calories, n=46), and 1993 ($F_{1,70}$=38.23, P<0.0001; mean wood = 7993$\pm$4869 calories, n=42; mean farm = 3718$\pm$2309 calories, n=42).

A number of studies have shown that earthworm abundance can be sensitive to microhabitat features such as soil structure, soil type or predominant plant species (Edwards and Lofty, 1972). Therefore in this study samples were restricted to localised areas within each habitat type. However, on one day in 1993, additional samples were

Table 5.7: Mean cover scores for hot-spot and non-hot-spot territories in early April. z values calculated from the Mann-Whitney test are given. No results were significant.

YEAR	HOT-SPOT	OTHER	z
1991	3.91±1.41 (29)	3.61±1.12 (19)	1.23
1992	3.86±1.33 (28)	3.68±1.12 (29)	0.88
1993	3.82±1.33 (26)	3.70±1.06 (31)	0.70

Table 5.8: Mean cover scores for hot-spot and non-hot-spot territories in early June. z values calculated from the Mann-Whitney test are given. ***P<0.001.

YEAR	HOT-SPOT	OTHER	z
1991	4.14±0.74 (29)	3.11±0.88 (19)	3.89***
1992	4.14±0.89 (28)	3.03±1.12 (29)	3.78***
1993	4.08±0.89 (26)	3.13±1.15 (31)	3.25***

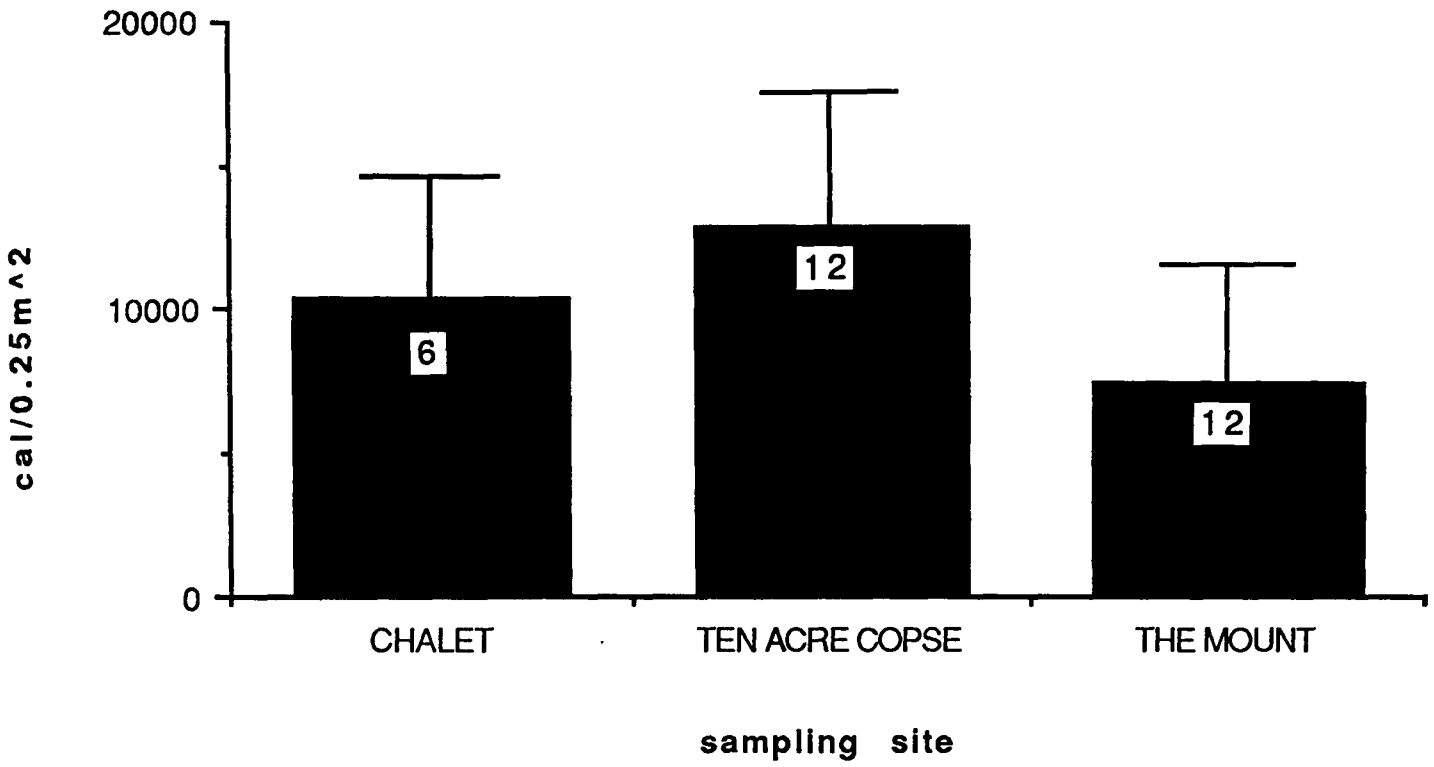


Figure 5.5: Mean earthworm abundance (cal/0.25m^2) at different sites within the woodland habitat. Error bars represent standard deviations. Numbers on columns represent sample sizes (i.e. number of sampling quadrats). The Chalet was the site used for sampling in the rest of the study

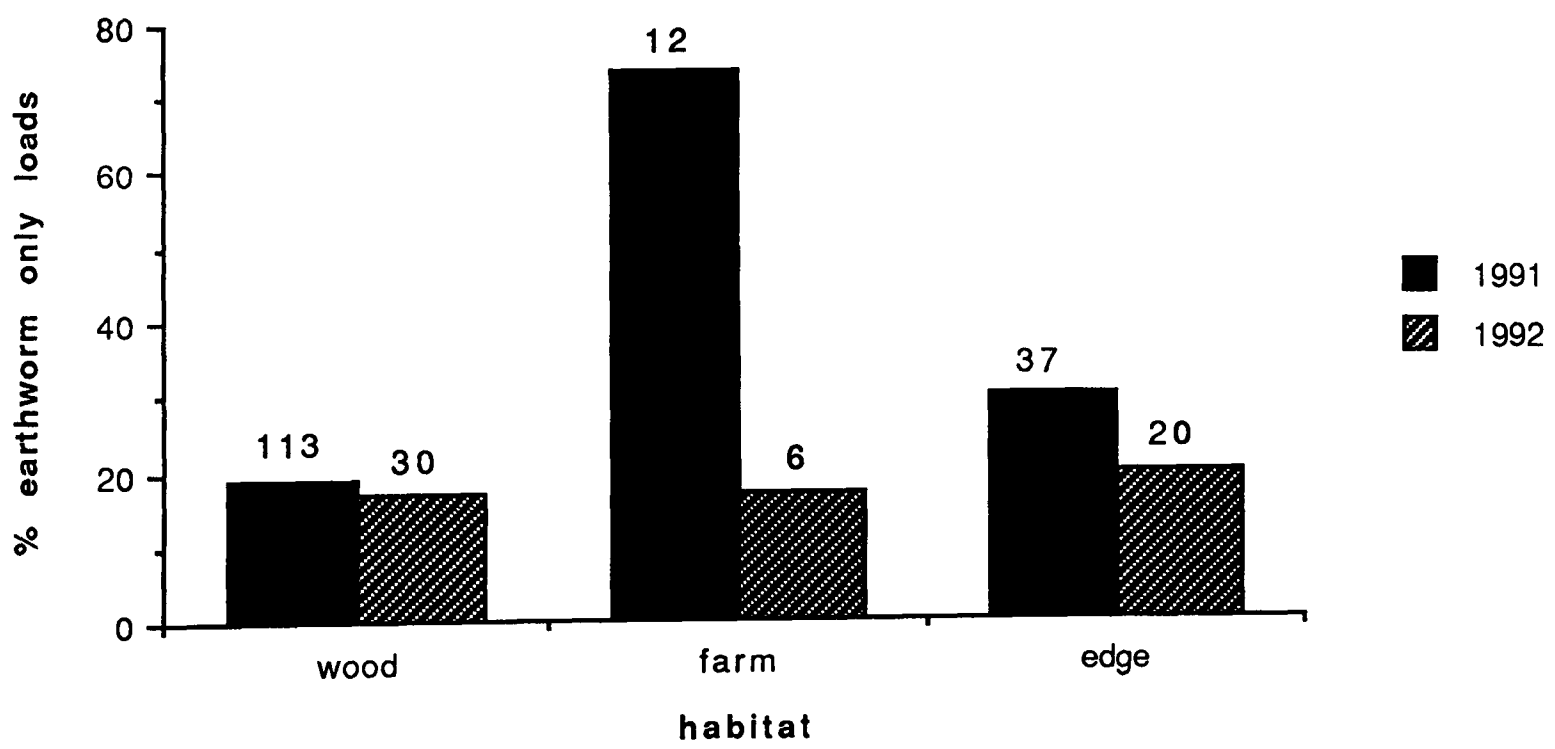


Figure 5.6: The proportion of worm-only loads delivered to nestlings during the 'caterpillar peak'. Numbers on columns represent sample sizes.

carried out at two other sites within the woodland habitat as well as the normal site. There were significant differences in mean calories per quadrat between these sites (ANOVA $F_{2,27}$=4.34, P=0.02- fig. 5.5), indicating that certain areas within a habitat may be of higher quality in terms of prey abundance. Therefore, some territories within a habitat may vary in prey availability. The effect that this will have on reproductive success could only become apparent with more detailed studies of prey availability and foraging site choice of provisioning parents.

5. Nestling Provisioning

There were no significant differences in the mean calories delivered (age 7-12) between habitat types, at either one or two hour observation periods (Table 5.9), when the appropriate adjustments for brood size had been made (Chapter 3). There were no significant differences in the mean delivery efficiency (Chapter 3) between habitats, but sample sizes in farm and edge habitats were very small (Table 5.10).

(i) Nestling Diet

If food sources alternative to earthworms are less available to farmland blackbirds, then the proportion of earthworms in the diet may be expected to differ between habitats when caterpillars are available in the wood.

Figure 5.6 shows the proportion of worm-only loads delivered to nests in each habitat type during periods when caterpillars were present in the diet (as inferred from fig. 4.3). In 1991 there were significantly more worm loads than expected in the farmland nestling diet (G-test=17.73, df=2, P<0.001); however in 1992 there was no significant difference between habitats (G-test=1.38, df=2, P<0.50). No results are presented from 1993 as unfortunately no nests were available to be watched from either farm or edge habitats during the caterpillar peak in this year.

One problem with the 1991 data is that 56% (9/16) of observations came from periods where earthworms formed over 80% of the diet even though caterpillars were present, so a large number of earthworms on farmland was not unexpected.

Table 5.9: Mean energy delivery rates in different habitats. Mean±standard deviation, sample sizes (parenthesis) and F values from ANOVA given. No differences were significant.

	SEX	WOOD	EDGE	FARM	F
cal/ hour	male	1849±1022 (22)	2053±368 (7)	1663±1294 (5)	0.22
	female	1135±642 (22)	1278±576 (7)	887±197 (4)	0.54
	total	3108±1102 (19)	3500±1632 (6)	2190±1020 (4)	1.44
cal/ 2hour	male	5056±1248 (18)	5482±2401 (5)	5814±2401 (4)	0.46
	female	2907±1448 (19)	2750±1744 (3)	1849±392 (3)	0.72
	total	8050±2300 (18)	9125±2783 (3)	7621±1673 (3)	0.37

Table 5.10: Mean energy gains (calories/min.) in different habitats (age 7-12). F values from ANOVA given. No differences were significant.

SEX	WOOD	EDGE	FARM	F
male	56.54±20.64 (17)	66.99±22.74 (5)	67.22±21.98 (4)	0.73
female	44.22±43.65 (15)	46.39±24.60 (5)	37.03±18.53 (3)	0.06

Considering only data from periods where caterpillars occurred at less than 20% calorific contribution, there are still significant differences in diet across habitats (G-test=6.21, df=2, 0.05>P>0.03; fig 5.7), although sample sizes are small. In this case both edge and farm habitats have a significantly higher proportion of earthworms in the diet.

As farmland birds tend to differ slightly from woodland and edge nesting birds in their diet (fig. 5.6 and 5.7), environmental factors may have differing effects on chick quality according to habitat. Combining data from both years, there was a significant positive effect of total rainfall in the previous eight days on day eight nestling weight in farmland only (fig. 5.8), which supports the theory that farmland blackbirds are more dependent on earthworms than woodland/edge birds. No significant effects of temperature on chick weight were found in any habitat (fig. 5.9).

6 Habitat Use

In 1992 and 1993, in addition to collecting data on nestling diet, an attempt was made to determine the habitat use of parents in edge habitats. In practice this proved difficult as the blackbirds typically foraged in cover, so no direct observations of foraging was possible. The only data that was collected was simple habitat choice data (i.e. whether the parent foraged in woodland or farmland). Given the differing effects of environmental variables on earthworm abundance in the two habitats (Section 4), and the assumed differences in caterpillar abundance (Section 1), it may be expected that habitat choices are influenced by environmental variables. If it is assumed that rainfall and temperature are the major effects on habitat choice, and brood size and chick age are relatively unimportant then each watch period may be considered as independent. When treating the data like this, there was no significant effect of rainfall index or temperature on the proportion of foraging visits to farmland from edge habitats (Spearman rank correlation: rainfall n=20, r=0.21, P=0.35; temperature n=20, r=-0.37, P=0.11), nor was there a significant effect of rainfall index on the proportion of

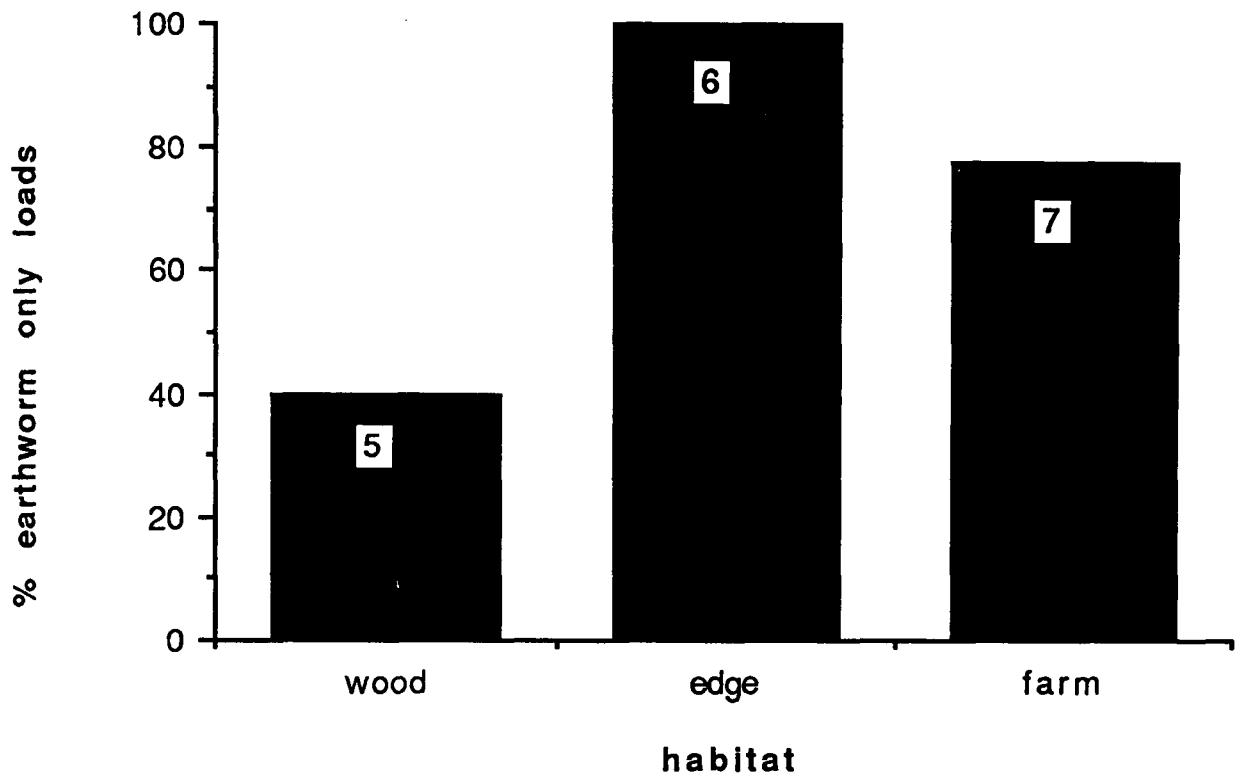
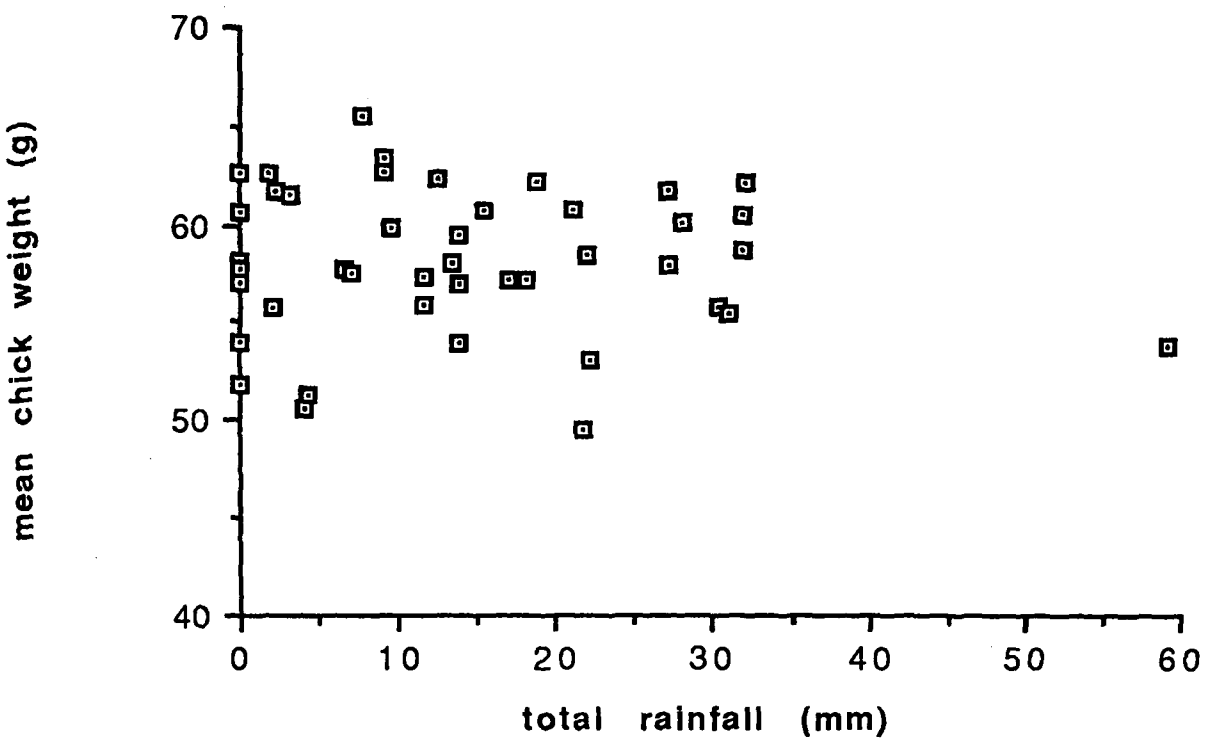
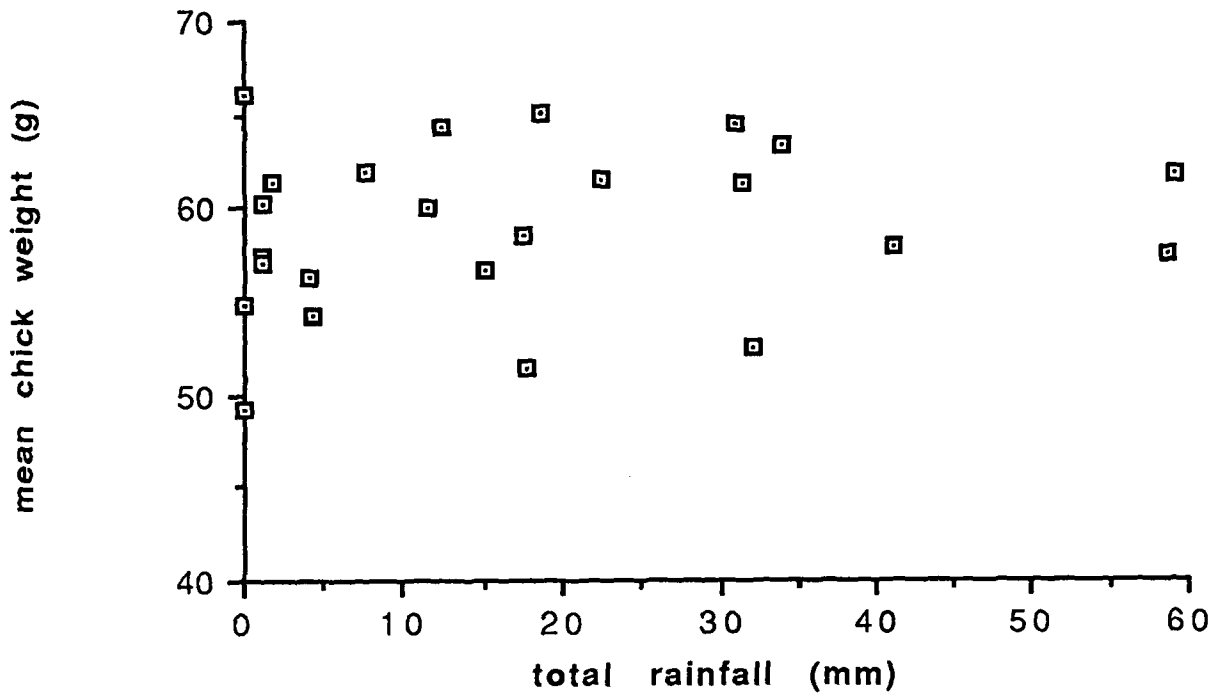


Figure 5.7: The proportion of earthworm-only loads in the nestling diet when earthworms contributed over 80% to the total diet (1991 only).

(A) Wood



(B) edge



(C) farm

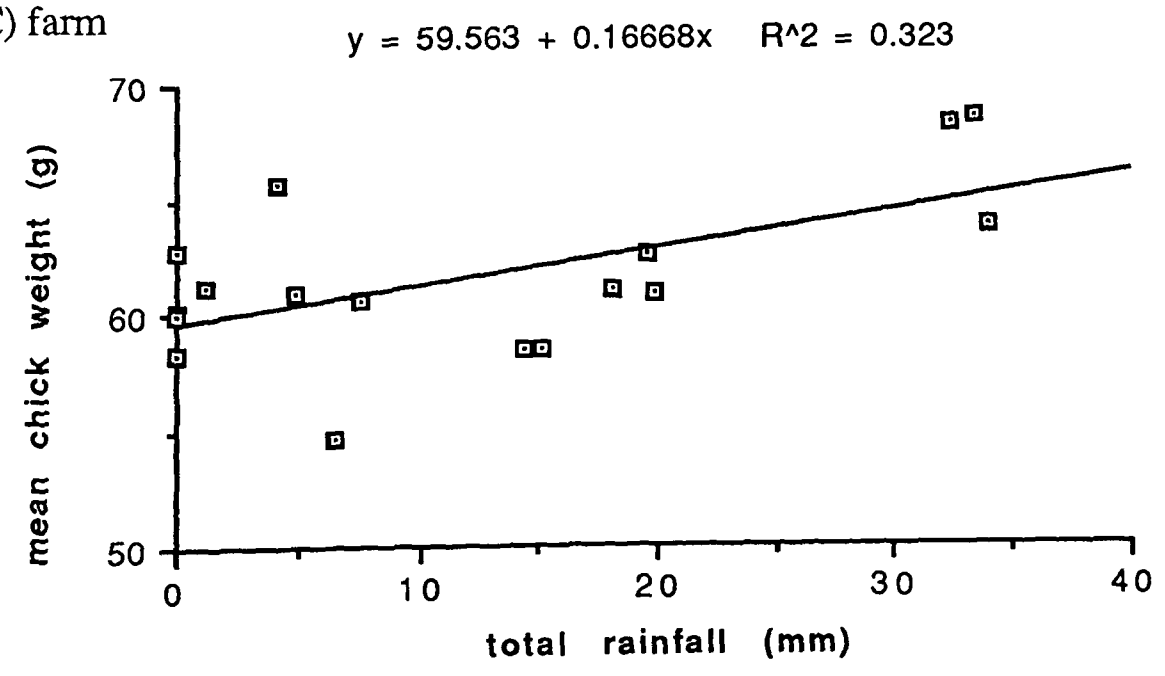
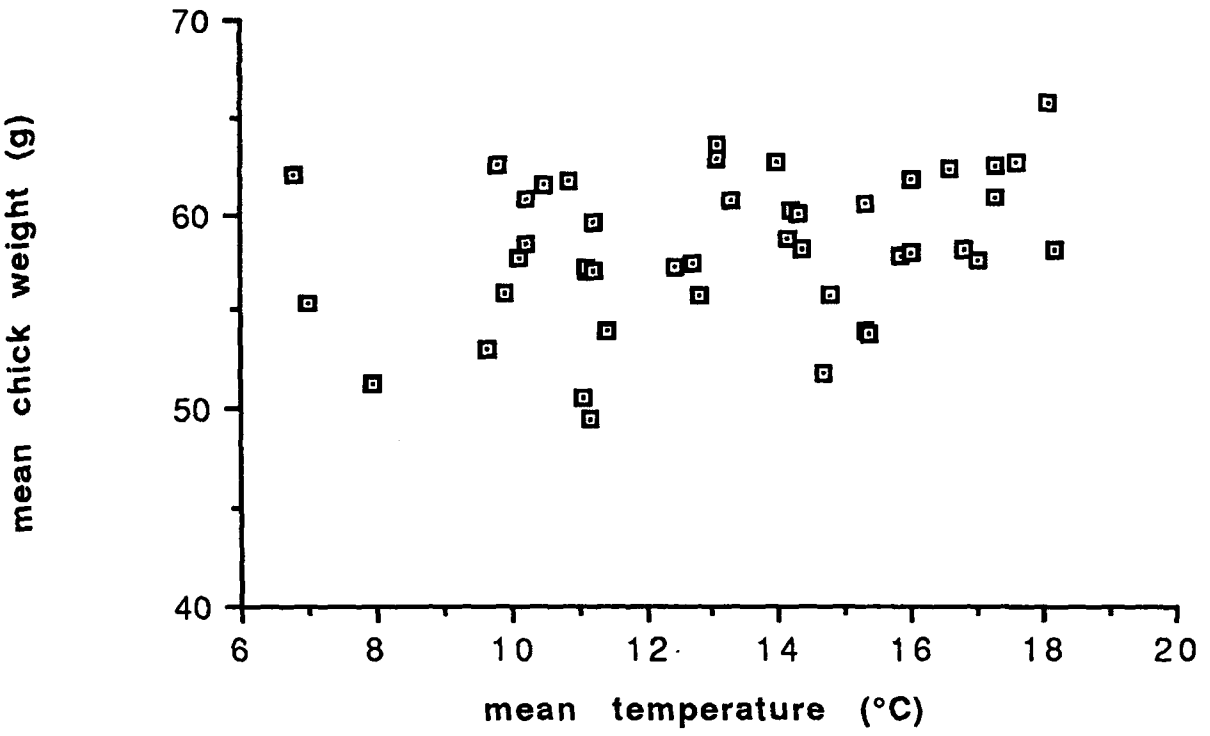
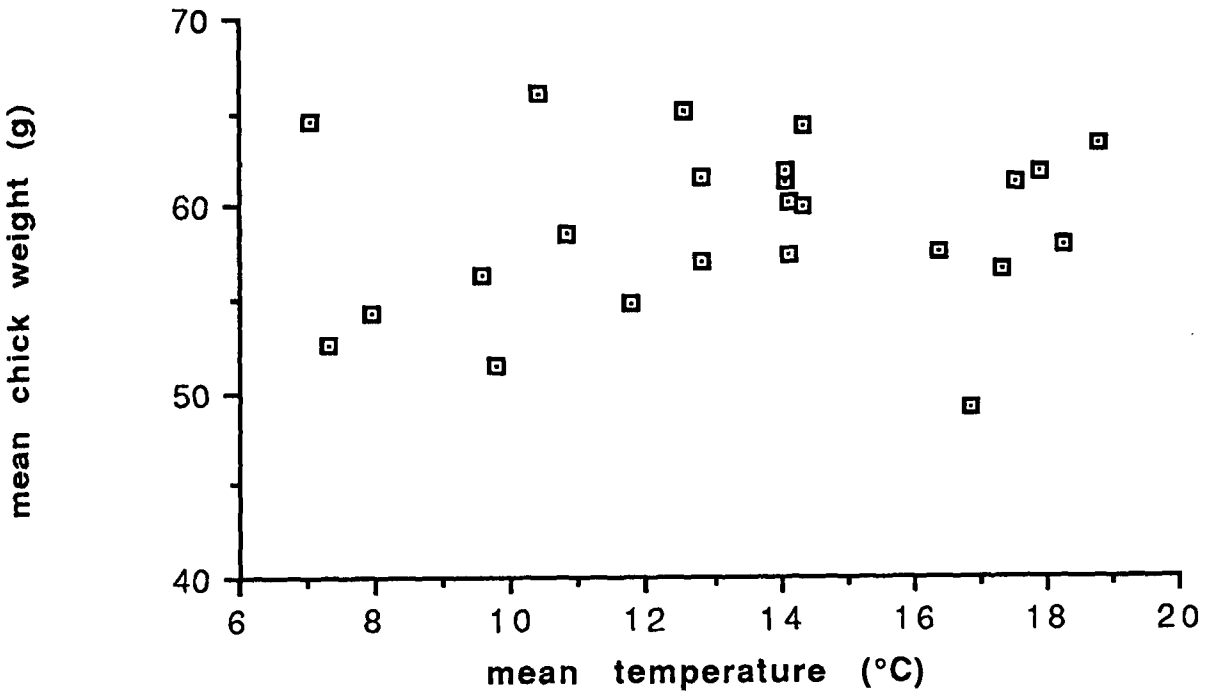


Figure 5.8: The effect of total rainfall in the eight days previous to weighing, on day eight chick weight. Wood r=0.10, edge r=0.17, farm r=0.57.

(A) Wood



(B) edge



(C) farm

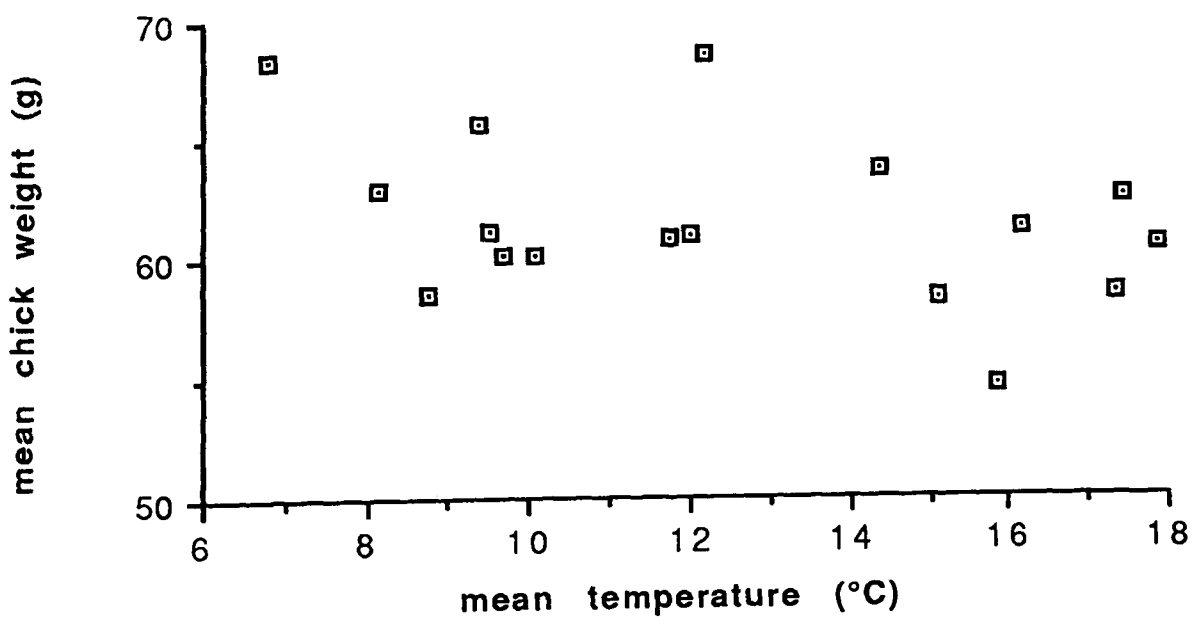


Figure 5.9: The effect of mean morning temperature eight days previous to weighing, on day eight chick weight. Wood r=0.29, edge r=0.15, farm r=-0.39.

farmland visits from farmland nests (n=13, r=0.03, P=0.90), but there was a significant negative effect of temperature (n=13, r=-0.57, P=0.03).

As parental effort increases with both chick age and brood size, then the above result may be invalid if habitat choice is mediated via the demand of the brood (compare Tinbergen, 1981). Only 5 edge nests and 4 farm nests had habitat choices recorded. If the total proportion of farmland visits from individual nests from ages 7-12 are used against mean rainfall and temperature in a repeat of the previous analysis, similar results are obtained (edge: rainfall index n=5, r=0.70, P=0.16; temperature n=5, r=0.50, P=0.32; farm: rainfall index n=4, r=0.20, P=0.73; temperature n=4, r=-0.86, P=0.16). Although the latter result was not significant when analysed this way, it was a fairly strong trend for such a small sample size and may indicate that some relationship does exist between habitat choice and temperature on farms, although a much larger sample is needed to make any firm conclusions. Ideally, radio-tracking of provisioning parents would provide a very detailed picture of habitat use, although this technique was not available to this study.

7 The Adult Population

In 1991, 74.07% (40/54) of breeding males and 59.26% (32/54) of breeding females were colour ringed. In 1992 the respective figures were 61.54% (40/65) and 69.23% (45/65), and in 1993, 69.86% (51/73) for both sexes. In all years, first year breeders were uncommon, accounting for 0% of identified breeding males and 8.11% (3/37) of breeding females in 1991 and 17.77% (8/45) of breeding males and 10.42% (5/48) of breeding females in 1992. In 1993, first year breeders were more common, accounting for 25.49% (13/51) of identified breeding males and 37.3% (19/51) of breeding females. Note that sometimes the age of birds were identified in the field without being ringed, thus sample sizes for ringed birds and aged birds will not necessarily be the same.

According to a number of studies (see Introduction) birds breeding in their first year tend to occupy sub-optimal habitats, thus the age structure of populations across

habitat types may provide evidence of habitat quality. In 1991 there were only 3 first year birds (all females) which were known to have bred, occupying two edge and one woodland territory. In 1992 there were significantly more first year males occupying farmland territories than other habitats, and significantly more older (2nd year+) males occupying woodland territories (G-tests: G=10.84, df=2, P<0.01). There were no significant differences in the age structure of the female population across habitats (G=1.75, df=2, P>0.50; Table 5.11). In 1993, there was no significant difference in age structure between habitats in either sex (male G=1.33, df=2, P<0.50; female G=0.30, df=2, P<0.75; Table 5.12).

Of the total number of breeding birds caught and ringed in 1991, 60% (n=43) were seen or captured again in 1992. When considered by habitat type, and combining sexes, there was a strong, although non-significant tendency for fewer birds to be relocated in farmland when compared with woodland and edge territories combined (χ^2=3.74, df=2, P=0.08; fig. 5.10). Therefore it would appear that either survival was lower on farmland territories, or that farmland birds were more likely to move territory than either woodland or edge nesting birds. There were a small number of movements across habitat type from year to year (fig. 5.11). All movements were either edge to woodland habitat, or farm to edge habitat. There were no detected movements from woodland to other habitats, and no movements onto farmland. There was a significant difference in the proportion of birds of either sex moving habitat (G-test=7.76, df=2, P<0.03).

In 1993 , 41% (n=20) of males and 43% of females (n=21) which had been present in 1992 were captured or relocated in 1993. When considering both sexes combined, there was no tendency for the number of birds relocated between years to be associated with habitat (χ^2=0.76, df=2, P>0.50; fig. 5.12). There were also no significant differences in the number of individuals moving habitats between years (G-test=4.16, df=2, P>0.10; fig. 5.13).

There were a number of birds caught which did not show any sign of breeding behaviour (e.g. birds ranging over a wide area, males singing throughout the breeding

Table 5.11: Age structure of breeding populations in different habitats in 1992.

	NUMBER OF MALES		NUMBER OF FEMALES	
HABITAT	1st year	2nd year+	1st year	2nd year+
WOOD	1	22	3	19
FARM	4	2	0	7
EDGE	3	13	2	17

Table 5.12: Age structure of breeding populations in different habitats in 1993.

	NUMBER OF MALES		NUMBER OF FEMALES	
HABITAT	1st year	2nd year+	1st year	2nd year+
WOOD	4	20	9	15
FARM	2	4	8	12
EDGE	7	17	2	5

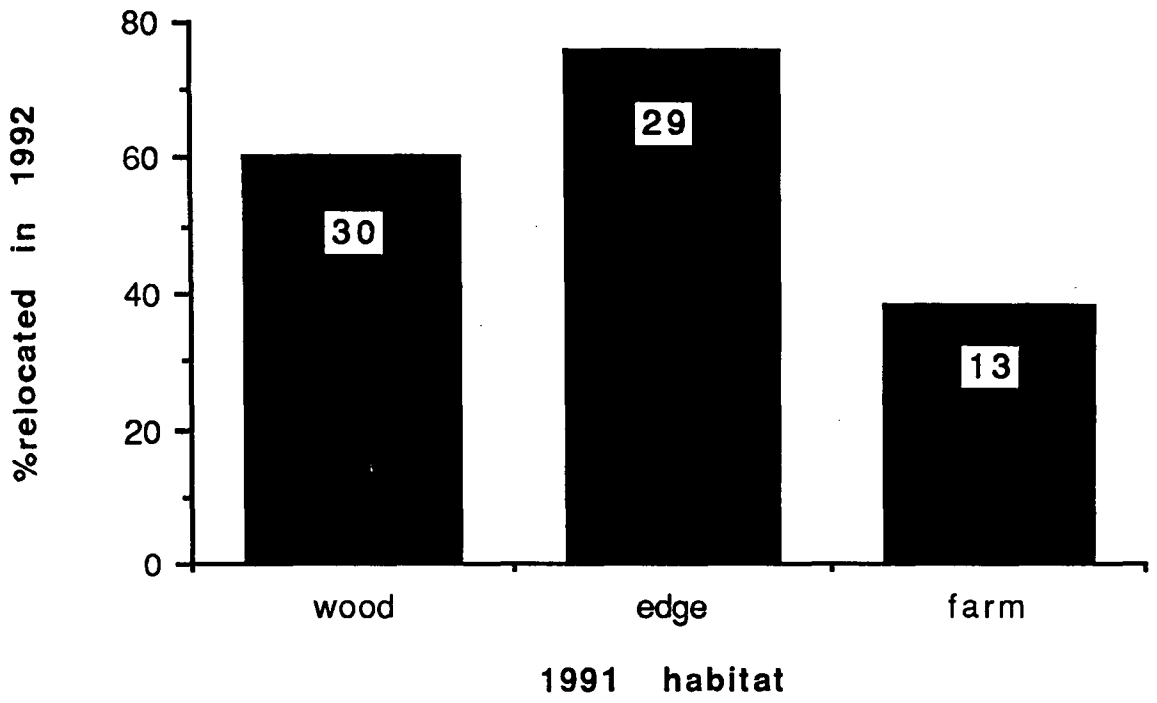


Figure 5.10: The proportion of birds breeding in 1991 which were relocated on the study site in 1992. Sexes were combined. Numbers on columns represent sample sizes.

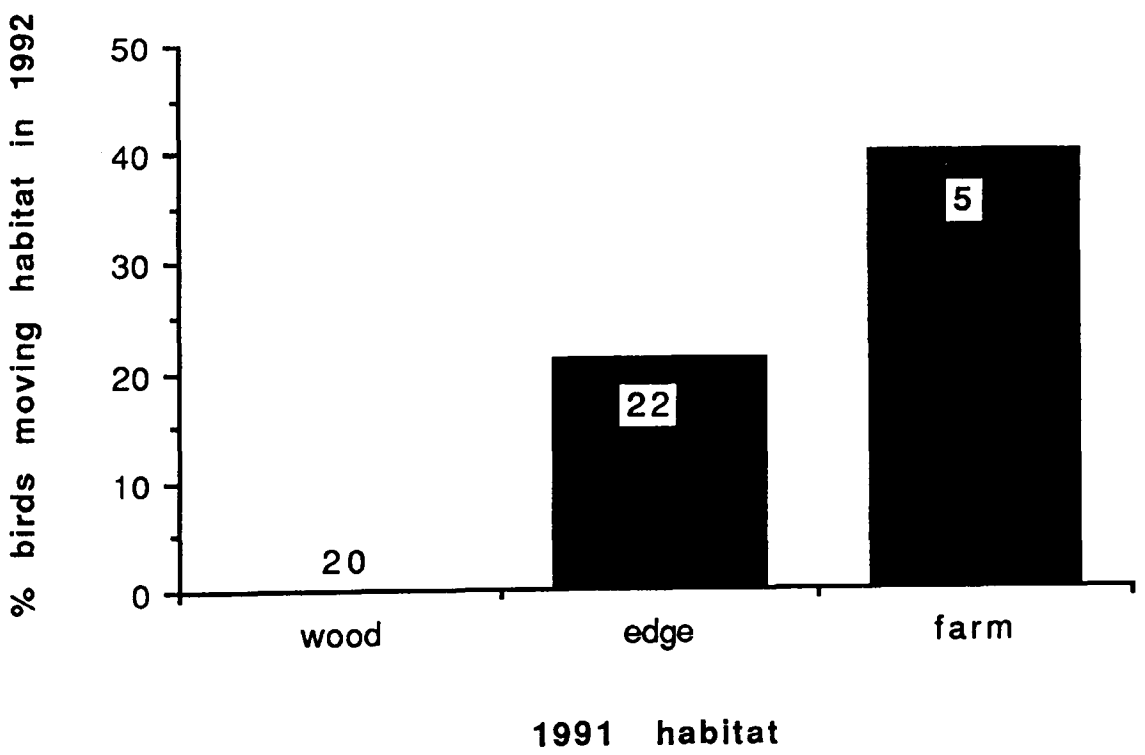


Figure 5.11: The porportion of birds which changed nesting habitat between 1991 and 1992. Sexes were combined. Numbers on columns represent sample sizes.

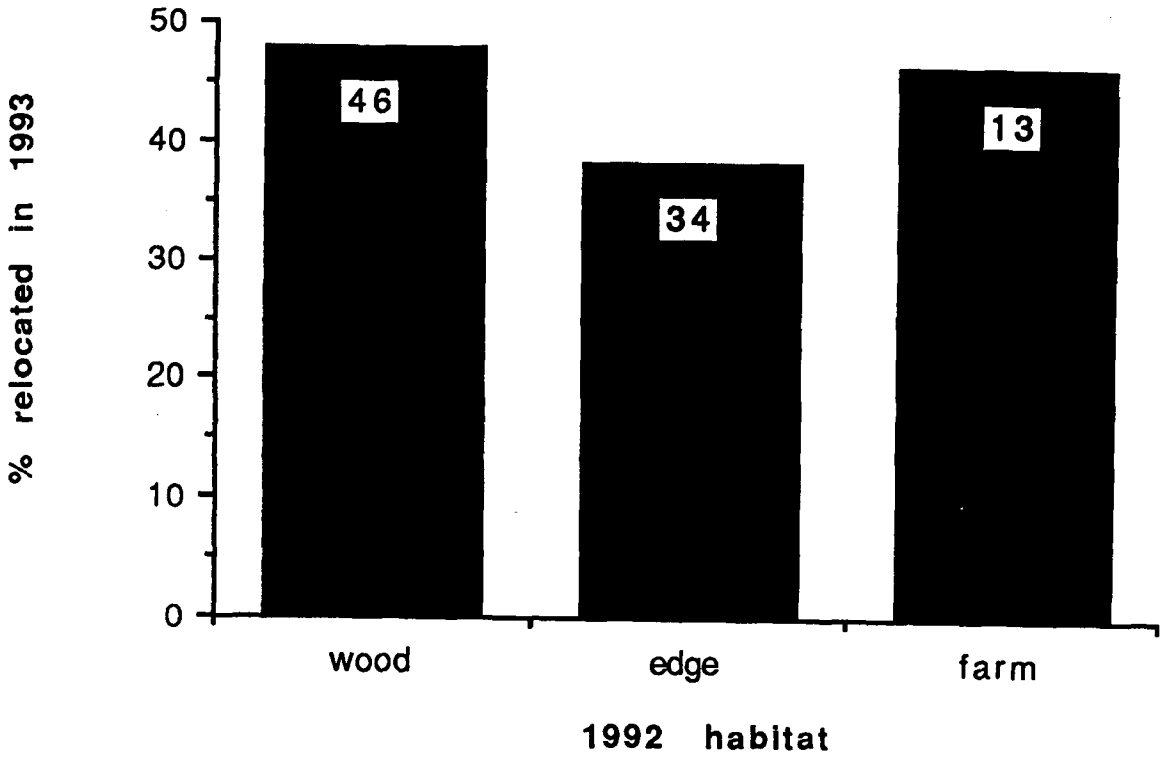


Figure 5.12: The proportion of birds breeding in 1992 which were relocated on the study site in 1993. Sexes were combined. Numbers on columns represent sample sizes.

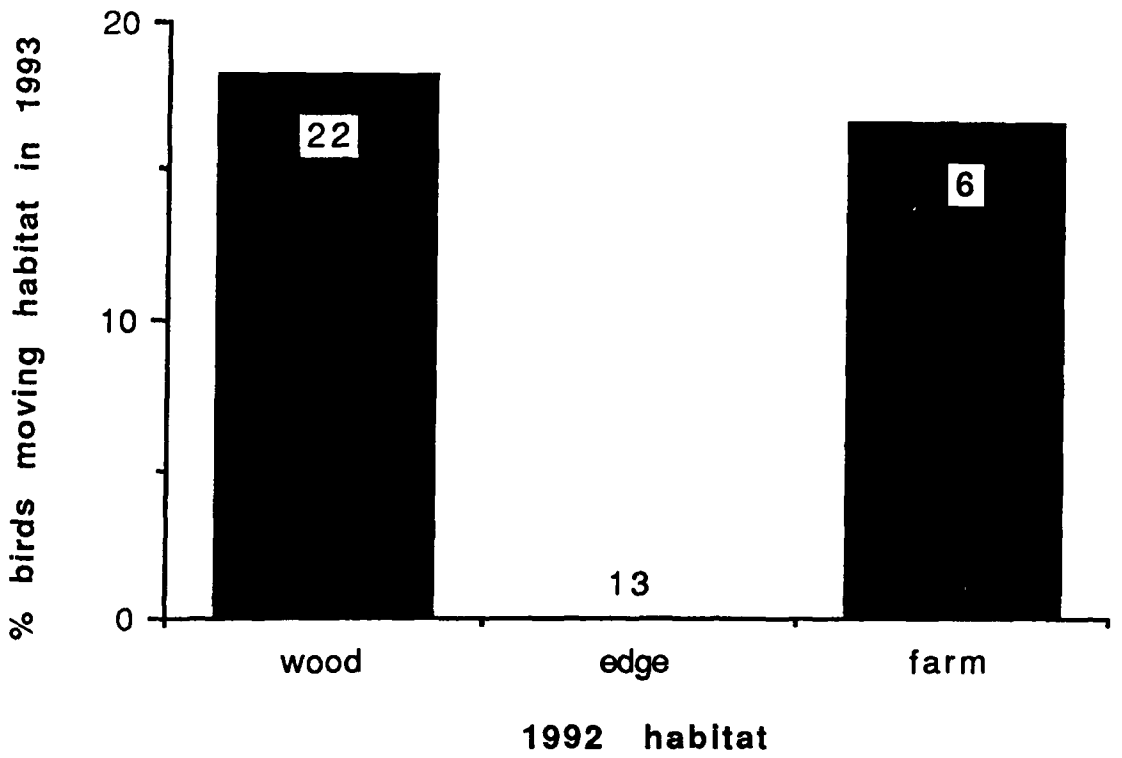


Figure 5.13: The proportion of birds which changed nesting habitat between 1992 and 1993. Sexes were combined. Numbers on columns represent sample sizes.

season, and no observations of mate guarding or provisioning behaviour). All suspected non-breeders were males.

In some species certain physical characteristics can be indicators of adult 'quality' in terms of occupation of the best territories or having a high reproductive success (e.g. pied flycatcher *Ficedula hypoleuca* Lundberg et al., 1981; meadow pipit *Anthus pratensis* Hötker, 1989; song sparrow *Melanospiza melodia* Hochachka et al., 1989). If size reflects quality in the blackbird, then significant differences in size may be expected between territories of differing quality. When comparing wing length, bill length and tarsus length between adults in hot-spots, farmland and other areas, no significant differences were found in either males or females in 1991 and 1992. However, there were significant differences in male tarsus length and bill length in 1993 (Table 5.13).

If measures of body size reflected quality, then larger individuals would be expected in more productive territories. In 1993, hot-spots, which held the most productive territories in two out of three years, had significantly smaller males than farmland or other woodland territories. This could have arisen due to there being a greater proportion of first year breeders on these territories, which tend to have smaller body size. However, removing all first year breeders from the analysis did not alter the results (ANOVA tarsus $F_{2,38}=4.18$, $P=0.02$; bill $F_{2,38}=3.72$, $P=0.03$) therefore even mature adult males were smaller in hot-spots.

Compared with 1991 and 1992, the adult population in 1993 showed some significant differences, particularly in the hot-spot territories. In this year an experiment was carried out in the edge hot-spot, when territories were supplied with additional food over the winter. This may have had an effect on the population in the hot-spot, therefore these results should be viewed with some caution when comparing them with other years. The food supplementation experiment and its effects are described in Chapter 7.

Table 5.13: Measures of adult body size in relation to nesting territory.

All measurements are in millimetres. F values for ANOVA given. **0.05>p>0.01.

(A) 1991

	HOT-SPOT	FARM	THE REST	F
male wing	133.57±3.03	133.88±2.48	133.40±2.46	0.07
	(21)	(8)	(10)	
tarsus	34.43±1.02	34.66±0.56	34.73±1.02	0.41
	(21)	(8)	(10)	
bill	25.66±0.95	25.53±0.97	25.74±0.72	0.13
	(21)	(8)	(10)	
female wing	127.33±2.78	127.647±3.39	129.50±2.38	0.96
	(21)	(6)	(4)	
tarsus	34.32±0.72	34.27±1.02	34.52±1.38	0.12
	(21)	(6)	(4)	
bill	25.42±0.91	25.63±0.89	25.68±0.63	0.23
	(21)	(6)	(4)	

(B) 1992

	HOT-SPOT	FARM	THE REST	F
male wing	134.11±2.73	132.00±3.24	134.07±3.24	0.44
	(19)	(6)	(15)	
tarsus	34.74±0.96	34.60±0.75	34.85±1.03	0.32
	(19)	(6)	(15)	
bill	25.62±0.66	26.05±1.05	25.71±1.18	0.58
	(19)	(6)	(15)	
female wing	127.35±2.71	128.31±2.29	127.93±2.56	0.44
	(23)	(7)	(14)	
tarsus	34.34±0.89	34.02±1.07	34.15±1.09	0.32
	(23)	(6)	(14)	
bill	25.69±0.88	25.70±0.64	25.38±1.01	0.58
	(23)	(7)	(14)	

(C) 1993

	HOT-SPOT	FARM	THE REST	F
male wing	133.64±3.33	131.00±2.97	133.50±4.23	1.37
	(28)	(6)	(16)	
tarsus	34.26±0.76	34.48±0.58	34.89±0.97	3.12**
	(28)	(6)	(16)	
bill	25.41±0.79	25.78±0.65	26.16±0.95	4.26**
	(28)	(6)	(16)	
female wing	127.85±2.81	127.29±1.60	127.19±2.61	0.37
	(27)	(7)	(16)	
tarsus	34.07±0.83	34.09±1.14	33.68±1.06	0.97
	(27)	(7)	(16)	
bill	25.40±0.89	25.50±1.07	25.46±0.88	0.05
	(27)	(7)	(16)	

Discussion

1 Reproductive Success

There were no significant differences in reproductive success per pair when comparing territories from wood, farm, and edge habitats. Given the differences in density between habitat types (wood and edge>farm), these results at first sight would appear to conform to an Ideal Free Distribution (Fretwell and Lucas, 1969) where the more profitable habitat is occupied at a higher density, but pay-offs (in this case reproductive success) are equal across habitat types due to disadvantages associated with a greater number of competitors (e.g. increased predation- Tinbergen et al., 1967; reduced food supply- Arcese and Smith, 1988).

There was a significantly higher mean brood weight in farmland nests compared with the other two habitat types. This is contrary to the prediction made in the introduction and what would be expected on the basis of the earthworm sampling results. Also there was no difference in provisioning rates between habitat (see below). There was a significantly lower clutch size in farmland, probably due to the higher numbers of first year breeders in this habitat (Snow, 1958). Although there was no detected effect of clutch size on chick weight, there may have been a subtle effect, enough to cause the difference in chick weight between habitats. When the results were considered by individual years, in only one year was the weight apparently higher, although this was not quite significant. The trend is therefore a weak one anyway.

The habitat definitions used above are somewhat crude as they do not take into account the large variation in nesting densities within the woodland habitat (c.f. figs 5.1, 5.2 and 5.3). When high density hot-spot areas were compared with farmland and other woodland territories, it was found that measures of nesting success in hot-spots tended to be higher than those in farmland territories, which in turn had higher nesting success than the remaining territories. Measures associated with nestling quality and starvation were, however, not significantly different between hot-spots and other woodland areas. Therefore it is differential predation across habitats, rather than feeding conditions, which cause differences in breeding success between areas.

Edwards (1983), working in an urban environment, found that reproductive success throughout the breeding season was related to the amount of cover on a territory, rather than food abundance (measured by earthworm density). Given that hot-spots tended to be areas of extensive cover, then it seems likely that cover is also the major territorial resource in rural environments.

On a finer level, Hatchwell (pers. comm.) found that the characteristics of individual nest sites had a strong effect on reproductive success in the Wytham population. Nests which successfully hatched were significantly less exposed than nests which were predated, thus confirming the effect of cover on habitat quality. There were also differences in nest exposure and nest bulk between habitats, with farmland nests being significantly less exposed and significantly smaller than woodland or woodland edge nests. Nest site selection on farmland may therefore be more constrained than in woodland or edge due to greater potential predation pressure. This is discussed further in Chapter 6.

When the results are considered in terms of hot-spots and non-hot-spots, rather than the broader definitions of woodland, edge and farmland, then there are clear differences in reproductive success between habitats, and therefore an Ideal Free Distribution (Fretwell and Lucas, 1969) is not reached. In this situation it may be expected that the better habitats are being occupied by birds of greater competitive ability. There was however, no evidence for this in terms of body size, but body size may not necessarily reflect competitive ability.

2 Prey availability

The significant differences in the effects of environmental variables on earthworm availability between habitats (Chapter 4) are probably due to differences in habitat structure. Grazed pasture is a much more exposed habitat than an oak woodland ground layer, thus it may be more sensitive to short term changes in climate. Woodland is more buffered by the canopy and leaf litter and so is more likely to reflect long term trends in earthworm abundance. This may also explain why earthworm availability was

higher in woodland, despite the fact that many studies quote grazed pasture as having higher earthworm populations (Kruuk, 1978; Hofer, 1988).

3 Provisioning and diet

There were no detectable differences in energy delivery rates to nestlings between habitat types. This seems to contradict the prey sampling results where earthworm availability was significantly higher in woodland; also caterpillars are likely to be much more abundant in woodland (see Introduction).

It is possible that the discrepancies between the two sets of results were due to the sampling method having differing effects according to the habitat (e.g. sampling efficiency may be influenced by soil type, or ground vegetation structure). Alternatively, the sampling method may not accurately reflect availability in the habitats sampled (see Chapter 3). A further problem with the data is that provisioning rates tended to be very variable, therefore sample sizes would have to be considerably larger than those presented to detect any significant differences.

There were differences in diet across habitats in 1991 which were consistent with predictions about prey availability. Farmland birds had a significantly lower proportion of caterpillars in their diet, tending to feed on earthworms when the predominant diet in woodland was caterpillars. Additionally, there was some evidence in 1992 and 1993 that farmland birds tended to forage more in woodland at higher temperatures, when earthworms are less available. Consequently, only farmland habitats exhibited a significant relationship between chick weight and rainfall. However, neither chick weight, brood reduction, or provisioning parameters were significantly different between farmland and woodland birds, so overall the apparent dependence of farmland birds on earthworms conferred no disadvantage to nestlings.

4 The Adult Population

A typical characteristic of sub-optimal habitats is that they tend to be occupied by sub-dominant (usually young) birds. In this study there were significantly more first

year males breeding on farmland, and significantly more older birds breeding in woodland in 1992. On this basis it would therefore appear that farmland is sub-optimal to woodland. In 1991 there were no significant differences between habitats in terms of age structure, but in this year there were very few first year breeders, and fewer birds altogether in the study area, possibly as a result of a poor breeding season followed by a harsh winter in the preceding year which caused high juvenile mortality.

In 1993 there was no significant difference in age structure of breeders between habitats. The higher proportion of first year breeders in 1993 was probably due to a mild winter and early spring increasing juvenile survival. This may have led to reduced competition for food during the winter, and therefore enabled young birds to compete on a more equal footing with adults.

The changes in the adult population from year to year also suggest that farmland is the less preferred habitat. A greater proportion of birds breeding in wood or edge habitats in 1991 were relocated in 1992. Additionally, all recorded habitat movements between years were either from farm to edge or from edge to woodland habitats. This result parallels the work of Krebs (1971), where removal experiments showed that great tits tended to move from sub-optimal farmland habitats to the more productive woodland habitat, vacant territories on farmland tending to be occupied by first year birds. There was however, no significant difference between habitats in 1993, and some movements from wood to edge nesting habitat were recorded, again possibly due to the milder winter. The situation could have been clarified by a removal experiment in woodland and edge territories in the early part of the breeding season, although this was not carried out due to practical difficulties.

The evidence presented on differences in provisioning and reproductive success between habitats is not consistent with the data on age structure and movements between habitats in the adult population, at least in 1992. Indeed a bird moving from farmland to a non-hot-spot territory is likely to have a lowered reproductive success in the subsequent breeding season. Although no difference was detected in energy delivery rates, there was evidence that farmland birds rarely fed on caterpillars. All

years of the study had fairly similar amounts of rainfall (Chapter 2), and the low incidence of brood reduction throughout the duration of the study indicated that food was generally abundant (Magrath, 1989). However in a dry year it seems likely that farmland birds would find it harder to find food and consequently, reproductive success would be lower, as occurs in urban populations in dry years (Snow, 1958; Batten, 1973; Magrath, 1989). Therefore nesting on farmland would yield a more variable (and probably never higher) success rate over a number of years compared to the woodland habitat where the food supply is less dependent on rainfall.

In 1992 there was a dry period in late May when farmland territory holders were seen to make foraging journeys into woodland, flying distances in excess of 300m in order to feed the brood (presumably on caterpillars, though unfortunately no loads were determined for these birds). These adults may have to increase energy expenditure during dry periods in order to adequately provision the chicks. Increased energy expenditure has been shown to affect subsequent survival (Nur, 1984) or fecundity (Slagsvold, 1984; Gustafsson and Sutherland, 1988), though this has not been the case in all studies (Pettifor, 1993). If there is a cost to reproduction in blackbirds, then it may be the adults rather than the chicks who bear the cost of nesting in the farmland habitat. The lower relocation rate of birds which nested on farmland in 1991 may therefore be indicative of a lower survival of adults on farmland.

Chapter 6

Nest Predation and Nest Density: an Experiment

Introduction

Nest predation rates may be affected by many factors, e.g. habitat patch size (Møller, 1988), degree of nesting cover (Edwards, 1983), nest size (Møller, 1990) or distance from human disturbance (Osborne and Osborne, 1980). However, the effects of the spacing of nests on predation rates have perhaps received the most attention (e.g. Tinbergen et al., 19647; Croze, 1970; Wilson, 1975, Caccamise, 1976; Andersson and Wiklund, 1978; Davies, 1978; Andrén, 1991). Tinbergen et al. (1967), used artificial nests to show that the degree of predation was positively related to nesting density, due to predators showing 'area restricted searching' (Smith, 1974) after a successful find. This work has received further support from both experimental (Gorransson et al., 1975; Andersson and Wiklund, 1978) and natural nests (Fretwell, 1972; Dunn, 1977). These findings have supported the theory that predation has been a major factor in the evolution of territoriality (Hinde, 1956; Davies, 1978).

In most natural populations, a relationship between nesting density and predation is unlikely to be observed if nests are distributed according to measures of habitat quality associated with predation. In these cases, and with individuals of equal competitive ability, an Ideal Free Distribution (Fretwell and Lucas, 1969) is likely to be reached, where better habitats are occupied at higher densities, but benefits (predation rates) are equal across habitat types.

Predation is clearly the major factor affecting reproductive success in the Wytham blackbird population (Chapter 2). The density of breeders within the woodland habitat is apparently related to the availability of nesting cover, although in high density 'hot-spot' areas, predation is actually lower than elsewhere (i.e. density and predation negatively related). This population does not therefore correspond to an Ideal Free Distribution, despite the fact that there was no evidence to suggest that individuals in these areas were of higher competitive ability (Chapter 5). In the farmland habitat, density was the lowest over the whole study site and predation rates were lower than non-hot-spot woodland territories. Despite this, the age structure and

between-year movements of farmland birds were characteristic of a sub-optimal habitat (Chapter 5).

The aim of this chapter is to attempt to further the understanding of the distribution of territories within the study area by conducting experiments using artificial nests. Two main questions were asked:- (i) did predation in hot-spots increase to a rate at least equal to that in the rest of the woodland when the density of nests was increased, and (ii) were density/predation effects different in the farmland habitat. Additionally, the type of nest predators was surveyed with the use of plasticine eggs (Groom, 1993).

Methods

The experiment took place from mid to late July in the final breeding season of the study (1993), after completion of the last known nesting attempt. This was an ideal time to perform the experiment, as nesting had finished by early July in 1993 (thus avoiding interference of natural nests), but the breeding season had carried on into July in the previous years, so real predation rates were available for comparison.

Old, well preserved nests were collected from known sites in the study area. Experimental nests were always removed from old sites and re-positioned so as to appear 'new' to predators. Nests were placed between 0.5 and 1.5 metres above the ground in sites which the experimenter considered to be typical (usually bramble or hawthorn), and which were exposed to less than 5% of ambient light, as measured by a light meter.

Two quails eggs (dyed light blue) and one light blue plasticine egg were placed in each experimental nest. In a similar experiment, Groom (1993) found total removal of plasticine eggs by predators was common, so in order to minimise this, plasticine eggs were sewn into the mud lining of nests.

Three experimental sites were chosen: woodland, woodland edge (both 'hot-spots') and farmland. In both woodland and woodland edge, nests were placed at two densities, high (10 per hectare) and medium (5 per hectare), with a minimum distance

of 5m and 15m respectively between nests within a hectare. The medium density was based on the highest natural nesting density observed on the study site. Additionally, low density nests (1 per hectare) were positioned in all areas over the woodland (n=6) and woodland edge (n=4; there was not enough space in woodland edge for a full quota of low density nests). Similar treatments were carried out on farm hedgerows, high density being 10 nests per 150m of hedge, medium, 5 per 150m, and low, 1 nest a minimum of 150m away from the next nearest nest.

For each treatment, the total number of nests was ten (except in low density edge and wood habitats), thus one high density, two medium density, and ten low density areas were set out for each study site. Nests were checked every five days up to day twenty-five (the approximate length of the nesting period). Plasticine eggs which had been 'predated' were collected and an attempt was made to identify the predator from the markings made in the plasticine.

Results

The percentage of nests remaining unpredated at five day intervals in each habitat is shown in figure 6.1. There were clearly different effects in different habitats, although no predation occurred in the first 5 days in any habitat. In the woodland, only two nests (out of 26) were predated after 25 days. A total of 10 out of 24 nests were predated in the woodland edge habitat at the end of the experimental period, the majority of this occurring in the last ten days. There was a relatively rapid depletion of nests on the farmland, the final predation rate being 20 nests out of 30. The difference in predation after 25 days between habitats was significantly different (χ^2=20.28, df=2, P<0.001).

The effect of nest density on predation in different habitat types is shown in figure 6.2. Only in the farmland habitat was there a significant difference between densities, low density nests clearly having lower predation than either medium or high density areas (G-test =18.14, df=2, P<0.001). In woodland edge, though the pattern

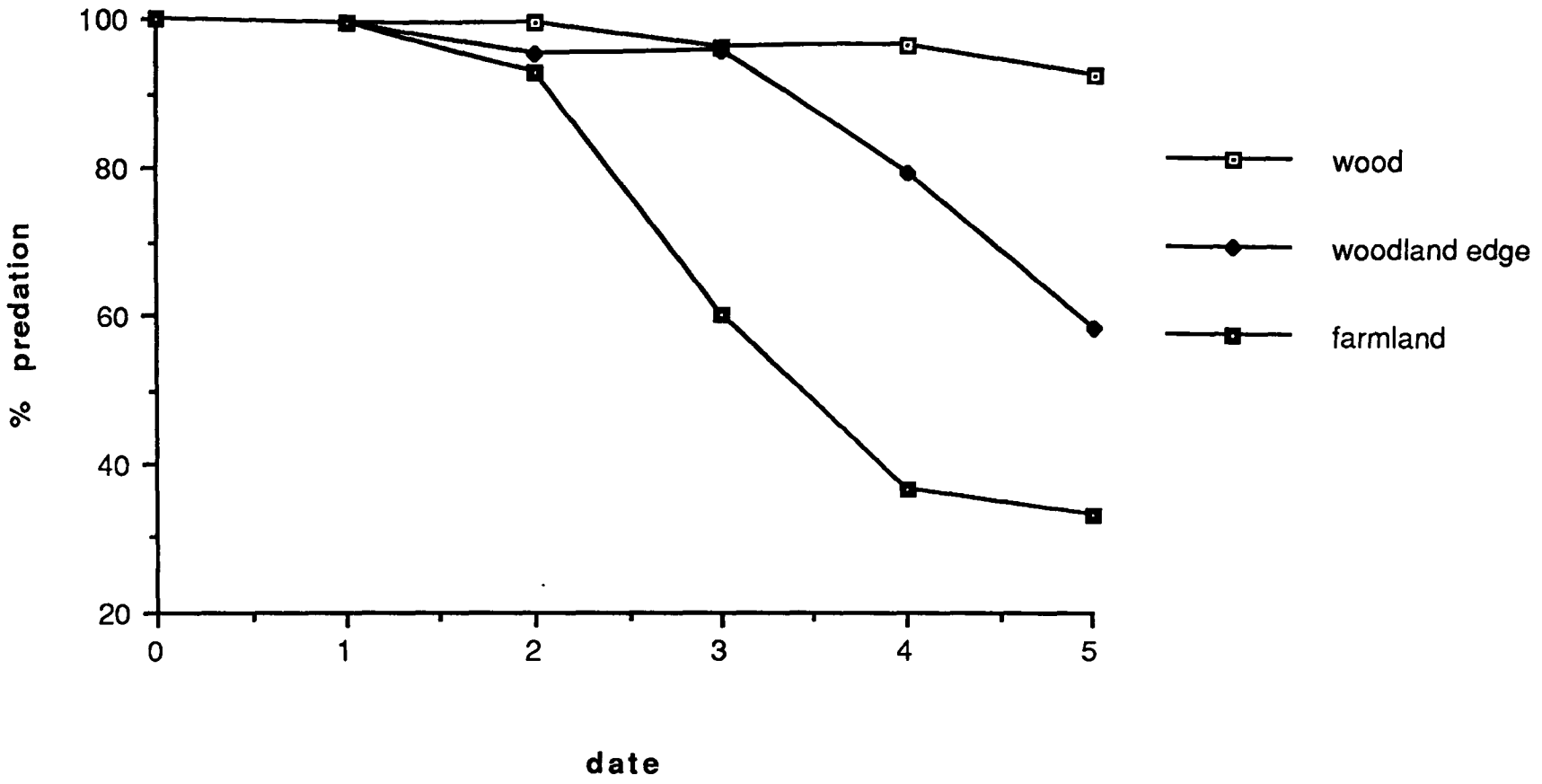


Figure 6.1: The percentage predation on artificial nests in different habitats over five day periods, where date 1=20/7/93.
Sample sizes: wood n=26, woodland edge n=24, farmland n=30.

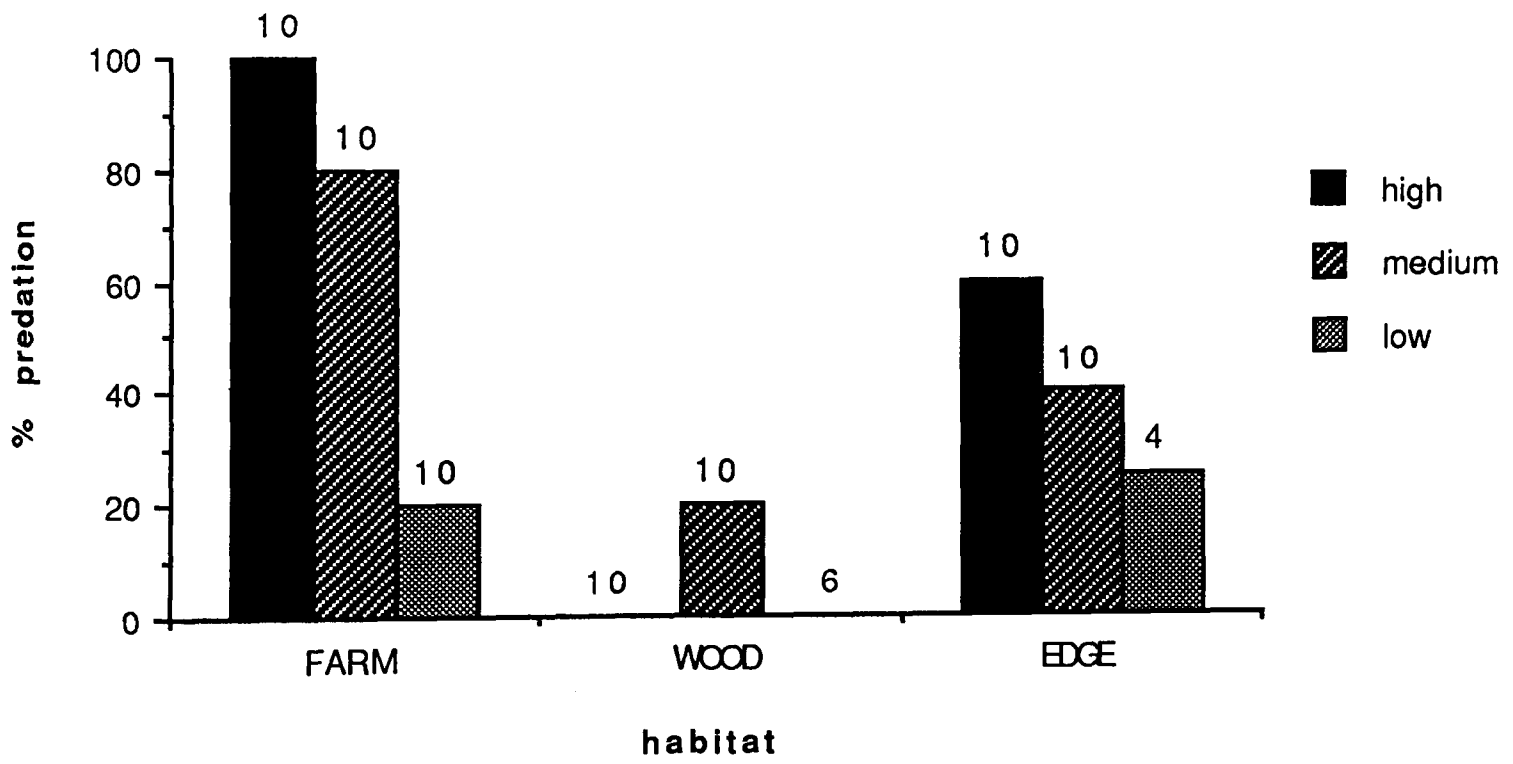


Figure 6.2: Predation on artificial blackbird nests at different densities in different habitats. Numbers above columns represent sample sizes.

was of increasing predation with density, the difference between treatments was not significant (G-test =1.68, df=2, P>0.50). Woodland showed no evidence of a density effect (G-test =4.10, df=2, 0.25>P>0.10).

When considering the effect of habitat type within density treatments, there were significant differences at high (G-test =28.02, df=2, P<0.001) and medium densities (G-test =7.97, df=2, 0.025>P>0.01), but there was no significant difference between habitats in the low density nests (G-test =2.40, df=2, P>0.25).

Of 33 nests predated, 22 (67%) showed some evidence of the type of predator responsible, due to marks in the plasticine eggs attached to the nest lining. Three of the unknown predations had the quails eggs removed, but the false eggs left unmarked; the rest had the entire contents of the nest removed. Table 6.1 shows the number of the identified nest predators in each habitat. This table clearly shows that in woodland edge, only avian predators were responsible for predations, whereas in the farm both avian predators and weasels were important predators. A Fisher exact test, combining results from woodland and woodland edge, showed that there was a significant difference between avian and mammalian predation across habitat types (P=0.05).

If the above results are evidence of area restricted searching, then the majority of predations in a single area should have been done by the same individual animal. In the farmland habitat there was some evidence of this, as all seven weasel predations came from the same (high density) experimental area, five of these occurring within the space of five days; with the exception of a single predation by a rat, all other identified predations in woodland edge and farmland were by corvids. Measures of the bite/beak marks on the plasticine eggs did not indicate that the same individuals were responsible for predations in the same area. However, these measurements were difficult to take as often an egg was so deeply and repeatedly marked that it was difficult to clearly define a given beak or mouth imprint. Also, as an ovoid shape does not have a uniform curvature to its surface, measurements may differ according to the location of the mark in question on the egg. These results should therefore be viewed with some caution.

Table 6.1: The number of predations by different predators in different habitat types.

	PREDATOR TYPE			
HABITAT	CORVID	WEASEL	FOX/BADGER	RAT
FARM	6	7	0	1
EDGE	6	0	0	0
WOOD	1	0	1	0

(i) Comparison with real nests

One problem with drawing conclusions from the above results is that the extent to which artificial nests reflect the situation with real nests is unknown. Figure 6.3 shows a comparison between predation on artificial nests and predation on real nests which had at least some of the nesting period in July. In both edge and farmland, there was no significant difference between real and artificial predation rates (G-tests: edge $G=0.05$, $df=1$, $P>0.80$; farm $G=0.23$, $df=1$, $P>0.50$, but note the small sample size of real farmland nests); however, in woodland predation was significantly higher in real nests (G-test $=51.31$, $df=1$, $P<0.001$). A more accurate analysis could compare predation rates within density types, but this is not possible as too few data exist for real nests, and the artificial high density nests were based on twice the highest observed densities, so real nests do not actually exist for this category. However, as real nests from a range of densities were used, the results still give some comparison between real and artificial predations.

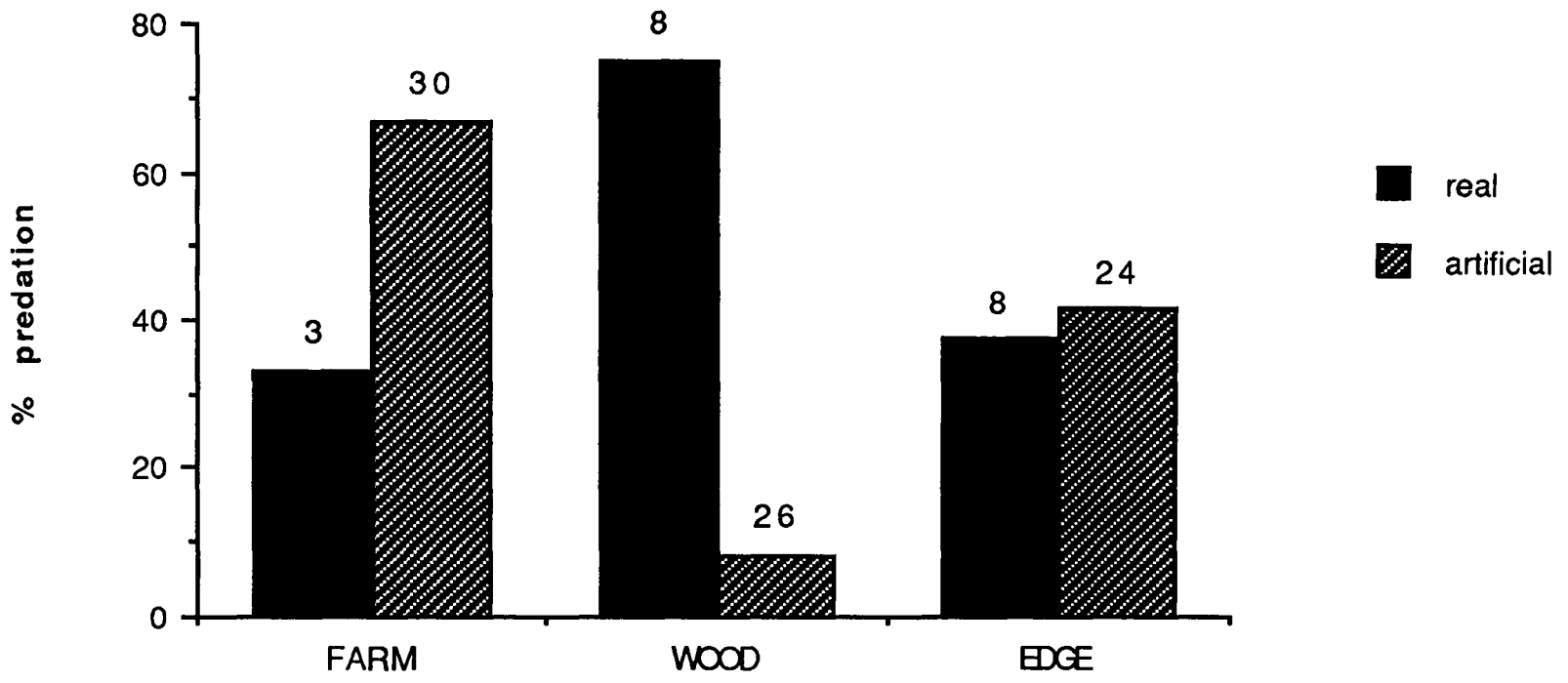


Figure 6.3: Predation on late (July) real nests and artificial nests in different habitats. Numbers above columns represent sample sizes.

Discussion

Artificial nests on farmland were subject to significantly higher predation than those in woodland or woodland edge in all but low density areas. Also farmland was the only habitat to exhibit significant differences in predation between densities (although woodland edge showed the expected trend), and to show some evidence of area restricted searching by the same individual predator. The reason for this may be due to differences in habitat structure; nesting habitat on farmland is invariably hedgerow, which may facilitate easy systematic search compared to woodland or woodland edge, which are more complex habitats in terms of plant species diversity and vertical structure.

Hatchwell (pers. comm.) found that both nest exposure and nest bulk were significantly lower in farmland than woodland or edge nests in the Wytham blackbird population. The former result may imply that hedges provide better quality nesting cover. However, the latter result and the results presented in this chapter suggest that nest site selection may be more constrained in the farmland habitat due to greater potential predation rates.

Predation was greater in woodland edge than in woodland. Many studies have shown similar effects for both real (Gates and Gysel, 1978; Brittingham and Temple, 1983) and artificial nests (Andrén et al., 1985; Wilcove, 1985). There is some evidence that predation on blackbird nests increases with decreasing habitat patch size within farmland habitats (Møller, 1988), presumably due to enhanced edge effects. The situation in this experiment can be viewed in a similar way, with woodland and hedges being respectively very large and very small habitat patches, with edge predation effects acting accordingly.

An additional point to consider is the abundance of predators across habitat types. Snow and Mayer-Gross (1967) reported predation to be higher in woodland than in farmland, which they suggested was due to a higher density of predators in woodland. In this study farmland had a total of two major predator types, corvids and weasels. In the woodland there was only one, corvids. Although nothing can be

concluded about the differences in the abundance of predators between habitats, a greater diversity of predators may result in higher predation rates due to different foraging techniques being used; for example a corvid will probably forage by sight from 'outside' a hedge, but a weasel will forage inside a hedge and may use odour as an additional cue, and therefore may predate some nests overlooked by corvids.

(i) Sources of error

When compared with predation rates on real nests, only the woodland habitat showed significant differences, predation on artificial nests being significantly lower. The experiment was started on 20 July, some two weeks after the last known nesting attempt; additionally, very few other passerines were still nesting at this time (M.R. Evans, pers. comm.; pers. obs.), so it seems likely that predators would have stopped searching for nests and switched to foraging for alternative prey types. Also, some predators may only start searching for nests when there is some evidence of nesting activity from the birds themselves, which there was some evidence for in natural nests (Chapter 2). Why these effects should occur in woodland and not farmland is unclear, although both habitat structure and predator density could be involved.

A further source of bias may be that certain predators did not perceive the artificial nests as prey items. In real woodland nests, an estimated 29% of predations were by either foxes or badgers (Chapter 2). These animals are likely to hunt by smell as much as sight, so the odour of the plasticine eggs and the dye on the quails eggs may have deterred these predators (although this did not apparently deter weasels).

(ii) Predation and the distribution of territories

The results of this experiment indicate that there is a cost to nesting at high densities in farmland. It is possible that the observed density/predation effect has consequences for nesting habitat choice in the blackbird, and therefore goes some way to explaining the low territory density observed in this habitat. However, this choice is unlikely to be mediated via experience of a predation/density effect, as the high

densities used in the experiment are unlikely to occur in any farmland habitat (Chapter 7), and the medium densities are also rare; in only one hedgerow was this density achieved in this study, and that was in a very tall, dense hedge, atypical of the surrounding habitat. Additionally, most birds were first year breeders, so could not have experienced any other nesting habitat.

It seems more likely that if birds settle in territories according to relative nest predation risk, then cover will be the resource selected (Chapter 5). A bird nesting in the farmland habitat may therefore require a large amount of hedgerow in order to have adequate cover within a territory, whereas in the woodland, territories may be smaller, but the amount of cover defended may be approximately the same.

There was little evidence to suggest that territories in woodland or woodland edge were at their maximum density (at least in terms of predation risk) as there was no significant difference between density treatments. (It should be noted that as there were significant differences between real and artificial predation rates in woodland, these results should be viewed with some caution). Therefore according to these results, an increase in nesting density in hot-spots would not increase predation risk significantly. The question as to why hot-spots were not occupied at a higher density therefore remains unanswered.

Chapter 7

Factors affecting the breeding density of the blackbird within and between habitats.

Introduction

Blackbirds show large differences in nesting density, both within and between woodland and farmland habitats (Chapter 5), which to a large extent are related to nesting cover. On a wider scale, there are very large differences in the breeding density of different populations (Table 7.1). Urban/suburban habitats support a consistently higher density than rural habitats, although there is apparently little difference between woodland and farmland populations, except in this study when the farmland density was much lower, and the Scilly Isles population which was unusually high. These widely differing figures may in part be due to differences in the way density was measured in the different studies. Most of the habitat on farmland will be unsuitable to nesting blackbirds (e.g. crops or open pasture), so densities approaching those observed in woodland would seem unlikely, unless density was measured only in terms of available nesting habitat. This was not the case in this study, hence the very low observed density. The likely reasons for the differences in density between rural and urban habitats are discussed below.

1 Nesting cover

As cover, rather than food supply, seems to be the major territorial resource (Chapter 5), then habitat differences in density could be explained by a greater availability of nest sites in urban environments. Parks and gardens may provide many good nest sites for breeding birds, but some areas of woodland and farmland (hedgerows) have very dense cover as well. The results of this study would indicate that there are many good potential nesting sites within the rural habitat which are not occupied. Thus it seems doubtful that differences in available nesting cover can fully account for differences in density between habitats.

2 Food supply

It seems unlikely that food resources account for differences in density between habitats. In the managed habitat of parks and gardens, mown lawns and flower beds

Table 7.1: Breeding densities of blackbirds in different habitats.

HABITAT	DENSITY (pairs/ha)	SOURCE
German oak forest	0.3	Niebuhr, 1948
Surrey oak wood	0.2-0.7[1]	Beven, 1952
Wytham woods	0.5-0.7[1]	Snow, 1958
woodland	0.9	Batten, 1973
woodland (Austria)	0.1	Schnack, 1991
Wytham woods	0.5	this study
Oxon. farmland	0.4	Chapman, 1939
Welsh farmland	0.3	Campbell, 1953
farmland	0.4	Batten, 1973
farmland	0.3	Edwards, 1977
Scilly Isles farm	1.0-1.4[1]	Robinson, 1991
Wytham farm	0.05	this study
Welsh garden	6.7	Campbell, 1953
suburban	1.8	Jackson, 1954
Botanic garden	5.0-7.3[1]	Snow, 1958
Parkland	1.2	Snow, 1958
suburban	7.3	Batten, 1973
suburban (Sweden)	1.7-2.7[1]	Karlsson and Kallander, 1977
suburban (Austria)	1.0	Schnack, 1991

[1]Figures give the range from different years.

doubtless provide very good foraging for earthworms in the right conditions; but it is unlikely that they provide the same diversity and overall abundance of food as woodland (Lack, 1968). Caterpillars in particular are an important source of food for woodland birds in mid-summer (Chapter 4). The probable scarcity of caterpillars in suburban environments means that woodland birds are better able to survive periods of drought during periods of caterpillar abundance. Typically, woodland birds have a higher mean weight at fledging and a much lower starvation rate than garden birds (Snow, 1958), which presumably reflects food availability (although the effect of greater competition in the more heavily populated suburban habitat cannot be ruled out (Lack, 1968)). Thus, there does not appear to be an 'Ideal Free Distribution' with respect to food supply.

3 Predation

Nest predation is undoubtedly higher in woodland than in urban populations (Snow, 1958; Snow and Mayer-Gross, 1967; Dyrcz, 1969), which is probably due to the number of predators, rather than differences in cover or habitat structure. Consequently the mean number of fledglings raised per pair per year is much higher in suburban habitats than in woodland habitats (Lack, 1968). Chick weight tends to be lower in gardens (Snow, 1958) so post-fledging survival is likely to be lower in urban habitats (Magrath, 1991), but the large difference in predation rates is probably sufficient to enable a greater proportion of chicks to survive to breed in the urban habitat.

4 Interactions between populations

Habitats occupied at a higher density may be expected to be more productive than those occupied at a lower density, either due to a distribution according to resources (Ideal Free Distribution; Fretwell and Lucas, 1969) or according to dominance (Despotic Distribution; Fretwell, 1972). Thus it could be possible that urban habitats are of greater quality. A typical characteristic of sub-optimal habitats is that they

will contain a higher proportion of subordinate (younger) birds (Chapter 5), but the suburban habitat generally has a higher proportion of first year breeders than rural habitats (Snow, 1958; Lack, 1968).

One assumption of the ideal free and despotic distributions is that animals must be free to move between habitats of differing quality (Fretwell, 1972). Lack (1968) suggested that one reason for the differences in density between rural and urban habitats is limited dispersal, there being little or no movement of individuals between the two major habitat types. This has received further support from studies showing that differences in behaviour between rural and urban individuals may have a genetic basis (Luniak and Mulsow, 1986; Walasz, 1990). Therefore it is unlikely that interactions between individuals across suburban and rural habitats lead to differences in their breeding density.

5 Winter survival

Havlin (1962) suggested that the major reason for the higher density in gardens is due to winter food supply (particularly that provided by man) which enables survival of many birds through to the next breeding season. Winter food supplementation experiments on other species have had some conflicting results, population increases having only been detected in about half of the studies (Boutin, 1990). In blackbirds, there is some indirect evidence that increased winter survival leads to higher breeding densities: Karlsson and Kallander (1977) found that breeding density in an urban population was positively related to winter temperature. Thus increased winter survival due to increased food supply, coupled with the probable habitat fidelity shown by blackbirds, could lead to the establishment and maintenance of the high breeding density in suburban habitats. This also suggests that comparing the chances of survival to breeding in terms of chick weight (as per Magrath, 1991) is not possible across habitat types.

In this chapter, Havlin's hypothesis is tested by supplying supplemental food to a rural population over the winter. If the hypothesis is correct, the density of breeding

birds should increase. An additional factor in the experiment is the effect of increased winter food supply on subsequent reproductive performance. Additional food supply prior to breeding has been shown to advance laying date in Paridae (Kallander, 1974), which is probably linked to the condition of the female prior to laying, and consequently her ability to form eggs (Perrins, 1970). However, few studies have shown an effect on clutch size (Boutin, 1990). Increasing the food supply in the Wytham blackbird population may therefore explain differences in the timing of first breeding attempts and first clutches between years.

Methods

Three habitats were chosen for the supplemental feeding experiment: a high density hot-spot area (Chapter 5) on the woodland edge; a previously unoccupied area of woodland, and a low density area of farmland.

In the hot-spot area, extra food was supplied to approximately half the area, encompassing about seven territories. Non-supplied areas acted as controls for comparison. In each site 5 (woodland and farmland) or 6 (hot-spot) feeding stations were chosen, spaced roughly according to typical territory size. Every two days, each feeding station was supplied with food consisting of apples, bread, rolled oats and cheese scattered on the ground. Hides were set up near selected feeding stations in order to ascertain the number of birds using the stations, and to identify individual birds, if ringed. Feeding was carried out from the beginning of February until 12th March in 1993.

Results

1 Differences between habitat.

The minimum number of individuals seen at feeding stations in each habitat is shown in Table 7.2. In the farmland and woodland habitats the food supply was not used consistently by blackbirds, and thus will not be considered in any subsequent analysis. By contrast, in the hot-spot, many birds came to the feeding stations. Of the

minimum 15 individuals seen in the hot-spot, 6 stayed onto breed in the area, 6 disappeared before the start of the breeding season, and the other three were unringed birds which may have stayed on to breed, as a number of unringed birds were present at the start of the 1993 breeding season.

2 Breeding density

Of the six individuals seen using the feeding stations in the edge hot-spot before the breeding season which were subsequently relocated (Section 1), all were occupying territories in the fed area. The number of breeding pairs whose territories either contained, or were adjacent to, a feeding station in 1993 is shown in Table 7.3 along side the number of pairs occupying the same area in 1991 and 1992. Also shown are the number of pairs occupying two control areas, the lower (unfed) part of the edge hot-spot, and the number of pairs occupying the woodland hot-spot. If the supplemental food had an effect on the number of breeding pairs in the experimental area, then there should be proportionately more pairs breeding in that area compared with the general population trends in the two control areas. There was no significant difference in the proportion of pairs breeding in the experimental area (G-test=0.63, df=4, P>0.95), the numbers in different years tending to follow the general population trend (Chapter 5).

One possible consequence of increased food abundance may have been the increased survival of birds of a lower dominance rank (first years). There was no significant difference between the fed area and the control areas in the proportion of first year breeders identified (χ^2=2.18, df=2, P>0.25; figure 7.1). If the feeding had any effect on the age structure of the population, then a different result would be expected in other years. For example, the analysis assumes that the other control areas are equally comparable with the experimental area. If for some reason the experimental area is of lower quality than the control areas, then the food supply may have just brought the area up to the standard of the other two, so no significant differences would be detected. When comparing the age structure of the three areas from 1992, there was

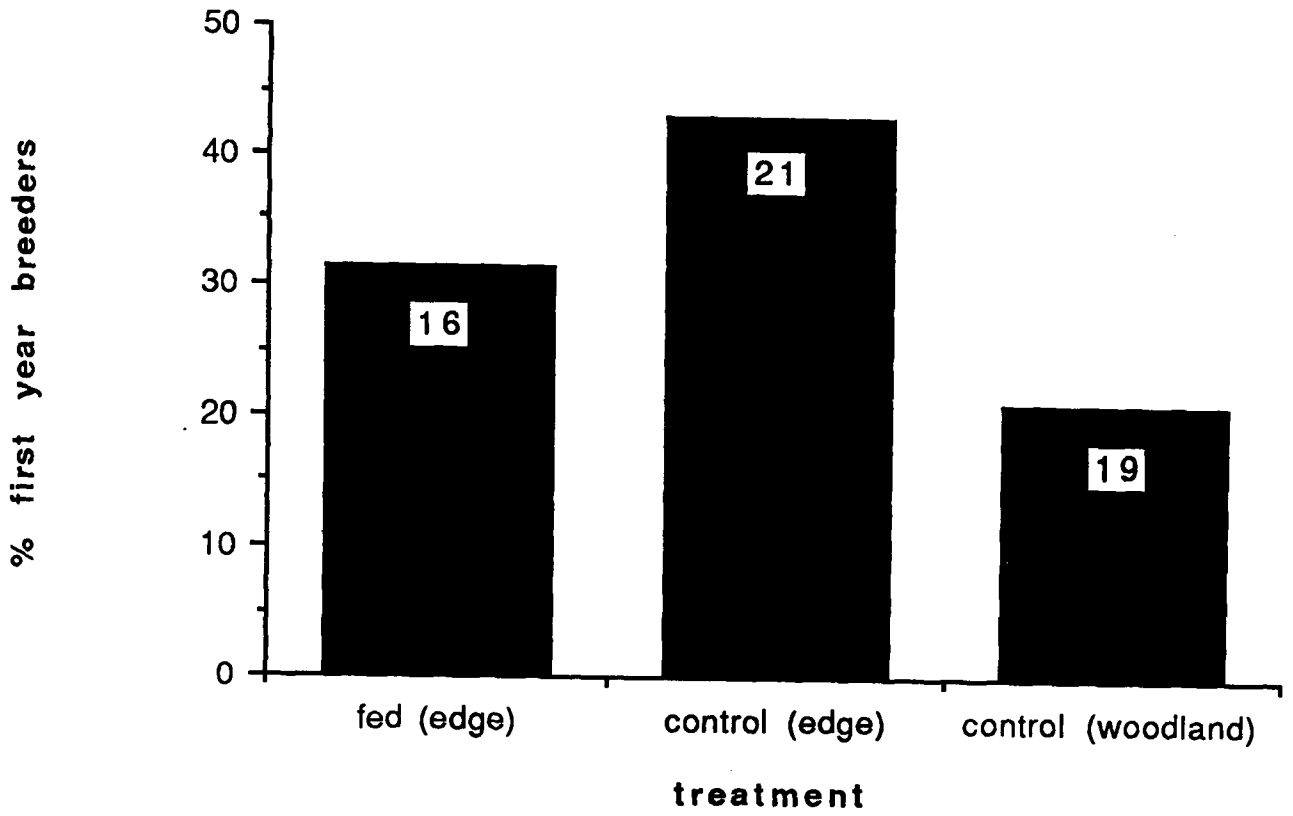
Table 7.2: The minimum number of individuals birds seen at feeding stations in different habitats.

HABITAT	NO. FEEDING STATIONS	TOTAL OBSERVATION TIME	MINIMUM NO. INDIVIDUALS
hot-spot	6	11.5 hrs.	15
wood	5	4.0 hrs.	2
farm	5	2.0 hrs.	0

Table 7.3: The number of breeding pairs for fed and control areas in 1993, and for the corresponding areas in 1991 and 1992.

YEAR	FED (edge)	CONTROL (edge)	CONTROL (woodland)
1993	8	13	12
1991	6	7	10
1992	7	9	12

(A) 1993



(B) 1992

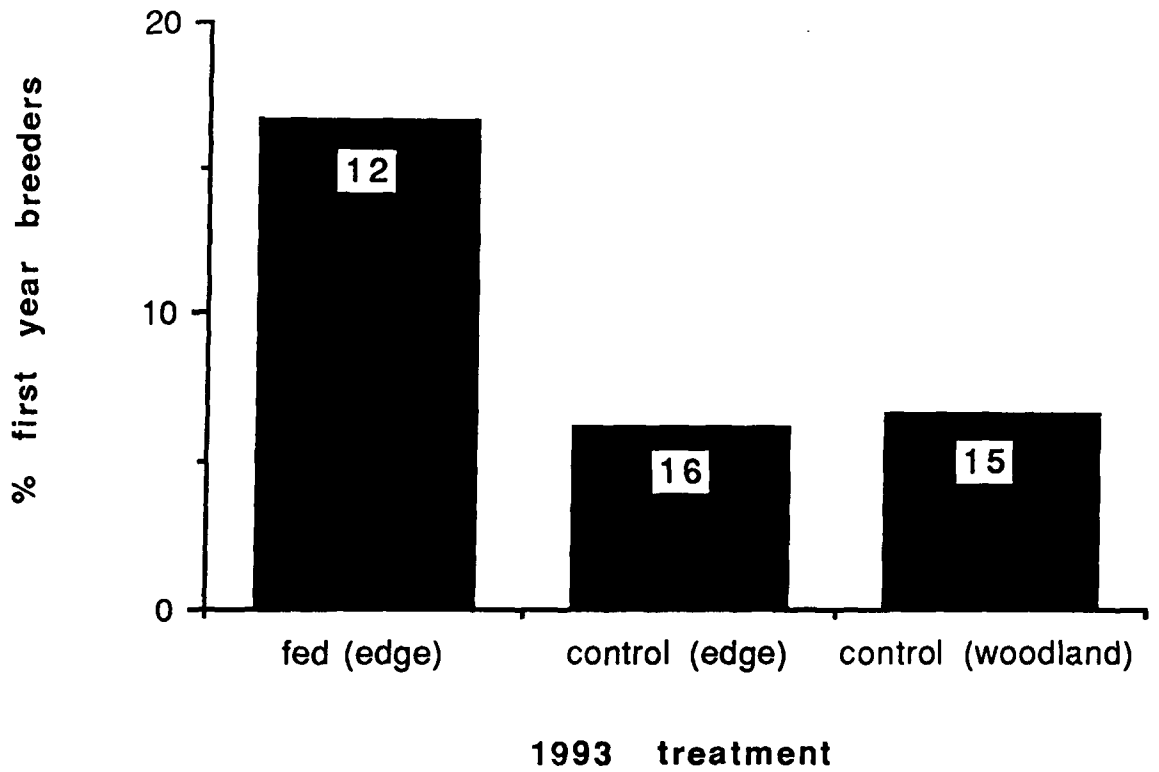


Figure 7.1: The proportion of first year breeders in fed and control areas in 1993, and in the corresponding areas in 1992. Numbers on columns represent sample sizes.

also no significant difference (G-test=0.96, df=2, P>0.50; figure 7.1), thus supplemental feeding had no effect on the age structure of the breeders in the fed area. No comparison is presented for 1991 as only two first year birds were known to have bred in the three areas.

3 Clutch size and timing of breeding

The mean size of first clutches from females in fed and control areas are shown in Table 7.4A. No clutches were used when it was suspected that earlier nesting attempts had not been found. There was no significant difference between fed and control areas (ANOVA $F_{2,17}$=2.19, P=0.14). The same comparison was also carried out on data from 1991 and 1992 (Table 7.4B and C), and again there was no significant difference (1991 $F_{2,5}$=1.41, P=0.41; 1992 $F_{2,13}$=0.67, P=0.53).

The mean dates of first breeding attempts from pairs in fed and control areas are shown in Table 7.5A. Two different dates are given. The first date represents the date of clutch completion, and the second date uses the date when the first sign of nesting was observed, which includes observations of females carrying nesting material and nests abandoned before completion. There was no significant difference between fed and control areas in either the date of clutch completion (Kruskal-Wallis H=0.62, n=25, P=0.73), or the date of the first sign of nesting (H=1.52, n=32, P=0.47). Tables 7.5B and C show the respective mean dates for 1991 and 1992. There was no significant difference between areas in either the date of clutch completion (1991 H=0.08, n=9, P=0.78; 1992 H=0.25, n=23, P=0.88), or the date of the first sign of nesting (1991 H=2.74, n=10, P=0.25; 1992 H=0.83, n=23, P=0.66).

Discussion

The additional food supply was only used regularly in an area which was known to be occupied at a high density in the breeding season. In the farmland feeding area, only two individuals birds were seen (a male and a female), and in the woodland, none was seen and the food supply did not decrease as it did in the hot-spot area. No

7.4: The mean size of first clutches in fed and control areas in 1993, and for the corresponding areas in 1991 and 1992. Sample sizes are given in brackets.

(A) 1993

FED (edge)	CONTROL (edge)	CONTROL (woodland)
4.0±0	3.43±0.54	3.44±0.53
(4)	(7)	(9)

(B) 1991

FED (edge)	CONTROL (edge)	CONTROL (woodland)
4.0±0	4.0±0	3.40±0.55
(2)	(1)	(5)

(C) 1992

FED (edge)	CONTROL (edge)	CONTROL (woodland)
3.33±0.58	3.17±0.75	3.57±0.54
(3)	(6)	(7)

Table 7.5: Mean laying date of first breeding attempts for fed and control areas in 1993, and for the corresponding areas in 1991 and 1993. Date 1=1/3. Sample sizes given in brackets.

(A) 1993

	FED (edge)	CONTROL (edge)	CONTROL (woodland)
date first clutch completion	39.71±10.29 (7)	36.11±7.96 (9)	37.67±5.94 (12)
date first evidence of nesting	34.75±7.78 (8)	31.17±11.79 (12)	33.83±9.69 (12)

(B) 1991

	FED (edge)	CONTROL (edge)	CONTROL (woodland)
date first clutch completion	47.00±6.08 (3)	46.00±0 (1)	43.20±8.04 (5)
date first evidence of nesting	31.75±10.40 (4)	24.00±0 (1)	40.00±7.97 (5)

(C) 1992

	FED (edge)	CONTROL (edge)	CONTROL (woodland)
date first clutch completion	40.67±9.69 (6)	42.67±8.14 (9)	41.38±8.50 (8)
date first evidence of nesting	33.33±12.24 (6)	31.33±8.69 (9)	35.50±7.93 (8)

breeding territories were set up in these areas in the following season. This could be due to a lack of birds moving through these areas, although this alone seems unlikely as at least 9/16 individuals seen feeding in the edge hot-spot were not relocated in the breeding season, which presumably must have been in part due to dispersal. An alternative explanation is that blackbirds are initially attracted to areas of high cover, the food supply having little bearing on territorial settlement.

There were no effects of an additional pre-breeding season food supply on either breeding density, breeding age structure, timing of breeding, or size of the first clutch. Therefore, the original hypothesis of Havlin (1962), that differences between urban and rural breeding densities in the blackbird are due to the greater food supply in urban environments, is not supported. The results also indicate that differences between years in age structure (Chapter 5) were not effects of the feeding experiment.

Food was only supplied for one and a half months before breeding commenced, whereas Havlin (1962) was assuming that food would be more plentiful throughout the whole winter. If the food was supplied after the critical period, when mortality is at its highest, then the additional food would have had less chance of having any effect. However, Batten (1978) found that during the winter months (October-March), the greatest mortality occurred in February and March (based on data gathered from all habitat types), thus the experiment probably did cover a critical period for blackbird mortality.

The year in which the experiment was carried out (1993) differed from the other two in terms of breeding density, age structure of breeders, and also clutch size (Chapter 5). This may have been due to the mildness of the winter, 1993 having a significantly lower number of freezing days than the other two years (Chapter 2). This result alone gives some indirect support to Havlin's hypothesis, if it is assumed that the number of freezing days is a good reflection of winter food availability.

The mildness of the weather during the experimental period may have meant that food was unusually abundant anyway, thus an additional food supply would have made little difference to overall trends. Kallander (1981) reported a similar situation,

when great tit breeding density was affected by a supplemental food supplied during a harsh winter, but there was no effect in a year when the winter beech mast crop was high. A harsh winter would probably have provided better conditions for a test of Havlin's hypothesis.

A problem with interpreting results from this type of experiment is that it is not known how the birds perceive the additional food supply. If it is seen as a short term abundance of food, then it may not have any effect on long-term reproductive strategy, particularly in rural environments where the birds will be unaccustomed to this type of food. Longer term food supplies and temperature over the whole winter may be more likely to effect population densities and clutch size in the blackbird, as seen from between-year differences, than a relatively short term abundance of food.

Chapter 8

Conclusions

1 Clutch size

The seasonal rise and fall in clutch size in blackbirds is apparently well adapted to conditions for raising young. Parents could adjust their provisioning rates according to the natural variation in brood size, and consequently there was no difference in mean chick weight in broods of different sizes. Although the rate of starvation increased with brood size, suggesting some cost to having a larger brood, the incidence of starvation was very low, and therefore the likely disadvantage this confers on larger broods will be low (Chapter 3).

The variation in clutch size over the breeding season is unlikely to be linked solely to the availability of food at periods of peak chick demand, as the seasonal pattern in peak demand (chick age 7 days onwards) did not correspond very closely to variations in food abundance (Chapter 4). Food availability to the chicks is probably still important to some extent, particularly at the end of the breeding season, but the pattern of clutch size and feeding conditions indicate that food supply may be just as important to the adults in determining clutch size.

Although supplementary feeding immediately prior to the breeding season had no effect on clutch size (Chapter 7), variations in early clutch size between years were consistent with the harshness of the winter (Chapter 2), therefore early clutch size is probably linked to pre-breeding season temperature (food supply and stress). It is unlikely that females can predict future food supplies on this basis (i.e. predict conditions at the time of peak chick demand based on pre-breeding season conditions) as earthworms, by far the most important prey type at this time, are not really 'seasonal' organisms, their availability being more closely linked to immediate rainfall and temperature.

It is possible that the early clutch size of females may be limited directly by an energetic constraint on their ability to produce eggs. This hypothesis is unlikely as females often laid many eggs within a short period early in the season, due to successive predations. A female in better condition may, however, be able to raise more young, as she may forage more efficiently and spend less time feeding herself; the same

argument will also apply to the male parent. Therefore the size of the first clutch may depend on how many chicks the female 'thinks' can be raised on the basis of her and her partner's condition. Brood manipulation experiments and manipulation of parental condition are needed to test these ideas further.

2 Reproductive success

Reproductive success, in terms of the number of chicks raised from a brood, was not apparently related to diet type or the abundance of prey. However, there was an effect of diet on nestling quality, chicks fed on predominantly caterpillar diets in dry periods being significantly lighter than chicks fed on predominantly earthworm diets (Chapter 4). Therefore, even when caterpillars are abundant, some earthworms are needed in the diet. This may present a problem to blackbirds in a dry summer.

There was no significant difference in nestling provisioning rates between parents in farmland, wood or edge habitats. There was some evidence that farmland birds were more dependent on earthworms in the diet, and consequently nestling quality was significantly related to rainfall in the farmland habitat (Chapter 5). However, there was no overall disadvantage to farmland nestlings either in terms of starvation or weight. In fact chick weight tended to be higher on farmland, although this result was probably not of any biological significance (Chapter 5).

Predation was by far the most important factor determining reproductive success (Chapter 2). Many pairs had all nesting attempts predated, and only very few pairs raised more than one brood in a season. Predation rates would almost certainly be very much higher if an estimate of post-fledging predation could have been made. There was no significant difference in predation rates between the three major habitat types, woodland, farmland and woodland edge. However, when defined in terms of nesting density, territories in high density (hot-spot) areas were found to have lower predation rates than farmland territories, which in turn had lower predation rates than territories in the rest of the wood (Chapter 5). Hot-spot territories had significantly better quality nesting cover than the rest of the wood, so blackbird nesting density

corresponded to the quality of nesting cover within the woodland habitat. The fact that there was differential nesting success between areas of differing nesting cover implies that some individuals were occupying a greater 'share' of the high quality habitat.

On a wider scale, differences in predation rate may be in part responsible for differences in population density between urban and rural habitats. If more attempts are successful in urban habitats, and there is less post-fledging predation, then the population will be larger so long as there is little or no dispersal out of the urban habitat (Chapter 7). This effect may also be enhanced by increased winter survival in urban habitats.

3 Is farmland a sub-optimal habitat ?

Neither parental provisioning rates or predation differed significantly across habitat types, and consequently there were no real differences in nestling quality, starvation, or reproductive success across habitat types. When considering hot-spot areas, farmland was intermediate in reproductive success between hot-spots and the rest of the woodland territories. Therefore on the basis of these results, farmland was not a sub-optimal habitat.

However, there were some features of the farmland population which were characteristic of a population in a sub-optimal habitat. In one out of three years, there was a significantly higher proportion of first year breeders on farmland, and in one out of two years, disappearance of individuals was significantly greater from farmland and movements between habitat were significantly greater from farmland (Chapter 5). These results show that in one year at least, the farmland adult population showed characteristics of a population in a sub-optimal habitat, which may indicate that costs on the parents are greater in farmland, which could be due to greater foraging effort of the parents (foraging in the wood when earthworms are unavailable on the farm, for example), greater predation rate of adults in the more open farmland habitat, or lower food supplies outside the breeding season.

There was a very low density of breeders on the farmland. A direct comparison between densities in woodland and farmland is difficult given that the majority of the farmland habitat will be completely unsuitable for nesting. However, personal observation of the cover of unoccupied hedgerows, and the fact that some hedges were occupied (and produced successful breeding attempts) in some years and not others suggests that there was not a shortage of suitable nesting habitat on the farmland. The simpler habitat of farmland may have meant that a greater minimum territorial area was required to nest in, as predation/density effects may be greater on farmland (Chapter 6), and therefore breeding densities were low in the farmland habitat.

Predation of young after fledging may be a major factor in reproductive success, although it was not possible to gather any data on this. The simpler structure of the farmland habitat could again come into play; with less 'volume' of cover to hide in, fledglings from farmland nests could suffer a greater predation rate than fledglings from woodland territories. If this was the case, then the survivorship curves relating nestling weight to the probability of survival to breed are likely to be different in woodland and farmland, and therefore nestling weight will not be strictly comparable as a measure of nestling quality across habitat types.

The answer to the question of whether farmland is a sub-optimal habitat within the rural environment is therefore not clear cut. The results presented from the three years of this study do not support the theory that farmland is a sub-optimal habitat. Despite this, certain features indicate that under certain conditions farmland could be a less profitable nesting habitat. Predation rate may increase sharply with an increase in nesting density, thus densities higher than those observed may result in a much lower breeding success. Predation on fledglings may also be higher in farmland. Also, farmland chicks are apparently more dependent on earthworms than those in the woodland, therefore in a very dry year they may not be able to raise as many chicks, or produce chicks of as good quality compared to their woodland counterparts. Costs on the parents may also be greater in the farmland habitat.

This study has revealed some differences in feeding ecology, reproductive success and the age structure of the adult population between woodland and farmland habitats. Whilst certain results indicate that farmland is a sub-optimal habitat, differences detected were subtle, and it is therefore difficult to draw firmer conclusions on the relative quality of farmland as a nesting habitat. However, the high predation rate on artificial farmland nests, and the greater apparent reliance of earthworms in the diet of farmland birds, suggests that farmland is potentially a suboptimal habitat if subject to different conditions (particularly rainfall) than those observed during the three years of this study.

References

Andersson, H. and Wiklund, C.G. (1978). Clumping verses spacing out: experiments on nest predation in Fieldfares (*Turdus pilaris*). Anim. Behav. 26:1207-1212.

Andrén, H. (1991). Predation: an over rated factor for over dispersion of birds' nests. Anim. Behav. 41:1063-1070.

Andrén, H., Angelstam, P., Lindström, E. and Widén, P. (1985). Differences in predation pressure in relation to habitat fragmentation: an experiment. Oikos 45:273-277.

Arcese, P. and Smith, J.N.M. (1988). Effects of population density and supplemental food on reproduction in Song Sparrows. J. Anim. Ecol. 57:119-136.

Arnold, T.W. (1993). Fledging success in experimentally manipulated broods of House Wrens. Wilson. Bull. 105:448-454.

Askenmo, C. (1979). Reproductive effort and return rate of male Pied Flycatchers. Am. Nat. 114:748-753.

Batten, L.A. (1973). Population dynamics of suburban Blackbirds. Bird Study 20:251-258.

Batten, L.A. (1978). The seasonal distribution of recoveries and causes of Blackbird mortality. Bird Study 25:23-32.

Berg, Å. (1993). Food resources and foraging success of Curlews *Numenius arquata* in different farmland habitats. Ornis Fenn. 70:22-31.

Best, L.B. (1977). Territory quality and mating success in the field sparrow (*Spizella pusilla*). Condor 79:192-204.

Beven, G. (1952). Further observations on the bird population of an oakwood in Surrey (Eastern Wood, Bookham Common). London Nat. 32:51-77.

Birkhead, T.R. and Møller, A.P. (1992). Sperm Competition in Birds. Academic Press, London.

Boutin, S. (1990). Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. Can. J. Zool. 68:203-220.

Brittingham, M.C. and Temple, S.A. (1983). How cowbirds have caused forest songbirds to decline. BioScience 33:31-35.

Brown, J. L. (1969). The buffer effect and productivity in tit populations. Am. Nat. 103: 347-354.

Bryant, D.M. (1973). The factors influencing the selection of food by the House Martin (*Delichon urbica* L.). J. Anim. Ecol. 42:539-564.

Burke, T., Davies, N. B., Bruford, M. W. and Hatchwell, B.J. (1989). Parental care and mating behaviour of polyandrous Dunnocks *Prunella modularis* related to paternity by DNA finger-printing. Nature 338:249-251.

Caccamise, D. F. (1976). Nesting mortality in the red-winged blackbird. Auk 93:517-534.

Campbell, B. (1953). A comparison of bird populations on 'industrial' and 'rural' farmland in South Wales. Rep. Trans. Cardiff Nat. Soc. 81:4-65.

Chapman, W. M. M. (1939). The bird population on an Oxfordshire farm. J. Anim. Ecol. 8:286-299.

Clutton-Brock, T. H. (1988). Reproductive Success: Studies of Individual Variation in Contrasting Breeding Seasons. University of Chicago Press, Chicago.

Crick, H. P. Q., Gibbons, D. W. and Magrath, R. D. (1993). Seasonal changes in clutch size in British birds. J. Anim. Ecol. 62:263-273.

Crossner, K. A. (1977). Natural selection and clutch-size in the European starling. Ecology 58:885-892.

Croze, H. (1970). Searching image in carrion crows. Z. Tierpsychol. 5:1-85.

Davies, N. B. (1978). Ecological questions about territorial behaviour. In Behavioural Ecology: An Evolutionary Approach . Blackwell, Oxford. Eds J.R. Krebs and N.B. Davies.

Davies, N. B. and Hatchwell, B. J. (1992). The value of male parental care and its influence on reproductive allocation by male and female dunnocks. J. Anim. Ecol. 61:259-272.

Desrochers, A. (1991). Age and reproduction in European Blackbirds *Turdus merula*. PhD Thesis, University of Cambridge.

Desrochers, A. (1992). Age and foraging in European Blackbirds: variation between and within individuals. Anim. Behav. 43:885-894.

Dunn, E. K. (1977). Predation by weasels (*Mustella nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. J. Anim. Ecol. 46:633-652.

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

Dyrcz, A. (1969). The ecology of the song thrush (*Turdus philomelos*) and blackbird (*T. merula*) during their breeding season in an area of joint occurrence. Ekol. Pol., Ser. A 17:735-793.

Edwards, C. A. and Lofty, J. R. (1972). The Biology of Earthworms. Chapman and Hall, London.

Edwards, P. (1977). 'Reinvasion' by some farmland bird species following removal. Polish Ecological Studies 3:53-70.

Edwards, P. J. (1983). Behavioural ecology of British thrushes. DPhil. Thesis, University of Oxford.

Ekman, J., Cederholm, G. and Askenmo, C. (1981). Spacing and survival in winter groups of willow tit *Parus montanus* and crested tit *P. cristatus*- A removal study. J. Anim. Ecol. 50:1-9.

Fretwell, S. D. (1972). Population in a Seasonal Environment. Princeton University Press, Princeton.

Fretwell, S. D. and Lucas, H. J. (1969). On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

Gates, J. E. and Gysel, L. W. (1978). Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871-883.

Gibb, J. A. (1950). The breeding biology of the Great and Blue Titmice. Ibis 192:507-539.

Gibb, J. A. and Betts, M. M. (1963). Food and food supply of nestling tits (Paridae) in Breckland pine. J. Anim. Ecol. 32:489-533.

Goransson, G., Karlsson, J., Nilsson, S. G. and Ulfstrand, S. (1975). Predation on birds' nests in relation to anti-predator aggression and nest density: an experimental study. Oikos 26:117-120.

Gosler, A. G. (1990). The birds of Wytham. An historical survey. Fritillary 1: 29-74.

Greenlaw, J. S. (1978). The relation of breeding schedule and clutch size to food supply in the Rufous- Sided Towhee. Condor 80:24-33.

Groom, D. W. (1993). Magpie predation on blackbird nests in urban areas. Bird Study 40:55-62.

Gustaffsson, L. and Sutherland, W. J. (1988). The costs of reproduction in the collared flycatcher *Ficedula albicollis*. Nature 335:813-815.

von Haartman, L. (1953). Was reizt den Trauerfliegenschäpper (*Musicapa hypoleuca*). Vogelwarte 16:151-164.

Hails, C. J. and Bryant, D. M. (1979). Reproductive energetics of a free-living bird. J. Anim. Ecol. 48:471-482.

Hamilton, W. D. (1971) Geometry for the selfish herd. J. Theor. Biol. 31:295-365.

Havlin, J. (1962). Environmental requirements in the blackbird *Turdus merula* L. Prace 33:1-47.

Hinde, R. A. (1956). The biological significance of the territories of birds. Ibis 98:340-369.

Hochachka, W. M. et al. Song Sparrow. In Lifetime Reproduction in Birds ed. I. Newton.

Hofer, H. (1988). Variation in resource presence, utilisation and reproductive success within a population of European Badgers (*Meles meles*). Mammal Rev. 18:25-36.

Högstedt, G. (1981). Effect of additional food on reproductive success in the magpie *Pica pica*. J. Anim. Ecol. 50:219-229.

Holm, C. H. (1973). Breeding sex ratios, territoriality and reproductive success in the red-winged blackbird *Agelaius phoenicius*. Ecology 54:356-365.

Hötker, H. (1989). Meadow Pipit. In Lifetime Reproduction in Birds ed. I. Newton.

Howe, H. F. (1976). Egg size, hatching asynchrony, sex and brood reduction in the Common Grackle. Ecology 57:1195-1207.

Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187-211.

Hussel, D. J. T. (1972). Factors affecting clutch-size in arctic passerines. Ecol. Monogr. 42:317-364.

Hussel, D. J. T. and Quinney, T. E. (1986). Food abundance and clutch size of tree swallows *Tachycineta bicolor*. Ibis 129:243-258.

Jackson, R. D. (1954). Territory and pair formation in the blackbird. Brit. Birds 67:123-131.

Janssen, C., Ekman, J. and von Brömssen, A. (1981). Winter mortality and food supply in tits *Parus* spp. Oikos 37:313-322.

Järvinen, A. (1982). Effects of exceptionally favourable weather on the breeding of the pied flycatcher *Ficedula hypoleuca* in Finnish Lapland. Ibis 124:196-198.

Järvinen, A. and Väisänen, R. A. (1984). Reproduction of pied flycatchers (*Ficedula hypoleuca*) in good and bad breeding seasons in a northern marginal area. Auk 101:439-450.

Kallander, H. (1974). Advancement of laying of great tits by the provision of food. Ibis 116:365-367.

Kallander, H. (1981). The effects of provision of food in winter on a population of the great tit *Parus major* and the blue tit *P. Caeruleus*. Ornis Scand. 12:244-248.

Karlsson, J. and Kallander, H. (1977). Fluctuations and density of suburban populations of Blackbird *Turdus merula*. Ornis Scand. 8:139-144.

Klomp, H. (1970). Clutch size in birds. Ardea 58:1-121.

Knupp, D. M., Owen, R. B. and Dimond, J. B. (1977). Reproductive biology of American Robins in Northern Maine. Auk 94:80-85.

Krebs, J. R. (1971). Territory and breeding density in the great tit *P. major*. Ecology 52:2-22.

Kruuk, H. (1978). Foraging and spatial organisation of the European Badger *Meles meles* L. Behav. Ecol. Sociobiol. 4:75-89.

Lack, D. (1947). The significance of clutch-size. Ibis 89:302-352.

Lack, D. (1948). Natural selection and family size in the starling. Evolution 2:95-110.

Lack, D. (1950). Family size in titmice of the genus *Parus*. Evolution 4:279-290.

Lack, D. (1954). The Natural Regulation of Animal Numbers. Oxford University Press, Oxford.

Lack, D. (1968). Population Studies of Birds. Clarendon Press, Oxford.

Lack, D., Gibb, J. A. and Owen, D. F. (1957). Survival in relation to brood size in tits. Proc. Zool. Soc. Lond. 128:131-326.

Lack, P. (1993). Birds on Lowland Farms. HMSO, London.

Lakhani, K. H. and Satchel, J. E. (1970). Productivity by *Lumbricus terrestris* (L.). J. Anim. Ecol. 39:473-492.

Lessels, C. M. (1992). The evolution of life histories. In Behavioural Ecology: an Evolutionary Approach, eds. J. R. Krebs and N. B. Davies. Blackwell, Oxford.

Lundberg, A., Alatalo, R. V., Carlson, A. and Ulfstrand, S. (1981). Biometry, habitat distribution and breeding success in the pied flycatcher *Ficedula hypoleuca*. Ornis Scand. 12:68-79.

Luniak, M. and Mulsow, R. (1986). Ecological parameters in the urbanisation of the European Blackbird. Acta XIX Congr. Int. Orn. Ottowa 1787-1793.

Magrath, R. D. (1989). Hatching asynchrony and brood reduction in the blackbird *Turdus merula*. PhD Thesis, University of Cambridge.

Magrath, R. D. (1991). Nestling weight and juvenile survival in the blackbird *Turdus merula*. J. Anim. Ecol. 60:335-351.

Marchant, J. H., Hudson, R., Carter, S. P. and Whittingham, P. (1990). Population Trends in British Breeding Birds. BTO, Tring.

Marchetti, K. and Price, T, (1989). Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. Biol. Rev. 64:51-70.

Martin, T. E. (1987). Food as a limit on breeding birds: a life history perspective. Ann. Rev. Ecol. Syst. 18:453-487.

Mason, C. F. (1970). Bioenergetic studies of populations of woodland molluscs. DPhil Thesis, University of Oxford.

Mertens, J. A. L. (1969). The influence of brood size on the energy metabolism and water loss of nestling great tits *Parus major*. Ibis 111:11-16.

Møller, A. P. (1982). Characteristics of magpie *Pica pica* territories of varying duration. Ornis Scand. 13:94-100.

Møller, A. P. (1988). Nest predation and nest site choice in passerine birds in habitat patches of different size: a study of magpies and blackbirds. Oikos 53:215-221.

Møller, A. P. (1990). Nest predation selects for small nest size in the blackbird. Oikos 57:237-240.

Murton, R. K. and Westwood, N. J. (1974). Some effects of agricultural change on the English avifauna. Brit. Birds 647:41-69.

Newton, I. (1976). Breeding of sparrowhawks in different environments. J. Anim. Ecol. 45:831-849.

Newton, I. (1989). Lifetime Reproduction in Birds. Academic Press, London.

Niebuhr, O. (1948). Die Vogelwelte des feuchten Eichen-Hainbuchenwaldes. Orn. Abhand. 1.

Nilsson, J. A. and Svensson, E. (1993). Energy constraints and ultimate decisions during egg laying in the blue tit. Ecology 74:244-251.

Nur, N. (1984). Feeding frequencies of nestling blue tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequency. Oecologia 65:125-137.

Nur, N. (1987). Nestlings and feeding frequencies: a model of optimal parental investment and implications for avian reproductive strategies. In Foraging Behaviour, eds. A. C. Kamil, J. R. Krebs and R. H. Pulliam. Plenum Press, New York.

Nur, N. (1988). The cost of reproduction in birds: an examination of the evidence. Ardea 76:155-168.

O'Connor, R. J. (1975). The influence of brood size upon metabolic rate and body temperature in nestling blue tits (*Parus caeruleus*) and house sparrows (*Passer domesticus*). J. Zool. 175:391-403.

O'Connor, R. J. (1984). Growth and Developement in Birds. Wiley and Sons, London.

O'Connor, R. J. (1986). Dynamical aspects of avian habitat use. In Wildlife 2000. Modelling Habitat Relationships in Terrestrial Vertebrates. Eds. J. Verner, H. C. Morrison and C. J. Ralph. Madison, Wisconsin.

O'Connor, R. J. and Fuller, R. J. (1985). Bird population responses to habitat. In Bird Census and Atlas Studies. Eds. K. Taylor, R. J. Fuller and P. C. Lack. BTO, Tring.

O'Connor, R. J. and Shrubb, M. (1986). Farming and Birds. Cambridge University Press, Cambridge.

Osborne, P. and Osborne, L. (1980). The contribution of nest site characteristics to breeding success among Blackbirds *Turdus merula*. Ibis 122:512-517.

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

Perrins, C. M. (1970). The timing of birds breeding seasons. Ibis 112:242-255.

Perrins, C. M. (1976). Possible effects of qualitative changes in the insect diet of avian predators. Ibis 118:580-584.

Perrins, C. M. (1979). British Tits. Collins, London.

Pettifor, R. A. (1993). Brood-manipulation experiments I. The number of offspring surviving per nest in blue tits (*Parus caeruleus*). J. Anim. Ecol. 62:131-144.

Pleszczynska, W. K. (1978). Microgeographic prediction of polygyny in the lark bunting. Science 201:935-937.

Raw, F. (1959). Estimating earthworm populations by using formalin. Nature 184:1661.

Reyer, H. U. and Westerterp, K. (1985). Parental energy expenditure: a proximate cause of helper recruitment in the Pied Kingfisher (*Ceryle rudis*). Behav, Ecol. Sociobiol. 17:363-369.

Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. Smithsonian Contr. Zool. 9.

Robinson, P. J. (1991). Breeding passerines at Lunnon Farm, St. Marys, Isles of Scilly. Isles of Scilly Bird Report, 1991.

Rogers, D. L. et al., (1977). Length-energy relationships in shrub-steppe invertebrates. Ann. Entomol. Soc. Am. 77:51-53.

Rosenberg, K. V. et al. (1982). Community organisation of riparian breeding birds: response to annual resource peak. Auk 99:260-277.

Roskaft, E. (1985). The effect of enlarged brood size on the future reproductive potential of the rook. J. Anim. Ecol. 54:255-260.

Royama, T. (1966). Factors governing feeding rate, food requirement and brood size of nestling Great Tits *Parus major*. Ibis 108:131-347.

Royama, T. (1969). A model for the global variation of clutch-size in birds. Oikos 20:562-567.

Royama, T. (1970). Factors governing hunting behaviour and selection of food by the Great tit (*Parus major* L.). J. Anim. Ecol. 39:619-668.

Schnack, S. (1991). The breeding biology and nestling diet of the blackbird *Turdus merula* and song thrush *T. philomelos* in Vienna and an adjacent wood. Acta Orn. 26:85-106.

Seel, D. C. (1969). Food, feeding rates and body temperature in the nestling house sparrow *Passer domesticus* at Oxford. Ibis 111:36-47.

Skutch, A. F. (1949). Do tropical birds rear as many young as they can nourish? Ibis 91:430-455.

Skutch, A. F. (1976). Parent Birds and Their Young. University of Texas Press, Austin.

Slagsvold, T. (1982). Clutch size variation in passerine birds: the nest predation hypothesis. Oecologia 54:159-169.

Slagsvold, T. (1984). Clutch size variation in birds in relation to nest predation: on the cost of reproduction. J. Anim. Ecol. 53:945-953.

Smith, H. G. et al. (1988). Feeding frequencies and parental division of labour in the double brooded great tit *Parus major*. Behav. Ecol. Sociobiol. 22:447-453.

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

Smith, J. N. M. (1978). Division of labour by song sparrows feeding fledged young. Can . J. Zool. 56:187-191.
Smith R. L. (1984). Sperm Competition and the Evolution of Animal Mating Systems. Academic Press, Orlando.

Snow, D. W. (1958). A Study of Blackbirds. British Museum, London.

Snow, D. W. (1962). A field study of the black and white manakin *Manacus manacus* in Trinidad. Zoologica 47:65-104.

Snow, D. W. and Mayer-Gross, H. (1967). Farmland as a nesting habitat. Bird Study 14:43-52.

Snow, D. W. and Snow, B. (1988). Birds and Berries. Poyser, Calton.

Stearns, S. (1992). The Evolution of Life Histories. Oxford University Press, Oxford.

Stephens, D. W. and Krebs, J. R. (1986). Foraging Theory. Princeton University Press, Princeton.

Sullivan, K. A. (1989). Predation and starvation: age specific mortality in juvenile juncos (*Junco phaenotus*). J. Anim. Ecol. 58:275-286.

Svensson, L. (1992). Identification Guide to European Passerines. Stockholm.

Tinbergen, J. M. (1981). Foraging decisions in starlings (*Sturnus vulgaris* L.). Ardea 60:1-647.

Tinbergen, N. et al. (1960). The dynamics of insect and bird populations in pine woods. Arch. Neerl. Zool. 13:259-472.

Tinbergen, N., Impeckoven, M. and Franck, D. (1967). An experiment on spacing out as a defence against predators. Behaviour 78:307-321.

Török, J. (1981). Food composition of nestling blackbirds in an oak forest bordering an orchard. Opusc. Zool. Budapest 17-18:145-181.

Török, J. and Ludvig, E. (1985). Seasonal changes in foraging strategies of nestling blackbirds. Behav. Ecol. Sociobiol. 22:329-333.

Walasz, K. (1990). Experimental investigations on the behavioural differences between urban and forest blackbirds. Acta Zool. Cracov 33:235-271.

Westerterp, K. (1973). The energy budget of the nestling starling *Sturnus vulgaris*, a field study. Ardea 61:137-158.

Wilcove, D. S. (1985). Nest predation in forest tracts and the decline of migratory song birds. Ecology 66:1212-1214.

Williamson, K. (1971). Habitat preferences of the wren on English farmland. Bird Study 16:53-59.

Wilson, E. O. (1975). Sociobiology. Belknapp Press, Cambridge Mass.

Zar, J. H. (1984). Biostatistical Analysis. Prentice-Hall, New Jersey.