EFFECTS OF NESTLING DIET QUALITY ON THE GROWTH AND ADULT SIZE OF PASSERINE BIRDS

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Thesis submitted for the degree of
Doctor of Philosophy.

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November, 1990.

For Mum and Dad,
for their x and y,
and their love and support.

The fruit of their loins is but a vegetable in disguise

'I knew then that the years would come and go
and the book would live.
It has taken more years than I ever could have imagined
and more battles than I ever felt I'd have to fight
but the fist I shook
and the rage I spent
has at last blossomed
and before it should fade
I'd like to say that I am glad'

J. P. Donleavy

ACKNOWLEDGEMENTS

The three years I have spent in Stirling have been the happiest of my life so far, apart from the early days as a blastula, and I would dearly like to thank all the people who were so helpful and so friendly to me. I wish them all the best of luck in the future.

Many friends provided a supportive, humorous and relaxed atmosphere in the office. Sorry for eating all your food. It is easier to be sincere on paper. Steve Newton gave me experience of continental driving, 90mph on the right-hand side of the road. I felt younger when we got back. Anne Hudson taught me that I should hope the ambulance arrives first if I am run-over. Helen Riley Ltd. provided single fares to Glendevon and also lent me a sunglass lens to replace my wok. Maimie Thompson and I lived together. We lit a flame that will burn forev... it went out. Thank you for your selfless generosity. Margaret Still took me to market, but couldn't get her reserve price. Mark Feltham, Ian Morgan, Scott Mathieson, Chris Wimham, Lulu Stader, Maria Alves, Sally Ward and Ian Johnstone also provided friendship and assistance, as latterly did John Robinson, Marcelo, Dora, Marcos and Audrey. To all those who inflated my already colossal ego on the squash court, badminton court and tennis court, I wasn't really trying. Khiayre and June provided gossip about all the staff and students. Mike Bell looked after my personal safety. Sandy Milner used his less-than-psychic powers ('I bet Hearts lose') to deprive me of my livelihood. Tony Berry was a constant source of amusement and interest.

Thanks to all the technical staff for their assistance, particularly Sandy Gardiner my laboratory pardner, who was a good friend throughout. Jim Weir analysed my hydrogens and put up with my hot air. Andrew Liddle solved a riddle. Sylvia Peters mended the meters. Lewis took all the photos with care and attention, but then we were raided by the vice squad. Lex was not lax. Jimmy Wright was always prompt with my demonstrating money and my very petty cash claims. Campbell and his meatballs were always helpful, particularly with the nestboxes. The animal house, whose reaction when I first went down with Dave was 'we haven't got a cage big enough', looked after the zebra finches. Jerry 'the

pen' and his fellow storesmen bought my messages. I didn't buy John 'the stores' his. The library staff were considerate, and interested in the human fly prostrate against their first floor window. They prevented me being prostrate against the ground below. The porters didn't wave their job descriptions at me when I made a request, but what use is a blank piece of paper anyway. John Broom of the Microprocessor Group supervised the construction of the infrared sensor which resulted in his purchase of a toupé. It worked despite my gobbets of solder, but it took two of us to lift the PCB. Thanks also to Gordon Brewster. SURRC at East Kilbride provided facilities for the doubly-labelled water analysis.

Rob and Gillian gave me permission to hold the fair hand of their fair daughter Tamara, who accompanied me to innumerable weddings and tolerated my unusual working hours, she didn't know when that hour would be. Burt bought me tickets for the Hearts, who were usually so awful that I could face going back to work ('ken Willie Bauld').

NERC provided funding through Studentship GT4/87/TLS/55. It is nice to know they think of you as a person rather than a number. Professor J.R. Sargent provided the facilities of DMBS, to someone he thought was called Scott.

My special thanks go to my supervisor, Professor David Murray Bryant, whose fund of ideas, constructive criticism, consideration and companionship guided me through the project. I could not have had a better supervisor. Congratulations on your chair and good luck in the future.

Thanks to all again,

Ross.

Ross

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ABSTRACT

The effect of nestling diet quality (limiting nutrient kj^{-1}) and quantity on the growth and adult phenotype of passerines was investigated in this study.

An increase in nestling diet quality resulted in faster growth and larger adult size of the zebra finch *Taeniopygia guttata*. The ultrasound technique revealed differences in *pectoralis* thickness between groups. Male zebra finch plumage may be affected by diet quality. Diet quality effects are likely to occur in wild zebra finch populations.

A decrease in diet quality resulted in slower growth, and smaller nestling size at fledging, of house martins *Delichon urbica*. Mechanisms for this effect in wild populations are discussed. Estimates of Field Metabolic Rate using the doubly-labelled water technique were the highest yet published. Possible explanations are discussed.

Brood manipulation affected great tit *Parus major* nestling growth, reduced broods grew faster than enlarged broods. Supplementary feeding did not alter diet quality but did increase food availability and result in faster growth of Supplemented broods. Breast strip size was affected by food availability, but this effect may not have been independent of body size. These effects are likely to occur in wild populations, and their implications are discussed. The pattern of female mass loss supported the hypothesis that feeding frequency is adjusted to maximise the difference between reproductive costs and benefits.

Variation in diet quality may affect individual life-histories through effects on growth rate, differential growth, growth curve shape, fledging size, adult size, fledging plumage and adult plumage. The results of the study support a key assumption of the brood reduction hypothesis. Implications of the results for evolutionary and ecological studies are discussed. It is suggested that parents may maximise the quality of nestlings through maximising the quality of their nutrition, and that the quality of nestlings is a more important component of fitness than has been considered previously.

1 INTRODUCTION

1.1 THE GENETIC AND ENVIRONMENTAL CONTRIBUTIONS TO BODY SIZE VARIATION

In most classical studies of wild birds, body-size variation is assumed to be largely genetically controlled. A common explanation for geographic morphological variation in the great tit *Parus major* (Snow 1954; Hamilton 1961), red-winged blackbird *Agelaius phoeniceus* (Power 1969), house sparrow *Passer domesticus* (Johnston & Selander 1971) and other species (James 1970) is that natural selection on polygenic traits leads to structural adaptations to local conditions (Endler 1977). For example, Bergmann's rule (Kendeigh 1972) proposes that individuals of a species are larger the further north the population lies, because of selection for the greater thermodynamic efficiency of larger size (Murphy, E.C. 1985; Paterson 1990; but see Geist 1987, 1990; Blaxter 1989; McGillivray 1989). This explanation assumes that the variation in body size has a genetic component but there has been little research into the possibility that clinal variation of this type is, at least in part, the result of environmental effects on body size.

James (1983) investigated this possibility for the red-winged blackbird. A stable cline of body size variation exists in the breeding population of the red-winged blackbird, despite massive winter movements, with larger birds being found in the north (Mosimann & James 1979). James (1983) transplanted eggs between populations and measured the growth of nestlings. Nestling morphology shifted in the direction of the foster parents, indicating that clinal variation in red-winged blackbird body size is influenced by environmental effects on growth. This effect was also demonstrated in a later transplant study on the red-winged blackbird (James & Nesmith 1986), but was not detected in an analagous transplant experiment on the coal tit *Parus ater* (Alatalo & Gustafsson 1988).

James (1983) offered three possible explanations for the clinal variation in red-winged blackbird body size. Firstly, if natural selection is maintaining the clinal variation then regional genetic variation must covary positively with

the environmental variation. Secondly, genetic differences between populations may be independent of the environmentally-induced differences, but the latter are associated with reproductive rate. For example, if genetic differences in morphology covary with environmentally-induced variation in clutch size, then the variation in clutch size may drive directional gene flow between localities. A third possible explanation is that the clinal variation is not adaptive in any sense. Whatever the correct explanation for the clinal variation, it is apparent from this experiment that environmental factors may have a role in geographical variation in body size, but their importance relative to genetic factors is unknown and this subject requires further research (Rising 1989), such as that on the wood frog *Rana climitans* (Berven & Gill 1983). If environmental factors are important then there are important taxonomic implications because morphological differences between populations, previously used for classification, may not reflect actual genetic differences (Gill 1987; Karl *et al.* 1987; Corbin & Wilkie 1988; Hackett & Rosenburg 1990). In future, genetic analyses should be used in preference to morphometric analyses, where possible, for speciation studies (Ahlquist *et al.* 1987).

Environmental factors have also been proposed to explain intraspecific body size variation between localities (Boag & Grant 1978; Ricklefs & Peters 1979; James 1983; Conant 1988), years (Lloyd 1979; Summers & Drent 1979; Boag 1983), seasons (Lloyd 1979) and weather conditions (Lack & Lack 1951; Dunn 1975); but the mechanisms by which the environment may influence body size have received little attention. One possible means is by influencing the nutrition of nestlings, thereby affecting growth and adult size. The aspect of nutrition most often studied is food availability.

1.1.1 *Food availability*

Two methodologies have been used to investigate the effect of food availability (i.e. the quantity of food fed to nestlings) on nestling growth. Some studies have provided supplementary food to parents in an experimental group and compared growth in this group with the growth of nestlings in a control group. Crossner (1977) demonstrated an increase in the growth of starling *Sturnus vulgaris* nestlings in the supplemented group. Similar results have been obtained with supplementary food in experiments on the crested tit *Parus*

cristatus (von Bromssen & Jansson 1980) and the song sparrow *Melospiza melodia* (Smith & Arcese 1986).

Other studies have measured natural food availability and correlated variations in food availability with variation in nestling growth. Positive correlations between food availability and nestling growth have been found for the great tit (van Balen 1973), house martin *Delichon urbica* (Bryant 1975a, 1978a), tree swallow *Tachycineta bicolor* (Quinney *et al.* 1986; Wiggins 1990b) and western kingbird *Tyrannus verticalis* (Blancher & Robertson 1987); but not in all experiments (e.g. Powell 1984).

These two methodologies have both produced results which indicate that nestling growth in some species is affected by the quantity of food supplied. Circumstantial evidence for this relationship is gained from studies of the effect of brood size on growth (Harris 1970; Crossner 1977) with larger brood size resulting in slower growth, presumably because less food is fed to each nestling in larger broods (Nur 1984a; Smith *et al.* 1988). Studies of the effect of breeding density on nestling growth have shown that higher density also results in slower nestling growth (Arcese & Smith 1988). This is likely to be the result of lower effective food availability for each individual (Minot & Perrins 1986). It seems, then, that environmental conditions are able to affect growth and body-size variation through an effect on the quantity of food supplied to nestlings. There is, however, another factor that may affect nestling nutrition and growth. Nestling diet quality may affect nestling growth because of the potential limiting effect on growth of a lack of specific nutrients in a nestling diet, but this aspect has received little attention.

1.1.2 *Nestling diet quality*

Poultry scientists have investigated the effect of diet quality in an attempt to identify the most economical means of maximising chick growth. Diet quality, limiting factor kj^{-1}, is usually defined in terms of protein content because protein is an essential requirement for growth and is easily assayed (Maynard & Loosli 1966; Robbins 1983). Their research has generally demonstrated that a high protein content increases growth rates of mallard *Anas platyrhyncos* (Street 1978), Japanese quail *Coturnix japonica* (Morse & Vohra 1971) and chickens

Gallus gallus (Woodward *et al.* 1977).

There have been very few studies of the effect of nestling diet quality on the growth of wild birds even though there is circumstantial evidence for the importance of nestling diet quality to growth. Frugivorous birds, for example, survive as adults on a diet almost entirely of fruit but feed their nestlings almost exclusively on insects (Morton 1973), presumably because fruits have a lower limiting factor content (eg protein) (Izhaki & Safriel 1989) and if fed to nestlings they will result in a slow growth rate (Berthold 1976, 1977). Protein content is also known to be important in the maintenance of body condition in adult birds (Martin 1968; Blem 1990).

There have been very few experimental investigations of the effect of nestling diet quality. A transplant of eggs between the black-browed albatross *Diomeda melanophris* and the grey-headed albatross *D. chrysostoma* (Prince & Ricketts 1981) showed faster nestling growth in transplanted grey-headed albatross chicks and slower growth in transplanted black-browed albatross chicks. Prince & Ricketts (1981) concluded that these differences in growth were caused by the difference in diet quality between the two species, with the squid diet of the grey-headed albatross being of lower quality than the krill and fish diet of the black-browed albatross. Krebs & Avery (1984) demonstrated that bee-eater *Merops apiaster* nestlings grew better on a mixed diet of insects than on a single taxon diet, and they concluded that a mixed diet provided more of the nutrients necessary for nestling growth; but this study investigated growth over a period of only two or three days. Westerterp *et al.* (1982) showed that nestling starlings *Sturnus vulgaris* grew more slowly when fed tipulid larvae with a higher water content, though this effect was thought to be due to unusually fluid faeces soiling the nest and reducing thermodynamic efficiency of nestlings.

There is only preliminary evidence, so far, for an effect of diet quality on nestling growth and there is clearly a need for further experimental studies to determine if variation in the quantity and quality of nestling diet are potential mechanisms by which environmental variation may influence intraspecific body size variation.

There is also a need to determine if environmental variation can influence

phenotypic characters other than body size, which has been the phenotypic character used in most studies of the effects of environmental variation.

Variation in adult plumage can influence the life-history of individuals in a species through variation in the size of plumage characters such as tail length (Andersson 1982), variation in the size of plumage badges (Møller 1987) or variation in the colour of plumage features (Hill, G.E. 1988), yet the environmental contribution to this variation is not known. Variation in adult body shape (Allen's rule, Fleischer & Johnston 1982) and adult bill shape (Schluter & Grant 1984) can also influence the life-histories of individuals. Experimental studies are needed to investigate the effect of variation in nestling diet quality, and quantity, on these characters of the adult phenotype.

The aim of this project was to fill these gaps in our knowledge of avian morphological variation through experimental studies of the effect of nestling diet quality (limiting factor kJ^{-1}) and quantity on both nestling growth and the adult phenotype. It was hoped that this aim could be achieved using recent technical advances where possible, such as the use of ultrasound to measure condition (Baldassare *et al.* 1990), and also that the manipulation of diet necessary for this study would enable the investigation of other aspects of avian life-histories, such as brood reduction (Lack 1954) and parental breeding effort (Nur 1984a).

2 EFFECTS OF AN INCREASE IN NESTLING DIET QUALITY ON A LABORATORY PASSERINE

2.1 INTRODUCTION

It is difficult to measure effects on adult size in wild populations of birds because mortality and dispersal occur between fledging and the attainment of adult size. There is the additional problem of catching unbiased samples of adult birds in the wild. It is possible that some birds will evade capture even if resident in the study area. For these reasons a study of the effect of nestling diet quality on adult size is most easily performed on a captive population where there is no predation and no dispersal. Captive populations also permit more rigorous control of nestling diet because the resources available to birds can be regulated. The aim of this chapter was to investigate the effect of nestling diet quality on the growth and adult size of a laboratory passerine.

No such study was present in the literature at the time of the project proposal, however, in the intervening period between the proposal and project, Boag (1987a) published a detailed study on the effect of diet quality on the growth and adult size of zebra finches *Taeniopygia guttata* (Clayton & Birkhead 1989). Zebra finch nestlings fed on a high quality diet grew faster and reached a larger adult size than nestlings fed on a low quality diet. The novelty of such work in the literature merited a repeat of Boag's study, both for the important scientific purpose of replication (Loehle 1987) and for the extension of the original experiment so that additional questions could be investigated.

2.1.1 *Nestling diet*

Boag (1987a) used a multicomponent, qualitative diet to vary the diet quality between each of the experimental treatments. Seed, greens, nestling mix and minced egg were supplied to the birds. These components of the diet may have been fed disproportionately to the nestlings by the parent birds, making it impossible to ascertain the actual composition of the nestling diet. If the composition of the nestling diet is unknown it is impossible to attribute the observed difference in growth and size between treatments to a difference in a

specific nutrient between treatments (Boag 1987a). If the zebra finches are supplied only with a semi-synthetic diet of uniform composition (Murphy & King 1982) then the composition of the diet fed to the nestlings by the parents will be known. Thus, by providing treatments with two semi-synthetic diets differing only in their protein contents it will be possible to attribute differences between treatments directly to the differences in protein content of the nestling diet. It was intended that semi-synthetic diets would be used in this study.

2.1.2 *Body condition*

Boag (1987a) demonstrated a significant effect of nestling diet quality on adult body mass in the zebra finch. The nestlings fed on a high quality nestling diet were significantly heavier as adults than the nestlings fed on a low quality nestling diet. This difference in body mass could have been due to either a difference in structural size or a difference in body condition (lipid content or protein content), or a combination of both these factors. Boag (1987a) did not measure body condition so he was unable to distinguish between the effect of structural size and the effect of body condition upon adult body mass. It is important, therefore, to measure body condition and gauge its effect on observed differences in adult body mass.

Nestlings from the experimental treatments were to be kept in mixed holding cages after fledging (Section 2.2.1) until adult size was reached. It was possible that dominance hierarchies might have developed in these cages because of competition for resources such as food, water and perching sites. One way to assess the dominance status of an individual is to compare its condition with other individuals in the cage. Better condition would indicate better nutrition, and therefore a more dominant bird. Relative dominance status of birds from the different experimental treatments was inferred in this way.

The major stores for proteins in birds are the pectoralis muscles used in flight (Ward 1969; Jones & Ward 1976). These muscles contain between 30% and 60% of the protein in the body (Kendall *et al.* 1973; Peters 1983) and their thickness varies according to the nutritional status of the bird (Kendall *et al.* 1973; Jones & Ward 1976; Owen & Cook 1977; Węglarczyk 1981; Marsh 1984; Zazula 1984; Bailey 1985; Jones 1986; Krementz & Ankney 1986).

Consequently a measure of the thickness of the pectoralis muscles can be used as an index of body condition. This was the measure of body condition used in this study.

2.1.3 *Plumage*

Intraspecific variation in plumage has been shown to be an important influence on the life history of some species of passerine birds, particularly in terms of dominance (Järvi & Bakken 1984; Watt *et al.* 1984; Richison 1985; Rohwer 1985; Newton 1989; Jones 1990; but see Jackson *et al.* 1988), individual recognition (Rohwer 1975; review in Whitfield 1987) and sexual attraction (Reskaft & Järvi 1983; Møller 1988, 1989d; Hoglund *et al.* 1990). A dietary influence upon plumage, in terms of pigment content, has been identified in poultry (Grav *et al*. 1989) and wild birds (Slagsvold & Lifjeld 1985; Spellman *et al.* 1987; Hudson & Brush 1989). It is possible, therefore, that nestling diet quality may influence the phenotype of an adult bird through an effect on the plumage of that adult bird. If this is the case, then the effect on plumage colouration may have important consequences for the life history of that bird.

Zebra finches have distinctive bill (Burley & Coopersmith 1987) and plumage characteristics (Burley & Bartels 1990) that may be important for individual recognition . Male birds have chestnut ear coverts, a finely barred throat and chestnut flanks with white dots; all of which are absent in the female (Plate 2.1). Variation in male plumage may result in assortative mating (Immelman *et al.* 1978). These conspicuous male features provide a means of measuring the effect of nestling diet on the plumage of zebra finches, and thus provide an additional measure of the influence of nestling diet quality on the phenotype of the adult bird.

2.2 METHODS

Two replicates of the following experiment were performed during the study, one from November 1988 to November 1989 and the other from January 1989 to January 1990. The methods for each replicate were identical.

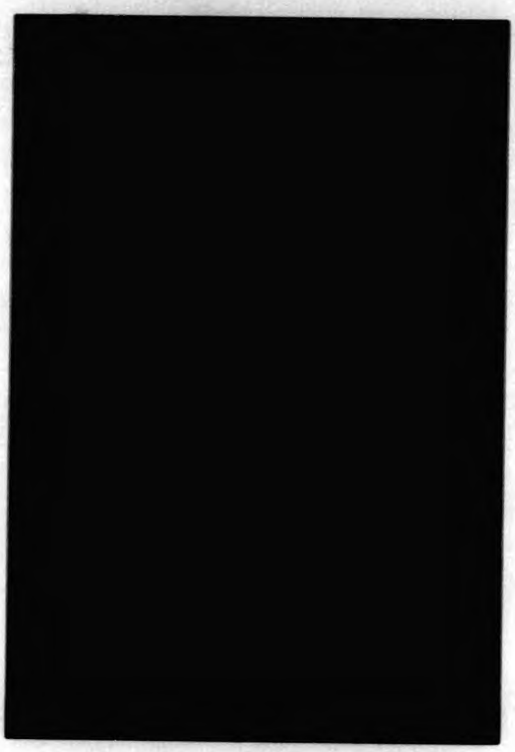

Plate 2.1 Adult zebra finch plumage

2.2.1 *Population*

The laboratory population used in this experiment was the colony of zebra finches at the University of Stirling. The zebra finch is a member of the Estrildidae, native to Australasia (Rogers 1977). It is granivorous with some opportunistic insectivory, especially during breeding (Rogers 1977). It was first used as a cage bird in Europe in the 1850's and it has since established itself as the most easily bred of all the domestic species of cage and aviary birds (Rogers 1977), thus it is ideal for nestling growth studies. The nest is built of straw and contains 3-8 eggs which are incubated for 11 -12 days. The nestlings are fed by both parents for a week after fledging (fledging date is at Day 16-18). Then the male takes responsibility for feeding the young until they are independent (approximately Day 40) while the female lays another clutch (Rogers 1977).

The University of Stirling colony is an outbred mainly wild-type colony kept in cages (150:30:30 cm) with 4-8 birds in a cage. During the experiment the room was kept at 25-30^{o}C with an LD cycle of 12:12. Seed with a vitamin supplement was supplied *ad libitum*. Water and cuttlebone were also provided.

Males and females were each given a code number and assorted into pairs using a random number generating facility on the BBC Microcomputer . The two birds were drawn from separate cages because individuals from the same holding cage often fought each other if paired (Feltham *pers. comm.*). Each pair was assigned to a treatment by means of random numbers, placed in a separate cage and then provided with a wickerwork nestcup and straw to encourage breeding. Pairs were also provided with Haith's Egg Biscuit food to enable them to attain breeding condition. Ten pairs were set up for each replicate. Birds that fought were returned to holding cages and replaced. Clutches were completed within four weeks of each other in both replicates. Fledglings were randomly assorted into holding cages at Day 40. Each holding cage contained 4-6 birds.

2.2.2 *Nestling diet quality*

2.2.2.1 *Semi-synthetic diet*

Two semi-synthetic diets were assembled using the recipe recommended by Murphy & King (1982). These diets differed only in their protein and amino-acid content with the metabolisable energy value kept constant. The diet was pelleted to make it more palatable (Morton & Davies 1983; Murphy & King 1986). The pelleted diet was ignored repeatedly by the finches for over a day in the absence of alternative food, therefore, techniques similar to those stated in Boag's paper (1987a) were used to alter nestling diet quality.

2.2.2.2 *Altering diet quality*

Two treatments were used in the experiment, one of high nestling diet quality (HIGH) and a control (CON) where nestling diet consisted of seed, the natural nestling diet in wild populations (Morton & Davies 1983; Zann & Straw 1984). The dietary regime of the two treatments is summarised in Table 2.1. The Haiths Biscuit egg food (composition in Table 2.2) was presented to the finches in small petri dishes after it had been soaked in warm water and the excess fluid drained off.

2.2.3 *Growth*

2.2.3.1 *Growth measurements*

Eight parameters of body size were measured during the experiment, as summarised below.

Body Mass (MASS) (g, 1 decimal place (dp)) - whole body mass, using a Mettler TP35 balance until Day 18, a Pesola 100g spring balance thereafter.

Wing Length (WING) (mm)- the length of the maximum wing chord, using a stopped rule (150mm).

Tarsus Length (TARS) (mm, 2 dp)- the distance from beneath the elbow to the top of the tarsus, using dial callpers.

Head & Bill Length (HEAD) (mm, 2 dp)- the distance from the back of the head

Table 2.1 Experimental dietary regime (food per day per cage)

Stage of Breeding Cycle	HIGH	Control
Until First Egg	Egg food (1 petri dish) + seed (*ad libitum*)	Egg food (1 petri dish) + seed (*ad libitum*)
Until Date of Hatch (Day 0)	Egg food (1 petri dish) + seed (*ad libitum*)	Egg food (1 petri dish) + seed (*ad libitum*)
Until Day 40	Egg food (1 or 2 dishes) + seed (*ad libitum*)	Seed (*ad libitum*)
Until Day 400	Seed (*ad libitum*)	Seed (*ad libitum*)

Table 2.2 Contents of Haith's Egg Biscuit Food (dry mass, from manufacturers label).

Component	mass/kg		Component	mass/kg	
Carbohydate	788	g	Vitamin B1	1.95	mg
Protein	132	g	Vitamin B6	1.5	mg
Oil	36	g	Biotin	50	mg
Fibre	2	g	Vitamin B12	6	mg
Ash	32	g	Choline Chloride	288	mg
Vitamin A	10	k iu	Iron	50	mg
Vitamin D3	2.5	k iu	Manganese	35	mg
Vitamin E	12.5	mg	Copper	2.5	mg
Vitamin B2	8	mg	Zinc	25	mg
Vitamin K MSB	2	mg	Iodine	0.5	mg
Nicotinic Acid	13.8	mg	Magnesium	330	mg
Cal Panto	5.5	mg	Sodium Chloride	750	mg
Folic Acid	0.2	mg	Phosphorus	3.18	g
			Calcium	47.3	g

to the tip of the bill, using dial calipers.

Bill Depth at Nares* (BDN) (mm, 2 dp)- vertical bill depth taken at the nares using dial calipers.

Bill Length at Nares* (BLN) (mm, 2 dp)- from the anterior edge of the nares to the tip of the bill, using dial calipers.

Lower Bill Base Width* (LBW) (mm, 2 dp)- the maximum distance across the base of the lower bill,using dial calipers.

Keel Length (KEEL) (mm, 2 dp)- the length of rigid material from the tracheal pit to the posterior edge of the sternum, using dial calipers.

* - In the first replicate bill measurements to Day 28 were made by the use of dividers stretched to the length of the parameter and then laid on a ruler to measure length in millimetres.

Measurements were made daily from Day 0 to Day 14, every two days from Day 14 to Day 32 and then at Day 36, Day 40, Day 62, Day 150 and Day 400. Bill measurements commenced at Day 10 as the bill of young nestlings was too pliable to attain accurate measurements. This was also the reason why KEEL was not measured until Day 20. All measurements were made between 07.30 and 10.00 hours. 'Adult size' was assumed to be attained by Day 400. Fledging date was recorded in the second replicate as the earliest day upon which a nestling was seen outside the nest.

Parent birds were measured twice before hatching and once after fledging. All parameters were measured as described above. The mean value for each bird was used to test for differences in parental size between treatments.

2.2.3.2 *Growth curve analysis*

Modern growth studies have described growth in terms of fitted curves. These curves produce biologically meaningful coefficients that may reveal relationships not obvious from the raw data or simple measures of growth such as mass at fledging (Pruitt *et al.* 1979). The improvement in computers has meant that these curves can be fitted to data using non-linear regression packages that produce quicker, more accurate results (Herlugson 1983; Ricklefs 1983) than the graphical method of fitting curves pioneered by Ricklefs (1967).

There are four curves commonly used for avian growth analysis. These are :

Bertanffly $S(t) = A\ (1 - be^{-kt})^3$

Richards $S(t) = A\ (1 \pm e^{(b-kt)})^{-1/m}$

Gompertz $S(t) = A\ (\exp(-b(e^{-kt}))$

Logistic $S(t) = A\ (1 + be^{-kt})$

where S(t) is size at time t, *A* is asymptotic size, *b* is the constant of integration (unimportant biologically (Zach *et al.* 1984)), *k* is the growth constant and *m* is a value representing the shape of the curve.

The Richards curve was derived from the von Bertanffly equation (Richards 1953). It has been recommended for growth studies (Brisbin *et al.* 1987) because it is the only curve with a shape coefficient, *m*, and it is thought that *m* may be more sensitive to environmental and experimental differences than the more commonly used *A* and *k* (Pasternak & Shalev 1983; Brisbin *et al.* 1987). The Richards curve has, however, proved to be very sensitive to small errors in data collection (Zach *et al.* 1984; Zach 1988). The coefficients *k* and *m* are highly correlated in most fitted curves and thus cannot be analysed independently (Brisbin *et al.* 1987; Zach 1988). These coefficients can be made independent by use of a reparameterised Richards curve and a process error model (White & Brisbin 1980; Bradley *et al.* 1984; Brisbin *et al.* 1986a,b) but this model assumes that no error is present in data collection (Zach 1988). This is an invalid assumption in measurements of nestling size parameters. In this project a Richards curve fitted by non-linear regression (SAS) has been used only to test for differences in the shape of growth curve (*m*) between treatments in Section 2 where the most extensive data set is present, including the asymptote of the curve. The value of *k* from the Richards curve was not used to test for differences in growth rate between treatments because it is not independent of *m*.

The simpler three-coefficient Gompertz and Logistic curves are derived from the Richards curve by having a fixed value of *m* of 0 and 1 respectively (Zach *et al.* 1984). These curves are less sensitive to errors in data collection than the Richards curve but achieve comparative fits to growth data (Rogers *et al.* 1987; Zach *et al.* 1984; Zach 1988) as measured by the coefficient of

determination. The Gompertz and Logistic curves were used in all three sections of the project to obtain values of *k* for comparison between treatments. A Wilcoxon Matched-pairs test was used to compare the coefficients of determination of the two curves and then the curve with the best fit to the growth data for each body size parameter was used to obtain the value of *k*.

The growth curve parameters are not absolute values, they are estimates with an asymptotic standard error obtained by a 'bootstrapping' procedure (Lanyon 1986) within the SPSS$_x$ NLIN program. This variation of parameter estimate has been ignored in previous studies of growth curves (but see Herlugson 1983) which have treated the parameters as absolute values and analysed them by ANOVA (e.g. Boag 1987a; Languy & Wanstaenwegen 1989). The variation of the estimates can only be ignored, however, if it is assumed that the variance of the estimates is similar within and between groups in an ANOVA, as it will not then influence the detection of significant variation between groups (Yates 1982; Rowell & Waters 1986; Potvin *et al.* 1990). This assumption can be tested by means of an ANOVA of the standard errors of the estimates. If there are significant differences between groups then an ANOVA is invalid and a non-parametric test such as the Kruskal-Wallis test must be used in the analysis of the growth curve parameter.

The asymptotic coefficient *A* was not used for analysis because the data sets in Section 3 and Section 4 were too small to accurately predict asymptotic size. In Section 2 the coefficient was not required because a direct measure of asymptotic size was present.

2.2.3.3 *Adult shape analysis*

The shape of the adults in each treatment can be compared by means of Principal Component Analysis (Boag 1987a; Bookstein 1989). The first principal component is the vector in hyperspace which explains the maximum possible variation of the data, thus when the characters are body-size parameters the first principal component (PC1) will be highly correlated with size (Lemen 1987). The subsequent principal components are orthogonal to the PC1 'size' axis and they are isometric. The second principal component (PC2) is interpreted, therefore, as 'shape', and in a plot of PC1 against PC2 'shape' is the single dimension along the PC2 axis (Bookstein 1989). PC2 was used as the measure of body shape in this experiment.

PC1 was used to test for overall differences in body size between treatments. Comparisons of single size parameters may well be misleading (Freeman & Jackson 1990) and it has been suggested that comparisons of body size between groups should only be made using multivariate measures such as PC1 which are a more accurate representation of body size (Rising & Somers 1989, Freeman & Jackson 1990).

The principal component analysis in this experiment used all size parameters except MASS in the calculation of the principal components. MASS was excluded from the analysis because it varies with body condition in adults and is not, therefore, an accurate measure of body size.

2.2.4 *Body condition*

A non-destructive ultrasound technique was used to measure the pectoralis thickness of experimental birds at Day 150 and Day 400. The physical principles of this technique are described by Baldassare *et al.* (1980) and Sears (1988) in studies of fat content and breast muscle thickness respectively. The portable Krautkramer instrument (model number USK 7) powered by six rechargeable Ni-Cd cells (NCA 2-6) was used in this experiment. The transducer comprises a small cylindrical probe (Alpha 2 Aerotech, 10 MHz) with a diameter of 9mm and a height of 11mm. The birds were held in the left hand and the sound emitting face of the transducer applied with the right hand to the pectoralis muscles which were exposed by wetting the breast feathers with alcohol then brushing them to one side. The probe was applied at three standard locations on the right hand side of the pectoralis; at the anterior and posterior ends and in the middle (Figure 2.1a). The face of the probe was moistened with alcohol to achieve full contact. The instrument's span and zero were checked using a stepped perspex block.

Arbitrary units were measured off the grid overlying the cathode ray tube (CRT) display as the interval on the x-axis from the origin to the first reflection (Figure 2.1c). This distance represents the return travel time of a sound pulse between the probe and the muscle:sternum interface and is directly proportional to the intervening thickness of the tissue. The probe was applied at a constant pressure and at an angle such that reflections from the keel did not

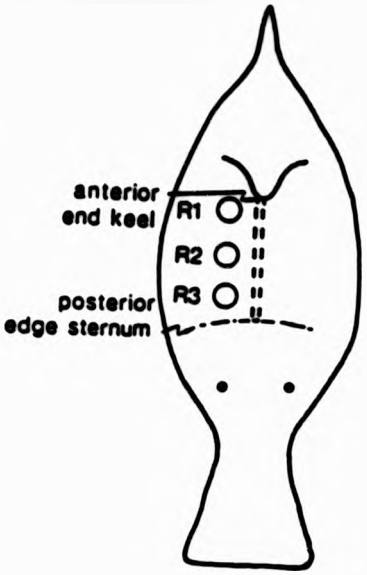

Figure 2.1a Positioning of probe for ultrasound measurements.

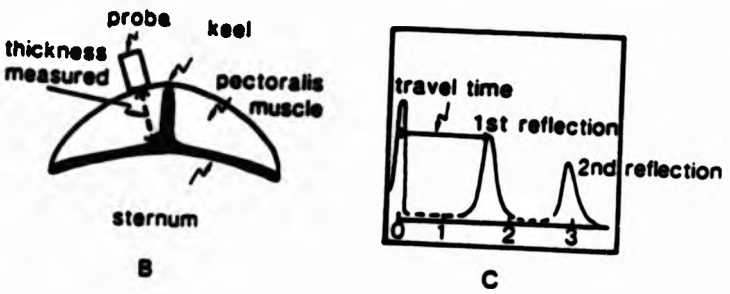

Figure 2.1b & c Cross-section of probe measurement, and monitor display.

interfere with the reading (Figure 2.1b). Several readings were taken at each location on the pectoralis until a consistent reading was achieved. Measurements were made at Day 150 and Day 400 and from the readings two indices of condition were calculated.
These were :
Mean Pectoralis Thickness (MPT) = (U1+U2+U3)/3

Corrected Pectoralis Thickness (CPT) = ((U1+U2+U3)/3)/KEEL

KEEL was used to correct pectoralis thickness for body size because it was the most highly correlated size parameter to MPT at both Day 150 ($n=31$, $r= .386$, $p < 0.05$) and Day 400 ($n=29$, $r=.465$, $p < 0.01$). MPT and CPT values were used to test for differences in condition between the HIGH treatment and the control.

2.2.5 *Male plumage*

Two of the most conspicuous and defined features of the plumage of the male zebra finch are the chestnut ear patch and the chestnut flank. These were the features measured during the experiment. Measurements were made with the birds held in a standard grip in the left hand. Their plumage was smoothed in an anterior-posterior plane. The measurements (Figure 2.2) were:

Ear Patch Width (PATWD) (mm, 1dp) - maximum width of patch along plane of bill, using dial calipers.
Ear Patch Height (PATHT) (mm, 1dp) - maximum vertical height of patch along plane orthogonal to PATWD, using dial calipers.
Ear Patch Area (PATCH) (mm^2, 1dp) - PATWD x PATHT.

Flank Length (FLKLE) (mm, 1dp) - maximum anterior-posterior length of flank, using dial calipers.
Flank Width (FLKWD) (mm, 1dp) - maximum width of flank in plane orthogonal to FLKLE, using dial calipers.
Flank Area (FLANK) (mm^2, 1dp) - FLKLE x FLKWD

An index of the total area of both the cheek patch and the flank was obtained by multiplying the length by the depth. These 'areas' were analysed

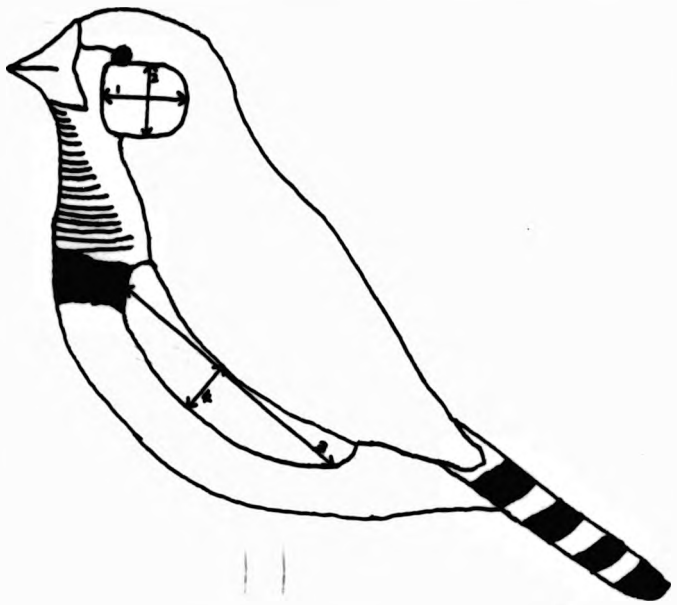

Figure 2.2 **Male plumage measurements at Day 150 and Day 400:**
1 = Ear Patch Width
2 = Ear Patch Height
3 = Flank Length
4 = Flank Width

along with the individual measurements to test for differences between the HIGH and CON treatments.

2.2.6 *Statistical Analysis*

Analysis of variance was used in this project for comparison of HIGH and LOW treatments in this Section, and also for comparison of treatments in Sections 3 and 4 of this project. Data from all nestlings in a treatment were assumed to be independent for these analyses. This assumption may not be valid because there may be a 'nest effect', associated with parental quality and the nestling environment, which invalidates clumping of nests, as detected by Ricklefs & Peters (1981) for the starling *Sturnus vulgaris*. For the purposes of this project, however, which involved intensive treatment of nests, and where the sample size of broods was therefore necessarily small, it would be preferable to treat nestling data as independent and thereby make analyses more powerful in their detection of a treatment effect, provided the assumption of statistical independence is not seriously violated. Such assumptions may be necessary where there is a conflict between statistical and biological requirements (Petranka 1990; Toft 1990), although they must always be explicitly stated.

There are, however, factors which may diminish the importance of the 'nest effect' in this project and make the above assumption tenable. For example, in the zebra finch experiment, birds were paired at random and the absence of assortative mating may have ameliorated differences in parental quality between nests. In all sections of the project, brood hierarchies may have resulted in a closer nutritional status for nestlings in similar positions in the brood hierarchy than existed between siblings. The genetic similarity of great tit and house martin nestlings from the same nest may be affected by egg-dumping, or extra-pair copulations (epc). Up to 30% of house martin nests may contain nestlings resulting from epc's (Riley *pers. comm.*). There was no difference between nests in the foraging environment of parents in the zebra finch or house martin experiments which probably minimised differences in the realised foraging abilities of parents. Furthermore, any difference in the foraging habitat or ability of great tits may be ameliorated in terms of nestling diet by the tendency to lay clutches representing an optimum investment (Pettifor *et al.* 1988), ie larger clutches in a better quality environment or with better quality parents.

The presence of a 'nest effect' was tested for by means of an analysis of variance. Nests were divided into the anova blocks used for analysis (eg. HIGH 1987 , LOW 1989 for Section 2; or RED early-hatch, CON early-hatch for Section 4) and within these blocks a one-way analysis of variance was used to test if variation between nests was a significant constituent of the overall variation between nestlings (Appendices 4 to 6). There were some indications of a nest effect for zebra finch MASS at Day 400 (Appendix 4), and great tit nestling PC1 at Days 15 and stripe width at Day 19 (Appendix 6). Nonetheless, it was decided to proceed with the statistical analysis as if nestling data were independent and to accept the risk of a Type II error. The conclusions should therefore be treated as preliminary.

2.3 RESULTS

Experimental broods contained some white morph nestlings. This is a recessive morph that appears in captive populations (Rogers 1977). It grows to a smaller adult-size than the wild-type morph (Carr & Zann 1986) therefore the white morph birds were excluded from analyses of growth, size and condition.

The following procedures and symbols were used in all sections of the project.

All variables in the analyses were assessed for normality by means of a frequency histogram. Skewness and kurtosis statistics were calculated using the FREQUENCIES procedure of $SPSS_x$ and used to assess the correspondence of the data to a normal distribution (Zar 1974). If a variable was not normally-distributed transformations were used to see if a normal distribution could be obtained (Sokal & Rohlf 1981). If transformation did not produce a normal distribution then non-parametric analyses were used. Non-parametric analyses were also used when the sample size was insufficient to describe the distribution of a variable (Sokal & Rohlf 1981).

Significance levels are two-tailed for all analyses and a value of p less than 0.05 was assumed to indicate a significant result. In the summary tables of analyses the following symbols were used to indicate significance level:

ns - $p > 0.05$
* - $p < 0.05$
** - $p < 0.01$
*** - $p < 0.001$

2.3.1 *Breeding data*

The breeding data for each treatment, and each replicate are summarised in Table 2.3 . There was no significant difference between treatments in clutch size, brood size, fledged young or adult young, for each replicate and for the replicates combined (Mann Whitney U-test (M-W), $p > 0.2$ for all tests). This indicates that breeding parameter effects, such as the effect of zebra finch brood

Table 2.3 Summary of Zebra Finch breeding data for both replicates (()=white morph).

Year	Treatment	Nest	Clutch Size	Brood Size	FledgedYoung	Fledging Date	Young at Day 400
1987	HIGH	1	5	4	4	-	4
		2	6	3	2	-	2
		3	6	5(2)	4(2)	-	4(2)
	CONTROL	1	6	3	2	-	2
		2	6	4	4	-	4
		3	5	5(2)	3(1)	-	3(1)
1989	HIGH	1	6	5	5	1 (Day 22), 4 (Day 23)	5
		2	4	4	4	2 (Day 18), 2 (Day 20)	4
		3	2	2(2)	1(1)	1 (Day 20)	1(1)
		4	5	1	1	1 (Day 18)	-
	CONTROL	1	6	3(1)	3(1)	1 (Day 23), 2 (Day 24)	2(1)
		2	6	5	2	1 (Day 20), 1 (Day 22)	2
		3	6	4	2	2 (Day 25)	2
		4	5	2	1	1 (Day 18)	1

size on growth (Skagen 1986) did not influence treatment effects. Fledging date in the second replicate was earlier in HIGH treatment than in the CON treatment. This difference was almost significant (M-W, n_h=11, n_c=8, U= 22.5, p = 0.075). This result may indicate that nestlings in the HIGH treatment developed slightly faster than nestlings in the control.

The survival of nestlings from the HIGH and control treatments can be calculated by subtracting the number of young reaching adult age (Day 400) from the initial brood size. This value was compared between treatments using the Mann Whitney U-test. No difference was detected for the 1988 and 1989 replicates but when the replicates were combined the success of the HIGH treatment was greater than that of the CON treatment. This difference was almost significant (n_h=7, n_c=7, U = 11.5, P = 0.075).

2.3.2 *Growth*

The growth of the nestlings in the experiment is shown in graphical form, for each size parameter, in Figures 2.3 to 2.18. Only measurements of nestlings surviving up to Day 150 are included in the graphs, and in the analyses of growth and size.

2.3.2.1 *Growth rate*

Growth rates for each size parameter, for each nestling, were obtained as the value of *k* , the rate coefficient, from a fitted curve. The choice of curve from either Logistic or Gompertz was made by comparing the coefficients of determination (percentage of variation explained by curve) of each curve for each size parameter using a Wilcoxon Matched-pairs test (Table 2.4). A significant difference between the curves was present for all parameters except BDN. The Gompertz curve was used to obtain *k* for this parameter because the mean value of d was negative (Table 2.4).

An ANOVA (Table 2.5) of the standard error of the estimate of *k* for each nestling (Table 2.6) showed no difference in standard errors between sexes or treatments, but there was a significant difference between replicates in the standard error of the *k* estimate for BWD.

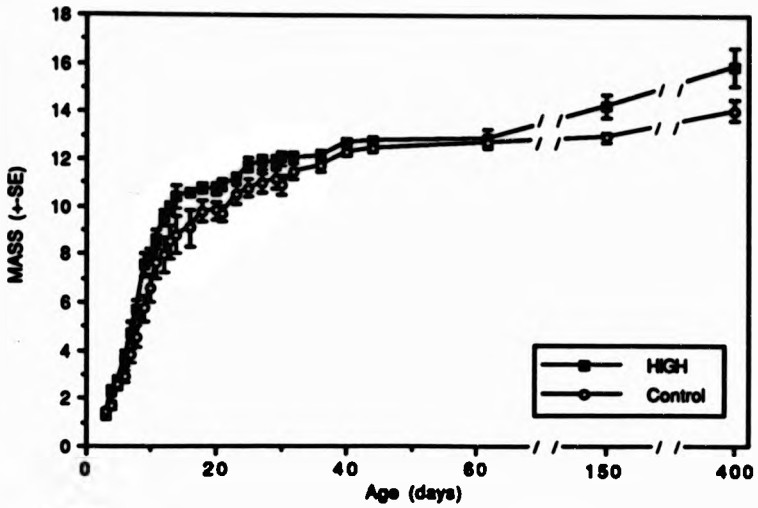

Figure 2.3 MASS growth of zebra finches, 1987.

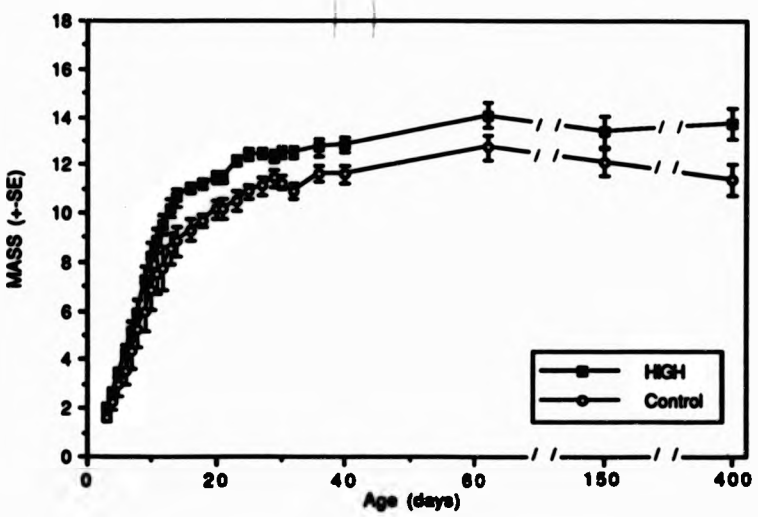

Figure 2.4 MASS growth of zebra finches, 1988.

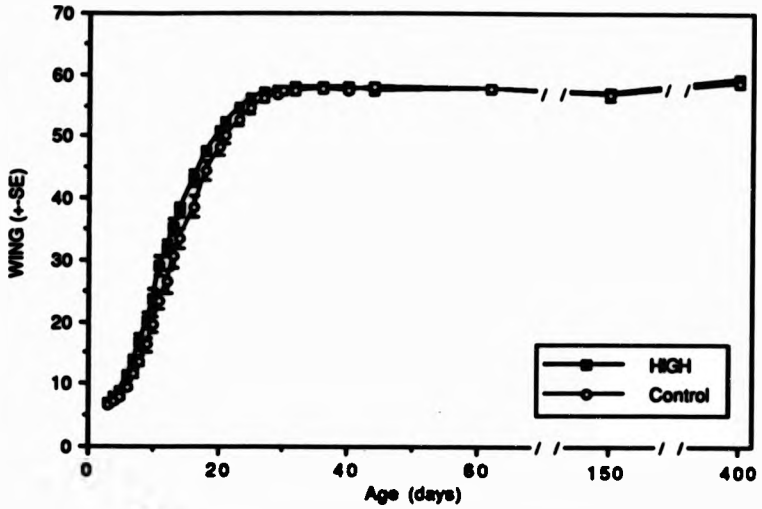

Figure 2.5 WING growth of zebra finches, 1987.

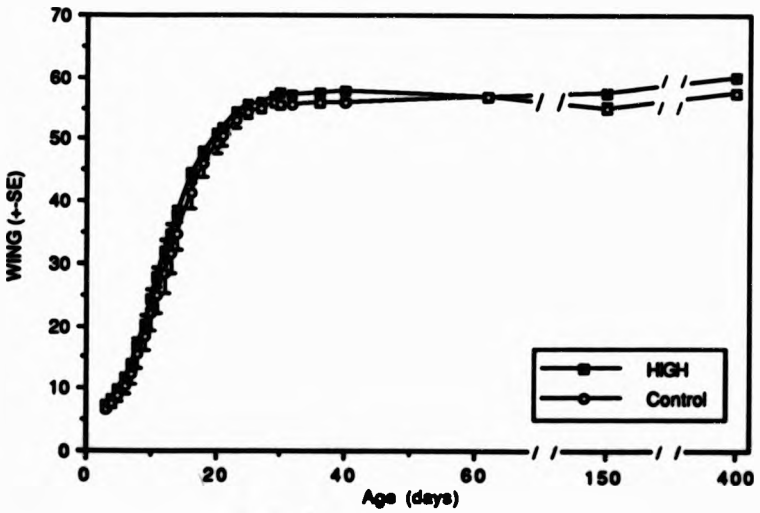

Figure 2.6 WING growth of zebra finches, 1989.

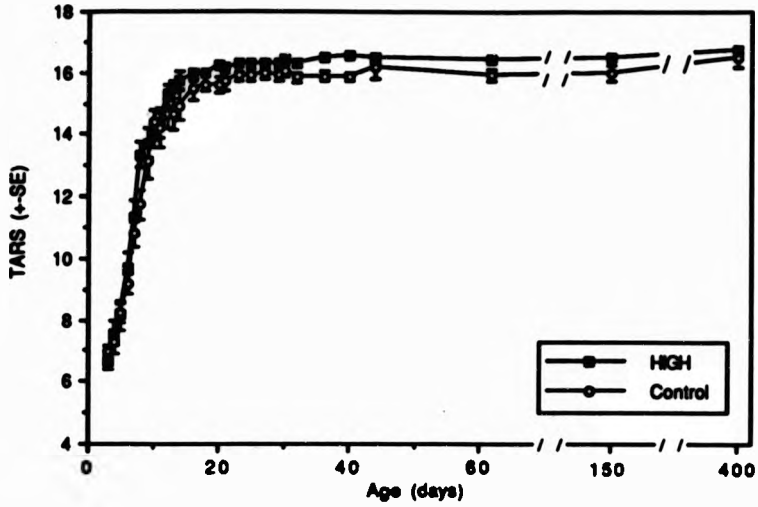

Figure 2.7 TARS growth of zebra finches, 1987.

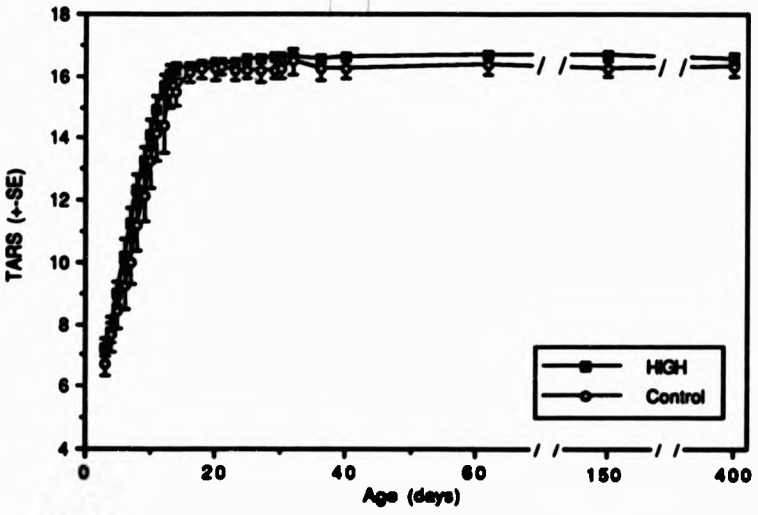

Figure 2.8 TARS growth of zebra finches, 1988.

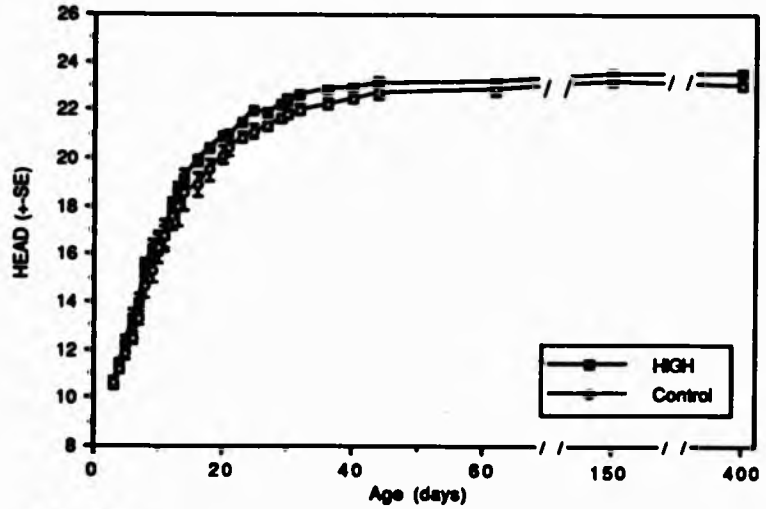

Figure 2.9 HEAD growth of zebra finches, 1987.

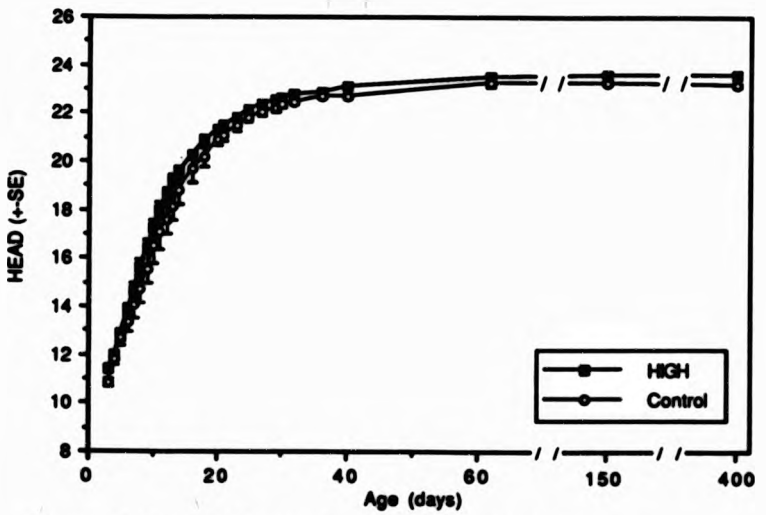

Figure 2.10 HEAD growth of zebra finches, 1989.

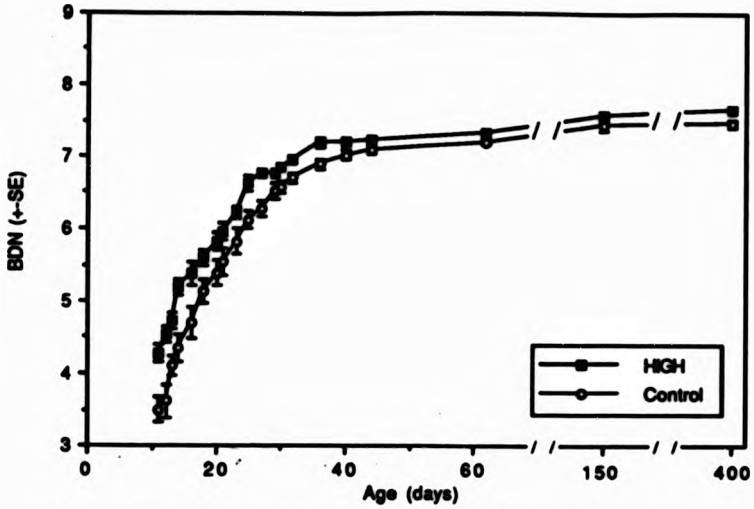

Figure 2.11 BDN growth of zebra finches, 1987.

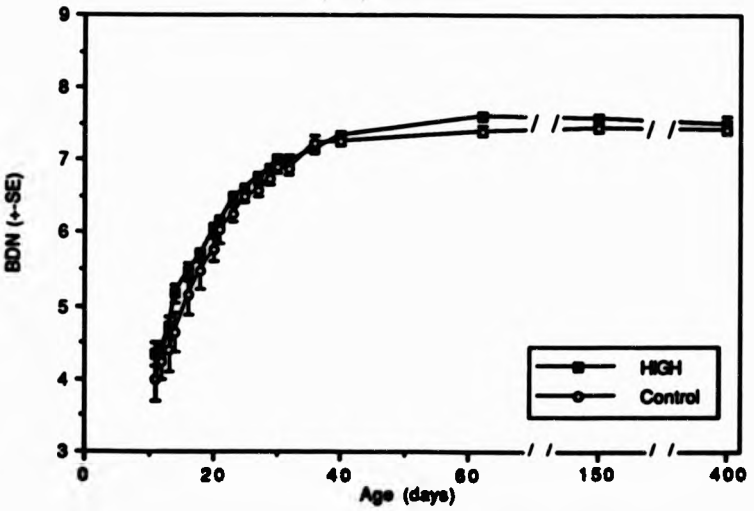

Figure 2.12 BDN growth of zebra finches, 1989.

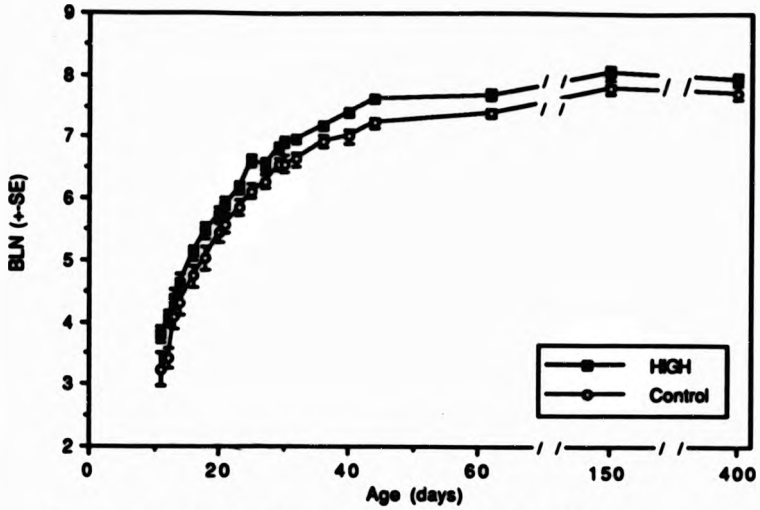

Figure 2.13 BLN growth of zebra finches, 1987.

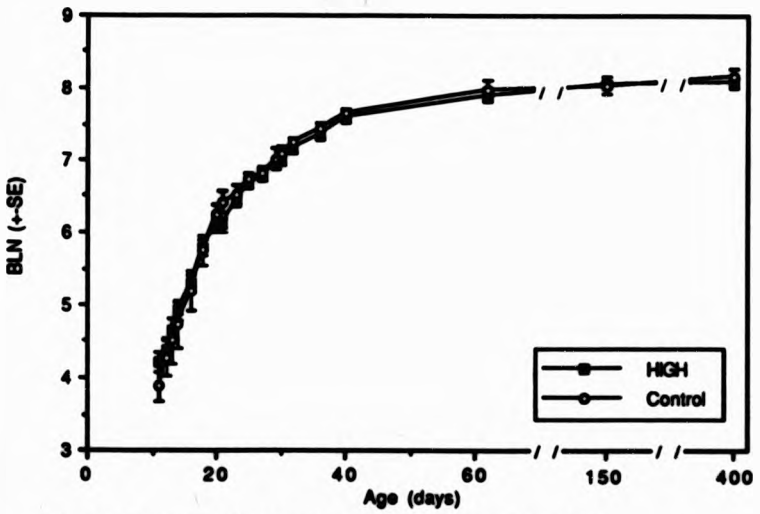

Figure 2.14 BLN growth of zebra finches, 1989.

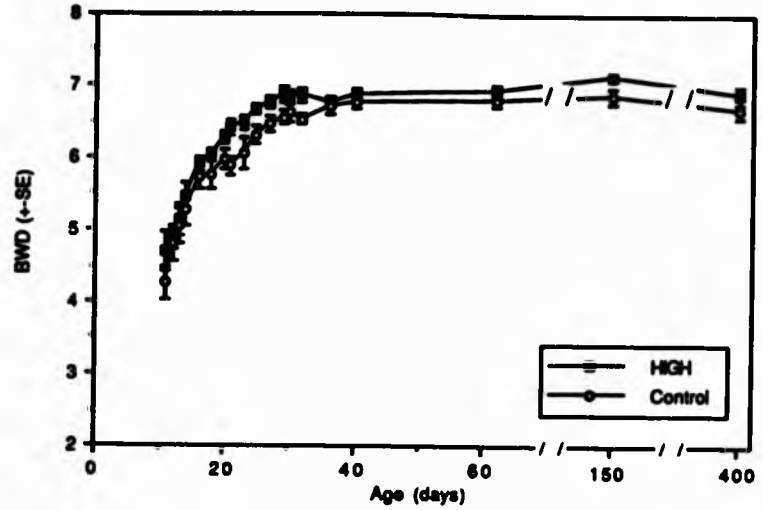

Figure 2.16 BWD growth of zebra finches, 1989.

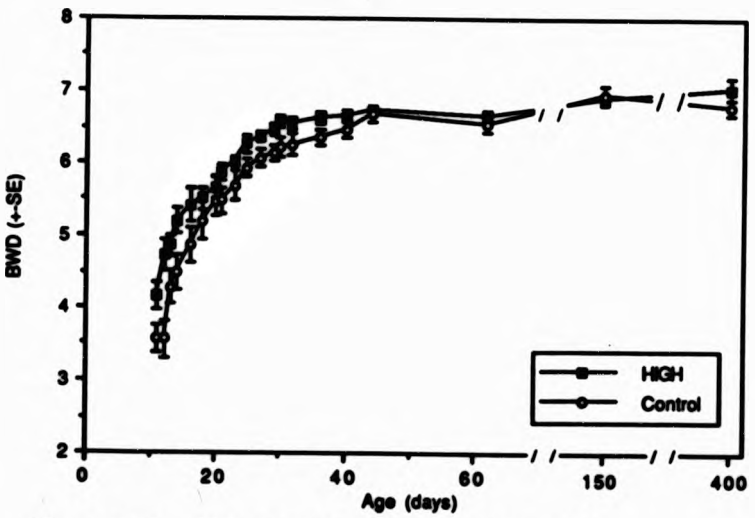

Figure 2.15 BWD growth of zebra finches, 1987.

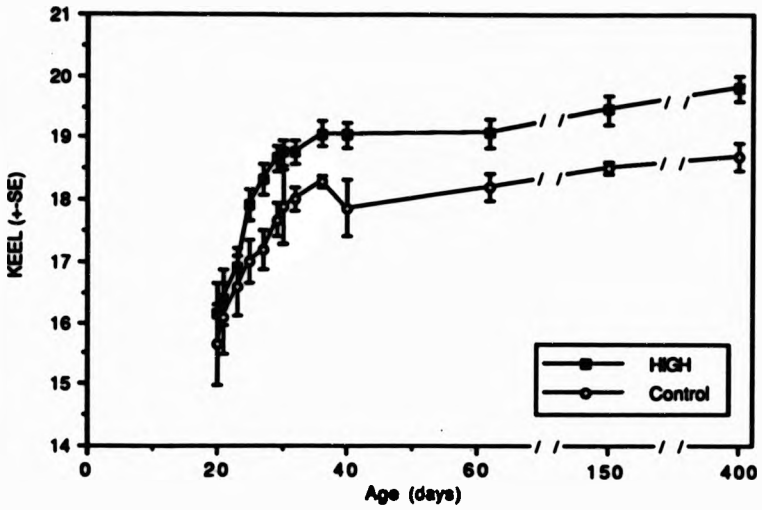

Figure 2.18 KEEL growth of zebra finches, 1989.

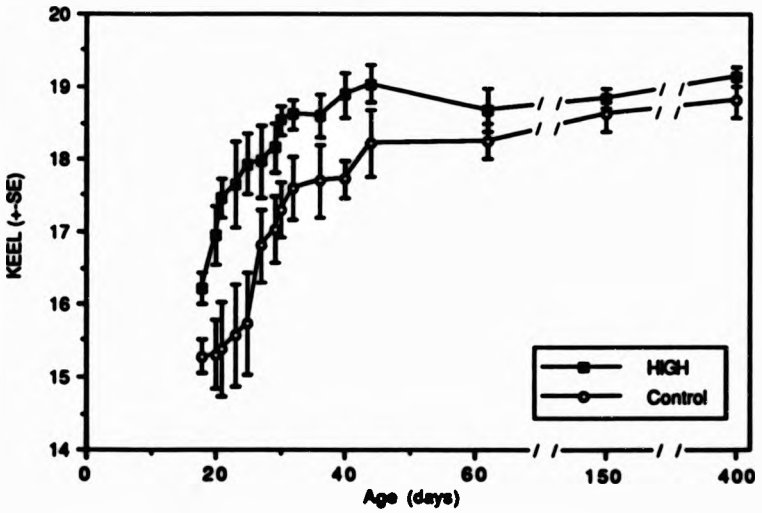

Figure 2.17 KEEL growth of zebra finches, 1987.

Table 2.4 **Comparison of the Logistic and Gompertz coefficients of determination of fitted equations for all zebra finch size parameters using the Wilcoxon Matched-pairs test.**

	1988 (n=16)			1989 (n=15)			Combined (n=31)			
Parameter	d^a	Z	p	d^a	Z	p	d^a	Z	p	Fitted Equation
MASS	-.010	-3.52	***	-.005	-3.35	***	-.008	-4.43	***	Gompertz
WING	.004	-3.46	***	.003	-3.24	***	.003	-4.73	***	Logistic
TARS	.005	-3.26	***	.007	-3.35	***	.006	-4.66	***	Logistic
HEAD	-.001	-1.58	ns	.000	-1.76	ns	-.001	-2.27	*	Gompertz
BDN	.000	-0.65	ns	-.001	-1.51	ns	-.001	-1.52	ns	Gompertz
BLN	-.003	-3.52	***	-.003	-3.42	***	-.003	-4.86	***	Gompertz
BWD	-.004	-1.91	ns	.001	-2.61	**	-.002	-3.03	**	Gompertz
KEEL	.013	-1.34	ns	.002	-0.99	ns	.008	-2.37	*	Logistic

a - d is the mean value of Logistic r^2 minus Gompertz r^2

Table 2.5 **Comparison by ANOVA of the standard error (ln(SE+1)) of the estimate of *k* between treatments, sexes and replicates (N = 31). (F values and significance level)**

Parameter	Treatment	Sex	Replicate	Interactions
MASS	2.00 ns	.38 ns	2.36 ns	ns
WING	.46 ns	3.71 ns	2.38 ns	ns
TARS	.95 ns	.63 ns	.81 ns	ns
HEAD	.15 ns	.01 ns	3.76 ns	ns
BDN	1.31 ns	1.27 ns	.03 ns	ns
BLN	3.11 ns	1.58 ns	2.71 ns	ns
BWD	.38 ns	.03 ns	8.73 * *	ns
KEEL	.75 ns	.01 ns	1.62 ns	ns

Table 2.6 **Mean values of asymptotic standard error of estimate of growth rate (*k*) for both treatments and both replicates.**

	FIRST REPLICATE		SECOND REPLICATE	
	HIGH(n=8)	CON(n=8)	HIGH(n=9)	CON(n=6)
Parameter	ln(SE+1)	ln(SE+1)	ln(SE+1)	ln(SE+1)
MASS	.023	.016	.016	.015
WING	.007	.006	.007	.007
TARS	.022	.022	.018	.023
HEAD	.006	.007	.005	.004
BDN	.007	.007	.008	.006
BLN	.006	.006	.006	.008
BWD	.019	.013	.022	.026
KEEL	.059	.034	.031	.042

An ANOVA (Table 2.7) was used to test for differences in the value of *k* between treatments, sexes and replicates. The value of *k* for KEEL was significantly larger for the HIGH treatment (i.e. growth was faster) than in the CON treatment (Table 2.8). The same pattern was present for MASS, WING, TARS, HEAD and BWD but the difference in values was not significant.

2.3.2.2 *Growth curve shape*

The shape of the growth curve was measured as the coefficient *m* of the Richards curve. The standard error of the estimate of *m* was analysed by ANOVA (Table 2.9), as described in Section 2.3.2.1. The value of *m* for TARS could not be analysed by ANOVA because the standard error of estimate was significantly larger in the control (Table 2.10) so a non-parametric analysis was used.

An ANOVA (Table 2.11) was used to test for differences in *m* between treatments, sexes and replicates for MASS, WING and HEAD. The mean value of *m* was smaller for the control than that of the HIGH treatment for all parameters (Table 2.12). This difference was significant for WING and HEAD . There was no significant difference in TARS *m* between treatments (M-W, u=79, n_h=17, n_l=14, ns) or replicates (M-W, u=75, n_h=17, n_l=14, ns).

2.3.3 *Body size*

2.3.3.1 *Parental size*

The body-size of parents was compared between treatments and replicates by means of an ANOVA (Table 2.13). There was no significant difference in parental size between treatments for any of the size parameters. TARS was significantly larger in the second replicate than in the first replicate (Table 2.14).

2.3.3.2 *Nestling size*

An ANOVA (Table 2.15) was used to test for differences in body size of nestlings between treatments, sexes and replicates at Days 5, 150 and 400 (Table 2.16). There were no significant differences in size between treatments at Day 5, but by Day 150 MASS, WING, TARS, HEAD, BDN and KEEL were significantly larger in the HIGH treatment than in the control. When adult size was measured at Day 400 MASS, WING, TARS and KEEL were still significantly

Table 2.7 **Comparison by ANOVA of values of k between treatments, sexes and replicates (n=31).** (F values with significance level)

Parameter	Treatment(T)		Sex(S)		Replicate(R)		Interactions	
MASS	1.52	ns	.14	ns	.87	ns		ns
WING	1.60	ns	.75	ns	4.22	ns		ns
TARS	2.12	ns	.18	ns	.60	ns		ns
HEAD	.54	ns	.27	ns	.16	ns		ns
BDN	.03	ns	.03	ns	7.97	*		ns
BLN	.01	ns	.94	ns	7.60	*	T-R	**
BWD	1.50	ns	.00	ns	10.56	* *		ns
KEEL	5.89	*	1.38	ns	1.82	ns	T-S	*

Table 2.8 **Mean values and standard errors of growth rates (*k*) of zebra finch for both treatments and both replicates.**

	FIRST REPLICATE				SECOND REPLICATE			
	HIGH (n=8)		CON (n=8)		HIGH (n=9)		CON (n=6)	
Parameter	*k*	se	*k*	se	*k*	se	*k*	se
MASS	.187	.011	.173	.023	.207	.010	.180	.013
WING	.253	.004	.240	.005	.256	.003	.258	.007
TARS	.347	.024	.315	.026	.330	.016	.296	.024
HEAD	.124	.004	.122	.012	.131	.005	.121	.011
BDN	.096	.004	.094	.004	.105	.003	.106	.002
BLN	.092	.003	.081	.003	.090	.003	.101	.002
BWD	.122	.008	.101	.006	.159	.013	.149	.021
KEEL	.281	.086	.122	.020	.168	.022	.140	.025

Table 2.9 **Comparison by ANOVA of the standard error (ln(SE+1)) of the estimate of *m* between treatments, sexes and replicates (n = 31).** (F values with significance level, df = 1 for all factors)

Parameter	Treatment	Sex	Replicate	Interactions
MASS	1.99 ns	.96 ns	.66 ns	ns
WING	.00 ns	.22 ns	.72 ns	ns
TARS	5.91 *	3.91 ns	5.68 *	ns
HEAD	2.55 ns	.52 ns	3.52 ns	ns

Table 2.10 **Mean values of asymptotic standard error of estimate of curve shape (*m*) for both treatments and both replicates.**

	FIRST REPLICATE		SECOND REPLICATE	
	HIGH (n=8)	CON (n=8)	HIGH (n=9)	CON (n=6)
Parameter	ln(SE+1)	ln(SE+1)	ln(SE+1)	ln(SE+1)
MASS	.322	.294	.377	.299
WING	.268	.333	.411	.348
TARS	.953	1.264	1.305	2.512
HEAD	.489	.692	.476	.448

Table 2.11 **Comparison by ANOVA of curve shape (*m*) between treatments, sexes and replicates (n=31).** (F values with significance level, df = 1 for all factors)

Parameter	Treatment		Sex		Replicate		Interactions
MASS	.13	ns	.08	ns	.78	ns	ns
WING	4.97	*	1.28	ns	.00	ns	ns
HEAD	5.73	*	1.38	ns	.16	ns	ns

Table 2.12 **Mean values and standard errors of curve shape (*m*) of zebra finch for both treatments and both replicates.**

	FIRST REPLICATE				SECOND REPLICATE			
	HIGH (n=8)		CON (n=8)		HIGH (n=9)		CON (n=6)	
Parameter	*m*	se	*m*	se	*m*	se	*m*	se
MASS	1.13	0.42	1.39	0.28	1.73	0.31	1.21	0.40
WING	2.35	0.18	2.95	0.26	2.36	0.25	2.93	0.44
TARS	4.35	0.25	6.77	1.71	8.63	2.68	12.49	2.28
HEAD	0.96	0.48	2.71	0.60	1.58	0.39	2.39	1.04

Table 2.13 Mean values (x) and standard errors of parental body size for both treatments in each replicate.

	FIRST REPLICATE				SECOND REPLICATE			
	HIGH (n=6)		CON (n=6)		HIGH (n=6)		CON (n=6)	
Parameter	x	se	x	se	x	se	x	se
MASS	13.60	.27	14.60	.70	15.95	1.18	14.79	.87
WING	57.67	.54	57.67	.54	58.50	.41	57.81	.33
TARS	16.35	.17	16.39	.15	16.73	.22	16.91	.17
HEAD	23.19	.21	23.25	.37	23.62	.12	23.28	.29
BDN	7.47	.06	7.53	.15	7.70	.10	7.74	.10
BLN	7.56	.11	7.65	.30	7.98	.15	7.90	.28
BWD	6.75	.15	7.01	.10	7.13	.06	7.02	.07
KEEL	19.12	.23	18.97	.20	19.11	.25	18.77	.07

Table 2.14 Comparison by ANOVA of parental size between treatments, sexes and replicates (n=28). (F values with significance level, df = 1 for all factors)

Parameter	Treatment(T)		Sex(S)		Replicate(R)		Interactions	
MASS	.00	ns	.04	ns	1.01	ns		ns
WING	.63	ns	1.63	ns	1.45	ns		ns
TARS	.44	ns	1.27	ns	7.65	*	T-S	*
HEAD	.20	ns	4.78	*	.53	ns		ns
BDN	.06	ns	9.14	**	2.97	ns		ns
BLN	.00	ns	8.76	**	2.23	ns		ns
BWD	.74	ns	5.60	*	2.77	ns		ns
KEEL	1.80	ns	.00	ns	.06	ns		ns

Table 2.15 Comparison by ANOVA of zebra finch body size at Days 5, 150 & 400 between treatments, sexes and replicates (n=31).
(F values with significance level, df = 1 for all factors)

Parameter	Treatment		Sex		Replicate		Interactions
Day 5							
MASS	.41	ns	.95	ns	2.41	ns	ns
WING	1.68	ns	.03	ns	1.10	ns	ns
TARS	.17	ns	1.08	ns	.85	ns	ns
HEAD	.27	ns	1.20	ns	4.74	*	ns
Day 150							
MASS	6.77	*	.01	ns	2.28	ns	ns
WING	5.94	*	8.78	**	.98	ns	T-R *
TARS	5.15	*	2.27	ns	.79	ns	ns
HEAD	8.68	**	10.68	**	.79	ns	ns
BDN	9.26	**	5.83	*	.00	ns	S-R * T-S-R *
BLN	3.46	ns	.24	ns	2.44	ns	T-S *
BWD[a]	1.92	ns	.43	ns	1.95	ns	ns
KEEL	7.72	*	.06	ns	1.74	ns	T-R *
Day 400							
MASS[b]	11.75	**	1.50	ns	13.01	**	S-R * T-S-R *
WING	11.71	**	.05	ns	.19	ns	ns
TARS	1.20	ns	.33	ns	1.20	ns	ns
HEAD	8.73	**	9.39	**	1.42	ns	ns
BDN	3.35	ns	12.87	**	6.54	ns	S-R **
BLN	.17	ns	.92	ns	8.10	**	ns
BWD	3.05	ns	2.27	ns	.97	ns	ns
KEEL	11.25	**	1.07	ns	2.37	ns	T-R * T-S-R *

a - n = 30
b - n = 29

Table 2.16 **Mean values (x) and standard errors of nestling body size at Days 5, 150 & 400 for both treatments and both replicates.**

	FIRST REPLICATE				SECOND REPLICATE			
	HIGH (n=8)		CON (n=8)		HIGH (n=9)		CON (n=6)	
Parameter	x	se	x	se	x	se	x	se
Day 5								
MASS	2.67	.27	2.58	.19	3.37	.29	2.97	.43
WING	8.90	.62	8.03	.35	9.67	.62	8.73	.71
TARS	8.15	.48	8.24	.30	8.98	.39	8.39	.55
HEAD	12.19	.31	11.81	.28	12.79	.21	12.69	.31
Day 150								
MASS	14.21	.48	12.86	.20	13.39	.66	12.12	.55
WING	57.00	.38	56.63	.87	57.11	.26	55.00	.82
TARS	16.48	.14	15.99	.24	16.66	.14	16.23	.27
HEAD	23.51	.08	23.15	.17	23.59	.13	23.26	.12
BDN	7.57	.05	7.42	.06	7.57	.06	7.43	.05
BLN	8.04	.10	7.80	.08	8.05	.04	8.04	.11
BWD	6.88	.06	6.95[a]	.13	7.13	.06	6.86	.11
KEEL	18.84	.13	18.71	.19	19.45	.23	18.50	.10
Day 400								
MASS	15.79	.82	13.98	.43	13.71	.67	11.40[b]	.63
WING	59.25	.37	58.63	.46	59.78	.28	57.25	.63
TARS	16.76	.13	16.46	.26	16.55	.16	16.29	.32
HEAD	23.45	.10	23.01	.17	23.53	.14	23.18	.10
BDN	7.66	.04	7.45	.05	7.49	.10	7.42	.07
BLN	7.93	.10	7.72	.10	8.07	.07	8.16	.11
BWD	7.03	.15	6.79	.10	6.88	.11	6.67	.10
KEEL	19.14	.13	18.89	.15	19.79	.20	18.71	.22

a - n = 7
b - n = 4

larger in the HIGH treatment than in the control.

Males and females were not significantly different in size at Day 5 but at Day 150 males had larger WING, HEAD and BDN than females. The differences in HEAD and BDN were still present at Day 400.

There were few differences between the two replicates of the experiment. At Day 400 nestlings were heavier in the first replicate than in the second replicate whereas BLN was longer in the second replicate than in the first replicate.

2.3.4 *Nestling shape at Day 400*

The First Principal Component (PC1) was significantly correlated with all nestling size parameters except BLN (Table 2.17). The Second Principal Component (PC2) was strongly correlated with BLN and weakly correlated with TARS and HEAD, indicating a very weak overall association with body size.

The plot of PC2 against PC1 for parents (Fig. 2.19) showed little difference in the distribution of the adults from each treatment along either axis, as delineated by the lines joining the boundary points. The plot of PC2 against PC1 for nestlings at Day 400 (Fig. 2.20) showed little difference in the distribution of nestlings from each treatment along the PC2 'shape' axis but a large difference between treaments in their distribution along the PC1 'size' axis

ANOVA (Table 2.18) was used to test for differences in the value of PC1 and PC2 between treatments, sexes and replicates . PC1 was significantly larger in the HIGH treatment than in the control. PC2 was significantly larger in the second replicate than in the first replicate. This difference in shape may be due to the pronounced difference in bill length between treatments (Table 2.15) as bill length is highly correlated with nestling PC2 (Table 2.17).

2.3.5 *Nestling condition*

MPT and CPT were compared between treatments, sexes and replicates by an ANOVA (Table 2.19) for Day 150 and Day 400 . CPT was significantly larger

Table 2.17 Correlation matrix of PC1 and PC2 with nestling size parameters at Day 400 (n=31). (Pearson correlation coefficient)

Parameter	PC1 r	PC1 sig	PC2 r	PC2 sig
WING	.630	***	.149	ns
TARS	.594	***	-.473	*
HEAD	.740	***	.449	*
BDN	.506	**	.180	ns
BLN	.117	ns	.839	***
BWD	.747	***	.069	ns
KEEL	.837	***	.060	ns
Eigenvalue	2.96		1.06	
Percentage of variation	49.4		18.0	

Table 2.18 Comparison by ANOVA of parent (n=28) and nestling (Day 400, n=31) PC1 and PC2 between treatments, sexes and replicates . (F values with significance levels, df = 1 for all factors)

	Treatment	Sex	Replicate	Interactions
PARENT				
PC1	.00 ns	7.27 *	3.70 ns	ns
PC2	.72 ns	3.64 ns	.45 ns	ns
NESTLING				
PC1	16.70 ***	7.54 **	.02 ns	ns
PC2	.23 ns	1.16 ns	5.64 *	ns

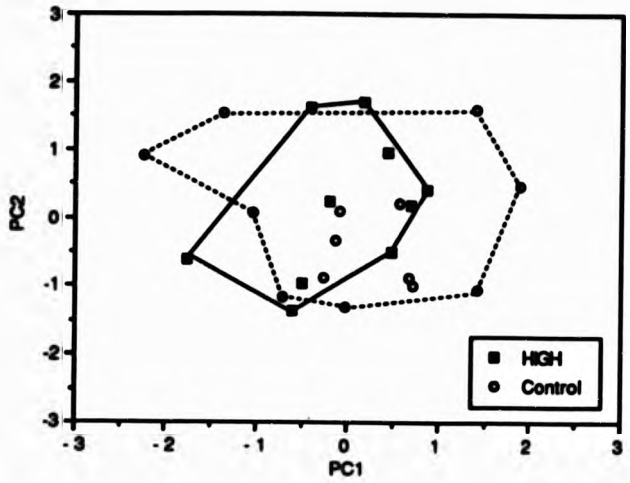

Figure 2.19 Comparison of parent PC1 & PC2 between treatments.

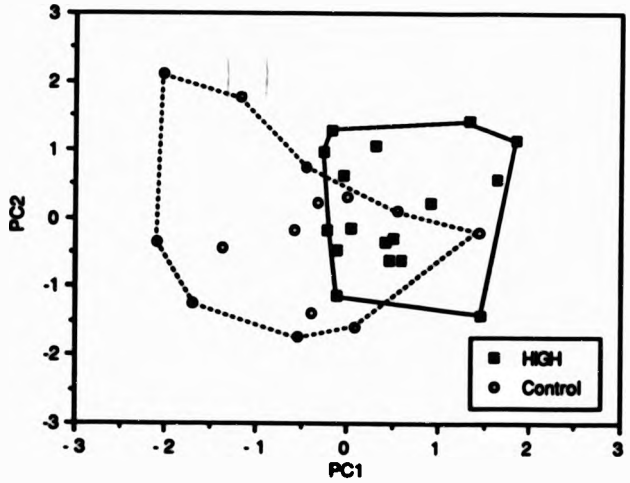

Figure 2.20 Comparison of nestling PC1 and PC2 at Day 400 between treatments.

(Table 2.20) in the control than in the HIGH treatment at Day 150. There was no difference in MPT between treatments.

At Day 400 there was no significant difference between treatments in CPT but MPT was, however, almost significantly larger in the HIGH treatment than in the control. This result indicates that the condition of birds from the HIGH treatment improved between Day 150 and Day 400 in comparison to birds from the control. Analysis of the change in CPT between Day 150 and Day 400 (d) of individual birds confirmed this indication. d was negative (mean = -.005) for birds from the control and positive (mean = .002) for birds in the HIGH treatment. The difference was significant when tested by ANOVA (Table 2.19).

2.3.6 *Male plumage*

Mann-Whitney U-tests were used to test for differences in plumage between treatments at Day 150 and Day 400 (Table 2.21) because the sample sizes were too small to describe a distribution for the plumage measurements (Sokal & Rohlf 1981). Ear Patch width was wider in the HIGH treatment than in the control at Day 400 when replicates were combined ($U=7$, $n=15$, $p < 0.05$). There were no other significant differences between treatments.

Table 2.19 **Comparison by ANOVA of zebra finch body condition indices at Day 150 (n=31) and Day 400 (n=29) between treatments, sexes and replicates.** (F values with significance level, df = 1 for all factors)

Parameter	Treatment(T)	Sex(S)	Replicate(R)	Interactions
Day 150				
CPT	4.62 *	.17 ns	.07 ns	ns
MPT	.03 ns	.05 ns	.63 ns	T-R *
Day 400				
CPT	.86 ns	1.95 ns	.72 ns	T-S-R *
MPT	4.24 ns[a]	.84 ns	.01 ns	T-S-R **
d	4.63 *	.96 ns	.41 ns	ns

a - p = 0.052

Table 2.20 **Mean (x) and standard error of body condition indices at Day 150 (n=31) and Day 400 (n=29) for both treatments and both replicates.**

	FIRST REPLICATE				SECOND REPLICATE			
	HIGH (n=8)		CON (n=8)		HIGH (n=9)		CON (n=6)	
Parameter	x	se	x	se	x	se	x	se
Day 150								
CPT	0.139	.002	0.143	.001	0.139	.001	0.142	.002
MPT	2.61	.04	2.68	.02	2.70	.02	2.63	.05
Day 400								
CPT	0.140	.003	0.140	.002	0.141	.001	0.133[a]	.011
MPT	2.69	.05	2.65	.04	2.79	.04	2.48[a]	.24

a - n = 4

Table 2.21 **Mean (x) and standard error of male ear patch and flank measurements at Days 150 & 400 for both treatments and both replicates.**

	FIRST REPLICATE				SECOND REPLICATE			
	HIGH (n=5)		CON (n=3)		HIGH (n=4)		CON (n=3)	
Parameter	x	se	x	se	x	se	x	se
Day 150								
PATWD	11.6	0.6	11.7	1.1	11.7	0.4	10.8	0.4
PATHT	10.9	0.2	11.8	1.2	13.7	2.5	10.7	0.7
PATCH	127.0	6.5	134.6	6.4	158.3	22.8	115.4	10.2
FLKWD	9.9	0.8	9.2	0.4	9.0	0.9	9.7	1.1
FLKLE	33.8	1.4	35.7	2.9	32.4	3.3	35.0	2.3
FLANK	331.8	24.9	327.3	29.1	299.0	55.4	339.8	57.8
Day 400								
PATWD	11.5	0.2	10.9	0.7	12.5	0.5	10.2	0.2
PATHT	11.7	0.7	12.6	0.4	11.4	0.4	11.8	0.7
PATCH	134.7	9.6	136.8	9.7	143.0	5.9	119.8	8.4
FLKWD	4.2	2.6	5.2	2.6	8.9	0.8	10.8	0.9
FLKLE	14.6	9.0	25.6	12.9	37.1	1.0	34.8	0.8
FLANK	154.6	95.1	201.3	101.9	330.5	28.7	374.6	33.1

2.4 DISCUSSION

2.4.1 *Effects of nestling diet quality*

Nestling diet quality affected the growth rate and adult size of zebra finch nestlings in this experiment. Higher nestling diet quality resulted in faster nestling growth and larger adult size. This effect is consistent with the results of Boag (1987a), and the results of Skagen (1988) who also demonstrated an effect of nestling diet in that increased food abundance resulted in faster nestling growth in a laboratory zebra finch population.

Growth rate was significantly different between treatments only for KEEL yet there were significant size differences between treatments in MASS, WING, TARS, HEAD and KEEL at Day 150 and in MASS, WING, HEAD and KEEL at Day 400. The fact that nestlings in the HIGH treatment fledged at a younger age than nestlings in the control indicates that they grew faster than nestlings in the control but growth rate analysis did not detect such a difference. This could be explained by the small sample size for the analysis. Alternatively the disparity between the results of growth rate analysis and analyses of size may be explained by the significant differences in growth curve shape between treatments. Growth may have started earlier in the HIGH treatment or continued for longer than in the control . Either of these differences in shape would result in larger adult size without necessitating a faster growth rate. Growth curve shape may be more sensitive to experimental and environmental differences than growth rate and it could prove to be a useful analytical tool in future investigations (Pasternak & Shalev 1983; Brisbin *et al.* 1987).

At Day 150 fledglings that had received a high quality nestling diet were larger than fledglings that had received the control. Many passerine fledglings experience enhanced competition at this age as winter approaches and resources become scarcer (Garnett 1981). The differences in body size resulting from differences in nestling diet quality may be important in determining access to these resources and will also influence the size of resource necessary for survival (Lehtikoinen 1986a).

There was some compensatory growth of young from the control between

Day 150 and Day 400 but adult size was still larger in birds that had received the high quality nestling diet. Compensatory growth may not occur in wild populations as food resources are likely to be more restricted than the *ad libitum* resources available to fledglings in this experiment. Adult body size is important in determining the ecology of an individual bird (Peters 1983) thus nestling diet quality may influence the life history of an individual bird through an effect on its adult size (Richner *et al.* 1989). Indeed there was some evidence from the experiment that the larger size of birds in the HIGH treatment may have put them at a competitive advantage to birds from the control . The body condition of adult birds from the HIGH treatment increased between Day 150 and Day 400 whereas the condition of birds from the control decreased, indicating that they were dominant in their access to food in the mixed cages between Day 150 and Day 400. This impression is also supported by the fact that the two birds which died between Day 150 and Day 400 were both from the control group. Aggression from other birds in the holding cage caused loss of neck and head plumage, bruising of head tissue and eventual death (*pers. obs.*). This dominance may have been a result of the larger size of birds from the HIGH treatment, or it may have been due to the influence of nestling diet quality on another component of the phenotype.

There was some evidence that the ear patch width of adult male zebra finches may be influenced by nestling diet quality. If so, it is possible that, in species where plumage variation is important in dominance and sexual selection, nestling diet quality may influence plumage variation thereby influencing the social role of individual birds. Plumage variation is important in individual recognition in the zebra finch (Burley & Bartels 1990). Different colour leg rings result in assortative mating in the zebra finch (Burley 1985; Burley *et al.* 1982) so it is possible that plumage variation may be a basis for mate choice in zebra finches.

There is evidence from this experiment that nestling diet quality influences the quality of zebra finch young. Higher nestling diet quality results in faster growth, earlier fledging, better survival, and larger, possibly more dominant, adults. These differences occurred under an experimental dietary regime and to assess their importance it is important to know if they are likely to occur in the natural situation. Does zebra finch nestling diet quality vary in the wild?

Wild zebra finches, when captured and bred in cages, produce F1 young that are significantly smaller than themselves (Carr & Zann 1986). This must be an environmental effect and nestling diet seems a likely factor. The zebra finch is granivorous and like many estrildid finches it often raises young on seed alone (Morton & Davies 1983; Zann & Straw 1984) and a granivorous diet can vary in quality according to its species composition (Shuman *et al.* 1990). Their natural habitat is, however, highly seasonal and there may be both opportunistic feeding on insects and also times of impoverished diet (Zann & Straw 1984). There is the potential, then, for zebra finch nestling diet to exhibit temporal and spatial variation in quality. This variation may well produce phenotypic differences between individuals in a wild population of a similar magnitude to those differences between individuals resulting from the manipulation of nestling diet quality in this experiment.

2.4.2 *Male and female differences*

The most conspicuous difference between males and females was the significantly larger bill of the male. This was noticeable in the comparison of parental size (Table 2.13), nestling size at Day 150 (Table 2.17) and nestling size at Day 400 (Tables 2.19 & 2.22). This difference in bill size also resulted in differences in HEAD measurements between sexes (Tables 2.13, 2.17 & 2.19).

2.4.3 *Differences between replicates*

Bill growth (Table 2.7) and bill size (Tables 2.19 & 2.22) were significantly greater in nestlings from the second replicate than in the first replicate. The difference in nestling bill size may have been due to the larger bill size of parents in the second replicate (Table 2.14). This would not, however, explain the faster growth in the second replicate. It is possible that this may have resulted from the use of calipers early on in the measurement of bills in the second replicate rather than the use of dividers as in the first replicate (Section 2.2.3.1). If so the difference in bill size represents a difference in methodology between treatments rather than representing an actual difference in growth. This instance illustrates the need for a rigid

methodology when performing experiments requiring replication (Zar 1974). A requirement satisfied for all other size parameters in the experiment.

3 EFFECTS OF A REDUCTION IN NESTLING DIET QUALITY ON A WILD INSECTIVOROUS PASSERINE

3.1 INTRODUCTION

There have been many studies of the effect of variation in the food supply on the growth of wild birds but almost all of these have studied the effect of food availability upon growth, assuming that food availability influences the quantity of food fed to nestlings. There have been very few studies of the effect of variation in nestling diet quality (defined as 'limiting nutrient' kj^{-1}) on passerines (great tit *Parus major*, Perrins 1976; European bee-eater *Merops apiaster*, Krebs & Avery 1984; starling *Sturnus vulgaris*, Westerterp *et al.* 1982; carrion crow *Corvus corone corone*, Richner 1989c) or other birds (Heath & Randall 1985; Massias & Becker 1990) and there is a need for further investigation of this effect. It is important to determine if the effect of nestling diet quality on growth demonstrated by Boag (1987a) is present in wild populations. If variation in nestling diet quality is important in determining variation in growth in wild populations, another influence of the environment on the phenotype of birds will have been identified and studies of heritability (Boag & Grant 1978; Smith & Zach 1979; Moss & Watson 1982), morphometric variation (James 1983; Murphy, E.C. 1985; St Louis & Barlow 1987; Corbin & Wilkie 1988) and selection (Fleischer & Johnston 1982, 1984; Schluter & Smith 1986) will have to consider the influence of diet quality as part of the wider interpretation of results.

It was the aim of this study to test for a causal effect of nestling diet quality, as opposed to food quantity, on nestling growth in a wild population. An important factor in making this investigation was to choose an appropriate methodology. Most studies of the effect of nestling diet on wild populations have investigated the effect of food availability during the nestling period on nestling growth and parental behaviour. Two methods have been used in these studies.

One method is to measure natural food availability and to correlate variation in this value with variation in nestling development and breeding parameters (van Balen 1973; Bryant 1975a, 1978a; Green 1984; Powell 1984; Hill 1985; Alatalo & Lundberg 1986; Quinney *et al.* 1986; Blancher &

Robertson 1987; Heezik 1990). This method has the advantage of measuring the effects of *natural* variation in food supply but there is the problem that any correlation detected may be the result of the effect of a covariate of nestling diet such as temperature, habitat or parental quality rather than an effect of nestling diet itself; therefore this method cannot demonstrate a causal effect of nestling diet (Bryant 1978a). There are also problems in measuring the variation in diet fed to nestlings in the wild, especially diet quality, as parents may be selective in their use of a food resource (Tinbergen 1981; Grundel 1990). This method was not used in this study because of these difficulties.

A second approach has been the experimental method which involves the alteration of nestling diet in an experimental treatment and the comparison of nestling growth in this treatment with that of a control where nestling diet was unaltered from its natural level. All other variables are kept constant between treatments. This method has the advantage of being able to demonstrate a causal effect of nestling diet upon nestling growth and it was chosen for this study.

Nestling diet can be altered in several ways. The most commonly used method is to provide parent birds with a supplement which they feed to the nestlings (Crossner 1977; Harris 1978; Bromssen & Jansson 1980; Smith *et al.* 1980; Ewald & Rohmer 1982; Daan *et al.* 1986; Smith & Arcese 1986; Arcese & Smith 1986, 1988; Mock *et al.* 1987; Hochachka & Boag 1988; Briggs 1989; Clamens & Isenmann 1989; Moreno 1989; Boutin 1990; Hörnfeldt & Eklund 1990; Simons & Martin 1990; Waite 1990). The assumption is made that the supplement is utilised by the parent birds and alters nestling growth. This may not be true, however, when natural food availability is such that it does not constitute a limiting factor to nestling growth because the supplement may not then be used, or if it is used it may be of no net nutritional benefit. The problem of non-use of the supplement can be overcome by hand-feeding the supplement to nestlings (Perrins 1976; Krebs & Avery 1984; Ricklefs *et al.* 1987) so this method was chosen for this study.

It is also necessary to validate the basic assumption that the realised nestling diet quality was different between treatments because parent birds may compensate for the supplement in their feeding. The assumption can be tested by recording all the food items fed to nestlings, however this is very difficult to do unless the nestlings are hand-fed only, in which case the experiment becomes very intensive and remote from the conditions experienced by the nestlings in the

wild. An alternative method is to collect all the faeces produced by nestlings and to use the remains in the faeces as a record of the nestling diet. This is not feasible in species where the parents remove nestling faeces from the nest for disposal but there are some species where the nestlings themselves deposit all faeces outside the nest, providing an accurate dietary record. One such species is the house martin *Delichon urbica* whose nestlings eject faeces from the nest from Day 9 onwards (Bryant & Gardiner 1979).

The house martin (Hirundinidae) is an aerial insectivore that breeds in the Palaearctic and winters in the Afrotropical and Oriental regions (Turner 1989). It is typically colonial though small groups and isolated individual nests are frequent. The house martins arrive at their breeding sites in late April and early May. Breeding commences almost immediately. Both male and female incubate the clutch of 2 to 5 eggs and feed the nestlings until fledging. All broods are raised monogamously, and one or two broods are raised during the season (Bryant 1975a, 1989; Turner 1989). The nestlings in a brood may not all be fathered by the same male because of extra-pair copulations by the female (Riley *pers. comm.*).

House martin nestling faecal sacs are removed from the nest by the parents until Day 8 when nestlings start to defaecate onto the ground immediately below the nest entrance (Bryant & Gardiner 1979). This behaviour provides an accurate record of the daily dietary intake of a brood of house martins from Day 9, if it is assumed that faecal mass is proportional to the fresh mass of insects fed to the nestlings (Bryant & Gardiner 1979, Feltham 1987), as has been demonstrated in other Hirundines (Bryant & Bryant 1988). The other characteristics that make the house martin suitable for a dietary study are its colonial nesting which provides a large sample size in a small area, and its tolerance of the disturbance involved in such studies (Bryant 1978a).

House martin nestlings are fed exclusively on insects caught on the wing by both parents (Bryant 1975a, 1978a). Insects contain a high percentage of protein. Samples of aerial insects present in Hirundine diets showed they contained 65% protein by dry weight (Turner 1980, 82). This protein has greater quantities of sulphur-containing amino-acids essential for feather growth (Murphy & King 1986b) than vegetable protein (Tristram 1953). Protein is an is an essential requirement for nestling growth (Ricklefs 1983).

Therefore natural diet of house martin nestlings was therefore considered a 'high' quality diet in this study, assuming protein to be a limiting factor to growth of house martin nestlings.

The experimental approach requires that nestling diet quality be manipulated so that different treatments experience different qualities of nestling diet. It is difficult to increase nestling diet quality because the natural diet is high quality and also because house martin parents may compensate in the food they deliver to nestlings. These problems may not apply to an experimental reduction of diet quality using a high energy dietary supplement. There is evidence that parents feed nestlings according to their energy demand and that when energy requirements are satiated the parents may feed nestlings on the basis of nutrient content (Tinbergen 1981; Grundel 1990). A high energy supplement, containing negligible amounts of nutrients, would supply the nestlings with a proportion of their Daily Energy Requirement (DER) thereby reducing the intensity of nestling begging. Parental feeding rate would in turn be lower, reducing the amount of insect food consumed by nestlings, consequently reducing the amount of protein consumed by nestlings receiving the supplement in comparison to naturally fed nestlings in the control. The energy intake of nestlings in both treatments will be similar but the intake of nutrients will be greater in the control. This technique is advantageous because parents will not compensate for the supplement because they respond to nestling begging as a cue (Bengtsson & Ryden 1983). It also has the advantage of being independent of variation in natural food abundance, unlike food supplement experiments where the supplement is provided to the parents.

3.2 METHODS

Two replicates of the following experiment were performed during the study, one in the summer of 1988 and one in the summer of 1989. The methods for each replicate were identical.

3.2.1 *Population*

The population of house martins used in this study was the colony of 10 to 15 pairs that nest on the University of Stirling library (NS 807 965).

This population had been used in previous studies of house martin biology (Feltham 1987). These studies provided the colony with an excess of artificial nest boxes (Plate 3.1) constructed of cement and sawdust, which were attached to brackets on the underside of the second floor ledge (3 metres above the first floor ledge) that allowed easy removal and replacement of the nest boxes for breeding studies. The design of the artificial nest boxes was altered for this particular study, so a ladder was no longer needed for checking the nest boxes. An aluminium nut was glued to the bottom of the nest box and the corresponding aluminium bolt was attached to a wooden pole so that the nest boxes could be removed from the brackets by use of the pole. This procedure minimised the time involved in removing a nest box, thereby reducing disturbance to the colony. Pairs were encouraged to use the artificial nest boxes by the destruction of natural nests upon partial completion. If a pair persisted with building they were left to complete the nest so that they did not desert the colony.

3.2.2 *Nestling diet quality*

Pork fat was used as the high energy supplement in this experiment. The mean DER of a brood of four house martin nestlings (Day 0 to Day 20) was obtained from Bryant & Gardiner (1979). These values were converted to the mean DER of an individual nestling. The digestible energy of pork fat (36.1 kj g^{-1}) for poultry was obtained from Scott *et al.* (1982). Digestible energies for poultry are not necessarily applicable to wild birds (Martin 1968) and a converted value of 21 kj g^{-1} was used for the experiment using the 60% dry mass assimilation efficiency figure calculated by Feltham (1987) in a study of house martin nestling digestion (cf. 52% for *Hirundo tahitica*, Bryant & Bryant 1988). The mass of pork fat required to satiate the mean DER of a house martin nestling was calculated for Day 0 to Day 20 (Table 3.1). This mass was not expected to satisfy the DER of all nestlings because the mass of fat was equivalent to the *mean* DER (Bryant & Gardiner 1979), not the maximum DER, so it would be expected that some nestlings in the FATFED treatment would still beg and receive food from their parents despite being fed the supplement. Also, it was expected that some fat would pass undigested through the gut of the house martin nestlings because of the large mass of fat fed at each feed.

Fresh pork fat was bought on the day of slaughter and cut into the masses calculated in Table 3.1. These pieces were kept in a freezer until use. Nestlings

Table 3.1 Derivation of mass of fat equivalent to the mean Daily Energy Requirement of house martin nestlings during growth from data in Bryant & Gardiner (1979).

Plate 3.1 Artificial nest *in situ*, with infra-red sensor.

Table 3.1 Derivation of mass of fat equivalent to the mean Daily Energy Requirement of house martin nestlings during growth from data in Bryant & Gardiner (1979).

Day[a]	Daily Energy Requirement of brood of 4 (kj)	Daily Energy Requirement per nestling (kj)	Mass of Fat (g)[b]
01	8.4	2.20	0.10
02	21.0	5.25	0.25
03	42.0	10.50	0.50
04	54.6	13.65	0.65
05	71.4	17.85	0.85
06	84.0	21.00	1.00
07	113.4	28.35	1.35
08	138.6	34.65	1.65
09	168.0	42.00	2.00
10	184.8	46.20	2.20
11	184.8	46.20	2.20
12	189.0	47.25	2.25
13	180.6	45.15	2.15
14	172.2	43.05	2.05
15	155.4	38.85	1.85
16	138.6	44.65	1.65
17	117.6	29.40	1.40
18	100.8	25.20	1.20
19	92.4	23.10	1.10
20	88.2	22.05	1.05

a - Date of Hatch = Day 0
b - assuming a Digestible Energy of 21 kilojoules g^{-1}

were fed from Day 3 to Day 16 because the nestlings were too weak to accept the fat until Day 3 and they were too animated to be fed from Day 17 onwards. The nestlings were fed twice a day, half the prescribed mass before 10.00h and half after 14.00h, to reduce the damage to nestlings through excessive gut expansion or excessive stress on digestive processes. The fat was chopped into small pieces using a scalpel. These pieces were placed in the mouth of a nestling (Plate 3.2). Nestlings usually swallowed voluntarily, however if a nestling refused the fat, it's mouth was prised open and the fat was placed in the back of the mouth where it was swallowed by reflex. Nestlings were not fed on days when they did not swallow food easily. This occurred very infrequently such as when they were subject to extreme cold stress or if they were unhealthy (e.g. sluggish, closed eyes).

3.2.3 *Monitoring nestling diet quality*

Two methods were used to determine if nestling diet quality differed between the experimental FATFED treatment and the Control. Both assessed the validity of the assumptions implicit in the experimental manipulation of diet quality in the FATFED treatment (Section 3.2.2).

3.2.3.1 *Parent feeding rate*

The experimental alteration of diet quality in this experiment assumed that nestlings in the FATFED treatment would beg less than nestlings in the Control and therefore receive fewer feeding visits from parent birds than nestlings in the Control. The validity of this assumption was assessed by measuring the number of feeding visits made to nests in each treatment during the experiment.

House martin parents enter the nest to feed the nestlings until Day 6 (Cramp *et al.* 1988) but from Day 6 onwards the parents increasingly feed the nestlings by perching at the entrance of the nest and putting their head into the nest. This behaviour was used to measure the number of feeding visits to a nest.

An infrared beam across the entrance of a nest will be blocked each time a bird arrives at the entrance and places its head inside the nest. When the adult withdraws its head the beam will be restored. An infrared sensor at the opposite side of the nest entrance to an infrared emitter can detect the blockage and restoration of the infrared beam (i.e. a parental feeding visit). This principle

Plate 3.2 House martin nestling being fed a piece of fat.

was used in the construction of a sensor to record the feeding visits of house martin parents.

The sensor could monitor two nests simultaneously. The overlap of nestling periods made it impossible to record feeding visits for all nests in the study so analysis of feeding visits was restricted to only a sample of nests in each treatment.

An infrared emitter (RS 635-296) was placed at one side of the nest entrance, directing a narrow beam towards an infrared sensor (RS 635-303) at the opposite side of the nest entrance. The sensor emits a voltage that varies in strength according to the intensity of infrared light it receives. The more intense the infrared light then the higher the voltage emitted. Blockage of the infrared beam greatly reduces light intensity, producing a distinct drop in the voltage emitted by the infrared sensor. The voltage rises to its previous level when the beam is restored. This switch in voltage was processed into a signal compatible with the RS 243 interface of a BBC microcomputer using an interface circuit designed and constructed in collaboration with the Academic Computing Support Group at the University of Stirling (Appendix 1). The circuit could process information from two nests simultaneously. A BBC BASIC program (Appendix 2) was written which used the signal from the interface to record the time at which the beam was blocked, the time at which the beam was restored and the duration of the blockage (i.e. the duration of the visit) for each nest. The duration of the blockage was used to filter out other causes of blockage such as nestlings begging, nestlings defaecating and adults entering and leaving the nest. Feeding visits blocked the beam for between .5 and 4 seconds (*pers. obs.*) whereas the other blockages were usually shorter than 0.5 seconds (*pers. obs.*). Only beam-blockages within this time range were recorded by the program.

A data logger stored this information on memory chips with a storage capacity of 8000 bytes, sufficient for 2 to 3 days' data. The BASIC program was synchronised with real time so that the sensor only operated from 10.00h to 21.00h each day. The sensor was started at 10.00h so that it was synchronised with the collection of faeces (Section 3.2.3.1) and the emptying of the suction trap (Section 3.2.4). Feeding visits were usually finished by 21.00h (*pers. obs.*), although when insect abundance is low parents feed until night falls (Bryant & Westerterp 1980). The University library opened at 09.00h on weekdays. The time until 10.00h was used to transfer data from the data logger to

a 5" floppy disc. Data were transferred from the discs onto the VAX mainframe using a BBC program. The data recorded by the sensor for an hour each day for each nest were compared with a visual record of feeding visits to the nest for that hour. The ratio of observed feeding visits to the number of visits recorded by the sensor (between 0.7 to 1.3) was used to calibrate the sensor data for each nest, for each day. The resultant value did not measure the actual number of feeding visits but was used as an index of the number of daily feeding visits. This index was divided by brood size to give an index of the number of feeding visits per day per nestling. This was the value used to test for differences in feeding visits between the FATFED treatment and the Control.

3.2.3.2 *Nestling faecal output*

Vinyl floor tiles were placed immediately below each nest. Nestling faeces were scraped off each tile at 10.00h (synchronous with feeding visit sensor (3.2.3.1) and suction trap (3.2.4)) using a plastic spatula. The faeces were placed in a plastic sachet which was sealed and placed in a freezer. The faecal samples were dried in a freeze drier to constant mass (3 days) and then weighed. The dried samples were placed in a SOXHLET apparatus (5:1 diethyl ether:chloroform)for 8 hours to remove lipid matter and the fat-free faecal mass was then measured. This value was divided by brood size to give a mean fat-free faecal mass per nestling for each nest for each day. This was the value used to test for differences between the FATFED treatment and the Control in the mass of insect food fed to the nestlings.

3.2.4 *Insect abundance*

The abundance of aerial insects varies considerably between breeding seasons and within breeding seasons (Bryant 75a; Turner 82). Differences between treatments in nestling diet may be caused, therefore, by differences in the natural food abundance experienced by the parents in each treatment. This possibility was investigated using data on the aerial insect abundance experienced by the colony provided by a suction trap in the grounds of the University.

The suction trap samples air vertically downwards at a height of 12.2m. The trap samples from a randomly distributed aerial insect population. It is non-selective for size and is neutral in attraction (Bryant 1978a; Turner 1982; Jones 1985). Massive insects not normally eaten by house martins (e.g. bumble bees *Bombus* sp.) were removed from samples before the volume of the catch was

measured. House martins feed lower to the ground than the height of the suction trap in poor weather conditions (Turner 1982; Waugh 1980). Values of insect abundance from hand-net sampling at 0.2-2m above ground are positively correlated, however, with suction trap volumes (Jones 1985) so the suction trap catch volumes still serve as an index of the insect abundance experienced by the house martins when they are foraging in poor conditions.

Samples were removed at 10.00h daily and stored in 10:1 methanol: glycerol solution. The settled volume of the catch was estimated in a measuring cylinder. Volumes were log-transformed because house martin breeding biology (feeding visits) is thought to have a logarithmic relationship to aerial insect abundance (Bryant 1975a, 1978a). This log-transformed value was used to test for differences between the FATFED treatment and the Control in the aerial insect abundance experienced by parents during the nestling period.

3.2.5 *Nestling energetics*

The growth of nestlings may be affected by their activity during the nestling period (Bryant & Gardiner 1979). The more energy nestlings expend by respiration in activity or in maintenance of homeothermy, the less energy remains for growth. Any difference in growth between the Control and the FATFED treatments could then be a result of a difference in respiration rates of nestlings between them. Of particular interest was whether the costs of begging, an activity lowered in the FATFED treatment, had a significant effect on nestling energy expenditure. This possibility was investigated in this experiment by use of the doubly-labelled water technique for measuring energy expenditure in free living animals.

The doubly-labelled water technique, first described by Lifson, Gordon & McClintock (1955), measures carbon dioxide output and hence daily energy expenditure. The oxygen of respiratory carbon dioxide is in isotopic equilibrium with the oxygen of body water, thus by injecting water doubly-labelled ($D_2{}^{18}O$), the oxygen of respiratory carbon dioxide and water are labelled. The deuterium labels the hydrogen of body water. The difference in turn-over rates between the labelled hydrogen (lost in expired water) and labelled oxygen (lost in expired water and carbon dioxide), measures the oxygen turnover due to carbon dioxide alone. This value is used to calculate energy expenditure to an accuracy of $\pm 4\%$

(Nagy 1980).

There are problems associated with the use of this technique in studies of nestling energetics, as there may be differential incorporation of the isotopes at non-exchangeable sites in the body (Williams & Nagy 1985; Williams & Prints 1986; Weathers *et al.* 1990). Also the water pool in the body decreases in size through growth (Konarzewski 1988) and this may influence the concentration of isotope in the body water. These effects are likely to be small (Williams & Nagy 1985; Weathers *et al.* 1990), however, and are unlikely to influence treatment differences in energy expenditure in this study.

3.2.5.1 *Field protocol*

House martin nestlings were removed from their nests on Day 14, between 07.00h and 09.00h, and their body measurements were taken. A calculated volume (nestling mass(g) * 0.005 ml) of a solution containing doubly-labelled water (20 atom% ^{18}O, 10 atom% D) was injected into the peritoneal cavity of the nestling. The nestling was left in a bird bag for one hour to allow for equilibration of the stable isotope labels with the body water. Blood samples were collected from a vein in the leg or wing into 5-10µl capillary tubes which were sealed using a flame torch. A second series of blood samples was taken 24 hours later. Once sealed, samples could be kept indefinitely for laboratory analysis.

3.2.5.2 *Laboratory procedure*

The blood samples were analysed in the Life Sciences Laboratory at the Scottish Universities Reactor Research Centre on the National Engineering Laboratory campus at East Kilbride.

The hydrogen/deuterium fraction of the blood was obtained by distilling water out of the blood under vacuum and passing it through a heated (800°C) uranium furnace. The water oxidises the uranium to liberate hydrogen/deuterium gas which is collected on activated carbon for subsequent analysis (Sackett 1978). The carbon dioxide fraction was obtained by microdistillation of blood water into a tube containing guanadine hydrochloride (Dugan *et al.* 1985). The tube was flame-sealed under vacuum, then baked in a muffle furnace (250°C) for ten hours. The guanadine tube was then broken under vacuum in a vessel containing 100% phosphoric acid, and the whole glass assembly was placed in an oven (80°C) for one hour. This releases the carbon dioxide. The carbon dioxide was then purified by freezing down into collection

vessels with liquid nitrogen under a vacuum. An isotope ratio mass spectrometer analysed hydrogen (X22VG.SIRA 9) and carbon dioxide samples (VG SIRA 10). Samples were analysed in duplicate to ensure that errors were identified. The mean value was used for analysis.

3.2.6 *Daily temperature*

The maximum daily temperatures during the experiment were recorded from a weather station at the site of the suction trap. The temperature was recorded as a supplement to the energy study because ambient temperature may influence the energy expenditure of nestlings in terms of the cost of homeothermy (Murphy, M.T. 1985). Differences between treatments in daily ambient temperature during the nestling period may result in differential costs of homeothermy between treatments which could result in differences between treatments in the energy available for growth.

3.2.7 *Nestling growth*

Five parameters of nestling and adult body size were measured during the experiment, as summarised below.

Body Mass (MASS) (g, 1 decimal place) - whole body mass, using a Pesola 100g spring balance.

Wing Length (WING) (mm)- the length of the maximum wing chord, using a stopped rule (150mm).

Tarsus Length (TARS) (mm, 2 dp)- the distance from beneath the elbow to the top of the tarsus, using dial calipers.

Head & Bill Length (HEAD) (mm, 2 dp)- the maximum length from the back of the head to the tip of the bill, using dial calipers.

Keel Length (KEEL) (mm, 2 dp)- from the tracheal pit to the posterior edge of the sternum, using dial calipers.

Nestlings were measured daily from Day 3 until Day 10 and once every two days from Day 10 until nestlings had fledged. All measurements were made between 08.00h and 11.00h. Fledging age is difficult to measure in house martins as nestlings return to the nest frequently after their first flight and the process of fledging takes five or six days to complete (Bryant 1975a). Age of fledging in this experiment was measured as the earliest age at which nestlings attempted to fly from the nest when the nest was removed from its bracket. KEEL was only measured from Day 20 onwards as the keel was too flexible at an earlier age to obtain a reliable measurement.

The First Principal Component (PC1) was used as an overall measure of body size (Section 2.2.3.3). It was calculated using WING, TARS, HEAD and KEEL measurements. MASS was not used as a variable in the calculation of PC1 because the peaked mass growth of house martin nestlings (Bryant & Gardiner 1979) means that MASS is not an accurate measure of nestling size at Day 20.

Parent birds were caught during incubation by placing a hand-held mist net over the entrance of the nest and then disturbing the nest until the bird(s) flew into the net. All five body dimensions were measured as described above. Parents were sexed by examining the extent of the brood patch (Bryant 1975b).

3.2.8 *Statistical analysis*

Statistical analysis of the data collected for this experiment was complicated by two factors. One of these factors was the presence of first and second broods within the data set for each year. These broods were not strictly independent and should have been analysed separately. One second brood in each year, however, was reared by a female with a different male and these different pair combinations were assumed to be independent. The remaining second broods were few in number (1 in 1988, 2 in 1989) and it was assumed that they were not an important source of bias in the analyses.

A similar problem arose when data from 1988 and 1989 were analysed together. Some birds bred in both years and thus, the data were not strictly independent. Only four out of 18 adults which bred in 1989, however, had bred in 1988. These four adults were also older and more experienced than in the previous year and may have exhibited a different breeding behaviour in 1989

than in 1988 (Dhondt 1989; Languy & Wansteenwegen 1989). It was assumed for these reasons that this factor was not an important sense of bias and that 1988 and 1989 could also be treated as independent in this respect.

3.3 RESULTS

The notation for analyses and results is as described in Section 2.3 .

3.3.1 *House martin breeding data*

There was no significant difference between treatments in any of the breeding parameters for 1988 or 1989 (M-W, $p > 0.05$ for all tests, Table 3.2), except for fledging age in 1989, which was significantly greater in the FATFED treatment than in the Control (M-W, $u=33$, $n_c = 20$, $n_t = 13$, $p < 0.01$).

There was no significant difference between years in breeding parameters but both Date of First Egg (DOE) and Date of Hatch (DOH) were almost significantly later in 1989 than in 1988 (M-W, $u=32$, $n_{1988} = 11$, $n_{1989} = 11$, $p = 0.061$).

3.3.2 *Success of fat feeding*

During the fat feeding period in 1988 and 1989 the mass of faecal fat per nestling of the FATFED treatment was greater than that of the Control (Figs 3.1 & 3.2). This difference was significant for each day from Day 10 to Day 17 for 1988 and from Day 7 to Day 17 in 1989 (M-W, mean mass per nestling was weighted by brood size, $p < 0.05$). After Day 17 the faecal fat content in the FATFED treatment declined to a value similar to that of the Control from Day 17 to Day 20. The mass of faecal fat was between 15% and 35% of the mass of fat fed to nestlings during the nestling period, 27% on average in 1988 and 24% on average in 1989 (Figs 3.1 & 3.2). There was no significant difference between years in the percentage of fed fat present in nestling faeces per day or in total for the nestling period (M-W, $p > 0.2$).

Less fat was fed early on to nestlings in the FATFED treatment in 1989 in comparison to nestlings in the FATFED treatment in 1988 (Figs. 3.1 & 3.2). These nestlings had received 2 g less fat on average by Day 12 although this difference was recovered by Day 17. The difference between years early in the nestling period was the result of a methodological error from Day 6 to Day 8 in 1990 when nestlings received half the quantity of fat prescribed.

Table 3.2 **Summary of House Martin breeding data for 1988 & 1989 (mean and standard error).**

Year	Treatment	N	Date of Hatch[a]	Clutch Size	Brood Size	Fledged Young	Age at Fledging[b]
1988	Control	6	67 (10)	3.5 (.4)	3.3 (.3)	3.0 (.5)	23.7 (.6)
	FATFED	5	54 (09)	4.4 (.3)	3.8 (.5)	2.4 (.5)	24.6 (.6)
1989	Control	7	79 (10)	3.4 (.2)	3.2 (.3)	2.9 (.3)	23.2 (.4)
	FATFED	4	70 (11)	4.0 (.0)	3.7 (.3)	3.3 (.5)	25.4 (.4)

a - Day 0 is May 1st

b - Age in days from Day 0 (Date of Hatch)

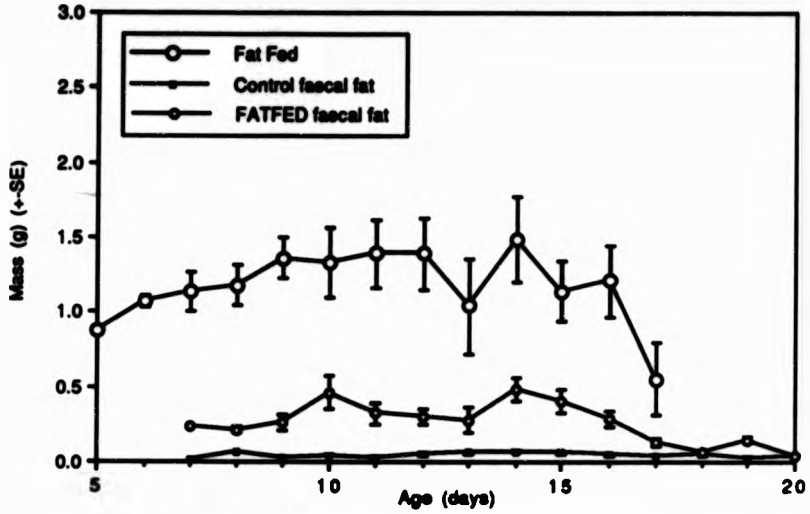

Figure 3.1 Mass of fat fed, and faecal fat per nestling in the Control and FATFED treatments, 1988.

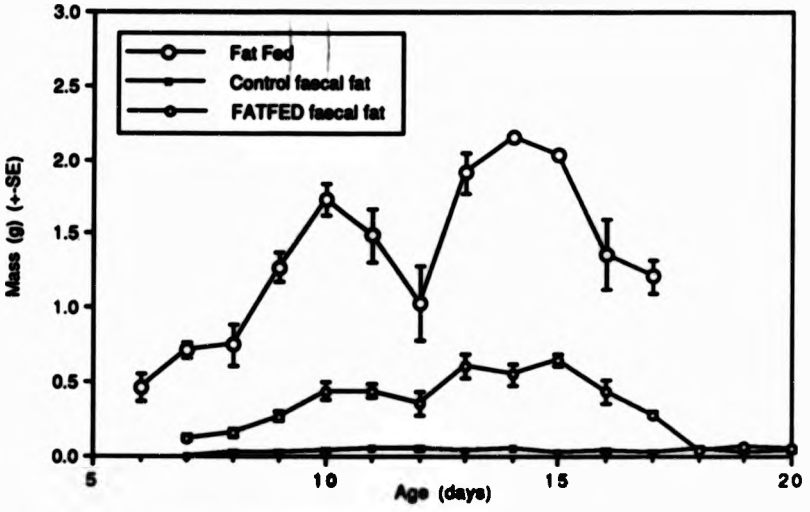

Figure 3.2 Mass of fat fed, and faecal fat per nestling in the Control and FATFED treatments, 1989

3.3.3 *Parental feeding visits*

3.3.3.1 *Comparison of parental visit index between treatments*

The number of parental visits to the nest was greater in the Control than in the FATFED treatment from Day 8 to Day 16, for both 1988 and 1989 (Figs 3.3 & 3.4). From Day 17 onwards, after the end of fat feeding, the visits to nests in the FATFED treatment increased to the same level as the nests in the Control. In 1988 the number of visits increased to a greater level than in the Control.

3.3.3.2 *Relationship of faecal mass to visit index*

The relationship of fat-free faecal mass per nestling to parental visit index per nestling was investigated by regression for both 1988 and 1989 (Figs 3.5 & 3.6). The significant linear relationships indicate that the visit index was an accurate index of the number of feeding visits made to a nest in each year, assuming feed mass was constant.

The regression equations for 1988 and 1989 were not significantly different (t-test of slope, $t = 0.22$, $df = 83$, $p > 0.5$) indicating that the sensor operated similarly in each year.

3.3.3.3 *Fat-free faecal mass*

In both 1988 and 1989 fat-free faecal mass per nestling was greater in the Control than in the FATFED treatment during the period of fat-feeding (Figs 3.7 & 3.8). After Day 17 the fat-free faecal mass of the FATFED treatment increased to the same level as that of the Control. There was a difference in pattern between years. In 1988 the fat-free faecal mass of nestlings in the Control peaked at Day 14 whereas in 1989 it peaked at Day 11. The fat-free faecal mass of nestlings in the FATFED treatment rose sharply in 1988 after fat-feeding ceased. This rise in mass was not present in the FATFED treatment in 1989. The trends in both treatments were more erratic in 1989 than in 1988. This was probably the result of natural food variation

3.3.3.4 *Factors influencing fat-free faecal mass*

The relationship of fat-free faecal mass per nestling to other experimental variables was investigated by means of a stepwise multiple regression (Sokal & Rohlf 1981, Table 3.3). The mass of fat fed per nestling was the most important

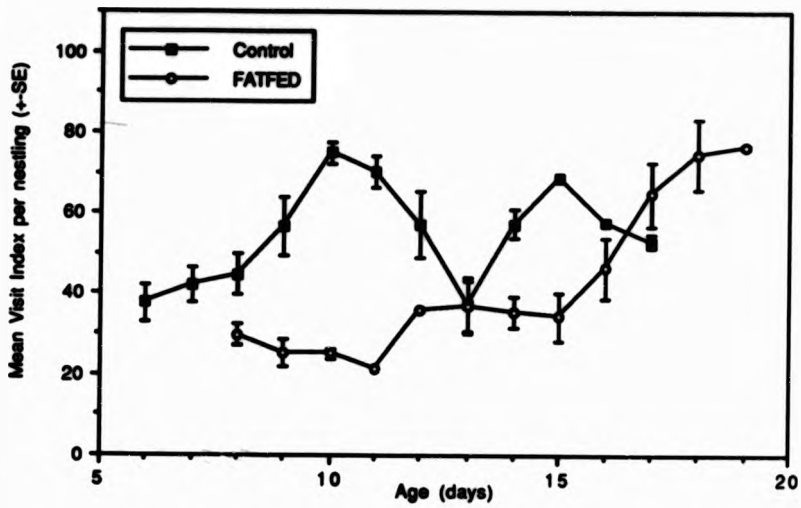

Figure 3.3 House martin parental visits, 1988.

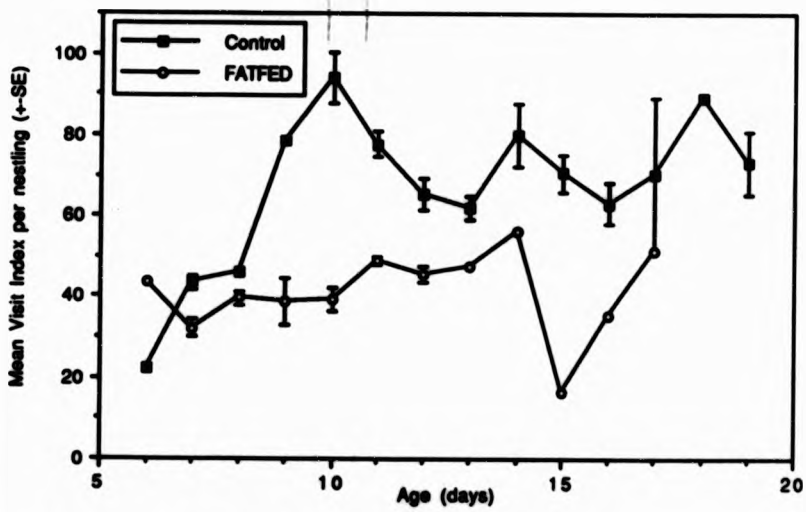

Figure 3.4 House martin parental visits, 1989.

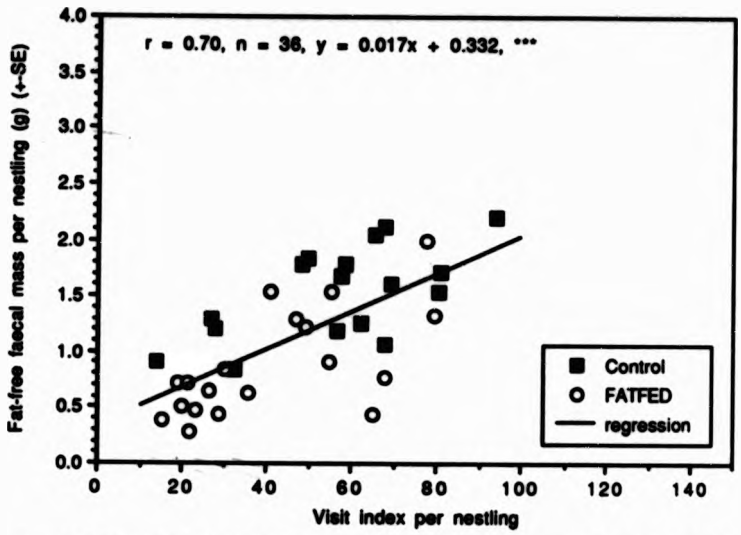

Figure 3.5 Relationship of faecal output to visit index, 1988.

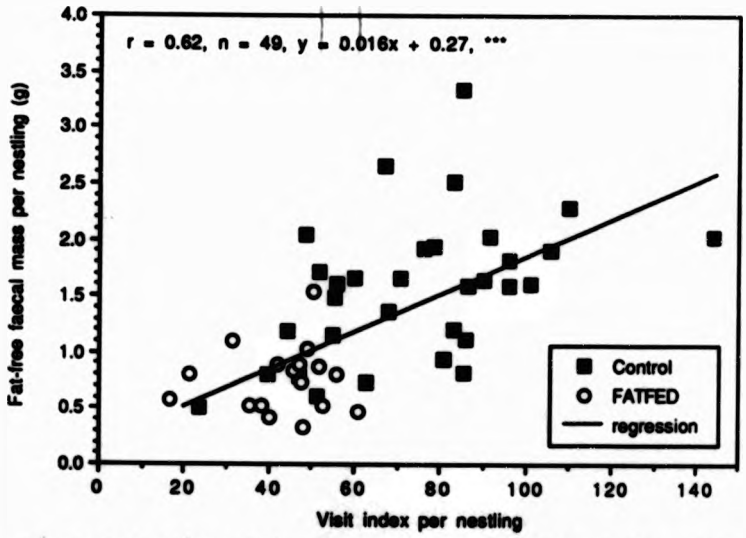

Figure 3.6 Relationship of faecal output to visit index, 1989.

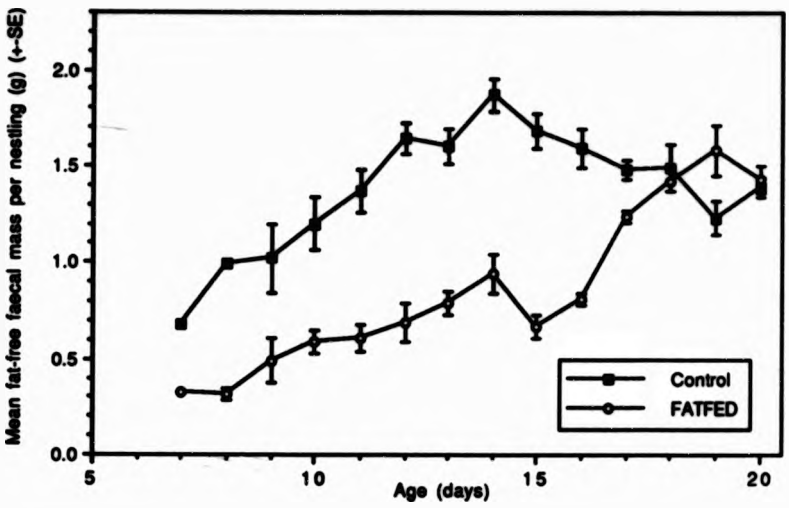

Figure 3.7 House martin nestling faecal output, 1988.

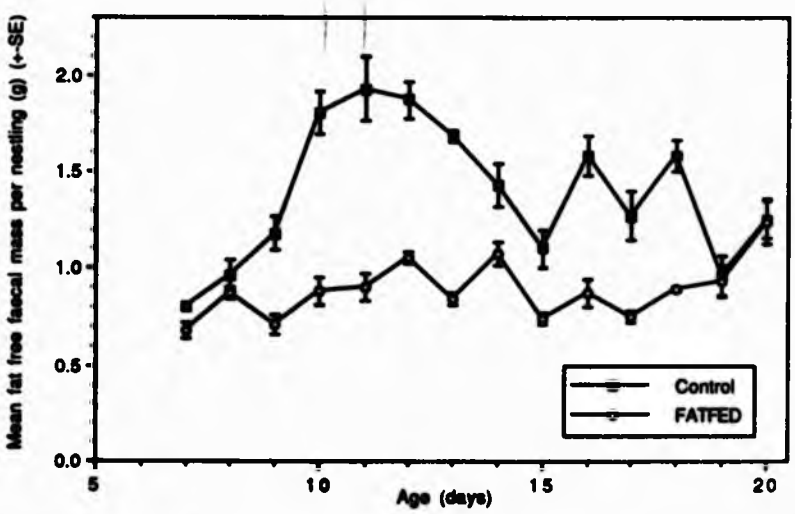

Figure 3.8 House martin nestling faecal output, 1989.

Table 3.3 **Stepwise multiple regression[a] of the relationship to fat-free faecal mass per nestling of the mass of fat fed per nestling (indfed), nestling age, log-transformed insect abundance (insect), brood size, year and maximum daily temperature.**

Variable	r^2_{eq}[b]	T	sig	F_{eq}	df	sig	beta[c]
indfed	.1039	-7.9	•••	41.1	1,354	•••	-.322
Age	.1567	-4.7	•••	32.8	2,353	•••	-.247
Insect	.1659	1.98	•	23.3	3,352	•••	.097

a - variables were rejected if p > 0.05 for T
b - correlation efficient for equation
c - dimension and direction of relationship for that variable.

factor determining fat-free faecal mass per nestling: the more fat fed the lower the fat-free faecal mass. A similar negative relationship was present between nestling age and fat-free faecal mass per nestling. The effect of age was not as pronounced as for the mass of fat fed (i.e. beta was smaller). There was also a weak positive relationship of fat-free faecal mass per nestling to insect abundance.

These three variables together explained only 17 per cent (r^2_{eq} x 100) of the variation of fat-free faecal mass per nestling. This is a small percentage but it is to be expected given the experimental errors in measurements of all variables, the relatively small sample size of the experiment and the inherent variability of natural systems.

3.3.4 *Insect abundance*

3.3.4.1 *Treatment differences*

There was little difference between treatments in insect abundance during the nestling period for both 1988 and 1989 (Figs. 3.9 & 3.10). Mann-Whitney U-tests showed no significant difference between treatments for any day during the nestling period.

3.3.4.2 *Year differences*

The only difference in insect abundance between years was late in the breeding season during September when insect abundance was consistently higher in 1988 than in 1989 (Figs 3.11 & 3.12). At this late stage most broods had fledged in both years.

3.3.5 *Daily temperature*

3.3.5.1 *Treatment differences*

There were no apparent differences between treatments in the maximum daily temperatures during nestling growth (Figs 3.13 & 3.14) except for a higher temperature in the FATFED treatment in 1989, from Day 6 to Day 10.

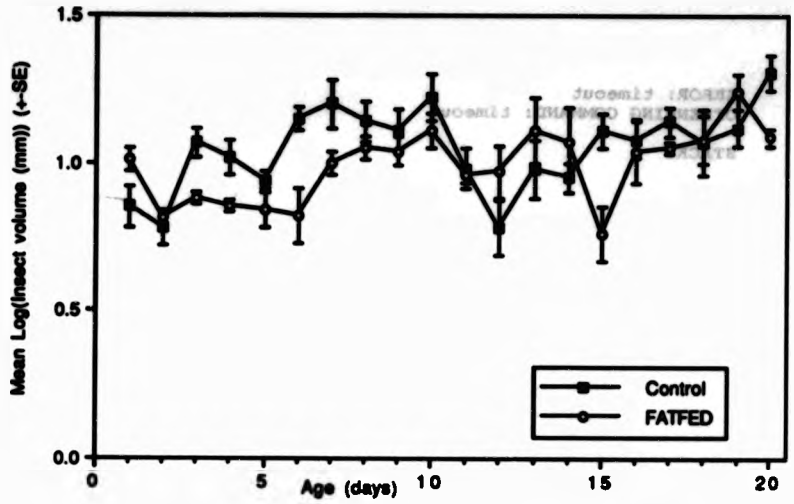

Figure 3.9 Aerial insect abundance during growth, 1988.

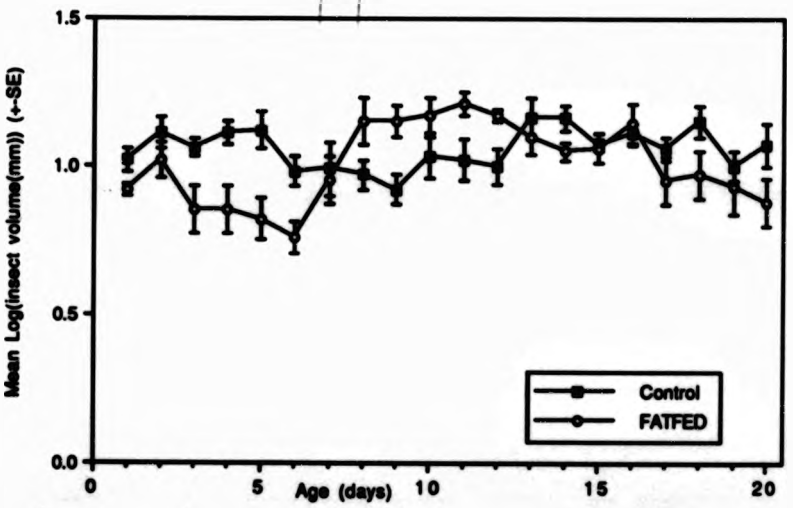

Figure 3.10 Aerial insect abundance during growth, 1989.

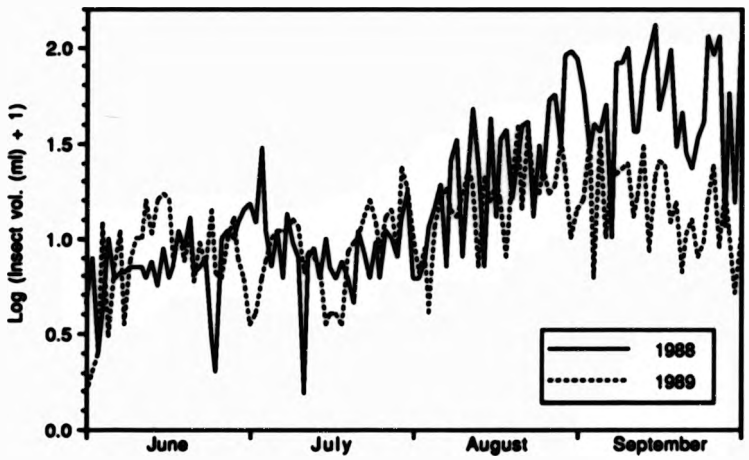

Figure 3.11 Daily insect abundance during the breeding season.

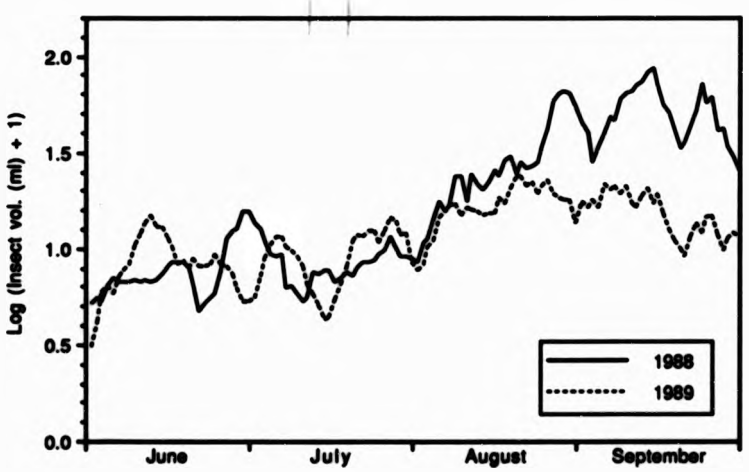

Figure 3.12 Five day running average of insect abundance during the breeding season.

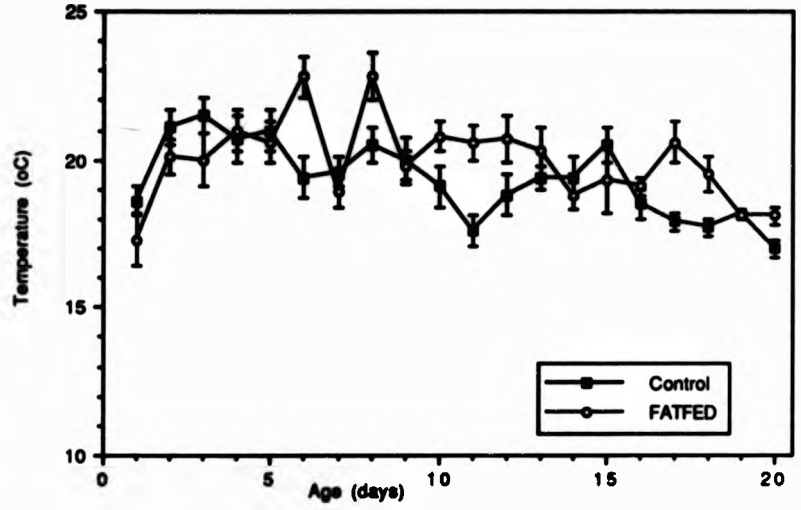

Figure 3.13 Maximum daily temperature during nestling growth, 1988.

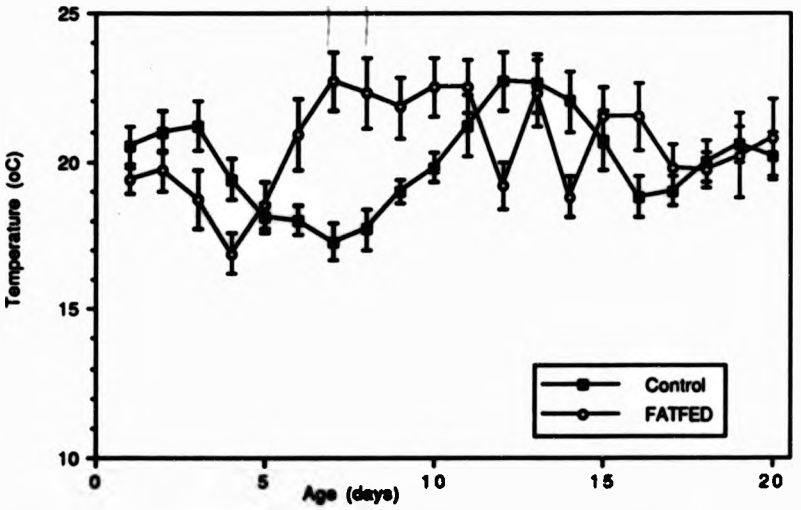

Figure 3.14 Maximum daily temperature during nestling growth, 1989.

3.3.5.2 *Year differences*

Comparison of the graphs for 1988 and 1989 indicated little difference between years in the maximum daily temperatures during growth. Maximum daily temperature ranged from 17 °C to 23 °C in both 1988 and 1989 although there was greater variability of temperatures in 1989.

3.3.6 *Nestling energetics*

There were no results from 1988 as the preliminary study in that year was used to gain familiarity with field techniques and it did not produce samples that could be used in the laboratory.

Analysis of the data was complicated by the difference in nestling diet composition between treatments. The respiratory quotient (RQ), which is used to calculate energy expenditure from carbon dioxide output, varies according to the substrate burnt for energy production. The RQ value for fat varies between different classes of fat (Weathers & Sullivan 1989) and an average fat RQ of 0.72 was used in this experiment (Masman 1986). This value was used to calculate energy expenditure for the FATFED nestlings as the abundance of fat and paucity of protein in the diet, would probably result in almost all the protein being diverted for growth deposition, and therefore not being used for the energy expenditure assessed by the doubly-labelled water technique. This would leave fat as the sole source of energy production.

The situation is more complicated for nestlings in the Control. The diet of control nestlings was aerial insects which contain a high proportion of protein (65% dry mass, Turner 1982) and a low proportion of fat (9% dry mass, Turner 1982). At this stage in house martin nestling development roughly half the energy available is burnt for respiration (Bryant & Gardiner 1979), and the other half is deposited for growth. The low amount of fat available in the diet for respiration almosty certainly means that protein was used as an energy source. Amino-acids, from digestion of protein, undergo gluconeogenesis when they are used as an energy source, and the process of gluconeogenesis affects the RQ value (Masman 1986). The RQ is about 0.92 when almost all the energy is obtained via gluconeogenesis of protein and about 0.74 when there is little gluconeogenesis (Masman 1986). The fat in the insect diet was probably used to provide energy in which case an intermediate level of gluconeogenesis was assumed. This resulted

in an estimated RQ value of 0.85 for the control nestlings. Calculations were also made with an RQ of 0.75 for the Control, to investigate the effect of variation in the RQ on the estimated energy expenditure of nestlings

There was no evidence of a difference between treatments in daily energy expenditure (Table 3.4, M-W, $n_c = 3$, $n_t = 7$, $U = 7$, $p > 0.5$), or daily energy expenditure/basal metabolic rate (Table 3.4, M-W, $n_c = 3$, $n_t = 7$, $U = 4$, $p > 0.1$) when an RQ of 0.85 was used . There was, however, a significant difference between treatments in DEE when an RQ of 0.75 was used (Table 3.4, M-W, $n_c = 3$, $n_t = 7$, $U = 1$, $p < 0.05$) so RQ determination is important when making comparisons between dietary treatments using the doubly-labelled water technique. Using corrected RQ values, nestling energy costs, as measured by the doubly-labelled water technique, did not differ between treatments.

3.3.7 *House martin growth*

House martin growth in 1988 and 1989 is plotted for each size parameter in Figures 3.15 to 3.22 . Most of these curves show a similar trend, with little difference at Day 5 in the size of nestlings in the FATFED treatment and the Control, then Control nestlings grew faster than the nestlings in the FATFED treatment reaching a larger size at Day 20. MASS (Figs. 3.15 & 3.16), however, peaked before Day 20 in both 1988 and 1989 and there was no difference between treatments by Day 20 in both years.

3.3.7.1 *Choice of growth curve*

Growth rates for each size parameter, for each nestling, were obtained as the value of k , the rate coefficient, from a fitted curve. The choice of either Logistic or Gompertz, was made by comparing the coefficients of determination of each curve for each size parameter using a Wilcoxon Matched-Pairs Test (Table 3.5).

3.3.7.2 *Standard error of k estimate*

The standard error of the estimate of k was compared between treatments and years using an ANOVA (Table 3.6). The values of standard error were log-transformed to obtain a normal distribution. The standard error of the estimate of WING k was significantly larger (Table 3.7) in 1988 than in 1989, so WING k was analysed separately for each year. The standard error of the estimate of

Table 3.4 House martin nestling energy expenditure at Day 14 in 1989 calculated by the doubly labelled water method.

Chick	Brood Size	Mass(g)	BMR[a]	DEE[b]	DEE/BMR	DEE[c]
FATFED						
1	4	24.5	43.4	81.5	1.88	-
2	4	24.7	43.6	79.5	1.82	-
3	4	23.1	41.6	76.7	1.82	-
4	4	23.4	42.0	71.2	1.70	-
5	2	26.3	45.6	107.3	2.35	-
6	4	25.2	44.2	69.9	1.58	-
7	4	26.7	46.1	92.7	2.01	-
Mean (SE)		24.8 (.5)	43.8 (1.6)	82.5 (5.0)	1.88 (.09)	
Control						
1	3	26.1	45.3	85.9	1.90	97.4
2	4	23.4	42.0	87.1	2.07	98.7
3	4	24.9	43.9	76.5	1.74	86.7
Mean (SE)		24.8 (.8)	43.7 (1.0)	83.1 (3.4)	1.90 (.09)	94.3 (3.8)

a - Basal Metabolic Rate (kj d^{-1}), from Aschoff & Pohl 1970 (BMR = 114.8 Mass (kg) $^{0.704}$)
b - Daily Energy Expenditure (kj d^{-1}), RQ = 0.72 for FATFED, RQ = 0.85 for Control (see text)
c - Daily Energy Expenditure (kj d^{-1}), RQ = 0.75 for Control (see text)

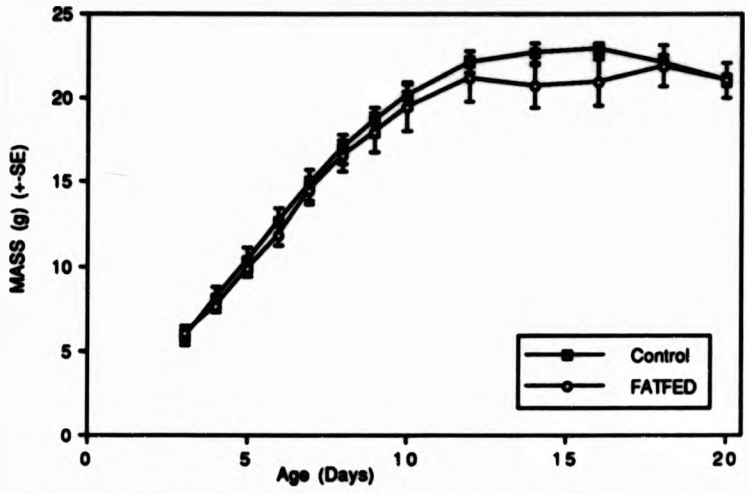

Figure 3.15 MASS growth of house martins, 1988

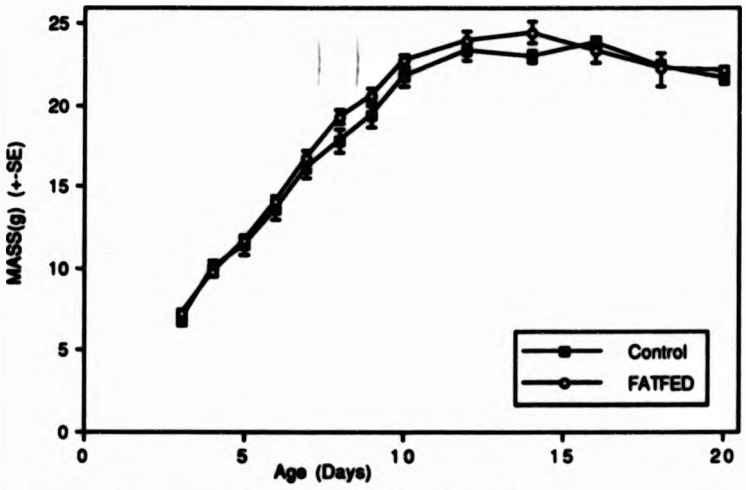

Figure 3.16 MASS growth of house martins, 1989

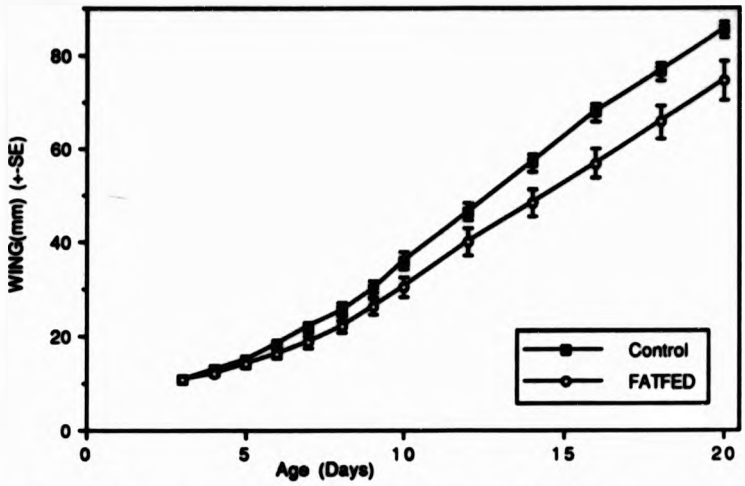

Figure 3.17 WING growth of house martins, 1988.

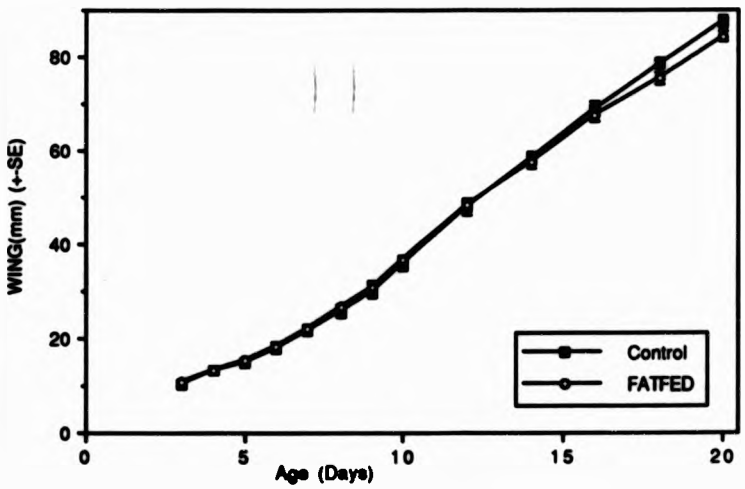

Figure 3.18 WING growth of house martins, 1989.

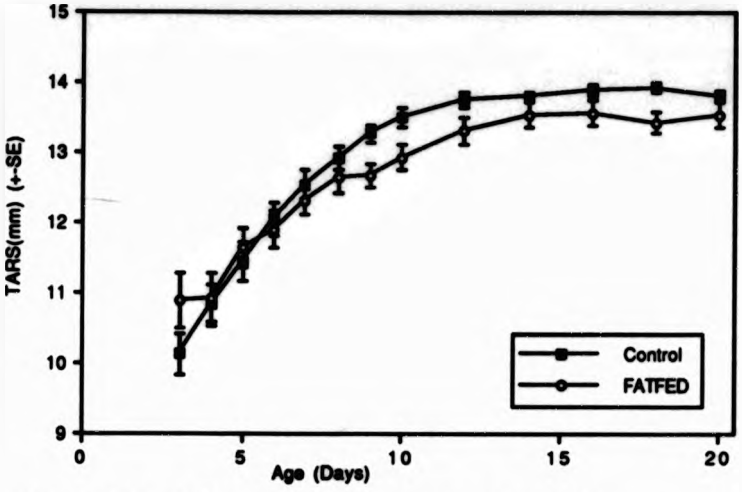

Figure 3.19 TARS growth of house martins, 1988.

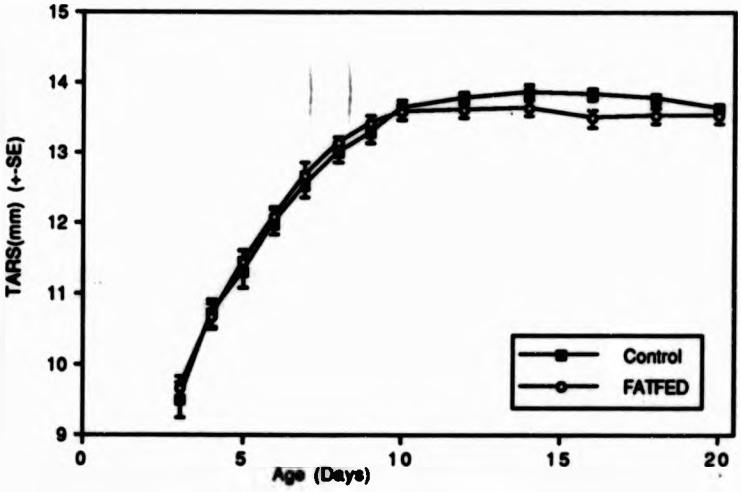

Figure 3.20 TARS growth of house martins, 1989.

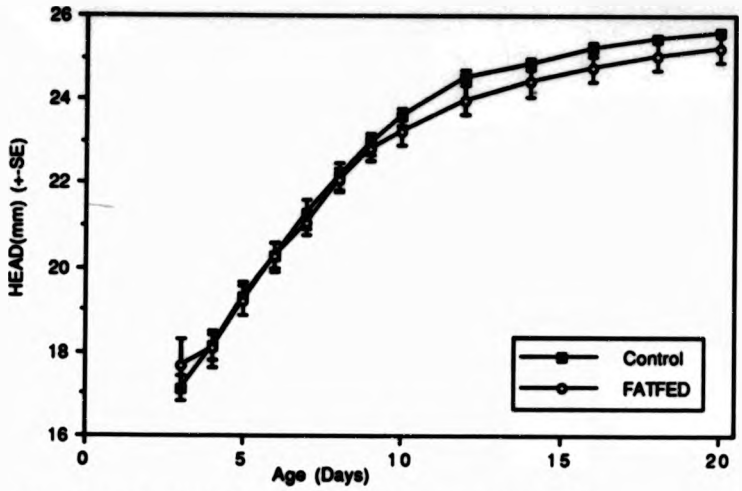

Figure 3.21 HEAD growth of house martins, 1988.

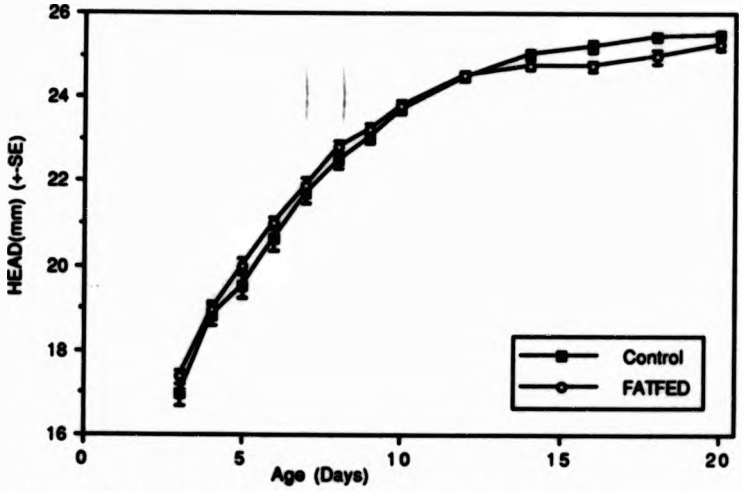

Figure 3.22 HEAD growth of house martins, 1989.

Table 3.5 **Comparison of the Logistic and Gompertz coefficients of determination (r^2) for house martin size parameters.**

	1988 (n=28)			1989 (n=31)			
Parameter	d[a]	Z	p	d[a]	Z	p	Growth Equation
MASS	.002	-2.78	* *	.001	-1.75	ns	Logistic
WING	.001	-2.92	* *	.001	-3.40	* * *	Logistic
TARS	.001	-1.99	*	.002	-4.39	* * *	Logistic
HEAD	.001	-1.95	ns[b]	.001	-2.83	* *	Logistic

a - d is the mean value of Logistic r^2 - Gompertz r^2.
b - p = 0.051

Table 3.6 **Comparison by ANOVA of the standard error (ln(SE+1)) of the estimate of *k* for house martin between treatments and years (N = 59).** (F values with significance level, df = 1 for all factors)

Parameter	Treatment		Year		Interaction
MASS	0.16	ns	0.16	ns	ns
WING	3.36	ns	5.66	*	ns
TARS[a]	3.85	ns	0.01	ns	ns
HEAD	6.88	*	4.94	*	ns

a - n = 58

Table 3.7 **Mean values of asymptotic standard error of estimate of house martin growth rate (k) for both treatments and both years.**

	1988		1989	
	Control (n=16)	Fatled (n=12)	Control (n=16)	Fatled (n=13)
Parameter	ln(SE+1)	ln(SE+1)	ln(SE+1)	ln(SE+1)
MASS	.035	.036	.036	.039
WING	.008	.011	.007	.007
TARS	.043	.045[a]	.039	.052
HEAD	.018	.022	.014	.018

a - n = 11

Table 3.8 **Comparison by ANOVA of k ($\ln(k+1)$) of house martin size parameters between treatments and years (N=59).** (F values with significance level, df = 1 for all factors)

Parameter	Treatment		Year		Interaction
MASS	.00	ns	.48	ns	ns
TARS[a]	.56	ns	25.80	**	ns

a - n = 58

Table 3.9 **Mean values and standard errors of house martin growth rate ($\ln(k+1)$) for both treatments and both years.**

	1988		1989	
	Control (n=16)	Fatled (n=12)	Control (n=16)	Fatled (n=13)
Parameter	$\ln(k+1)$	$\ln(k+1)$	$\ln(k+1)$	$\ln(k+1)$
MASS	.345 (.021)	.323 (.024)	.318 (.011)	.335 (.009)
WING	.192 (.003)	.184 (.003)	.206 (.002)	.205 (.003)
TARS	.288 (.014)	.267 (.018)[a]	.336 (.009)	.376 (.020)
HEAD	.214 (.007)	.217 (.009)	.229 (.006)	.247 (.007)

a - n = 11

HEAD*k* was significantly larger in the FATFED treatment than in the Control, and it was also significantly larger in 1988 than in 1989. Parametric analyses could not, therefore, be performed on HEAD *k*.

3.3.7.3 *Analysis of k*

MASS*k* andTARS*k* were compared between treatments and years by ANOVA (Table 3.8). TARS *k* was significantly larger (Table 3.9) in 1989 than in 1988. WING *k* was compared between treatments by a t-test for 1988 and 1989. There was no significant difference between treatments in 1989 ($t = .07$, $df = 29$, ns) but in 1988 WING *k* was significantly larger in the Control than in the FATFED treatment ($t = 2.06$, $df = 25$, $p < 0.05$).

HEAD*k* was significantly larger in 1989 than in 1988 (M-W, $n_{1988} = 27$, $n_{1989} = 30$, $U = 238$, $p < .01$) so years were analysed separately. There was no significant difference between treatments in either 1988 (M-W, $n_c = 15$, $n_f = 12$, $U = 83$, ns) or 1989 (M-W, $n_c = 19$, $n_f = 11$, $U = 63$, ns).

3.3.7.4 *Factors affecting the linear stage of growth*

The relationship of the linear stage of growth to experimental variables was investigated by means of a stepwise multiple regression (Table 3.10, Sokal & Rohlf 1981). MASS growth during the linear phase was greater in 1989 than in 1988 and lower in larger broods. WING growth was positively correlated with the fat-free faecal mass. It was also greater in 1989 than in 1988, when data up to Day 20 were analysed.

3.3.8 *Body size*

3.3.8.1 *Parental size*

Parental body size (Table 3.11) was compared between treatments, sexes and years by ANOVA (Table 3.12). There were no significant differences.

3.3.8.2 *Nestling size at Day 3*

Nestling size at Day 3 (Table 3.14) was compared between treatments and years by ANOVA (Table 3.13) to test for differences in size between treatments before fat-feeding began. There were no significant differences between years. Both MASS and TARS were significantly larger in the FATFED treatment than in

Table 3.10 Stepwise multiple regression[a] of the relationship of fat-free faecal mass per nestling (Fwt), brood size, year and maximum daily temperature, to the linear phase[b] of house martin growth.

Variable	r^2_{eq}	T	sig	F_{eq}	df	sig	beta
MASS							
Year	.208	3.16	• •	10.0	1,38	• •	.456
Brood size	.340	-2.72	• •	9.5	2,37	• • •	-.423
WING							
Day 10							
Fwt	.443	5.64	• • •	31.8	1,40	• • •	.666
Day 20							
Fwt	.152	5.49	• • •	25.5	1,142	• • •	.390
Year	.206	3.10	• •	18.3	2,141	• • •	.234
TARS							
no significant linear relationships							
HEAD							
no significant linear relationships							

a - variables were rejected if $p > 0.05$ for T

b - linear phase of growth is until Day 10 for all variables, extended until Day 20 for WING

Table 3.11 **Comparison by ANOVA of house martin parental size between treatments, sexes and years (n=24).** (F values with significance level, df = 1 for all factors)

Parameter	Treatment(T)		Sex(S)		Year(Y)		Interactions	
MASS	.54	ns	.14	ns	.06	ns		ns
WING	.32	ns	.00	ns	2.61	ns		ns
TARS	.13	ns	7.30	*	2.01	ns		ns
HEAD	.34	ns	2.37	ns	.75	ns		ns
KEEL	.07	ns	.09	ns	.58	ns	T-S	*
PC1	.18	ns	.89	ns	7.58	* *		ns

Table 3.12 **Mean values (x) and standard errors of house martin parental body size for both treatments in each year.**

	1988				1989			
	Control (n=12)		FATFED (n=10)		Control (n=14)		FATFED (n=8)	
Parameter	x	se	x	se	x	se	x	se
MASS	19.02	.20	18.94	.35	18.84	.30	19.36	.17
WING	111.60	.70	111.90	.50	112.50	.50	112.80	.50
TARS	13.83	.07	13.79	.08	13.72	.06	13.71	.08
HEAD	26.54	.14	26.26	.14	25.64	.76	26.54	.13
KEEL	19.09	.13	18.94	.22	18.86	.13	18.99	.15
PC1	0.38	.26	-0.17	.36	-0.24	.29	0.08	.27

Table 3.13 Comparison by ANOVA of house martin nestling size at Day 3 between treatments and years. (F values with significance level, df = 1 for all factors)

Parameter	n	Treatment(T)		Year(Y)		Interaction
MASS	55	7.51	**	0.54	ns	ns
WING	55	0.95	ns	0.41	ns	ns
TARS	55	9.70	**	2.29	ns	ns
HEAD	55	0.56	ns	2.19	ns	ns
PC1	55	2.31	ns	1.80	ns	ns

Table 3.14 Mean values (x) and standard errors of house martin nestling body size at Day 3 for both treatments in each year.

	1988				1989			
	Control (n=14)		FATFED (n=10)		Control (n=18)		FATFED (n=13)	
Parameter	x	se	x	se	x	se	x	se
MASS	5.8	0.4	6.0	0.5	6.9	0.4	7.3	0.3
WING	11.0	0.5	10.9	0.4	10.3	0.4	10.9	0.3
TARS	10.13	0.30	10.89	0.38	9.50	0.26	9.68	0.16
HEAD	17.13	0.29	17.68	0.64	16.95	0.25	17.37	0.18
PC1	0.09	0.29	0.47	0.38	-0.33	0.26	0.03	0.15

the Control.

3.3.8.3 *Nestling size at Day 20*

Nestling size at Day 20, when most growth is completed (Bryant & Gardiner 1979) was compared between treatments and years by ANOVA (Table 3.15). WING, HEAD and KEEL were significantly larger (Table 3.16) in the Control than in the FATFED treatment. WING was significantly larger (Table 3.16) in 1989 than in 1988.

3.3.8.3 *Nestling size at fledging*

Nestling size at fledging was compared between treatments and years by ANOVA (Table 3.17). MASS, TARS, BWD & KEEL were significantly larger (Table 3.18) in the Control than in the FATFED treatment.

Table 3.15 Comparison by ANOVA of house martin nestling size at Day 20 between treatments and years. (F values with significance level, df = 1 for all factors)

Parameter	n	Treatment(T)		Year(Y)		Interaction
MASS	63	0.2	ns	2.8	ns	ns
WING	63	10.7	**	6.0	*	ns
TARS	63	3.6	ns	1.0	ns	ns
HEAD	62	5.2	*	0.0	ns	ns
KEEL	61	33.6	***	0.7	ns	ns
PC1	61	10.0	**	0.5	ns	ns

Table 3.16 Mean values (x) and standard errors of house martin nestling body size at Day 20 for both treatments in each year.

	1988				1989			
	Control (n=17)		FATFED (n=12)		Control (n=21)		FATFED (n=13)	
Parameter	x	se	x	se	x	se	x	se
MASS	21.00	.40	21.00	1.00	21.70	.40	22.10	.30
WING	85.60	1.70	74.60	4.10	87.30	1.10	84.30	1.20
TARS	13.81	.08	13.53	.18	13.64	.06	13.52	.11
HEAD	25.62[a]	.08	25.21	.32	25.55	.08	25.25	.14
KEEL	17.37[a]	.19	15.52	.45	17.33[b]	.16	16.09	.30
PC1	0.48[a]	.11	-0.83	.52	0.30[b]	.10	-0.29	.15

a - n =16
b - n =20

Table 3.17 Comparison by ANOVA of house martin nestling size at fledging between treatments and years. (F values with significance level, df = 1 for all factors)

Parameter	n	Treatment(T)		Year(Y)		Interaction
MASS	55	6.24	*	.05	ns	ns
WING	55	.01	ns	9.48	* *	ns
TARS	55	8.80	* *	2.39	ns	ns
HEAD	54	1.77	ns	4.31	*	ns
KEEL	55	9.92	* *	.39	ns	ns
PC1	55	5.29	*	3.24	ns[a]	ns

a - p = 0.082

Table 3.18 Mean values (x) and standard errors of house martin nestling body size at fledging for both treatments in each year.

	1988				1989			
	Control (n=17)		FATFED (n=10)		Control (n=15)		FATFED (n=13)	
Parameter	x	se	x	se	x	se	x	se
MASS	19.32	.40	18.85	.51	19.71	.40	18.10	.40
WING	97.90	1.30	95.20	.60	99.70	1.20	102.00	1.30
TARS	13.82	.07	13.55	.12	13.68	.08	13.41	.10
HEAD[a]	26.00	.10	25.89	.18	25.79	.09	25.60	.12
KEEL	18.09	.11	17.36	.28	18.07	.16	17.65	.20
PC1	0.15	.23	-0.81	.26	0.32	.25	0.06	.28

a - n = 16

3.4 DISCUSSION

3.4.1 *Year differences*

Nestlings in 1989 grew faster than in 1988 (Table 3.8, Section 3.3.7.3). They had longer WING at Day 20 and at fledging, and larger HEAD at fledging (Tables 3.15 to 3.18) even though there was no significant difference in nestling size at Day 3 between years (Table 3.14) and there was a smaller parental size (PC1) in 1988 (Table 3.11). The nestlings grew faster in 1989 because they received a larger amount of insect food until Day 16 than did nestlings in 1988, as demonstrated by the larger cumulative mass of FWT by Day 16 in 1989 (2.4 g greater for FATFED, 0.7g for the Control). This may have been the result of greater insect abundance in 1989 than in 1988 during September and the latter half of August (Fig. 3.12), especially as mean DOE and DOH were later in 1989. It may also have been the result of less fat being fed early on to nestlings in the FATFED treatment in 1989 in comparison to nestlings in the FATFED treatment in 1988 (Section 3.3.2).

3.4.2 *Nestling diet quality*

The experimental treatment was successful in altering nestling diet quality in the house martin colony. Nestlings in the FATFED treatment received fewer parental visits per nestling (VISIT) than nestlings in the the Control, in both 1988 and 1989 (Figs 3.3 & 3.4). There was a positive correlation between VISIT and fat-free faecal mass per nestling (FWT) in both years (Figs 3.5 & 3.6), so the lower number of parental visits resulted in less insect food and a lower FWT in the FATFED treatment than in the Control for both years (Figs 3.7 & 3.8). The lower amount of insect food fed to nestlings in the FATFED treatment meant that they received less of the nutrients in the insect food, such as protein, whilst receiving a similar amount of energy because energy was provided by the fat supplement. The nestlings in the FATFED treatment received therefore, a lower quality diet.

The difference in FWT between treatments was directly attributable to the feeding of the fat supplement. A stepwise multiple regression of variables that might influence FWT showed that the mass of fat fed to nestlings was the variable

which explained most variation in FWT (Table 3.3). The heavier the mass of fat fed to nestlings the smaller the FWT. The age of nestlings also affected FWT. The older the nestling the lighter the FWT. This relationship can be explained by the fact that FWT was measured from Day 9 until nestlings fledged. The DER of house martin nestlings reaches a peak around Day 12 and declines from then until fledging as the energy requirement for growth declines (Bryant & Gardiner 1979), therefore FWT will decline from Day 12 onwards as the nestlings require less food (Figs 3.7 & 3.8) and this is probably the cause of the relationship shown by the multiple regression. This cannot have been a cause of the difference in FWT between treatments because nestling age was measured in the same way for both treatments and FWT was compared by day. Insect abundance also explains a significant amount of the variation in FWT. The higher the insect abundance the heavier the FWT. Insect abundance was not likely to be a cause of the difference in FWT between treatments as insect abundance during the nestling period was very similar for both treatments (Figs 3.10 & 3.11).

The fat-feeding caused a reduction in FWT through its effect on nestlings in the FATFED treatment which then resulted in fewer parental visits. The most plausible mechanism for this effect is that the fat-feeding made the nestlings in the FATFED treatment beg less than nestlings in the control. The fat may have satiated metabolic energy requirements when digested and this may have acted as a stimulus for a reduction in begging. Alternatively, the fat may have reduced begging simply through gut occupancy time. Gut passage time in nestling insectivores is usually about 6 hours (Waugh 1978; Krebs & Avery 1984), while 15% to 35% of the fat was undigested, so there is a possibility that large amounts of fat remained in the gut for a few hours and that this physical stimulus reduced begging by the house martin nestlings. Both these effects may have operated at once. Another explanation might be that the fat, or a constituent of the fat, has a sub-lethal toxic effect on the nestlings, inhibiting growth and/or begging. This is improbable as nestling house martins have a large lipid index under normal circumstances (Bryant & Gardiner 1979) so their metabolism is adapted to deal with large quantities of lipid, although it is possible that their digestion may not show the same adaptation. Also, the FWT of nestlings in the FATFED treatment increased to the same level as that of nestlings in the Control as soon as fat-feeding was stopped (Figs 3.7 & 3.8). A sub-lethal toxic effect is not easily compatible with the rapid recovery in feeding rate

3.4.3 *Treatment differences*

Nestlings in the Control were significantly larger than nestlings in the FATFED treatment at Day 20 and at Fledging (Tables 3.15 to 3.18) even though there were no significant differences between treatments in growth rate, except for faster WING growth in the Control in 1988 (Section 3.3.7.3). These differences in size were probably not the result of differences in genotype between treatments as there were no differences in parental size between treatments in either year (Tables 3.11 & 3.12). Differences in egg size between the two treatments are unlikely to have caused the difference in size at Day 20 and at fledging as neonate size is not related to fledging size in house martins (O'Connor 1977; Bryant 1978a). There is evidence that there was a difference in growth rates between the two treatments which the growth curve analysis failed to detect, but which can be seen on the graphs of growth (Figs 3.15 to 3.22) and was detected by comparisons of nestling size at Day 3, Day 20 and at fledging. Nestlings in the Control grew faster in terms of linear measurements than nestlings in the FATFED treatment. This statement is supported by the fact that nestlings in the Control fledged earlier in 1989 (Section 3.3.1), indicating quicker attainment of maturity.

The growth curve analysis may have failed to detect the difference in growth rate because the longitudinal data sets were too short for accurate fitting of the growth curves (Zach 1988; Jehl *et al.* 1990), indeed only the curve for TARS growth reached the asymptote of the curve. MASS growth analysis was complicated by the unusual peaked curve of nestling house martins. The analysis could also have been affected by differences in growth curve shape between treatments as detected for zebra finch nestlings (Section 2.3.2.2).

The faster growth of nestlings in the Control was probably due to differences in nestling diet quality between treatments. Evidence for this is provided by the multiple regression of factors influencing the linear phase of growth in house martin nestlings (Table 3.10). Analysis of the parameter with the longest period of linear growth, WING, revealed an effect of FWT on growth, the heavier the FWT, the greater the growth of WING. In this experiment the most important factor affecting FWT was the feeding of fat to nestlings which resulted in a lower FWT for nestlings in the FATFED treatment. There is, then, evidence for an effect of the experimental treatment on growth with a lower FWT in the FATFED treatment resulting in slower growth.

There are other possible causes of the difference in growth rates between treatments such as the effects of parasites (Møller 1989c, 1990b), toxins (Perrins 1976) and nestling energy expenditure (Bryant 1978a), but these effects can all be discounted in this experiment.

House martin nestlings are host to three main arthropod parasites, a hipoboscid (*Stenepteryx hirundinis*) and two species of flea (*Ceratophyllus hirundinis* & *C. farreni*) (Bryant 1975a). These can be very numerous in natural nests (*pers. obs.*; Bryant 1975a), and could possibly affect growth but in the experiment the effect of these parasites was standardised as nestboxes in both treatments were cleaned in the winter, and hipoboscids were removed from nestlings when they were measured. It is unlikely, therefore, that arthropod parasitism would have had a differential effect on the growth of nestlings in the two treatments. There are other, internal parasites of nestlings whose effect was not controlled for in this experiment but it is assumed that they did not differentially affect the treatments.

A toxic effect of the fat fed to nestlings in the FATFED treatment could have impaired development in relation to nestlings in the NATURAL treatment. This is unlikely as nestlings showed natural begging rates as soon as fat-feeding was stopped (Section 3.4.1). Also, the fat was kept frozen until it was fed to nestlings so the chance of incidental bacterial infection of the nestlings in the FATFED treatment was small.

There was no evidence of a difference in nestling energy expenditure between the two treatments as calculated by the doubly-labelled water method (Table 3.3). Different feeding rates are unlikely to result in differences in energy expenditure because activity is a minor component of overall energy expenditure (approx. 5%) in house martin nestlings (Feltham 1987).

The evidence from this experiment indicates that there is an effect of nestling diet quality on the growth of house martin nestlings up to fledging. It is difficult to determine if these effects persist to adult size as the sample size of fledglings returning to the colony as adults was very small. House martins continue to grow after fledging (Bryant & Gardiner 1979) and it is possible that nestlings from the FATFED treatment may grow after fledging more than nestlings from the Control, as occurred for zebra finch nestlings (Section 2.3.3.2).

Fledgling size, however, is highly correlated to adult size in some species of passerine including house martins (Riley *pers. comm.*) which implies that small nestlings do not show complete compensatory growth after fledging. If this holds true for the experiment then the smaller fledging size of nestlings in the FATFED treatment will persist to adult size.

3.4.3.1 *Nestling energetic studies using doubly labelled water*

Nestling energetic studies relied upon the use of respirometry before the development of the doubly-labelled water technique. Respirometry is problematic because accurate measurement of carbon dioxide production relies upon the use of an enclosed system, which can only be achieved by removing nestlings from their natural environment. A partially enclosed system allowing parental visits will result in some carbon dioxide escaping from the system and therefore an underestimate of carbon dioxide production (Bryant & Gardiner 1979). A comparison of doubly-labelled water and laboratory respirometry estimates of carbon dioxide production in savannah sparrows (Williams & Prints 1986) found that the laboratory estimate was 36% lower than the doubly-labelled water estimate. This difference was explained by William & Prints (1986) as reflecting the increased energy expenditure for thermoregulation and activity of nestlings in the wild.

The advantage of field measurements of energy expenditure over laboratory measurements of energy expenditure has resulted in the increasing use of doubly-labelled water in field studies of nestling energetics. There are ten studies (Table 3.19) of which eight are in the literature and two unpublished (this study & Feltham 1987). The estimate of field metabolic rate in this study is the highest yet obtained for nestlings (Table 3.19).

This high result may be explained by the error associated with net fat deposition in nestlings (Weathers & Sullivan 1989). Fat synthesis produces carbon dioxide (0.73 litres per gram of fat deposited) and although this carbon dioxide production contributes to the total carbon dioxide production measured by the doubly-labelled water technique, the carbon dioxide it produces has a low energy equivalent and will therefore result in an overestimate of FMR. House martin nestlings have large fat resources as an adaptation to their unpredictable food supply (O'Connor 1977; Bryant & Gardiner 1979) and this greater emphasis on fat deposition in comparison to nestlings of other species may well

Table 3.19 Summary of doubly-labelled water studies of nestling energetics. (underlined values calculated from text of study)

Study	Species	Nest[a]	Age[b]	Age2[c]	Mass(g)	CO_2prod[d]	Energy[e]	FMR[f]
Fiala & Congdon 1983	*Agelaius phoeniceus*	O	6	0.60	28.2	5.12	25.2	3.12
Gettinger *et al.* 1985	*Carpodacus mexicanus*	O	8	0.80	15.8	4.17	24.7	2.47
Williams & Nagy 1985	*Passerchulus sandwichensis*	O	7	0.88	14.6	4.17	24.6	2.46
Williams & Prints 1986	*Passerchulus sandwichensis*	O	7	0.88	13.0	5.32	24.6	3.14
Feltham 1987	*Cinclus cinclus*	C	18	0.78	56.5	3.24	23.7	1.85
Weathers & Sullivan 1989	*Junco phaenotonus*	O	7	0.58	14.8	3.90	26.2	2.45
Bryant & Tatner 1989	*Merops viridis*	C	17	0.63	33.3	2.01	25.0	1.21
Weathers *et al.* 1990	*Melanerpes formicivorous*	C	20	0.67	74.3	3.32	25.5	2.04
This study 1990	*Delichon urbica*	C	14	0.58	24.8	6.02	25.0	3.61
Klaasen *et al.* 1989	*Sterna paradisaea*	O	11	0.5	82.0	3.97	25.0	2.38

a - Type of nest, C = closed, O = open
b - Age in days, Day 0 = Date of Hatch
c - Age as a fraction of age at fledging
d - Carbon dioxide production ($cm^3 g^{-1} h^{-1}$)
e - Energy equivalent of carbon dioxide ($j\ cm^{-3}$)
f - Field Metabolic Rate ($KJ\ g^{-1} d^{-1}$)

explain the high value of carbon dioxide production obtained in this study. Another explanation may be that night-time brooding of house martin nestlings resulted in labelled nestlings inhaling unlabelled carbon dioxide exhaled by other nestlings and adults. This would also result in an overestimate of the carbon dioxide production of house martin nestlings (Nagy 1980). These sources of error may contribute to the difference in the estimate of FMR between this study and other studies, but would not contribute to variation between FATFED and Control treatments within this study. There may also be a source of error in this experiment associated with the use of the X22VG.SIRA9 to estimate hydrogen expenditure. The equations available for interpretation of the results from this machine may no longer be applicable because of a change in the machine reference gas (Newton *pers. comm.*), however, this error is unlikely to be large or to affect the two treatments differently (Tatner *pers. comm.*). The raw data from this study are included in Appendix 4 for recalculation, if necessary.

The sources of error described above, and in Sections 3.2.5 and 3.3.6, may also contribute to the variation in estimates of nestling FMR between published studies (Table 3.19), as evidenced by the different estimates of sandwich sparrow nestling energy expenditure found by the studies of Williams & Nagy (1985) and Williams & Prints (1986).

There is no linear relationship between FMR and mass or age as a proportion of the nestling period, but there is an almost significant negative correlation between FMR and age in days (n=10, r = -.615, p = 0.059). This relationship is significant if the result of Klaassen *et al.* (the only seabird study), and of this study (possibly an overestimate) are excluded (n = 8, r = -.798, p = 0.018). FMR may decline with age because increased feathering reduces the cost of thermoregulation.

The small number of studies enable a preliminary comparison of FMR between open-nesting and closed-nesting species (Table 3.19) to test the theory that energetic costs of nestlings in closed-nests are lower than those of nestlings in open-nests because of the greater degree of insulation. The mean FMR of open-nesting species (excluding Klaassen *et al.* 1989) is 2.58 kj g^{-1} d^{-1} whereas the mean FMR for closed-nesting species (excluding this study) is 1.70 kj g^{-1} d^{-1} and this difference was significant (M-W, n_o = 5, n_c = 3, U = 0, p = 0.036). This result is preliminary, however, and may well be an artefact of the older age at which nestlings were measured in the closed-nest studies (M-W, U = 0, p =

0.036). More doubly-labelled water studies are required before interspecific trends and differences in nestling FMR can be elucidated.

3.4.4 *Natural variation of house martin nestling diet*

The experimental effect of variation in house martin diet quality on the growth of nestlings is an important result but it is also important to determine if such a phenomenon could occur under natural conditions in the house martin population. It is possible that the experimental variation in nestling diet quality is much greater than that which occurs in the natural diet of house martins. If so, the effects on growth present in the experiment may be absent in the wild.

The state diet of house martins is highly variable (Fig. 3.11, Bryant 1975a, 1978a) with insect abundance affected by wind, rain and temperature. House martin nestlings are adapted to this variable food supply, though mortality may occur after prolonged periods of rain (Rheinwald 1971). Nestlings accumulate large lipid reserves during growth which provide energy during periods of fast (Bryant & Gardiner 1979). This adaptation means that reduced food intake does not impose a short term mortality risk on the nestlings (O'Connor 1977). Nestlings can also go torpid in fasting conditions with metabolic rate decreasing by 90%, thereby saving energy (Prinzinger & Siedle 1986). These adaptations are principally concerned with survival and Bryant (1975a, 1978a) demonstrated an effect of natural variation in insect abundance upon nestling growth, and also house martin breeding parameters. This effect was also found in this study (Tables 3.3 & 3.9) though the importance of insect abundance was masked by the experimental regime. Bryant (1988) also demonstrated an effect of insect abundance during the breeding season on the adult size of males from the cohort of that year. There is, then, an effect of food abundance on house martin nestling growth. This does not demonstrate an effect of nestling diet quality on growth. Indeed, the insectivorous diet of the nestlings is unlikely to vary as greatly in terms of quality such as protein content as it will in quantity because there are so many different taxa, from different habitats, which make up the aerial fauna and fluctuations in the number or composition of any one of these taxa will not influence the overall quality of the diet.

Variation in the availability of protein may occur through a different mechanism. When energy is the limiting factor to growth, the retention of

protein may be reduced because protein is metabolised for energy rather than for the construction of tissues (Masman 1984) thereby reducing the mass of protein available for growth. It is possible that the experimental result is not reflected by an effect of natural variation in the protein intake of nestlings because energy intake is the more frequent limiting factor to growth.

4 EFFECTS OF NESTLING DIET VARIATION ON THE PHENOTYPE OF A WILD PASSERINE

4.1 INTRODUCTION

Most studies of the effects of variation in food availability and nestling diet quality on the phenotype of birds have used body size parameters as phenotypic characters (Boag 1987a; Richner 1989c). There are, however, other components of the phenotype which may influence the life history of individual birds.

The shape of a bird is important in determining its thermodynamic properties and therefore the energy cost of homeothermy (Kendeigh 1972). Allen's rule (Mayr 1956) states that variation in the core to limb ratio of individuals in a species is correlated with ecogeographic variation; the colder the climate the higher the core to limb ratio. This rule is supported by a study which demonstrated that cold weather conditions selected for a higher core to limb ratio in a house sparrow *Passer domesticus* population (Fleischer & Johnston 1982).

Intraspecific variation in the area of plumage characters is important in determining dominance relationships in some passerines such as size of the black bib of the house sparrow (Richison 1985; Møller 1987), the extent of chestnut streaking on the breast of the yellow warbler *Dendroica petechia* (Studd & Robertson 1985b), the extent of the chestnut plumage on the breast and abdomen of the dipper *Cinclus cinclus* (Newton 1989) and the extent of black plumage on the head and the crown of the Harris sparrow *Zonotrichia querula* (Rohwer 1985; but see Jackson *et al.* 1988).

Variation in the colour of plumage characters may also correlate with dominance in some species such as overall brightness in the black-headed grosbeak *Pheucticus melanocephalus* (Hill, G.E. 1988), plumage darkness in the dark-eyed junco *Junco hyemalis* (Holberton *et al.* 1989, 1990), brightness of the crown in the white-crowned sparrow *Zonotrichia leucophrys gambelii* (Fugle *et al.* 1987) and plumage darkness in the least auklet (Jones 1990).

Male plumage variation may also be an agent for female mate choice such as the darkness of plumage in Darwin's medium ground finch *Geospiza fortis* (Price 1984) and pied flycatcher *Ficedula hypoleuca* (Roskaft & Järvi 1983), the extent of chestnut streaking on the breast of the yellow warbler (Studd & Robertson 1985a), the extent of the black badge of male house sparrows (Møller 1989d, 1990b); overall brightness of male plumage in the house finch *Carpodacus mexicanus* (Hill, G.E. 1990) and the whiteness of the tail of male great snipe *Gallinago media* (Hoglund *et al.* 1990).

The relative contribution of environment and genetic factors to this variation in plumage remains unknown, although these plumage characters may be heritable in some species, for example the badge size of male sparrows (Møller 1990b). One possible means by which the environment may influence variation in adult plumage is through variation in the food fed to nestlings, either in terms of food quantity or diet quality. Nestling diet quality, in terms of pigment content, has been shown to affect the colour of adult plumage in poultry (Grav *et al.* 1969) and wild species such as woodpeckers *Cloaptes auratus* & *C. cafer* (Test 1969), house finches (Brush & Power 1976), great tits, (Slagsvold & Lifjeld 1985), cedar waxwings *Bombycilla cedrorum* (Hudson & Brush 1989, Brush 1990) and least terns *Sterna elegans* (Hudson & Brush 1990); but as yet there has been no research published on the effect of nestling diet quality on the magnitude of plumage characters. The aim of this experiment was to investigate the effect of food quantity and diet quality on the size of a plumage character as well as on body size.

The experiment required a study species that exhibited a quantifiable plumage character, preferably of biological importance. One such species is the great tit (*Parus major*). The great tit is a small (18-20g) passerine resident from Northwest Europe through to Southeast Asia. It is an abundant species in Britain and readily occupies nestboxes (Perrins 1979). Laying commences in late April/early May and the clutch of 4 to 10 eggs is incubated for 14 days by the female. Nestlings fledge at Day 21 and they continue to be dependent upon the parents for a further week. Second broods are infrequent in Britain (Perrins 1979).

Dominance within the great tit is influenced by the width of the black

stripe on the breast, the wider the breast stripe the more dominant the individual (Järvi & Bakken 1984; Järvi *et al.* 1987; Winge & Järvi 1988). This quantifiable plumage characteristic of the great tit, of known biological importance, together with its preference for nestboxes made it an ideal species for the study of the effect of diet quality and food quantity on plumage characters, as well as body size.

4.2 METHODS

Two experiments were performed, one in the summer of 1989 and one in the summer of 1990. The 1990 experiment incorporated changes in methodology suggested by experience of the 1989 experiment therefore the experiments were analysed separately. These changes in methodology are described in the text.

4.2.1 *Population*

The great tit population studied in this experiment was a nestbox population in the surrounds of the University of Stirling campus (NS 907 865). The centre of the campus contains a loch and some parkland. The campus is fringed by mixed woodland, the largest block of which is Hermitage Wood, a steep south-facing slope covered by a mature sycamore *Acer pseudoplatanus* plantation containing some oak *Quercus petraea*, ash *Fraxinus excelsior* and spruce *Picea norvegicus*. Sixty nestboxes were sited around the campus in February 1989, with 30 of these placed in Hermitage Wood.

The nestbox top was changed to a lid so that the nestlings could be extracted, and a metal hook was attached to the back of the boxes to enable them to be hung from a nail. They were hung on the south face of a tree trunk at a height of 2-3 metres (Plate 4.1). This method of attachment meant that a nestbox could be removed by placing a hook inside the nestbox entrance and lifting the box off the nail. Two nails either side of the base of the boxes prevented them from swinging in the wind. Nestboxes were cleared of nest material in the autumn.

4.2.1.1 *Year differences*

In February 1990 forty more nestboxes were placed around the campus to

Plate 4.1 Great tit nestbox *in situ*.

increase the breeding population for the 1990 experiment. Twelve of these boxes were placed in Abbey Craig (NS 912 852), a deciduous woodland south of the campus and the rest were used to fill gaps in the distribution of nestboxes around the campus and Hermitage wood.

4.2.2 *Nestling diet*

4.2.2.1 *Food quantity*

Food quantity (mass of food fed per nestling) was varied between treatments using brood size manipulation. Brood enlargement results in smaller nestlings (Ross 1980; Wiggins 1990a), and Perrins (1979) has demonstrated a reduced nestling mass in enlarged broods of the great tit in comparison to control broods. Recent research has confirmed this effect in the great tit on the continent (Tinbergen 1987; Lindén 1988; Smith *et al.* 1989), whilst also demonstrating a reduced tarsus length (Lindén 1988; Smith *et al.* 1989) and wing length (Smith *et al.* 1988) of nestlings in enlarged broods. Reduced broods have heavier nestlings with longer tarsi than control broods (Lindén 1988).

This variation in growth between brood manipulation classes in the great tit is explained by variation in the feeding frequency per nestling by parents (Smith *et al.* 1988). Parent birds do not raise their feeding effort in proportion to the increase in brood size, therefore each nestling in an enlarged brood receives less food, and there is slower mean growth of the nestlings in these broods than in control broods. Parents of reduced broods make more feeding visits per nestling than parents of control broods. Brood manipulation provides, therefore, a method by which food quantity per nestling can be varied between treatments.

Broods that hatched on the same day were divided randomly into groups of three and each nest in a group of three was randomly assigned to one of three treatments. These three treatments were Enlarged (+3 nestlings), Reduced (-3 nestlings) and Control (0 nestlings removed or added). A genuine control would have been to add three nestlings to a control brood and then to remove three nestlings so that the disturbance caused by the manipulation procedure was

present in all treatments. This procedure was not performed in this experiment because the disturbance due to manipulation was thought to be minimal in comparison to the disturbance due to growth measurements, and also because of the lack of time available due to nestling measurement and feeding, and the effort required to capture females. The effect of 'strange' young in the brood was not, however, controlled for in the experiment but no study has demonstrated an effect of 'strange' young so this should not be a source of bias in the experiment.

Three nestlings were removed from a brood in the Reduced (RED) treatment on the morning of Day 2 (Day 0 = Date of Hatch, when first nestling observed) and transferred immediately to a nest in the Enlarged (ENLA) treatment. After the synchronous broods had been divided into groups of three the remaining broods were allocated to treatments. These were put in the Enlarged and Reduced treatments if two broods remained, and the Control (CON) treatment if just one brood remained.

In this way, variation in food quantity was induced between treatments. Comparisons of nestling growth and plumage development between treatments were used to test for an effect of food quantity.

4.2.2.2 *Nestling diet quality*

Nestling diet quality in this experiment was varied by the use of a supplementary food. Broods were randomly selected from the Enlarged treatment and put in the SUPP treatment where a supplement was fed to half the nestlings (half - 1 in odd-sized broods) during the nestling period. The nestlings in the FED treatment were the first nestlings brought out of the nest for measurement at Day 5. This may have been a possible source of bias, as evidenced by the smaller mass of nestlings receiving the supplement (FED) in comparison to nestlings not receiving the supplement (UNFED) at Day 5 in 1990. This bias should not, however, influence the detection of a difference in growth between the FED and UNFED nestlings.

The FED nestlings were expected to have a higher quality diet than the UNFED nestlings in the brood. The ENLA treatment was used to supply broods for the SUPP treatment because nestlings in the ENLA treatment were expected to be under most nutritional stress, therefore the effect of the supplement would be

greatest in these broods. The ENLA broods also provided a larger sample size of nestlings for comparison of FED and UNFED nestlings.

It was assumed that the supplement contained a higher percentage of nutrients necessary for growth than was present in the natural food. It was expected that feeding the supplement to nestlings in the brood would reduce their begging activity for a period (Bengtsson & Ryden 1983; Hussell 1988) and that during this period parents would concentrate on feeding the unfed nestlings which would continue to beg. In this way the quantity of food fed to nestlings in the FED and UNFED treatments would be similar whereas it was expected that the quality of the diet would be greater in the FED treatment. Comparisons of nestling growth and phenotype could then be made between FED and UNFED treatments to test for an effect of nestling diet quality.

The supplementary feed used in this experiment consisted of 90% steak mince, 5% 'PYM Bird Tonic', 3% calcium phosphate ($Ca_3(PO_4)_2$) and 2% 'Vitasol' by mass. The dry mass of the mixture was approximately 60% of the wet mass. Fat comprised 40% of this dry mass with protein assumed to constitute almost all the remaining 60% dry mass. The components were mixed thoroughly and the mixture divided into 20g portions which were then frozen in individual packets. Packets were thawed overnight before use.

Nestlings were fed twice daily, morning (07.00h to 11.00h) and evening (16.00 to 20.00), from Day 7 to Day 13 . Boli of diet were placed in the nestling's mouth upon begging. If the nestling was reluctant to feed the boli were placed in the back of the mouth until they were swallowed by reflex. Upon satiation (0.6g - 1g), the remaining supplement was returned to the packet and the packet weighed to determine the mass of supplement fed to the nestling.

The four treatments are summarised below-

Reduced (RED)- 3 nestlings removed Day 1-2, no supplement

Control (CON)- no brood manipulation, no supplement

Enlarged, Unfed (ENLA) - 3 nestlings added Day 1-2, no supplement

Enlarged, Fed (SUPP)- 3 nestlings added Day 1-2, supplement fed to half brood (FED) and the rest receiving a natural diet (UNFED)

4.2.2.3 *Year differences in nestling diet*

In 1990 the sample size of ENLA and SUPP broods was increased by using all the nestlings in synchronous broods in Abbey Craig to enlarge broods in the rest of the field site. This method also facilitated a shorter time gap between measurements of nestlings as it was found that a circuit of nestboxes in the Abbey Craig added an hour on to the circuit of nests as a whole. This time was saved during the nestling period by only using Abbey Craig as a source of nestlings for manipulation.

Nestlings were fed from Day 6 to Day 12 in 1990 because it was found difficult to feed Day 13 nestlings in 1989 because of their maturity.

4.2.3 *Growth measurements*

Five parameters of body size were measured during the experiment, as summarised below.

Body mass (MASS) (g, 1 decimal place)- whole body mass, using a Pesola 100g spring balance.

Wing Length (WING) (mm) - the maximum length of the wing chord, using a 150mm stopped wing-rule.

Tarsus Length (TARS) (mm, 2 dp) - the distance between the elbow and the top of the tarsus, using vernier calipers.

Head & Bill Length (HEAD) (mm, 2 dp) - the maximum distance from the back of the head to the tip of the bill, using vernier calipers.

Keel Length (KEEL) (mm, 2 dp) - the distance from the tracheal pit to the posterior edge of the sternum, using vernier calipers.

Measurements were made on Days 5,7,9,11,13,15 & 19. KEEL was

measured at Day 19. All measurements were made between 07.00h and 12.00h. Nestlings were too frail to be measured accurately before Day 5. Day 15 is the latest stage at which the nestlings can be disturbed without the risk of them prematurely 'exploding' from the nestbox (Perrins 1979) and it was at this age that the nestlings were ringed, both with a unique combination of colour rings and with a BTO metal ring. Day 19 was the latest stage at which normal fledging is unlikely (Perrins 1979) and thus the oldest age at which measurement of broods could be expected. Some broods, however, fledged or were predated between Day 15 and Day 19.

Principal component analysis was used to calculate PC1, a multivariate measure of body size (Lemen 1987, Section 2.2.3.3), for each nestling; using MASS, WING, TARS and HEAD values.

4.2.3.1 *Year differences in size measurements*

Measurements were reduced to Days 5, 15 & 19 in 1990 because there was more pressure on time. There was a larger sample size and also the extra feature of female measurements during the nestling period. Comparison of size at Days 5, 15 & 19 was used to detect differences in growth.

4.2.4 *Adult measurements*

Females were captured during incubation (ten days after the last egg in the clutch was laid) by removing the nestbox from the tree and placing a handnet over the lid. When the lid was removed the birds either flew into the handnet or were trapped on the nest by hand. The females were measured as described above for the nestlings and ringed with a BTO metal ring.

4.2.4.1 *Female feeding effort*

The effect of the experimental treatments on parental feeding effort was investigated in 1990. The feeding frequency of female great tits affects their mass change during the nestling period, with higher feeding rates resulting in a higher mass loss (Smith *et al.* 1988). This relationship was used to infer the feeding rates of females in the different treatments by comparing the mass loss during the nestling period of females in the different treatments. Females were caught and weighed at twilight (21.00h to 22.30h) on Day 13 of the nestling

period while they roosted in the boxes with the nestlings (Smith *et al.* 1988). This mass measurement was compared with the mass during incubation to obtain a value of the mass change during the nestling period.

4.2.5 *Plumage Measurements*

Measurement techniques for adult breast stripe have varied between the different studies of the great tit. Winge & Järvi (1988) measured stripe width on a subjective scale with stripe width ranked from 1 (narrow) to 10 (wide), by two independent observers. This type of subjective ranking produces qualitative data which must be analysed by non-parametric statistics as opposed to the more powerful parametric analysis of quantitative data (Sokal & Rohlf 1981). There are also problems of observer bias in a subjective ranking. These can be overcome by use of an independent observer (Järvi & Balden 1984), however in this study an independent observer was not available. For these reasons a subjective ranking of breast stripe was not used in this study.

A more sophisticated, quantitative, measure of breast stripe was used by Norris (1990). This study measured stripe size as the area of stripe calculated from photographic negatives of birds photographed in a set position within a frame, under constant illumination. This method, though very accurate, was too time-consuming to be considered for this experiment given the numbers of nestlings that would have to be photographed. Järvi & Balden (1984) used a simpler quantitative measure of breast stripe. They measured breast stripe width as the width of the stripe at the base of the sternum as measured by the calipers. This measurement was checked using independent observers to rank stripe width from photographs of the experimental birds. These rankings were highly correlated to the caliper measurements. This method provides quantitative data that is quick to collect and which should be relatively free of observer bias, and this was the method used in this study. It was hoped that a photographic record of nestling plumage could be used to check the accuracy of the caliper measurements and a camera was used for this purpose, taking photographs under a standard illumination and at a set distance (Plate 4.2). This photography was, however, too time-consuming to be used for all the broods in the experiment in 1989 and the few photographs obtained were of little value as the breast stripe was usually disturbed in the process of obtaining the photograph (e.g. Plate 4.3).

Plate 4.2 Great tit nestling showing undisturbed plumage.

Plate 4.3 Great tit nestling showing disturbed plumage.

Therefore photography was not used in the 1990 experiment.

Nestlings were held in a set position in the left hand and breast stripe measurements were taken with the callpers in the right hand. Plumage was smoothed with the right hand in the plane of the keel before measurements were taken, so that the error in measurement due to disturbance of plumage was minimised. Stripe length was measured in addition to stripe width so that there was an additional measurement of breast stripe development. Measurements were made at Day 19 when the stripe was more clearly delineated than at Day 15 (*pers. obs.*).

The stripe measurements are summarised below (Figure 4.1)-

Stripe Width (SWID)- widest width of stripe along the keel.

Stripe Length (SLEN)- length of continuous black plumage from bottom of cheek patch down along the plane of the keel.

4.2.5.2 *Year differences in plumage measurements*

Breast stripe was measured at Day 15, as well as at Day 19, so that all nestlings would have their stripe size measured instead of missing those nestlings that fledged or died between Day 15 and Day 19, as had happened in 1989. Stripe length was chosen as the measure at this age because stripe width was too difficult to measure consistently. The method of measuring stripe length was altered from that used in 1989 so that measurements were less subjective. The keel was used as a reference point for measurements instead of other plumage features. It was hoped that in this way there would be greater consistency of method than was achieved in 1989.

The plumage measurements are summarised below (Figure 4.1)-

Stripe Width (SWID) - width of stripe at posterior end of keel

Stripe Length (SLEN)- length of continuous black plumage from the anterior end of the keel down along the plane of the keel.

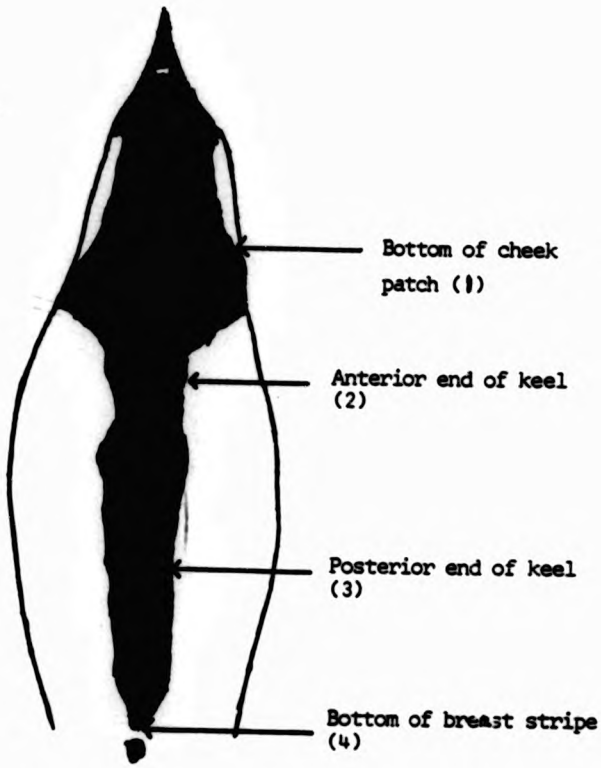

Figure 4.1 Ventral view of great tit nestling breast stripe:
(1) - (4) = stripe length measure in 1989;
(2) - (3) = range of stripe width measure in 1989;
(2) - (4) = stripe length measure in 1990;
(3) = site of stripe width measure in 1990.

4.2.6 *Fledgling survival*

The relative survival and dispersal of fledglings from the treatments was investigated by means of mist-netting at feeding stations in the winter of 1989/1990. The feeding stations were set up around the campus. It would have been preferable to net at sites outside the campus as well to try to catch juveniles that had dispersed from the campus but these sites were not used because of the difficulty of obtaining access and permission to net . Some nestlings were also expected to be caught as breeding females during the 1990 experiment.

4.2.6.1 *Year differences in nestling survival*

Nestling survival was not assessed for the 1990 experiment to release time for writing the thesis.

4.3 1989 Results

Analysis of the results from the 1989 experiment involved the use of ANOVA to test for differences between treatments. Date of hatch (DOH) was included as a factor in this analysis, where possible, to account for the influence of the timing of breeding on nestling growth during the experiment (Perrins 1979). Broods were divided into two categories of DOH. Those broods that hatched before the mean DOH (22.3) were assigned to category 1. Those hatching after the mean were assigned to category 2. Only two categories of DOH were used because further subdivison would have resulted in empty blocks, thus invalidating the use of ANOVA.

4.3.1 *Breeding data*

4.3.1.1 *Comparison of Reduced, Control and Enlarged broods.*

There were no significant differences in breeding parameters between RED, CON and ENLA treatments (Table 4.1; K-W tests, $x^2 < 1.4$, $p > 0.5$) but there was a significant difference between treatments in manipulated brood size (MS) (Table 4.1; K-W test, $x^2 = 12.3$, $p < 0.01$).

4.3.1.2 *Comparison of Enlarged and Supplemented broods*

There were no significant differences in breeding parameters between ENLA and SUPP treatments (Table 4.1, M-W tests, $U > 4$, $p > 0.69$).

4.3.2 *Growth curves*

Nestling growth of each size parameter is summarised for each treatment in Figures 4.2 to 4.5 . Growth curves were calculated for growth up to Day 15 using the non-linear regression procedure of the $SPSS_X$ computer package.

4.3.2.1 *Choice of growth curve*

A Wilcoxon Matched-Pairs test (Table 4.2) was used to test which curve of either Logistic or Gompertz, fitted the data most accurately and would therefore be used for growth curve analysis.

Table 4.1 Great tit breeding parameters in 1989 (Mean (x) and SE).

	Treatments							
	RED (n=8)		CON (n=8)		ENLA (n=3)		SUPP (n=3)	
Parameter	x	se	x	se	x	se	x	se
Date of First Egg[a]	32.8	2.2	38.9	4.5	32.0	4.0	30.0	3.5
Date of Hatch[b]	20.5	2.0	26.8	4.1	21.7	3.8	18.7	3.9
Clutch Size	6.1	0.2	6.0	0.4	7.3	1.5	6.3	1.5
Brood Size	5.9	0.4	5.5	0.6	6.7	1.2	6.0	1.7
Manipulated Size	2.9	0.4	5.5	0.6	9.7	1.2	9.0	1.7

a - April 1st is 1
b - May 1st is 1

Table 4.2 Comparison of the Logistic and Gompertz coefficients of determination for great tit size parameters using the Wilcoxon Matched-pairs test (n = 115).

Parameter	d[a]	Z	p	Growth equation[b]
MASS	.002	-4.33	***	Logistic
WING	.002	-7.38	***	Logistic
TARS	.002	-7.45	***	Logistic
HEAD	-.001	-2.63	*	Gompertz

a - d is the mean value of Logistic r^2 - Gompertz r^2.

b - choice of equation to be used in analysis of growth rate.

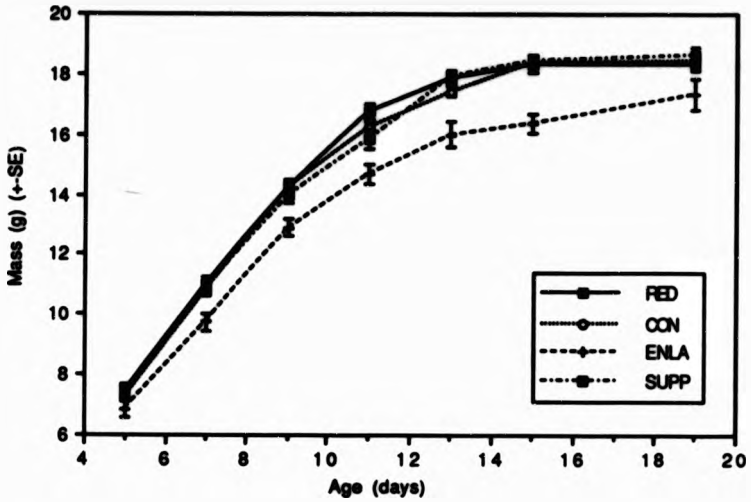

Figure 4.2 Mass growth of great tit nestlings, 1989.

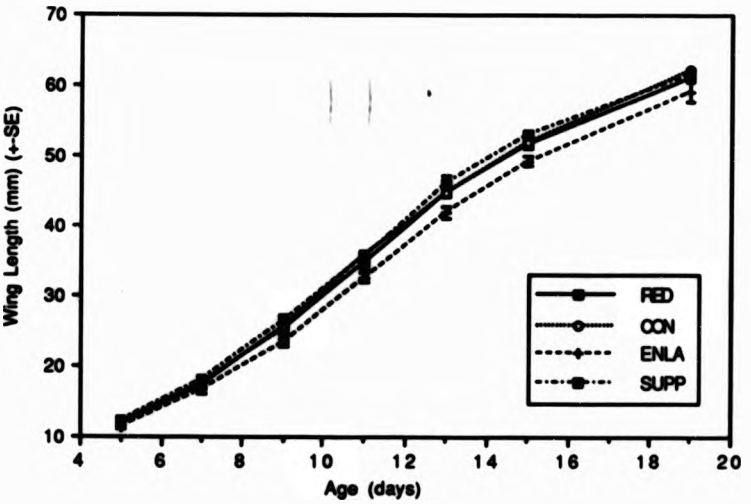

Figure 4.3 Wing growth of great tit nestlings, 1989.

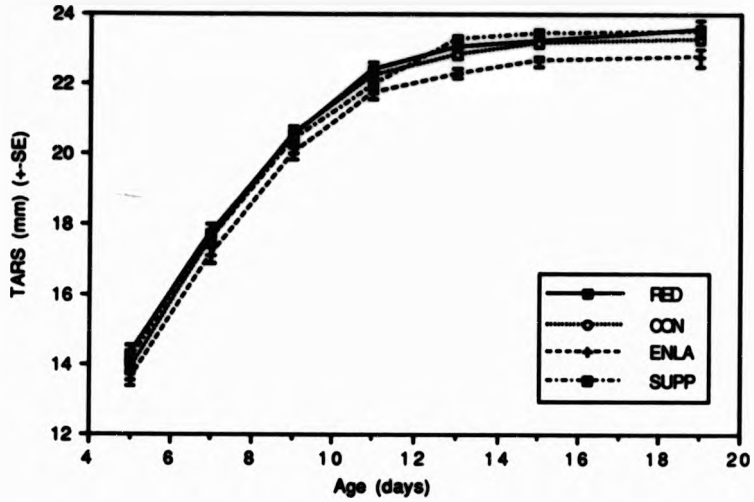

Figure 4.4 TARS growth of great tit nestlings, 1989.

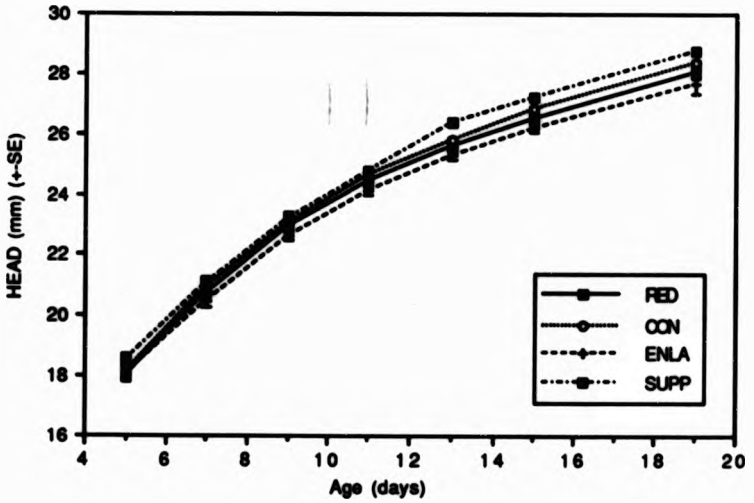

Figure 4.5 HEAD growth of great tit nestlings, 1989.

4.3.2.2 *Comparison of Reduced, Control and Enlarged broods*

The standard error of the *k* estimate (Table 4.3) was log-transformed to achieve a normal distribution. The standard errors of the estimates of MASS *k* and WING *k* were significantly different between treatments (Table 4.4) so MASS *k* and WING *k* were analysed using non-parametric statistics (Section 2.2.3.2).

There was no difference in TARS *k* or HEAD *k* (Table 4.5) between treatments (Table 4.6). TARS *k* was larger in early-hatched nestlings than in late-hatched nestlings (Table 4.6).

WING *k* was significantly different between treatments (Table 4.5, K-W test, $x^2 = 15$, $p < 0.001$) and dates of hatch (M-W test, $U = 237$, $p < 0.001$). WING *k* was largest (i.e. growth was fastest) in the CON treatment and smallest in the ENLA treatment, and larger in early-hatched nestlings than in late-hatched nestlings. There was no significant difference in MASS *k* between treatments (Table 4.5, K-W test, $x^2 = 1.2$, $p > 0.5$) or dates of hatch (M-W test, $U = 105$, $p > 0.2$).

4.3.2.3 *Comparison of FED and UNFED nestlings in Supplemented broods*

FED nestlings each received an average of 1 g of supplement each per feed. This amounted to 2 g a day and 14 g of supplement in total during the nestling period.

The growth of FED and UNFED nestlings in the SUPP treatment is summarised graphically (Figures 4.6 to 4.9). There were no significant differences between FED and UNFED nestlings in either the standard error of the *k* estimate (Table 4.7) or *k* (Table 4.8).

4.3.2.4 *Comparison of ENLA and SUPP*

The standard error of the MASS *k* estimate (Table 4.3) was significantly larger in the ENLA treatment than in the SUPP treatment (Table 4.9) so MASS *k* was compared between treatments by a Mann-Whitney U-test.

WING *k* (Table 4.5) was significantly larger in the SUPP treatment than in the ENLA treatment (Table 4.9).

Table 4.3 **Standard error of growth rate estimate for all treatments. (mean (x))**

	TREATMENT							
	RED (n=21)		CON (n=43)		ENLA (n=26)		SUPP (n=25)	
Parameter	x	se	x	se	x	se	x	se
MASS	.038	.003	.043	.004	.057	.005	.023	.003
WING	.028	.005	.020	.002	.029	.003	.030	.003
TARS	.049	.007	.039	.007	.041	.004	.041	.004
HEAD	.024	.002	.020	.002	.028	.002	.021	.002

Table 4.4 **Comparison by ANOVA of the standard error (ln(SE +1)) of the growth rate (k) estimate between RED, CON & ENLA treatments and dates of hatch (N = 90).** (F values with significance level, df = 2 for treatment, df = 1 for Date of Hatch)

Parameter	Treatment		Date of Hatch		Interaction
MASS	3.65	•	1.60	ns	ns
WING	6.68	• •	37.68	• • •	ns
TARS	1.49	ns	0.32	ns	ns
HEAD	3.02	ns	0.11	ns	ns

Table 4.5 **Mean values and standard errors of great tit growth rate (*k*) for all treatments.**

	TREATMENT							
	RED (n=21)		CON (n=43)		ENLA (n=26)		SUPP (n=25)	
Parameter	*k*	se	*k*	se	*k*	se	*k*	se
MASS	.406	(.011)	.392	(.010)	.386	(.017)	.383	(.007)
WING	.272	(.004)	.290	(.005)	.256	(.007)	.292	(.006)
TARS	.375	(.011)	.390	(.006)	.387	(.012)	.375	(.008)
HEAD	.182	(.007)	.181	(.004)	.165	(.006)	.170	(.006)

Table 4.6 **Comparison by ANOVA of great tit growth rate (*k*) between RED, CON & ENLA treatments and dates of hatch (N=90).** (F values with significance level, df = 2 for treatment, df = 1 for Date of Hatch)

Parameter	Treatment		Date of Hatch		Interaction	
TARS	1.89	ns	12.29	**	8.29	**
HEAD	2.61	ns	1.82	ns	4.16	*

Table 4.7 **The standard error of great tit growth rate estimate for UNFED and FED nestlings in the SUPP treatment.**(x = mean)

	TREATMENT						
	Unfed (n=15)		Fed (n=10)				
Parameter	x	se	x	se	t	*df*	sig
MASS	.024	.004	.021	.004	0.57	23	ns
WING	.030	.003	.032	.006	-0.45	23	ns
TARS	.045	.006	.038	.003	0.91	23	ns
HEAD	.022	.003	.020	.003	0.43	23	ns

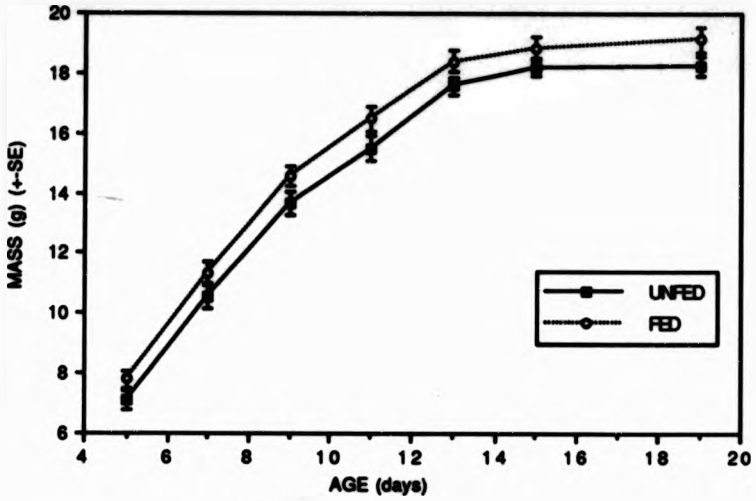

Figure 4.6 MASS growth of nestlings in the SUPP treatment.

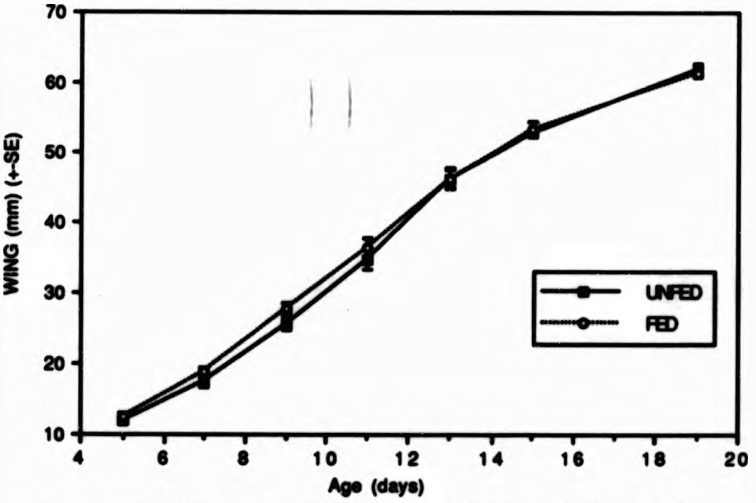

Figure 4.7 WING growth of nestlings in the SUPP treatment.

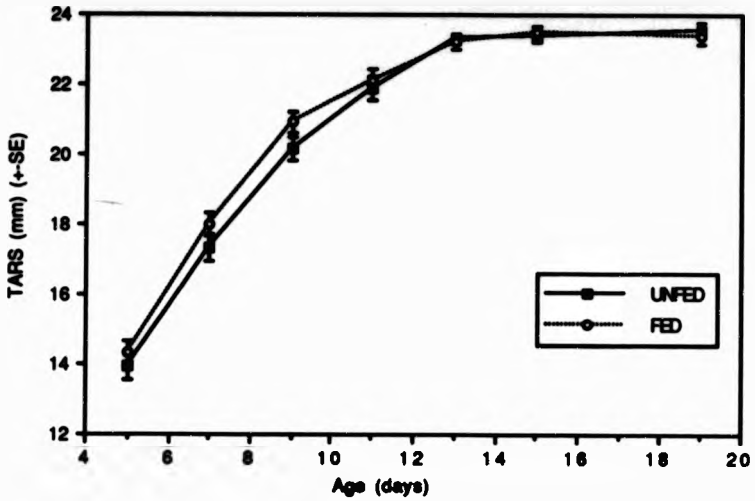

Figure 4.8 TARS growth of nestlings in the SUPP treatment.

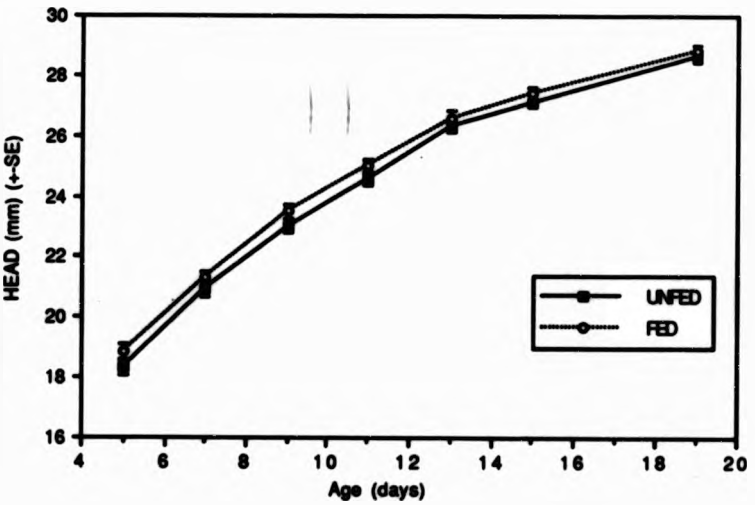

Figure 4.9 HEAD growth of nestlings in the SUPP treatment.

Table 4.8 Mean values and standard errors of great tit growth rate (*k*) for UNFED and FED nestlings in the SUPP treatment.

	TREATMENT							
	UNFED (n=15)		FED (n=10)					
Parameter	*k*	se	*k*	se	t	*df*	sig
MASS	.380	.013	.388	.010	-0.47	23	ns
WING	.293	.007	.291	.010	0.14	23	ns
TARS	.365	.010	.390	.011	-1.65	23	ns
HEAD	.171	.008	.169	.007	0.13	23	ns

Table 4.9 Comparison between ENLA and SUPP treatments of the standard error of the *k* estimate and nestling growth rate (*k*), 1989.

	SE of *k* estimate			*k*		
Parameter	t	df	p	t	df	p
MASS	5.44	49	••			ns[a]
WING	-0.23	49	ns	-4.21	49	•••
TARS	-0.07	49	ns	0.79	49	ns
HEAD	-0.57	49	ns	1.14	49	ns

a - Mann-Whitney U-test

4.3.3 *Nestling size*

Only nestlings which were measured up to at least Day 15 were included in the nestling size analyses. There were very few deaths within broods. Only one brood, in the SUPP treatment, was predated before Day 15 and this brood was excluded from analyses.

4.3.3.1 *Comparison of Reduced, Control and Enlarged broods*

An ANOVA (Table 4.10) showed no significant differences between treatments or dates of hatch in the size of nestlings at Day 5 (Table 4.11) but by Day 15 there were highly significant differences between treatments (Table 4.10) in all nestlings size parameters (Table 4.11). Nestlings in the RED and CON treatments were similar in size but those in the ENLA treatment were considerably smaller (Table 4.11). The pattern was similar at Day 19 (Table 4.11) but the differences were not as significant (Table 4.10) These results indicate that nestlings in the RED and CON treatments grew more between Day 5 and Days 15 & 19 than nestlings in the ENLA treatment.

Early-hatched nestlings were significantly larger at Day 15 than late-hatched nestlings in all size parameters except mass (Table 4.11)

4.3.3.2 *Comparison of FED & UNFED nestlings in supplemented broods*

There were no significant differences between FED and UNFED nestlings in nestling size at Days 5, 15 or 19 (Table 4.12). These results indicate that there was no difference in growth between FED and UNFED nestlings in the SUPP treatment.

4.3.3.3 *Comparison of Enlarged and Supplemented broods*

Nestlings in the SUPP treatment were significantly larger (Tables 4.10 & 4.13) at Day 5 than nestlings in the ENLA treatment. This difference in nestling size was much more significant at Day 15 (Table 4.13) with nestlings in the SUPP treatment considerably larger in all measures than nestlings in the ENLA treatment (Table 4.11). The pattern was the same at Day 19 (Table 4.11) though the differences were less significant (Table 4.13). These results indicate that nestlings in the SUPP treatment grew more than nestlings in the ENLA

Table 4.10 Mean values (X) and standard errors of great tit nestling size in 1989, for all treatments at Days 5, 15 and 19

	TREATMENT							
	RED (n=21)		CON (n=43)		ENLA (n=26)		SUPP (n=25)	
Parameter	x	se	x	se	x	se	x	se
Day 5								
MASS	07.4	0.3	07.2	0.1	06.8	0.20	7.4	0.2
WING	12.0	0.4	11.7	0.2	11.5	0.31	12.2	0.3
TARS	14.26	0.29	13.86	0.15	13.58	0.21	14.10	0.27
HEAD	18.04	0.24	18.13	0.11	18.10	0.16	18.54	0.19
PC1[a]	0.07	0.24	-0.07	0.12	-0.27	0.18	0.33	0.25
Day 15								
MASS	16.3	0.2	16.4	0.1	16.4	0.3	16.5	0.2
WING	51.5	0.5	52.0	0.3	49.2	0.7	53.0	0.6
TARS	23.23	0.17	23.16	0.12	22.65	0.15	23.44	0.15
HEAD	26.52	0.13	26.61	0.09	26.17	0.15	27.22	0.12
PC1[b]	0.04	0.16	0.21	0.11	-0.93	0.24	0.57	0.14
Day 19[c]								
MASS	16.3	0.2	16.4	0.2	17.4	0.5	16.7	0.3
WING	61.3	0.8	62.2	0.3	59.3	1.5	61.8	0.5
TARS	23.53	0.28	23.28	0.12	22.76	0.24	23.49	0.15
HEAD	26.07	0.20	26.37	0.09	27.66	0.32	26.75	0.14
KEEL	15.5	0.3	15.5	0.1	14.9	0.5	15.6	0.2
PC1[d]	-0.03	0.26	0.14	0.12	-0.97	0.50	0.39	0.16

a - Eigen value = 3.63, 90.8% of variation explained
b - Eigen value = 2.95, 73.8% of variation explained
c - n_r = 8, n_c = 42, n_e = 11, n_s =13
d - Eigen value = 2.86, 71.2% of variation explained

Table 4.11 Comparison by ANOVA of great tit nestling size in 1989 between RED, CON & ENLA treatments and dates of hatch (N=90). (F values with significance level, df =2 for treatment, df = 1 for Date of Hatch)

Parameter	Treatment		Date of Hatch		Interaction
Day 5					
MASS	1.44	ns	1.63	ns	ns
WING	0.57	ns	2.69	ns	ns
TARS	1.66	ns	1.55	ns	ns
HEAD	0.17	ns	1.13	ns	ns
PC1	0.45	ns	2.31	ns	ns
Day 15					
MASS	24.54	***	1.15	ns	ns
WING	8.10	***	10.09	**	ns
TARS	3.52	*	5.78	*	ns
HEAD	8.00	**	6.99	*	ns
PC1	10.62	***	5.11	*	ns
Day 19[a]					
MASS	3.81	*			
WING	4.78	*			
TARS	2.64	ns			
HEAD	5.11	**			
KEEL	2.40	ns			
PC1	3.40	*			

a - N = 61, n_r = 8, n_c = 42, n_e = 11

Table 4.12 Mean values (X) and standard errors of nestling size for UNFED and FED nestlings in the SUPP treatment, 1989.

Parameter	UNFED (n=15) x	se	FED (n=10) x	se	t	*df*	sig
Day 5							
MASS	7.3	0.4	7.9	0.3	-1.20	23	ns
WING	12.3	0.5	12.7	0.5	-0.52	23	ns
TARS	14.35	0.43	14.60	0.39	-0.41	23	ns
HEAD	18.48	0.31	18.96	0.32	-1.05	23	ns
PC1	0.18	0.34	0.58	0.34	-0.77	23	ns
Day 15							
MASS	18.2	0.3	18.9	0.3	-1.63	23	ns
WING	52.8	0.7	53.4	1.1	-0.48	23	ns
TARS	23.39	0.16	23.52	0.16	-0.54	23	ns
HEAD	27.08	0.15	27.42	0.20	-1.35	23	ns
PC1	0.43	0.16	0.79	0.24	-1.28	23	ns
Day 19[a]							
MASS	18.2	0.3	19.1	0.4	-1.77	11	ns
WING	62.0	0.8	61.5	0.7	0.46	11	ns
TARS	23.57	0.20	23.39	0.22	0.60	11	ns
HEAD	28.41	0.23	28.84	0.28	-0.83	11	ns
KEEL	15.4	0.3	15.7	0.2	-0.84	11	ns
PC1	0.30	0.21	0.49	0.62	-0.56	11	ns

a - $n_U = 7$, $n_f = 6$

Table 4.13 Comparison between ENLA and SUPP treatments of nestling size at Days 5, 15 and 19, 1989.

Parameter	Day 5 t	df	sig	Day 15 t	df	sig	Day 19 t	df	sig
MASS	-1.87	51	ns[a]	-5.28	51	***	-2.37	22	*
WING	-2.04	51	*	-4.19	51	***	-1.65	22	ns
TARS	-2.35	51	*	-4.25	51	***	-2.56	22	*
HEAD	-1.94	51	ns[b]	-5.33	51	***	-3.14	22	*
KEEL							-1.30	22	ns
PC1	-1.47	51	ns	-4.24	51	***	-2.75	22	*

a - p = 0.067
b - p = 0.058

Table 4.14 Mean values (X) and standard errors of great tit nestling plumage measurements at Day 19, 1989.

Parameter	RED (n=8) x	se	CON (n=42) x	se	ENLA (n=11) x	se	SUPP (n=13) x	se
SLEN	41.3	1.6	40.1	0.8	39.7	1.4	38.2	1.6
SWID	4.3	0.2	4.4	0.2	3.9	0.3	5.3	0.4

Table 4.15 Comparison by ANOVA and ANCOVA of great tit nestling plumage at Day 19 between RED, CON & ENLA treatments with PC1 as the covariate (N = 61), 1989. (F values with significance level, df = 2 for treatment, df = 1 for PC1)

Parameter		Treatment		PC1	
SLEN	ANOVA	0.29	ns	---	
	ANCOVA	2.25	ns	21.53	***
SWID	ANOVA	1.26	ns	---	
	ANCOVA	0.10	ns	14.67	***

treatment between Day 5 and Days 15 & 19.

4.3.4 *Breast stripe*

4.3.4.1 *Comparison of Reduced, Control and Enlarged broods*

Stripe measurements (Table 4.14) were normally distributed. There were no significant differences between treatments as analysed by ANOVA (Table 4.15) but stripe measurements were correlated with overall body size (PC1) and this relationship could mask actual differences in stripe measurements independent of body size. This possibility was investigated by analysis of covariance (ANCOVA) with PC1 as the covariate representing body size (Table 4.15) yet there was still no significant difference between treatments.

4.3.4.2 *Comparison of FED & UNFED nestlings in supplemented broods*

There were no significant differences in stripe measurements between FED and UNFED nestlings, with or without PC1 as a covariate (Table 4.16)

4.3.4.3 *Comparison of Enlarged and Supplemented broods*

Stripe Width was significantly wider in the SUPP treatment than in the ENLA treatment (Tables 4.14 & 4.17). This difference was still significant when PC1 was included as a covariate (Table 4.17). There was no significant difference in stripe length between ENLA and SUPP treatments.

4.3.5 *Nestling survival*

The mist-netting in the winter of 1989/90 was unsuccessful. It was difficult to attract great tits to feeding stations because of the mild weather (Perrins 1979). Only 22 individual great tits were caught of which 12 were unringed. Twelve juveniles were caught. Five of these were nestlings from the 1989 experiment.

Forty-three females were caught at the nest during the 1990 experiment. Nineteen of these birds were birds hatched in 1989 but only two were from the

Table 4.16 Mean values (x) and standard errors of great tit nestling plumage at Day 19 for UNFED and FED nestlings in the SUPP treatment, 1989. (ANOVA & ANCOVA, PC1 is covariate, *df* = 1 for Fed and PC1)

Parameter	Unfed (n=7) x	se	Fed (n=6) x	se		Fed		PC1	
SLEN	38.1	1.7	38.3	3.0	ANOVA	0.00	ns	- - -	
					ANCOVA	0.03	ns	1.82	ns
SWID	5.5	0.4	5.2	0.7	ANOVA	0.18	ns	- - -	
					ANCOVA	0.15	ns	0.02	ns

Table 4.17 Comparison by ANOVA and ANCOVA of great tit nestling plumage at Day 19 between ENLA & SUPP treatments with PC1 as the covariate (N = 24), 1989. (F values with significance level, *df* = 1 for treatment and PC1)

Parameter		Treatment		PC1	
SLEN	ANOVA	0.51	ns	- - -	
	ANCOVA	3.57	ns	2.78	ns
SWID	ANOVA	10.49	* *	- - -	
	ANCOVA	5.26	*	6.18	*

experiment.

There were thus only seven nestlings from the 1989 experiment known to have survived until the winter. Four of these nestlings were from the SUPP treatment (three UNFED, one FED), two were from the CON treatment and one from the ENLA treatment. This sample size was too small for any statistical comparison of survival between treatments. The mist-netting was performed at one of four netting sites around campus on forty days during November and December 1989. More juveniles would have been caught had sites outside the campus been netted, however the survival of juveniles is very low (7%-22% approx., Perrins 1979), and of the 115 nestlings surviving to Day 15 in 1989 only around twenty would be expected to survive until 1990 (assuming 15% survival). The probability of catching all these surviving juveniles was very small because of dispersal.

4.4 1990 Results

Two categories of DOH were used for analysis of the results from the 1990 experiment, as for the 1989 experiment (Section 4.3). Mean DOH in 1990 was 14.4 . Those nestlings hatching before the mean were assigned to category 1 (early-hatched)and those hatching after the mean to category 2 (late-hatched).

4.4.1 Breeding data

4.4.1.1 *Comparison of Reduced, Control and Enlarged broods*

There were no significant differences between treatments in any breeding parameter (Table 4.18; K-W tests, $x^2 < 3.0$, $p > 0.21$) except MS which was, as expected, smallest in the RED treatment and largest in the ENLA treatment (Table 4.18; K-W test, $x^2 = 18.2$, $p < 0.001$).

4.4.1.2 *Comparison of Enlarged and Supplemented broods*

There was no significant difference between ENLA and SUPP treatments in breeding parameters (Table 4.18, M-W tests, $U > 19$, $P > 0.11$)

4.4.2 *Nestling size*

4.4.2.1 *Comparison of Reduced, Control and Enlarged broods*

An ANOVA (Table 4.19) showed a significant difference between treatments in MASS, WING and TARS at Day 5 with nestlings in the CON treatment larger than nestlings in the RED and ENLA treatments (Table 4.20).

At Day 15 there was a significant difference between treatments for all size parameters including PC1 (Table 4.19). Nestlings in the RED and CON treatments were now larger than those in the ENLA treatment in all size measures (Table 4.20). Early-hatched nestlings were significantly heavier at this age than late-hatched nestlings (Table 4.19). This pattern remained at Day 19 (Table 4.20) but the differences were no longer significant.

Table 4.18 Great tit breeding parameters in 1990 (Mean (x) and SE)

	RED (n=13)		CON (n=9)		ENLA (n=8)		SUPP (n=9)	
Parameter	x	se	x	se	x	se	x	se
Date of First Egg[a]	24.3	2.0	24.2	2.4	24.3	1.8	24.9	1.9
Date of Hatch[b]	14.5	1.6	13.9	1.9	14.9	1.8	14.3	1.7
Clutch Size	7.5	0.4	7.3	0.5	8.1	0.5	7.1	0.5
Brood Size	7.0	0.4	5.8	0.7	7.3	0.7	6.6	0.6
Manipulated Size	4.0	0.4	5.8	0.7	10.3	0.7	9.6	0.6

a - April 1st = Day 1
b - May 1st = Day 1

Table 4.19 Mean values (x) and standard errors of great tit nestling size in 1990, for all treatments at Days 5, 15 and 19

	TREATMENT							
	RED (n=50)		CON (n=40)		ENLA (n=71)		SUPP (n=83)	
Parameter	x	se	x	se	x	se	x	se
Day 5								
MASS	7.6	0.2	8.2	0.2	7.6	0.2	7.9	0.1
WING	12.1	0.2	12.8	0.2	12.1	0.2	12.6	0.2
TARS	13.92	0.17	14.65	0.20	14.27	0.16	14.31	0.13
HEAD	18.44	0.13	18.84	0.16	18.61	0.12	18.74	0.10
PC1[a]	-0.24	0.13	0.23	0.20	-0.03	0.11	0.06	0.11
Day 15								
MASS	18.9	0.3	19.0	0.2	18.1	0.2	18.3	0.1
WING	53.4	0.3	54.0	0.5	52.4	0.4	53.7	0.3
TARS	23.59	0.12	23.09	0.11	22.86	0.08	22.99	0.08
HEAD	27.56	0.08	27.53	0.14	27.22	0.09	27.27	0.06
PC1[b]	0.31	0.11	0.27	0.19	-0.32	0.14	-0.05	0.09
Day 19[c]								
MASS	18.8	0.2	18.3	0.4	18.1	0.2	17.6	0.1
WING	63.1	0.4	62.7	0.8	62.4	0.4	62.8	0.3
TARS	23.24	0.15	23.49	0.21	23.03	0.11	23.25	0.10
HEAD	28.87	0.11	28.83	0.20	28.20	0.27	28.59	0.07
KEEL	15.6	0.2	15.6	0.2	15.4	0.1	15.6	0.1
PC1[d]	0.33	0.17	0.32	0.32	-0.20	0.17	-0.10	0.13

a - Eigen value = 3.70, 92.4% of variation explained
b - Eigen value = 2.54, 63.6% of variation explained
c - $n_r = 31$, $n_o = 10$, $n_b = 44$, $n_s = 48$
d - Eigen value = 2.12, 48.6% of variation explained

Table 4.20 Comparison by ANOVA of great tit nestling size in 1990 between RED, CON & ENLA treatments and dates of hatch (N = 161). (F values with significance level, df = 2 for treatment, df = 1 for Date of Hatch)

Parameter	Treatment		Date of Hatch		Interaction	
Day 5						
MASS	3.08	*	0.13	ns	ns	
WING	2.57	*	0.14	ns	ns	
TARS	3.14	*	1.30	ns	ns	
HEAD	2.66	ns	0.02	ns	ns	
PC1	0.89	ns	1.06	ns	ns	
Day 15						
MASS	4.97	**	4.09	*	ns	
WING	3.97	*	0.00	ns	4.51	*
TARS	6.92	**	0.07	ns	ns	
HEAD	3.58	*	0.15	ns	5.11	**
PC1	3.05	*	2.20	ns	ns	
Day 19[a]						
MASS	2.82	ns	0.11	ns	ns	
WING	0.38	ns	0.08	ns	7.72	**
TARS	2.36	ns	1.04	ns	ns	
HEAD	2.02	ns	0.00	ns	ns	
KEEL	1.33	ns	3.61	ns	ns	
PC1	2.54	ns	0.01	ns	3.72	*

a - N = 85, n_r = 31, n_b = 10, n_e = 44

These results indicate that nestlings in the RED and CON treatments grew more quickly between Day 5 and Days 15 & 19 than nestlings in the ENLA treatment.

4.4.2.2 *Comparison of FED and UNFED nestlings in SUPP*

FED nestlings received an average of 1.2 grams of supplement each per feed. This is equivalent to 2.2 grams per day and 15.4 grams in total during the experiment.

UNFED nestlings were significantly larger than FED nestlings at Day 5 in all measures except TARS (Table 4.21). At Day 15 the difference in MASS had diminished but the differences in WING and PC1 were more significant. At Day 19 UNFED nestlings were still larger in most parameters but this difference was only significant for KEEL. This is equivocal evidence that UNFED nestlings grew faster than FED nestlings.

4.4.2.3 *Comparison of Enlarged and Supplemented broods*

There was no significant difference in nestling size at Day 5 between ENLA and SUPP treatments (Table 4.22) but at Day 15 WING and PC1 were significantly larger in the SUPP treatment than in the ENLA treatment (Tables 4.20 & 4.22)

4.4.3 *Breast stripe*

4.4.3.1 *Comparison of Reduced, Control and Enlarged broods*

There was no significant difference in stripe length at Day 15 (Table 4.23) between treatments (Table 4.24). At Day 19 however, stripe length was significantly different between treatments (Table 4.24). This difference was still present after PC1 was included as a covariate to allow for the effect of body size on stripe length. Stripe length was longest in the RED treatment and shortest in the ENLA treatment (Table 4.23)

There was no significant difference between treatments in SWID

Table 4.21 Mean values (X) and standard errors of nestling size for UNFED and FED nestlings in the SUPP treatment, 1990.

	UNFED (n=45)		FED (n=41)				
Parameter	x	se	x	se	t	*df*	sig
Day 5							
MASS	8.1	0.1	7.6	0.2	2.11	84	•
WING	12.9	0.2	12.1	0.3	2.48	84	•
TARS	14.51	0.16	14.09	0.21	1.65	84	ns
HEAD	18.93	0.31	18.52	0.32	2.17	84	•
PC1	0.28	0.11	-0.19	0.18	2.29	84	•
Day 15							
MASS	18.4	0.1	18.1	0.2	1.31	84	ns
WING	54.5	0.3	52.9	0.51	2.71	84	• •
TARS	23.11	0.12	22.87	0.11	1.51	84	ns
HEAD	27.40	0.07	27.12	0.11	2.19	84	•
PC1	0.17	0.09	-0.29	0.14	2.83	84	• •
Day 19[a]							
MASS	17.4	0.2	17.7	0.2	-1.04	49	ns
WING	63.4	0.4	62.1	0.5	1.95	49	ns[b]
TARS	23.25	0.15	23.25	0.14	-0.02	49	ns
HEAD	28.72	0.09	28.46	0.11	1.85	49	ns
KEEL	15.9	0.2	15.3	0.2	2.06	49	•
PC1	0.25	0.19	-0.08	0.18	0.53	49	ns

a - $n_u = 27$, $n_f = 24$

b - $p = 0.057$

Table 4.22 Comparison between ENLA and SUPP treatments of nestling size at Days 5, 15 and 19, 1990.

Parameter	Day 5 t	df	sig	Day 15 t	df	sig	Day 19 t	df	sig
MASS	-0.83	152	ns	-0.68	152	ns	2.54	81	*
WING	-1.27	152	ns	-2.74	152	* *	-0.59	81	ns
TARS	0.07	152	ns	-1.14	152	ns	-1.51	81	ns
HEAD	-0.35	152	ns	-0.44	152	ns	-1.46	81	ns
KEEL							-0.91	81	ns
PC1	-0.35	152	ns	-2.11	152	*	-0.76	81	ns

Table 4.23 Mean values (X) and standard errors of great tit nestling plumage measurements, 1990.

Parameter	RED (n=50) x	se	CON (n=40) x	se	ENLA (n=71) x	se	SUPP (n=83) x	se
Day 15								
SLEN	10.5	0.6	10.2	0.6	9.6	0.4	8.9	0.5
Day 19[a]								
SLEN	17.8	0.6	14.6	1.5	13.2	0.7	14.1	0.6
SWID	4.1	0.2	3.7	0.3	3.7	0.1	3.6	0.1

a - $n_r = 31$, $n_c = 10$, $n_e = 44$, $n_s = 48$

Table 4.24 **Comparison by ANOVA & ANCOVA of nestling plumage between RED, CON & ENLA treatments with PC1 as the covariate (N = 161).** (F values with significance level, df = 2 for treatment, df = 1 for Date of Hatch and PC1)

Parameter		Treatment		Date of Hatch		Interaction		PC1	
Day 15									
SLEN	ANOVA	0.87	ns	0.14	ns	3.87	*	---	
	ANCOVA	0.12	ns	0.02	ns		ns	14.59	***
Day 19[a]									
SWID	ANOVA	1.40	ns	0.05	ns		ns	---	
	ANCOVA	1.06	ns	0.03	ns		ns	7.79	**
SLEN	ANOVA	8.71	***	2.89	ns		ns	---	
	ANCOVA	6.63	**	3.58[b]	ns		ns	20.50	***

a - N = 85, n_r = 31, n_b = 10, n_g = 44
b - p = 0.056

Table 4.25 **Mean values (x) and standard errors of great tit nestling plumage for UNFED and FED nestlings in the SUPP treatment.** (ANOVA & ANCOVA, PC1 is covariate, *df* = 1 for Fed and PC1)

	UNFED (n=45)		FED (n=41)					
Parameter	x	se	x	se		Fed		PC1
Day 15								
SLEN	10.0	0.7	7.7	0.7	ANOVA	5.09	*	---
					ANCOVA	1.29	ns	25.97 ***
Day 19[a]								
SWID	3.5	0.2	3.9	0.2	ANOVA	1.26	ns	---
					ANCOVA	0.81	ns	10.83 **
SLEN	15.3	1.0	13.1	0.8	ANOVA	3.12[b]	ns	---
					ANCOVA	2.55	ns	11.65 **

a - n_g = 27, n_r = 24
b - p = 0.084

4.4.3.2 *Comparison of FED & UNFED nestlings in Supplemented broods*

SLEN at Day 15 was significantly longer in UNFED nestlings than in FED nestlings (Table 4.25). This difference was not significant when the effect of body size was allowed for by including PC1 as the covariate.

There were no significant differences in plumage measurements between FED and UNFED nestlings at Day 19 (Table 4.25).

4.4.3.3 *Comparison of Enlarged and Supplemented broods*

There was no difference between enlarged broods in stripe measurements at Day 15 or Day 19 before and after inclusion of body size in the analysis (Tables 4.23 & 4.26).

4.4.4 *Female mass change*

Female mass change was normally distributed. The body mass of great tits varies diurnally (Cherel *et al.* 1988; Haftorn 1989) but there was no correlation between female mass at Day 10 of incubation and time of capture in this experiment (Figure 4.10) so mass at Day 10 of incubation was not corrected for time of day. No correction was required for female mass at Day 13 of the nestling period as all females were weighed between 21.00h and 22.30h on this day.

An analysis of variance showed a significant difference in female mass at Day 13 and mass change between RED, ENLA and SUPP treatments (Table 4.27). Mass at Day 13 was greatest in the RED treatment and least in the SUPP treatment. Mass loss was significantly greater in the ENLA treatment than in the RED treatment (Table 4.28). Mass loss in the SUPP treatment was less than in the ENLA treatment (Table 4.27) but this difference was not significant (Table 4.28).

There was a more significant difference between treatments in mass change after size correction (Table 4.27) and mass change was still significantly greater in the ENLA treatment than in the RED treatment (Table 4.28). Size-corrected mass during incubation was significantly different between treatments (Table

Table 4.26 Comparison by ANOVA & ANCOVA of nestling plumage between ENLA & SUPP treatments with PC1 as the covariate (N = 154). (F values with significance level, df = 1 for treatment, Date of Hatch and PC1)

Parameter		Treatment		Date of Hatch		Interaction	PC1
Day 15							
SLEN	ANOVA	1.11	ns	1.20	ns	ns	...
	ANCOVA	3.33[a]	ns	0.08	ns	ns	26.08 ***
Day 19[b]							
SWID	ANOVA	1.56	ns	0.08	ns	ns	...
	ANCOVA	2.25	ns	1.53	ns	ns	12.91 **
SLEN	ANOVA	0.23	ns	5.34	*	ns	...
	ANCOVA	0.12	ns	1.96	ns	ns	23.47 ***

a - p = 0.070
b - N = 92, n_o = 44, n_s = 48

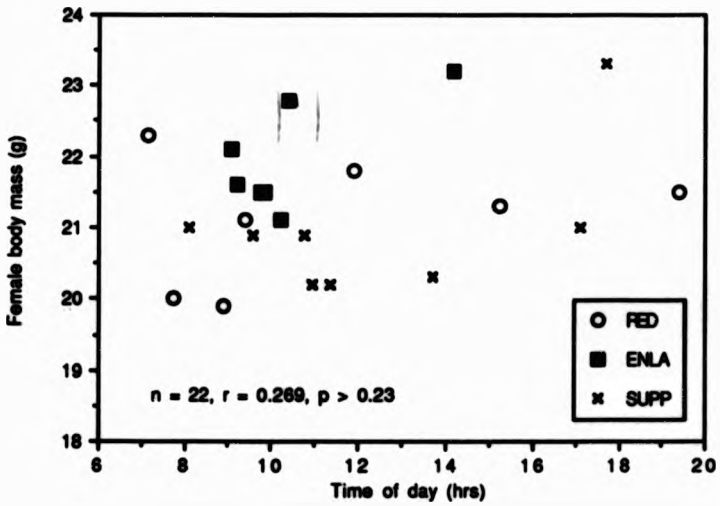

Figure 4.10 Relationship of female mass to time of weighing during incubation.

Table 4.27 Mass change of breeding great tit females during the nestling period, 1990.(Mean (x) and standard error (se)).(ANOVA, n = 22, df = 2)

	TREATMENTS						ANOVA	
	RED (n=7)		ENLA (n=7)		SUPP (n=8)			
Parameter	x	se	x	se	x	se	F	sig
Uncorrected mass								
Mass during incubation[a]	21.1	0.3	22.0	0.3	21.0	0.3	2.57	ns
Mass at Day 13[b]	19.6	0.1	19.1	0.2	18.8	0.3	4.02	*
Mass change	-1.6	0.3	-2.9	0.4	-2.2	0.3	3.77	*
Size corrected mass[c]								
Mass during incubation	0.92	0.01	0.96	0.01	0.91	0.01	4.94	*
Mass at Day 13	0.85	0.01	0.84	0.01	0.81	0.01	2.96	ns
Mass change	-0.07	0.01	-0.13	0.02	-0.10	0.01	4.13	*

a - caught at nest 10 days after the last egg in the clutch was laid
b - caught at nest in the night on Day 13 of the nestling period
c - corrected for body size by dividing mass by TARS (DeLast & Dhondt 1989)

Table 4.28 Comparison between RED & ENLA treatments, and ENLA and SUPP treatments, of female mass during breeding, 1990.

	RED v ENLA			ENLA v SUPP		
Parameter	t	df	p	t	df	p
Uncorrected mass						
Mass during incubation[a]	-1.89	12	ns[b]	2.13	13	ns[c]
Mass at Day 13[d]	-2.16	12	ns[e]	1.10	13	ns
Mass change	-2.66	12	*	1.37	13	ns
Size corrected mass[f]						
Mass during incubation	-2.80	12	*	3.04	13	*
Mass at Day 13	0.69	12	ns	1.72	13	ns
Mass change	-2.81	12	*	1.45	13	ns

a - caught at nest 10 days after last egg in clutch laid
b - p = 0.083
c - p = 0.053
d - caught at nest on the night of Day 13 of the nestling period
e - p = 0.055
f - corrected for body size by dividing mass by TARS (De Last & Dhondt 1989)

4.27). Females were significantly heavier in the ENLA treatment than females in the RED treatment and females in the SUPP treatment (Tables 4.27 & 4.28).

4.5 DISCUSSION

4.5.1 *Effect of supplement*

4.5.1.1 *Growth of FED and UNFED nestlings in the SUPP treatment*

Supplemental feeding was intended to induce variation in nestling diet quality between FED and UNFED nestlings in SUPP broods, and also to explore the interactions with food quantity by comparison of ENLA and SUPP broods. The variation in nestling diet quality was expected to be expressed by a difference in growth rates between FED and UNFED nestlings, with nestlings in the FED treatment growing larger than nestlings in the UNFED treatment. There was, however, no difference in the growth of FED and UNFED nestlings in 1989, and in 1990 there was some evidence that the UNFED nestlings grew more than FED nestlings. The supplement did not, therefore, confer a nutritional advantage to FED nestlings over UNFED nestlings and the assumption in Section 4.2.2.2 proved to be unfounded. Indeed, in 1990 there was evidence that the supplement conferred a nutritional disadvantage to FED nestlings which grew less between Day 5 and Day 15 than did UNFED nestlings in that year.

The supplement was evidently not of sufficiently high nutrient quality to produce the expected increase in growth in FED nestlings. This may have been a result of the relatively high fat content of the supplement (40%) which could have satiated the energy demand of FED nestlings, and thereby reduced begging by these nestlings (Section 3). The dry mass ratio of protein to fat in the natural diet of nestlings (caterpillars) is 2:1 (Mertens 1977) whereas the supplement provided protein:fat in a ratio of 1.5:1 . If energy intake regulated feeding then the nutrition received by the UNFED nestlings from the parents in 1990 was probably equivalent to, or superior to , the nutrition provided by the supplement.

The difference between 1989 and 1990 in the effect of the supplement was not due to a difference in the quality of supplement fed to nestlings as the supplement was made to an identical formula in both years. Nor was the

difference in effect the result of different amounts of supplement fed to nestlings as this too was effectively the same in both years. It is probable that the difference between years was a result of a difference between years in the breeding environment. Females laid earlier, and laid larger clutches in 1990 than in 1989 and the growth of nestlings in all treatments, especially the Control, was greater in 1990 than in 1989. This suggests that natural food availability was higher for broods in 1990 than in 1989. If this was the case then the difference between years was a result of UNFED nestlings in 1990 receiving more food, while the FED nestlings were satiated, than did UNFED nestlings in 1989. In conclusion nestling diet quality did vary between FED and UNFED nestlings but only in 1990, and then in the opposite direction to that which was intended, with UNFED nestlings receiving a higher quality diet than FED nestlings.

4.5.1.2 Growth of nestlings in enlarged broods

There was more growth between Day 5 and Day 15 of nestlings in the SUPP treatment in comparison to nestlings in the ENLA treatment in both 1989 and 1990. This difference in growth was not the result of a difference in breeding parameters between SUPP and ENLA treatments. It is probable that the difference was a result of the supplement-feeding in the SUPP treatment. This feeding may have resulted in a greater quantity of food fed per nestling in SUPP broods than in ENLA broods thus producing the difference in growth. There is support for this view from the analysis of female mass loss. Female feeding effort, as indicated by mass loss (Nur 1984a; Jones 1987; Smith *et al.* 1988), was lower in the SUPP treatment than in the ENLA treatment. Mass loss in the SUPP treatment was still, however, greater than that in the RED treatment even though the effective brood size when FED nestlings were digesting the supplement was similar to the brood size in the RED treatment. This suggests that the UNFED nestlings in the SUPP treatment were fed more by the parents than nestlings in the ENLA treatment and that this resulted in greater nestling growth in the SUPP treatment (FED and UNFED combined) than in the ENLA treatment.

The difference in the magnitude of this effect between 1989 and 1990 may have been the result of greater food availability in 1990 and which meant parents were able to feed a greater quantity of food to nestlings. In these conditions nestlings in enlarged broods were under less nutritional stress than in 1989,

therefore the supplement had less impact on the growth rate of the enlarged broods.

4.5.2 *Effect of brood manipulation*

The brood manipulations were successful in inducing significant differences in nestling growth between treatments. In both 1989 and 1990 nestlings in the RED and CON treatments were significantly larger in all body size measures at Day 15 than nestlings in the ENLA treatment. These results are similar to those from previous brood manipulation experiments with the great tit (Tinbergen 1987; Lindén 1988; Smith *et al.* 1989) but they extend the phenomenon to HEAD and to a multivariate measure of body size (PC1). The explanation for this difference in nestling growth is that although the parents of the ENLA broods raised their feeding rate, as inferred from the high mass loss of females in the ENLA treatment, they still delivered a lower quantity of food per nestling, relative to their requirements, in comparison to parents in the RED and CON treatments. This was true for both 1989 and 1990 despite the apparently greater food availability in 1990.

4.5.3 *Effect of variation in nestling diet on breast stripe*

Interpretation of the analyses of breast stripe size is complicated by the fact that male great tits have a larger breast stripe than female great tits (Svensson 1975). It is assumed in the following discussion that the sex ratio of nestlings did not differ between treatments and that this phenomenon would not therefore bias the results. This assumption was also made for analyses of size.

4.5.3.1 *Diet quality*

Variation in nestling diet quality was present between FED and UNFED nestlings in 1990 (Section 4.5.1.1). SLEN was apparently larger in UNFED nestlings than in FED nestlings at Day 15 and Day 19 in 1990 but this difference was not significant when the effect of body size was removed. This suggests that the increase in SLEN may simply have been a result of the increase in body dimensions. This contrasts with the results of Norris (1990) who found that adult stripe size varied independently of body size and those of Lemel (1989) who

found that chin stripe area varied independently of body size.

4.5.3.2 *Food quantity*

The higher food quantity fed to nestlings in the SUPP treatment in comparison to nestlings in the ENLA treatment did not result in a significant difference in SLEN in 1989 but there was a significantly larger SWID in the SUPP treatment. This difference was still significant, though less so, when the larger body size in the SUPP treatment was taken into account. This is evidence that there is a differential effect of food quantity fed to nestlings on breast stripe in comparison to body size. This evidence is equivocal though, as the sample size for the analyses was only 24 and the difference between male and female stripe size could have biased this small sample. Also, the measurement of stripe width was not consistent in 1989 and the measure was changed in 1990 to be less subjective. In 1990, with a larger sample size and a more repeatable measure, there was no evidence of a difference in stripe size between SUPP and ENLA treatments. This may just be a reflection of the smaller difference between treatments in nestling growth in 1990.

The difference in nestling growth between RED, CON and ENLA treatments in 1989, thought to be due to a difference in the quantity of food fed to nestlings, was not reflected in a difference in stripe size between treatments. This may be explained, as with the comparison of SUPP and ENLA treatments above, by the fact that the sample size was small and that the stripe measures were thought not to be repeatable. In 1990, with a slightly larger sample size and more reliable measures of breast stripe, there was a significant difference in SLEN between treatments. SLEN was longer in the RED treatment than in the CON treatment with the shortest SLEN in the ENLA treatment. These differences were similar to the differences between treatments in body size at Day 19 but they were of a greater magnitude and were still significant after the analysis allowed for the effect of body size. So there is evidence of a differential effect of diet quantity on growth of breast stripe in comparison to growth in body size.

4.5.4 *Do experimental effects occur in natural populations?*

Extrapolation of the experimental results to the natural situation may be complicated by the effect of using nestboxes in this study (Møller 1989c;

Robertson & Rendell 1990). Fledging success is higher in broods from nestboxes than in broods from natural nest sites (Drent 1984). This may be due to lower predation in nestboxes (Drent 1984) or higher growth rates due to lower levels of parasitism in nestboxes, which may be cleaned each year (Møller 1989c). These nestbox effects may mean that the experimental effects described below are of less importance in truly wild populations where parasitism and predation are more prevalent.

4.5.4.1 *Diet quality*

There is some evidence that nestling diet quality varies within populations of the great tit. Great tit parents may select prey items which provide a particular nutrient for nestling growth such as spiders for sulphur containing amino-acids for feather growth (Royama 1970), and snail shells (Perrins 1979) or ash (Ficken 1989) containing calcium for bone growth. Variation in the supply of these prey items will result in variation in nestling diet quality.

The bulk of great tit nestling diet consists of caterpillars. The tannin content of caterpillars may vary according to the composition of the foliage they consume and Perrins (1976) demonstrated that nestling growth decreases with an increase in the intake of tannins. Natural variation in the tannin content of caterpillars may therefore result in variation in nestling growth in the wild (Weathers *et al.* 1990). Variation between individuals, and between years, may occur in the selection of species of caterpillar (Simons & Martin 1990) and this may lead to variation in diet quality (but see Redford & Dorea 1984). It is possible, then, that the diet quality effects demonstrated in these experiments will also be present under natural conditions.

4.5.4.2 *Food quantity*

There is considerable evidence that the food quantity fed to great tit nestlings varies in the wild. Great tit nestlings in coniferous woodland are smaller at fledging than nestlings in deciduous woodland and this difference has been explained by the greater abundance of prey items in deciduous woodland (van Balen 1973; Drent 1984; Björklund & Westman 1986; Lemel 1989). Perrins (1986) suggested that variation in great tit nestling body size is due mainly to variation in nestling nutrition. This statement is supported by the results of van

Noordwijk (1986) who demonstrated that most variation in great tit nestling size was explained by environmental variation of which the most important factor was thought to be variation in the food supply. Variation in food supply may also be caused by changes in population density and competition from other species, such as the blue tit (Minot & Perrins 1986). It is probable, therefore, that the food quantity effect demonstrated in the experiment is also present under natural conditions.

4.5.5 *The importance of diet-induced variation in nestling breast stripe*

Greater food quantity and higher diet quality resulted in a larger nestling breast stripe in this experiment, and this effect may well exist in great tit populations under natural conditions (Section 4.5.4; see Ear Patch Width in Section 2.3.6). There was equivocal evidence that this effect was more pronounced than the effect of diet on body size. It is not known if an effect of diet on breast stripe persists until the nestlings reach adulthood. Only seven nestlings from the 1989 experiment were identified post-fledging and this sample was too small to correlate post-fledging stripe measures with nestling breast stripe measures. Great tit nestling size at Day 15, however, correlates with adult size (Garnett 1981; Smith 1986; Noordwijk *et al.* 1988) and this relationship may be similar for nestling plumage and adult plumage, although adult breast stripe (Norris 1990) and other adult plumage features (Lemel 1989) appear to vary independently of size.

If the diet-induced stripe variation does persist in the adult phenotype then it may have profound consequences on the life-history of individual birds. Järvi & Bakker (1984) showed that stripe width is a correlate of dominance in great tits. They suggested that this conspicuous plumage feature acted as a status-signal (Whitfield 1987) in that it signalled to other great tits the dominance status of individual birds. Further support for this theory was provided by Winge & Järvi (1988) who demonstrated that great tit males with larger breast stripes were more successful in defending nestboxes against pied flycatcher *Ficedula hypoleuca* males. Also, Norris (1990) demonstrated that males with larger breast stripe area bred with females laying larger clutches than males with small breast stripe area. He suggested that females paired selectively with

males and that breast stripe, as a conspicuous visual cue, may act as a signal of male quality. Variability in a character is necessary for mate choice to occur (Reid & Weatherhead 1990) and the experiment above indicates that variation in adult breast stripe size may be influenced by nestling nutrition in which case females may be choosing males with a better nutritional history as has been demonstrated in the house finch *Carpodacus mexicanus* where females select colourful males and plumage colouration is a function of the dietary intake of carotenoids (Hill, G.E. 1990). This study provides, therefore, equivocal support for the 'honest advertisement' hypothesis (Andersson 1986), assuming a genetic influence on great tit breast stripe size (*cf.* badge size of house sparrow, Møller 1990a). This theory proposes that sexually selected characters are phenotypically plastic and reflect the outcome of an individual's interaction with its environment (Hill, G.E. 1990).

Norris (1990) also demonstrated that the great tit's breast stripe increases in size after the first adult moult. There is generally a difference in plumage between one year old males and older males in passerines (Rohwer *et al.* 1980). This phenomenon has been explained as a status signal that indicates to females that one year-old males are of lower status than older males, and it is most likely to occur in species where males defend a nesting territory (Lyon & Montgomerie 1986). Norris's results (1990) are consistent with this explanation. Great tit males defend a nesting territory (Krebs 1982; de Laet 1984) and females select males with a larger breast stripe (Norris 1990). Breast stripe size increases after the first moult (Norris 1990) therefore females are more likely to select older males than one year old males.

If the diet-induced stripe variation persists until the winter it may affect the survival and dispersal of juveniles. The dominance status of juvenile great tits of both sexes is largely determined by the nestling environment (Westman 1990) and this may be mediated by variation in plumage stripe indicating the quality of individual juveniles. Dominant juveniles may have greater access to food resources (Garnett 1981) in the month after fledging when there is high mortality due to competition for food (de Laet 1985). Aggression of juveniles increases during the summer and reaches a peak in October when dispersal takes place (de Laet 1985). Less dominant individuals may be forced to disperse to unfavourable environments (Lehikoinen 1986a). The number of recaptured

juveniles from the 1989 experiment was too small (n = 7) to make a statistical comparison between treatments, yet the one obvious feature of the data was a higher number of juveniles from the SUPP treatment than might be expected. This provides some weak evidence that nestlings from the SUPP treatment, with a wider stripe and larger size than other treatments, either survived better or dispersed less than nestlings from other treatments. Both of these possibilities are consistent with the theory that stripe width indicates dominance status.

Variation in breast stripe may also facilitate individual recognition in the great tit (Whitfield 1987). This may help in the maintenance of the dominance hierarchy in wintering flocks (Whitfield 1987) or enable territorial males to recognise novel birds to which they are more aggressive (Curio 1989).

The results of this experiment indicate that some of the variation in adult breast stripe within a population may be caused by variation in nestling diet independent of its pigment content. Variation in nestling diet is likely to be present in wild populations and it is possible that it may contribute to the variation in breast stripe within a great tit population with profound consequences for the life-history of individual birds.

4.5.6 *Cost of reproduction*

Brood enlargement in this experiment resulted in greater female mass loss. This was probably the result of a higher parental feeding frequency in enlarged broods (i.e. higher parental effort, Smith *et al.* 1988). Further evidence for the effect of feeding frequency is provided by the fact that females in the SUPP treatment, where nestling begging was probably reduced by supplemental feeding, lost less mass than females in the ENLA treatment. This result agrees with those of de Laet & Dhondt (1989) but contrasts with those of Tinbergen (1987), Lindén (1988) and Smith *et al.* (1988).

Tinbergen (1987) demonstrated that mass loss from Day 7 of the nestling period to Day 12 was not affected by brood manipulation. It is possible that the shorter gap between the two mass measurements in Tinbergen's experiment was not sufficient to detect the effect of brood manipulation on the cost of reproduction of the parents. Lindén (1988) demonstrated that brood manipulation did not

affect female mass at Day 13 of the nestling period but mass change during the nestling period may be masked in this case by variation in the basal mass of females, such as the variation in mass at incubation between treatments found in this experiment (Tables 4.27 & 4.28). This possibility is acknowledged by Lindén (1988). Another possibility for the difference in results between Lindén (1988) and Tinbergen (1987), and this study, is that their experiments were performed on double-brooded European great tit populations, where as the study reported here was on a single-brooded population in which females may invest more effort in rearing their one brood rather than females that may rear a second brood (Lindén 1988).

4.5.7 *Feeding frequency and brood size*

Lack (1954) and Gibb (1955) first proposed the theory that feeding frequency was limited by parental ability, and that the brood size reared by parents represents the maximum number of nestlings that the parents can adequately feed. This theory predicts that parents of experimentally enlarged broods should not be able to raise their feeding frequency. Some brood manipulation experiments have, however, demonstrated that parents can increase feeding frequency when broods are enlarged (Nur 1984; Smith *et al.* 1988) and other brood manipulation experiments, including this study, have shown an increased mass loss of parents rearing enlarged broods (Hussell 1972; Askenmo 1977; Bryant 1979; Westerterp *et al.* 1982) which may indicate increased feeding effort by parents (Nur 1984a; Jones 1987; Smith *et al.* 1988; Slagsvold & Lifjeld 1990). These results contradict the predictions of the Gibb-Lack hypothesis.

An alternative hypothesis was proposed by Nur (1984) to explain the results from his study of blue tit feeding frequency. He proposed that given a genetic influence on feeding behaviour, natural selection should favour a feeding frequency which maximises the difference between reproductive costs (e.g. parental mass loss) and benefits (e.g. nestling survival). This theory was supported by Smith *et al.* (1988) who identified both a cost and benefit of higher feeding frequency for the great tit. Their study demonstrated a cost of increased feeding frequency in terms of an increase in the mass lost by parents over the nestling period. Everything else being equal, an increase in feeding frequency

should also result in larger nestlings (Smith *et al.* 1988). Larger great tit nestlings tend to survive better (McCleery & Perrins 1988; Tinbergen & Boerlijst 1990) so there is an identifiable benefit of a higher feeding frequency.

The results of the 1990 experiment also support Nur's hypothesis (1984a) as great tit nestling size decreased with increasing brood size (Tables 4.10 & 4.19), presumably because feeding effort per nestling declined as brood size increased. Nur's hypothesis is also supported by the effect of the supplement on female feeding frequency in 1990. Female feeding frequency, as evidenced by mass loss, was lower in SUPP broods than ENLA broods in 1990. Females did not continue to feed the brood with the same frequency which would have resulted in greatly enhanced growth of UNFED nestlings in SUPP broods albeit at a greater cost to the females. Instead it seems that there was a trade-off, with females in the SUPP treatment reducing their feeding frequency and therefore their mass loss (i.e. cost) whilst still achieving a greater benefit (i.e. larger nestlings) than females in the ENLA treatment. This supports Nur's prediction that feeding frequency is adapted to maximise the difference between reproductive costs and benefits.

5 DISCUSSION

5.1 THE USE OF DIETARY SUPPLEMENTS IN STUDIES OF AVIAN BIOLOGY

5.1.1 *The effect of supplement quality on nestling growth*

The results of Chapters 3 and 4 of this study demonstrate that variation in nestling diet quality affects nestling growth. These results were achieved through the use of a dietary supplement administered directly to the nestlings.

The difference in supplement quality (defined as limiting nutrient kJ^{-1}) between experiments was reflected in the effect of each supplement on nestling growth. The bulk of dry mass growth is through protein deposition (Robbins 1983) and a supplement could therefore be expected to have an increasingly positive effect on growth as it increases in quality, through increasing protein intake by nestlings (Fig. 5.1a), provided protein was limiting to growth. The experimental results, however, do not fit this model (Fig. 5.1b). This can be explained by the fact that the effect of a supplement will vary with the quality of the control diet that is supplemented. A control diet providing more of the limiting nutrient will result in less effect of the supplement on nestling growth, and if the control quality is higher than supplement quality the supplement will have a negative effect on growth, assuming food quantity itself is not limiting, because the supplement provides less of the limiting nutrient. This relationship can be incorporated into the model by redefining the *x*-axis as 'relative limiting nutrient content' (Fig. 5.2a). The results from the three experiments fit this model more closely (Fig. 5.2b), indicating that relative limiting nutrient content, assumed to be protein, did affect the outcome of the supplementation experiments in this project, although a test of this relationship is not justified with such a small sample size. Future studies should define supplement composition, and control composition, more precisely in order that their results can be interpreted fully.

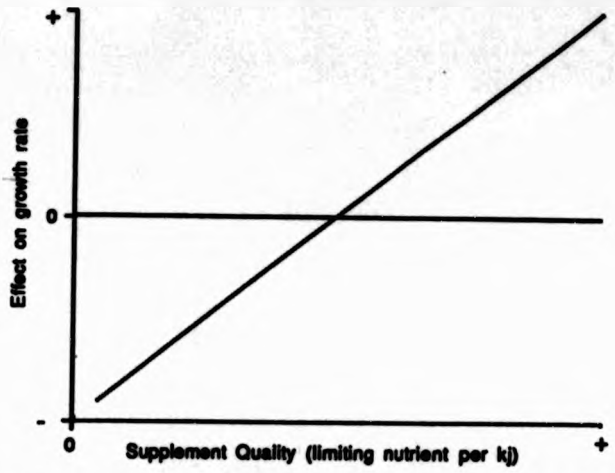

Figure 5.1a Theoretical relationship of supplement quality to effect on growth.

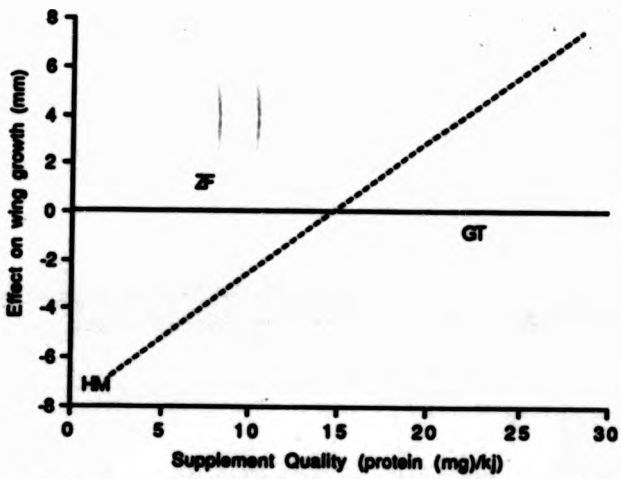

Figure 1.b Relationship of supplement quality to effect on wing growth.

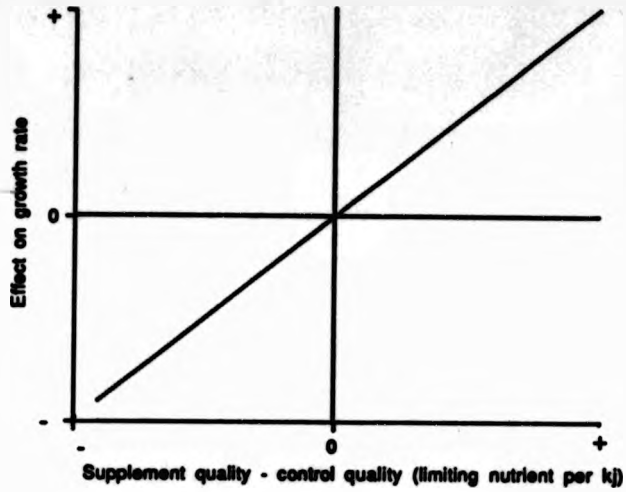

Figure 5.2a Theoretical relationship of supplement effect to relative supplement quality.

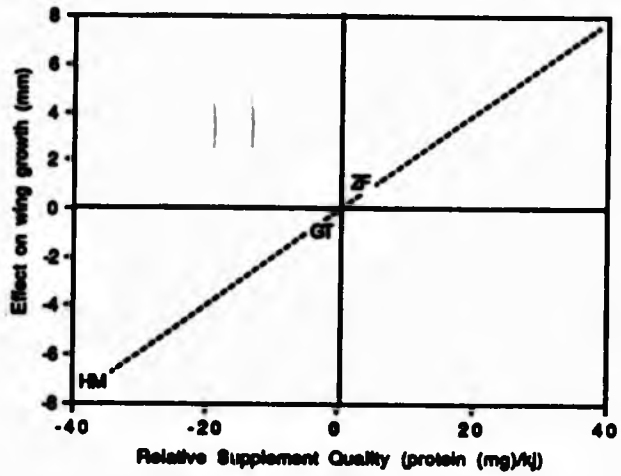

Figure 5.2b Relationship of relative supplemental quality to effect on wing growth.

5.1.2 *The effect of variation in supplement quality on the results of other supplement experiments*

Supplement quality may also affect the results of supplementation experiments investigating other aspects of avian biology. Recent reviews of food supplementation experiments (Martin 1987; Boutin 1989) have highlighted the need for improvements in the methodology of these experiments by regulating the time period over which the supplement is supplied, by controlling for the effects of natural variation in diet and by repeating the experiment to allow for year-to-year variability. The influence of the quality of the supplement is ignored in these reviews even though it may affect experimental results, such as those for the effect of supplemental feeding on clutch size. A supplement may provide extra resources for females and these exogenous resources may be important in determining clutch size, either directly through an increase in the resources for egg formation (Jones & Ward 1976), or indirectly through acting as a signal of higher food resources in future which encourages females to lay a larger clutch.

There is equivocal evidence for a positive effect of supplemental food on clutch size. Martin (1987) found that three out of nine studies had detected a positive effect of a supplement on clutch size. This positive effect on clutch size is usually accompanied by an earlier laying date (Meijer *et al.* 1990). Since Martin's review (1987) three more studies have demonstrated a positive effect of supplement upon clutch size (Arcese & Smith 1988; Korpimaki 1989; Hörnfeldt & Eklund 1990) and four have failed to detect an effect (Hill, W.L. 1988; Knight 1988; Clamens & Isenmann 1989; Dhindsa & Boag 1990). This difference in results between studies could be the result of differences in methodology such as the timing and technique of supplement provision, or the result of differences in the relative natural abundance of food during experiments (Martin 1987). Alternatively, the difference between results may be explained by variation in the quality of supplement provided to females.

Five of the seven studies which demonstrated a positive effect of supplementation used fish, chick or mouse carcasses. The majority of carcass dry weight is protein (Maynard & Loosli 1969; Robbins 1983). The remaining study used dog food containing 21% protein by dry mass (Table 5.1). The ten experiments which failed to demonstrate an effect of supplement on clutch size included one that used a carcass, and one that used dead chicks and eggs. The other

Table 5.1 **Comparison of supplement quality between those studies demonstrating a positive effect of supplement on clutch size and those studies showing no effect of supplement on clutch size.**

Paper	Species	Supplement
Positive effect		
Hogstedt 1981	*Pica pica*	Minced fish
Newton & Marquiss 1981	*Accipiter nisus*	Pigeon carcasses
Dijkstra *et al.* 1984	*Falco tinnunculus*	Mice carcasses
Harper 1984	*Erithacus rubeia*	n.a.
Arcese & Smith 1988	*Melospize melodia*	Dog food (21% protein)
Korpimaki 1989	*Aegolius funereus*	Mice
Hörnfeldt & Eklund 1990	*A. funereus*	Mice and chicks
No effect detected		
Kallander 1974	*Parus major*	Mealworms
Yom Tov 1974	*Corvus corone*	Eggs and chicks
Bromssen & Jansson 1980	*Parus montanus* & *P. cristatus*	Sunflower seeds & tallow containing soya
Ewald & Rohwer 1982	*Aegolaius phoeniceus*	Sunflower seeds & dog food
Smith *et al.* 1982	*M. melodia*	n. a.
Davies & Lundberg 1985	*Prunella modularis*	Oats, maggots & mealworms
Clamens & Isenmann 1987	*P. major* & *P. caeruleus*	Mealworms and caterpillars
Hill 1988	*Fulica atra*	26% protein animal feed
Knight 1988	*Pica pica*	Carcass + insects in carcass
Dhindsa & Boag 1990	*Pica pica*	25% protein & 12% fat

studies used foods of lower protein content than carcasses (Table 5.1). There is a possibility, therefore, that the discrepancy in results between experiments may be the result of a difference in the nutritional quality of the supplement, in terms of its protein content per kilojoule, with a lower protein content providing less material for egg formation. The relative importance of fat and protein supplies for egg formation has been the subject of many poultry studies (Spratt & Leeson 1987; review in Stadelman & Pratt 1969) but has yet to be determined in most wild birds (Briggs 1969a), although overall food abundance has been related to clutch size in some species (e.g. great tit, Perrins 1979; house martin, Bryant 1978a; tree swallow *Tachycineta bicolor*, Hussell & Quinney 1987).

Pre-laying red grouse *Lagopus lagopus scoticus* select heather *Calluna vulgaris* containing a higher concentration of nitrogen and phosphorus (Moss 1972, 1977). The nitrogen content of heather may relate to protein requirements for egg-laying (but see Moss *et al.* 1990). Eldridge & Krapu (1988) demonstrated that mallards *Anas platyrhynchos* which received a higher protein diet laid larger clutches than those birds on a lower protein diet. Naylor & Bendell (1989) showed that an increase in protein intake by female spruce grouse *Dendragapus canadensis* may lead to a larger clutch size. There is evidence, therefore, that protein intake may determine clutch size in wild birds (but see Hepp *et al.* 1987). More experiments are required to elucidate the relative roles of fat and protein resources in egg formation and their role in the limitation of clutch size in wild birds. This could be achieved through supplement experiments which make comparisons between the effects of supplements that differ in protein and fat content (Hill 1989).

The results of Chapters 2 & 3 of this study and a review of the literature suggest that the quality of the supplement must be considered for the wider interpretation of the results of food supplementation experiments.

5.2 DOES NESTLING DIET QUALITY VARY IN THE WILD?

The experimentally-induced variation in nestling diet quality described in Chapters 2 and 3 produced a variety of effects on the growth of zebra finches and house martins. These experimental effects may be present in wild populations if nestling diet quality shows sufficient variation.

Zebra finch nestling diet quality may well vary in wild populations as zebra finches are facultative insectivores and those parents with access to a source of insect prey will probably feed their nestlings a greater number of insects, and therefore more protein than parents without a source of insect prey. Also, the quality of seeds varies between species (Shuman *et al.* 1989) and seed supply is highly seasonal so there may be spatial and temporal variation in quality of a purely granivorous nestling diet. These causes of variation in nestling diet quality may well be present in other granivorous birds.

The alate diet of nestling aerial insectivores, such as the house martin, may not vary in terms of quality as much as that of granivores, even though it varies greatly in abundance. The alate population consists of so many taxa from different sources that any variation in the abundance, or quality of any one taxon, is unlikely to bias the overall quality of the diet. There is another mechanism, however, that may result in an effective reduction in diet quality. Protein retention in lean tissue is reduced when the energy intake is at maintenance level (Blaxter 1989) thus food supply only at the energy maintenance level may have a lower 'effective' quality in terms of protein content.

5.3 THE IMPORTANCE OF DIET QUALITY EFFECTS

5.3.1 *Diet quality effects in other animals*

Research has revealed environmental effects on growth in many different orders of animal. These effects may be mediated by variation in the diet quality available to the growing animal.

Some insect larvae exhibit plasticity in growth (e.g. speckled wood butterfly *Pararge aegeria* (Nylin *et al.* 1989) and this plasticity may be the result of variation in the diet quality available to larvae. Low diet quality, in terms of the nutrient quality of foliage, results in slower growth of lepidopteran larvae (*Papilio polycenes*, Finke & Scriber 1988; *Gymnaephoria groenlandica*, Kukal & Dawson 1989; *Samea multiplicatus*, Taylor 1989; *Hemiluca lucina*, Stamp & Bowers 1990) and larvae may show adaptations to combat low diet

quality (Taylor 1989). Growth and adult size of hymenoptera (*Bombus rufocinctus*, Owen 1989) and orthoptera (*Myrmeloetettix maculatis* & *Chanthippus brunneus*, Atkinson & Begon 1988) may also be affected by variation in larval diet quality, but not all insects show this response (e.g. *Pogemus chaiceus*, Desender 1989).

Variation in diet quality may also result in differential growth of orthopterans. Bernays (1986) showed that diet quality affected the size of the head in *Pseudoleca unipuncta*; a lower quality of leaf supplied to larvae resulted in a greater development of the head in imagines. The larger size of the head enabled the larvae to chew the tougher leaves.

Vertebrates also show environmental effects on growth; for example in fish (*Poeciopsis*, Wetherington *et al.* 1989; *Salmo salar*, Metcalfe & Thorpe 1990), amphibians (*Rana climitans*, Berven *et al.* 1979; *Bombina orientalis*, Kaplan 1989) and reptiles (Ford & Siegel 1989; Grant & Dunham 1990). These effects may be caused by variation in factors such as temperature or quantity of food. It is possible that diet quality may be important but more research is needed before this potential role of diet quality can be evaluated.

Mammals have been studied more intensively than other orders and there is direct evidence that diet quality can affect the growth and body size of mammals (e.g. *Rattus norvegicus*, Smart *et al.* 1987; *Mus musculus*, Toyomizu *et al.* 1988; *Sigmodon hispidus*, Dering 1989). This relationship between diet quality and growth has been invoked to explain temporal and spatial intraspecific variation in the body size of the reindeer *Rangifer tardus* (Klein *et al.* 1987), the Columbian ground squirrel *Spermophilus columbianus* (Dobson 1988) and baboons *Papio* spp. (Vitzhum 1988; Dunbar 1990). A detailed study of a population of pocket gophers *Thomomys bottae* (Patton & Bryiski 1987) showed that males were 25% heavier in alfalfa fields than in the natural habitat of pocket gophers. This difference was not the result of genetic differences between males as there was considerable gene-flow between the alfalfa fields and the natural habitat. Laboratory growth rate of gophers increased when diet quality was increased. Patton & Bryiski (1987) suggest that in this mammal growth rate is labile and that the adult size which is characteristic of a particular population results in part from differing initial growth rates which are related to the quality of food in

each habitat.

There is evidence, then, that diet quality variation in the wild can affect growth and adult size of invertebrates and vertebrates but these organisms are assumed to show relatively indeterminate growth in comparison to birds (Atchley 1984; Alatalo *et al.* 1990). For this reason it is necessary to obtain empirical data for an effect of diet quality on birds rather than simply extrapolate from the phenomena demonstrated for other organisms.

5.3.2 *Growth rate*

Nestling growth rate was faster in nestlings that received a higher quality diet (Chapters 2 & 3). This difference in growth was not always detected by growth rate analysis in this study. It is possible that growth rate analysis was not appropriate for the short data sets in Chapters 3 & 4 of this study because they did not permit accurate fitting of the growth curve; for example the asymptote was not reached in many of the curves. Growth studies collecting relevant data over a short time period should use growth curves for descriptive purposes only and use other, simpler, measures of growth for analysis (Zach 1988; Jehl *et al.* 1990) such as comparisons of size at the beginning and end of the experiment (Chapters 2, 3 & 4).

The faster growth of nestlings receiving a higher quality diet resulted in earlier fledging of nestlings (Chapters 2 & 3). Earlier fledging can be advantageous because it reduces the time for which nestlings are vulnerable to nest predation (Lack 1968) and also because it gives an advantage to early fledglings when in competition with other fledglings for the exploitation of a limited food resource (Perrins 1979; Arcese & Smith 1985).

Lack (1968) hypothesised that growth rate was a compromise between mortality risk in the nest and the availability of food, with higher risk of nestling mortality resulting in higher rates of nestling growth. Ricklefs (1973) proposed an alternative hypothesis. He suggested that nestlings grow at a physiological maximum to minimise the nestling period and therefore reduce the risk of predation. This maximum rate may be determined by the rate of

differentiation of myoblasts into skeletal muscles (Ricklefs 1973). Ricklefs' theory may explain growth rate variation in precocial birds (review in Martin 1987) but the situation for altricial birds is more complicated.

There is considerable evidence that growth rate is below the physiological maximum in altricial species (Martin 1987). For example the growth rate of tropical birds is slower than that of ecologically and morphologically similar species in temperate regions (Ricklefs 1976), whereas Ricklefs (1973) theory would expect similar growth rates within taxa, in both temperate and tropical regions. This difference in growth rates between tropical and temperate species also contradicts Lack's (1968) hypothesis, in that growth is slower in the tropics even though there is a higher risk of predation in the tropics (Skutch 1966). Martin (1987) suggested that growth rate of altricial birds is food limited. The results of this study, which demonstrated that diet quality affects growth rate (Chapters 2 & 3), also provide evidence that growth is limited but that this food limitation may take the form of a limitation in nestling diet quality as well as in food supply.

5.3.3 *Differential growth*

Growth is the process whereby an animal incorporates into its molecular structure a portion of the external chemical environment (Robbins 1983). Patterns of growth differ between altricial and precocial modes of development (Ricklefs 1983) and also within these modes (O'Connor 1977, 1978a,b). It has been suggested that a nestling may differentially apportion chemicals to those organs and tissues of greatest value at each stage of growth, and that variation in the priority of structures within and between altricial and precocial birds, results in the differences in the pattern of growth (O'Connor 1977; Kushlan 1977; Ricklefs 1983; Slagsvold 1983; Tatner 1984).

The three Chapters of this study induced differences in the resources available for nestling growth. The effects of this difference on each size parameter will depend on the priority of that structure to the individual nestling. Passerine nestlings require protein for growth (Robbins 1983) and when protein supply is limited a nestling may allocate protein and other nutrients for the growth of high priority structures at a cost to other, lower priority, organs and tissues. This implies a smaller difference between treatments in high

priority structures than in low priority structures.

There were significant differences between treatments in zebra finch nestling size at Day 40 (Table 5.2), the age at which the difference in dietary regimes ceased. The nestlings in the HIGH treatment were larger in may aspects than nestlings in the control. The only parameter for which there was not a significant difference was bill width, indicating that this parameter was of high priority to the finch nestlings. The bill morphology of nestling birds can be different to that of adult birds (Royama 1966; O'Connor 1977; Feltham 1987). This difference may be due to the different priorities of nestlings and adult birds. Dipper nestlings, for example, maximise the target area of their gape to maximise their signal to parents and also to accomodate large feeds. Later in the nestling phase the bill assumes an adult shape more suited to independent feeding (Feltham 1987). This may also be the case for zebra finch nestlings given the apparent priority for bill width development. Bill width may determine the gape size of zebra finch nestlings. If so, it is possible that nestlings in the control diverted some resources from other tissues to increase bill width growth and thereby increase their gape size so that they maximised begging efficiency, in terms of the signal to parent birds and the ability to handle large food items.

House martin nestlings in the FATFED treatment received less protein than nestlings in the control (Chapter 3). This difference in nutrition resulted in a significant difference between treatments at Day 20. The two size parameters that were not significantly larger in the control than in the FATFED treatment were body mass and tarsus length.

Tarsus growth is usually completed earlier than the growth of other structures (Austin & Ricklefs 1977; Feltham 1987) presumably because a highly developed tarsus assists in maintaining a feeding position in the nest (O'Connor 1977; Marsh 1979; Ryden & Bengtsson 1980). The high priority of tarsus growth for FATFED nestlings probably resulted in a diversion of resources for tarsus growth in these nestlings, thus explaining the lack of a significant difference between treatments in tarsus size at Day 20. There was no significant difference in body mass because of the large amounts of body fat present in nestlings from the FATFED treatment.

Brood manipulation did not differentially affect great tit nestling structures. Differences between FED and UNFED nestlings, and supplemented (SUPP) and enlarged (ENLA) broods, however, were most pronounced for wing length in 1990 (Chapter 4). Impoverished nestlings may have diverted resources away from wing growth, which requires large amounts of protein (Robbins 1983) and specific amino-acids (Murphy & King 1986a), to other components of the body which were not significantly different between treatments. This suggests that wing growth is a low priority in great tit nestling development. Great tit fledglings do not need to fly long distances, instead they fly from perch to perch where they stay while the parents continue to feed them (Perrins 1979). Wing growth need not, therefore, be a priority for nestlings as compensatory growth may occur after fledging without incurring a competitive disadvantage as a result of a short initial wing length (Slagsvold 1983). Indeed great tit nestlings which explode from the nest at Day 15 can still survive to become adult (Perrins 1979). This apparently low priority of wing growth for nestlings may also be present in other passerine species as there appears to be adaptive explanation for intraspecific variation in wing growth (Redfern 1989).

One component of growth that was not investigated in this study was the growth of the digestive system. The rate of gut development may be adapted to the particular requirements of a species (Lightbody & Ankney 1984) and growth may be limited in some species by a limitation in the growth of gut capacity (Konarzewski *et al.* 1989). In passerines the size of the digestive organs, as a percentage of body mass, reaches a peak early on in development (O'Connor 1977; Bryant & Gardiner 1979; Feltham 1987) before the dietary regimes were in place in the house martin and great tit experiments (Chapters 3 & 4). It is unlikely, therefore, that diet quality affected gut development in these experiments. It is possible, however, that variation in diet quality may influence gut development in wild passerine nestlings as adult gut dimensions of some species are affected by diet quality, for example the white-cheeked bulbul *Pycnonotus leucogenys* (Al-Dabbagh *et al.* 1987), mallard (Kehoe *et al.* 1988) and various frugivorous birds (Levey & Karasov 1990; Walsberg & Thompson 1990). More experiments are needed to investigate this relationship in wild birds.

5.3.3.1 *Use of body condition indices*

Variation in diet quality affects the accumulation of protein and fat in the tissues of growing poultry (Woodward *et al.* 1977; Baghel & Pradhan 1989; Fancher & Jensen 1989a,b,c; Summers *et al.* 1989; Marks 1990; Whitehead 1990). This has important commercial consequences in the poultry industry because producers try to maximise the lean carcass mass of birds. Extrapolation of phenomena demonstrated in poultry to wild birds is difficult because of the highly inbred nature of poultry populations, which may even result in a variation in response to diet quality between strains of the same species (Marks 1987, 1990; Whitehead 1990). Empirical studies of wild birds are needed to investigate the dynamics of protein and fat deposition in wild birds.

Chapter 2 of this study used an ultrasound probe to assess the body condition of zebra finches in terms of pectoralis thickness. This technique was sensitive enough to detect differences between treatments in these small birds suggesting that it may have applications in other studies investigating the relation of pectoralis thickness (i.e. protein resources) to other life history parameters, such as overwinter survival (Newton 1989). Previously such studies would have used carcass analysis to measure body composition, thus precluding a continuous measure of pectoralis measurements on individual birds but technological advances have now made available accurate non-destructive measures of body condition and composition such as the ultrasound probe, total body electrical conductivity (TOBEC, Walsberg 1988; Castro *et al.* 1990) and nuclear magnetic resonance (NMR, Lewis *et al.* 1986). These techniques may allow more accurate monitoring of protein and fat deposition during nestling growth and adult life than is possible through the use of crude indices of condition (e.g. Slagsvold 1982; Briggs 1989b; Castro & Myers 1990; Ormerod & Tyler 1990) or subjective measures such as fat-scoring (Krementz & Pendleton 1990), thus opening up more areas of investigation into the dynamics of fat and protein deposition in wild birds.

5.3.4 *Growth curve shape*

There was evidence from Chapter 2 of this study that nestling diet quality may influence the shape of nestling growth curves as well as nestling growth rate. Growth curve shape may be more sensitive to environmental perturbation than

growth rate (Brisbin *et al.* 1987) and the results of this study suggest that it may be a beneficial tool for future research into areas such as the adaptive function of reduction of peak brood demand (Bryant & Gardiner 1979), and the differential provision of male and female nestlings (Howe 1977; Stamps 1990). The alteration of growth curve shape may also have important economic benefits in the future of the poultry industry (Pasternak & Shalev 1983). The major drawback of this technique of analysis is that it requires a complete longitudinal data set for accurate curve-fitting such as existed in Chapter 2 of this study for the analysis of zebra finch growth. In wild bird populations complete growth curves are difficult to obtain as birds do not usually reach the asymptote of the growth curve until after fledging, when they are difficult to catch for repeated measurements (but see TARS, Chapters 2, 3 & 4).

5.3.5 *Fledging size*

The faster growth of nestlings fed a higher quality diet (Chapter 2 & 3) resulted in larger nestling size at, or near, the time of fledging. There is evidence that larger nestlings have greater survival than small nestlings in the period after fledging from studies of the great tit (Perrins 1966; Dhondt 1979; Garnett 1981; Drent 1984; McCleery & Perrins 1988; Smith *et al.* 1988; Tinbergen & Boerlijst 1990), dipper *Cinclus cinclus* (Newton 1989), dunnock *Prunella modularis* (Davies 1986), starling *Sturnus vulgaris* (Krementz *et al.* 1989), sparrowhawk *Accipiter nisus* (Newton *et al.* 1983), blue tit (Nur 1984b), house sparrow (Schifferli 1978), kittiwake *Rissa tridactyla* (Coulson & Porter 1985) and also from interspecific comparisons (Saether 1989). Some studies have not, however, detected this effect (Arcese & Smith 1988; Ross & McClaren 1981). The recapture rates of fledglings from the experiments in this study (Chapters 3 & 4) were too small for any conclusions to be made on the relative survival of fledglings fed different qualities of nestling diet. The evidence cited above suggests that the larger size of nestlings fed a high quality nestling diet is likely to be of advantage in terms of survival to the next breeding season.

Two mechanisms have been suggested for this greater survival of large nestlings. Large size may represent a larger fat reserve (Chapter 2) and hence greater reserves to withstand periods of food shortage (Smith 1988) but maintenance of a high fat level may be costly and may only be beneficial in harsh conditions (Lehikoinen 1986b). It is also possible that large size confers a

dominance advantage reflected in a greater access to a food resource, both in flocking species (Smith 1988) and territorial species (Newton 1989), and that this effect results in the greater survival rate of large nestlings.

5.3.6 *Adult size*

Direct evidence for an effect of diet quality on the adult size of zebra finches was presented in Chapter 2 of this study. An effect of nestling diet quality on the adult size of a passerine has only been demonstrated twice before (Boag 1987a; Richner 1989). There was no direct evidence for an effect of nestling diet quality on adult size in the other experiments (Chapters 3 & 4), but the differences in fledging size in these experiments are likely to extrapolate to differences in adult size because adult size is correlated to fledging size in both the house martin (Riley *pers. comm.*) and great tit (Noordwijk *et al.* 1988; Smith 1988), although compensatory growth may occur (Lindén 1988).

Body size is the most important determinant of individual life histories in mammals (Clutton-Brock & Harvey 1983; Lindstedt & Swain 1988). The allometric physiological relationships detected in mammals are also found in birds with metabolic rate, locomotion, ingestion and growth all related to body size (Peters 1983).

Larger birds have a lower metabolic rate, a higher total energy requirement and a greater thermodynamic efficiency than smaller birds (Kendeigh 1972). The greater thermodynamic efficiency of large birds may enhance survival during periods of cold stress (Fleischer & Johnston 1982, 1984; Lehikoinen 1986a; Monaghan & Metcalfe 1986; but see Searcy 1979 & Jones 1987b) and extend winter range (McNab 1970). Winter survival may also be enhanced by dominance (Kikkawa 1980; Ekman 1984; Desrochers *et al.* 1989) which may result in better access to food resources whether in feeding flocks (Alatalo & Moreno 1987; Hogstad 1988; Wagner & Gauthreaux 1990; Chapter 2 of this study) or in territories (Lehikoinen 1986a; Collins & Paton 1989; Newton 1989).

There is some evidence of a cost of dominance, however, in terms of a higher metabolic rate (Reskaft *et al.* 1986; Hogstad 1987). Smaller recessive

individuals may survive by exploiting a different niche suited to their morphology and lower total energy requirements in comparison to dominant birds (Johnston & Fleischer 1981; Goudie & Ankney 1986; Lehikoinen 1986b; Moermondt & Howe 1986; Collins & Paton 1989). Winter survival appears to be determined by the interaction of the dominance status of an individual, its total energy requirement and its feeding behaviour (Lehikoinen 1986a).

The dominance status conferred by larger size may also influence breeding success with larger individuals breeding more successfully than smaller individuals in some species such as the house martin (Bryant & Westerterp 1982; Bryant 1989), swallow (Møller 1988, 1989a) and carrion crow (Richner 1989b). Smaller individuals of territorial species may be forced by larger birds into inferior breeding territories (Ulfstrand *et al.* 1981; Lemel 1989; Richner 1989a,b).

Females may also choose to pair with males on the basis of the size of a morphological feature, such as tail length in the long-tailed widowbird *Euplecte progne* (Andersson 1982), barn swallow *Hirundo rustica* (Møller 1988) and shaft-tailed whydah *Vidua regia* (Barnard 1990). Longer tail length is thought to be a handicap in terms of flight cost (Møller 1989a) and it has been hypothesized that these conditions of sexual selection for a handicapping trait favour the evolution of phenotypic plasticity of these traits (Nur & Hasson 1984), because optimal development of the handicap will correlate positively with the nutritional state of the organism. Variation in nestling diet quality, causing variation in growth, is one mechanism by which nutrition may induce phenotypic plasticity of these traits.

The studies cited above have usually assumed that adult size is a constant but recent studies have demonstrated that adult size may vary after the growth phase is complete (Smith *et al.* 1986; Alisauskas 1987; Francis & Wood 1989). This variation may also apply to bill measures (Gosler 1987; Jordan 1987; Morton & Morton 1987; Matthysen 1989). Variation in feather measurements may be explained by nutrition during the moult (Waite 1990) whereas variation in bill measures may be the result of abrasion or an adaptive response to a variation in food supply (Matthysen 1989). Whatever the mechanism, there is some evidence that the concept of an absolute adult phenotype may be mistaken and

that in future we may have to consider adult phenotype as a plastic parameter.

In summary, the larger adult size resulting from higher nestling diet quality appears to confer an advantage to individuals in terms of dominance, survival and breeding success. This advantage is, however, balanced by the greater total energy requirements of larger size and the cost of maintaining dominance status.

5.3.7 *Adult plumage*

Diet quality and food quantity were found to influence nestling breast stripe size in the great tit. There was equivocal evidence that this effect was independent of the effect of diet variation on nestling body size. The importance of diet-induced breast stripe variation has been summarised in Section 4.4. The most telling indication from the experiment is that diet quality, independent of pigment content, may influence the dimension of plumage features which act as a status signal. If this is the case then the dimension of the plumage character may reflect the nutritional history of an individual bird, as well as its genotype (Møller 1989d), and a long term consequence of variation in nestling diet is thereby identified.

Other environmental factors may also influence plumage characters which act as status signals. The level of parasitism is related to male colouration in the stickleback (Milinski & Bakker 1990) and a similar phenomenon occurs may also occur in birds (review in Loye & Zuk 1990), for example the comb size of red jungle fowl (*Gallus gallus*) is inversely related to the number of gut parasites (Zuk *et al.* 1990). This may be viewed as an indirect effect of nutrition on growth of birds as a higher number of gut parasites will reduce digestive efficiency and parasites in other parts of the body will divert resources away from growth, for example the nematode parasite *Trichostrongylus tenuis* on of the red grouse *Lagopus l. scoticus* (Hudson & Rands 1988).

More experiments are needed to further investigate the possible influence of nestling diet on adult plumage in wild birds. One aim of these experiments should be to establish if the differences observed in nestling plumage persist in adult plumage.

5.4 BROOD REDUCTION

Hatching asynchrony is a widespread phenomenon amongst bird species. It is facilitated by starting incubation prior to clutch completion so that young may hatch on separate days (Lack 1968). It has been commonly assumed that this asynchrony has an ultimate, adaptive, value (Slagsvold 1984; but see Meads & Morton 1986). Several hypotheses have been proposed to explain the assumed adaptive value of hatching asynchrony such as the nest failure hypothesis (Clark & Wilson 1981), the peak load reduction hypothesis (Hussell 1972; Bryant & Gardiner 1979) and the reduced sibling rivalry hypothesis (Hahn 1981).

Lack (1954) proposed the brood reduction hypothesis which explains hatching asynchrony as an adaptation which enables adult birds of species with unpredictable food supplies to reduce brood size in times of food shortage by selectively starving the smaller, later hatched young (O'Connor 1978c). Hatching asynchrony is not, however, a pre-requisite for the occurence of brood reduction as brood reduction also occurs in synchronous broods (Ricklefs 1965; Ligon 1970; Shaw 1986), as predicted by O'Connor (1978c). This is explained by the fact that the mechanism of brood reduction is a size hierarchy within a brood and these hierarchies may result from egg size differences as well as hatching asynchrony (e.g. Schifferli 1973; Bryant 1978b, Edwards & Collopy 1983; Slagsvold 1984).

There are a number of assumptions inherent in the idea of an adaptive value of brood reduction; important amongst these is the assumption that brood reduction operates under conditions of food shortage when parents are unable to provision all the brood (Lack 1954). This assumption can be tested using data from this study.

Chapters 3 and 4 of this study induced nutritional variation between broods of house martins and great tits respectively. If the above assumption is correct, then broods which are nutritionally stressed will exhibit a greater tendency to brood reduction, implied by a more pronounced size hierarchy, than broods which are not nutritionally stressed. This prediction can be tested by comparing the degree of size hierarchy between treatments in Chapters 3 & 4. The degree of size hierarchy (DOSH) was calculated by dividing the range of nestling mass within a brood by the mean nestling mass of that brood.

5.4.1 *House martin*

There was no difference between years in the values of DOSH (Table 5.2) at Day 4 (M-W, U = 49, p = 0.94) or Day 16 (M-W, U = 20, p = 0.11) so the data for 1988 and 1989 were combined for analysis. There was no significant difference in DOSH between treatments at Day 4 (M-W, U = 43, p = 0.60), the age at which the fat-feeding (i.e. the difference in nutrition) began. There was, however, a significant difference in DOSH between treatments at Day 16 (M-W, U = 8, p = 0.009), with DOSH being larger in FATFED broods than in Control broods (Table 5.2).

These results are consistent with the prediction that there should be a greater size hierarchy in broods which are nutritionally stressed. The FATFED broods received less protein than Control broods and showed a correspondingly higher degree of asynchrony.

5.4.2 *Great tit*

There were no significant differences between years in the value of DOSH (Table 5.3), either as a whole (M-W, U = 346, p = 0.57) or by treatment (M-W tests, U > 6, p > 0.17), so data for 1989 and 1990 were combined.

There was no difference in DOSH between Enlarged and Supplemented broods at Day 5 (M-W, U = 63, p = 0.85), but at Day 15 DOSH was larger in Enlarged broods than in Supplemented broods (Table 5.3) though this difference was not significant (M-W, U = 48, p = 0.27).

DOSH was significantly different between Reduced, Control and Enlarged broods at Day 5 (K-W, x^2 = 12, p < 0.01) Day 15 (K-W, x^2 = 6.6, p < 0.05), with Enlarged broods having a larger DOSH than Control or Reduced broods (Table 5.3). This indicates that there was an effect of brood size on DOSH between Day 2 when manipulations took place, and Day 5 when measurements started.

These results support the prediction of the brood reduction hypothesis. The degree of size hierarchy was higher in the Enlarged broods (least food per nestling) than in the Control or Reduced broods (more food per nestling), or in the Supplemented broods (more food per nestling), although the difference was

Table 5.2 DOSH[a] values (Mean + (SE)) of house martin broods in FATFED and Control treatments in 1988 and 1989.

	1988		1989		COMBINED	
	Control (n = 5)	FATFED (n = 3)	Control (n = 6)	FATFED (n = 4)	Control (n = 11)	FATFED (n = 7)
Day 4	.369 (.184)	.356 (.143)	.287 (.069)	.210 (.076)	.324 (.134)	.273 (.127)
Day 16	.125 (.020)	.493 (.122)	.070 (.016)	.198 (.082)	.095 (.021)	.324 (.173)

a - DOSH = Degree of Size Hierarchy = (range of nestling mass/mean nestling mass)

Table 5.3 DOSH[a] values (mean + (SE)) for great tit broods in all treatments in 1989 and 1990.

	TREATMENT			
	Reduced	Control	Enlarged	Supplemented
Day 5				
1989[b]	.217 (.068)	.337 (.040)	.491 (.059)	.458 (.152)
1990[c]	.257 (.042)	.308 (.049)	.479 (.071)	.479 (.089)
Combined[d]	.244 (.045)	.323 (.034)	.482 (.063)	.474 (.094)
Day 15				
1989[b]	.067 (.009)	.130 (.018)	.258 (.036)	.174 (.035)
1990[c]	.142 (.044)	.129 (.021)	.193 (.048)	.134 (.014)
Combined[d]	.125 (.047)	.130 (.015)	.211 (.052)	.144 (.031)

a - DOSH = Degree of Size Hierarchy = (range of nestling mass/mean nestling mass)
b - $n_r = 6$, $n_c = 8$, $n_e = 3$, $n_s = 3$
c - $n_r = 13$, $n_c = 8$, $n_e = 8$, $n_s = 9$
d - $n_r = 19$, $n_c = 16$, $n_e = 11$, $n_s = 12$

not significant in the latter case.

5.4.3 *Is brood reduction adaptive?*

The evidence from this study is consistent with the prediction made by the brood reduction hypothesis that brood reduction will operate under conditions of food shortage when parents are unable to provision all the nestlings. The brood reduction hypothesis was also supported by the results of an experimental study on the blackbird *Turdus merula* (Magrath 1989) which demonstrated that in times of food shortage, asynchronous broods were more productive than synchronous broods. Magrath (1989) proposed that brood reduction was more efficient in asynchronous broods because the size hierarchy within these broods was more pronounced. The results of Magrath's study (1989), and of this study, provide experimental support for the brood reduction hypothesis and thereby question the assertion of Amundsen & Stokland (1988) who concluded from a study of the shag *Phalacrocorax aristotelis* and a review of the literature that the 'brood reduction hypothesis does not provide an explanation of hatching asynchrony in general'. More experiments are needed on the influence of food availability on the adaptive value of brood reduction, to determine if the effects found in this study, and Magrath's study (1989) are present in other species.

5.5 IMPORTANCE OF NESTLING DIET QUALITY IN ECOLOGICAL AND EVOLUTIONARY STUDIES

There are two possible causes of intraspecific variation in life-history characteristics. Populations of a species may be genetically differentiated or there may be plastic responses to different local environmental conditions (e.g. Berven *et al.* 1979; Stearns 1983; Patton & Brylski 1987; Atkinson & Begon 1988; Dobson 1988; Ford & Siegel 1989; Williams & Moore 1989, 1990; Grant & Dunham 1990; Metcalfe & Thorpe 1990). If temporal and spatial differences in phenotype are a result of genotypic differences within a population then natural selection can be invoked as an explanation, such as for changes in body size and bill shape in Darwin's finches (*Geospiza* spp.). Variation in the body size and bill shape of the finches has a genetic component (Boag & Grant 1978, 1981; Boag 1983, 1984; Grant & Grant 1989), and natural selection has been

used to explain changes in these characters following a climatic change (Gibbs & Grant 1987b) which altered the food supply thus providing a selective advantage to birds of a particular size and bill shape (Schluter & Grant 1984; Schluter 1986; Schluter & Smith 1986; Gibbs & Grant 1987a; Grant & Grant 1989); a phenomenon described for an African finch *Pyrenestes ostrinus* (Boag 1987b; Smith 1990a,b).

5.5.1 *Heritability studies*

Usually a genetic basis for a character is tested for in field studies by means of a heritability study. These rely upon the calculation of heritability values by performing a regression of offspring values on adult values (Boag 1983). The slope of the regression directly estimates heritability, which is defined as being the proportion of the phenotypic variance which is additive genetic (Falconer 1981).

Significant heritability values have been obtained for many body size parameters and life-history characteristics with values ranging from 0.3 to 0.7 (review in Boag & van Noordwijk 1987). The remaining proportion of the variation in characters may be explained by environmental variation and measurement error. The results of my study provide evidence that variation in diet quality is one means by which environmental variability can cause variation in body size. These values may be exaggerated in some cases by the existence of prolonged parental care, with larger adults providing more food and therefore raising larger young (Smith & Dhondt 1980).

Heritability of male and mid-parent values may be underestimated because of the existence of extra-pair copulations. There will be more variation about the regression line, and a lower heritability if some nestlings in a brood are fathered by a non-pair male. This potential difference between male and female heritabilities has been used to test for the presence of extra-pair copulations in a population (Alatalo *et al.* 1984, 1989; Møller 1989b; Norris & Blakey 1989). This technique has been criticized by Lifjeld & Slagsvold (1989) who argued that the standard error of the regressions was too high, with realistic sample sizes, for differentiation between the slopes of males and females. They also argued that growth of characters is influenced by food provisioning and that this may lead to

the observed differences in male and female heritabilities. Møller (1989b) refuted these criticisms, pointing out that nestlings are unlikely to be differentially provisioned according to the tarsus length of parents. Even so, this technique is at best relatively imprecise in detecting the frequency of nestlings from extra-pair copulations, in comparison to genetic fingerprints (Burke & Bruford 1987; Wetton *et al.* 1987); and where possible genetic fingerprinting studies should be used to establish the frequency of extra-pair paternity and egg-dumping which are known to occur in some species (e.g. house martin , H. Riley *pers. comm.*) .

Variation in nestling diet quality may reduce the heritability value of a character by increasing the environmental contribution to character variation. This environmental contribution may vary from year to year because environmental conditions during growth vary from year to year, and these conditions affect heritability values (Noordwijk *et al.* 1988). Variation in nestling diet quality will not, however, contribute to the difference in heritability values between males and females.

5.5.2 *Phenotypic plasticity*

If environmental (non-heritable) variation contributes significantly to the determination of the phenotype of individuals in a population, then spatial or temporal variation in the environment will result in spatial or temporal variation in phenotype. This phenomenon is termed phenotypic plasticity. Plasticity may be influenced by selection (Via & Lande 1985) and environmental factors may compete with genetic factors to produce a given selected level of phenotypic variance (Bull 1987).

Plastic responses of individuals may be either environmental modulations of phenotype or developmental conversions (Smith-Gill 1983). In passerines an example of an environmental modulation of phenotype is the variation of adult bill size and shape in response to seasonal differences in food supply (Gosler 1987; Jordan 1987; Morton & Morton 1987; Matthysen 1989) which may result from different rates of abrasion from different food sources (Matthysen 1989). The results of this study (Chapters 2 & 3) provide evidence that passerines may also exhibit a plastic response through a developmental conversion dependent upon

nestling diet quality.

Why, then, does phenotypic plasticity occur? It is possible that in passerines, where mortality is relatively high, the possibility of producing young that survive to a critical size (e.g. great tit, Tinbergen & Boerlijst 1990) is maximised by also maximising the environmental variation in growth (Houston & McNamara 1990) because this produces a variety of phenotypes that will be adapted to a variety of environmental conditions (Schultz 1989). This environmental variation may, however, be diminished in the adult population by selection on fledglings which removes undernourished nestlings from the population. Such a phenomenon has been demonstrated for tarsus length in the great tit (van Noordwijk 1986; van Noordwijk *et al.* 1988) and the collared flycatcher *Ficedula hypoleuca* (Alatalo *et al.* 1990). Positive selection on environmental deviation in a parameter, such as fledgling mass, may be common in species where food limitation occurs during growth (Alatalo *et al.* 1990) and this study provides evidence that food limitation may take the form of a limitation in nestling diet quality.

This type of positive selection produces no evolutionary response because it is only acting upon environmental variation. Alatalo *et al.* (1990) suggest that the existence of selection on environmental variation reduces the utility of simple measures of selection and creates problems in the interpretation of morphological evolution. They recommend that future studies of selection and evolution use 'norms of reaction' (the mean phenotypic value over a range of environmental conditions, Via & Lande 1985; Boag & van Noordwijk 1987; Alatalo *et al.* 1990) as the parameter for study.

In conclusion, the effect of diet quality demonstrated in this study provides a new agent by which the environment may influence growth. This is an important result because the role of environmental variation in evolution and selection is an area demanding much further research (Noordwijk *et al.* 1988; Rising 1989; Alatalo *et al.* 1990) and diet quality effects will have to considered in this research.

5.5.3 *Life history theory*

One of the fundamental tenets of life history theory is that the particular breeding strategy of an individual represents a trade-off between reproductive benefits and the cost to future reproduction (Lindén & Møller 1989). The most studied aspect of reproductive strategy in birds is clutch-size. The clutch-size laid by an individual should be that which maximises individual fitness, as has been demonstrated in the great tit (Tinbergen & Daan 1990) and the kestrel (Daan *et al.* 1990). The larger the clutch size of a bird, the more young it can produce, but an increased clutch size also means greater parental effort to rear the young and the potential for a correspondingly greater parental cost in terms of survival or subsequent fecundity. The mass loss of female great tits in this study (Chapter 4) was consistent with the proposition that a greater cost is incurred by parents of enlarged broods.

Other experimental studies have also established a parental cost of reproduction through brood enlargement, but there is little evidence that this cost is important enough to affect life-histories (Lindén & Møller 1989). The main determinant of life-time reproductive success is parental survival (Clutton-Brock 1988) and survival may be more affected by multiple-brooding than variation in the size of individual clutches (Dobson 1990).

There is considerable evidence that the average clutch size is smaller than the most productive clutch size in some species of bird (Charnov & Krebs 1974). A smaller clutch size may have more reproductive benefit by producing a few high quality (i.e. well-nourished) fledglings rather than more low quality (i.e. undernourished) fledglings, as the survival of the high quality young will be greater (see Section 5.3.5), and their subsequent fitness may be greater. This emphasis on the quality of progeny may be more important in light of the results of life-history studies which show that a small proportion of birds, presumably of high quality, produce the majority of progeny (Newton 1989). There were insufficient data on the survival and reproduction of nestlings in this study to test the proposition that a high quality nestling diet produces nestlings which survive better and breed more successfully than nestlings fed a low quality diet. This is an area for future investigation, as part of the wider study of the importance of nestling quality in the life-history strategy of birds.

6 SUMMARY

6.1 INTRODUCTION

In most classical studies of wild birds, phenotypic variation is assumed to be largely genetically controlled with little attention given to environmental effects on the phenotype. There is, however, evidence that environmental variation may influence temporal and spatial intraspecific variation in the adult phenotype. Research into the mechanisms by which the environment can influence the adult phenotype has concentrated on the effect of food availability on nestling growth and adult body size. The role of diet quality has not been studied in detail. A need to investigate the possible role of diet quality in determining nestling growth and adult body size was identified. Investigation should also be extended to the effect of nestling diet on other features of the adult phenotype which are of importance in determining life-histories, but which have not yet been investigated in this context, such as body shape and plumage.

6.2 EFFECTS OF AN INCREASE IN NESTLING DIET QUALITY ON A LABORATORY PASSERINE

6.2.1 *Introduction*

Use of a laboratory population of passerines, rather than a wild population, enables repeated measurements of size to be made until the adult phenotype is attained, with minimal problems of mortality and no dispersal. Laboratory conditions also permit rigorous control of nestling and adult diet. In the period between the proposal and the project, Boag (1987a) published a laboratory study demonstrating an effect of nestling diet quality on the growth and adult size of the zebra finch *Poephila guttata*. This study was repeated with additional features such as the measurement of plumage and the measurement of condition using ultrasound. An attempt to use a semi-synthetic diet failed because it proved unpalatable.

6.2.2 *Methods*

The study was performed on a zebra finch colony at the University of Stirling. Two replicates were performed, one in 1987 and the other in 1989. Methods for each replicate were identical. Pairs were put in individual cages and divided into two treatments. The HIGH treatment received seed *ad libitum* and Haith's egg food supplement during the nestling period and until fledglings were 40 days old. The Control group received seed *ad libitum* only. After Day 40 all fledglings were placed in holding cages where they received only seed until they were measured as adults. Eight parameters of body size (mass, wing, tarsus, head plus bill, keel, bill measures) were measured at regular intervals until Day 40, and then at Days 44, 62, 150 and 400. Adult shape and size were analysed using principal components analysis. Growth curves were fitted to measure growth rate and growth curve shape. Body condition at Day 150 and Day 400 was measured as the thickness of the *pectoralis* muscles, using an ultrasound probe. Male ear patch and flank plumage characters were measured at Day 150 and Day 400.

6.2.3 *Results*

There was no difference between treatments in any breeding parameter. Growth rate was faster in the HIGH treatment for almost all parameters. This difference was significant for keel length. Growth curve shapes of wing length and head & bill were significantly different between treatments. There was no difference between treatments in parental size or nestling size at Day 5. At Day 150 and Day 400 nestlings were significantly larger in the HIGH treatment than the Control for most size parameters. There was no difference in the adult shape of nestlings between treatments. Nestlings in the Control had relatively thicker *pectoralis* muscles at Day 150 but lost more condition between Day 150 and Day 400 than nestlings in the HIGH treatment. Male Ear Patch was wider at Day 400 in the HIGH treatment than in the Control.

6.2.4 *Discussion*

It was concluded that the higher nestling diet quality in the HIGH treatment resulted in faster growth and larger adult size of nestlings, although compensatory growth of Control nestlings did occur. These results support those of Boag (1987a). It was suggested that the greater loss of condition of Control

fledglings between Day 150 and Day 400 may have been due to their subordinance in the holding cages to the 'higher quality' nestlings from the HIGH treatment. The effect of diet quality on Ear Patch provided evidence that diet quality may influence adult plumage, which is an important feature. Zebra finch nestling diet quality is likely to vary in the wild and these experimental effects may well be present in natural populations.

6.3 EFFECTS OF A REDUCTION IN NESTLING DIET QUALITY ON A WILD INSECTIVOROUS PASSERINE

6.3.1 *Introduction*

There have been very few experimental studies of the effect of nestling diet quality on growth in a wild bird population and these have usually only investigated the effect on growth over a short period of time rather than the whole nestling period. It was the aim of this chapter to perform an experiment on the effect of nestling diet quality on nestling growth throughout the nestling period of a wild passerine. The house martin *Delichon urbica* was chosen for this study because house martin nestlings are safe from predators and deposit faeces below the nest from Day 6 onwards, providing a record of their food intake. This record provided a means of comparing nestling diet between treatments. The insect diet of house martins is of high quality and it was hoped that mean nestling diet quality could be reduced by feeding nestlings a high energy supplement which reduced nestling demand, and therefore parental feeding, but provided no protein. This would provide nestlings with a similar energy intake to control nestlings but fewer nutrients (i.e. lower diet quality).

6.3.2 *Methods*

A colony of house martins on the University of Stirling library (NS 807 965) was used for the study. Artificial nests were provided to ease access to nestlings. Two replicates were performed, one in 1988 and one in 1989. Methods were identical for each. Pork fat was used as a high energy supplement. A quantity of fat equivalent to the mean daily energy requirement of a nestling was fed to nestlings in the FATFED treatment from Day 3 to Day 16, half the prescribed mass in the morning and half in the evening. Parental visits were

monitored by an infra-red sensor. Faeces were collected daily under nests from Day 8 until fledging, then freeze-dried and the fat removed by a SOXHLET. Daily temperature and insect abundance were monitored. Nestling energy expenditure at Day 14 was measured using the doubly-labelled water technique. Nestling size (mass, wing , tarsus, head & bill, keel) was measured regularly from Day 3 until fledging.

6.3.3 *Results*

There were no significant differences in breeding parameters between treatments. Parental visit rate and fat-free faecal mass were correlated, and both were lower in the FATFED treatment than in the Control. Mass of fat fed explained more variation in fat-free faecal mass than any other variable. There was no difference in insect abundance, daily temperature or nestling energy expenditure between treatments. There were no significant differences in growth rate or parental size between treatments. Wing growth was positively correlated to fat-free faecal mass. Body mass and tarsus length were larger in the FATFED treatment at Day 3, but by Day 20 Control nestlings had significantly larger wing, tarsus, keel and overall size (PC1) than FATFED nestlings. Control nestlings were still larger at fledging.

6.3.4 *Discussion*

It was concluded the fat-feeding was successful in reducing nestling diet quality in the FATFED treatment. Fat-feeding reduced parental visits, presumably through reduced nestling begging, which resulted in a smaller intake of insects by nestlings as shown by the lower fat-free faecal mass. A lower insect intake resulted in lower intake of protein and other nutrients in comparison to Control nestlings, whereas energy intake was similar. Therefore nestling diet quality was lower in the FATFED treatment. The smaller size of nestlings in the FATFED treatment was not caused by differences in insect abundance, daily temperature or energy expenditure. It is unlikely to have been the result of different levels of parasitism or due to a sublethal toxic effect of fat. It was concluded that lower nestling diet quality resulted in slower growth of FATFED nestlings and the smaller nestling size at Day 20 and at fledging. Aerial insect abundance is highly variable, providing scope for an effect of food abundance on nestling growth as demonstrated by Bryant (1975, 1978). Nestling diet quality is unlikely to vary directly because of the many taxa that make-up the aerial

insect population. Effective diet quality may vary, however, when nestlings are fed at their energy maintenance level as some of the protein in the diet will be used to produce energy (Masman 1984) rather than deposited as tissue.

The field metabolic rate of house martin nestlings in this study was higher than those obtained by the other doubly-labelled water studies of nestling energetics. This difference was probably caused by fat deposition and some inhalation of carbon dioxide exhaled by other nestlings in the brood.

6.4 EFFECTS OF NESTLING DIET ON THE PHENOTYPE OF A WILD PASSERINE

6.4.1 *Introduction*

Intraspecific plumage variation affects dominance and mate choice in passerines, but the relative importance of genetic and environmental factors in determining plumage characters is unknown. The pigment content of nestling diet influences plumage colour but the effect of general nestling diet quality has not been investigated. The aim of this chapter was to investigate the effect of variation in nestling diet quality and quantity on the development of a plumage characteristic of known importance to individual life-history. The great tit *Parus major* was chosen as the study species because great tits have a readily quantifiable plumage character, breast stripe, which is related to dominance.

6.4.2 *Methods*

The great tit population studied was a nestbox population in the surrounds of the University of Stirling campus (NS 807 965). Sixty nestboxes were present in the first experiment in 1989, one hundred in the second experiment in 1990. The two experiments differed slightly in methodology, so they were not combined for analysis. Food quantity was varied between treatments by brood manipulation. Three nestlings were removed from Reduced (RED) broods at Day 2, three nestlings were added to Enlarged (ENLA) broods at Day 2, and Control (CON) broods were unmanipulated. Diet quality was varied by feeding a fortified mince supplement to half the nestlings (FED) in randomly chosen enlarged broods (SUPP). Mince was fed from Day 7 to Day 13 in 1989, and from Day 6 to Day 12 in 1990. Nestling size (mass, tarsus, wing, head and bill, keel) was measured

every two days from Day 5 to Day 15 , and then at Day 19 in 1989 and growth curve analysis performed. In 1990, nestling size was measured at Days 5, 15 and 19. Nestling breast stripe width and length were measured at Day 19 in 1989. Different measurements of width and length were made at both Day 15 and 19 in 1990. Females were caught and measured during incubation. In 1990, females were also caught at Day 13 of the nestling period to calculate mass loss during the nestling period. Nestling survival from broods in the 1989 experiment was assessed by winter mist-netting at feeding stations around the campus.

6.4.3 *1989 Results*

Breeding parameters did not differ between treatments except for manipulated brood size. Wing growth was significantly faster in RED broods than in ENLA broods. Comparison of size at Days 5, 15 and 19 showed faster growth of RED and CON nestlings. There was no significant difference in stripe size, before or after correction for body size.

There was no difference in growth rates, size at Days 5, 15 or 19 or stripe measures between FED and UNFED nestlings.

Wing growth was faster in SUPP broods than in ENLA broods. Comparison of size at Days 5, 15 and 19 indicated faster growth of SUPP nestlings. Breast stripe was wider in the SUPP treatment than in the ENLA treatment, even when corrected for body size.

Seven nestlings were recaptured in winter 1989 or in the spring of 1990. Four were from the SUPP treatment but the sample size was too small to test for differences in survival rates.

6.4.4 *1990 Results*

There was no difference between treatments in any breeding parameter except manipulated brood size. Comparison of sizes showed faster growth of RED and CON nestlings than ENLA nestlings. Stripe length was longer in the RED treatment than in the ENLA treatment.

Comparison of sizes indicated faster growth of UNFED nestlings than FED nestlings. Breast stripe was longer in UNFED nestlings at Day 15, but not when corrected for body size.

Comparison of sizes indicated faster growth of SUPP nestlings than ENLA nestlings. There was no difference in stripe size between the two treatments.

Female mass loss was greater for ENLA broods than SUPP or RED broods.

6.4.5 *Discussion*

It was concluded from comparisons of nestling growth, that brood manipulation was successful in altering food intake and that SUPP broods had greater food availability than ENLA broods. FED nestlings did not have a higher quality diet than UNFED nestlings and they may have been fed a lower quality diet in 1990. It was concluded that food availability influences nestling breast stripe, but there was only equivocal evidence that this effect was independent of body size. Diet quality and quantity are likely to show natural variation in great tit populations and diet-induced variation in breast stripe may have important consequences for individual life-histories. Further investigation of the relationship of diet to breast stripe is required, especially to determine if differences in nestling plumage extend to adult plumage. The pattern of female mass loss provided evidence for Nur's (1984) proposition that feeding frequency is adjusted to maximise the difference between reproductive costs and benefits.

6.5 DISCUSSION

The effect of the supplements used in this study varied according to their relative quality and this influence of relative supplement quality may also be present in other supplemention studies, such as the effect of supplementary feeding on clutch size. Supplement quality should be explicitly stated in studies so that results can be fully interpreted.

Diet quality varies in wild populations of other animals and nestling diet quality is likely to vary in wild bird populations. The results of this study indicate that variation in nestling diet quality may affect individual life-histories through effects on growth rate, differential growth, growth curve shape, fledging size, adult size, and adult plumage.

The results of this study also provide evidence that supports a key assumption of the brood reduction hypothesis proposed by Lack (1954), that the tendency for brood reduction, as evidenced by the degree of size hierarchy, will be lower in times of higher food availability.

The effects demonstrated in this study may explain low heritability values obtained in some studies and may also contribute to the phenotypic plasticity present in some species. Phenotypic plasticity may serve to produce a suite of

phenotypes that will be adapted to the range of conditions produced by a variable environment.

The results of this study could also explain why the most frequent clutch size is often not the most productive. It may be beneficial to raise fewer, well-nourished, 'high quality' nestlings, because high quality progeny may contribute disproportionately to future generations.

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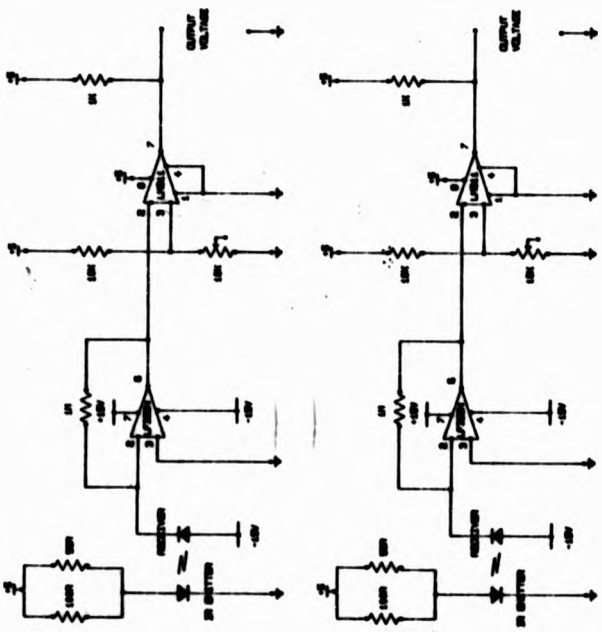
8 APPENDICES

Appendix 1 **Circuit diagram for the infrared sensor used to record house martin visits.**



Appendix 2 BBC BASIC program to operate feeding visit sensor for house martin nests.

```
10      REM  sets printer setting
20      @%=&0005
30      REM  limit of memory space for programme operation
40      HIMEM=&4000
50      REM  gives address of input port
60      PORTA=&FE01
70      REM  gives address of data direction register
80      DDRA=&FE03
90      REM  set DDRA to input
100     ?DDRA=16
110     REM  so data storage above HIMEM
120     BASE=&4001
130     REM  gives PORTA a 00000100 configuration so that first two
        ports are  input
140     ?PORTA=4
150     REM  give initial values of parameters used in program
160     VISIT%=0
170     ITH=0
180     ITH1=0
190     ITH2=0
200     ITM=0
210     ITM1=0
220     ITM2=0
230     ITS=0
240     ITS1=0
250     ITS2=0
260     OTH=0
270     OTH1=0
280     OTH2=0
290     OTM=0
300     OTM1=0
310     OTM2=0
320     0TS=0
330     OTS1=0
340     0TS2=0
350     NEST=0
360     NEST1=0
370     NEST2=0
380     X0=0
390     X1=0
400     X2=0
410     T=0
420     T1=0
430     T2=0
440
450     REM  start sensor or load data onto disc
460     INPUT"DO YOU WANT TO LOAD DATA ONTO A DISC"
470     IF B$="YES" THEN PROC?PRINT
480
490     REM  set sensor to real time
500     CLS
```

```
510     INPUT"HOUR";HO
520     INPUT"MIN";MIN
530     TIME=((HO*60+MIN)*60)*100
540     PRINT "TIME=", TIME
550
560     REM  memory test, takes three minutes approximately
570     FOR Y=&4000 TO &8000
580     ?Y=255
590     Z=?Y
600     IF Z<>255 THEN PRINT "ERROR AT  ";Y
610     NEXT Y
620
630     REM  delay before starting sensor
640     INPUT"PRESS Y TO START SENSOR",B$
650     IF B$="Y" THEN GOTO 670
660
670     CLS
680     PRINT "  NEST  HOUR  MIN  TIME"
690
700     PROCSCAN
710
720     DEF PROCSCAN
730     REM constantly reads input from PORTA
740     TIMER=(TIME DIV 360000) MOD 24
750     IF TIMER<10 GOTO 770
760     IF TIMER<21 GOTO 780
770     GOTO 740
780     X1=?PORTA
790     X2=X1 AND 3
800     VISIT%=X0-X2
810     IF VISIT%=0 THEN GOTO 740
820     IF VISIT%=-3 THEN PROCNEST1OUT:PROCNEST2OUT:GOTO 740
830     IF VISIT%=-2 THEN PROCNEST2OUT:GOTO 740
840     IF VISIT%=-1 THEN PROCNEST1OUT:GOTO 740
850     IF VISIT%=1 THEN PROCNEST1IN:GOTO 740
860     IF VISIT%=2 THEN PROCNEST2IN:GOTO 740
870     IF VISIT%=3 THEN PROCNEST1IN:PROCNEST2IN:GOTO 740
880     ENDPROC
890
900     DEFPROCNEST1IN
910     REM  records time at which beam broken at nest1
920     ITH1=(TIME DIV 360000) MOD 24
930     ITM1=(TIME DIV 6000) MOD 60
940     ITS1=(TIME DIV 10) MOD 600
950     X0=X2
960     ENDPROC
970
980     DEFPROCNEST2IN
990     REM  records time at which beam broken in nest2
1000    ITH2=(TIME DIV 360000) MOD 24
1010    ITM2=(TIME DIV 6000) MOD 60
1020    ITS2=(TIME DIV 10) MOD 600
1030    X0=X2
1040    ENDPROC
1050
1060    DEFPROCNEST1OUT
```

```
1070    REM  records time at which beam restored,calculates duration of
1080    REM  blockage and loads data from nest1 to memory chips of data
        logger
1090    OTH1=(TIME DIV 360000) MOD 24
1100    OTM1=(TIME DIV 6000) MOD 60
1110    OTS1=(TIME DIV 10) MOD 600
1120    ?BASE=253
1130    BASE=BASE+1
1140    NEST1=1
1150    ?(BASE)=NEST1
1160    BASE=BASE+1
1170    ?(BASE)=ITH1
1180    BASE=BASE+1
1190    ?(BASE)=ITM1
1200    BASE=BASE+1
1210    T1=ITS1+(600*ITM1)+(360000*ITH1)
1220    T2=OTS1+(600*OTM1)+(360000*OTH1)
1230    T3=T2-T1
1240    ?(BASE)=T3
1250    BASE=BASE+1
1260    IF T3>40 GOTO 1280
1270    IF T3>4 GOTO 1300
1280    BASE=BASE-5
1290    GOTO 1310
1300    PRINT NEST1   ITH1   ITM1   T3
1310    X0=X2
1320    IF BASE>&7FF0 THEN END
1330    ENDPROC
1340
1350    DEFPROCNEST2OUT
1360    REM  records time at which beam restored,calculates duration of
1370    REM  blockage and loads data from nest2 to memory chips of data
        logger
1380    OTH2=(TIME DIV 360000) MOD 24
1390    OTM2=(TIME DIV 6000) MOD 60
1400    OTS2=(TIME DIV 10) MOD 600
1410    ?BASE=253
1420    BASE=BASE+1
1430    NEST2=2
1440    ?(BASE)=NEST2
1450    BASE=BASE+1
1460    ?(BASE)=ITH2
1470    BASE=BASE+1
1480    ?(BASE)=ITM2
1490    BASE=BASE+1
1500    T1=ITS2+(600*ITM2)+(360000*ITH2)
1510    T2=OTS2+(600*OTM2)+(360000*OTH2)
1520    T3=T2-T1
1530    ?(BASE)=T3
1540    BASE=BASE+1
1550    IF T3>40 GOTO 1570
1560    IF T3>4 GOTO 1590
1570    BASE=BASE-5
1580    GOTO 1600
1590    PRINT NEST2   ITH2   ITM2   T3
1600    X0=X2
```

```
1610    IF BASE>&7FF0 THEN END
1620    ENDPROC
1630
1640    DEFPROCPRINT
1650    REM  loads dat from memory chips onto floppy disc
1660    @%=&00004
1670    CLS
1680    BASE=&4001
1690    INPUT" DATA FILE NAME ";D$
1700    X=OPENOUT (D$)
1710    M=?BASE
1720    IF M=253 GOTO 1760
1730    BASE=BASE+1
1740    NEST=255
1750    GOTO 1780
1760    BASE=BASE+1
1770    NEST=?(BASE)
1780    BASE=BASE+1
1790    ITH=?(BASE)
1800    BASE=BASE}+1
1810    ITM=?(BASE)
1820    BASE=BASE+1
1830    T3=?(BASE)
1840    BASE=BASE+1
1850    PRINT NEST  ITH  ITM  T3
1860    PRINT£X,NEST,ITH,ITM,T3
1870    FOR W=1 TO 1000
1880    NEXT W
1890    IF NEST<>255 GOTO 1710
1900    CLOSE£ X
1910    PRINT "END OF DATA REPLAY"
1920    END
1930    ENDPROC
```

Appendix 3 **Raw data for house martin doubly-labelled water analysis.** (ppm - parts per million)

Chick	Brood Size	Mass(g)	Time(h)	Initial O_2 Delta 2	Final O_2 Delta 2	Initial H_2 ppm	Final H_2 ppm
FATFED							
1	4	24.5	24.4	595.95	325.38	730.30	566.83
2	4	24.7	23.8	627.27	367.49	771.53	612.11
3	4	23.1	23.9	609.68	310.29	731.55	534.15
4	4	23.4	23.8	555.60	286.52	708.98	526.19
5	2	26.3	24.0	590.91	313.90	717.02	573.44
6	4	25.2	24.8	622.02	271.65	669.22	490.00
7	4	26.7	23.2	640.30	282.21	753.00	524.25
Control							
1	3	26.1	23.3	535.87	242.97	682.57	485.81
2	4	23.4	24.1	536.30	271.65	669.22	490.00
3	4	24.9	24.0	619.22	323.65	769.15	575.64

Appendix 4 Results (p values) of tests for nest effect in the ANOVA blocks used for analysis in Section 2 for zebra finch nestling size at Day 400.

	ANOVA BLOCK			
Parameter	1987, High	1987, Control	1989, High	1989, Control
MASS	.059	.014	.391	.040
WING	.842	.067	.478	.087
TARS	.304	.004	.821	.194
HEAD	.267	.132	.631	.953
BDN	.538	.391	.598	.337
BLN	.189	.994	.767	.932
BWD	.244	.126	.840	.056
KEEL	.791	.108	.224	.013
PC1	.452	.211	.185	.284

Appendix 5 Results (p values) of tests for a nest effect in the ANOVA blocks used for analysis in Section 3 on house martin nestling size at Day 20.

	ANOVA BLOCKS			
Parameter	Control, 1988	FATFED, 1988	Control, 1989	FATFED, 1989
PC1	0.723	0.078	0.444	0.102

Appendix 6 Results (p values) of tests for a nest effect in the ANOVA blocks used for analysis in Section 4 on great tit nestling size at day 15, and plumage at Day 15 and Day 19.

	ANOVA BLOCKS							
Parameter	**Red,early**	**Red,late**	**Con,early**	**Con,late**	**Enla,early**	**Enla,late**	**Sup,early**	**Sup,late**
1989								
Day 15								
PC1	.117	.214	.071	<u>.019</u>	.087	<u>.004</u>	.110	.308
Day 19								
SLEN	.161		<u>.002</u>		<u>.035</u>		.088	
SWD	.670		.192		.765		.908	
1990								
Day 15								
PC1	.757	.110	.458	.123	<u>.001</u>	.720	.067	.852
SLEN	.366	.299	.768	.119	.321	.271	<u>.031</u>	.231
Day19								
SLEN	.201	.206	.109	.999	.902	.108	<u>.034</u>	.651
SWD	.530	.186	.752	.999	.531	.772	.890	.970