# Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies

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**Summary**

**1.** When faced with increased brood demand, parent birds provisioning young in the nest can make a variety of adjustments to their foraging and food allocation strategies. Logical extensions of classic optimal foraging theory predict increased provisioning effort to larger broods to be accompanied by changes in load size, foraging distance from the nest, as well as possible changes in the type and size of prey delivered.

**2.** We assessed such behavioural adjustments and their consequences in pairs of European starlings (*Sturnus vulgaris*) responding to a range of experimental brood sizes. Parents feeding larger broods increased their visit rates by spending less time in the nestbox and less time around the nestbox colony. High visit rates to larger broods were also associated with larger loads per visit and changes in the type of prey delivered to the nest. As a consequence, chicks in large and small broods received similar rates of food intake, but experienced differences in the nutritional quality of their food. Parents feeding larger brood sizes were able to increase their provisioning effort despite feeding in the same foraging sites, travelling at comparable flight speeds and maintaining similar body masses to parents feeding smaller broods.

**3.** Parental energetic expenditure, measured through doubly labelled water analyses, showed no effect of the brood size treatment. The greater proportion of indigestible material per gram of food delivered to the larger experimental brood sizes (i.e. soil from the guts of earthworms) was probably responsible for the fact that these chicks grew at slower rates and fledged at lower body masses, although we cannot rule out the possibility of lower growth rates due to higher energetic costs of sibling competition within larger broods. Lighter fledglings from large broods disappeared from the local area earlier in the summer, probably as a result of differential mortality rather than premature natal dispersal.

**4.** We discuss the adaptive significance of the provisioning trade-off between quantity and quality of food items delivered by parents to the nest, with reference to natural variation in foraging conditions and brood demand.

*Key-words:* chick nutrition, diet choice, energetic costs, parental care, starlings.

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## Introduction

For many bird species, adult energy expenditure peaks during the nestling rearing phase (Bryant & Westerterp 1980; Drent & Daan 1980). Provisioning young in the nest involves a series of critical behavioural

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decisions by parent birds, each with direct consequences for their lifetime reproductive success. During foraging trips, central-place foraging theory predicts that parents will maximize the net energetic gain per foraging effort (Kacelnik 1984). This is achieved by selecting the best (i.e. the nearest and most profitable) foraging patches and exploiting the most energetically efficient prey types (e.g. Royama 1966; Tinbergen 1981; Westerterp, Gortmaker & Wijngaarden 1982; Lifjeld & Slagsvold 1988; Wright & Cuthill 1989, 1990a). Patch residence times at feeding sites can also be adjusted and load sizes optimized according to the distance between nest and foraging patch (e.g.

Kacelnik 1984; Cuthill & Kacelnik 1990; Kacelnik & Cuthill 1990).

Any increase in parental provisioning effort should have energetic costs, and a potential increase in the risk of predation, which will have consequences for the survival and future reproduction of parents. Parental provisioning effort per brood should therefore be optimized in order to maximize lifetime reproductive success (Trivers 1972). However, regardless of total provisioning effort, classical optimal foraging models predict that on any one visit parents should always forage so as to maximize net energetic gain. This is because provisioning behaviour will always be selected to deliver energy to the nest as efficiently as possible. Any spare time or energy should be used to derive additional fitness benefits from non-parental activities, such as self-feeding or maintenance (e. g. Kacelnik & Cuthill 1990; Martins & Wright 1993), or additional social and reproductive activities (e.g. Westneat 1988; Wright & Cuthill 1990a,b; Wright & Cotton 1994). Following this reasoning, as brood demand increases parents should increase their provisioning effort at the expense of any non-parental behaviours. Therefore, even though parents may provision young at very different rates, they should always pursue the same optimal foraging strategy per visit, at least within normal limits of provisioning effort.

If brood demand exceeds normal maximum provisioning rates, parents following the optimal foraging strategy of net energetic returns may be unable to deliver sufficient prey to maintain brood fitness. Models by Houston & McNamara (1985a, 1985b) show that by being less selective regarding prey types collected, and thereby decreasing travel times by foraging nearer to the nest, the frequency of feeding events can be increased adaptively. Additionally, Houston (1985) shows that a reduction in handling time, such as that achieved by switching to smaller and more easily managed prey items, could be a better option for a central place forager than simple rate maximization. Under certain conditions, these strategies could increase the level of provisioning and reduce the immediate probability of chick starvation, despite an overall decrease in the efficiency of biomass delivery. In addition, different prey types may represent different energetic returns for foraging parents, either in their search or handling costs, or in their energetic content. A model by Lifjeld (1989) explores the consequences of differences in prey type for parents under a range of brood demands, and suggests that if the sacrifice of greater foraging costs are worth it, parents may switch from net energy maximization to gross energy maximization. This is predicted to lead to increases in optimum load sizes, as a result of changes in the type of prey delivered to hungrier broods.

Provisioning rates could be sustained above some parental maximum for net energy delivery if some other factor (or 'currency') is traded-off against energetic returns. The most obvious possibility is for parents to compromise the nutritional quality of prey delivered to the nest. The combination of nutritional compounds in the diet of chicks can be optimized for maximum growth and development (e.g. Johnston 1993), but prey types that provide the best energetic returns may not always contain every nutritionally important element (e.g. Krebs & Avery 1984). Unlike the short-term energy delivery strategies above, compromising prey quality would not necessarily require parents to pay higher energetic costs per unit of food delivered. Adaptive trade-offs could be made concerning the type of prey delivered, in order to balance both the nutritional and energetic requirements of growing young. In times of energy shortage, we might therefore expect the optimum nutritional content of chick diets to be traded-off against rates of energy delivery. This is because parents should first ensure short-term survival of chicks, and secondarily concern themselves with maximizing long-term growth rates of their offspring. Evidence exists for complex foraging strategies involving changes in prey types, mostly from studies which show that when feeding enlarged broods parents appear to switch the type or range of prey items that they feed to their young (e.g. Royama 1966; Ward 1973; Tinbergen 1981; Westerterp *et al.* 1982; Lifjeld & Slagsvold 1988; Wright 1990; Wright & Cuthill 1989, 1990a,b). For whatever reason, switching the type of prey delivered to the nest appears to represent a 'best-of-a-bad-job' strategy for parents, to be used only when faced with excessive brood demand. As such, prey switching should result in reduced future fitness (i.e. residual reproductive value) of parents or chicks, or both. Otherwise, any foraging strategy that increased provisioning efficiency in the long term would already be being used by *all* parents from the start. Therefore, in natural situations we would expect prey switching to function as an adaptation to clutch sizes that prove to be too large in unpredictable environments, to periods of depressed foraging conditions, or similarly unpredicted reductions in parental provisioning ability.

In this study, we experimentally manipulated brood size in the European starling (*Sturnus vulgaris*) to investigate adjustments made in parental provisioning strategies. We collected data on parental feeding rates, the size of loads and the prey types delivered to the young, as well as analysing the nutritional components of each prey type. Parental foraging sites, flight speeds and return times to the nest (i.e. patch residence time plus return travel time) were also recorded. We assessed daily energetic expenditure of parents using the doubly labelled water techniques (Tatner & Bryant 1988; Lifson, Gordon & McLintock 1995), and the effect of parental provisioning on chick fitness by weighing chicks daily, measuring chick tarsus length prior to fledging, and following fledged young until disappearance from the breeding site.

## Methods

### STUDY SITE

This study was carried out in 1993 at the Oxford University Farm, Wytham, Oxon., UK. The starling flock consists of over 300 birds resident at the site throughout the year, and each spring about 45 pairs breed in the 60 nestboxes provided. Over 90% of pairs are monogamous, although extra-pair matings are frequent (Wright & Cotton 1994). The starlings feed mainly on soil invertebrates in the farm's pasture fields bordering the River Thames, but they also use nearby gardens, roadside verges, and the margins of arable fields. The farm buildings provide the starlings with additional artificial food sources from animal feeds, as well as night-time roost sites in nearby coniferous trees and daytime 'loafing' areas around the barns on which the nestboxes are positioned.

### EXPERIMENTAL PROCEDURE

All 25 nests used in this study were exclusively defended and provisioned by only one male and one female, and were therefore considered socially monogamous. In all nests, the first chicks hatched within 4 days of each other (30 April to 3 May 1993). On the evening of 6 May (chick age 3–6 days), five pairs were randomly assigned to each of five experimental brood sizes. Chicks were swapped between nests so that every nest contained similarly aged chicks, and any small 'runt' chicks were removed and replaced with healthy chicks of similar age from non-experimental nests. No nest received more than two of its original brood, nor more than two chicks from the same donor nest. Parental desertion from four nests with artificially small broods and the disappearance of one chick from a brood of six during the initial stages of data collection resulted in the following experimental broods: (i) three chicks ($n = 3$); (ii) four chicks ($n = 3$); (iii) five chicks ($n = 6$); (iv) six chicks ($n = 4$); and (v) seven chicks ($n = 5$).

There were no significant differences between the experimental groups in terms of minimum estimated parental age, body size, body mass, original brood hatch-date, and original clutch size (all *P*-values > 0·1).

### PARENTAL FORAGING DATA

All birds were colour-ringed for individual identification, and parental foraging data were collected from 7 to 21 May 1993. Observations were performed simultaneously by two people, one recording the parental provisioning at the nestbox using a 15–60 × telescope, and the other recording parental foraging with 8 × 30 binoculars from a high vantage point on top of grain silos. The two observers were in visual contact and by synchronizing stopwatches many of the parental provisioning and foraging events could be linked. Parental provisioning observations included: the number of visits per hour; the prey type delivered (broadly classified by size and shape from nest-box camera pictures: Wright & Cuthill 1989; Wright 1990); and the time spent in nestbox. Parental foraging observations included: flight-time from box to foraging patch; foraging patch location (to nearest 50 m); any pauses in flight; and whether the flight path of parents was direct, curved or indirect (i.e. including stop-offs at other foraging sites).

Each of the 21 pairs was watched for 1 hour, between 07.00 and 20.00 h, two days out of every three. Observations were not performed between 16.00 and 18.00 hours when chicks were being weighed, nor in the evenings when parents were being trapped in the nestbox for doubly labelled water analysis, or on days when their chicks were collared to collect prey (see below). In total, each nest was watched for at least 10 separate hours of observation. By rotating observers and the order in which nests were watched, it was possible to avoid any biases in observation (e.g. time of day). Data from non-manipulated starling broods (Westerterp *et al.* 1982; Wright 1990) suggests that there is little variation in parental visit rates once chicks are older than 1 week, so that for a given brood size we would expect largely similar visit rates across the 15 days of the observation. Any differences between days, such as those due to changes in weather, were balanced across brood size treatment groups by the order of observations.

### CHICK GROWTH AND DIET DATA

Each chick was weighed (to nearest 0·5 g using Pesola balances) between 16.00 and 18.00 hours every day from hatching until 15 days of age, after which time most chicks were too large to handle without risking premature fledging. At 15 days of age, each chick was colour-ringed for individual identification, with colours specific to the experimental brood size included in the ring combinations in case of partial identifications. On day 15, chick tarsus lengths were also taken (to the nearest 0·05 mm using calipers). Following fledging, observations were made every day (26 May to 31 July) in and around the farm in order to compare survival/dispersal dates of fledglings from the different brood size treatments.

The diet of nestlings was examined using the neck collar method (Kluyver 1933). Small lengths of pipe-cleaner were used to prevent nestlings from swallowing their food, and the prey were then collected from their throats. This method has the potential problem of changing the begging behaviour of the chicks. Parents reacted to the chick neck collars by reducing their provisioning effort and spent more time brooding, which in itself could have affected parental foraging strategies. Collared chicks can also eject the food out of their mouths, and parents often remove it

from the nestbox. In order to minimize the problems associated with chick collars, and to reduce any disturbance of normal parental provisioning, neck collars were used for only one parental visit, with collars being used on all the chicks in the brood at the same time. Each nest was sampled on only one day, and during this day prey items from 6 to 12 separate visits were collected at hourly intervals. Four or five nests were collared simultaneously, with a range of different experimental brood sizes used on any one day. Parental loads were divided into different taxonomic prey type categories and the wet mass was taken for each prey type separately in the nearby field station laboratory. Samples were stored at –30 °C prior to nutritional analysis.

We tested the effect of neck collaring on the growth of chicks by comparing the mean change in mass of nestlings during the day of collaring with the mean mass change during the day before and after the data collection. The growth of the chicks was significantly negatively affected by the neck collaring (mean mass change $= -3.86$ g: paired $t$-test, $t = 6.78$, $n = 21$, $P < 0.001$). However, there was no significant difference in the mass change of chicks in the different experimental brood sizes as a result of the neck collaring ($F_{1,19} = 0.07$, $P = 0.790$). We therefore assume that there was no brood size bias in the detrimental effect of the neck collars.

### NUTRITIONAL ANALYSIS

To investigate the differences in nutritional quality of the different prey types, we analysed the dry–wet mass relationship, and the protein, lipid, carbohydrate and energy contents of different prey types. Following storage, dry mass of the chick neck collar samples were obtained by heating in a drying oven at 50°C, until mass remained constant (for $\approx 10$–20 days according to the size of prey). Prey items were analysed individually, except for small invertebrates which were combined into batches of five for ash and lipid content analyses in order to ensure that mass differences were large enough to be measurable. When tests were destructive, prey items were divided up and randomly allocated to the different tests.

Protein content was determined using a version of the Kjeldahl process (Robins 1983). Organic nitrogen was converted to ammonium sulphate by boiling individual dried samples in concentrated sulphuric acid using a Selenium tablet as catalyst and until the solution became colourless (taking up to 5 hours). Ammonium ions were then measured using a Technicin Auto-Analyser to give a percentage of total organic nitrogen (N), which when multiplied by 6·25 gives the protein content as a percentage of the dry mass. The final values were confirmed using the same extraction procedure on a second set of samples following the extraction of lipids (see below). In samples where this showed that the protein values were

reduced slightly by the lipid extraction and the values for percentage lipid content were adjusted downwards accordingly (i.e. by the percentage difference in the two sets of protein content values).

Lipid content was determined by extracting the lipids with organic solvents (Robins 1983). Individual dried samples were steeped in petroleum ether (b.p. 60–80 °C) for 48 h. Approximately 90% of the solvent was removed with a pasteur pipette and the remainder allowed to evaporate. The samples were then ground-up and steeped in a solution of 75% methanol and 25% chloroform for 96 h and most of the solvent removed. This was repeated for a further 48 h, the solvent was again removed and the remainder allowed to evaporate. Samples were then oven dried at 50°C for 24 h to remove any remaining solvent, weighed and the percentage of lipid removed was calculated.

Energy content (kJ per gram) was calculated from the above analyses by adding the mean calorific values for protein (21·35 kJ), lipid (39·77 kJ) and carbohydrate (17·17 kJ) given by Cummins & Wuycheck (1971). Ash content was determined by burning dried samples in a Muffle furnace at 500°C for 5 h. Carbohydrate content was determined by the difference after subtraction of protein, lipid and ash contents.

### DOUBLY LABELLED WATER ANALYSIS

The doubly labelled water (DLW) technique (Tatner & Bryant 1988; Lifson *et al.* 1995) was used to measure the energetic expenditure of parents feeding the different experimental broods between 8 and 14 May 1993 (chick ages 6–13 days old). This involved catching the parents with nestbox traps in the early evening between 18.00 and 20.00 h, and removing them temporarily to the nearby field station laboratory.

The DLW for injection into the subjects was prepared using: 7 mL 97 atom percentage $H_2^{18}O$; and 1·6 mL 99·996 atom percentage $D_2O$. When caught, birds were weighed (to nearest 0·5 g using a Pesola), and given an intraperitoneal injection with 0·005 mL per gram body mass of the DLW. It was assumed that 63% of body mass was water. Blood samples were collected from the brachial vein after allowing 1 hour for equilibrium and where possible after 24, 48, and 72 h. Blood was collected and stored in flame-sealed capillary tubes. For comparison, blood samples were also collected from six starlings not involved in DLW measurements, over 2 days during the experimental period, to assess natural isotope abundances. Blood samples were collected from a total of 26 experimental birds, but the samples from only 24 birds could be used for analysis. When both were available, the samples from the first 24 h were preferred to the 24–48 hour samples because of higher isotope concentrations.

Analysis of DLW samples was carried out at the Scottish Universities Research and Reactor Centre, following the procedures described by Tatner & Bry-

ant (1988). Water was extracted from blood samples under vacuum and converted to deuterium/hydrogen by reduction when passed over a uranium furnace at 800 °C. D/H was subsequently absorbed onto chilled activated charcoal (Sackett 1978; Wong & Klein 1986). Gas samples for oxygen analysis were obtained by converting water from blood to $CO_2$ using guanidine hydrochloride (Boyer *et al.* 1961). D/H and $^{18}O/^{16}O$ ratios in gas samples were determined by isotope ratio mass spectrometry on a VG OPTIMA. Rates of isotope turnover and estimates of $CO_2$ production were calculated using the 'two point' method (Lifson & McClintock 1966), which included corrections for fractionation of isotopes during water loss (Lee & Lifson 1960). All blood samples were analysed in duplicate and mean values used for both D/H and $^{18}O/^{16}O$. Background isotope concentrations obtained in this study were: D = 151·05 p.p.m., and $^{18}O$ = 2005·80 p.p.m. $CO_2$ production was converted to its equivalent energy expenditure using 1 cm$^3$ $CO_2$ = 24·86 J. Basal metabolic rate (BMR) was calculated from the appropriate equation of Aschoff & Pohl (1970) (i.e. passerines, resting phase).

### STATISTICAL ANALYSES

All data were reduced to single parameter estimates for each bird or nest prior to analyses. Sample sizes were typically 21 nests or 42 birds in the following tests. For estimating the effect of experimental brood size on such variables as nest visitation rates, the unit of analysis was the mean number per hour for each bird averaged across all observation periods. Brood size was treated as a continuous linear variable and parental sex as a categorical variable in all GLIM regression analyses (Crawley 1993).

Prey choice in part reflects feeding site (e.g. Tinbergen 1981), so each prey item does not constitute an independent statistical event. Thus, the prey type data were reduced as follows. The proportion of each prey type delivered, expressed as a percentage of total observed prey, was calculated for each bird. These arcsine-transformed proportions were then subjected to multivariate ANCOVA, which tested the changes in all prey types simultaneously (expressed in overall Wilks' lambda statistic, SPSS Inc. 1988), as well as performing univariate tests on each prey type separately within the same model. A 5% level of significance is applied throughout and all *P*-values presented are two-tailed.

## Results

### PARENTAL PROVISIONING

Parents feeding larger broods showed significantly higher visit rates to the nest, with no significant effect of parental sex or interaction between parental sex

and brood size (Table 1a, Fig. 1a). Visit rates per chick significantly decreased with increasing brood size, and again there was no significant effect of parental sex or any interaction between parental sex and brood size (Table 1a, Fig. 1b). There was a significant reduction in the time that parents spent in the nestbox with increasing brood size, but no significant difference between the sexes or any interaction between parental sex and brood size (Table 1a).

Overall, there was a significant effect of experimental brood size on the type of prey delivered by parents (Wilk's lambda = 0·60, $F_{1,34}$ = 4·61, $P$ = 0·003). The effect of parental sex approached significance (Wilk's lambda = 0·75, $F_{1,34}$ = 2·30, $P$ = 0·067), but there was no interaction between parental sex and brood size (Wilk's lambda = 0·80, $F_{1,34}$ = 1·68, $P$ = 0·166). As can be seen from univariate tests on each prey type separately (Table 1b), these overall effects were largely the result of significant decreases in the proportion of larval prey and increases in the proportion of earthworms delivered to larger broods (Fig. 2). The effects of brood size and parental sex on prey types delivered resulted from a stronger effect of brood size on the amount of pig pellets delivered by males (Table 1b, Fig. 2).

### PARENTAL FORAGING

There were no significant effects of experimental brood size, parental sex or the interaction between the two, on the mean distance of parental foraging sites from the nest, the mean time that parents took to return to the nest following arrival at foraging sites (i.e. foraging time plus flight time back to nest) or mean flight speed (calculated from the distance from nestbox to the foraging site divided by the time taken on the outward flight) (Table 1c).

Parents of both sexes feeding smaller broods paused significantly more often around the breeding colony after leaving the nestbox (Table 2a, Fig. 3), but there were no significant differences in the proportion of visits in which parents paused off colony on their way to foraging sites. There were no significant effects of experimental brood size, parental sex or any interaction between the two on whether parents flew in curved or indirect flight-paths from the nestbox to the foraging site (Table 2a).

There were no significant effects of experimental brood size, parental sex or the interaction term on the types of habitats that parents visited (Table 2b). In general, these results support the lack of differences in mean distance to feeding site and return times (Table 1c). There is, however, some question as to the reliability of these habitat use results, because differences in the delivery of pig pellets (Table 1b) were not reflected in differential usage of the pig pens by males feeding larger broods. Presumably, this was because more than one feeding site was sometimes used per

**Table 1.** The results of GLIM regressions testing for the effects of experimental brood size, parental sex and the interaction between the two on: **(a)** parental provisioning variables; **(b)** separate univariate tests within multivariate ANCOVA on the arcsine-transformed proportions of each prey type delivered; **(c)** parental foraging variables; and **(d)** parental body mass and DLW analysis of parental energetic expenditure. (See text for further explanation of variables.)

| Variable | Brood size | | Parental sex | | Sex *Brood size | |
|---|---|---|---|---|---|---|
| (a) | $F_{1,38}$ | $P$ | $F_{1,38}$ | $P$ | $F_{1,38}$ | $P$ |
| Visit rate | 17·26 | <0·001 | 0·01 | 0·944 | 0·41 | 0·523 |
| Visit rate per chick | 12·50 | 0·001 | 0·02 | 0·894 | 0·61 | 0·440 |
| Time in nest | 5·23 | 0·028 | 2·44 | 0·127 | 0·07 | 0·787 |
| (b) | $F_{1,38}$ | $P$ | $F_{1,38}$ | $P$ | $F_{1,38}$ | $P$ |
| Larvae | 11·47 | 0·002 | 0·11 | 0·738 | 0·08 | 0·781 |
| Earthworms | 4·18 | 0·048 | 0·22 | 0·638 | 0·12 | 0·744 |
| Large-winged | 0·90 | 0·349 | 1·97 | 0·168 | 1·81 | 0·187 |
| Small invertebrates | 0·00 | 0·962 | 0·67 | 0·418 | 0·31 | 0·580 |
| Pig pellets | 13·87 | 0·001 | 5·93 | 0·020 | 4·28 | 0·045 |
| (c) | $F_{1,38}$ | $P$ | $F_{1,38}$ | $P$ | $F_{1,38}$ | $P$ |
| Distance to site | 0·59 | 0·446 | 0·15 | 0·697 | 1·34 | 0·255 |
| Return time | 0·46 | 0·501 | 1·87 | 0·180 | 3·21 | 0·081 |
| Flight speed | 0·09 | 0·764 | 0·41 | 0·528 | 1·48 | 0·231 |
| (d) | $F_{1,20}$ | $P$ | $F_{1,20}$ | $P$ | $F_{1,20}$ | $P$ |
| Change in mass | 0·19 | 0·670 | 0·81 | 0·373 | 3·22 | 0·081 |
| $CO_2$ production | 1·01 | 0·319 | 0·58 | 0·449 | 0·07 | 0·789 |
| Energy expenditure | 0·45 | 0·768 | 0·24 | 0·631 | 0·09 | 0·966 |

parental round-trip, maybe reflecting different site use for self-feeding vs. collection of food for young.

PARENTAL BODY MASS AND ENERGETIC EXPENDITURE

The DLW results from this study (Table 3; mean energy expediture $= 3·5 \times$ BMP, range 1·57–5·08 $\times$ BMR) lie well within the ranges of previous non-experimental studies on parent European starlings (e.g. Ricklefs & Williams 1984; Westerterp & Drent 1985), providing evidence for the reliability of the estimates presented here, as well as a consistency in estimates from different study areas. This comparison also suggests that the experimental procedures used here did not elevate or depress energetic expenditures so that they lay outside natural ranges.

There was no significant effect of experimental brood size on the mean body mass of parents during the nesting period ($F_{1,38} = 0·15$, $P = 0·697$). Overall, males were significantly heavier than females ($F_{1,38} = 22·37$, $P < 0·001$), but there was no significant interaction between parental sex and brood size ($F_{1,38} = 0·04$, $P = 0·846$). Although nearly all parents lost mass during the period of chick feeding, mean changes in parental body mass between captures for DLW analyses showed no significant effect of brood size, parental sex or any interaction (Table 1d). Nor

were there any significant effects of experimental brood size, parental sex or the interaction terms regarding any of the estimates of energetic expediture (Table 1d). In addition, there was no relationship between individual parental body mass and daily energetic expenditure ($r^2 = 0·04$, $n = 24$, $P = 0·359$). Values for body mass and DLW measures for the different brood size treatments are given in Table 3.

CHICK NUTRITION

Both the dry and wet mass of loads delivered per parental visit increased significantly with experimental brood size (Table 4a, Fig. 4a), probably reflecting the larger proportion of earthworms delivered (Table 1b). As a result of these load size differences, the amount of food delivered per chick per visit did not differ significantly between experimental brood sizes in either wet or dry mass (Table 4a). This result, combined with the decreases in feeding visits per chick (Table 1a), resulted in the wet and dry mass of food delivered per chick per hour being consistent across brood sizes (Table 4a, Fig. 4b). In addition, total rate of energy delivery per chick per hour (calculated using visit rates, load sizes and prey types, with the energy content per gram summed over all nutritional components for each type of prey) showed no significant difference across brood sizes (Table 4a)
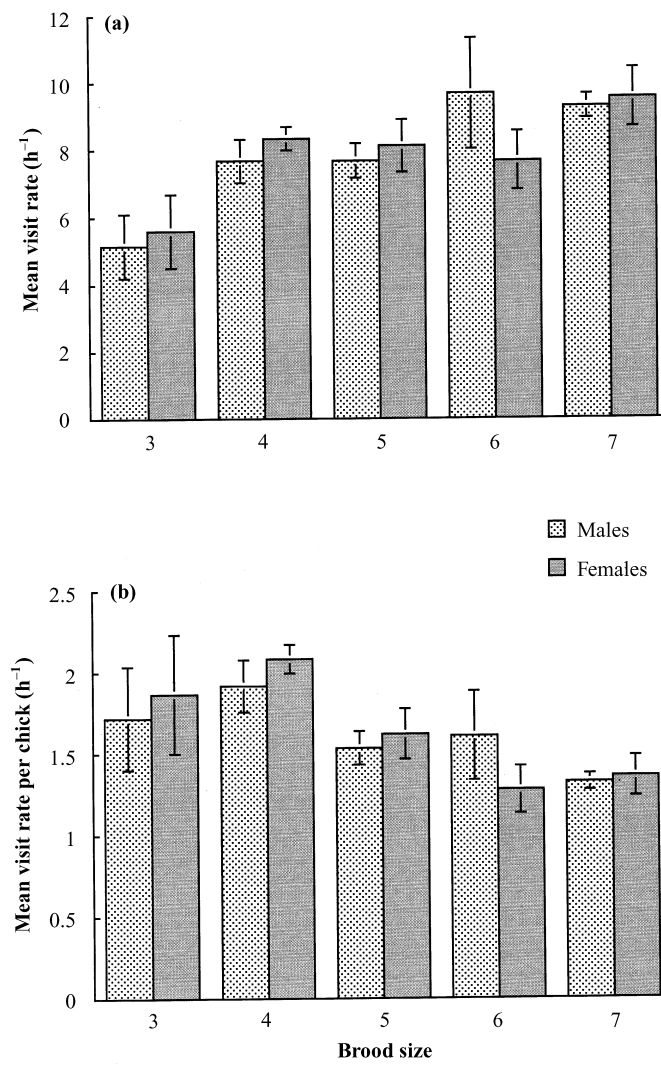
**Fig. 1.** The effect of experimental brood size on: (a) mean ($\pm$ SE) parental visit rate per hour, split by parental sex; and (b) mean ($\pm$ SE) parental visit rate per chick, split by parental sex.
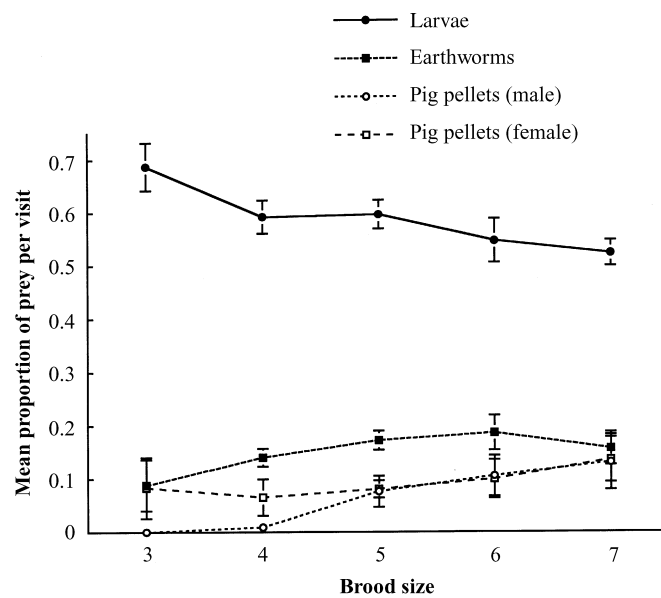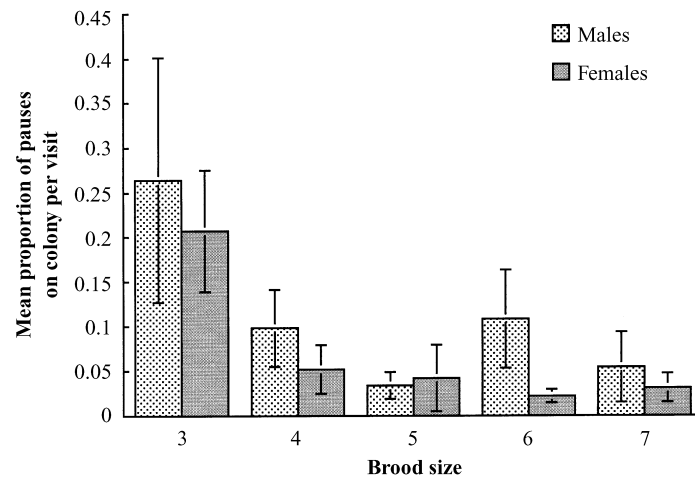


**Fig. 2.** The effect of experimental brood size on the mean ($\pm$ SE) proportion of prey delivered per visit for three of the seven prey type categories, split by parental sex in the case of pig pellets.

**Table 2.** The results of GLIM logistic regressions testing for the effects of experimental brood size, parental sex and the interaction between the two on the proportion of visits in which parents (a) did not fly direct from the nest to the foraging site; and (b) used different types of foraging habitats (see text for further explanation of variables)

| Variable (a) | Brood size $\chi_{1,38}$ | $P$ | Parental sex $\chi_{1,38}$ | $P$ | Sex *Brood size $\chi_{1,38}$ | $P$ |
|---|---|---|---|---|---|---|
| Pauses on colony | 7·09 | 0·008 | 0·94 | 0·332 | 0·29 | 0·591 |
| Pauses off colony | 0·12 | 0·725 | 0·00 | 0·964 | 1·92 | 0·166 |
| Curved flight-paths | 0·51 | 0·477 | 0·28 | 0·596 | 0·30 | 0·582 |
| Indirect flights | 1·22 | 0·270 | 0·62 | 0·430 | 0·03 | 0·862 |
| (b) | $\chi_{1,38}$ | $P$ | $\chi_{1,38}$ | $P$ | $\chi_{1,38}$ | $P$ |
| Stay on colony | 0·56 | 0·456 | 1·25 | 0·263 | 0·96 | 0·326 |
| Pig pens | 0·39 | 0·533 | 0·67 | 0·413 | 0·08 | 0·782 |
| Aerial | 0·02 | 0·877 | 0·00 | 0·975 | 0·00 | 1·00 |
| Gardens and edges | 1·48 | 0·224 | 0·07 | 0·786 | 1·12 | 0·291 |
| Arable fields | 3·14 | 0·077 | 0·33 | 0·567 | 0·44 | 0·510 |
| Pasture fields | 1·24 | 0·265 | 0·18 | 0·671 | 0·35 | 0·554 |



**Fig. 3.** The effect of experimental brood size on the mean ($\pm$ SE) proportion of foraging trips in which parents paused within the nestbox colony on their way to the feeding site, split by parental sex.

**Table 3.** Parental body mass (g), parental mass change (g/d), ADMR (average daily metabolic rate $CM^3$ $CO_2$/g/h), daily energy expenditure (kJ/d), xBMR, and sample sizes for each of the brood size treatment groups. Values given are means $\pm$ SD (minimum and maximum values in parenthesis)

| Variable | Brood size 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|
| Parental body mass | 82·0 $\pm$ 1·4 (81·0–83·0) | 83·0 $\pm$ 1·8 (81·5–85·5) | 82·9 $\pm$ 4·1 (80·0–89·0) | 83·9 $\pm$ 5·0 (78·0–92·0) | 83·2 $\pm$ 3·0 (78·5–88·0) |
| Parental mass change | −6·0 $\pm$ 0·0 (−6·0–6·0) | −1·3 $\pm$ 1·0 (−0·5–2·5) | −4·7 $\pm$ 0·8 (−0·5–2·5) | −1·8 $\pm$ 1·7 (−0·0–4·5) | −2·0 $\pm$ 0·5 (−1·5–3·0) |
| ADMR | 5·7 $\pm$ 0·2 (5·6–5·8) | 6·1 $\pm$ 1·5 (5·3–8·4) | 5·0 $\pm$ 0·9 (4·0–5·9) | 5·9 $\pm$ 1·5 (3·5–7·7) | 6·3 $\pm$ 0·8 (4·7–7·5) |
| Energy expenditure | 267·4 $\pm$ 19·0 (254–281) | 291·6 $\pm$ 69·1 (246–394) | 240·0 $\pm$ 47·0 (189–285) | 280·3 $\pm$ 63·5 (180–356) | 296·5 $\pm$ 38·4 (234–363) |
| $\times$ BMR | 3·5 $\pm$ 0·1 (3·4–3·6) | 3·7 $\pm$ 0·9 (3·2–5·1) | 3·1 $\pm$ 0·5 (2·4–3·6) | 3·6 $\pm$ 0·9 (2·2–4·7) | 3·8 $\pm$ 0·5 (2·9–4·6) |
| Sample size | 2 | 4 | 4 | 7 | 7 |

**Table 4.** The results of GLIM regression testing for the effect of experimental brood size on: **(a)** food delivery variables; **(b)** arcsine squareroot transformed proportions of nutritional components in chick diets; and **(c)** chick body size variables at chick age 15 days. (See text for further explanation of variables.)

| Variable (a) | Brood size $F_{1,19}$ | $P$ |
|---|---|---|
| Wet weight per visit | 12·21 | 0·002 |
| Dry weight per visit | 15·98 | <0·001 |
| Wet weight per chick per visit | 3·45 | 0·079 |
| Dry weight per chick per visit | 0·469 | 0·502 |
| Wet weight per chick per hour | 0·09 | 0·767 |
| Dry weight per chick per hour | 1·05 | 0·317 |
| Total energy delivered per hour | 2·09 | 0·165 |

| (b) | $F_{1,19}$ | $P$ |
|---|---|---|
| Proportion protein | 1·11 | 0·306 |
| Proportion carbohydrate | 0·00 | 0·950 |
| Proportion lipids | 10·13 | 0·011 |
| Proportion ash | 6·32 | 0·021 |

| (c) | $F_{1,19}$ | $P$ |
|---|---|---|
| Chick body mass | 6·44 | 0·020 |
| Chick tarsus length | 0·01 | 0·967 |

From the chicks' point of view, the effect of prey types and their different nutritional content can be summarized as the proportion of the different nutritional components received in chick diets. Table 4b shows that chicks in different brood sizes received diets that were not significantly different in the proportion of protein and carbohydrates. However, as brood sizes increased the proportion of lipids decreased significantly and the proportion of indigestible ash content increased significantly. The differences in ash content were probably the result of greater numbers of earthworms consumed by chicks in larger broods. Earthworms contained significantly more ash than the other prey types, probably as a consequence of the soil in their gut (Fig. 5; $F_{4,39} = 5.76$, $P = 0.002$).

CHICK GROWTH AND SURVIVAL

Despite receiving similar rates of biomass delivery (Table 4a), chick mass data at chick age 15 days showed that nestlings in smaller broods achieved significantly greater mass than those in larger broods (Table 4c, Fig. 6a). However, there were no significant differences in chick tarsus lengths between experimental brood sizes (Table 4b).

Given these differences in chick mass at age 15 days, we predicted that after leaving the nest fledglings from larger broods would suffer some disadvantage in terms of survival. All young were sighted at least once (and

most of them many times) following fledging. The mean day of last sighting of fledglings was significantly earlier for broods with lower mean body mass at chick age 15 days ($r^2 = 0.27$, $F_{1,19} = 7.10$, $P = 0.015$). The result of this was that experimental brood size had a significantly negative effect on the mean day of last sighting (Fig. 6b, $r^2 = 0.28$, $F_{1,19} = 7.47$, $P = 0.013$).

**Discussion**

PARENTAL VISIT RATES

There was a strong effect of experimental brood size on parental visit rates, irrespective of parental sex, with little evidence for any asymptote to visit rates. Previous work on starlings at this study site has shown an apparent ceiling to individual parental effort at about 20 visits per hour (Wright & Cuthill 1990b), possibly reflecting some physiological limit to parental energetic expenditure (Drent & Daan 1980), or a practical limit on the rate at which food could be found and delivered to the nest in this environment. Therefore, despite the experimental increases in brood size, parents in the present study appeared to be operating well within such limits for the maximum provisioning rates.

As with other studies on birds (e.g. Nur 1984b; Kacelnik & Cuthill 1990; Wright & Cuthill 1990a,b; Martins & Wright 1993), the increase in parental visits with brood size was not proportional to the number of chicks, so that visit rate per chick declined as brood size increased. This may seem strange when the visit rate evidence suggests that parents could have increased their provisioning effort at a greater rate. However, the decrease in number of visits per chick was compensated for by the increase in the size of the load delivered per visit in larger experimental broods. Hence, the rate of food delivery, in terms of biomass delivered per chick per hour, remained in proportion to the number of chicks in the brood. This is apparently contrary to predictions from life history models (e.g. Sibly & Calow 1983; Nur 1984a), as well as reports from other empirical studies (reviewed by Klomp 1970; Nur 1984a, 1988). However, the present data set does represent one of the most detailed estimates so far for food intake rates for chicks in the nest.

PARENTAL COSTS OF PROVISIONING
BEHAVIOURS

Parents seemed well able to absorb the extra provisioning effort required by the larger experimental brood sizes. However, there was some evidence that they did so at the expense of non-parental and foraging activities. When feeding smaller broods, parents of both sexes were often able to remain around the colony rather than return directly to the fields. It is possible that staying around in the colony carried
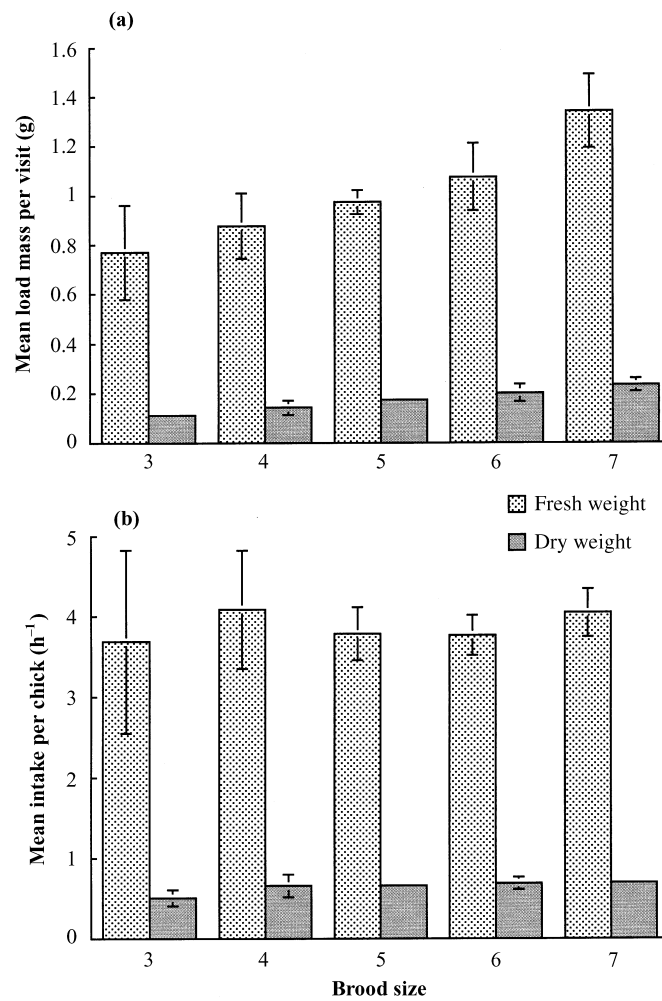
**Fig. 4.** The effect of experimental brood size on (a) the mean ($\pm$ SE) load wet and dry weights per parental visit; and (b) the mean ($\pm$ SE) food intake per chick per hour wet and dry weights.
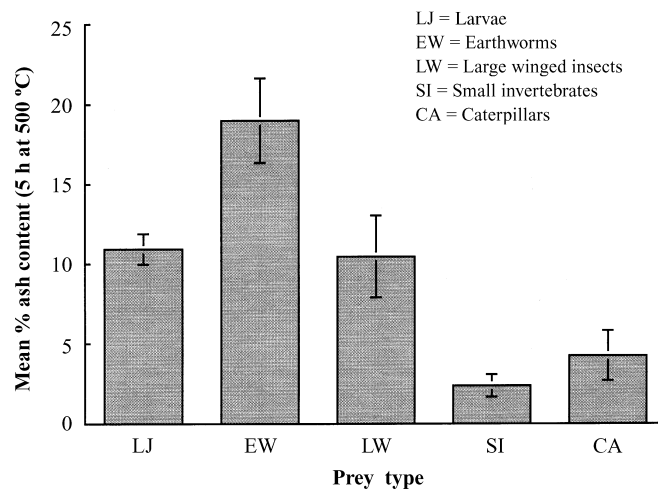


**Fig. 5.** The mean ($\pm$ SE) percentage ash (i.e. indigestible material) in the different types of prey delivered by parents.

fewer predation risks, or that some benefits (i.e. extra-pair matings) were to be gained from involvement in social interactions around the nestbox colony.

Models of allocation of food between parent and young in central place foragers (Kacelnik 1984; Kacelnik 1988; Kacelnik & Cuthill 1990) predict that the proportion of food allocated to the young should be positively related to brood size because of changes in
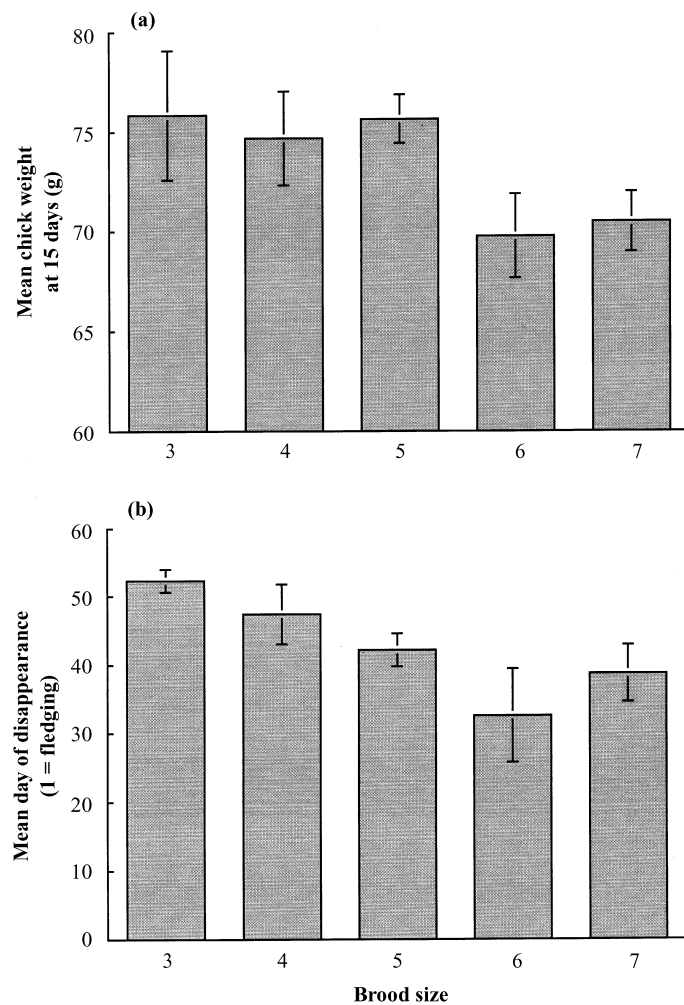
**Fig. 6.** The effect of experimental brood size on (a) the mean ($\pm$ SE) chick mass at day 15; and (b) the mean ($\pm$ SE) day of disappearance of fledglings from the colony.

the reproductive value of the brood. On a visit-by-visit basis, Kacelnik & Cuthill (1990) confirmed that an increase in brood size in starlings caused an increase in the proportion of food allocated to the chicks by adults using artificial feeders. Similar adaptive shifts in parental allocation are suggested by data showing substantial mass loss in parents that were feeding larger brood sizes (e.g. Hussell 1972; Askenmo 1977; Martins & Wright 1993). However, in the present study there was no evidence for differential mass loss by parents feeding larger broods. Even though most parents did lose body mass between successive captures for DLW analyses, this was early in the nestling period and matches earlier results of brood size manipulations on parental body mass in starlings by Ricklefs & Hussell (1984). Therefore, these adult mass reductions may well have represented adaptive seasonal changes in mass between incubation and chick feeding (Freed 1981; Norberg 1981) rather than the detrimental result of excessive energetic effort.

There was little evidence that parents feeding larger broods did so by expending greater amount of energy, suggesting that the extra foraging effort required was no more expensive than the alternative activities that parents with smaller broods were performing. Previous studies have shown positive effects of parental effort on daily energy expenditure (Bryant 1988; Tatner & Bryant 1988; Tinbergen & Dietz 1994; Deerenberg, Pen, Dijkstra, Arkies, Visser & Daan 1995). However, data from the present study, along with mixed results from more recent DLW estimates of parental expenditure (e.g. Moreno, Cowie, Sanz & Williams 1995; Verhulst & Tinbergen 1997), suggest that this relationship may not be a straightforward as previously expected. Parent birds may have a previously unforeseen capacity to avoid energetic costs of reproduction through subtle adjustments in their behavioural and physiological allocation of energetic effort. Indeed, such flexibility in parental responses may explain the lack of empirical evidence of long-term survival or future fecundity costs following brood size manipulations in some studies (for recent

reviews see, Lindén & Møller 1989; Dijkstra, Bult, Bijlsma, Daan, Meijer & Zijlstra 1990; Lessells 1991; but see also Deerenberg *et al.* 1995).

PARENTAL FORAGING AND PREY TYPES COLLECTED

Calculated flight speeds were unaffected by provisioning effort of parents (see also McLaughlin & Montgomerie 1990), confirming theoretical models that suggest parent starlings behave so as to maximize net energy delivery rather than simply rate of gain (Kacelnik 1984). Alternatively, increased parental visit rate to larger broods may have been possible through reductions in amount of time spent in the nestbox or time spent around the breeding colony. However, increases in load sizes delivered to larger broods tend to suggest changes in parental foraging strategies. The Lifjeld (1989) model suggesting a switch from net to gross energy maximization could explain the result here for increased load sizes being delivered to larger broods. However, such gross energy maximization requires that parents feeding larger broods had greater energy costs, which do not appear in our data. From the parental body mass data, it seems unlikely that there was a reduction in parental self-feeding per trip and re-allocation of prey to the chicks (Kacelnik & Cuthill 1990). So, parents must have been able to increase load size by some other mechanism.

The types of habitats and foraging locations used and the foraging distances from the nestbox colony showed no effect of experimental brood size, suggesting that parents did not achieve a greater load mass by changing where they fed. The return times to the nest, which included patch residence times (i.e. search time, self-feeding time plus prey loading time) and travel times back to the nest also showed no brood size effects. So, the heavier loads delivered by parents feeding larger broods did not appear to take birds longer to find, load in their beaks or carry back to the nest; although we cannot exclude the possibility that some trade-off was made between these variables. It therefore seems that parents feeding larger broods simply performed a greater number of trips whilst foraging in approximately the same places for the same lengths of time per trip. As predicted by Lifjeld (1989), this suggests that these parents took more food per unit patch residence time, and had loading curves that were above and/or steeper than parents feeding smaller broods.

These differences in foraging and hence the load sizes delivered by parents with the larger experimental broods may be explained by the change in the type of prey delivered. Parents feeding larger broods delivered a lower proportion of the larval prey types (mostly Tipulid larvae), whilst delivering more earthworms and pig pellets. Similar switches in prey types away from larval prey have been associated with increased parental provisioning rate in previous studies on starlings at this study site (Wright & Cuthill 1989, 1990a). The alternative prey type chosen in these previous studies was small invertebrates and not the earthworms, reflecting the temporal availability of different prey types in the environment. Similarly, Tinbergen (1981) showed that at a site in the Netherlands a female European starling provisioning at artificially increased rates switched from caterpillars (the preferred prey type in that study site) and towards Tipulid larvae.

Therefore, at first glance, it appears possible that the changes in prey types delivered to larger broods were the result of the types of mechanisms modelled by Lifjeld (1989). However, despite their presumably higher rate of gross gain, earthworms did represent a lower nutritional value per gram ingested by the chicks – a trade-off in parental foraging which is not part of the Lifjeld model. Therefore, a switch in diet of the kind shown here may be more likely to allow prey types of inferior nutritional quality, but of greater availability, to be concentrated upon in order to provide for the immediate needs of a hungry brood. This has been observed for other species, such as chicks of glaucous-winged gulls (*Larus glaucescens*) in larger than normal broods, which received a greater proportion of garbage in their diets (Ward 1973). This trade-off between the quality and quantity of food delivered to the nest provides the best explanation for the changes in prey type in the present study.

The changes in prey types may reflect an adaptive reduction in parental discrimination of prey types in order to save valuable foraging time (Houston & McNamara 1985a, 1985b) or handling time (Houston 1985). If this were the case, with less discriminate foraging by parents feeding larger brood sizes, we might predict that the change in diet recorded here simply reflects a move towards representing general prey availabilities in the environment. Increases in diet width have been reported for widowed parents (Sasvari 1986) and handicapped parents (Lifjeld & Slagsvold 1988), presumably reflecting selective prey choice by normal pairs of birds feeding on a potentially wide array of prey types available in the environment (see Lifjeld 1989). Instead, what we see in the present study is a change in the proportions of one prey type in favour of another. Taking greater proportions of smaller prey types would allow a finer adjustments of load sizes, which could result in savings in travel costs (see Cuthill & Kacelnik 1990). Shifts to smaller prey types (e.g. Lifjeld 1988), or even reductions in load size (e.g. Royama 1966) may indicate the possible importance of changing flight costs by adjusting the prey types loaded. However, such trends are the opposite of those reported here, and a switch to larger heavier earthworms which increased load sizes seems unlikely to have assisted the birds in achieving optimal load size for the purpose of reducing travel costs.

CHICK NUTRITION, BODY MASS AND
FLEDGLING SURVIVAL

Despite similar levels of food delivery per chick per hour across experimental brood sizes, the chicks in larger broods showed a lower individual mass prior to fledging. Variations in chick diets, resulting from the changes in the proportions of different prey types delivered, represent the only difference in the nutrition of chicks in the different experimental broods. It is not entirely clear which of the nutritional components measured here is important in chick growth and development. However, as a result of differential proportions of earthworms delivered, there were notable differences in the proportion of indigestible material that chicks in different broods sizes received. This may explain the fact that chicks in larger broods attained fledging masses below those of chicks in smaller broods, despite being fed similar amounts of prey biomass per hour. Surprisingly, differences in diet were reflected only in the mass of chicks and not in their tarsus lengths, possibly confirming that any brood size effects operated through the amount of digestible material delivered per chick, rather than a limitation in any one particular nutritional component of chick diets.

Lower chick mass in larger broods could also have been the result of chicks in larger broods experiencing greater sibling competition in the nest. When more chicks compete within a brood, there may be greater individual costs to acquiring food. This is because of the greater energetic effort spent pushing and struggling against more nestmates for the position closest to the nest entrance, where the parent arrives and chicks are most likely to get fed (Kacelnik, Cotton, Stirling & Wright 1995; Cotton, Kacelnik & Wright 1996). It may be difficult to gather empirical evidence for such escalating costs of begging in larger broods in the field, and we cannot exclude this as a possible explanation of the patterns in chicks mass.

Lower body mass of nestlings in larger broods would be expected to result in lower fledging mass, and eventually in lower survival chances (Perrins 1965; Gustafsson & Sutherland 1988; Tinbergen & Boerlijst 1990). This might have been especially true in the present study, since fledglings from larger broods were relatively light for their body size (see Magrath 1991). There was a clear effect of chick mass at day 15 on the date at which fledglings were last seen around the farm and breeding colony (see also Krementz, Nichols & Hines 1989), therefore showing a negative effect of the experimental brood size treatment on fledging fitness. We assume that last date seen reflects differences in fledgling survival, rather than variation in timing of natal dispersal dates. As in previous years, it was only later on in the summer that there was any mass exodus of fledglings dispersing from the study site. Presumably, this is because of the exceedingly good foraging conditions for young starlings around the nestbox

colony. The farm buildings provided starling flocks with safe day-time 'loafing' areas, although predation of starlings by domestic cats, corvids (mostly *Corvus corone corone*), and especially sparrowhawks (*Accipter nisus*) is not uncommon at this site. The greatest source of ringing recoveries at this site has always been through the mortality of young birds in their first year within a few kilometres of the breeding colony. So, predation in the first months may represent the most dangerous aspect of postfledgling survival, especially during dispersal. However, we do not have any useful data concerning the success of young birds from different experimental brood sizes once they dispersed from the breeding colony.

## Conclusions

The experimental manipulation of brood sizes revealed a flexibility in parental foraging strategies involving adjustments in rates of food delivery in response to changes in brood demand. Parents appeared to be able to avoid any direct measureable cost of feeding enlarged broods, mostly through passing any detrimental effects onto the chicks in terms of reduced fledgling survival. By being able to increase provisioning rates, and adjusting prey types in order to sustain those higher feeding rates, parent starlings may be able to cope with unpredictable variations in conditions during chick feeding. Factors such as changes in prey availability due to adverse weather conditions, or even the desertion or death of a mate, may require such behavioural flexibility. The trade-off between prey quality and quantity shown here represents an adaptive strategy for parents to produce viable young despite a temporary shortfall in the amount of prey that can be collected using the optimal foraging strategy for maximizing net energetic returns to the young in the nest. Clearly, such adjustments in parental provisioning behaviour would be ineffective in the long term, and are therefore avoided on the whole by birds rearing normal and reduced brood sizes.

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