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THE ENERGETICS OF NESTLING BIRDS

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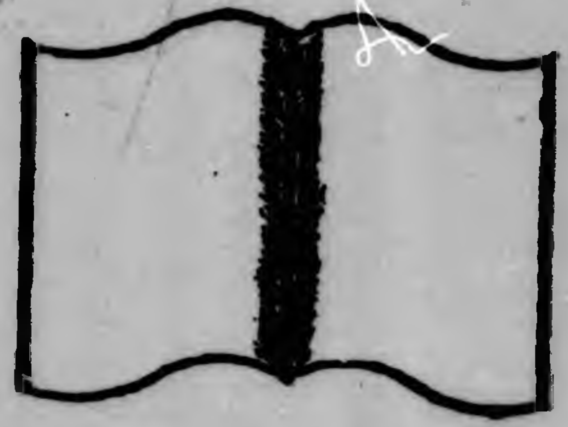
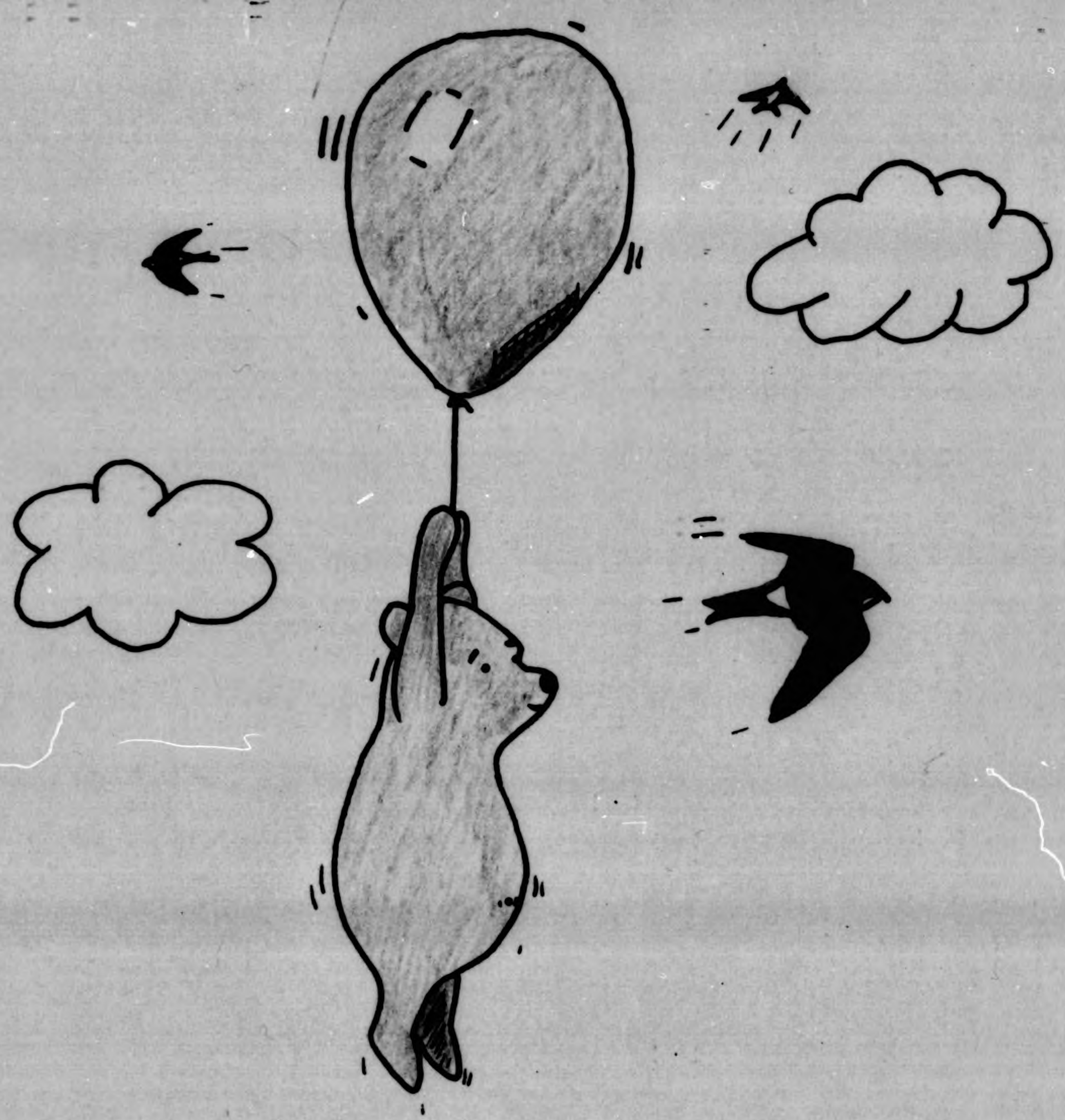


FOR

MARY



'Cottlestone, cottlestone, cottlestone pie,
Why does a chicken?
I don't know why .... '

A. A. Milne

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ABBREVIATIONS USED IN THE TEXT

A	Activity costs
ABT	After-begging Time
AL	'Alertness' costs
ALDM	Ash free lean dry mass
Bc	Brooding costs
BMR	'Basal' metabolic rate
DEB	Daily Energy Budget
DED	Dry Energy Density
DEE	Daily Energy Expenditure
DME	Daily Metabolisable Energy
DU	Doppler Units (= DAU)
EGUT	Elevated giving-up time
FCR	Field Cooling Rates
FEE	Field Energy Expenditure
FRR	Field Reheating Rates
FUC	Fixed Unit Cost (for activity)
GEI	Gross Energy Intake
GUT	Giving-up Time
GUT_{pre}	Prefeed giving-up time
GUT_{post}	Post feed giving-up time
H	Rate of heat loss
H_f	" " " " in the field
H_n	" " " " in a nest in the lab
H_o	" " " " out of a nest in the lab
h	Heat transfer coefficient
HT	Handling Time
HIF	Heat Increment of Feeding Costs

Abbreviations used in the Text (contd.)

IHS	Index of Hierarchy Stability
LCR	Lab Cooling Rates
LI	Lipid Index
LDM	Lean Dry Mass
M	Metabolism (= BME) Costs
MTA	Mouth Target Area
MUC	Mean Unit Activity Cost
N1	Single Nestling
N2	Paired Nestlings
P	Growth Costs
PDT	Parental Decision Time
PLR	Peak Load Reduction
PUV	Proportionate Unit Activity Cost
r	Cooling rate ($^\circ C^\circ Ch^{-1}$)
RDBM	Relative Difference in Body Mass
RDHM	Relative Difference in Hatching Mass
RLDM	Relative Lean Dry Mass
RRHP	Relative Resonance Holding Power
RSR	Reduced Sibling Rivalry
T_a	Ambient Temperature
T_b	Nestling Body Temperature
T_{lc}	Lower Critical Temperature
T_n	Nest Temperature
TR	Thermoregulation Costs
w	mass of nestling
w_b	brood mass
WED	Wet Energy Density
WMR	Wing-length/mass ratio
WTR	Wing-length/tarsus ratio

ABSTRACT

The nestling energy budget is examined with particular reference to the Dipper. Dippers showed an adaptive strategy of differential growth allowing premature fledging. Sex-specific differences in energetics and growth dynamics were observed which may result in differential mortality between the sexes.

Field thermoregulation costs were lower than laboratory estimates, however heat loss did not obey the 0.67 exponent rule in the Dipper. Adults appear to adjust their brooding behaviour in response to nestling body temperature.

Activity costs measured directly were only about 10% of previous indirect estimates. Brood activity costs increased exponentially with increasing brood-size thus offsetting any reduction in thermoregulation costs through huddling; implications of these results are discussed.

Time-activity-laboratory estimates of daily energy expenditure provided excellent agreement with field measurements using doubly-labelled water on 'mature' Dipper nestlings. TAL estimates, however, progressively over-estimated daily metabolised energy (DME) in younger nestlings. Sources of this error are evaluated, and a predictive equation for nestling DME presented. Influences of brood DME on parental care are discussed.

Energetic implications of hatching asynchrony were examined in the House Martin. Four hypotheses are discussed.

(1) Nest failure;
(2) Brood reduction;
(3) Peak load reduction, and
(4) Reduced sibling rivalry.

The latter two were modelled and tested in the field. Little evidence was found for the hypotheses considered, lending support to the view that hatching asynchrony is an incidental trait, and moreover one in which costs may outweigh benefits.

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CHAPTER ONE

INTRODUCTION

1. INTRODUCTION

Selective pressures on the allocation of time and energy to major resource-demanding stages in the annual cycle of birds, such as moult, migration and reproduction, are likely to be strong. Reproduction involves trade-offs such that fitness will be maximized for those individuals which evolve adaptive strategies to optimize investment between current and future reproductive attempts (Williams, 1966; Schoener, 1971).

In any current reproductive attempt, "patterns of energy utilization from hatching until independence of the young have two components; the allocation of time and energy by the parents food gathering and direct care of the young, and the use of energy by the young themselves. These two components are ultimately related through strategies of development and parental care". (Ricklefs, 1974). Nonetheless, the interests of parents, offspring, siblings and individuals may conflict (Brockelman, 1975; Smith & Fretwell, 1974; Trivers, 1974). Selection may therefore favour offspring which induce parents to invest more in the current, rather than subsequent, reproductive attempts. Equally, as trade-offs exist between the quality and quantity of young produced at a given time (Brockelman, 1975), parents are often likely to underinvest in the current reproductive attempt, from an individual offspring's point of view. This being so natural selection will favour the evolution of nestling development patterns that result in efficient use by parent and brood of limited energy resources. The study of nestling energetics allows such efficiencies to be quantified and explored and therefore play an important part in increasing our understanding of the complex interactions between parent and offspring, on which the evolution of reproductive strategies depends.

Previous studies of nestling development provide a base from which to examine nestling energetics from this broader behavioural perspective. The nestling energy budget has been simply represented by the following equation:-

$$GEI - FU = P + R \qquad \text{eqn. 1.1}$$

where GEI is the gross energy intake; FU is that energy voided as faecal and urinary waste; P is that energy accumulated as tissue growth; and R is the energy used in respiration (Kendeigh et al., 1977). The latter is often sub-divided into basal metabolism, thermoregulation and 'activity' costs. Initial interest in nestling development centred on two of the components of equation 1.1;

(i) the study of growth, primarily body mass and external measurements as functions of nestling age, and

(ii) thermoregulation (see Calder and King, 1974; King & Farner, 1961, for early reviews).

The study of growth progressed from detailed examinations of inter-specific differences in mass changes with age, using curve fitting techniques (Ricklefs, 1967a), and constraints on growth rate (Ricklefs, 1979a; 1984), to the energetics of growth and the differential growth of body components, in particular with respect to developmental mode (Austin & Ricklefs, 1977; Blem, 1978; Brisbin & Tally, 1973; Bryant & Gardiner, 1979; Bryant & Hails, 1983; Cain, 1976; Clay et al., 1979; Diehl & Myrcha, 1973; Dunn & Brisbin, 1980; Hockey, 1984; Kohl, 1962; Kushlan, 1977; Montevecchi et al., 1984; Ricklefs, 1967b; Ricklefs & White, 1981; Tatner, 1984).

Previous studies of nestling thermoregulation have concentrated on laboratory measurements of metabolism, and examined the ontogeny of thermoregulation (Dawson et al., 1976; Diehl & Myrcha, 1973; Dunn, 1976a; Gotie & Kroll, 1973; Marsh, 1979); brood-size effects (Dunn, 1976b, 1979; Mertens, 1969; O'Connor, 1975), and factors affecting the timing of the onset of endothermy (Dunn, 1975).

Estimations of energy intake and assimilation efficiency (Blem, 1973; Bryant & Bryant, in press; Diehl, 1971; Gibb, 1957; Myrcha et al., 1972; Tiainen, 1983; Turner, 1980; Westerterp, 1973) together with measurements of nestling growth metabolism and thermoregulation have however only allowed the construction of daily energy budgets for a handful of species (Blem, 1975; Bryant & Gardiner, 1979; Cain, 1976; Diehl & Myrcha, 1973; Dunn, 1976, 1980; Koelink, 1972; Norton, 1970; Tiainen, 1983; Wijnandts, 1984; Williams & Prints, 1986; Westerterp, 1973). Furthermore current published energy budgets are incompletely partitioned; few have measured biosynthesis costs directly, and no measurements of nestling activity costs are presently available.

Recently the doubly-labelled water technique (Lifson et al., 1955) previously used largely for measuring daily energy expenditure in free-living adult birds (Bryant et al., 1985; Bryant & Tatner, 1984; Bryant & Westerterp, 1980; Hails, 1979; Nagy et al., 1984; Westerterp & Bryant, 1984; Westerterp & Drent, 1985) has been applied to nestlings thus allowing comparisons to be made between nestling energy budgets calculated from laboratory measurements and time budget data, and energy expenditure measured directly in the field (Fiala & Congdon, 1983; Williams & Prints, 1986).

One way in which such studies of nestling energetics may be used as tools for assessing the interactions between parents and offspring, and for quantifying costs and benefits of different behavioural strategies for both parties, is by examining one specific behaviour phenomenon. One example common in altricial birds that may have shaped patterns of energy utilization by nestlings, as well as patterns of parental care, is hatching asynchrony.

The asynchronous hatching of nestlings, as a result of incubation starting prior to the completion of the clutch, may result in a disproportionate allocation of food to some young at the expense of others, and may appreciably alter patterns of brood energy demand and parental behaviour. A number of hypotheses have been advanced to explain the adaptive significance of asynchronous hatching.

Lack (1954) proposed that by producing offspring of different ages (and hence sizes) competitive hierarchies would be established within broods, which would tend to adjust allocation of food brought to the nest to prevailing food availability. In times of food shortage the later hatched nestling(s) would starve thus allowing remaining chicks to thrive. This 'brood reduction hypothesis' has been elaborated by O'Connor (1978c) who proposed that natural selection may under certain extreme circumstances favour suicide of the smallest nestling, since its inclusive fitness would be increased as a result of genes shared with its surviving siblings and parents.

The brood reduction hypothesis has been challenged by Clark & Wilson (1981) who proposed that hatching asynchrony has evolved to minimise total nest failure through predation. They examined the survival probabilities of nest contents during the period of egg laying until fledging of the last chick in 87 altricial species and concluded that the ratio of nest failures during the egg stage to nest failures during the nestling phase (= nest failure ratio) is of primary importance in selection for hatching asynchrony in birds. Two other hypotheses have received some support; the 'peak load reduction (PLR) hypothesis' (Bryant & Gardiner, 1979; Hussell, 1972) and the 'reduced sibling rivalry (RSR) hypothesis' (Hahn, 1981).

The 'PLR hypothesis' suggests that by spreading out hatching times, parents also spread out the peak energy demand of nestlings, in turn reducing the brood energy demand and maximum work load for the parent, itself limited by constraints on reproductive effort (von Haartman, 1955; Royama, 1966). The 'RSR hypothesis' suggests that by causing a size hierarchy to be established by asynchronous hatching, in which nestlings have specific positions within the hierarchy, energy is not dissipated on sibling competition that would occur if nestlings were of similar size (and hence competitive ability) and the outcome of contests for food was not clear to participants (Hamilton, 1964).

The main aims of this thesis are twofold: Firstly, to measure the activity component of the daily energy budget thus far unavailable for any species, and reassess the importance of all components of the energy budget, including activity costs, to nestling development and quality, using the Dipper, Cinclus cinclus, as a principal subject. Energy budget data derived from laboratory studies will be compared with daily energy expenditure measured in the field, and adaptive strategies of nestling development discussed. Secondly, the energetics of parent/offspring interactions will be examined with respect to hatching asynchrony in the House Martin, Delichon urbica: sib-sib competition in the House Martin and the Zebra Finch, Taeniopygia castanotis; and brooding behaviour and optimal inattentiveness in the Dipper.

By synthesizing ecological, behavioural, physiological and functional approaches using the techniques of 'behavioural energetics', a common rationale for exploring the many interrelated aspects of nestling development and parental care was adopted.

CHAPTER TWO

MODELS AND THEORY

2.1 THE DAILY ENERGY BUDGET OF A THEORETICAL 25g PASSERINE

2.1.1 The nestling growth curve

A theoretical Daily Energy Budget (DEB) was calculated for a 25g passerine from a synthesis of data in the literature, with the aim of using it to predict the consequence of various nestling strategies, for nestling growth and survival (see Sections 2.2 and 2.3). It was planned to examine the causes and consequences of the various strategies in the field using the House Martin, Dipper and other species as subjects. Using Ricklefs' curve fitting technique (Ricklefs, 1967a) the growth curve for a nestling with a 1.0g hatching mass and a 25g asymptotic mass was constructed (Figure 2.1). The equation is -

$$w = \frac{25.0}{1 + e^{-0.588(t-5.175)}} \qquad \text{eqn. 2.1}$$

where w = mass of nestling (g), and t = age (days).

No mass recession (Ricklefs, 1968) was assumed to occur and the nestling period was arbitrarily set at 18 days, at which time the asymptotic mass was reached. From this basic growth curve the following components of the nestling energy were calculated; Basal Metabolic Rate (M), Activity (A), Growth (P), specifically the energy accumulating in tissue growth (biosynthetic costs were not included in this preliminary model, see Chapter 5 for discussion) and Thermoregulation (TR).

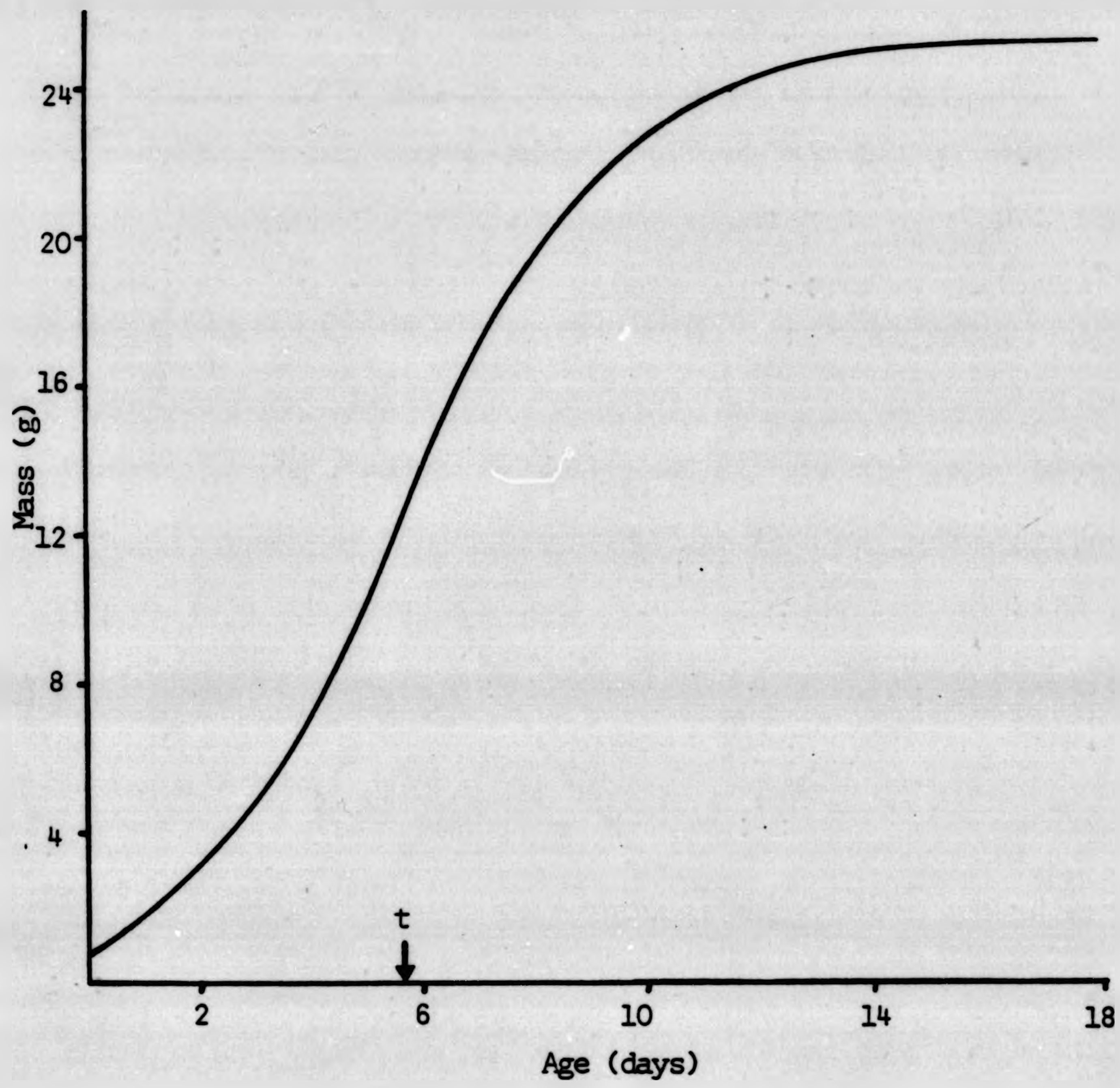


Figure 2.1

Growth curve for a theoretical 25g passerine.

t = inflexion point = 5·175 days

2.1.2 Basal metabolic rate

Strictly speaking the term basal metabolic rate (BMR) defined as: the metabolic rate of quiescent, non-growing, post-absorptive birds at thermoneutrality in the dark (Ricklefs, 1974; Calder & King, 1974) cannot be applied to nestling birds. Since nestling birds are growing, resting metabolism will contain a proportion of biosynthetic costs, this is likely even if no mass change is observed during experimental periods (see Section 4.6.2). Biosynthesis costs are composed of two components; replacement of degraded tissue and synthesis of new tissue during growth (Section 4.6.5). BMR of adult birds may contain some of the former cost, particularly during the daytime (Section 4.6.1) but nestlings resting metabolism will contain the latter cost also. By measuring nestling resting metabolism under suitable conditions the contribution of biosynthesis costs to resting metabolic costs may be minimised (Section 4.6). BMR is thus used in this study to signify resting metabolism in which the biosynthetic cost has been minimised, or when using equations of adult BMR to calculate basal metabolic costs in nestlings (see below). Nestling birds have water contents often up to 30% higher than adult birds (Section 4.2.1), and thus the amount of metabolising tissue for a given mass will be less in nestlings. The use of adult BMR equations will therefore tend to overestimate actual nestling 'BMR', all things being equal. This tendency to overestimate will decrease as nestlings mature, since water content (and hence dry mass and lean dry mass) approach adult proportions towards fledging (Section 4.2). Thus whilst it is recognised that adult BMR equations are imperfect predictors of nestling resting metabolism, they remain the most suitable alternative for calculating basal costs at the present time. They are therefore used below for the construction of the theoretical DEB, and elsewhere in this study.

BMR was calculated from the following two equations put forward by Aschoff and Pohl (1970).

$$\text{BMR resting phase} = 114.8w^{0.726} \quad \text{eqn. 2.2}$$

$$\text{BMR active phase} = 140.9w^{0.704} \quad \text{eqn. 2.3}$$

where w = mass of nestling (Kg), and resting phase is the night-time resting metabolism in postabsorptive birds, at thermoneutrality in the dark. The active phase BMR is the equivalent measurement for daytime resting metabolism. For the purpose of constructing the theoretical DEB a 12 hour diurnal cycle was assumed, and so the mean of equations 2 and 3 were taken to predict daily resting metabolism (mean BMR, Table 2.1). Results for the final energy budget are expressed as watts bird^{-1}.

2.1.3 Growth

Daily energy increment (P) was calculated assuming the energetics of nestling growth to be a composite of available data (see Appendix I). Cumulative energy content was constructed from the following equations, and the daily increment arrived at by subtraction.

(a) Water content

Water content (%) calculations were based on the House Martin (Bryant & Gardiner, 1979), in which % water decreased from approximately 90% to 60% during growth. For simplicity the

TABLE 2:1 Calculated BMR for a hypothetical 25g passerine

		BMR			
Age (days)	Mass (g)	Night-time	Daytime	Mean of Night/Day BMR	
		(~~kJ~~ Cal d^{-1})	(~~kJ~~ Cal d^{-1})	(~~kJ~~ Cal d^{-1})	(Watts bird^{-1})
0	1.00	0.762	1.089	0.926	0.044
1	1.64	1.091	1.543	1.317	0.064
2	2.75	1.588	2.218	1.903	0.092
3	4.41	2.238	3.095	2.667	0.129
4	6.83	3.074	4.215	3.645	0.177
5	9.91	4.028	5.472	4.750	0.230
6	13.35	5.000	6.749	5.870	0.284
7	16.68	5.878	7.895	6.890	0.334
8	19.39	6.557	8.777	7.670	0.372
9	21.45	7.056	9.424	8.240	0.399
10	22.84	7.385	9.850	8.570	0.415
11	23.72	7.591	10.116	8.853	0.429
12	24.24	7.711	10.271	8.990	0.436
13	24.55	7.783	10.364	9.070	0.440
14	24.75	7.829	10.423	9.126	0.442
15	24.86	7.854	10.456	9.155	0.444
16	24.92	7.868	10.473	9.171	0.444
17	24.96	7.877	10.485	9.181	0.445
18	25.00	7.882	10.491	9.187	0.445

change was assumed to be linear and was described by the following equation (see Figure 2.2);

Water content (%) = 9.0 - 2.14 Age eqn. 2.4

After 14 days of age water content was assumed to remain at 60%, comparable with a stable phase from House Martin data (Bryant & Gardiner, 1979). Water content, and hence dry mass (%) and dry mass (g) are presented in Table 2.2.

(b) Lipid mass and lean dry mass.

Dry mass was divided into lipid mass and lean dry mass (assumed to be protein, since ash content and other components are generally small, and the few data on change in ash content with age are inconclusive). Lipid mass was calculated from change in lipid index with age (Figure 2.2), based on the early change in lipid of House Martins (Bryant & Gardiner, 1979). Lipid index was assumed to change linearly and remain stable at 1.0, after day 14. The equation is;

Lipid index = 0.1 + 0.0643 Age eqn. 2.5

Since lipid index equals lipid mass/lean dry mass it was possible to calculate lean dry mass from the above equation (Table 2.2) since total dry mass was also known. Lipid and lean dry mass was converted to energy equivalents, using Lipid = 39.748 kJ g^{-1} (9.6 Kcal g^{-1}) and LDM (Protein) = 23.64 kJ g^{-1} (5.65 Kcal g^{-1}) (Brody, 1945). Daily energy increments of growth were calculated as described above and expressed as Watts $bird^{-1}$ (Table 2.2).

2.1.4 Activity

The cost of nestling activity was initially calculated

TABLE 2.2: Calculated daily energy increments of growth (P) for a 25g passerine

Age (days)	Mass (g)	Water (%)	Dry Mass (%)	Dry Mass (g)	Lipid Index	Lipid (%)	Lipid Mass (g)	Lean Dry Mass (g)	Energy as Lipid (kJ)	Energy as protein (kJ)	Cumulative Energy (kJ)	Daily energy increment (kJ d^{-1})	(w bird
0	1.00	90.0	10.0	0.10	0.100	0.09	0.01	0.09	0.36	2.15	2.51	-	-
1	1.64	87.86	12.14	0.20	0.164	0.14	0.03	0.17	1.11	4.07	5.18	2.67	0.031
2	2.75	85.72	14.28	0.40	0.228	0.19	0.08	0.32	3.02	7.66	10.68	5.50	0.064
3	4.41	83.58	16.42	0.73	0.293	0.23	0.17	0.56	6.68	13.29	19.97	9.29	0.108
4	6.83	81.44	18.56	1.27	0.357	0.26	0.33	0.94	13.11	22.22	35.33	15.36	0.178
5	9.91	79.30	20.70	2.05	0.422	0.30	0.62	1.44	24.44	34.04	58.48	23.15	0.269
6	13.35	77.16	22.84	3.05	0.486	0.33	1.01	2.04	40.14	48.22	88.36	29.9	0.347
7	16.68	75.02	24.98	4.17	0.550	0.36	1.50	2.67	59.60	63.19	122.79	34.43	0.399
8	19.39	72.88	27.12	5.26	0.614	0.38	2.00	3.26	79.49	77.07	156.56	33.77	0.391
9	21.45	70.74	29.26	6.27	0.679	0.40	2.51	3.76	99.77	88.89	188.80	32.30	0.375
10	22.84	68.60	31.40	7.17	0.743	0.43	3.08	4.09	122.42	96.69	219.11	30.31	0.351
11	23.72	66.46	33.58	7.97	0.807	0.45	3.59	4.38	142.69	103.54	246.23	27.12	0.314
12	24.24	64.32	35.68	8.65	0.872	0.47	4.07	4.58	161.77	108.27	270.04	23.81	0.276
13	24.55	62.18	37.82	9.28	0.936	0.48	4.45	4.83	176.88	114.18	291.06	21.02	0.243
14	24.75	60.00	40.00	9.90	1.000	0.49	4.45	4.95	192.82	117.0	309.82	18.76	0.217
15	24.86	60.00	40.00	9.94	1.000	0.50	4.97	4.97	197.55	117.49	315.04	1.29	0.015
16	24.92	60.00	40.00	9.96	1.000	0.50	4.98	4.98	197.95	117.73	315.68	0.64	0.007
17	24.96	60.00	40.00	9.98	1.000	0.50	4.99	4.99	198.34	117.96	316.30	0.62	0.007
18	25.00	60.00	40.00	9.99	1.000	0.50	5.00	5.00	198.74	118.70	316.94	0.64	0.007

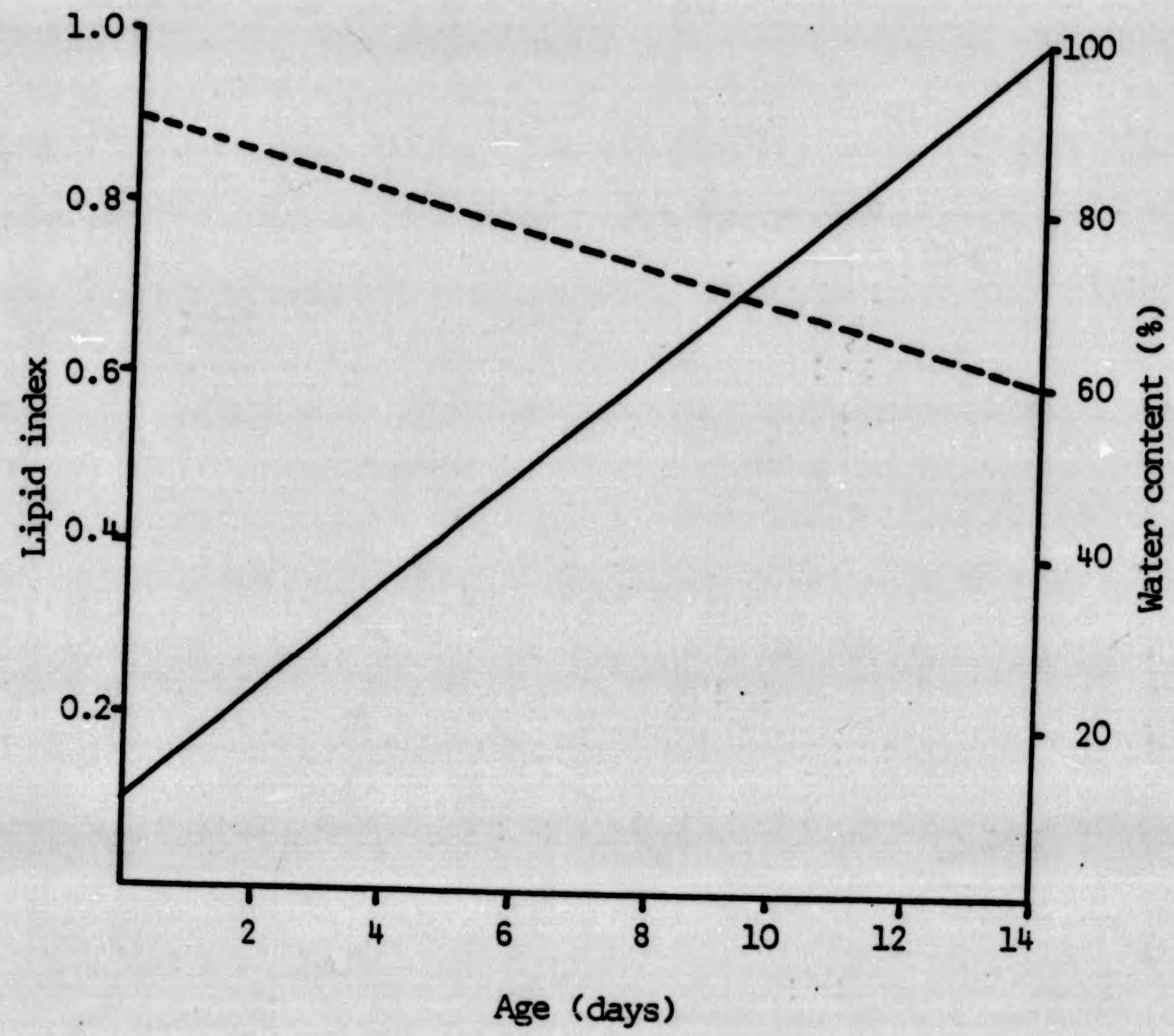


Figure 2.2

Lipid index and water content as a function of age for a theoretical 25g passerine.

in two different ways. Before this study costs of activity had not been measured directly in nestlings; figures appearing in the literature were usually obtained by subtracting all other DEB components from the total and apportioning this residual to activity. By this method values of up to 100% BMR activity costs were calculated for the Double Crested Cormorant Phalacrocorax auritus (Dunn, 1980), up to 40% BMR for the Starling Sturnus vulgaris (Westerterp, 1973) and up to 70% BMR for the House Sparrow (Passer domesticus, Blem, 1975). An approximate mean value applicable over the whole nestling period was calculated as 70 ? 50% BMR, and this was used to produce an estimate of activity costs (Table 2.3). Dunn (1980), however, presented a diagram of activity costs changing as a proportion of BMR in a similar way to Figure 2.3, for the Double Crested Cormorant, although the costs were higher. This pattern of changing activity costs was considered realistic since the locomotory capacity of nestlings change with increasing age (Ryden & Bengtsson, 1980) and parental inattentiveness. A value for activity costs at peak closer to those of the House Sparrow (70%) was however considered more realistic for a 25g passerine species on the basis of similarity in size.

The equations for sections a - c, Figure 2.3, are;

(a) Activity cost = 1.82 Age (0 - 5 days) eqn. 2.6

(b) Activity cost = 40 Age - 200 (5 - 7 days) eqn. 2.7

(c) Activity cost = 100 - 2.85 Age (7-14 days) eqn. 2.8

where activity cost is expressed as percentage BMR. Total activity costs for the whole nesting period calculated using

TABLE 2.3: Calculated activity costs for a 25g passerine

Age (days)	BMR (W.bird^{-1})	50% BMR activity cost (W.bird^{-1})	[a]Variable % BMR activity cost (% BMR)	Variable % BMR activity cost (W.bird^{-1})
0	0.051	0.02	0.0	0.0
1	0.064	0.03	1.82	0.001
2	0.092	0.04	3.64	0.003
3	0.129	0.06	5.46	0.007
4	0.177	0.09	7.28	0.013
5	0.230	0.12	9.10	0.021
6	0.284	0.14	40.0	0.114
7	0.334	0.17	80.0	0.267
8	0.372	0.19	77.15	0.287
9	0.399	0.20	74.29	0.296
10	0.415	0.21	71.43	0.296
11	0.429	0.22	68.57	0.294
12	0.436	0.22	65.72	0.286
13	0.440	0.22	62.86	0.277
14	0.442	0.22	60.00	0.267
15	0.445	0.22	57.95	0.258
16	0.445	0.22	54.29	0.249
17	0.445	0.22	51.43	0.229
18	0.445	0.22	48.57	0.216
TOTALS:	6.074	3.03	-	3.381

[a] See equations 2.6, 2.7 and 2.8

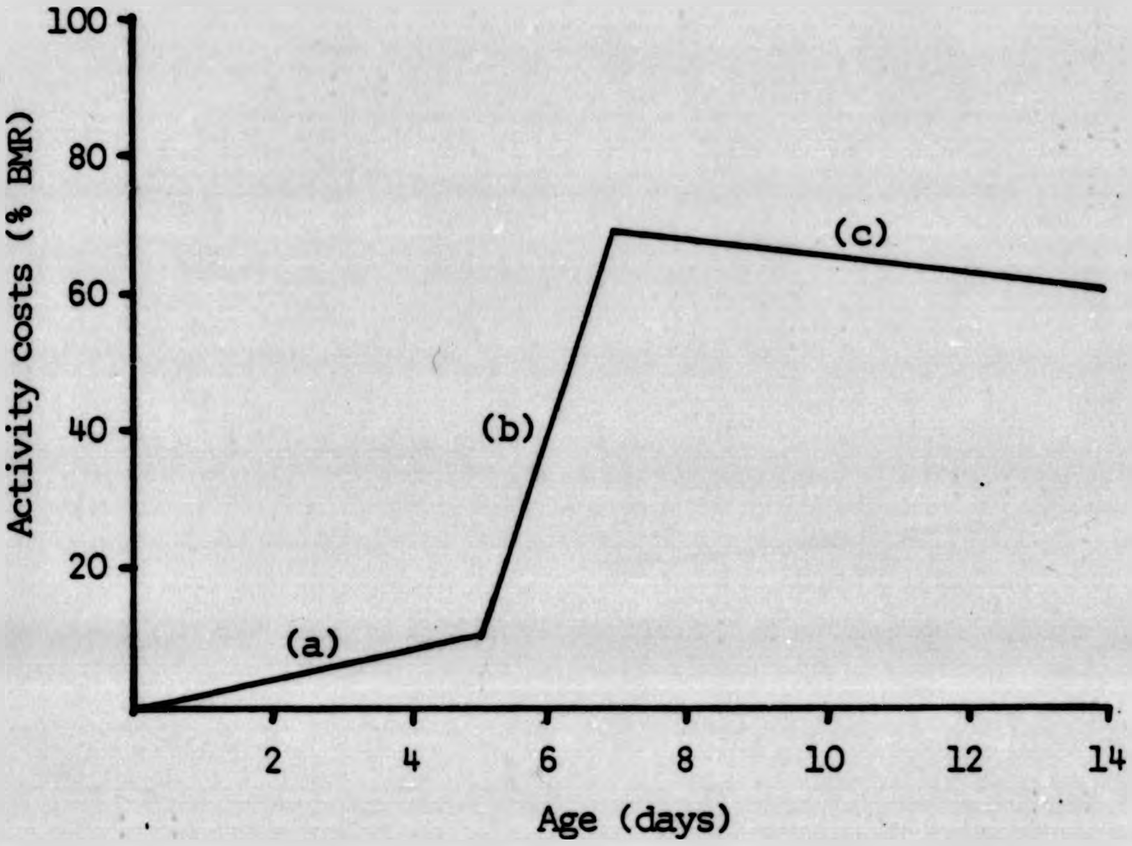


Figure 2.3

Activity costs as a function of age, expressed as percentage BMR.

For regression equations (a - c) see text.

these equations is 11% higher than those calculated by the constant BMR proportion model (Table 2.3). The model in Figure 2.3 was used in subsequent calculations of DEB.

2.1.5 Thermoregulation

Three different equations were used to calculate thermoregulatory costs (Table 2.5, Fig. 2.4). Aschoff (1981) investigated heat loss in passerines and non-passerines and produced three predictive equations, one for non-passerines, and two for daytime and night-time resting passerines respectively (see below).

$$M\alpha = 0.857\ w^{-0.463} \qquad \text{eqn. 2.9}$$

$$M\rho = 0.576\ w^{-0.410} \qquad \text{eqn. 2.10}$$

where $M\alpha$ and $M\rho$ are daytime and night-time conductances in ml $O_2.g^{-1}.h^{-1}.^{\circ}C^{-1}$, and w is nestling mass in grams. A third model is Mertens (1977) model for heat loss in Great Tit broods.

$$M = 0.0035\ w^{0.613} \qquad \text{eqn. 2.11}$$

where M = heat loss of nestling/brood in Watts nestling/brood bird^{-1} and w is the mass in grams. The latter is close to that predicted by Aschoff and Pohl for daytime conductance and lies between it and the night-time conductances (Figure 2.4, Table 2.5). Mertens' model was therefore used to calculate the net thermoregulatory cost for the theoretical passerine at 15°C (T_a), assuming a body temperature (T_b) of 40°C to calculate gross costs and then subtracting BMR. This additional cost was added to the Gross energy intake (GEI) to give GEI at 15°C (Figure 2.6). Calculating thermoregulatory cost in this

TABLE 2.4: Calculated DEB for a theoretical 25g passerine

Age (days)	Mass (g)	BMR (w bird^{-1})	P (w bird^{-1})	A (w bird^{-1})	Assimilation efficiency %	DEB calculated (w bird^{-1})	DEB Kendeigh et al. (w bird^{-1})	GEI (w bird^{-1})
0	1.00	0.051	0.000	0.000	92.3	0.051	0.056	0.055
1	1.64	0.064	0.031	0.001	90.0	0.096	0.084	0.107
2	2.75	0.092	0.064	0.003	87.7	0.159	0.128	0.181
3	4.41	0.129	0.108	0.007	85.4	0.244	0.187	0.285
4	6.83	0.177	0.178	0.013	83.1	0.368	0.268	0.443
5	9.91	0.230	0.269	0.021	80.8	0.520	0.362	0.644
6	13.35	0.284	0.347	0.114	78.5	0.745	0.461	0.949
7	16.68	0.334	0.399	0.267	76.2	1.000	0.553	1.312
8	19.39	0.372	0.391	0.287	73.8	1.050	0.626	1.423
9	21.45	0.399	0.375	0.296	71.5	1.070	0.679	1.497
10	22.84	0.415	0.351	0.296	69.2	1.062	0.715	1.535
11	23.72	0.429	0.314	0.294	66.9	1.037	0.737	1.550
12	24.40	0.436	0.276	0.286	64.6	0.998	0.754	1.545
13	24.55	0.440	0.243	0.277	62.3	0.960	0.758	1.540
14	24.75	0.442	0.262	0.268	60.0	0.972	0.763	1.162
15	24.86	0.445	0.015	0.258	60.0	0.718	0.766	1.197
16	24.92	0.445	0.007	0.249	60.0	0.701	0.767	1.157
17	24.90	0.445	0.007	0.229	60.0	0.681	0.768	1.135
18	25.00	0.445	0.007	0.216	60.0	0.668	0.769	1.113
	TOTALS:	6.074	3.644	3.388	-	13.100	10.201	18.786

P = Productivity   A = Activity

TABLE 2.5: Thermoregulation costs for a theoretical 25g Passerine at 15°C. Body temperature assumed to be 40°C.

Age	BMR	[1] α	[2] ρ	[3] m	[4] mean gross	[5] mean net
0	0.051	0.118	0.075	0.088	0.094	0.043
1	0.064	0.150	0.103	0.118	0.124	0.060
2	0.092	0.200	0.150	0.163	0.171	0.079
3	0.129	0.275	0.175	0.217	0.222	0.093
4	0.177	0.325	0.225	0.275	0.275	0.098
5	0.230	0.400	0.275	0.350	0.342	0.117
6	0.284	0.475	0.325	0.425	0.408	0.124
7	0.334	0.525	0.350	0.475	0.450	0.116
8	0.372	0.575	0.400	0.534	0.503	0.131
9	0.399	0.600	0.425	0.572	0.532	0.133
10	0.415	0.625	0.437	0.545	0.552	0.137
11	0.429	0.645	0.450	0.610	0.568	0.139
12	0.436	0.650	0.450	0.618	0.573	0.137
13	0.440	0.658	0.453	0.623	0.578	0.138
14	0.442	0.663	0.455	0.625	0.581	0.139
15	0.444	0.668	0.458	0.628	0.585	0.141
16	0.444	0.672	0.460	0.629	0.587	0.143
17	0.445	0.675	0.463	0.630	0.589	0.144
18	0.445	0.675	0.465	0.630	0.590	0.145

---

[1] Aschoff & Pohl, Daytime conductance = α

[2] Aschoff & Pohl, Night-time conductance = ρ

[3] Mertens Model = m

[4] Mean Gross = mean of α and ρ and is basal metabolism plus thermoregulation

[5] Net = Mean Gross-BMR

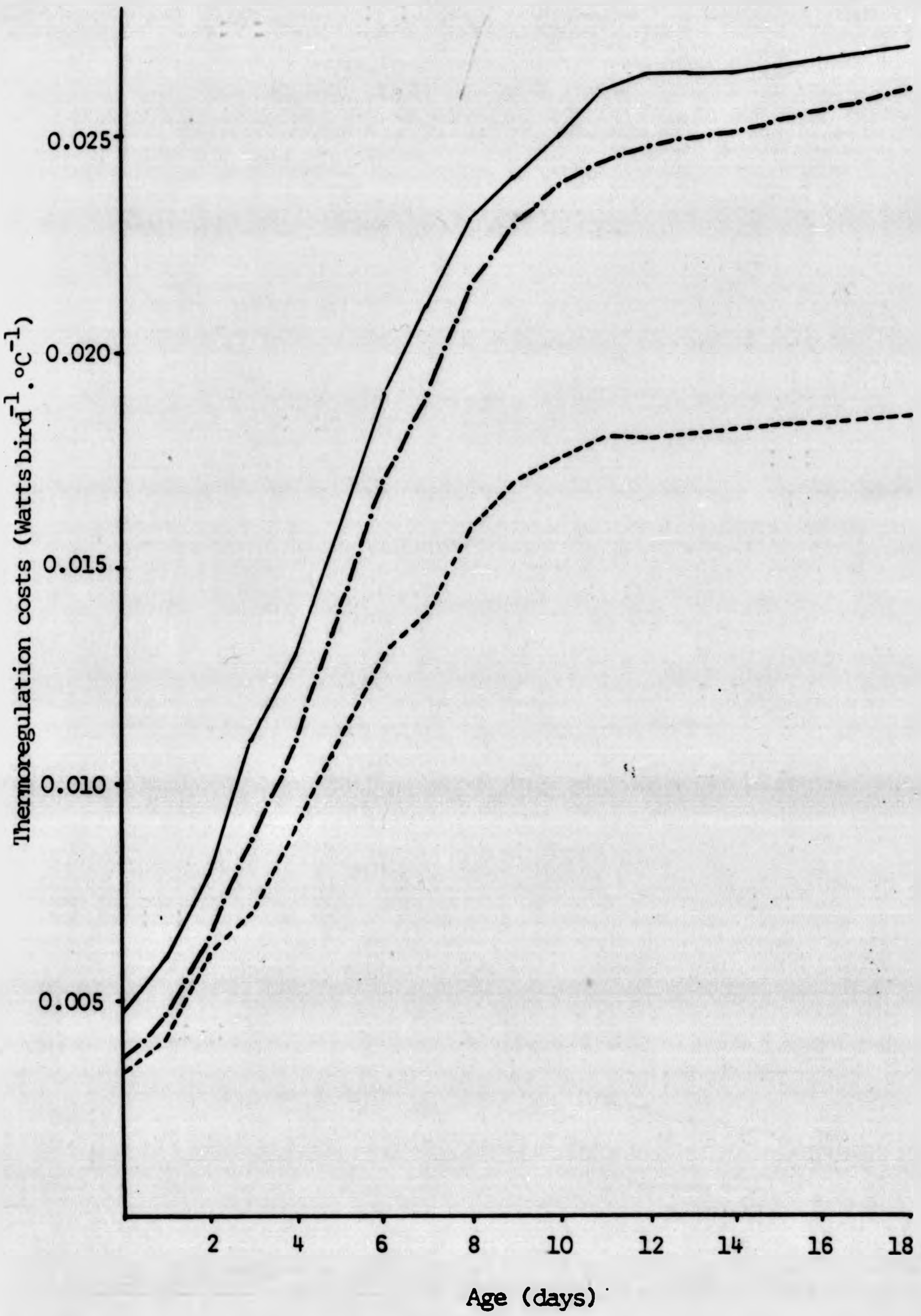


Figure 2.4

Thermoregulation costs calculated from three different equations as a function of age for a theoretical 25g passerine.

——————— Aschoff & Pohl, daytime model

—·—·—·—·— Mertens model

- - - - - - - - - - Aschoff & Pohl, night-time model way shows that the Lower Critical Temperature (T_{lc}) and hence the thermoneutral zone changes as nestlings get older (Figure 2.5). Smaller nestlings can only tolerate relatively high ambient temperatures and so have to increase metabolism to compensate for heat loss relatively earlier than larger nestlings (Figure 2.5). For simplicity in subsequent calculations of nestling energy savings from various strategies, birds were assumed to be at thermoneutrality and hence have zero thermoregulation costs. This was because the strategies considered were concerned primarily with the activity and growth components of the energy budget, and assume TR cost is constant (see Sections 2.2, 2.3).

2.1.6 Assimilation efficiency and GEI

DME was calculated as the sum of M, P and A and is presented in Table 2.4, assuming nestling is at thermoneutrality. Gross Energy Intake (GEI) was calculated retrospectively, using the following equation;

Assimilation Efficiency (%) = 92.3 - 2.308 Age eqn. 2.12

based on data for the Willow Warbler (Phylloscopus trochilus, Tiainen, 1983), and is presented in Table 2.4.

2.2 PEAK LOAD REDUCTION

2.2.1 Theory

Nestling food (energy) demand reaches a peak during the nestling period and then declines (Sections 2.1.7, 4.6). By spreading out hatching times, parents also spread out the individual nestling demand curves. The amount of food needed

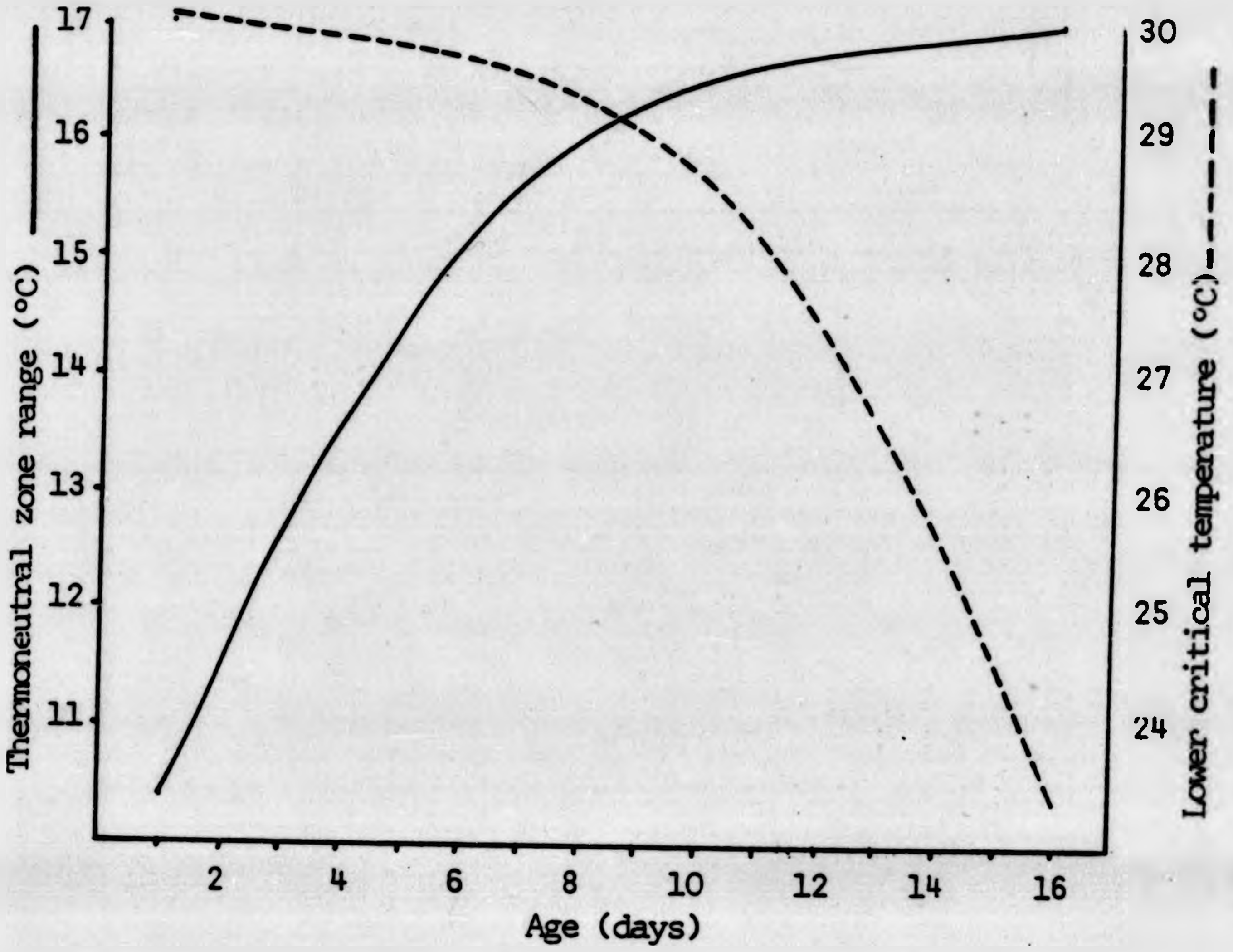


Figure 2.5

Range of thermoneutral zone (i.e. within which thermoregulatory costs are met by BMR), and the lower limit of the range (lower critical temperature).
Based on the Aschoff & Pohl (1970) equation for daytime resting conductance (see text).

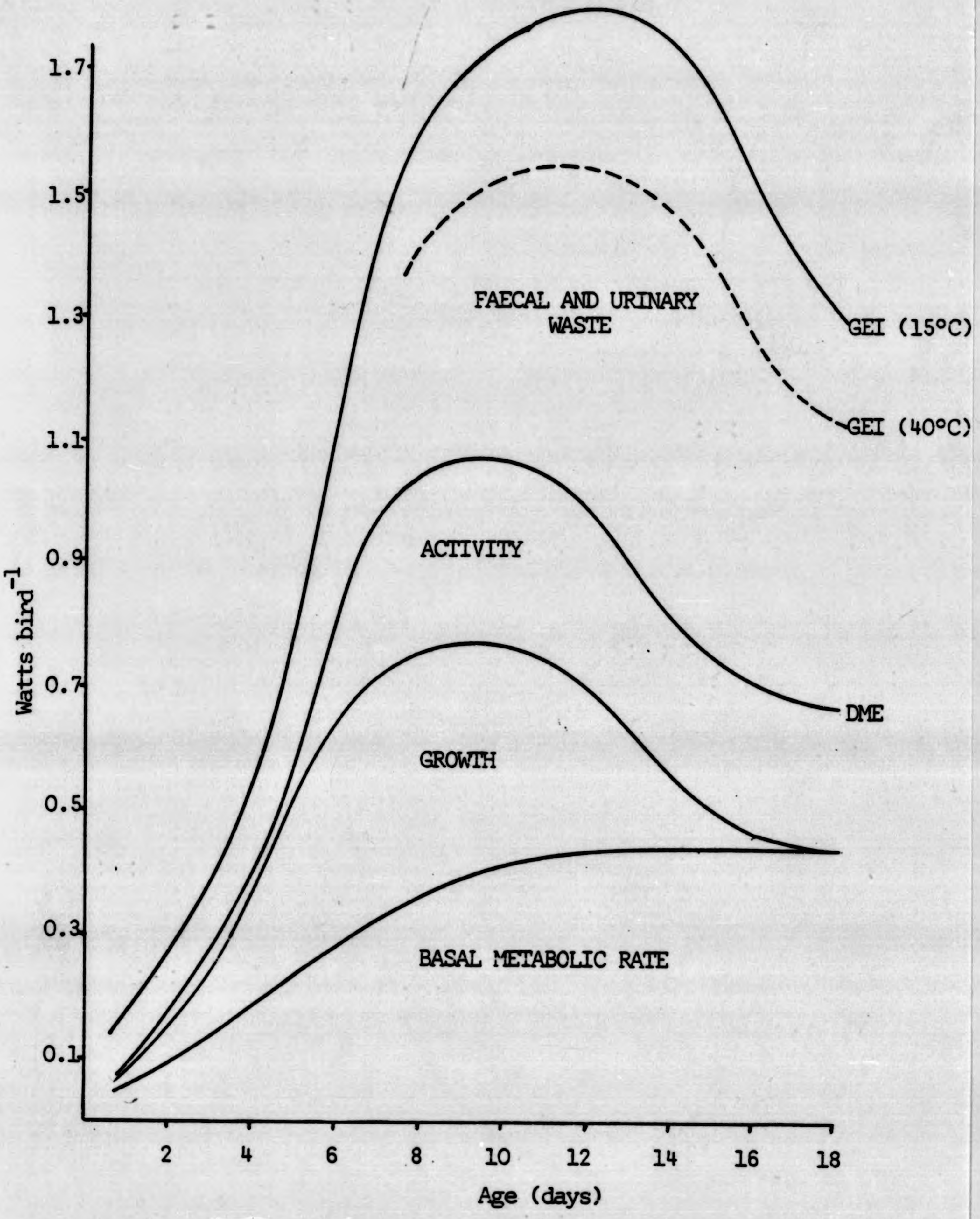


Figure 2.6

The daily energy budget for a theoretical 25g passerine nestling.

by the brood at any one time therefore may be reduced, compared with synchronously hatched young in which the peak demand of individuals is expected to coincide (Bryant & Gardiner, 1979; Feltham, unpublished; Hussell, 1972). This may be particularly important in species which are limited by the amount of time during which they may forage, or those in which the nestling peak demand curves have more pronounced peaks; for example, the House Martin (Bryant & Gardiner, 1979; Section 4.8). Peak load reduction was investigated in the latter (see Sections 3.6, 4.8).

2.2.2 The PLR model

Peak Load Reduction was modelled from the daily energy budget in Section 2.1. The peak energy requirement was arbitrarily defined as the three days of highest demand, and calculated for a brood of four nestlings (Figure 2.7) hatching over different periods. Asynchrony is expressed in days and represents the time between the first and the last hatched chicks, all others are assumed to have hatched at equal intervals during this period. Figure 2.7 shows the reduction in peak energy demand when compared to synchronous broods of four young.

Peak energy demand was calculated as 8.7 Watts brood^{-1} from the model (Figure 2.7), and energy saving acquired by reducing the peak energy demand with increasing asynchrony, was calculated as the difference between peak energy demand for a synchronous brood of four (i.e. Watts brood^{-1}) and the peak energy demand for broods with varying degrees of asynchrony. The results are presented in Figure 2.8. The model predicts

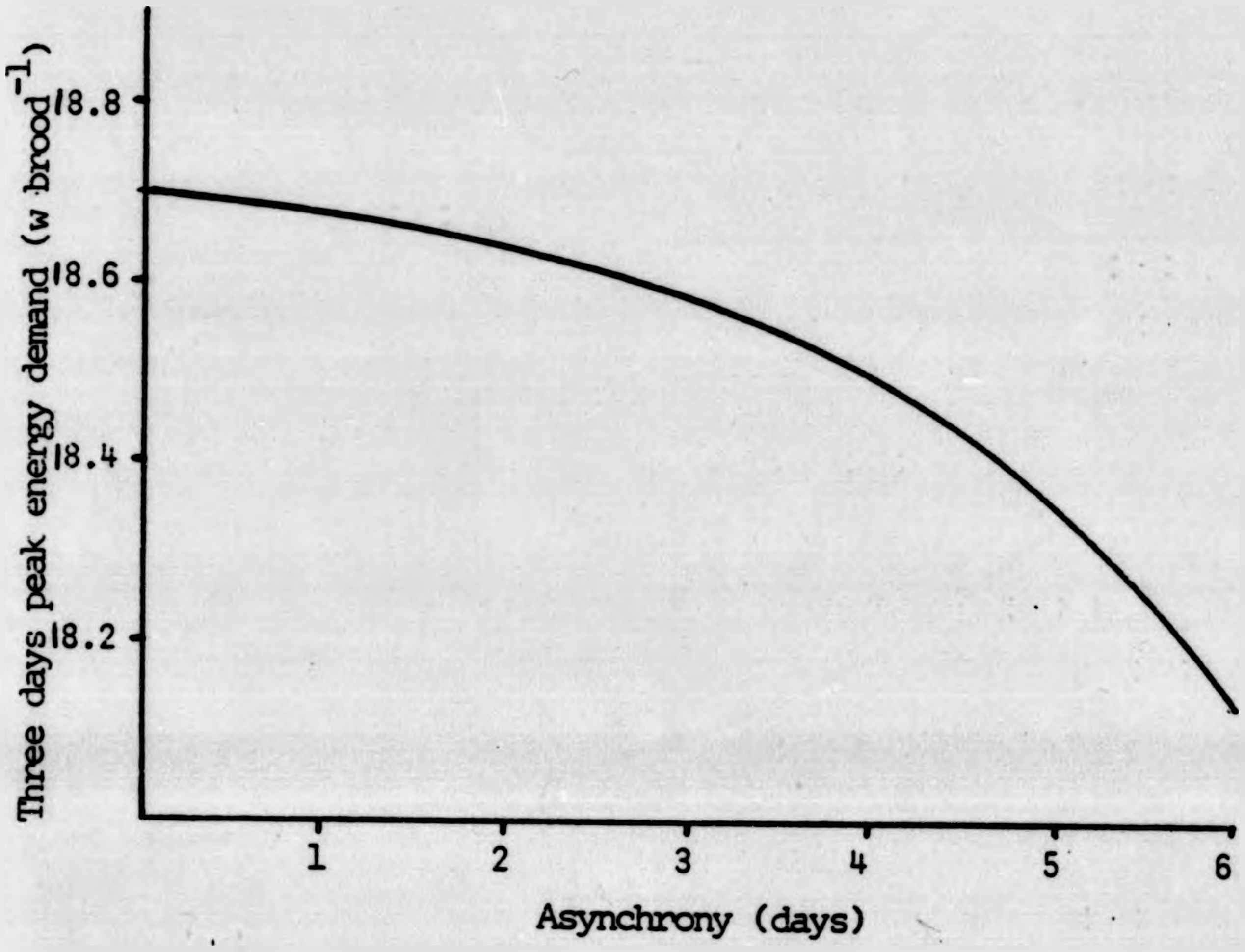


Figure 2.7

Three day peak energy demand as a function of hatching asynchrony for a brood of four theoretical 25g passerine nestlings.

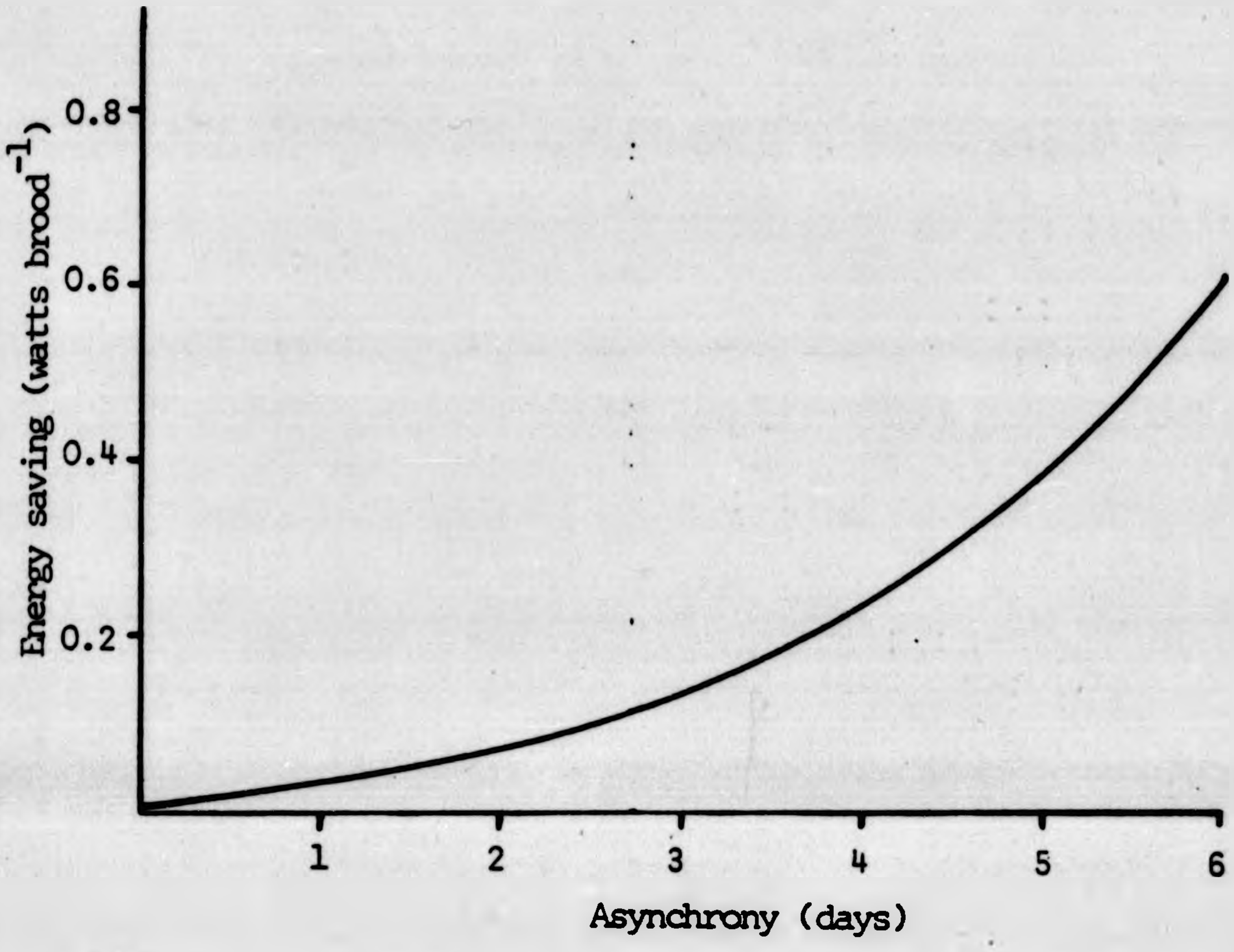


Figure 2.8: Energy saving from 'peak load reduction' in a brood of four theoretical 25g passerine nestlings, as a function of hatching asynchrony.

that increasing asynchrony should produce an exponential increase in energy savings.

The potential benefits of an asynchronous hatching strategy, in terms of energy saved at peak load, increases with brood-size (Figure 2.9). This shows that the peak energy saving calculated from the model DEB for brood-sizes 2 - 4, as a function of asynchrony. The values (maximum of approximately 9.5×10^{-2} Watts brood^{-1} in brood-size four) are small. This represents a 1.1% reduction in DME, or a 1.7% reduction in GEI at thermoneutrality. This compares with a 0.1% reduction in DME and a 2.2% reduction in GEI respectively for broods of four House Martins (Bryant & Gardiner, 1979) calculated over the seven days of peak energy demand. The shape of the DME curve as a function of age is very important when considering energy saving from PLR. The more pronounced the peak the greater the reduction in energy demand. By measuring energy intake of broods of varying asynchrony the model of exponential increase in energy savings with increasing asynchrony may be tested.

2.3 REDUCING SIBLING RIVALRY

2.3.1 Theory

Hamilton (1964) suggested advantages to the brood and adults of reducing energy wastage during sibling-sibling competition, and suggested that even in a season with average food resources an increased survival of young would be aided by economic use of energy. The link between asynchrony and reduced sibling rivalry was discussed by Parker (1974), who stated that by imposing asynchronous hatching on the brood, the

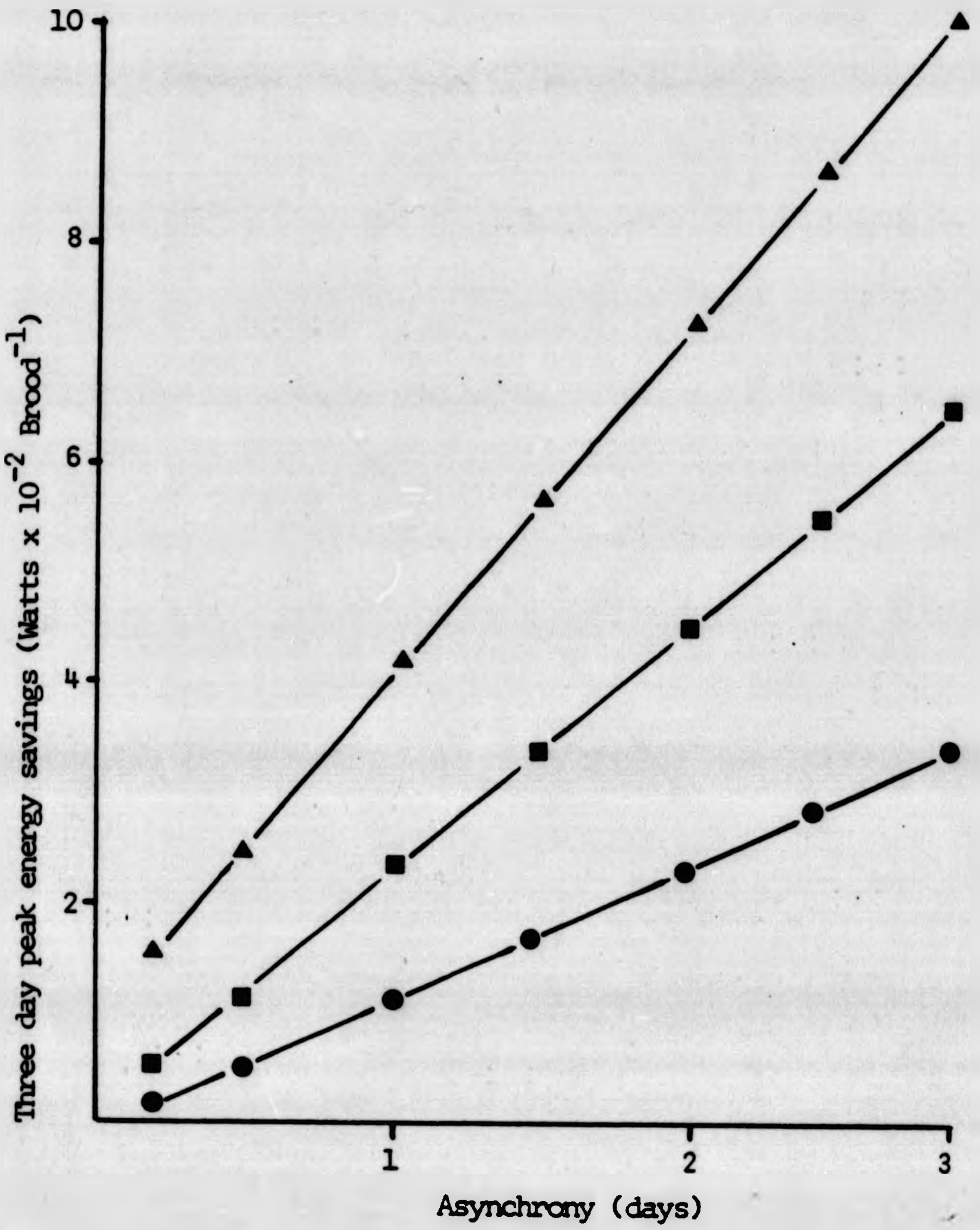


Figure 2.9

Energy savings for the three days of peak energy demand in brood sizes (▲)4, (■)3, and (●)2 respectively for a theoretical 25g passerine. The regression equations are;

Brood size 4: $y = 0.0343x - 0.000462$
Brood size 3: $y = 0.0217x - 0.000381$
Brood size 2: $y = 0.0115x - 0.000204$

Assumes linearity between days 0-3, see Figure 2.8

disparity in size of young would result in marked differences in the "Resource Holding Power" of competing siblings; and thus should reduce the probability of conflict. There is, however, no evidence to suggest that "Resource Holding Power" is a fixed parameter. It is likely that RHP changes in an individual in response to a number of factors. For example, hunger level, position in the nest, the behaviour of siblings and of parents, nestling size, mass, age, etc. It is therefore more realistic to view RHP as a plastic parameter. The 'Relative Resource Holding Power' (RRHP) of an individual with respect to the above factors, is a way of interpreting the probablistic approach to sibling conflict suggested by Parker, and is used instead of RHP to indicate the plasticity of the parameter.

2.3.2 Assumptions of the RSR Model

A model of reduced sibling rivalry (RSR) was proposed based on the following assumptions:-

(i) The relative resource holding power of individuals is directly proportional to the size difference between those individuals (Parker, 1974);

(ii) Mass differences (see below) are a suitable measure of size difference between individuals due to correlation with body size (and hence physical 'dominance') and age (and hence greater locomotory development) (Bryant, 1978a);

(iii) Disparity of size between nestlings should be optimised and actively maintained either throughout growth, or long enough to allow the establishment of a dominance hierarchy which then remains fixed even if size differences between individuals are not maintained;

(iv) The cost of sibling competition is energetically expensive;

(v) Energy saved from RSR is reinvested into some component of fitness. For example, increased probability of brood survival (see below) or reduced reproductive cost to the parent.

2.3.3 Index of Hatching Asynchrony

If hatching asynchrony produces size differences between individuals (from the model, mass differences) these differences can be used as a more accurate measure of the importance of asynchrony in regulating competitive energy expenditure (CEE). The difference in body mass (DBM) between individuals (usually the first and last hatched) is a misleading index of asynchrony, and fails to reflect the importance of growth on the size hierarchy. For example, a DBM of 1.0g between two nestlings of average mass of 2.0g, is clearly more important than a similar DBM between nestlings of mean mass 20.0g, since it represents 50% of body mass in the small nestlings but only 5% in the larger nestlings. This discrepancy was overcome by using Relative Difference in Body Mass (RDBM) as an index of asynchrony and calculated as:-

$$\text{RDBM} = \frac{\text{Mass of heaviest nestling-Mass of lightest nestling}}{\text{(Brood mass/Brood size)}} \qquad \text{eqn.2.13}$$

Since hatching masses of nestlings, on which the model was to be tested were difficult to obtain without frequent disturbance to the birds (due to closed nest structure), the Relative Difference in Hatching Mass (RDHM) was used. This is the size difference between individuals after the hatch of the last chick, and hence that mainly attributable to hatching asynchrony. This was calculated by plotting RDBM for several ages for each brood against mean nestling mass and extrapolating a line through these points to a nestling mass of 2.0g, which is a close estimate of mean hatching mass based on the House Martin, in which asynchrony was to be investigated (Bryant, 1975b). For a discussion of how RDBM changes with growth see Section 4.11.2.

2.3.4 Predicted Changes in Competitive Energy Expenditure

Figure 2.10 shows how competitive energy expenditure (CEE) and energy savings may change with asynchrony (RDHM). As RDHM increases then the probability of the smallest sibling winning a contest decreases; or RRHP of the smallest sibling decreases. It is envisaged that at some maximum RDHM, the RRHP of the largest sibling will be maximal, i.e. it wins all contests. If a sibling is not receiving any feeds as a result of reducing it's own competitive costs (Hamilton, 1964), and 'waiting it's turn', then it will be eventually forced to expend increasing amounts of energy in competition in order to receive some energy returns (Part B, Figure 2.10). Part A, Figure 2.10, may therefore be viewed as nestlings maximising returns, by reducing competition, whilst Part B may be viewed as ensuring a net energy gain but at a much reduced level. The optimal asynchrony corresponds to the point at which net energy gains are maximised by the greatest reduction in CEE. This was tested on the House Martin (Section 4.10).

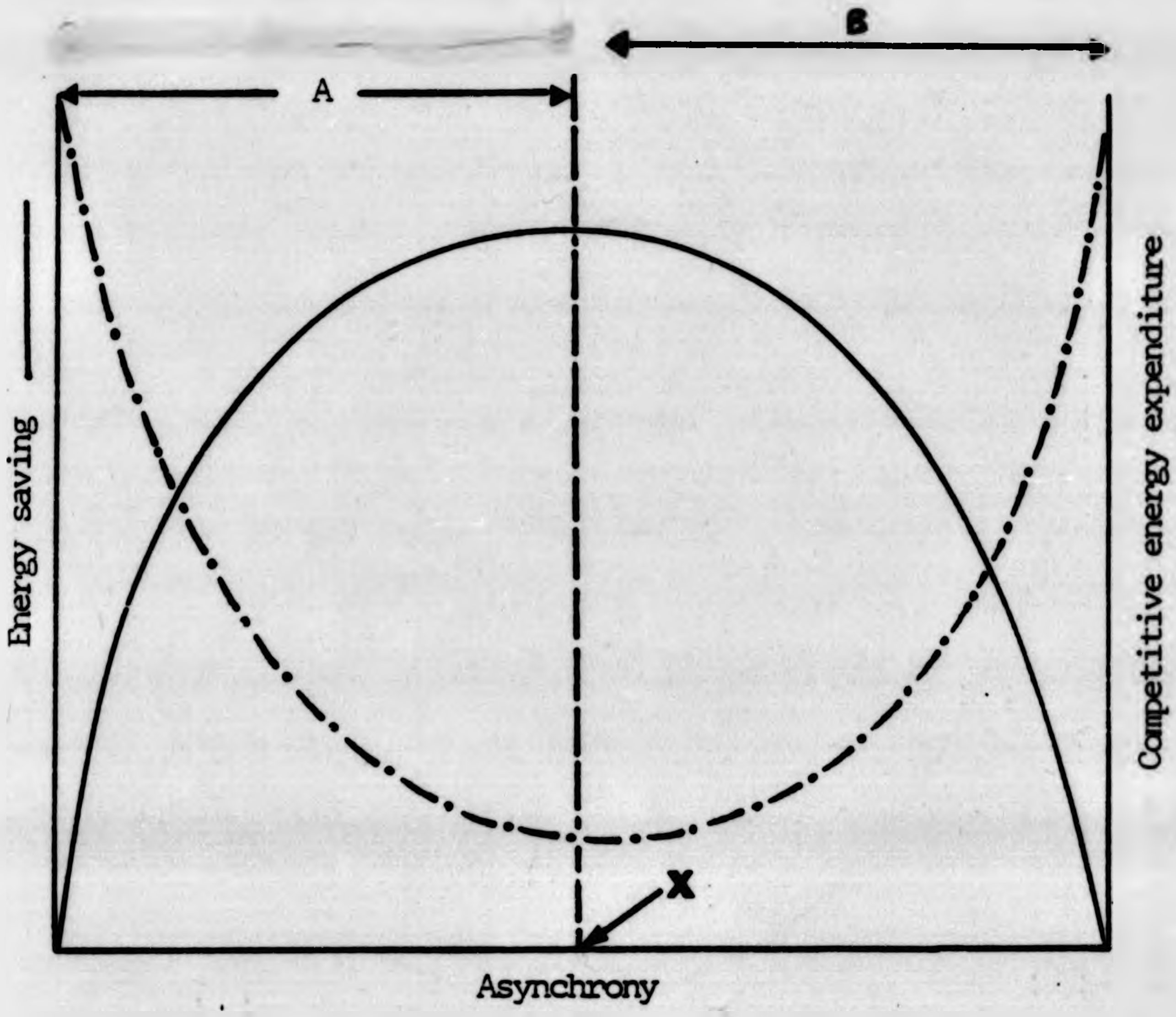


Figure 2.10

Model of reduced sibling rivalry (see text).

X = optimal asynchrony

2.3.5 Predicted Changes in Peak Body Mass of Nestlings

Assumption (v) of the RSR model requires demonstration of some component of fitness that may be expected to follow the form of the energy saving curve (Figure 2.11). House Martins show a particularly flexible growth response (O'Connor, 1977) since food supply to nestlings is often unpredictable (Bryant, 1978b). They have developed a strategy (Resource Storage Strategy; O'Connor, 1978a) of laying down substantial fat deposits to buffer against periods of food shortage.

One way in which energy saved from reduced sibling-competition might be invested would be as fat deposits, or an acceleration of the growth rate, which would be reflected in peak nestling mass (Section 4.11.1). The proportion of nestling activity that can be assumed to be sibling-sibling competition is not known. The energy saved from reducing total activity cost from between 0% and 100% was calculated. The energy equivalent mass of body tissue was then calculated assuming either it was 100% Fat, 100% Protein or 75% Fat:25% Protein respectively and assuming a biosynthetic efficiency of 50% (Wijnandts, 1984) (Figure 2.11). This mass was then expressed as the percentage increase above the 25g peak mass of the theoretical passerine. Theoretically a maximum increase in body mass of between 11% and 19% might be achieved for each nestling if such savings were reallocated to growth. This was investigated in the House Martin (see Section 4.11.1).

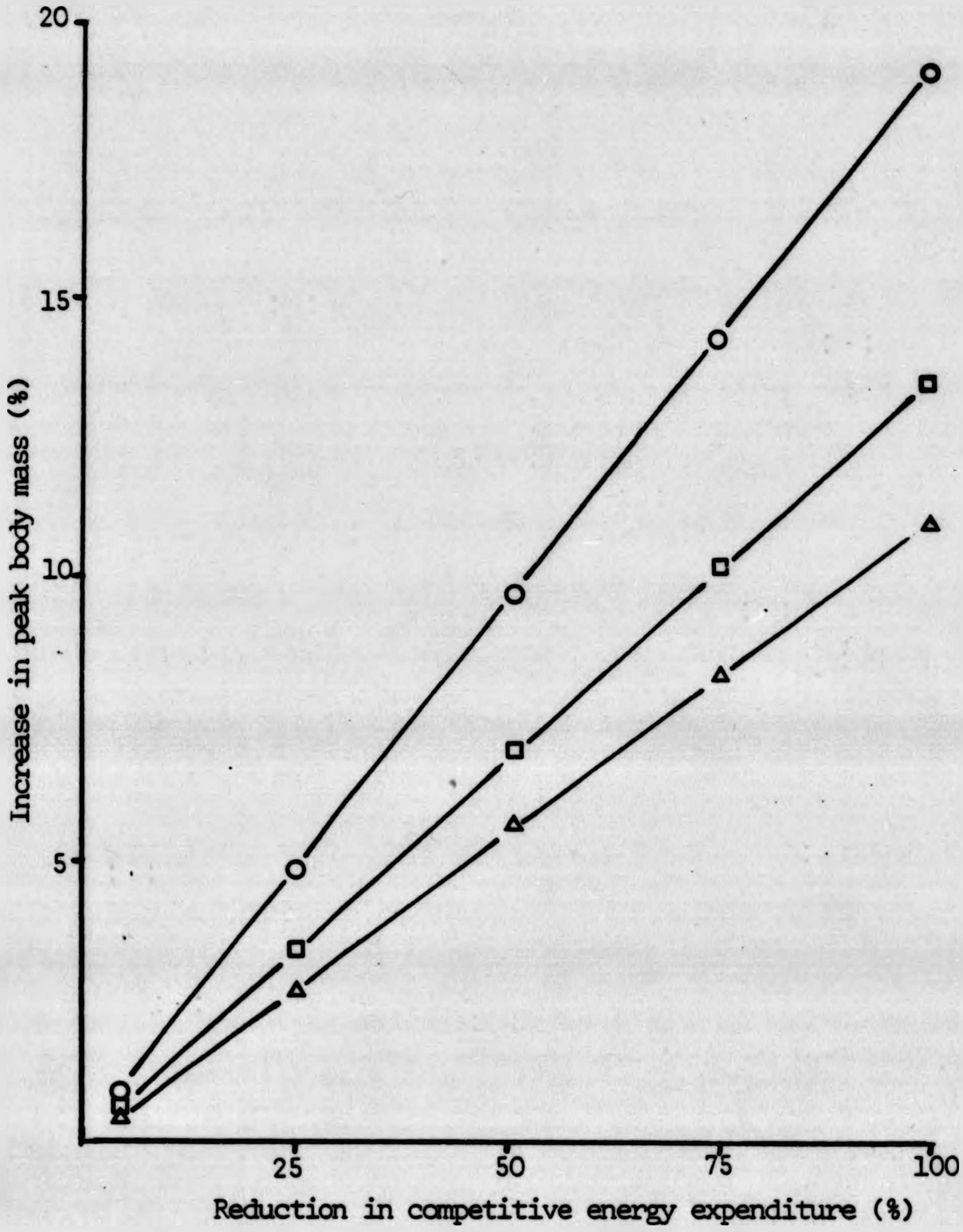


Figure 2.11

Percentage increase in peak body mass obtained by converting energy saving from reduced sibling-sibling competition, into growth as (○) 100% Protein, (□) 75% fat:25% protein, (△) 100% fat respectively (see text for explanation).

2.4 THE COST OF MAINTAINING BROOD HOMEOTHERMY

2.4.1 Nestling Cooling Rates

(a) The rate of heat loss (H) of adult birds is usually approximated satisfactorily by the following linear equation (Scholander et al., 1950);

$$H = h(T_b - T_a)$$

where h is the heat transfer coefficient and usually expressed as calories per gram-hour-degree Celsius. h is also sometimes called the 'thermal conductance', but actually includes radiative and convective heat losses as well as conductive ones (Calder & King, 1974). Herreid and Kessel (1967) determined heat transfer coefficients from the cooling curves of thirteen species of bird carcasses, with and without plumage and produced the following two equations (Figure 2.12a);

$$h = 4.57\ w^{-0.52} \text{ with feathers} \qquad \text{eqn. 2.14}$$

$$h = 7.24\ w^{-0.44} \text{ without feathers} \qquad \text{eqn. 2.15}$$

(b) Predicted nestling heat transfer coefficient (h_c)

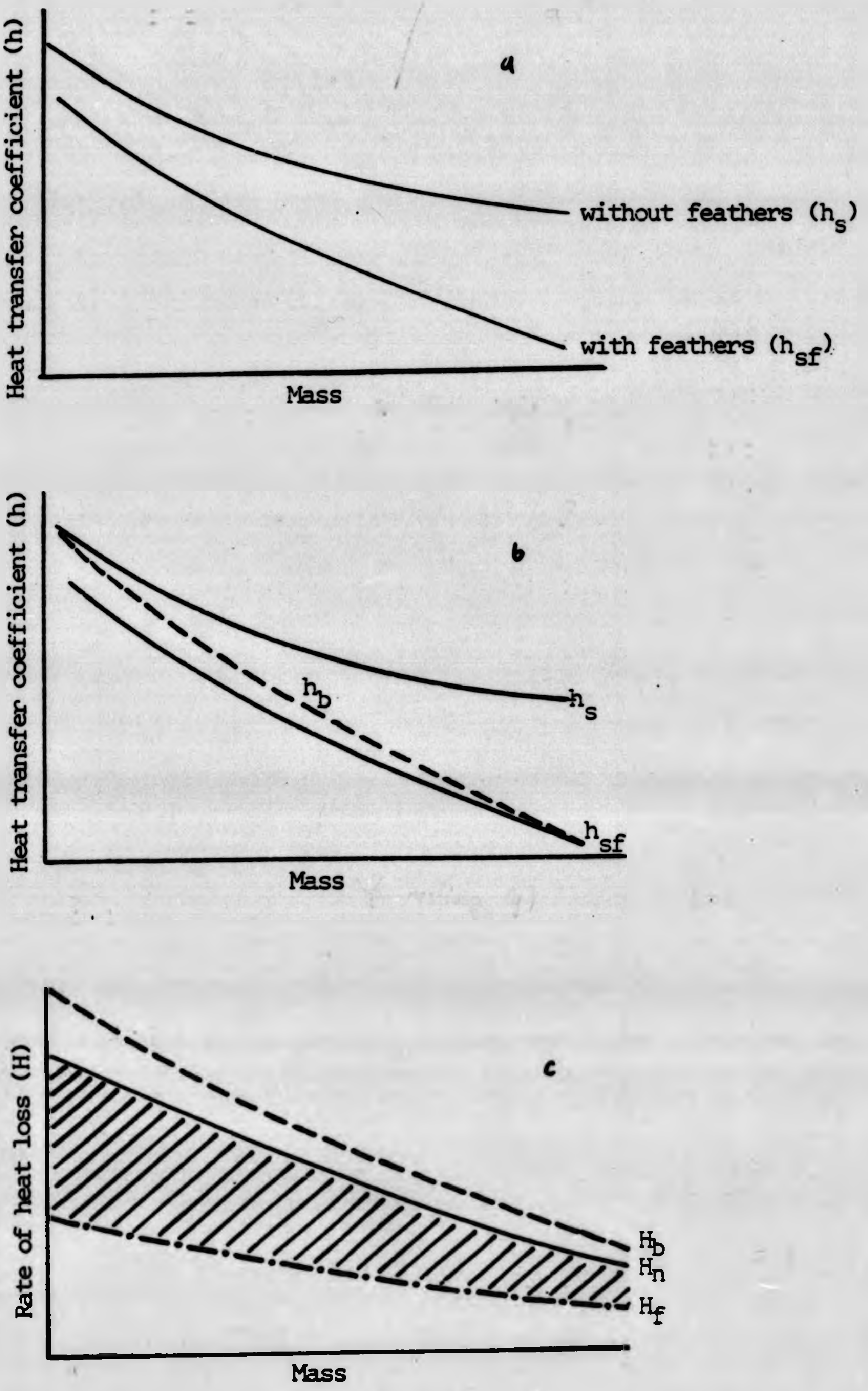
Smaller nestlings might be expected to have heat transfer coefficients nearer the second equation and older nestlings towards the first equation once feather growth occurs. This change between the two adult curves is illustrated by the pecked line in Figure 2.12b, and may be called the heat transfer coefficient of a nestling (h_c) or brood (h_b) if the brood behaves as a single mass (see Section 2.41(c)).

Figure 2.12

(a) Heat transfer coefficients for adult birds with (h_{sf}) and without feathers (h_s) (Herreid & Kessel, 1967).

(b) Heat transfer coefficient suggested for nestlings, h_b (see text).

(c) The rate of heat loss for a poikilothermic brood in the laboratory (H_b), in a nest in the wild (H_n) and a partially homeothermic brood in a nest in the wild (H_f). The hatched area represents the cost of nestling thermoregulation.


a
Heat transfer coefficient (h)
without feathers (h_s)
with feathers (h_{sf})
Mass
b
Heat transfer coefficient (h)
h_b
h_s
h_{sf}
Mass
c
Rate of heat loss (H)
H_b
H_n
H_f
Mass

(c) The 'field' heat transfer coefficient (h_f) and the 'field rate of heat loss' (H_f)

The ability of nestlings to raise their own metabolism at temperatures below their lower critical temperature varies as a function of age (Dawson et al., 1976; Dunn, 1976; Dyer, 1968; Gotie & Kroll, 1973) and causes under-estimates of true heat transfer coefficients (Ricklefs, 1974).

The apparent heat transfer coefficient of nestlings (not corrected for metabolism, Bartholomew & Tucker, 1963), may be used as an index of nestling thermoregulatory capacity under field conditions. This is referred to below as the field heat transfer coefficient, h_f. It is a combination of the influence of nest insulation (see below, Figure 2.12c) and a nestling's ability to thermoregulate (Figures 2.12a and b). A predicted reduction in hf for nestlings is further modified by brood size. Dunn (1976c,1979) demonstrated that the age of effective homeothermy decreased with increasing brood-size in the Tree Swallow <u>Iridoprocne bicolor</u>, and the House Wren <u>Troglodytes anedon</u>, although she was unable to calculate hf from her data, since body temperature was expressed as the percentage of adult body temperature (% adult thermoregulation) and T_a was variable. Mertens (1969) demonstrated that the earlier onset of homeothermy in large broods of Great Tits <u>Parus major</u> was a result of the reduced surface area/mass ratio of the brood and was described by the following equation:

$$m = 0.0732\ w^{0.672} \qquad \text{eqn. 2.16}$$

where m = brood metabolic rate (Watts) and w is brood mass in grams. This led him to later model heat loss in Great Tit broods and calculate the 'heat transfer coefficient' h_n (including convective and radiative heat loss) for broods in a nest box as:

$$h_n = 0.0719\, w_b^{0.613} \qquad \text{eqn. 2.17}$$

where h_n is the heat transfer coefficient of a brood within the nest (see below) and w_b is brood mass in grams (Mertens, 1972). This demonstrates the importance of measuring heat loss under field conditions, since nest structure modifies the "ambient" environment and will affect h_f. Nest structure has been shown to be important in reducing heat loss in incubating birds (Skowron & Kern, 1980) and birds roosting in the nest compared with conspecifics roosting nearby (Walsberg & King, 1978). A number of studies have shown that the heat transfer coefficients of nests (2.78-12.35 $Wm^{-2}\ {}^{\circ}C^{-1}$) indicate that they are generally good insulators (Whitton & Berger, 1977; Walsberg & King, 1978; Skowron & Kern, 1980).

For a given set of ambient conditions (e.g. $T_b - T_a$ = constant) the rate of heat loss (H) is proportional to the heat transfer coefficient (h) (Calder & King, 1974), i.e.

$$H = h(T_b - T_a) \qquad \text{eqn. 2.18}$$

When $T_b - T_a$ is constant the field rate of heat loss (H_f) may be substituted for the field heat transfer coefficient (h_f). Figure 2.12c shows the rate of heat loss of a brood of nestlings within its nest measured within the laboratory (H_n), compared with that of a brood not enclosed within a nest (H_b) the latter being proportional to the brood heat transfer coefficient (h_b) (Section 2.4.1b, Figure 2.12b). H_f is equal to H_n (for a given brood mass) in unfeathered nestlings, but declines with age, as nestlings contribute more and more to their thermoregulatory requirements (Figure 2.12c), until $H_f = 0$, when nestlings are fully homeothermic. This implies that the field heat transfer coefficient is also 0, but the true heat transfer coefficient is not.

The nest structure of the Dipper usually consists of a large moss ball with an inner nest cup of grass lined with dry leaves (see plates) and can be expected to have a marked effect on h_f. Mertens (1977b) measured the heat transfer coefficient of the nest material (primarily moss) in Great Tits' nests in relation to the relative proportions of water and air in the nest material, and found that the conductance increased by up to 13.6% when the volume water fraction of the nest (ϕ_w) was doubled. A number of points emerge from this discussion of heat loss. The first is that laboratory measurements of heat transfer coefficients are inadequate in trying to produce generalised predictive models of heat loss in field conditions. Detailed knowledge of a particular species and its nest environment can lead to workable (though very complex) predictive models (Mertens, 1972,1977a,b) applicable to that particular species and under specified conditions. Laboratory measurements of heat loss for nestlings, within nests in the presence of siblings, and under realistic 'ambient' temperature conditions may improve estimates of h_f and H_f. Nestlings may behave differently under laboratory conditions with respect to heat loss (see Section 4.4.2), and nests often dry out. For example, Dipper nest domes are often moist in the field whereas the use of old nests in metabolism studies (Section 4.4) means that the physical properties of the nest structure differ from field conditions.

(d) Factors affecting h_f and H_f

Whilst it is often difficult to model heat loss of growing nestlings in the field, a number of factors may be identified which will be expected to affect H_f of individual nestlings. They are (1) nestling age, (2) brood mass, (3) nestling mass (since nestlings may not huddle all of the time), (4) brood-size; important with respect to its effect on brood mass but also since it will affect (5) position within the brood, nestlings in the middle of a huddle will expose less of their surface area than nestlings at the edge of a huddle, (6) T_b, nestling body temperature, which will vary with age (Gotie & Kroll, 1977; Mertens, 1977), (7) T_a, ambient temperature outside nest, (8) T_n, temperature within nest (see Section 3.3.3) this will be dependent on T_b and T_a as well as parental heat input to the brood and nest and also (9) nest insulation, which will affect the equilibrium nest temperature, and hence the temperature gradient to which the nestlings are exposed.

The heat transfer coefficient (h_f) can be calculated from the cooling rates of nestlings measured under field conditions and compared with theoretical predictions based on the simple equations introduced earlier.

The calculation of h_f from field data allows one to examine the ontogeny of thermoregulation of wild nestlings and calculate the costs of brooding the young by the parent bird.

2.4.2 Brooding costs

A model of brooding costs for female Dippers (single sex brooders) is presented below and is modified from Kend$\overset{ei}{\text{ie}}$gh's (1963) model of incubation costs. The equation allows for the contribution of the brood to overall brood thermoregulatory costs by measuring field cooling rate which is expected to decrease as nestlings get older, due to their own partial homeothermy (Chapter 5).

(a) An equation for calculating brooding cost

$$B_c = w_b \times S \times r \times (T_b - T_n) \times i \times (1-ca)/1000 \times K \qquad \text{eqn. 2.19}$$

where B_c = Brooding costs (Watts)

w_b = Mass of brood (g)

S = Specific heat of nestlings ($\mathrm{cal.g^{-1}.°C^{-1}}$)

r = Cooling rate ($\mathrm{°C°C^{-1}.h^{-1}}$)

T_b = Nestling body temperature (°C)

T_n = Nest air temperature (°C)

i = Interval (h)

c = Proportion of brood surface covered by brooding bird assumed constant at 20% though it will actually decrease somewhat as nestlings grow

a = Proportion of time bird spends brooding

K = A constant, transforming $\mathrm{Kcals.day^{-1}}$ to Watts.

All of these variables were measured with the exception of S, the specific heat of nestlings. This is dealt with below. Brood costs were calculated for the Dipper and are discussed in Section 4.4.7.

(b) The specific heat of nestling birds

The specific heat of nestlings was calculated for the Dipper assuming a specific heat of water of 1.0, and a specific heat of dry animal tissue of 0.4 cal.g^{-1} °C (Klieber, 1961). The percentage water content of Dipper nestlings with age was measured (see Section 4.2.1) and S calculated as;

$$\frac{(\text{Percent water} \times \text{Wet mass}) + (\text{Percent dry mass} \times \text{Wet mass} \times 0.4)}{\text{Wet mass}} \qquad \text{eqn. 2.20}$$

and expressed as cal.g^{-1}.°C^{-1} (see Section 4.4.6).

2.4.3 Models of Parental Inattentiveness

(a) The likely failure of the "net energy gain" model to explain observed inattentiveness in incubating birds

During the early stage of nestling rearing, female Dippers brood the nestlings whilst males provide food for the growing young. The female leaves for short periods in order to feed, even on the day of hatch (pers.obs.) even though males may feed the female in the nest during the first few days of the nestling rearing period (pers.obs., and D. M. Bryant, pers.comm.). Females therefore must make decisions similar to those made by incubating birds, between keeping the brood warm and self feeding (Jones, 1985). Data on changing attentiveness by brooding birds are scarce though a pattern of progressive reduction in brooding as young become homeothermic has been demonstrated in the European Starling (*Sturnus vulgaris*, Clark, 1984 , Red-backed Shrike, Diehl & Myreha, 1973; House Sparrow, Seel, 1966; Willow Warbler, Tiainen, 1983; Pied Flycatcher, Winkel & Berndt, 1972), and reductions in brooding with increasing nestling age have been measured in some species (Johnson & Best, 1982; Wittenberger, 1982). The approximate causes of reduced brooding with increased nestling age have not been identified, although Clark (1984) has shown that decisions are based upon thermoregulatory considerations rather than brood feeding requirements *per se*. Jones (1985) constructed a model of optimal inattentiveness for incubating female swallows (*Hirundo rustica*) based upon maximization of net energy gain through foraging, once the cost of reheating the cooled clutch had been taken into account. He found that the modal inattentiveness periods of Swallows were shorter than those predicted by the optimality model, and suggested that an additional constraint of reduced embryonic development or increased mortality below a temperature threshold may have forced females to return earlier to reheat the clutch, even though net energy gains would be increased by remaining away. This would also explain why birds do not have a single inattentive period each day (the theoretical optimal strategy considering the decelerating shape of egg cooling curves) which was not explained by the net foraging gain model.

(b) The 'minimal temperature' model

A model of temperature threshold restrictions on parental inattentiveness is presented in Figure 2.13. Line A represents the cooling curve of a nestling with a high cooling rate. The horizontal temperature threshold is crossed at time t_a, whilst in curve B the temperature threshold is crossed at time t_b, where $t_a < t_b$. Factors likely to cause cooling rates to approach curve A are young age, small brood-size and low ambient temperatures; whilst curve B would tend to occur with higher ambient temperatures, bigger brood-sizes and older nestlings. The temperature threshold line may represent the line below which growth is slowed significantly, thereby extending the developmental period and exposing the young to increased risks of predation (Koskimies, 1948). Conversely it may represent the temperature below which irreversible hypothermia occurs leading to death of the nestlings.

Although the temperature threshold is not known, a number of predictions may be made regarding cooling rates measured in the field, if such a model is operating.

(i) Minimal nestling body temperature should be independent of length of inattentive period;

(ii) The variation in minimal body temperature should be small, since parents should stay away as long as possible in order to maximise net energy gain (Jones, 1985);

(iii) Parental inattentiveness should be positively correlated with nestling age, brood-size and with ambient temperature. This model is discussed with respect to the Dipper in Section 4.4.5.

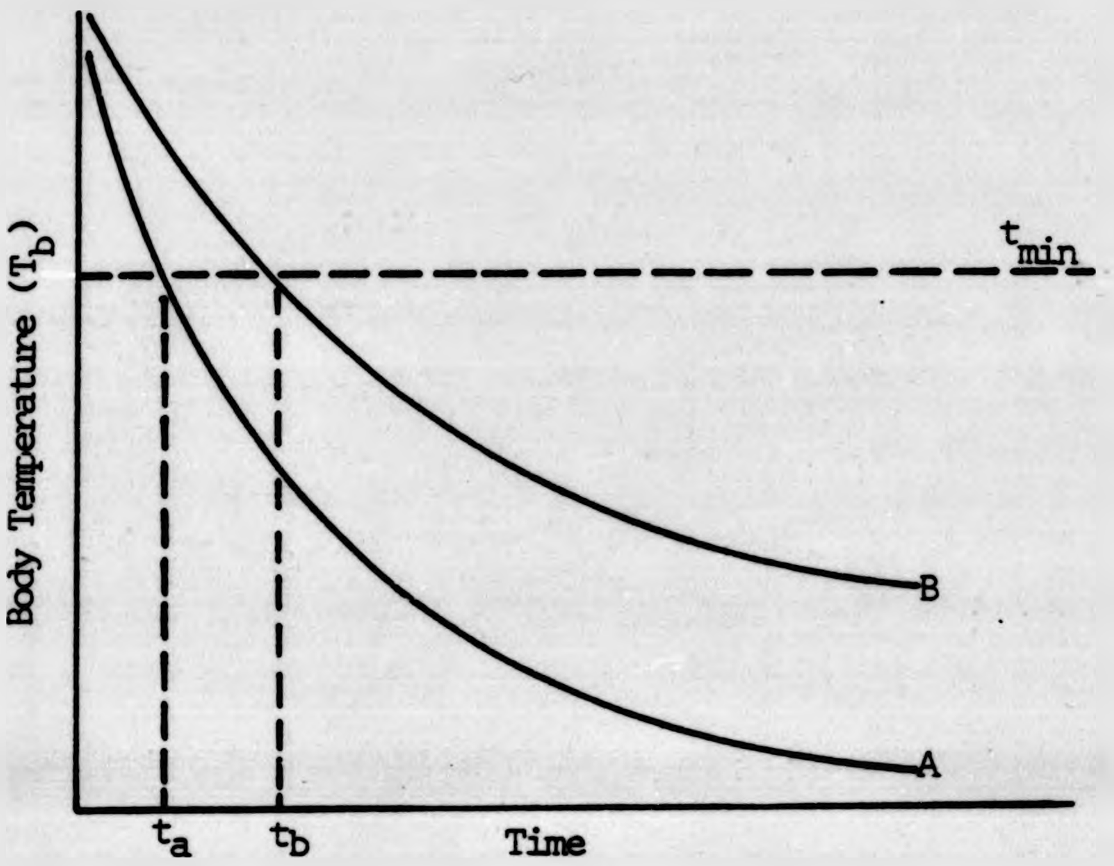


Figure 2.13

Model of maximum inattentive periods (t_a,t_b) for broods with high cooling rates (A) and low cooling rates (B).
t_{min} is the temperature threshold below which nestlings are not allowed to cool (see text).

(c) The 'maximal brooding time' model

An alternative model may also explain why parent birds return to their young earlier than predicted from the net energy gain consideration discussed previously. This model is similar to that of Jones (1985) but incorporates an additional cost which operates to reduce the time spent away by the female. It is based on the fact that brooding costs are composed of two separate costs, one borne directly by the female and the second, the most costly, borne indirectly. Figure 2.14a shows the cooling curve of a poikilothermic nestling (or brood). The horizontal line represents the normal nestling body temperature. The hatched area between the two curves is thus directly proportional to the cost of reheating the nestling when the parent returns. As nestlings get older and begin to thermoregulate they resist cooling by metabolic heat production (Figure 2.14b) and hence their cooling curves are shallower. The cost of brooding to the female is thus progressively reduced (the area between curves and horizontal line, Figure 2.14c), as nestlings get older, until they become fully homeothermic at which time the full cost of maintaining body temperature is borne by the nestling.

Whilst it costs the same amount of heat energy to maintain a brood at a given body temperature (whether this heat is produced by the brood or the brooding adult) there is an additional cost when this is produced by the brood.

Figure 2.15a shows the theoretical costs involved in delivering the energy for thermoregulation. A parent will

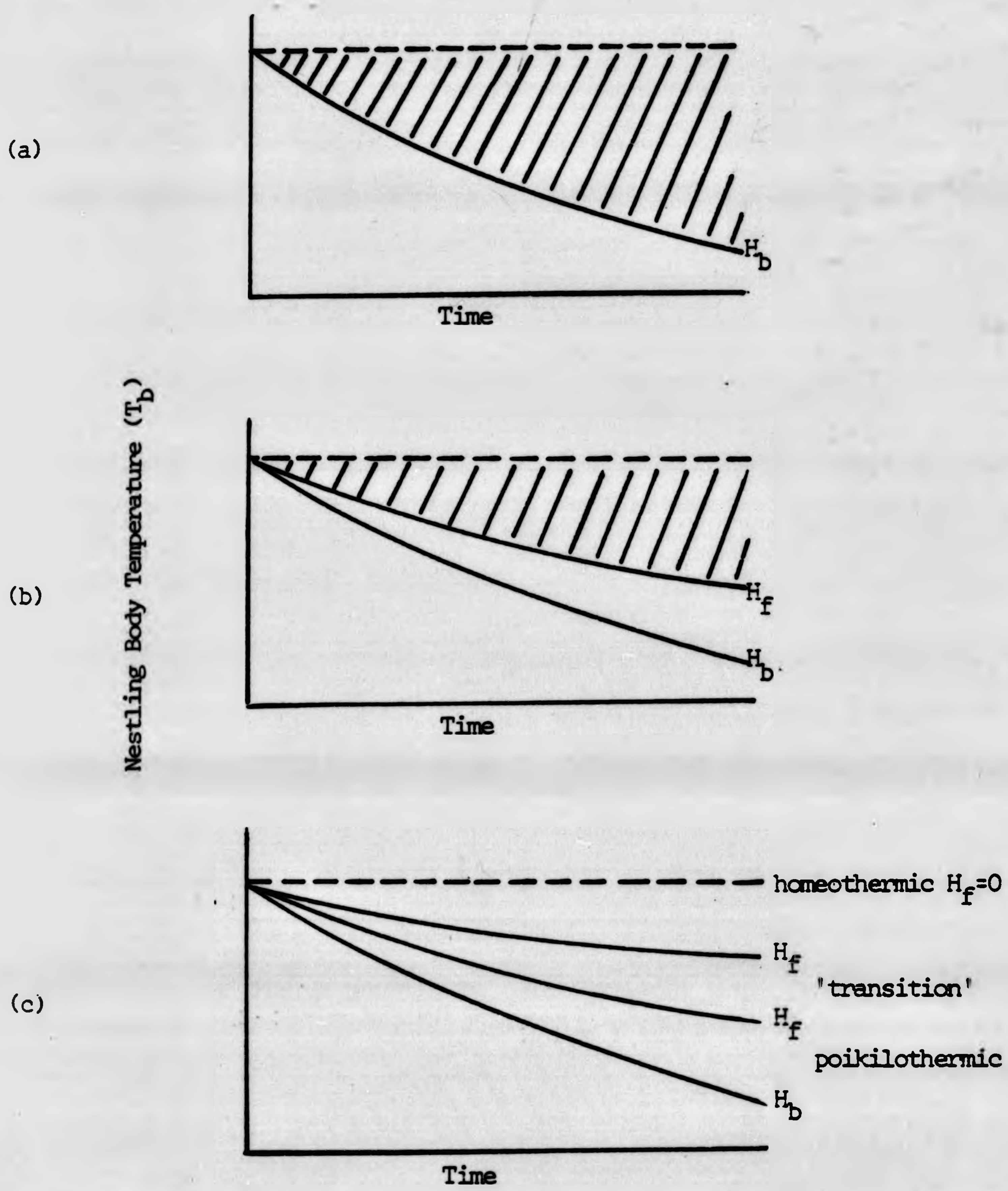


Figure 2.14

(a) Cooling curve of poikilothermic nestling/brood (H_b).

(b) Cooling curves of poikilothermic and partially homeothermic nestlings/brood (H_b and H_f respectively). Hatched areas represent the cost of reheating the brood (i.e. brooding cost).

(c) Change in cooling curves with age (see text).

bear a foraging cost (searching for and catching prey) and a travel cost (to and from the nest) during brooding. In order to collect and deliver a given amount of food energy to the brood requires making several trips to and from the nest. It is less costly for the female to brood the young herself than incur the additional travel costs necessary for provisioning of the brood in order that they may thermoregulate themselves.

Figure 2.15b shows the combined cost of foraging/travelling and maintaining brood temperature at near adult body temperature, assuming in this case that nestlings and parents contribute equally to brood thermoregulation costs (e.g. Figure 2.15(b)). It would therefore benefit the parent to reduce the amount of time that the young try to thermoregulate to a minimum or equally maximize the time spent brooding. There is another consideration which will force the parent to adjust its brooding level, and that is the energy demand of the growing brood. Most altricial species share in the feeding of their young, at least in the later part of the nestling period, and it seems unlikely that in the Dipper a single parent could adequately provide for the brood.

The 'maximal brooding model' predicts that
(i) the length of inattentive period should be affected by the same factors as for the minimal T_b model, but without any constraint on the minimal T_b experienced by nestlings,
(ii) minimal T_b should therefore be negatively correlated with the length of the inattentive period. The predictions of this model and the 'minimal temperature model' are compared with data from the field measurements of nestling cooling rate (Section 4.4.3) and discussed in Chapter 5.4.2

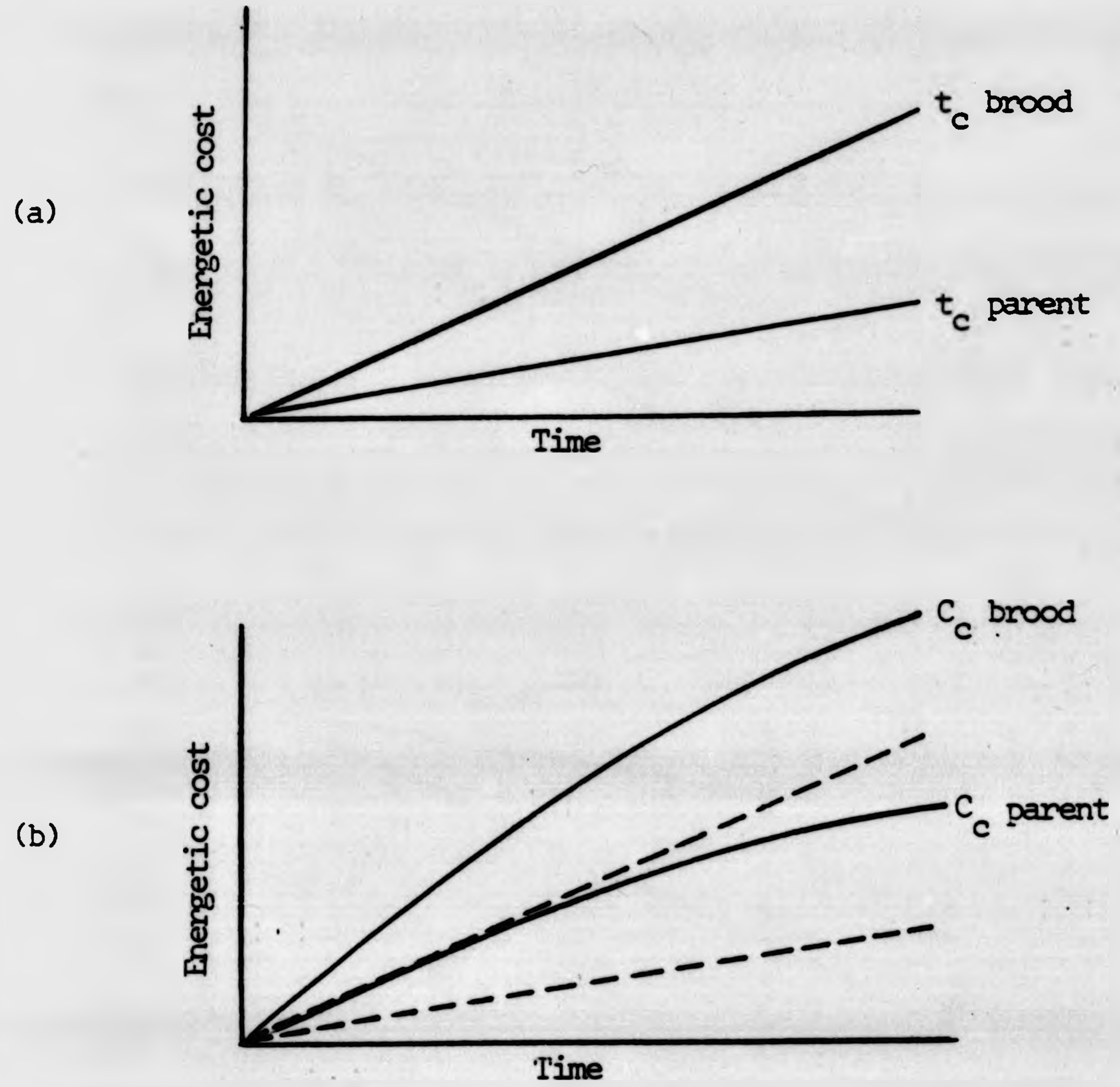


Figure 2.15

(a) Parental foraging costs to supply thermoregulatory energy requirement of the brood (t_c brood) and when brooding the young only (t_c parent).

(b) The cost of parental (brooding) component of nestling thermoregulation (C_c parent) and the nestling (self-heat) component of nestling thermoregulation (C_c brood); based on equal heat input by parent and brood (Figure 2.14b).

CHAPTER THREE

MATERIALS AND METHODS

PART ONE: THE NESTLING ENERGY BUDGET

3.1 GROWTH

3.1.1 Body Measurements of nestling House Martins and Dippers

Growth data were collected daily or every two days for the Dipper and House Martin nestlings. Body measurements for the House Martin were as follows: wing-length (maximum chord, mm), mass (to the nearest 0.1g) and tarsus (to the nearest 0.1mm) following Svensson (1975). Growth curves for individual nestlings were constructed to compare peak masses (Section 4.11.1). It was not possible to fit growth curves to individual nestling growth data as the daily change in body mass was often erratic (Section 4.11.2). Growth curves for the House Martin are therefore presented as the original data. All measurements on the House Martin were made between 1400-1700 hours.

Measurements on the Dipper were confined where possible to the morning hours and the following measurements were recorded: wing-length, mass, tarsus (as above), body-length; measured from the vent to tip of bill with neck gently extended to full stretch, bill-length; measured from the posterior edge of the fleshy gape to the tip of the bill, and thus differs from the typical measure of bill-length (Svensson, 1975); and gape-width; measured as the maximum width of the mouth from the edges of the fleshy gape. Mass was measured to the nearest 0.1 grams, wing-length and body-length to the nearest millimetre and tarsus, bill-length and gape width to the nearest 0.1 millimetre. Growth curves were fitted through these data (Section 4.1) using Ricklefs (1967a) graphical method, using the logistic model which fitted the data better than the Gompertz or von Berttalanffy curves. The Richards curve was not tested on these data (Richard, 1959). Dipper nestlings were aged to the nearest 0.5 day and from this sample a regression of wing-length on age (Section 4.1.1) was calculated for ageing young of unknown age.

3.1.2 Sexing Dipper Nestlings

Dipper nestlings were ringed and colour marked so that those recaptured postfledging might be sexed. Adult Dippers are sexually size-dimorphic and sexes may be separated on the basis of wing length and body mass (Anderson & Wester, 1971; Galbraith & Broadley, 1980). Since Dipper nestlings may disperse to other river systems (S. Newton pers.comm.) some recapture data was collected outwith the study area, and some adults recaptured in the study area were from nests on different river systems and therefore lacked the full set of body measurements as nestlings (Section 4.1.4). Further nestlings were sexed directly during carcass analysis (Section 4.2). Discriminant analysis was performed on nestling growth data for which the sex of nestlings had been subsequently established by one of the above methods (Section 4.1.4). Discriminant analysis is a method of combining several growth measurements to produce a single coefficient (the unstandardized canonical function coefficient) that will allow the discrimination of two populations (Sokal & Rohlf, 1969). This has been used with some success on adult birds (Anderson, 1975;

Dunnet & Anderson, 1961; Green, 1982) but has yet to be applied to nestlings. Using the above coefficient 'unknown' nestlings were retrospectively sexed, and the growth curves for males and females are presented in Section 4.1.5.

3.1.3 The energetics of Dipper nestling growth

A sample of Dipper nestlings at various ages was taken under licence from the Nature Conservancy Council and sacrificed for carcass analysis. Eighteen birds were taken and these were supplemented by six birds which had died naturally (five deserted, one predated) making a total of twenty-four nestlings. Nestlings were weighed, measured and then killed by chloroform inhalation. Carcasses were frozen and later thawed for dissection into components. Once thawed nestlings were reweighed and dissected into: head, neck, gizzard and oesophagus, wings, legs, skin and body feathers, body shell, pectoral muscle, liver, kidney, heart, lung, intestine (empty), gut contents, primaries and secondaries, and tail feathers. Carcasses were then freeze dried for ten days, weighed to the nearest 0.0001g and lipids extracted for five days. The solvent was five parts diethyl ether:one part chloroform and refluxed in a soxhiet apparatus. The carcasses were then freeze dried for a further week and lipid free mass (Lean Dry Mass) measured. Total carcass analysis yielded the following data; Wet Mass (WM), Dry Mass (DM), percentage water or Water Content (WC), Lean Dry Mass (LDM), Lipid Mass (LM), Lipid Index (LM/LDM), Water Index (WC/LDM), Ash Mass (AM), Ash-free Lean Dry Mass (ALDM), Wet Energy Density (WED) and

Dry Energy Density, DED. The results are discussed in Section 4.2. A sample of carcasses was then reduced to ash in a muffle furnace at 500°C for twenty-four hours and ash free lean dry mass derived by difference. Energy density was then calculated by multiplying lipid mass and ash free lean dry mass, by the energy equivalents of lipid and protein respectively (see Section 4.2.6).

3.2 METABOLISM

3.2.1 The respirometry equipment

The respirometry equipment used is shown in Figure 3.1. It consisted of a metabolism chamber enclosed within a controlled temperature incubator, which could either be lit or left in the dark for overnight runs. Carbon dioxide was removed from incurrent air using carbasorb. Air leaving the respirometry chamber was dried with drierite and filtered before entering first the MSA Infrared gas analyser for monitoring carbon dioxide production, and then through a Beckman OM2 polarographic oxygen analyser. The analysers and chart output were zeroed using 100% nitrogen and spanned at 1% carbon dioxide and 21% oxygen respectively. The mean flow rate during experimental runs (Section 3.2.2) was 56 litres h^{-1}. Calibration was intermittently checked using 0.5% carbon dioxide.

3.2.2 Resting Metabolism of Dipper nestlings

The respirometer was used in three ways, firstly to monitor metabolic rate of nestlings during short-term experiments on the cost of activity (Section 3.4). Secondly, to

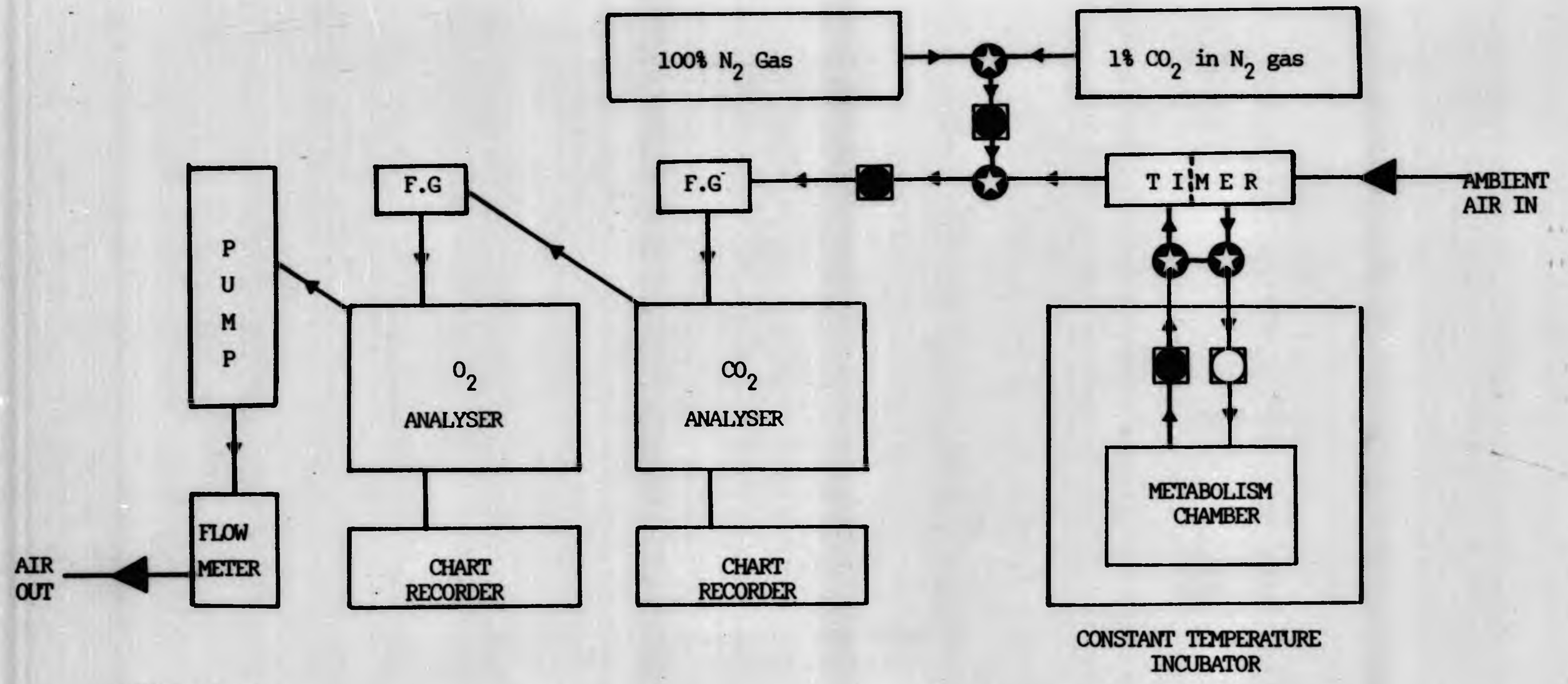


Figure 3.1

Diagram of the respirometry 'train' used for nestling metabolism measurements

✪ Three-way valves/stopcocks

→ Air flow

■ Drying agent

○ Carbasorb; removes CO_2

F.G. Flow gauge

measure the cost of huddling (Section 3.3.7) and, finally, it was used to measure overnight resting metabolism (overnight runs) in Dipper nestlings. The method for the latter is dealt with here.

An entire abandoned Dipper nest was placed in a large metabolism chamber. Homeothermic Dipper nestlings aged ≥ 12 days were brought to the laboratory just before dusk and placed in the nest within the chamber, having noted the mass of each nestling and the barometric pressure. For each of three broodsizes (1, 2 and 3) three replicates were performed at 5°C, 15°C and 25°C (see Section 4.3). Each overnight run was performed at just one temperature (± 0.5°C) and was divided into two hour sample periods interspersed with sampling of ambient air to check for zero and span drift. The first two hour period was not included in the calculation of mean night-time resting metabolism since nestlings were settling down during this period. Metabolism was higher during this period initially and then levelled off. Nestlings were returned to their own nest just after dawn the next morning having been reweighed. All results were then corrected to standard temperature and pressure and are discussed in Section 4.3.

In the metabolism measurements on single Zebra Finch and House Martin chicks a small (500ml) chamber was always used to replace the large (3500ml approximately) chamber used with the Dipper broods. All overnight runs were carried out in the dark.

3.3 THERMOREGULATION

3.3.1 The microprocessor system

Software is given in Appendix II, discussion here is confined to the function, use and limitations of the major components of the system. Figure 3.2 shows a stylized drawing of the components and where they would be situated in the field (see also Plate 3.1).

The main microprocessor (a) was housed in a wooden box about the size of a large car battery. This contained the two nickel-cadmium rechargeable batteries which provided power for ten hours continuous data collection. It also contained the microprocessor board (Eurocube), A- to D- converter, additional battery backed RAM and microphone interface. Microphone sensitivity was set from the main box by adjusting a knob until an L.E.D. went out, this meant that background noise, such as waterflow and nearby traffic would not trigger the microphone and give false readings. "Replay"/"record" mode was also controlled from the main box as was "Run Program" and "Recharge" modes. A metre long cable joined the main microprocessor to a separate waterproofed box which contained the thermistor interface (b) to which seven miniature bead thermistors (c) were connected on 30 centimetre leads. The thermistors were insulated and waterproofed using a silicon rubber compound so as to retain their flexibility. They were first calibrated in air against a mercury thermometer (± 0.5°C) and then more accurately against a quartz digital thermometer. The microprocessor was programmed to read all thermistors

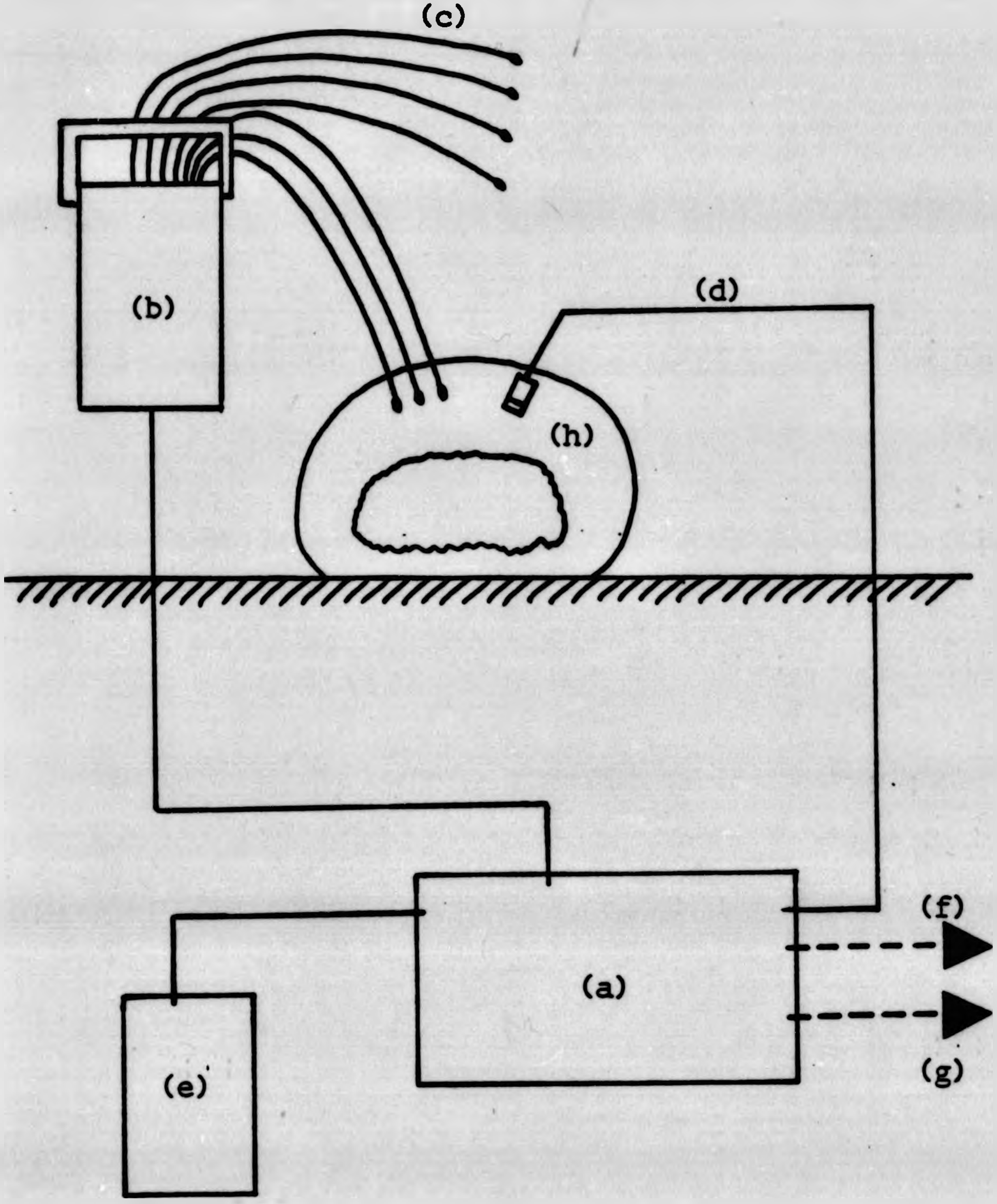


Figure 3.2

Diagram of microprocessor components at a Dipper nest
(see also plate31)

(a)	The microprocessor
(b)	Thermistor interface
(c)	Thermistor probes (1-7)
(d)	Condenser microphone
(e)	Remote switch box for logging parental visits
(f)	Output to VDU for laboratory work
(g)	Output to DEC VAX mainframe computer for data transfer

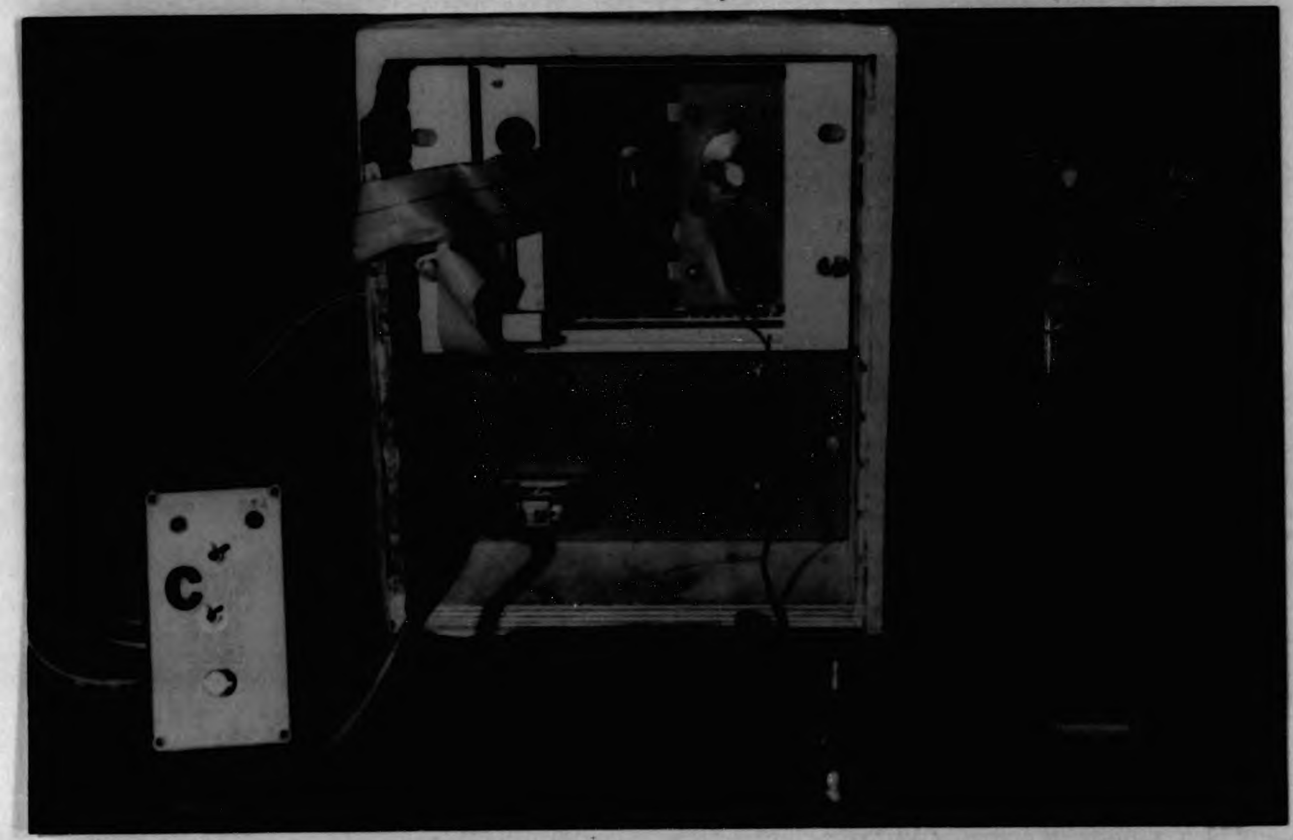


Plate 3.1:

Field portable microprocessor system used for measuring nestling cooling rates and begging behaviour.

A = Main microprocessor box

B = Thermistor interface with attached thermistors

C = Switch box to record parental arrival and departure, and to check microphone (Red LED) and micros memory (Green (LED)

D = Microphone

(a) every time a parent arrived or departed (see below);

(b) every time the nestlings begged, and

(c) every sixteen seconds during periods when the chicks were not being brooded and until the smallest nestling regained body temperature prior to parental departure.

Parental arrival and departure was observed and logged into the computer memory by throwing one of two switches on the switch box (e). This was connected to the microprocessor by a twenty metre cable. On/Off positions of each switch were converted to 'Male In'/'Male Out' and 'Female In'/'Female Out' data records, by the microprocessor and logged against the internal clock. The clock was set to zero automatically when the 'record' programme was activated and data collection commenced. All data collected was logged against time, providing accurate time budgeting at nests. Switch box (e) also had two L.E.D's - Red and Green. The red was programmed to come on each time chicks begged and acted as a check that the microphone (d) was working. The microphone was connected to box (a) by a thin three metre lead and acted as a simple sound switch. On/Off converted to 'BEG'/'NO BEG' signals for logging as previously. The green L.E.D. was programmed to come on when the memory of the microprocessor was full.

The main microprocessor (a) had two output lines. Line (f) could be connected to a V.D.U. for use in laboratory measurements and during calibration and also to a B.B.C. computer for development or modification of software. The software was stored in a PROM with 'Turnkey' facility which meant that the programme started when the system was 'powered up' without any need to prime the system from a keyboard with a 'RUN' command, before taking it into the field. Output line (g) provided a direct link with a DEC VAX mainframe computer for transfer of data from the microprocessors RAM to VAX data files, for detailed analysis. The system is hence fully portable but retains a great deal of flexibility with respect to reprogramming and linking to other pieces of laboratory equipment.

3.3.2 Field protocol

The microprocessor was used to record begging behaviour in the House Martin (Section 3.8.3) and nestling body temperature in the Dipper (see below). The Dipper nestling measurements required the full microprocessor 'package' to be set up at the nest (see also Section 3.8.3). In House Martins the software was modified to ignore thermistors and switch box (e) and to record only begging of nestlings (see below). This required the minimum of preparation. The main microprocessor box (a) stood below a House Martin nest and the microphone was inserted into the nest, either through a hole bored in the mud of the nest or through the lid of the nest box, where it was taped in place with masking tape. The microphone lead was then restrained to prevent it flapping in the wind.

It was not possible to place the main microprocessor box very far from the nest during work on the Dipper due to the short length of cable between (a) and (b). Prior to experimental measurements the birds were acclimatized to the equipment by gradually building up a dummy set around the nest. Initially this was done over a period of days but this was gradually reduced to three or four hours without detrimental effect. In some cases the main microprocessor box had to be raised several feet above the water, usually by building a stone cairn below the nest; but in most cases it was possible to stand the box (within its waterproof jacket) half in the river or burn, and half out so that it resembled a rock. Box (b) was usually draped with vegetation at open sites or left as it was (matt black) in a tunnel or under bridge sites. In all cases where parents were watched during the setting up of 'dummies' they returned to the nest without apparent hesitation, or concern for the change in their surroundings.

On the morning of the experiment the dummy equipment was replaced with the microprocessor system during the first inattentive period of the female. Thermistors were placed in and around the nest and attached to the nestlings (see below); the microphone was pushed into the moss of the nest roof so that it just penetrated into the nest space and the system switched on. The parent bird was allowed to return to brood or feed the young and the switch on box (e) triggered to make the start of the observations. Data previous to this was edited out of the file prior to analysis. In some cases the cable to switch box (e) was too short to allow its use and so in such cases observations of parental arrival and departure were noted and timed using the second hand of a watch that had previously been synchronized to the microprocessor's internal clock. These data were added to the file at the computer terminal.

3.3.3 Dipper nestling body temperature measurements

Body temperature measurements were logged on 6-7 day nestlings simultaneously with ambient temperature using the microprocessor and miniature bead thermistors. This was done to test the accuracy of skin temperature as an indicator of body (core) temperature, so breast, back, leg-pit (see Figure 3.3(a)), wing-pit and temperature was measured. This study showed that leg-pit temperature provided the best approximation to cloacal (body core) temperature. The regression is;

$$\text{Cloacal temperature} = -6.72 + 1.23 \text{ leg pit temperature}$$

$$r^2 = 53.8,\ n = 50,\ p < 0.001 \qquad \text{eqn. } 3.1$$

Hence leg-pit temperature lies below cloacal temperature by about one degree Celsius in the usual range of body temperatures shown by Dipper nestlings in the field. Cloacal temperature, whilst it perhaps provides the best approximation to core temperature (Calder & King, 1974), was found to be impractical to use, since the thermistors became dislodged. Leg-pit temperature was therefore chosen as the most suitable alternative; and hereafter when discussing body temperature it refers to leg-pit temperature.

Thermistors were attached by strapping them to the top of the left leg with a thin strip of sticking plaster, making sure that the head of the thermistor fitted snugly between the flap of skin between the leg and body, and the body itself (Figure 3.3(a-b)). Thermistor leads were long enough to allow movement within the nest (including defaecating out of it), and tangling of leads was never observed. At the end of

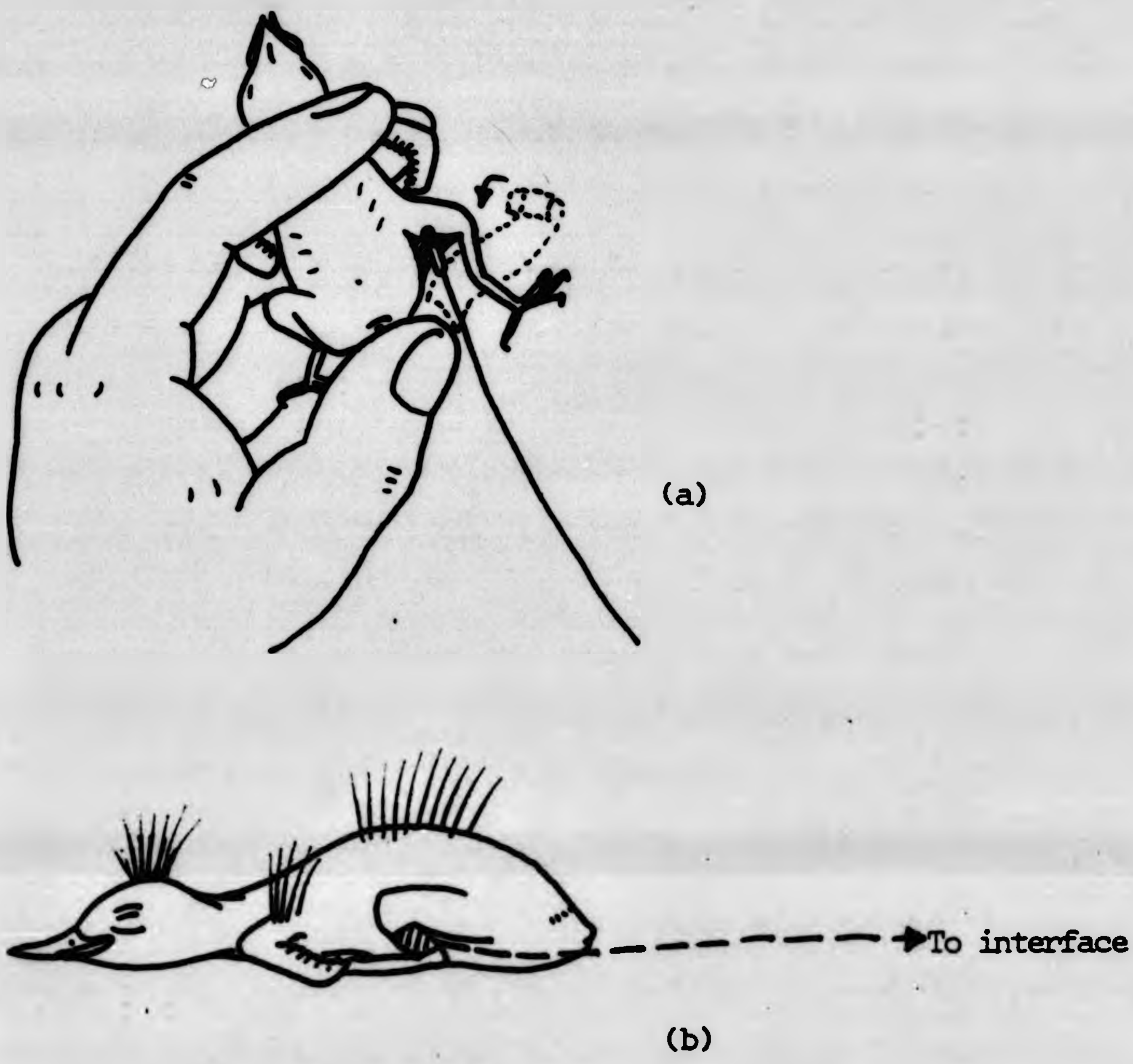


Figure 3.3

(a) Diagram showing attachment of thermistor in leg-pit.

▼ Flap of skin   Strip of sticking plaster

(b) Thermistor in place in a one week old Dipper nestling.

an experimental period it was sometimes found that a thermistor had become detached from the leg. Such events were immediately obvious on examination of the data as they were accompanied by a sudden drop in 'body' temperature of up to 10°C followed by a more gradual drop in nest temperature. This was confirmed independently in laboratory experiments (Section 3.3.4). Such data were excluded from further analysis.

Other abberant temperature readings were caused by movement of nestlings (e.g. defaecation) which temporarily resulted in partial exposure of the thermistor and subsequent reheating. Such changes usually occurred subsequent to arrival or departure of a parent, and might last for several minutes. Temperature changes were less than for total thermistor loss but too rapid to reflect true body temperature changes. It could be argued that nestling activity may produce rapid short-term increases in metabolism, and hence heat output. There is, however, no sound explanation to account for rapid short-term drops in body temperature. In such instances where it occurred therefore the data were noted but not included in calculation of cooling or reheating rates, which were measured over periods of temperature change consistent with the normal functioning of thermistor probes.

3.3.4 Cooling rates of Dipper nestlings in the laboratory

Many laboratory studies of nestling thermoregulation are carried out on single nestlings either out of the nest or occasionally within the nest (Dawson et al., 1976;

Dawson & Bennet, 1980; Dunn, 1976; Dyer, 1968; Gotie & Kroll, 1977). In this study of Dipper nestling thermoregulation, the cooling rate of nestlings in broods of three were examined in chicks of aged seven to eight days. Single nestlings were not investigated since this represents an infrequent brood size in the Dipper; no broods of one were found in this study. Broods were placed in uninsulated glass chambers, held at a constant temperature in a water bath to investigate the importance of the nest in insulating nestlings (Section 4.4.2). Thermistors were connected as above and cooling rates measured. It was not possible to measure cooling rates of nestlings out of the nest in the field, since thermistors were first threaded through the nest dome before attachment to the nestlings. By the time the thermistors had been removed and re-attached the nestlings would already have cooled considerably. Results are discussed in Section 4.4.2.

3.3.5 Cooling rates of Dipper nestlings in the field

All measurements were carried out between 0500-1200 hours. The equipment was set up as mentioned in Section 3.3.2 and some of the thermistors attached to nestlings (Section 3.3.3). The others were placed through the roof of the nest to monitor nest temperature, and outside the nest to monitor ambient temperature. The following data were collected; cooling rates, reheating rates, duration of attentive and inattentive periods. Results are presented in Section 4.4.3. Begging rate and duration as well as feeding rate and duration, was also automatically logged and is discussed in Section 4.10.

From previous observations at the nest, chicks were categorized, for the purpose of measurements, as young (3-5 days old, poikilothermic), transition (6-8 days old) and old (9-12 days old, homeothermic). Chicks of less than three days were too small for the attachment of thermistors. The categories were assigned to be realistic for all brood-sizes examined (i.e. brood-sizes three to five). All nests used for cooling rate analysis were of the typical moss dome type (see plates 3.2, 3.3). Additional time budget data was obtained from nests in which no equipment was present, these also included 'hole' and 'pipe' nests (see plates 3.4, 3.5). After the field data had been collected, nestlings were weighed and measured and the sticking plaster removed with scissors. Nestlings were returned to the nest and the equipment removed. If broods were used more than once for an experiment it involved different age categories and different individual nestlings were monitored.

3.3.6 A mate removal experiment and female inattentiveness in the Dipper

The possible trade off for female Dippers, between feeding and brooding one week old nestlings (i.e. transition) was investigated. Male Dippers were caught on the roost just before dawn and placed in a bird bag. The microprocessor equipment was set up as before and the behaviour of the nestlings logged. The data were then compared with nests where males were not removed. All treatments were carried out on brood size three. At the end of the experiment chicks were weighed and measured and returned to the nest. The male was

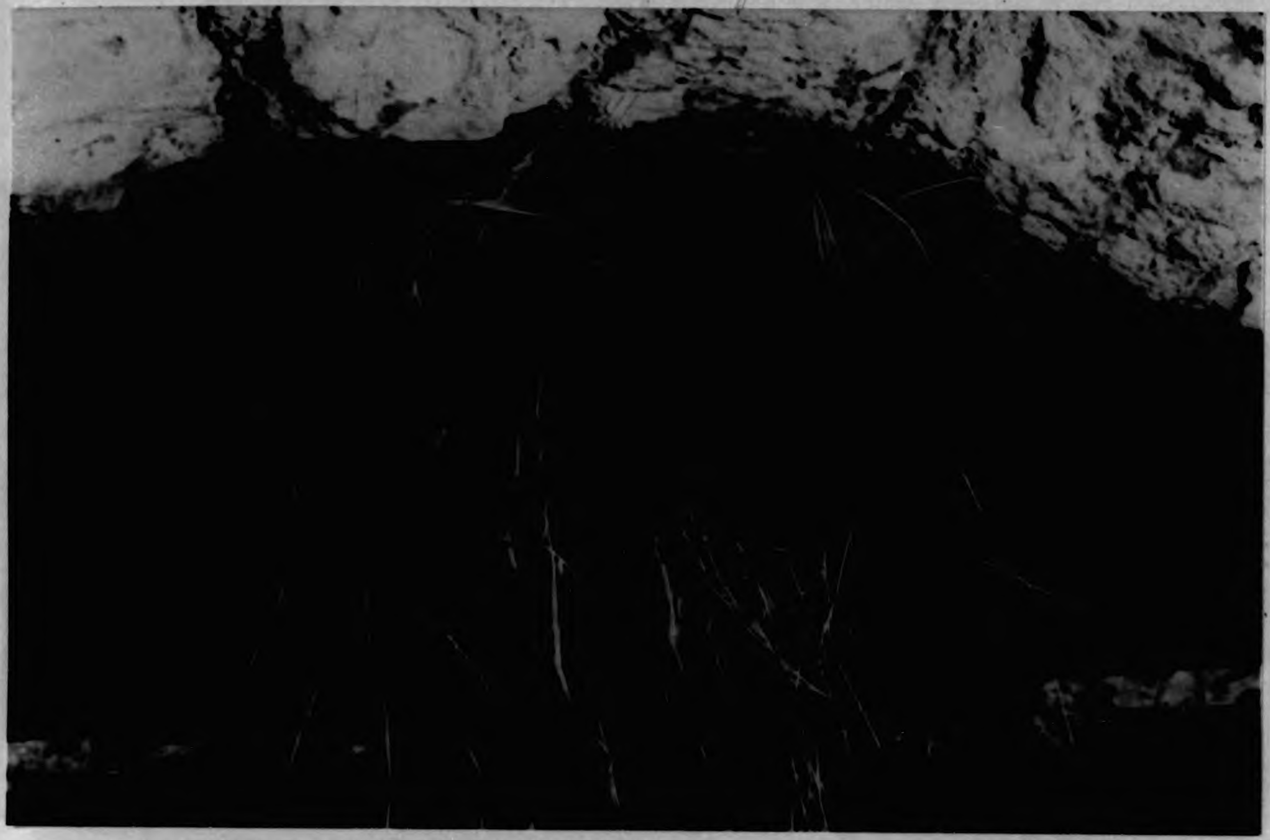


Plate 3.2:

Plate 3.3:

Natural Dipper nest, exposed moss 'ball' type.

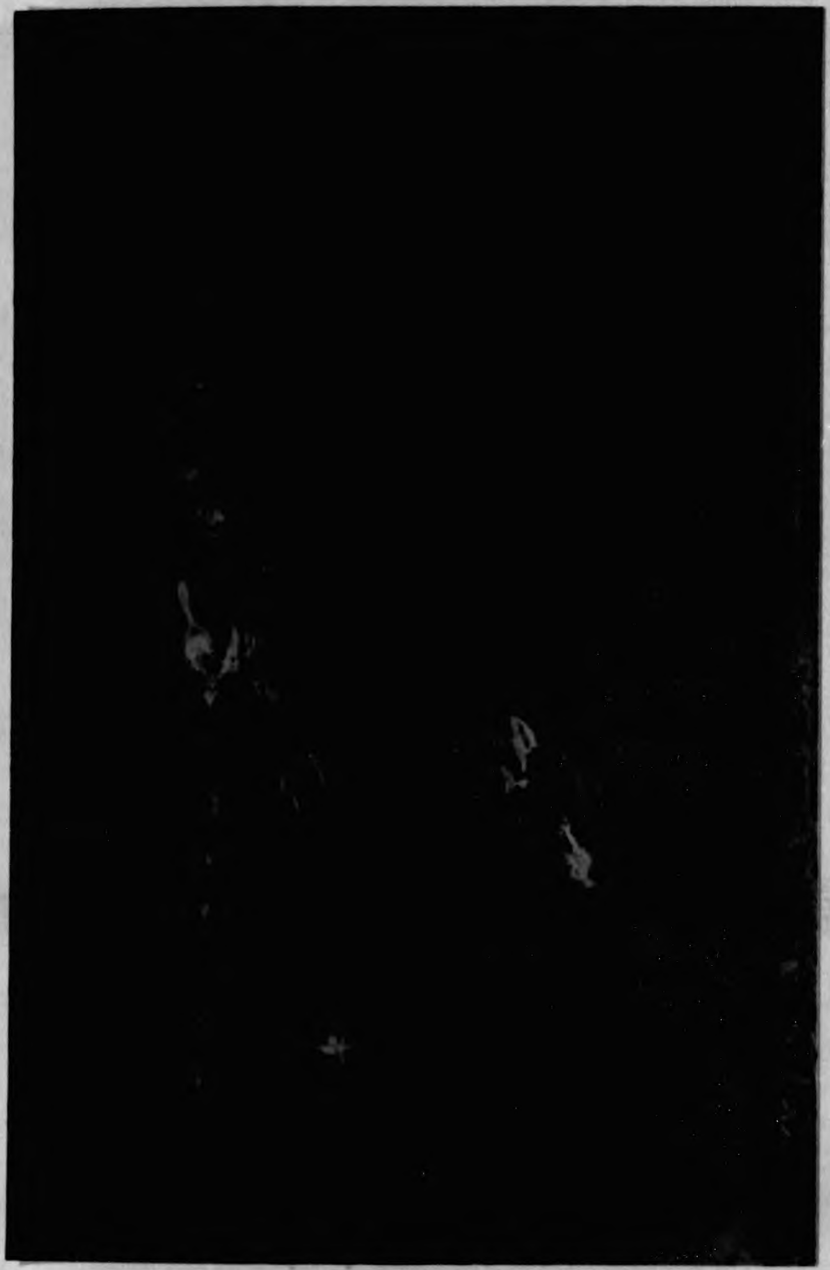


Plate 3.4:

Dipper pipe nest of the enclosed type.

Plate 3.5:

Site of pipe nest shown in Plate 3.4.

released and watched to confirm that he returned to the young. The results are presented in Section 4.4.5.

3.3.7. The use of heated dummy nestlings in examining the relative contribution of individual nestlings to brood homeothermy

This experiment consisted of three dummy nestlings, each of which contained a heating element and small thermostatic device so that temperature could be controlled from the main switch box (plate 3.6). The electrical part of each dummy was set in a resin which heated up uniformly to produce a warm block of known surface area.

Two of the dummy nestlings had a surface area of 16.95 cm^2 and the third was larger at 21.56 cm^2. Each dummy was set at a surface temperature 40°C to mimic a nestling. This was done by placing the dummy in the metabolism chamber prior to insertion of any chick and the dummy's temperature measured using a mercury thermometer strapped to it with rubber bands. The temperature control knob on the main box was locked and the dummy removed from the chamber. The metabolism chamber (Section 3.2.1) was then allowed to equilibrate with the temperature of the incubator, which was set between 2-5°C (see plate 3.6, Figure 3.4).

A nestling of known mass and age was then placed in the chamber and metabolism was monitored for 30 minutes without a dummy present. A heated 'dummy' was then placed alongside the nestling, so that it might benefit from the heat output. Metabolism was monitored for thirty minutes and then the dummy removed and metabolism monitored for a further thirty minutes.

Plate 3.6:

Heated 'dummy' nestlings (A) and control unit (B).

This experiment was repeated with another nestling and then finally the metabolism of the two nestlings together in the absence of the dummy was measured. Results are presented in Section 4.4.7.

3.4 ACTIVITY

3.4.1 A Doppler radar device for quantifying nestling activity

Figure 3.4 shows an X-band Doppler radar module (RS Doppler module 308-017) (a) that was used to detect movement of nestlings in metabolism chambers (c) or artificial nests. It detects Doppler shift in reflected microwave radiation by comparing microwaves emitted from a Gunn oscillator with those reflected from the target; in this case the nestling. The output was amplified and displayed as a digital output (d). The amount of movement generated by a nestling is linearly related to Doppler output i.e. number of Doppler units (D.U.) registered during a given time. The sensitivity could be adjusted but since this affects the number of D.U. registered it was kept set near maximum sensitivity for all measurements. Distance from the target, in this case the nestling, also affects the Doppler score (Figure 3.5). This was tested using a metronome set at 128 beats per minute, with the weight covered with aluminium foil to aid reflectivity. As the figure shows, the closer to the target, the higher the Doppler score.

In all experiments nestlings were placed the same distance (within five centimeters) of the Doppler head and prevented from moving further away by inserting a cardboard partition behind them. Since microwaves can pass through

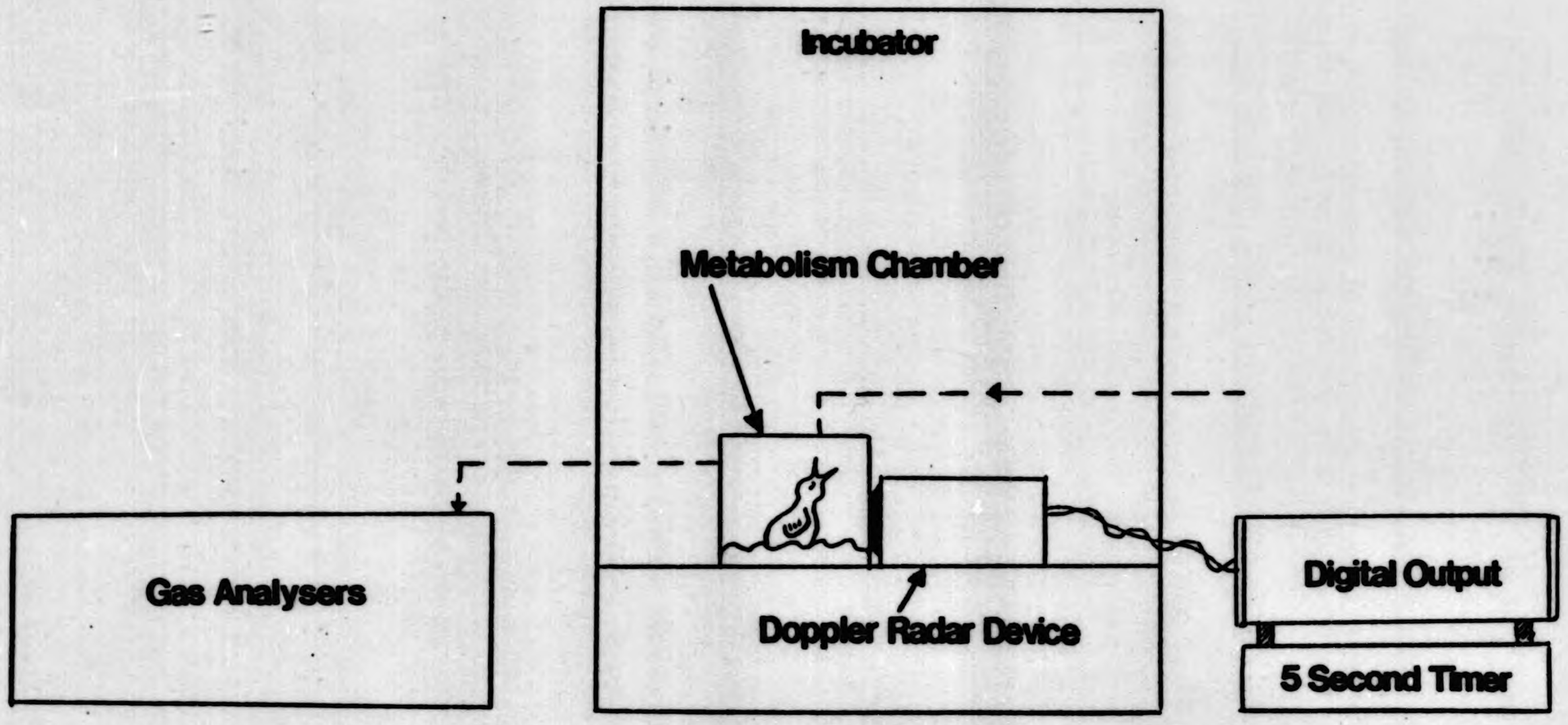


Figure 3.4: System for measuring energy expenditure during bouts of nestling activity (see text).

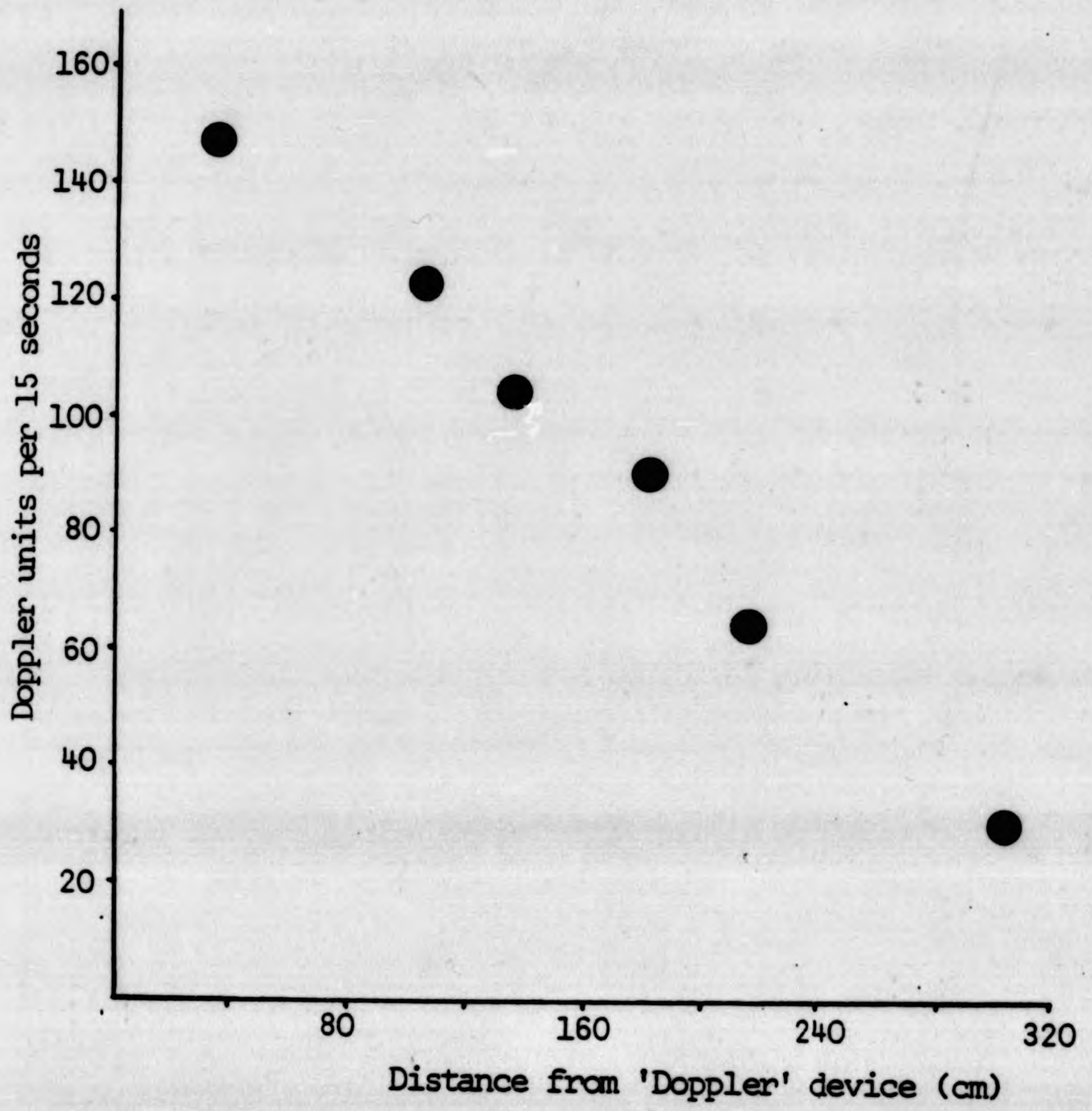


Figure 3.5

Number of Doppler activity units registered per 15 seconds as a function of distance between Doppler device and 'target'.

The regression equation is;

$$y = 163-0.425x$$

Target area = 7.52 cm^2

Metronome set at 128 beats min^{-1} (see text) objects, care was taken to ensure that there was no extraneous triggering of the device from other sources, including the observer. The Doppler was isolated from other pieces of electrical equipment by using a different 'bank' of plug sockets, since it was found that the thermostat cutting in and out on the incubator (f) caused the Doppler to trigger, giving higher scores than possible from chick movements alone. Since movement of the Doppler head itself will cause a reading it was clamped in position with a retort stand. The digital display box (d) also had a "freeze" button, which when pressed stopped the Doppler registering and displayed the current score. This was most useful since during intense activity it was often difficult to read the rapidly changing output. A reset button allowed for resetting the score to zero and a 'run' button allowed the device to register again.

3.4.2 The energetic equivalent of one activity (Doppler) unit

Individual House Martin and Zebra Finch nestlings were placed in a glass metabolism chamber which was connected via its exhalent part to the gas analysers (g) (see Section 3.2.1). The Doppler head was positioned so that it touched the chamber wall and was clamped in place. The chamber and Doppler head were kept within an incubator set at 24°C, whilst the digital display (d) remained outside. It was thus possible to measure metabolism and nestling activity (quantified using the Doppler score of movement) simultaneously. The metabolism data (carbon dioxide and oxygen levels) were recorded on a chart recorder, whilst the cumulative Doppler score was read every five seconds, prompted by a five second bleeper. Data were converted to kJ h^{-1} and DU h^{-1} for each five second interval, taking into account the lag in the system between the chamber and analysers (35 seconds at mean flow rate 56 (h^{-1})). The slope of the metabolism/Doppler unit regression yields the cost (kJ) of one Doppler unit (Figure 4.26).

Since metabolic rate remains high after activity until the oxygen debt incurred during that activity is repaid (Section 4.5.3) and activity may be either continuous or interrupted, the averaging of Doppler scores over periods in excess of five seconds may give more accurate results. Hence five second Doppler readings would only be expected to relate well to metabolism data (a) if activity occurred in discrete pulses, and (b) if these pulses (including repayment of oxygen debt) were less than or equal to five seconds. Patterns of activity varied considerably however between and amongst nestlings and so a computer programme was constructed to analyse the data in a stepwise fashion, until the best fit for a given set of data was found. This was achieved by progressively increasing, in five second steps, the period over which metabolism and Doppler scores were averaged (i.e. 5, 10, 15, 20 ... n seconds). The mean slope of the 'best fit' regression was then used to calculate energy costs (Section 4.5.3, 4.6.3, Chapter 5). The mean intercept represented metabolic rate at zero activity and is compared with predicted values in Section 4.5.

3.4.3 Measuring nestling activity costs in the laboratory

Nestling activity was quantified in captive Zebra Finch nestlings and in hand-reared 'wild' House Martin nestlings. The equipment was set up as previously except that the metabolism chamber was replaced with an artificial nest which consisted of an open-topped glass pot with a cotton wool 'nest cup'. Experiments were carried out on the laboratory bench top, or in the Zebra Finch controlled temperature room (mean 23.9 ± 0.12). Data collection was carried out as part of other experiments on begging behaviour in the Zebra Finch (Section 4.9) and assimilation efficiency in the House Martin (Section 3.6.2, 4.8.2). House Martin nestlings were also removed from the field and brought to the laboratory for calculating their energetic equivalents of Doppler units (previous section). These were also used to quantify nestling activities. Nestlings were stimulated to beg either by touching lightly (Zebra Finches, see below) or by offering food (House Martins), and the duration of the begging activity recorded by stop-watch or speaking into a tape recorder. At the same time the Doppler device was set running (after having removed the stimulus to the nestling, to prevent false Doppler readings) and stopped at the end of the activity. The result was expressed as D.U. sec^{-1}. The same procedure was followed for spontaneous behaviour such as moving about the nest, defaecating, scratching and feeding from an artificial bill (see Section 3.7.2). If nestlings appeared distraught or cold the test was abandoned.

In addition to measurements on single nestlings the total number of Doppler units registered by broods of four House Martins in their nest box was also recorded. (This is discussed in Sections 4.6 and 4.10).

Recovery times and their Doppler scores were measured in House Martins only (Section 4.5) and for the purpose of subsequent discussion it is assumed that recovery time as a proportion of activity time will not vary between the two species.

3.5 THE DAILY ENERGY BUDGET

3.5.1 The Time-Activity-Laboratory Method

Components of the Dipper nestling energy budget (Section 4.6) were measured in the laboratory and applied to time budget data collected in the field. The energetics of nestling growth were measured directly via carcass analysis (Section 4.2). Thermoregulatory costs were calculated from laboratory data (Section 4.3) and field data (Section 4.4). Activity costs were measured in the House Martin and Zebra Finch (Section 4.5) and applied to time-budget data collected for the Dipper (Section 3.3.2). 'Alertness' (Section 4.6.6) and biosynthesis costs (Section 4.6.5) were calculated using data in the literature. The daily energy budget calculated by this method was compared with the field metabolic rate (FMR) of eighteen day old Dipper nestlings, measured using the doubly-labelled water technique (see below).

3.5.2 The doubly-labelled water method

The doubly-labelled water method for measuring carbon dioxide output and hence daily energy expenditure was first described by Lifson, Gordon & McClintock (1955). The oxygen of respiratory carbon dioxide is in isotopic equilibrium with the oxygen of body water, thus by injecting water doubly-labelled (D_2O^{18}), the oxygen of respiratory carbon dioxide and water are labelled, whilst the deuterium labels the hydrogen of body water. By measuring the difference in turn-over rates between the labelled hydrogen (lost in expired water) and labelled oxygen (lost in expired water and carbon dioxide), the oxygen turnover due to carbon dioxide production alone can be calculated (see equation Section 4.7). This was then converted to energy expenditure assuming an R.Q. of 0.86 (Section 4.7).

(a) Field Protocol

Dipper nestlings were removed from the nest and body measurements taken. The dosage of the isotope (cm^3) to be injected (20 atom % O^{18}, 10 atom % D) was calculated as nestling mass (g) divided by 95. The isotope was then injected into the peritoneal cavity and the bird left for one hour in a bird bag, to allow for equilibration of the isotope with the body water. Blood samples were then taken from a vein in the leg (after having warmed the nestling for a few minutes to raise the vein) using 5-10 µl glass capillaries, which were then flame sealed using a fine-flame torch. In this state the blood samples could be kept for as long as required before analysis was performed. The nestling was then returned to the nest. Twenty-four hours later a second series of blood samples were taken. Natural background isotope levels were obtained at the start of the experiment from individuals which were not subsequently labelled.

(b) Analysis of blood samples

The hydrogen/deuterium fraction of the blood was obtained by distilling water out of the blood under vacuum and passing it through a uranium furnace that had been heated to 800°C (Wong & Klein, 1987). The water oxidizes the uranium to liberate hydrogen/deuterium gas which is collected on activated carbon for subsequent analysis (Sackett, 1978). The carbon dioxide fraction of the blood was obtained by micro-distillation of blood water into a tube, containing guanadine hydrochloride (Dugan et al., 1985; Tatner & Bryant, in press). The tube was flame sealed under vacuum and then baked in a muffle furnace for ten hours at 250°C. The guanadine tube was then broken under vacuum, in a vessel containing 100% phosphoric acid, and the whole assembly placed in an oven at 80°C for one hour. During this period the carbon dioxide is liberated (Tatner & Bryant, in press). The carbon dioxide gas was then purified by freezing down with liquid nitrogen under a vacuum, into collection tubes. Both hydrogen and carbon dioxide samples were then analysed on an isotope ratio mass spectrometer. All samples were analysed in duplicate to ensure that errors were quickly identified.

A total of eight eighteen-day old Dipper nestlings were used in this study, and the results are presented in Section 4.7.

PART TWO: HATCHING ASYNCHRONY: IMPLICATIONS FOR NESTLING ENERGETICS

3.6 PEAK LOAD REDUCTION (PLR)

3.6.1 Faecal collection and analysis

House Martin faeces were collected in association with the manipulations mentioned in Section 3.8.1. Plastic funnels were suspended about half a metre below House Martin nest boxes, with the funnel spout blocked. Faeces were collected at least every other day from about eight days after brood hatch. Before this time parents carried all or some faeces away from the nest. Faeces from each funnel, together with those voided by chicks during handling, were placed in separate petri-dishes, labelled and placed in a freezer. Faeces were then freeze dried to constant mass, and the daily dry faecal output per brood calculated, see Section 4.8.1.

3.6.2 Hand-rearing nestlings

House Martin nestlings were brought to the laboratory and hand reared from the age of seven to nine days in a nest box. The box contained a nest lining from an abandoned nest, it was kept at 35-40°C by placing a cloth over the open nest box and positioning an anglepoise lamp with a 60 watt bulb over the nest. The air temperature in the nest was monitored with a mercury thermometer and heat output adjusted to keep within the temperature range required by raising or lowering the lamp. Nestlings were fed exclusively on Blowflies <u>Calliphora</u> spp. that had been hatched from maggots and killed by freezing. Chicks were fed hourly in the brood of two and half-hourly in the brood of four. Flies were offered to the chicks on forceps. Each feed consisted of between ten and twenty flies per chick, depending upon how quickly the chicks became satiated. Nestlings were collected in the early afternoon on the day before the experiments, and fed until 2230 hours without collecting any data during this period, to allow them to adapt to the experimental conditions.

Nestlings begged spontaneously on the first offer of food and there was never any problem in getting them to take food. On the day of the experiment the times of each feed, the number of flies taken, their mass and the mass of any faeces collected were recorded for calculation of the dry mass assimilation efficiency (see below).

3.6.3 Assimilation efficiency

From 0400 hours until 2230 hours nestlings were offered flies as mentioned above. Flies had been placed in small polythene bags after freezing to provide convenient batches for each feed, then returned to the freezer to keep them fresh. They were then thawed about an hour before a feed. During the period of feeding bags of flies were set aside for freeze-drying to calculate any changes in water content, during storage. Since each bag of flies was of known wet mass, the mass of flies eaten by each chick was known for each feed. Nestlings regularly defaecated during feeding bouts or soon after, and it was always clear to which chick the faecal sac belonged. Faecal sacs were placed into polythene bags, sealed, and labelled with their owner's identity. Bags were then frozen and freeze-dried to constant mass together with samples of the flies set aside previously. Faeces were collected up until, and including, the first defaecation of the next day (i.e. with the 0400 hour feed).

For each nestling therefore it was known how much food had been eaten, its water content, and the faecal output for a twenty-four hour period. The mass of each nestling was taken at the beginning and end of this period to check that nestlings had indeed gained mass. Dry mass assimilation efficiency was then calculated as;

$$\text{Assimilation efficiency} = \frac{\text{Dry mass of flies eaten} - \text{Dry mass of faeces}}{\text{Dry mass of flies eaten}} \qquad \text{eqn. 3.2}$$

Results are discussed in Section 4.4.

The energy intake was calculated for each nestling as a double-check against under-nourishment (Section 4.8.2).

3.7 NESTLING COMPETITION I: A LABORATORY STUDY ON THE ZEBRA FINCH

3.7.1 Experimental treatments

Begging behaviour was examined in nestling Zebra Finches. A breeding population of adults had been established from which nestlings were removed either singly (N1) or as pairs (N2) from the same nest, and subjected to a variety of experimental treatments (see below). All experiments were carried out within the room where adult birds were breeding in cages, so that nestlings could hear adult birds as they would in the nest. Nestlings were removed an hour before the experiment and placed in an artificial nest which consisted of a small glass pot covered with brown paper and lined with cotton wool. During the hour before treatments no food was offered to nestlings. After 50 minutes the crop-score of each nestling was estimated (see below).

Nestlings were induced to beg by lightly touching each chick on the back of the head. This usually induced begging within 2 seconds. On some occasions, however, this failed, and if no begging was induced after 15 seconds of continual stimulation a value of zero was recorded. In the tests with two siblings both were simultaneously stimulated in this way, since induction of begging in one chick rarely induced begging in its sibling.

Nestlings were subjected to one of the following two treatments, and each treatment was replicated several times separated by two minute intervals. This produced an artificial but constant parental visit rate of 30 visits per hour, which was taken to be a realistic mean over all ages and natural brood sizes. Where additional treatments were carried out on particular individuals, they were separated by 10 minute 'rest' periods.

If nestlings appeared obviously disturbed or were cold the test was immediately terminated and the previous replicate removed from analysis. All treatments were carried out at 24°C and during daylight hours.

Treatment 1.

The time taken for a nestling to give up begging without being offered a feed (GUT = Giving-up Time) was timed to the nearest second. This was repeated 5 times. On the 6th occasion a feed was offered at one of two profitabilities, F = 1 or F = 0 (i.e. standard seed mix or nothing, see Section 3.7.2), and handling time measured. After a two minute interval another series of 5 measurements of GUT (without reward) were performed. The mean pre-feed GUT (GUTpre), mean post-feed GUT (GUTpost), and the ratio of GUTpre/GUTpost was calculated. In addition nestling mass, nestling age, crop-score, and in pairs Relative Difference in Body Mass (see RDBM previously) was also recorded.

Treatment 2

As above, but nestlings were offered food each time they were stimulated to beg. GUT was therefore not measured in treatment 2 tests. In treatments involving pairs, feeds were offered at random to one chick only, and the behaviour of the unfed sibling recorded. The handling time and behaviour of the fed sibling was timed to the nearest second as previously.

3.7.2 Handling time and feed profitability

Standard Finch Panicum Mix was offered to nestlings on a dummy bill. This consisted of a blunt wooden probe, 3mm in diameter, dipped first into a petri dish of water, and then into one half filled with the seed mix. The seed stuck to the wet tip and provided reasonably consistent load sizes 48.9 ± 4.2 mg). This corresponded to food profitability F = 1. Empty moist probe tips were also offered, F = 0. Food profitability was randomised with respect to chicks being offered a feed.

Immediately begging was induced the inside of the nestlings' bill was touched lightly with the dummy parent bill. Nestlings spontaneously 'fed' from the dummy bill (which was held still to minimise any variation in its stimulation effect) until they had finished feeding, when they voluntarily disengaged from the dummy bill and made no further attempt to feed. The dummy bill was then withdrawn so as not to interfere with any subsequent behaviour. This handling time (start to cessation of feeding) was recorded on a stop-watch. Handling time measurements were also randomised with respect to paired or single treatments, cropscore, length of each experimental run, previous handling experience and time of day. Hence handling time measurements were judged to be independent of each other even though several measurements were made on one individual. Results are therefore presented as individual handling time measurements versus the independent variables examined (Section 4.9).

No measure of natural loadsizes brought by parents were available, so the F = 1 profitability is arbitrary. However only very small chicks (< 3 days old) were unable to take food from the dummy bill with or without seed. Chicks older than 3 days were able to remove all seed without apparent difficulty.

3.7.3 Crop-score as an index of nestling hunger level

A measure of initial hunger level was made on all chicks by examination of crop contents. Zebra Finch nestlings have relatively transparent crops which bulge either side of the neck (Figure 6.1a), allowing the contents to be seen. By gently

Figure 3.6

Crop-scoring in Zebra Finch nestlings

A. Natural arrangement of partly full crop

B. Crop displaced by finger for scoring - this would score a '6'.

displacing the crop to one side with a finger (Figure 3.6), the proportion of the crop filled was estimated and ranked as follows;

0	Empty	
1	Some food present	
2	Approximately	one-quarter full
3	"	one-third full
4	"	one-third to one-half full
5	"	one-half full
6	"	two-thirds full
7	"	three-quarters full without 'air bubbles'
8	"	three-quarters full with 'air bubbles'
9	"	completely full but 'air bubbles'.

Hunger level was assumed to be inversely proportional to crop-score since individuals with low crop-scores still begged vigorously suggesting that they had not just emptied their crops and were therefore satiated. However, nestlings with more full crops often refused food, suggesting that they were somewhat more satiated.

3.7.4 Nestling age and nestling mass

Growth data was collected on a limited number of Zebra Finch nestlings. Nestling mass was found to be linearly related to age between day 3 and day 9 after hatch inclusive. The regression equation is;

$$\text{Mass} = 1.05 + \text{Age} \times 0.4 \qquad \text{eqn. 3.3}$$

$r^2 = 0.76$, $n = 29$, $p < 0.005$

Nestling mass was used instead of age for comparing begging behaviour data for two reasons. Firstly, previous considerations of nestling competition (of which begging behaviour is considered important) have been based upon the relationship between the size of an individual and its siblings and how this will affect nestling dominance hierarchies, (Section 2.4) hence nestling mass is more pertinent to such discussions than age per se. Secondly, the age of nestlings used was often not known, but mass was always accurately measured. Nestling mass is therefore the independent variable against which other nestling parameters are considered (Section 4.9).

3.8 NESTLING COMPETITION II: A FIELD STUDY ON THE HOUSE MARTIN

The hypothesis of Reduced Sibling Rivalry (RSR) proposed in Section 2.3 is based on five assumptions (Section 2.3.2); four of these were examined in the House Martin.

3.8.1 Peak mass and hatching asynchrony

Nestling mass hierarchies were manipulated on broods of House Martins. Manipulations were of two types; synchronous and asynchronous. Synchronous broods were those in which individuals of similar mass were placed together from different broods and relative differences in body mass at hatch (RDHM) were small ≤ 0.35. Asynchronous broods were those in which nestlings were known to have hatched from different broods between three and five days apart. These broods ranged from 0.4-2.0 RDHM. Unmanipulated broods acted as controls. To these data were added a number of unmanipulated brood data from another site provided by D. M. Bryant. These included the brood-size two data (Section 4.111) which were lacking at this investigator's sites. Most manipulations were set at the more usual brood-sizes of three to five (mostly three to four, Sections 3.8, 4.10). Nestling mass was measured regularly (Section 3.1.1) and growth curves plotted from which peak masses could be obtained. These were compared with degree of hatching asynchrony (RDHM) to test the hypothesis that there is an optimal asynchrony which will be reflected in a maximal peak mass (Section 2.3.5). These results are presented in Section 4.11.1.

Peak masses of individuals within a given brood were taken as being independent with respect to asynchrony since hatching mass is independent of hatching order (Section 4.11.2).

3.8.2 Hierarchy stability and the flexibility of nestling growth

Consideration of the factors affecting nestling mass hierarchies showed that under certain circumstances changes in hierarchy structure may be expected to occur. Changes in hierarchy positions of individuals within given broods were examined from the growth data collected above in relation to initial hatching asynchrony (RDHM). The maintaining or prolonging size differences between individuals was thought to be important in considerations of sibling rivalry (Section 2.3, assumption (iii)). The relative difference in body mass (RDBM) between individuals was therefore monitored throughout growth as a test of this assumption of the RSR model. Results are presented in Section 4.2.

3.8.3 Competitive costs and the Reduced Sibling Rivalry (RSR) model

The examination of sibling rivalry and competitive costs in House Martin nestlings can be split into three stages;

(a) Laboratory costs of competitive activities (Section 3.4)

(b) Brood manipulations (Section 3.1)

(c) Field measurements of begging behaviour.

The latter was carried out in two ways. The microprocessor system (Section 3.3.1) was modified so that it did not include the thermistor and thermistor interface. The software was modified so that only begging behaviour was recorded and logged. The system was placed below a House Martin nest at the time of the experiment. There was no need to build up a dummy prior to this (see Section 3.3.2). The condensor microphone was either inserted under the lid of the nest box and taped in place, or a small hole was bored into the side of a natural nest and the microphone fitted snuggly. The microphone lead was taped down to stop it flapping about since this was found to distract the parent birds. The microphone position within the nest was chosen to eliminate the risk of false triggering by nestlings brushing against it, or wind blowing across the nest entrance. Sensitivity was adjusted to eliminate external noise

(Section 3.3.2), nonetheless it was not practicable to record begging behaviour in this way at some nests. An alternative method was therefore applied. The microphone was connected to a cassette player and begging behaviour recorded on C120 cassette tapes. These were later transcribed, they provided additional information on the intensity of begging behaviour and therefore supplementing the frequency and duration measurements of the microprocessor (Section 4.10).

CHAPTER FOUR

RESULTS

PART ONE: THE NESTLING ENERGY BUDGET

4.1 BIOMETRICS OF DIPPER NESTLINGS

4.1.1 Mass, wing-length, body-length and tarsus

Nestling body mass as a function of age (to the nearest 0.5 day) is plotted in Figure 4.1. Nestlings reach peak mass (56.1 ± 3.88g, n = 25) around day 17, and then undergo a slight mass recession until fledging at about twenty-three days (mean = 23.1 ± 0.9d, n = 36). The mass at peak is 87.8% of adult body mass whilst at fledging (55.2 ± 2.70, n = 14) it is 86.4% of adult body mass. Variation around the latter part of the growth curve is partly explained by the divergence of the male and female growth curves, mentioned earlier but reported and discussed below. Wing-length increased almost linearly with age (Figure 4.2) and is a good predictor of the latter ($r^2 = 0.97$, $n = 486$, $p < 0.001$). Nestling wing-length is 80.8% of adult wing-length by fledging. Tarsus growth was completed by about day twelve (Figure 4.3) suggesting that leg growth is an important early requirement, not only related to nestling competition (Ryden & Bengtsson, 1980) but also as a nestling 'escape' mechanism from predation. Dipper nestlings can "explode" out of the nest after day twelve if danger threatens (pers.obs., Shaw, 1978). The ability to be mobile on the ground is clearly enhanced by the developed tarsi (see Chapter 5).

Nestling body-length increases quickly until day seven and then slows down (Figure 4.4). Body-length measurements of nestlings older than 17.5 days are impracticable but it seems that this levels off to about 138mm in older

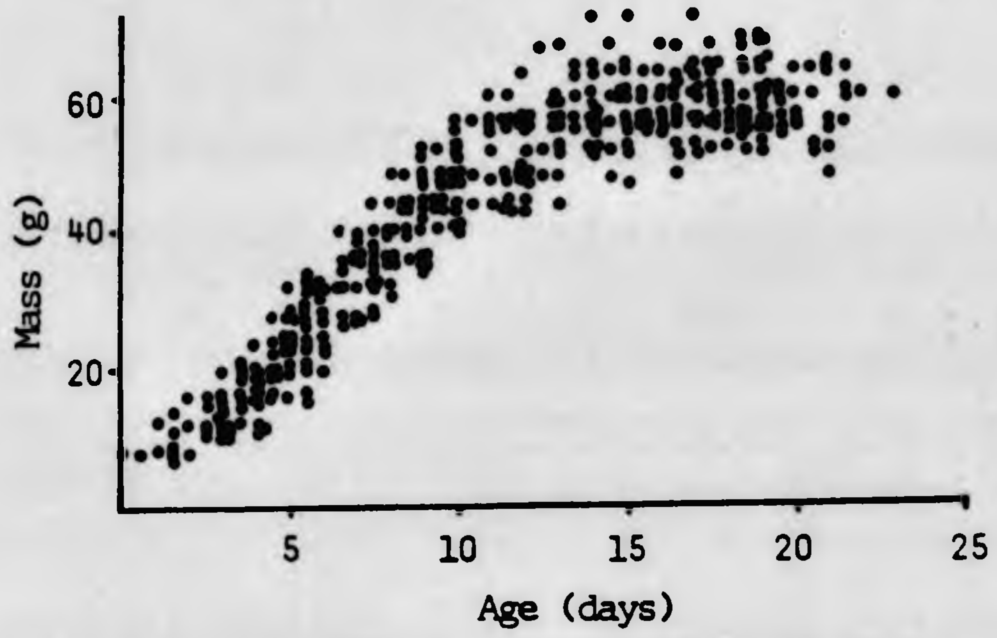


Figure 4.1: Nestling body mass as a function of age in the Dipper

(n = 490)

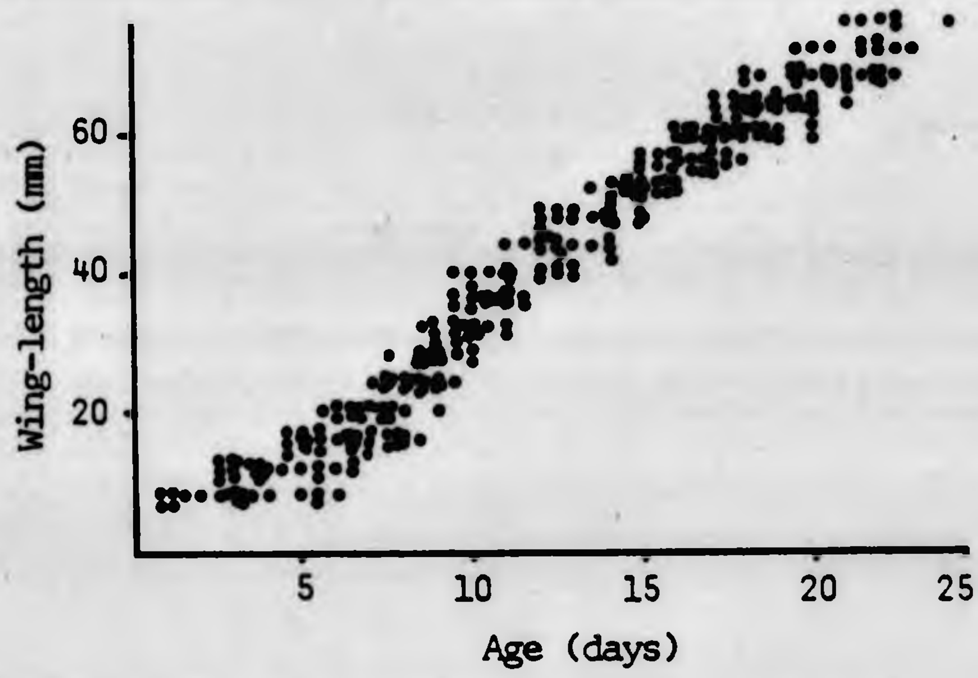
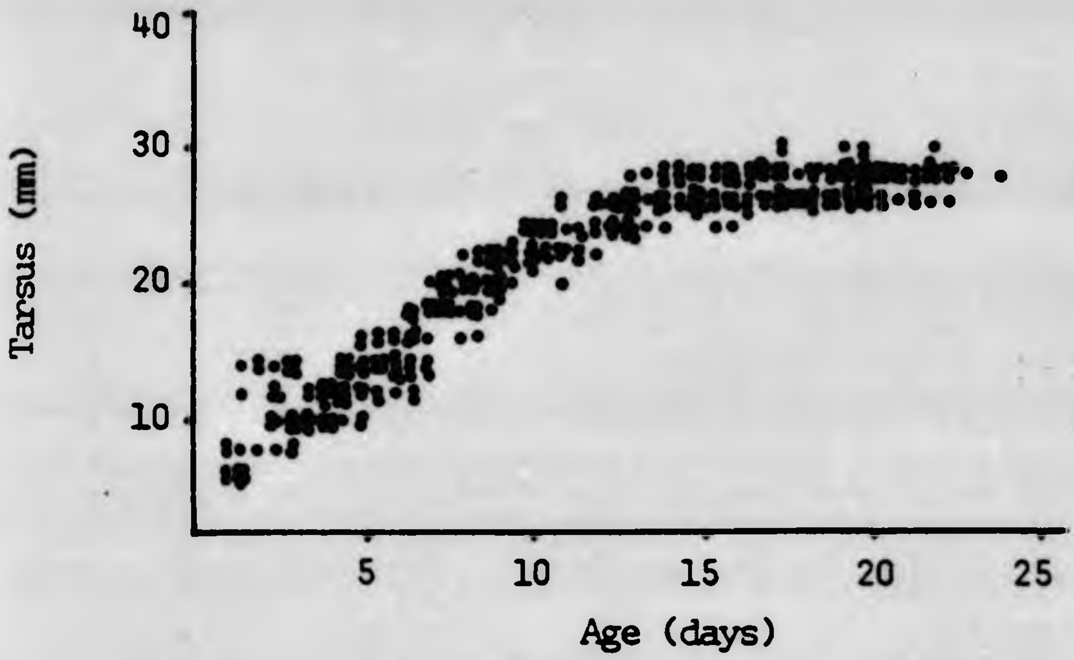


Figure 4.2: Wing-length as a function of age in the Dipper

(n = 486)

Wing-length = 1.61 + 3.45 Age

$r^2 = 0.97$, $p < 0.001$



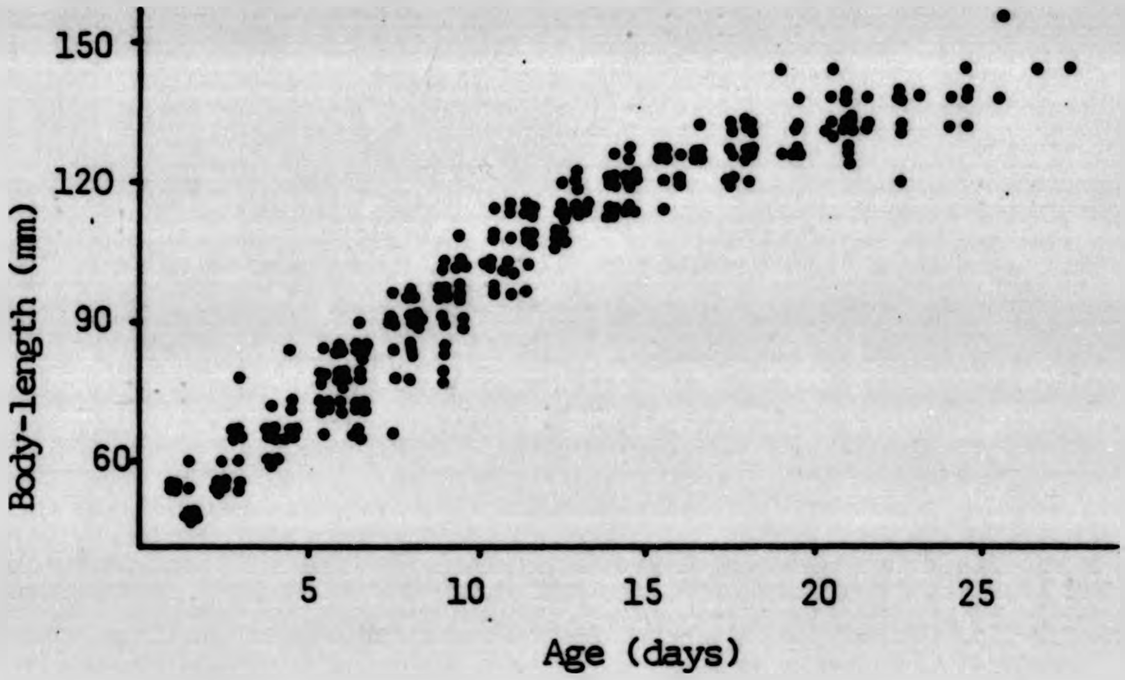


Figure 4.3 (top): Tarsus length as a function of age in the Dipper.

n = 486

Figure 4.4 (bottom): Body-length as a function of age in the Dipper.

n = 367

nestlings. Body-length is a crude indicator of how far a nestling can stretch out its head when competing with siblings for food. Since establishment of mass hierarchies takes place early in the growth period, a rapid increase in body-length might be adaptive. Other features associated with the procurement of food show a similar early increase in size.

4.1.2 Gape and bill-length growth and their relationship to mouth "target area"

Gape width (Figure 4.5) increases until day twelve and then decreases markedly whilst bill-length growth (Figure 4.6) increases linearly up to this point and then levels off. This tends to support O'Connor's (1977) view of adaptive growth of the bill, initially to increase the target area for parental feeding and then changing in shape towards fledging, to resemble the adult. Figure 4.7 shows that the reduction in gape width is more important in bringing this about than is bill-length growth.

An indicator of the importance of bill morphology to nestling food procurement is mouth 'target' area (MTA). MTA reflects both changes in bill-length and gape width, and in addition provides a measure of the effectiveness of combining gape width and bill length measurements. Two derivations of MTA were calculated and are shown in Figures 4.8 and 4.9. Figure 4.8 (MTA I) follows closely the pattern of gape with age but suggests that as chicks get older (> 12 days) mouth area decreases and presumably the ability to handle larger food items decreases as well. Figure 4.9 (MTA II) suggests that target area reaches an asymptote at

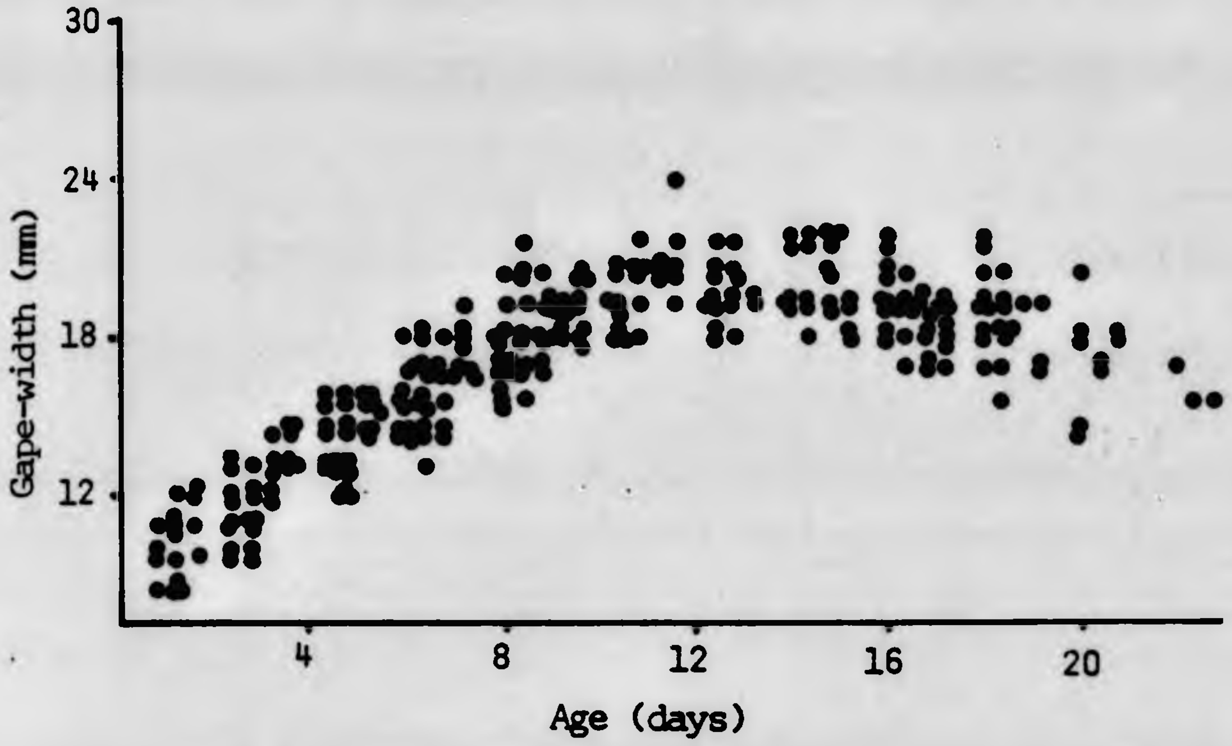


__Figure 4.5:__ Gape-width as a function of age in the Dipper (n = 395)

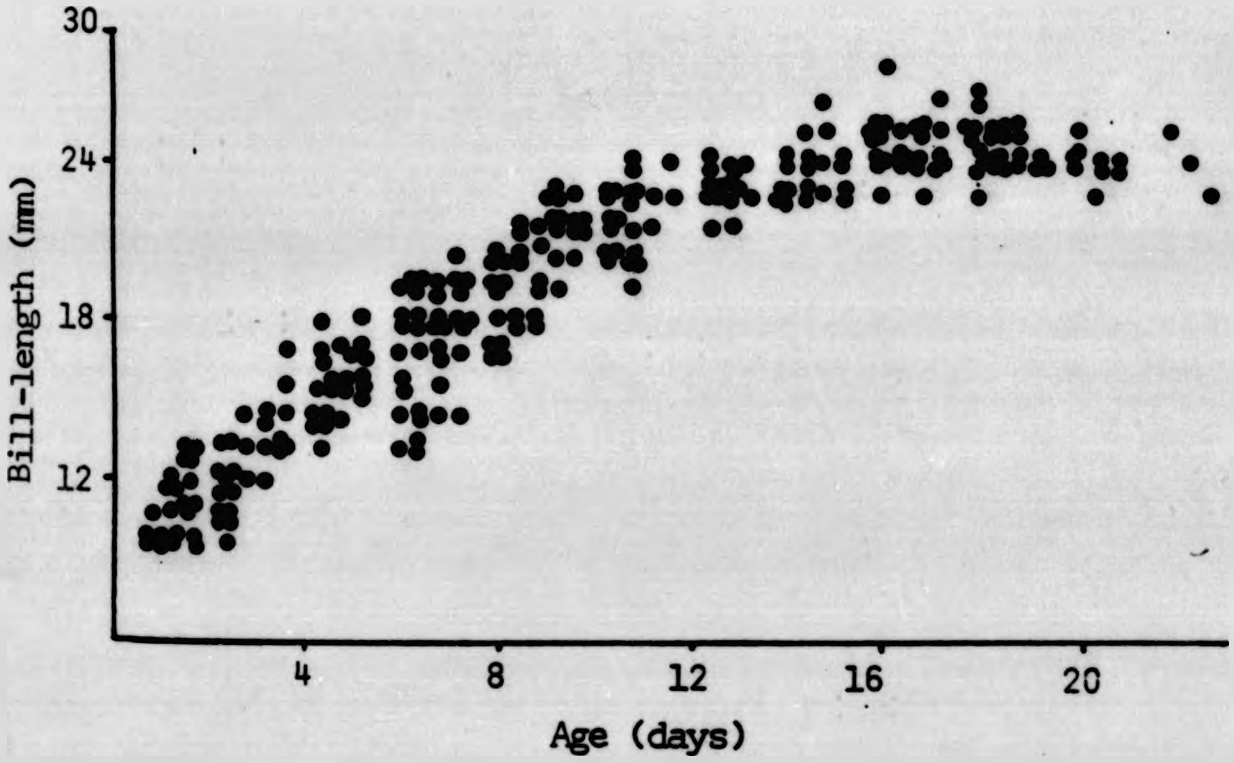


__Figure 4.6:__ Bill-length as a function of age in the Dipper (n = 367)

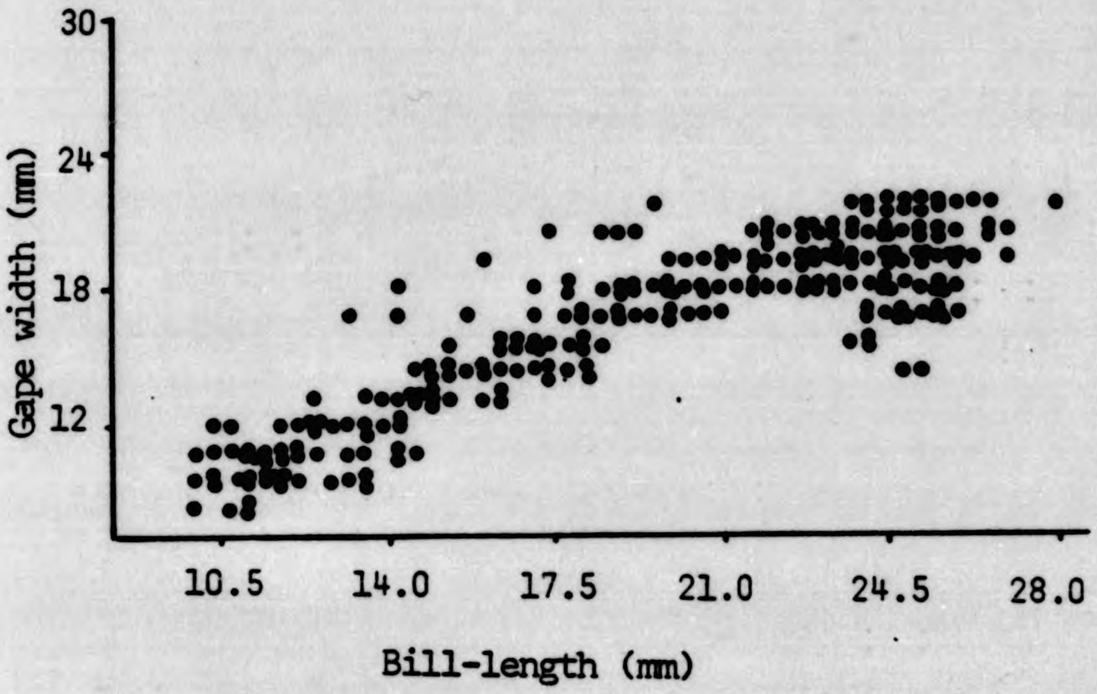


Figure 4.7: Gape width as a function of bill-length in the Dipper.

The regression equation is:

$y = 4.38 + 0.644x$

$r^2 = 0.76$, $n = 365$, $p < 0.001$

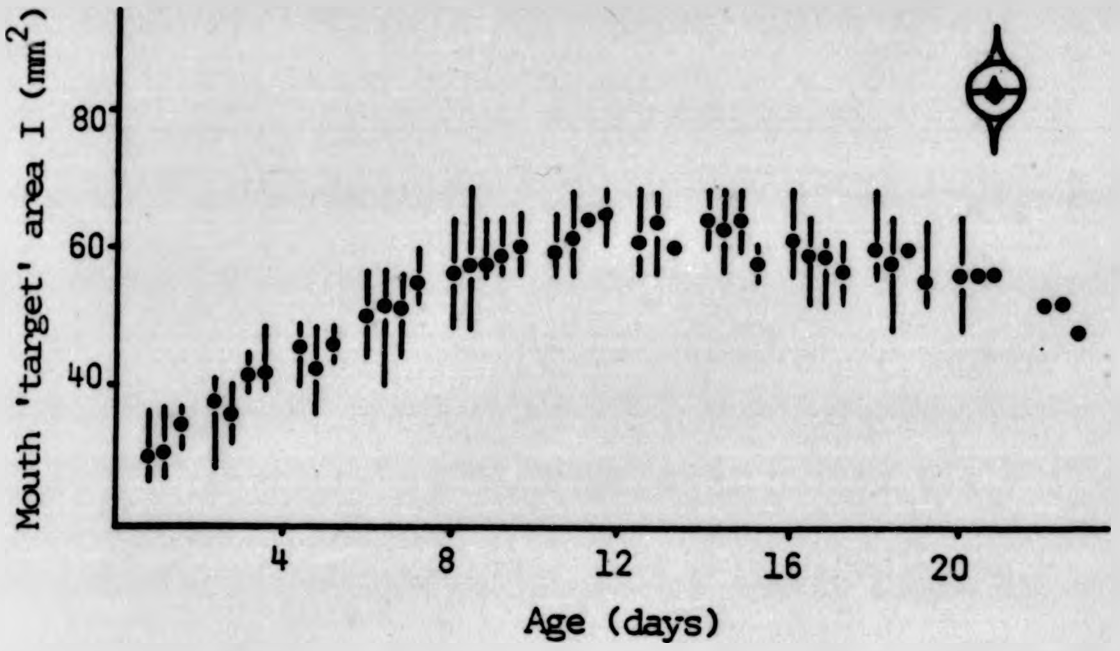


Figure 4.8: Mouth 'target' area as a function of age in the Dipper.
MTA I = $\pi \times \left(\frac{\text{gape width}}{2}\right)^2$ (mm) n = 365

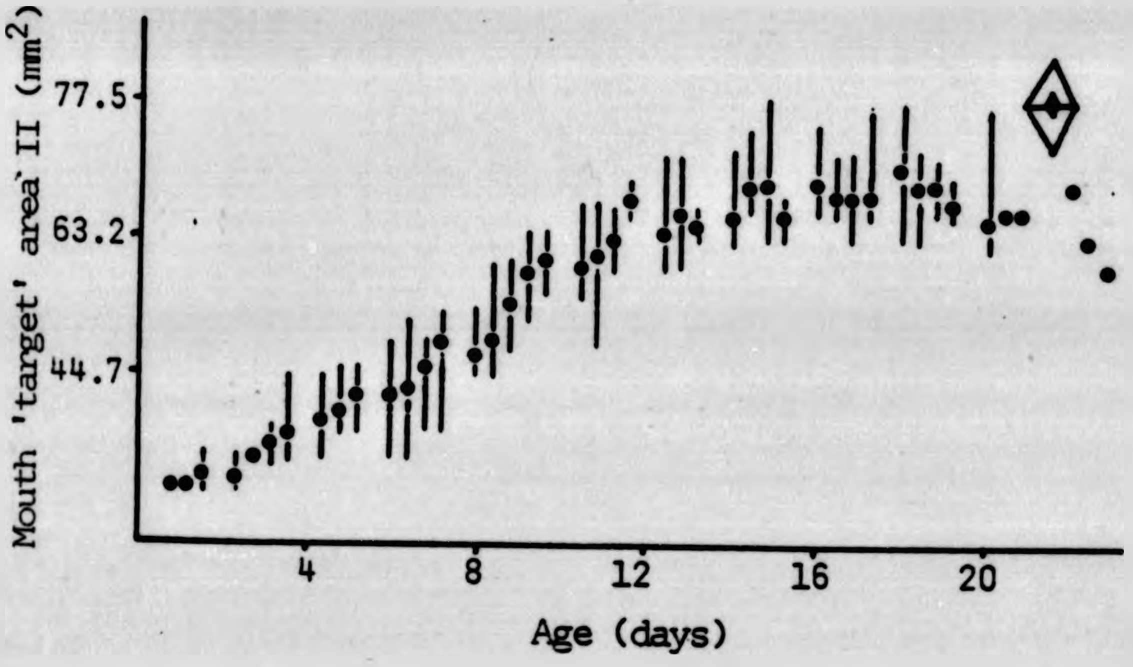


Figure 4.9: Mouth 'target' area as a function of age in the Dipper.

MTA II = Gape width (mm) x $\sqrt{(\text{Bill-length}^2 - \frac{\text{gapewidth}^2}{2})}$
n = 365

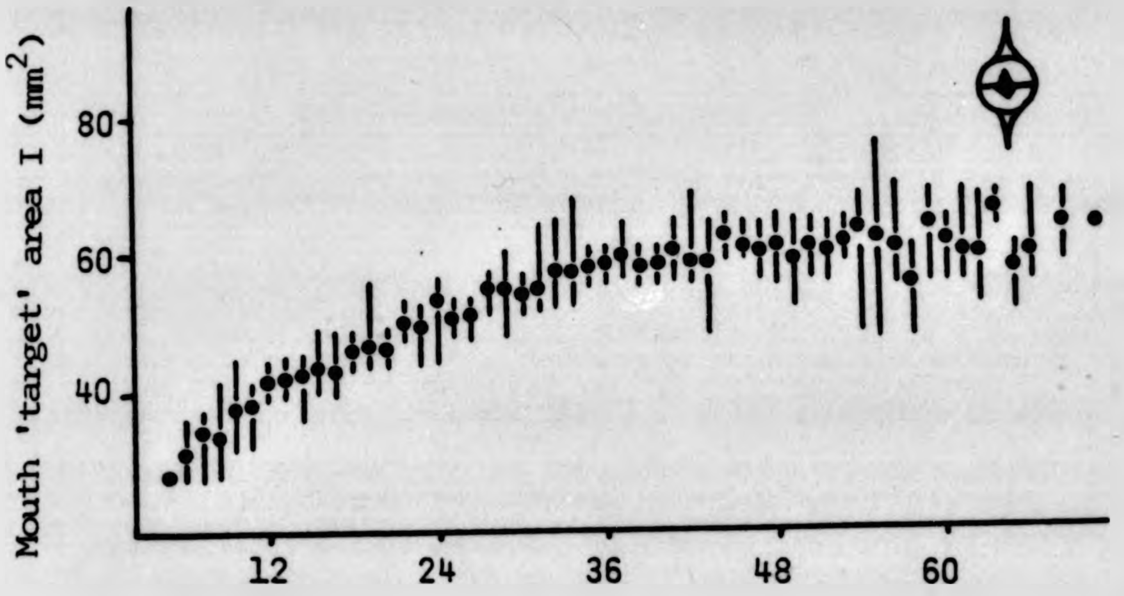
(Means and ranges)

about 14 days. The slopes of both curves during the linear phase (zero to eight days), are very similar. Indeed personal observations suggest that mouth shape changes from MTA I to MTA II as the nestling grows.

When MTA is compared with nestling growth as shown by body mass, then two different patterns emerge (Figures 4.10 and 4.11). Both begin with a linear increase ($b = 1.2$ for both) but in Figure 4.11 the growth continues at this rate (i.e. is directly proportional to body mass), whilst in Figure 4.10, MTA levels off at around 60mm^2. The possible adaptation of changing bill morphology in relation to nestling growth will be discussed in Chapter 5.

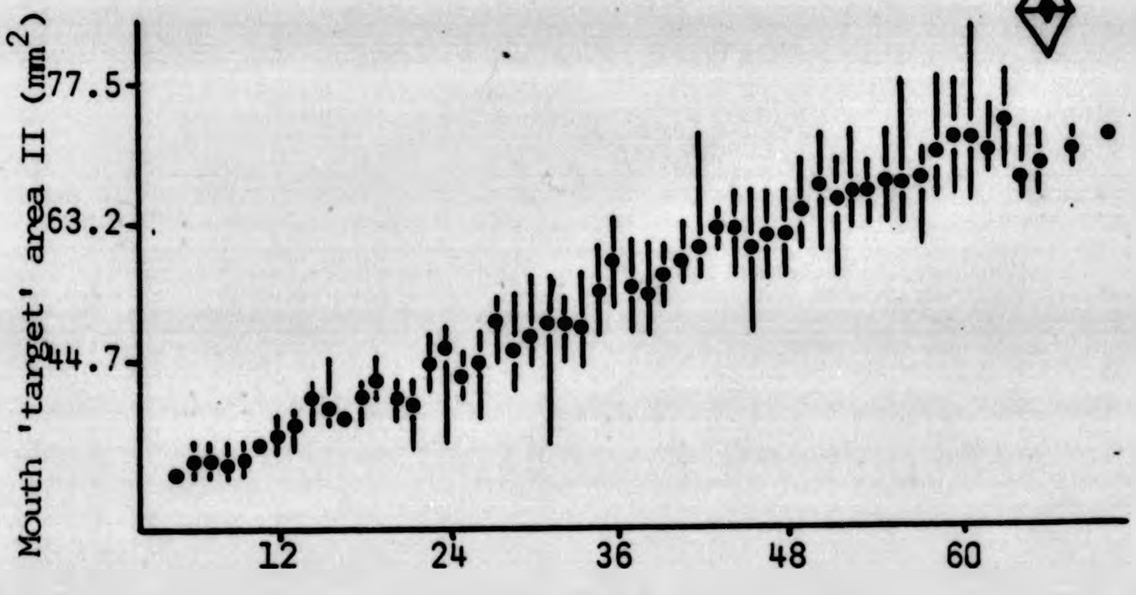
4.1.3 Feather growth

The development of feathers in the Dipper is summarized in Table 4.1. Feathers prick first on the head at about day 3.5, followed by wing coverts (day 4.0), back (5.3), primaries (5.4) and belly (6.1). The first ones to split are the back (day 5.7), head (6.2) and belly (6.7), whilst the primaries and wing coverts split later (8.3 and 7.7 days respectively). Since young are becoming homeothermic at around seven to eight days of age, energy put into growth of insulating feathers, specifically the exposed back, but also the head, will be energetically beneficial. Feathers on the belly presumably provide little insulation since this part of the nestling is rarely exposed. Development of feather covering on the wings will also provide insulation, although early development of primary and secondary feathers



Nestling mass (g)

Figure 4.10: MTA as a function of nestling mass in the Dipper
MTA I = π x (Gapewidth)^2 (mm) n = 365



Nestling mass (g)

Figure 4.11: MTA as a function of nestling mass in the Dipper

MTAII = Gapewidth (mm) x $\sqrt{\frac{(\text{Bill-length}^2 + \text{gapewidth}^2)}{2}}$

The regression equation is:

$y = 12.5 + 1.196x$

$r^2 = 0.91$, $n = 365$, $p < 0.001$

(Means and ranges)

TABLE 4.1: The relationship of feather growth (length) with age for nestling Dippers

Feathers	Pin			'Tuft'			Total			Adult length			Mean Growth completed at day 23 % Adult
	b	Mean day [b]pricked	Rank order pricking	b	Mean day split	Rank order split	b	r^2	significance	$\bar{x}$	±	S.E	
Primary 1	1.97	5.4	4	1.07	8.3	5	2.86	93.4	$p<0.005$	63.6		2.84	89.6
Wing Coverts	1.60	4.0	2	0.62	7.7	4	2.28	86.7	$p<0.005$	47.7		2.50	90.9
Back	0.75	5.3	3	0.75	5.7	1	1.55	98.2	$p<0.005$	25.7		5.86	100.0
Belly	0.56	6.1	5	0.49	6.7	3	1.37	85.8	$p<0.001$	26.7		5.90	86.8
Head	0.26	3.5	1	0.32	6.2	2	0.39	30.4	$p<0.05$	9.5		5.88	80.3

a 'Tuft' refers to the portion of feather split from the pin.

b 'Pricked' refers to the time when the feather pin just begins to break (prick) through the skin (see text).

= the slope of the feather length (mm) versus age (days) regression.

might increase problems of heat loss (Section 4.4) due to long periods of pin exposure prior to splitting; three to four days for primaries and wing coverts. The main insulating feathers however (with the exception of the head) split almost as soon as the pins prick through the skin. The back feathers are by far the most important insulating group of feathers, and have completed growth by fledging. Primaries and wing coverts have completed almost 90% of growth at fledging whilst the head feathers have completed 80% of growth. The relative mass of the head is large in small nestlings and decreases as nestlings become older (Figure 4.19(d)), thus one might expect that the head becomes decreasingly important as an avenue of heat loss, whilst the body, leg, belly and back remain at a similar relative mass (Figure 4.19(a)). Early growth of head feathers may therefore initially reduce heat loss but slower growth later may not affect heat loss through the head appreciably. Table 4.2 shows the $\log_e/\log_e$ slopes of each feather area versus mass. It can be seen that back feathers grow considerably quicker than the body as a whole and more so than the other feather areas, whilst the belly is the slowest feather growing area. The high exponents are due to the fact that feather growth only commences about a third of the way through body growth.

4.1.4 Sexing Dipper nestlings from body measurements

It was often possible in mature ($\geq$ 18 day old) Dipper nestlings to separate members of a brood into one of two size classes, depending on whether they were relatively large or

TABLE 4.2: The exponent b, of the loge feather length (mm) versus loge nestling mass (g) relationship for the major areas of feather growth in the Dipper

The relationship is described by: feather length = a mass^b.

Feather area	b	r^2	significance
Primary	3.42	83.4	$p < 0.005$
Wing Coverts	3.94	75.7	$p < 0.005$
Back	12.9	93.9	$p < 0.005$
Belly	2.94	99.3	$p < 0.005$
Head	3.28	35.9	$p < 0.05$

small for their age. It was suspected that this difference might be an early indication of sexual dimorphism found in the adult (Anderson & Wester, 1971). It was possible to sex eighty-three nestlings retrospectively; sixty-six from retrap measurements as adults and seventeen from carcass analysis (Section 3.1.2). Tarsus measurements were only available for twenty-seven nestlings.

Nestling mass, wing-length, tarsus length, age, wing/mass ratio (WMR) and wing/tarsus ratio (WTR), for these nestlings were entered into two and three-way discriminant analyses, using the 'Discriminant' program of SPSSX (Nie et al., 1983). One set of measurements per nestling was entered into the analysis, or where several were available the measurement from the oldest chick was used. Nonetheless growth data were not confined to the latter part of the growth period and so a stepwise approach was used in which data was analysed progressively eliminating younger birds, so that the effect of age on the ability to discriminate the sex of a nestling was examined. Table 4.3 shows the significances of the various analysis performed. It can be seen that three-way analyses provide consistently better discrimination than two-way analyses, although the addition of a fourth parameter did not improve the relationship. Older birds (> 18 days old) produced a greater number of significant relationships than younger birds. Two analyses provided the most significant relationships; Age:Mass:Tarsus and Wing:Mass:Tarsus. The latter was the most significant and was therefore used to sex

TABLE 4.3: The significance of variables entered into a discriminant analysis in predicting the sex of nestling Dippers (Nie et al., 1983, SPSSX 'discriminant' program)

	Minimum age of nestlings considered (days)[a]			
Variables entered into Analysis	5	14	16.5	18
Age:WMR	0.0249*[b]	0.0525	0.0076**	0.0040***
Age:MWR	0.0994	0.0858	0.0121*	0.0042***
Age:WTR	0.2040	0.2118	0.1216	0.1446
Wing:WMR	0.0140*	0.0263*	0.0072**	0.0055**
Wing:MWR	0.0484*	0.0401*	0.0109*	0.0050***
Wing:WTR	0.2414	0.2893	0.2048	0.1281
Wing:Mass	0.0124*	0.0165*	0.0076**	0.0048***
Age:Mass:Wing	0.0322*	0.0364*	0.0207*	0.0138*
Age:Mass:Tarsus	0.0211*	0.0023***	0.0048***	0.0119*
Wing:Mass:Tarsus	0.0201*	0.0022***	0.0030***	0.0119*
Wing:Mass:Tarsus:Age	0.0440*	0.0064**	0.0089**	0.0296*

[a] 5 is all data; 14 is birds with 49^{+}_{mm} wing length; 16.5 is birds with 59^{+}_{mm} wing length; 18 is birds with 65^{+}_{mm} wing length

[b] * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.005$

'unknown' birds for the subsequent comparison of male and female growth curves (Section 4.1.5).

The equation used to sex Dipper nestlings, calculated from the discriminant unstandardized canonical function coefficients is:-

$$\text{sex} = (0.101*\text{Mass}) - (0.076*\text{Wing}) + (1.041*\text{Tarsus}) - 29.65 \qquad \text{eqn. } 4.1$$

Values that are negative are classified as females and those that are positive are males.

Table 4.4 shows the percentage of birds correctly sexed using the above equation. The proportion of correctly sexed birds increases with nestling age. At age $\geq$ 18 days all females were correctly classified. At all ages the ability to discriminate females was higher than for males, due to the incorrect sexing of small males.

4.1.5 The effect of sex on nestling growth

The Dipper growth data were re-analysed, and nestlings for which growth data measurement were available for the latter part of the growth period (i.e. $\geq$ 14 days, see Figure 4.1) were sexed using the discriminant function.

Figure 4.12 shows male and female masses as functions of age. After five days males were significantly heavier than females of the same age, and averaged 11% heavier at fledging. Males had longer tarsi than females and averaged 5% longer towards the end of the growth period. Both sexes had completed tarsal growth after approximately twelve days (Figure 4.13(a-b)).

TABLE 4.4: **The percentage of Dipper nestlings correctly sexed from a discriminant analysis of mass (g), winglength (mm) and tarsus length (mm) for three age classes**

Sex	≥ 14 days		≥ 16.5 days		≥ 18 days	
	% correct	n	% correct	n	% correct	n
Male	78.6	14	80.0	10	83.3	6
Female	84.6	13	90.0	10	100.0	8
TOTAL:	81.5	27	85.0	20	92.86	14

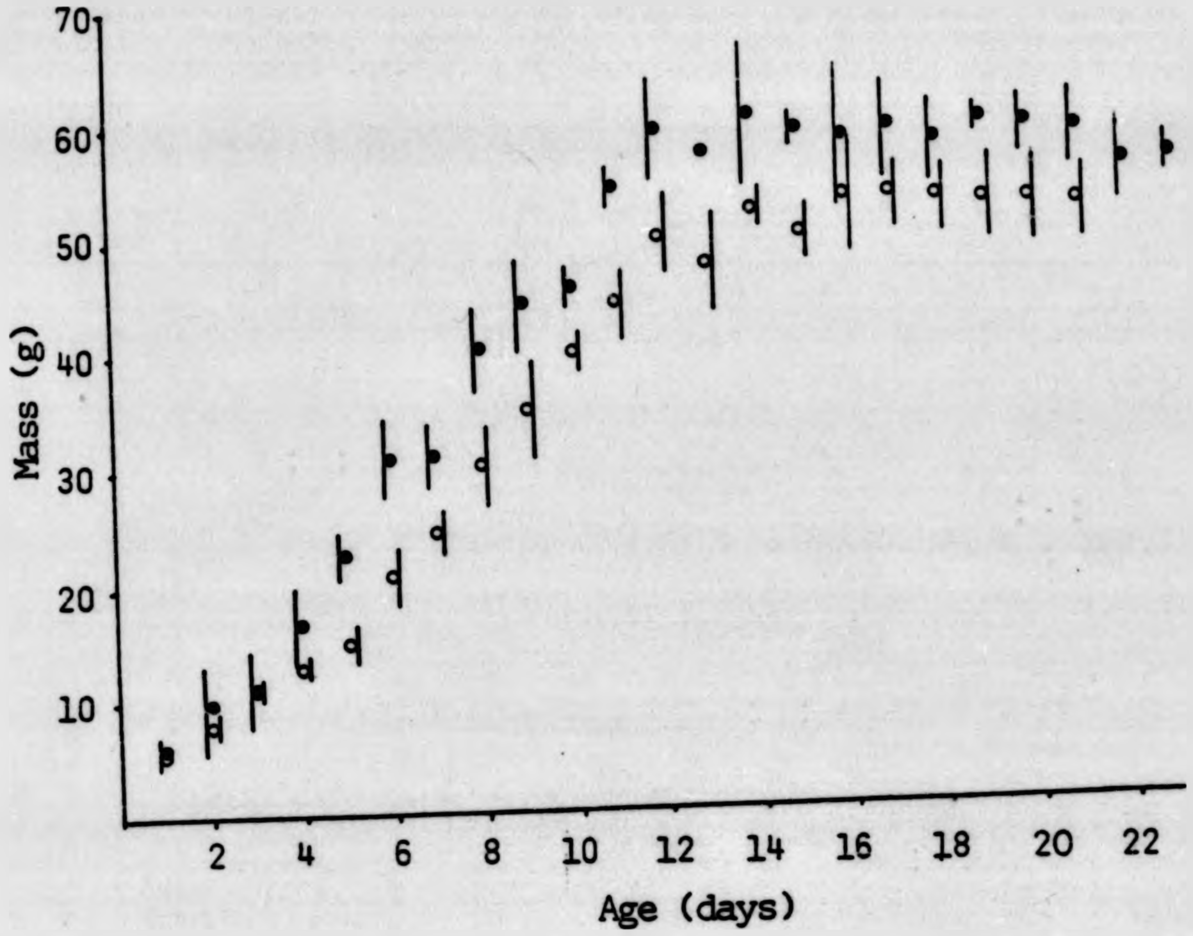


Figure 4.12: Nestling mass as a function of age for male (●) and female (O) Dippers. Means ± 1 standard deviation

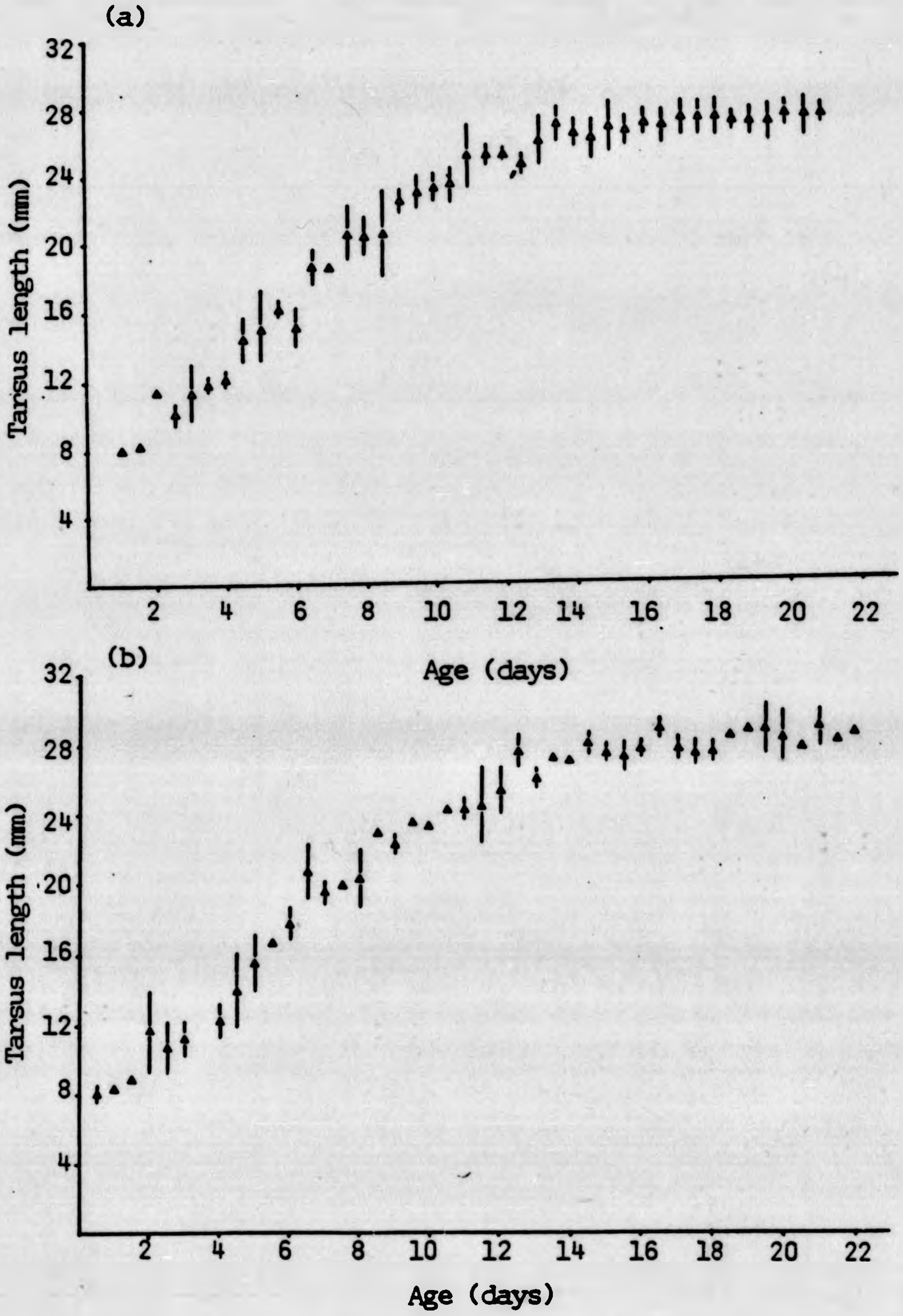


Figure 4.13: Tarsus length (mm) as a function of age in the Dipper.

(a) Males ▵ (b) Females ▲

Means ± 1 standard deviation

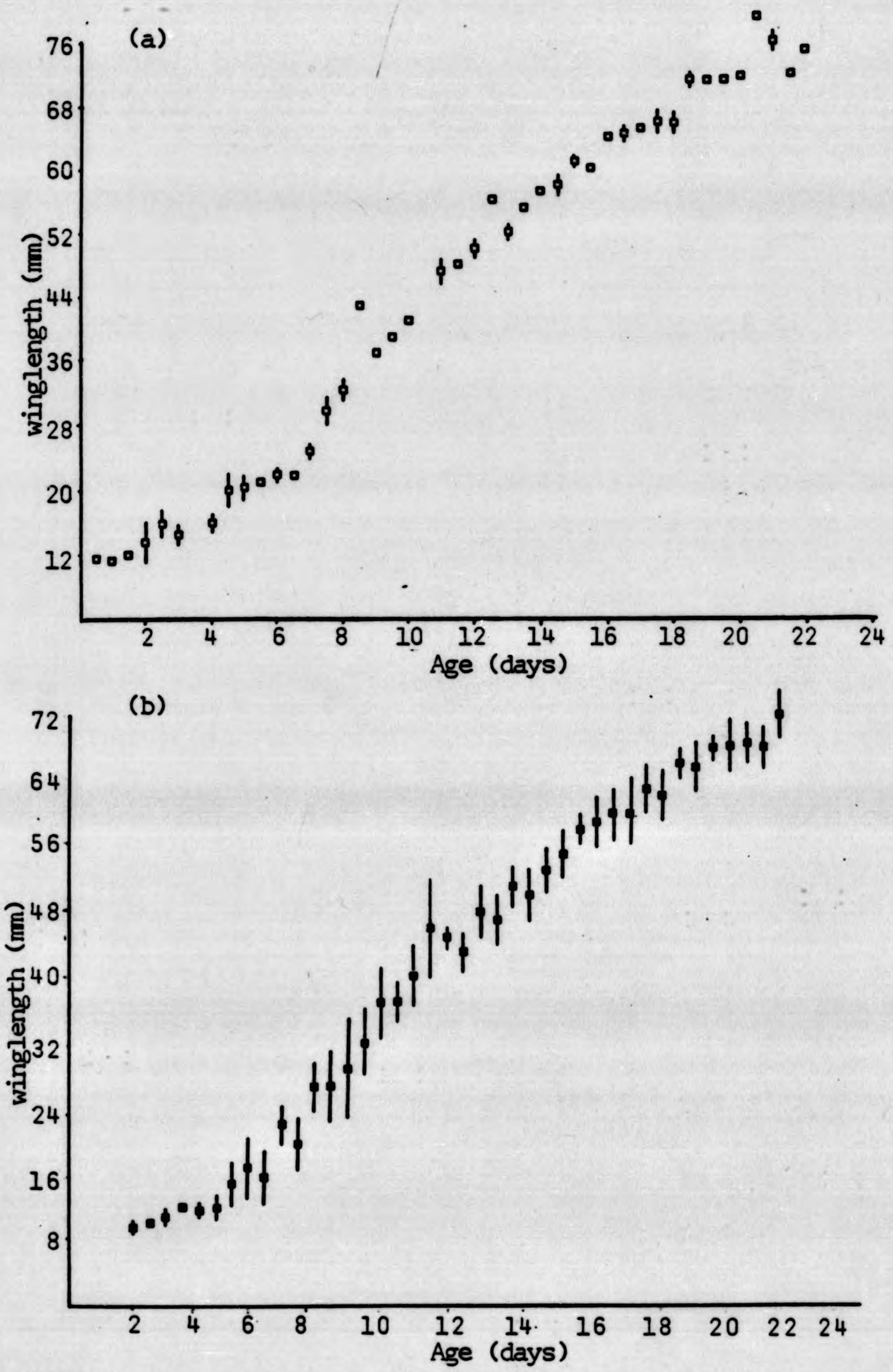


Figure 4.14: Winglength (mm) as a function of age in the Dipper

(a) males (b) females

means ± 1 standard deviation

The slopes of male and female regressions of wing-length on age did not differ significantly, though males had slightly longer wing-lengths for a given age, as indicated by the intercept of the regression (Figure 4.14(a-b)).

At fledging females had completed 90% of adult growth for mass and wing-length, and males 84% and 83% respectively. Although males tended to be larger than females, especially late in the growth period, females grew proportionately faster. Table 4.5 shows the parameters for the fitted growth curves for male and female nestlings. The growth rate constants for mass and tarsus-length on age, are higher for females. This suggests that males are bigger at hatch and that this size difference is maintained during growth. The implications of this size dimorphism with respect to the energetic cost of rearing males and females is further discussed in Section 4.6 and Chapter 5.

A number of factors other than sex were thought to influence Dipper nestling growth. Two of these factors were analysed - nest type and brood-size. Dipper nests can be divided into two types; exposed and enclosed. Exposed nests consist of a large mass "ball" with usually a slightly downward facing nest entrance hole (Plates 3.2 and 3.3), and an inner nest cup of grass lined with dry leaves. Enclosed nests are built within holes, for example in stone bridges, or sometimes within drainage pipes (Plate 3.4).

4.1.6 The effect of nest type on nestling growth

Enclosed nests can become noticeably cramped, especially as the young increased in size. A two-way analysis

TABLE 4.5: [a]Fitted growth parameters for male and female Dipper nestlings

Variable	Male[b]	Female[b]
Asymptotic Mass (g)	58.02	51.75
Growth rate (k)	0.300	0.380
Age of Inflexion (days)	6.26	6.08
Asymptotic Tarsus (mm)	28.28	26.94
Growth rate (k)	0.298	0.362
Slope Wing (b)	3.43	3.48
Intercept Wing (a)	2.03	0.934

[a] Data fitted using logistic equation from Ricklefs (1967). Asymptote for mass estimated as the mean mass of 14-23 day old nestlings. Tarsus asymptote estimated from 17-23 day old nestlings.
The logistic curve = $A/[1 + e^{k(t-age)}]$

[b] Sexed from discriminant analysis, but including birds sexed directly as adults and through carcass analysis (Section 4.1.4)

of variance showed that nest type did not explain a significant amount of the variance in either peak nestling mass (asymptote) or growth rate. The latter was measured as the mass of nestling at the inflexion point on the fitted growth curve for all data (i.e. 6.3 days).

4.1.7 The effect of brood-size on nestling growth

Brood-size explained a significant amount of the variance and was therefore entered into a two-way analysis of variance with sex of nestling. The results are presented in Table 4.6. Sex of nestling accounts for 29.1% and 36.3% of the variance in growth rate and maximum mass respectively. Brood-size explained less of the variance but was still significant. Both brood-size and sex of nestling explained a higher percentage of the variance in maximum mass than growth rate.

4.2 THE ENERGETICS OF NESTLING GROWTH IN DIPPERS

4.2.1 Whole body water content, lean dry mass, lipid and water indices

Figures 4.15 and 4.16 show LDM, water indices, water content and lipid indices for nestlings as a function of age. They are presented with comparative data for fledged juveniles and adults. LDM increases linearly with age; ($y = -0.186 + 0.630x$, $r^2 = 94.7$, $n = 18$, $p < 0.001$).

Nestlings fledging at twenty-three days have attained 81% of adult LDM. Water indices (Figure 4.15(b)) decreased with age as tissues matured, and nestlings fledged with water indices about 11% higher than for adults. Whole body lipid index (Figure 4.16(a)) was considerably more

TABLE 4.6: The percentage variation in Dipper growth rate and asymptotic mass attributable to brood size and sex of nestlings, from a two-way analysis of variance

Source of variation	Growth rate[a]	Asymptotic mass[b]
Error	61.2%	53.9%
Brood size	4.7%	7.2%**
Sex	29.1%***[c]	36.3%***
Interaction	3.9%	2.7%

a Mass at inflexion. Inflexion was calculated from the logistic curve fitted through combined Dipper nestling growth data (Section 4.1.1) and is equal to age 6.3 days

b Mean mass 14-23 days of age

c ** = $p < 0.02$; *** = $p < 0.005$

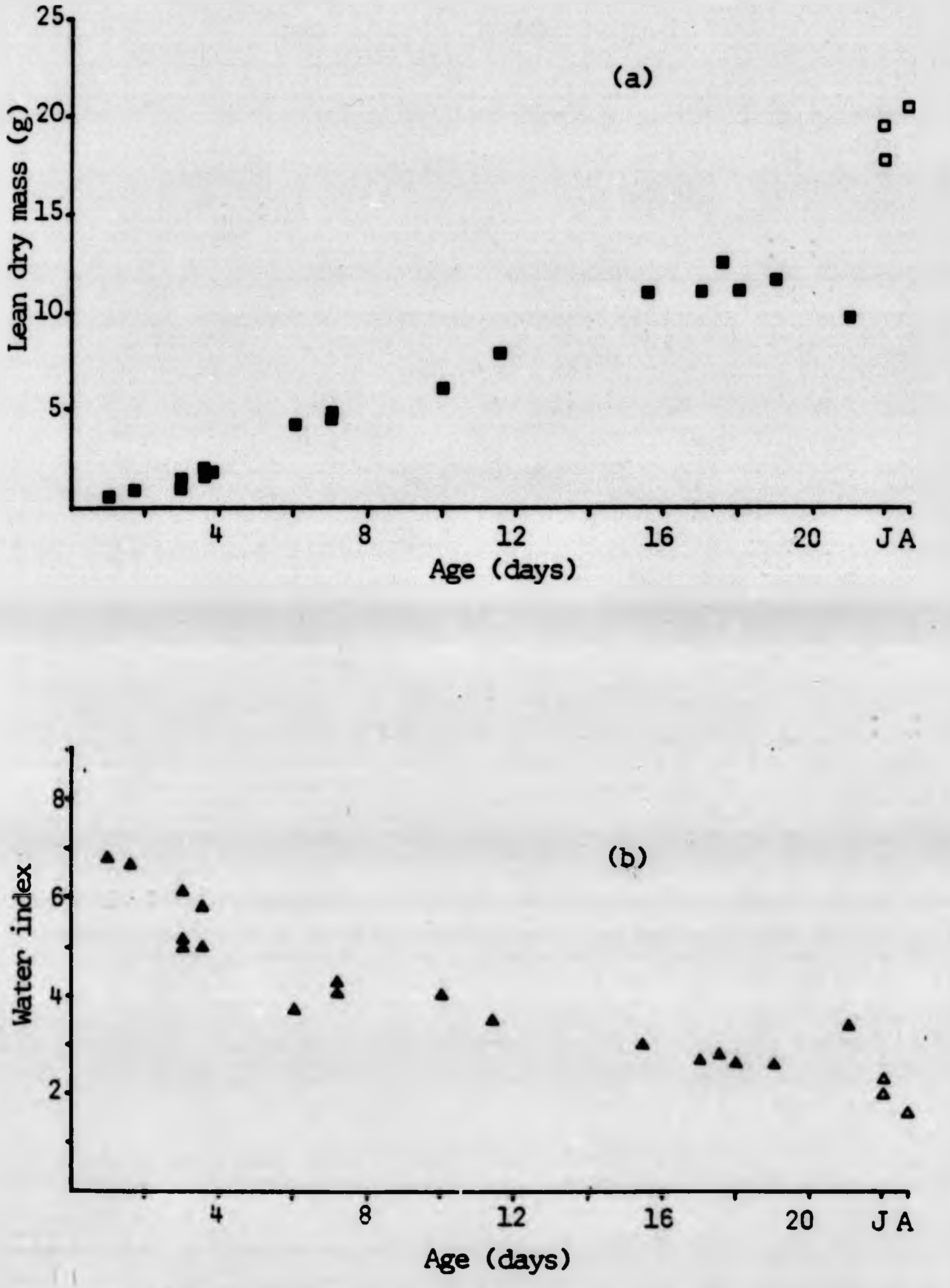


Figure 4.15: (a) Lean dry mass as a function of age in the Dipper.

(b) Water index as a function of age in the Dipper.

J = Juveniles   A = Adults

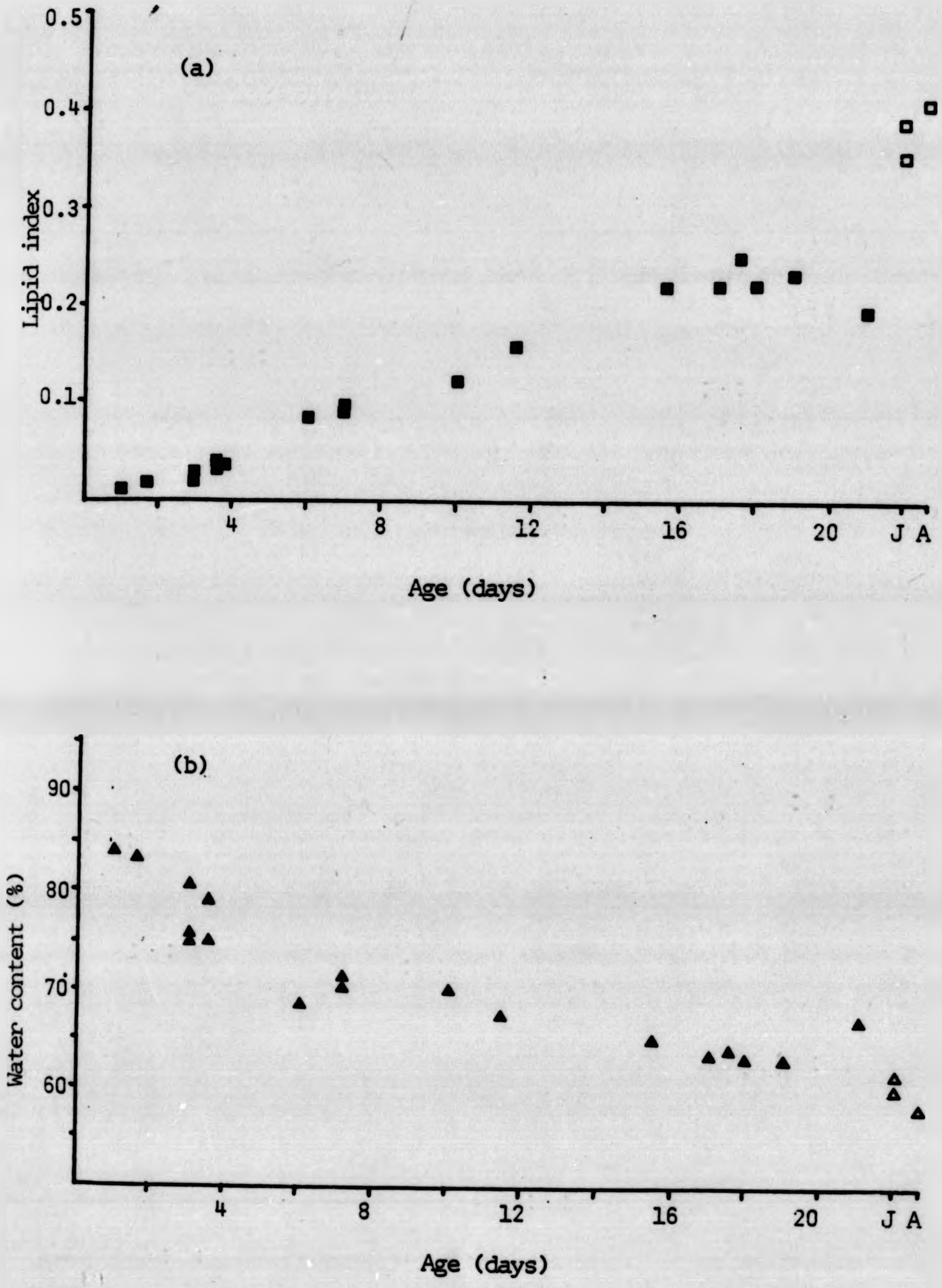


Figure 4.16: (a) Lipid index, and (b) water content as a function of age in the Dipper.
J = Juveniles
A = Adults

variable than either LDM or water index, but increased with age, so that fledglings had lipid indices twice those of adults and juveniles. This can be viewed as a mechanism for ensuring sufficient fat reserves at fledging, when energy demands may increase sharply on leaving the nest. Young are capable of leaving the nest and surviving as early as day twelve. Even at this early age, lipid indices are substantially similar to those of adults and juveniles, Figure 4.16(a).

The mean whole body ash index (Ash mass/LDM) is 0.112 ± 0.015 (Figure 4.21(m)), although individual variation among components with age is marked (Figure 4.21(a-l)). The calorific equivalent of tissue was obtained by multiplying lipid mass by 39.75 and ALDM by 23.64, carbohydrate was assumed to be negligible. Wet energy density (WED = kJ g^{-1} wet weight) and dry energy density (DED = kJ g^{-1} dry weight) were calculated using the mean ash index for the whole body and are plotted in Figure 4.17. WED increased with age so that nestlings fledged with similar WED's to adults and juveniles. DED was, however, more constant with the suggestion of a slight upward trend before tailing off to the lower adult and juvenile levels.

4.2.2 Lean dry mass of body components

All body components increased in LDM with age (Figure 4.18(a-l)), and with the exception of lungs and intestine appear to have lower LDM component masses than juveniles and adults. Differential growth rate of components was examined by calculating the relative lean dry mass of

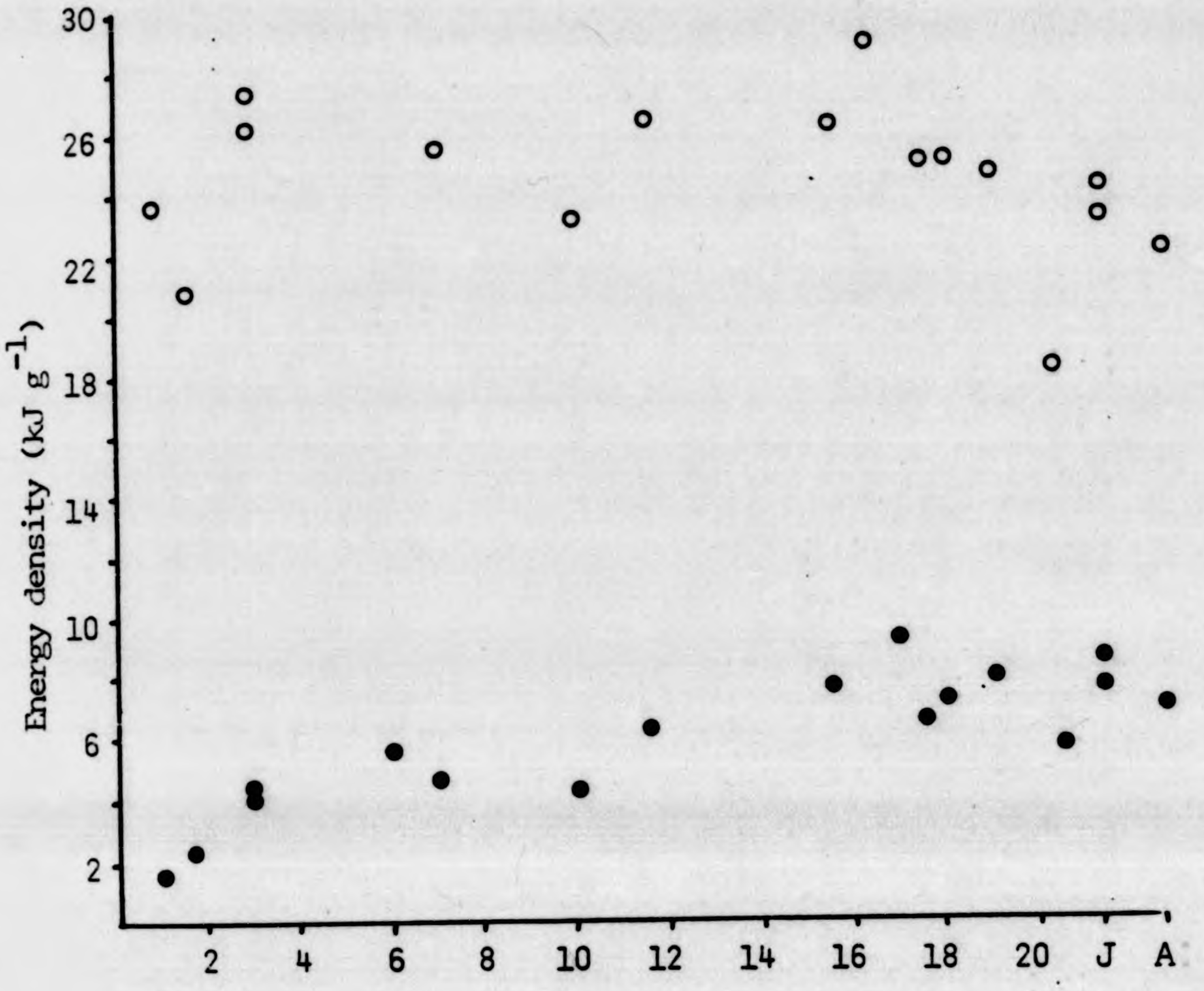


Figure 4.17: Energy density as a function of age in the Dipper

(○) Dry energy density

(●) Wet energy density

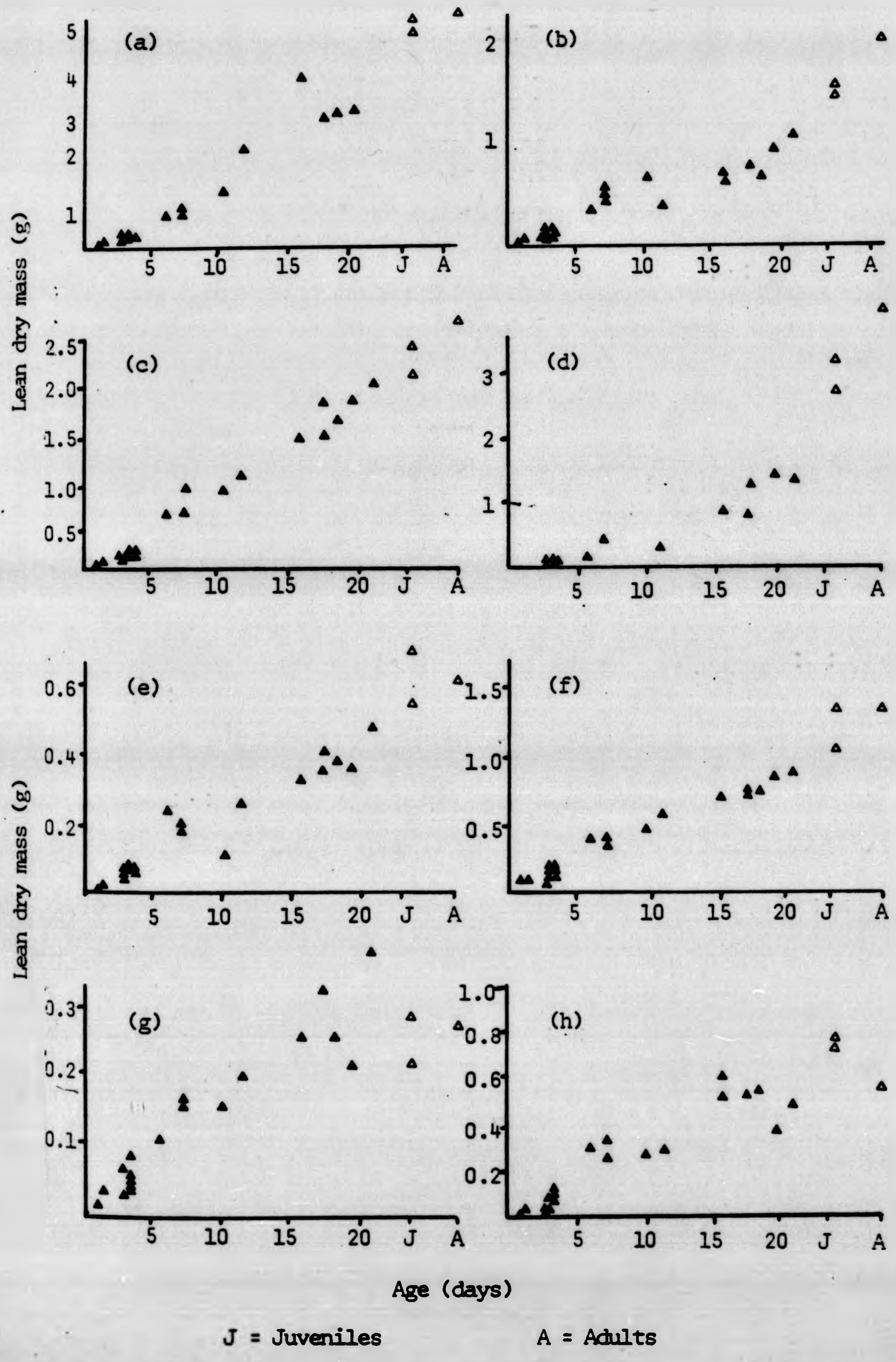
The regression equation for wet energy density is:

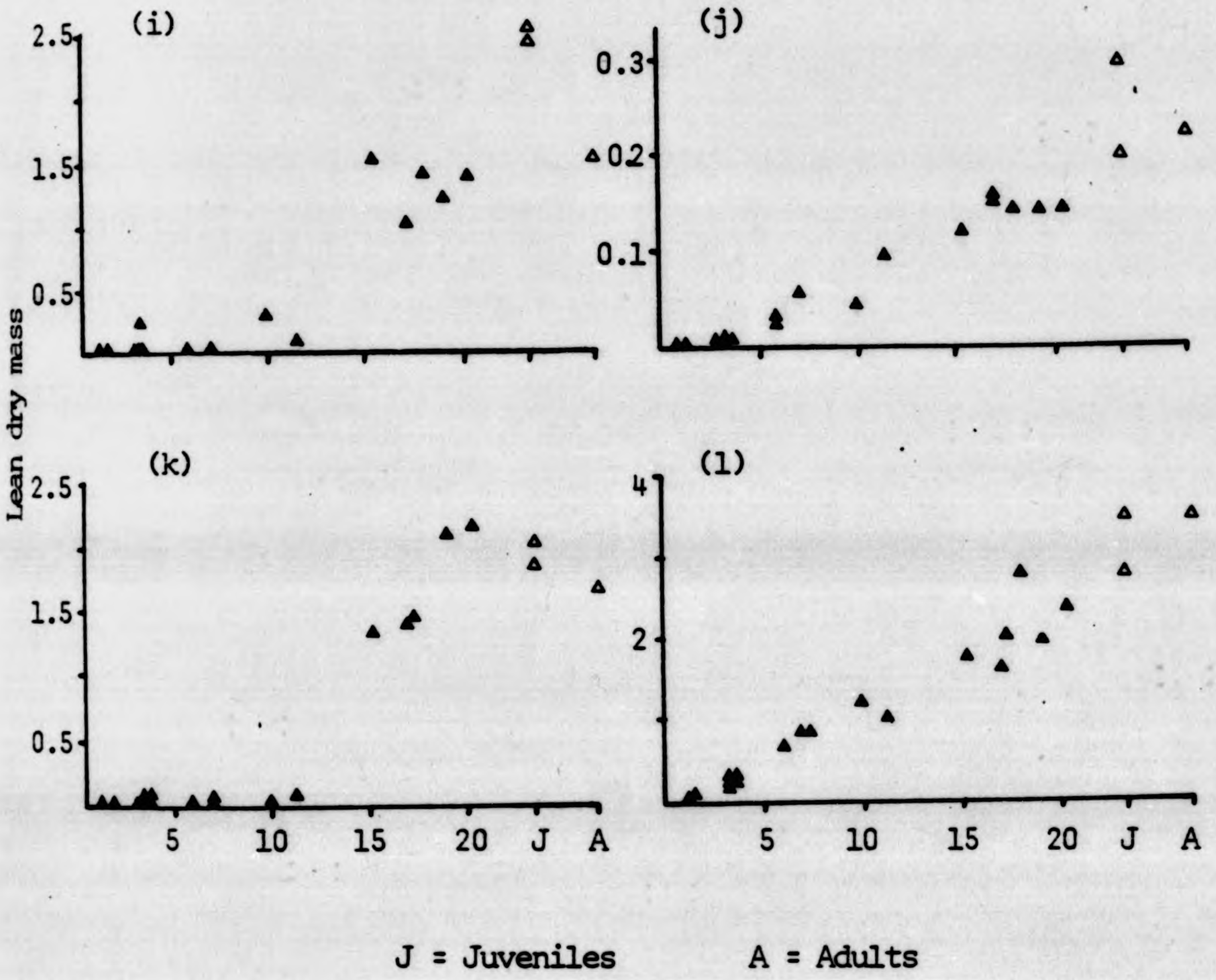
$y = 3.33 + 0.212x$

$r^2 = 63.8$, $F = 23.9$, df 1,12, $p < 0.001$

Figure 4.18: Lean dry mass of Dipper body components as a function of age

(a) Skin and feathers
(b) Wings
(c) Legs
(d) Pectoral muscle
(e) Neck
(f) Head
(g) Intestine
(h) Liver
(i) Heart
(j) Kidneys
(k) Lungs
(l) Body shell


Lean dry mass (g)
(a)
1
2
3
4
5
(b)
1
2
(c)
0.5
1.0
1.5
2.0
2.5
(d)
1
2
3
Lean dry mass (g)
(e)
0.2
0.4
0.6
(f)
0.5
1.0
1.5
(g)
0.1
0.2
0.3
(h)
0.2
0.4
0.6
0.8
1.0
5
10
15
20
J
A
Age (days)
J = Juveniles
A = Adults



(i)
(j)
(k)
(l)
Lean dry mass
2.5
1.5
0.5
0.3
0.2
0.1
4
2
5
10
15
20
J
A
J = Juveniles
A = Adults

each component (RLDM);

$$\mathrm{RLDM}_{\mathrm{component}} = \frac{\mathrm{LDM}_{\mathrm{component}}}{\mathrm{LDM}_{\mathrm{total}}} \times 100 \qquad \text{eqn. 4.2}$$

These are plotted in Figure 4.19 for each component. Growth of body components can also be related allometrically to LDM;

$$\mathrm{LDM}_{\mathrm{component}} = a\ \mathrm{LDM}^{b}_{\mathrm{total}}$$

where a is a constant, and b is the exponent of component LDM on total LDM (e.g. Jones (1985), O'Connor (1977), Tatner (1984)).

In Table 4.7 allometric growth constants for Dipper nestling LDM are also presented. RLDM is initially high and then decreases in the head, neck and liver as also demonstrated by the low values of b (Table 4.7). The RLDM of the gizzard actually peaks at around day six although the height of the peak may be exaggerated by the single high value at 4.5 days. This reflects the importance of the ability of the young to process food and grow rapidly. The peak RLDM of intestine and liver (6% and 7-8% of total LDM) in the Dipper are lower than for some other passerines (Blue Tit, House Sparrow, House Martin; O'Connor (1977)), and resembles more closely the figures for Double Crested Cormorants (8 and 6-7%, Dunn (1975)), and Herring Gulls, Larus argentatus, (8 and 6-7%, Hall (1979)). Ricklefs gives a figure of 7-9% for the liver fraction in the Cactus Wren, Campylorhynchus brunneicapillus (1975) which is also a passerine.

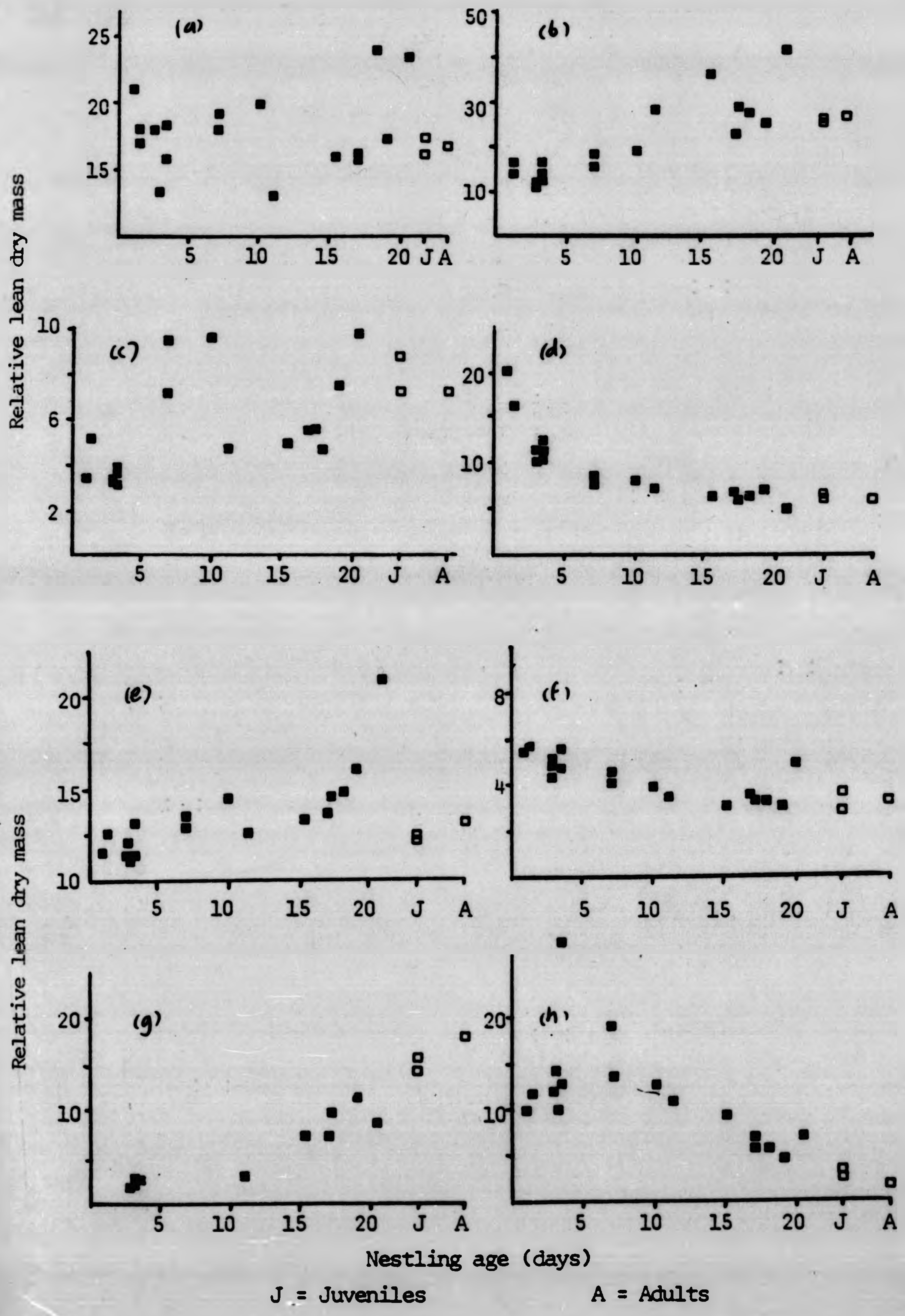
TABLE 4.7: **Allometric growth constants for the lean dry mass of Dipper nestling body components.** The relationship is described by;

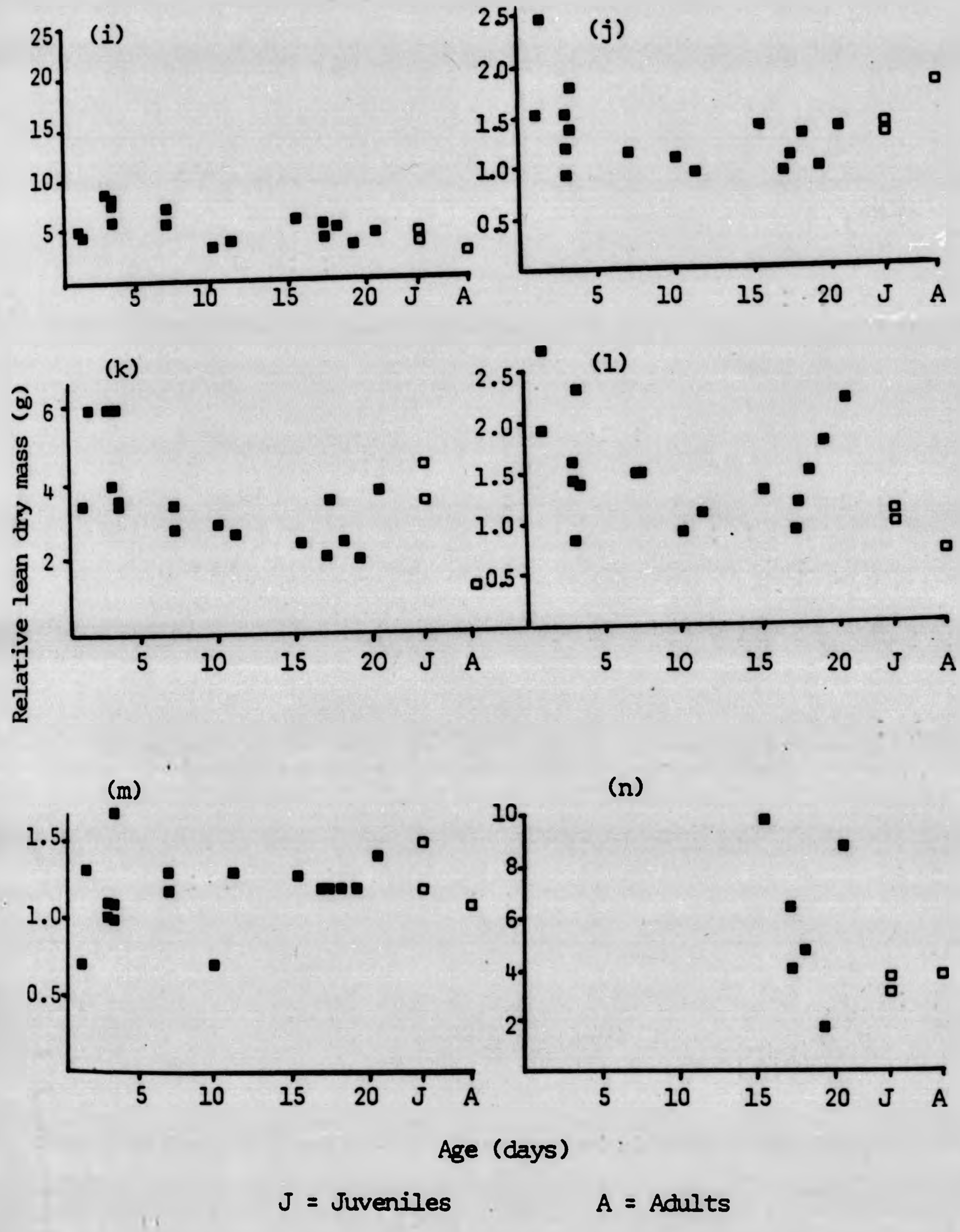
Lean dry mass of component = a lean dry mass of whole body^{b}

Body Component	Slope b	SE of b	Intercept $\log_e$ a	SE of $\log_e$ a
Skin and feathers	1.09	0.026	-1.71	0.060
Pectoral muscles	1.76	0.038	-4.25	0.050
Wings	1.10	0.025	-2.92	0.054
Legs	0.96	0.017	-1.87	0.048
Body Shell	0.90	0.018	-1.42	0.034
Head	0.68	0.012	-1.90	0.036
Gizzard and Oesophagus	0.49	0.028	-1.64	0.055
Intestine.	0.73	0.019	-3.01	0.038
Liver	0.80	0.020	-2.67	0.038
Kidneys	0.98	0.020	-4.36	0.039
Lungs	0.60	0.030	-3.39	0.060
Heart	0.86	0.017	-4.06	0.034

Figure 4.19: Relative lean dry mass of Dipper body components as a function of age

(a) Body shell
(b) Skin and feathers
(c) Wings
(d) Head
(e) Legs
(f) Neck
(g) Pectoral muscles
(h) Gizzard and oesophagus
(i) Liver
(j) Heart
(k) Intestine
(l) Lungs
(m) Kidneys
(n) Flight feathers and tail


(a)
25
20
15
5 10 15 20 J A
(b)
50
30
10
5 10 15 20 J A
Relative lean dry mass
(c)
10
6
2
5 10 15 20 J A
(d)
20
10
5 10 15 20 J A
(e)
20
15
10
5 10 15 20 J A
(f)
8
4
5 10 15 20 J A
Relative lean dry mass
(g)
20
10
5 10 15 20 J A
(h)
20
10
5 10 15 20 J A
Nestling age (days)
J = Juveniles
A = Adults


(i)
(j)
(k)
(l)
(m)
(n)
Relative lean dry mass (g)
5
10
15
20
J
A
Age (days)
J = Juveniles
A = Adults

O'Connor (1984) has shown a relationship between the relative growth of the liver (coefficient of allometry during the first few days of growth) and total body growth expressed in terms of the growth constant K. The Dipper fits well into this relationship: Relative growth of liver = 1.4, K = 0.328.

Skin and feather, leg and pectoral RLDM increase with age and have exponents of allometry of greater than b = 1 demonstrating that they grow faster than the body as a whole.

4.2.3 <u>Lipid content of body components</u>

In Table 4.9 nestling lipid content is given for each component as a function of total lipid. Lipid content combines that fraction of lipid within the tissues and the subcutaneous lipid deposits. Lipid content is therefore not a measure of actual fat stores, although it is likely to be directly proportional to these. The slope b partitions component lipid over the nestling period. Hence the skin and feathers component accounts for 31%, body shell 21% and legs 7.6% of total body lipid. Body lipid in the skin and feather component is subcutaneous hence feathers do not contribute to lipid content. The exponents in treatment II suggest, however, that lipid is preferentially stored in the skin, pectoral muscle and wing fractions of the body. Wings and pectoral muscle only account for about 10% of total body lipid however.

Correcting for autocorrelation (i.e. removing component lipid in turn) between component lipid content and

TABLE 4.8: Allometric growth constants for the water indices of Dipper nestling body components. The relationship is described by;

Water index of component = a water index of whole body^b

Body Component	Slope b	SE of b	Intercept $\log_e$ a	SE of $\log_e$ a
Skin and feathers	1.78	0.029	-1.41	0.040
Pectoral muscles	0.86	0.020	0.42	0.025
Wings	1.30	0.012	-0.37	0.016
Legs	0.97	0.014	-0.12	0.019
Body Shell	0.76	0.010	0.34	0.013
Head	0.93	0.026	0.38	0.035
Neck	0.88	0.007	0.31	0.011
Gizzard and Oesophagus	0.40	0.023	0.57	0.031
Intestine	0.312	0.029	1.12	0.038
Liver	0.51	0.016	0.72	0.021
Kidneys	1.21	0.031	0.20	0.041
Lungs	0.67	0.035	0.91	0.047
Heart	0.81	0.041	0.58	0.054

TABLE 4.9: Fat content of Dipper nestling body components expressed as a function of total body fat

[a]Component	I Component fat as a function of total fat		II $\log_e$ (component fat) as a function of $\log_e$ (total fat)			III Component fat as a function of "corrected" total fat	
	b	r	b	SE of b	r	b	r^2
Skin and feathers	0.308	0.905	1.10	0.031	0.894	0.389	0.634
Pectoral muscles	0.056	0.544*	1.27	0.084	0.787	0.053	0.215*
Wings	0.050	0.845	1.17	0.019	0.963	0.051	0.684
Legs	0.076	0.911	0.957	0.028	0.879	0.080	0.803
Body Shell	0.210	0.905	0.960	0.027	0.894	0.247	0.712
Head	0.039	0.864	0.699	0.024	0.843	0.040	0.726
Gizzard and Oesophagus	0.015	0.640	0.420	0.028	0.615	0.015	0.391
Intestine	0.045	0.827	0.826	0.039	0.782	0.046	0.653
Liver	0.029	0.666	0.678	0.023	0.8473	0.030	0.389
Kidneys	0.010	0.587	0.650	0.026	0.811	0.011	0.294
Lungs	0.004	0.752	0.658	0.021	0.872	0.004	0.514
Heart	0.005	0.711	0.886	0.022	0.915	0.005	0.551

[a] Components were dissected as in Section 3.1.3

All regressions significant to $p < 0.001$, except * pectoral Treatment I ($p < 0.01$), and Treatment III ($p < 0.05$), $n = 20$

total lipid content, reduced the significance of the regression in all cases, although all still remained significant; the pectoral muscles just so (see Table 4.9(II)). The rank order of component lipid deposition as expressed by b in the Dipper is identical to that found in the Sand Martin (Jones, 1985), although the values differ slightly.

4.2.4 Water indices of body components

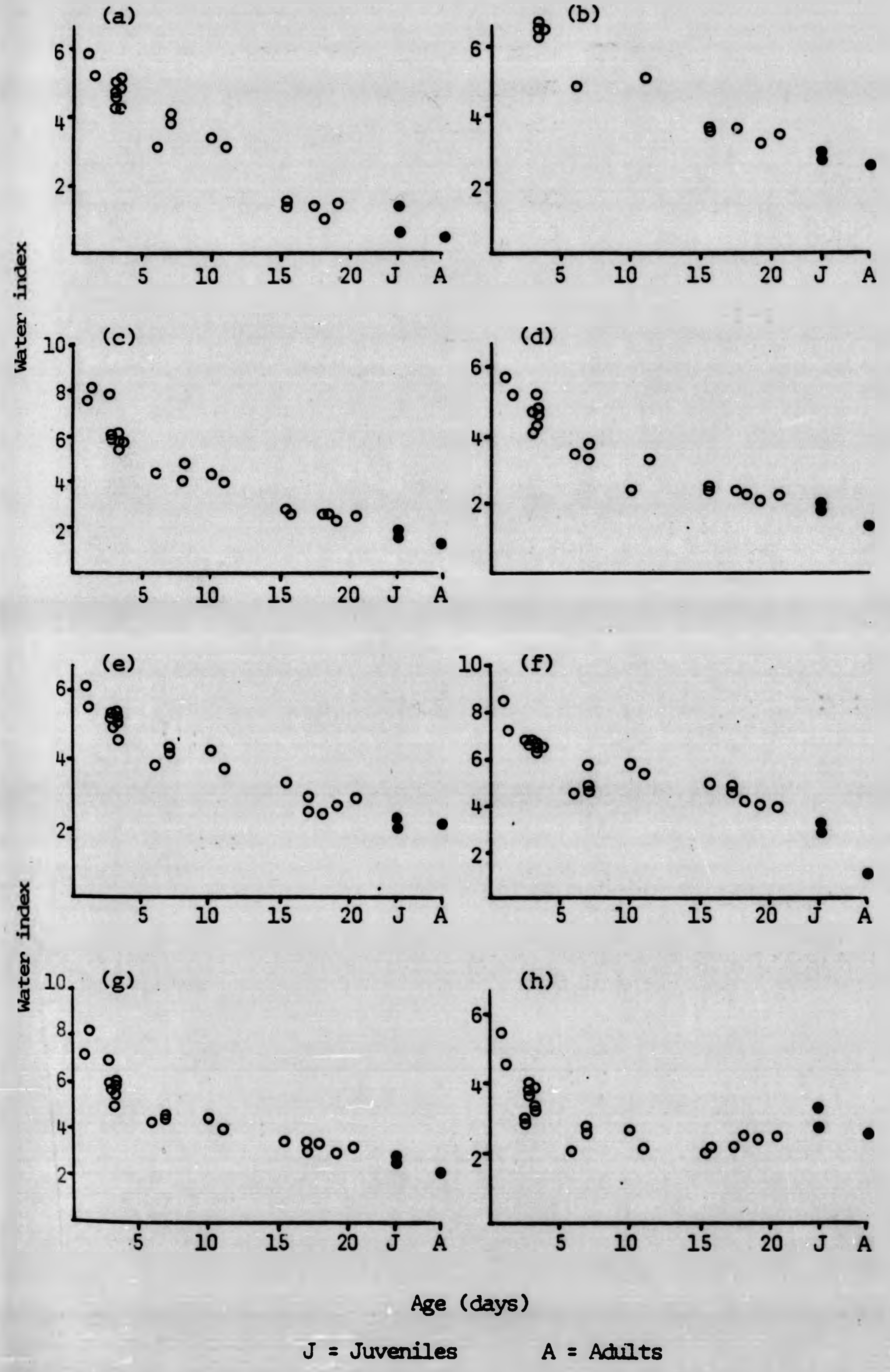
Water indices are plotted as a function of age in Figure 4.20 for nestling body components. Water index decreased in all cases with age, but the gizzard, liver and lungs have declined to likely adult levels by the first week of growth, whilst the other components remain slightly higher than adults even among fledglings. Since low water indices are considered to represent advanced functional maturity of components (Ricklefs, 1974), then those associated with digestion (see above) become functionally mature relatively early as well as being of large size (see Section 4.2.2). This is borne out by the exponents in Table 4.8, for the liver, intestine and lungs which all have very low values suggesting they have lower water indices than the body as a whole. Skin, feather, and wings appear to mature notably slower than the rest of the body.

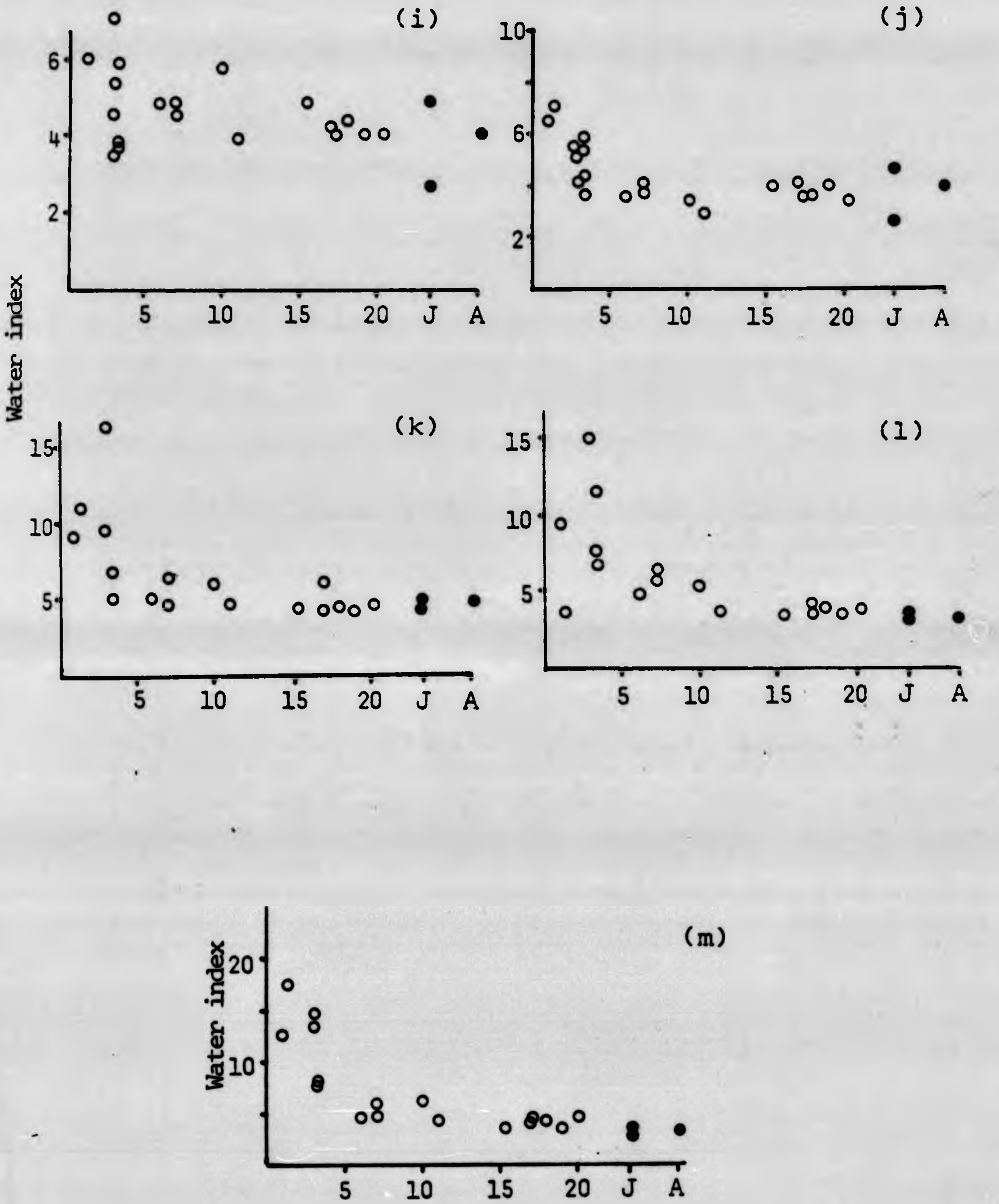
4.2.5 Ash indices of nestling body components

Data for whole body ash indices are scarce and exist for only a handful of species (Austin & Ricklefs, 1977; Bryant & Gardiner, 1979; Ricklefs, 1967,1975). Data for mean ash indices of individual body components have been

Figure 4.20: Water index of Dipper body components as a function of age

(a) Skin and feather
(b) Pectoral muscles
(c) Wings
(d) Legs
(e) Body shell
(f) Head
(g) Neck
(h) Gizzard and oesophagus
(i) Intestine
(j) Liver
(k) Kidneys
(l) Lungs
(m) Heart


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Water index
Water index
2
4
6
8
10
5
10
15
20
J
A
Age (days)
J = Juveniles
A = Adults



J = Juveniles A = Adults

published for only two species; the House Martin (Bryant & Gardiner, 1979) and the Red-winged Blackbird, Agelaius phoeniceus, (Ricklefs, 1967b). These data are compared with those found in this study for the Dipper in Table 4.10. In each case the way ash index changes with age is noted and the range of values (maximum and minimum) representing changes from smaller chicks to older chicks (but see (c) Table 4.10) are also shown. The full data for the Dipper are plotted in Figure 4.2~~0~~1, and the significance of regression lines fitted through the data are presented in Table 4.11.

Ranges and trends for all components that contain skeletal material (wings, neck, legs, head) are remarkably similar, despite the difference in the size of the species concerned. The percentage of ash in those components which do not contain skeletal material (integument, heart, liver, gizzard, intestine) are more variable. House Martins have ash indices for these components about half that of Dippers, whilst the Red-winged Blackbird integument figures resemble those of the Dipper, perhaps due to its similar total body mass. The regression equations in Table 4.11 were used to calculate ash free lean dry mass (ALDM) for calculation of the energy content of body tissues with age (see 4.2.6).

Whilst there was no obvious increase or decrease of whole body ash index with age (Figure 4.21(m), Table 4.11), there is a suggestion that ash index falls from a high value at hatching until about day ten and then increases again. In this respect it is worth quoting Ricklefs' (1967b) work on the

TABLE 4.10: A comparison of ash index for nestling body components in three passerine species as a function of age. Table shows trend with age and range of values measured.

Ash Index = Ash mass/lean dry mass

Body Component	Red-Winged Blackbird[a]	Dipper	House Martin[b]
Wings	Increases 9-23%	Increases 9-24.5%	Increases 9-23%
Legs	Increases 11-21.0%	Increases 11.7-19.3%	Increases 11.6-16.55%
Head	Increases 12.0-18.0%	Increases 15.0-17.8%	No change[c] 14.4%
Integument	Decreases 10.0-3.0%	Decreases[d] 8.5-1.0%	No change 3.0%
Pectoral Muscle	Decreases -	No change 4.0%	-
Heart	Decreases -	No change 10.5%	No change 5.2%
Liver	Decreases	Decreases 16.7-0.6%	-
Neck	-	Increases 13.1-16.8%	No change 13.2%
Gizzard and Oesophagus	-	No change 9.0%	No change 4.9%
Intestine	-	No change 16.0%	No change 6.9%

[a] Ricklefs, 1967

[b] Bryant & Gardiner, 1979, range shows minimum and maximum value for the early part of the growth period only

[c] Single figures are mean values

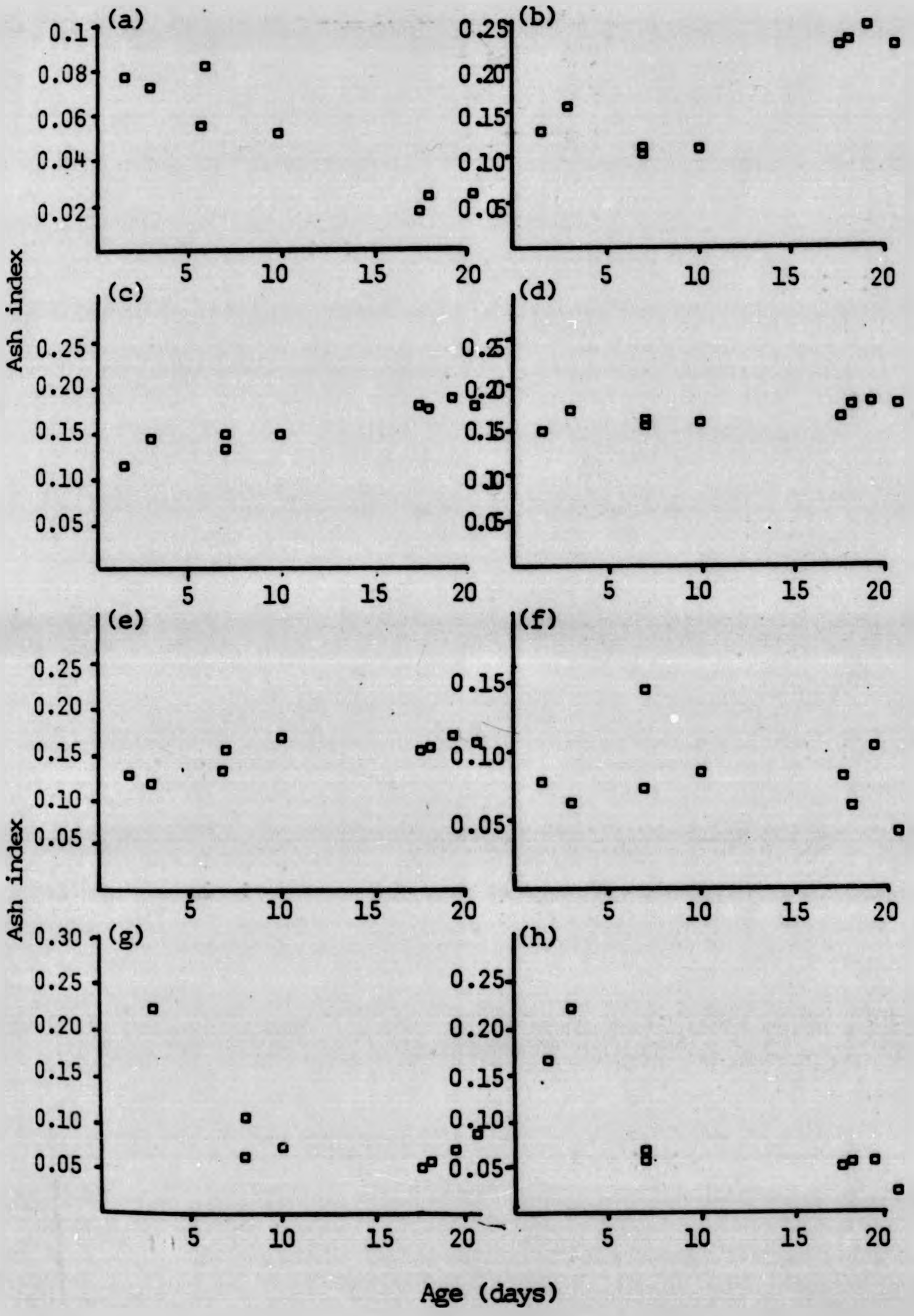
[d] Skin and feather

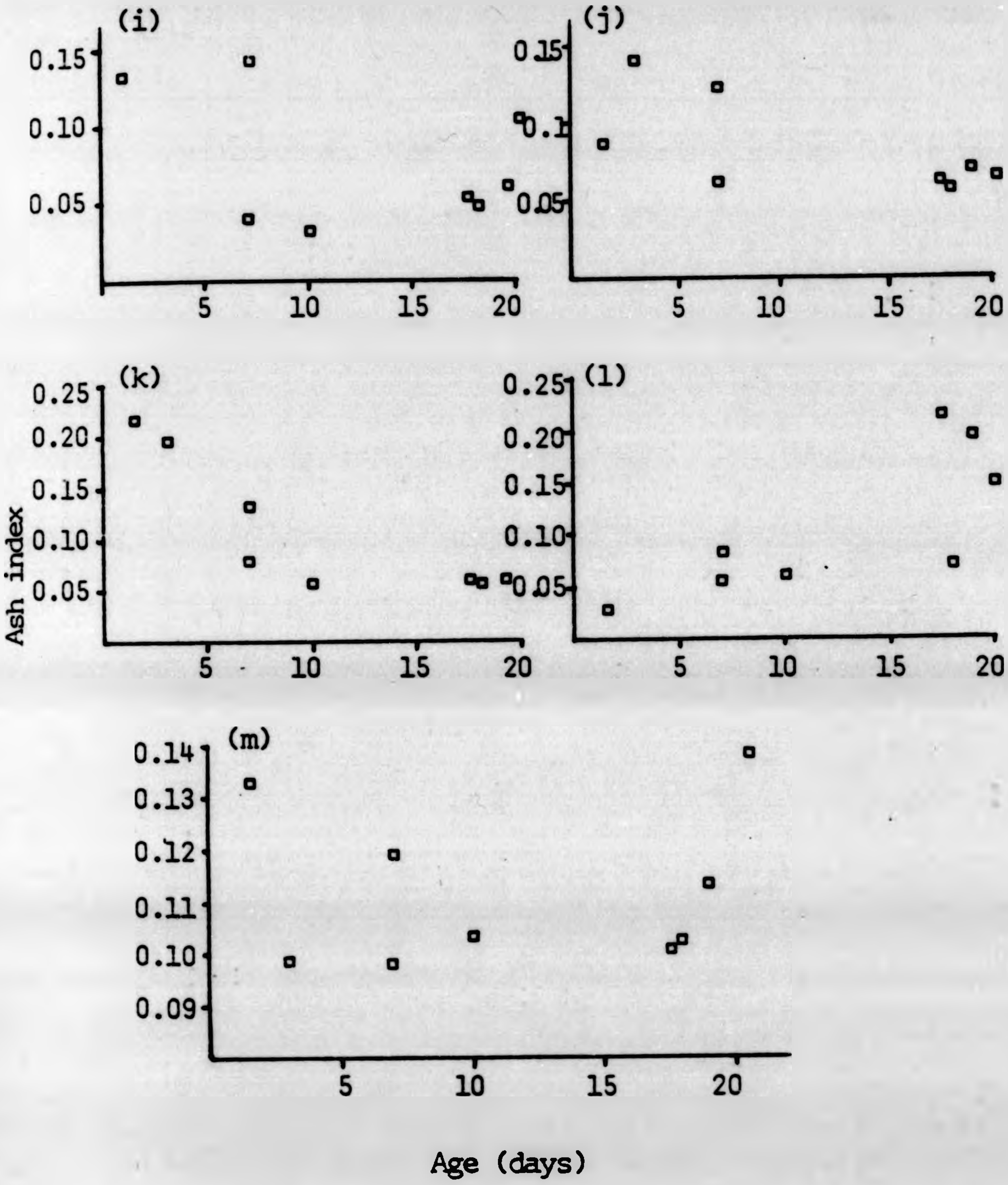
TABLE 4.11: Regression equation parameters for the change in ash index with age (days) for Dipper nestling body components

Body Component	Intercept a	SE of a	Slope b	SE of b	r^2	significance
Skin and feathers	0.085	0.003	−0.0033	0.0004	34.4	$p < 0.005$
Wing	0.089	0.008	+0.0068	0.0006	66.8	$p < 0.01$
Legs	0.117	0.002	+0.0033	0.0002	83.8	$p < 0.001$
Head	0.150	0.002	+0.0012	0.0001	51.7	$p < 0.02$
Neck	0.131	0.003	+0.0016	0.0002	44.9	$p < 0.05$
Gizzard and oesophagus	0.090	0.007	−0.0009	0.0005	0.0	NS
Intestine	0.160	0.014	−0.0053	0.001	31.9	NS
Liver	0.167	0.012	−0.0070	0.0008	55.9	$p < 0.05$
Heart	0.105	0.013	−0.0026	0.0009	0.0	NS
Lungs	0.115	0.006	−0.0027	0.0005	34.8	NS
Kidney	0.191	0.010	−0.0082	0.0008	64.7	$p < 0.02$
Body Shell	0.104	0.006	+0.0031	0.0004	50.8	$p < 0.05$
Whole body	0.110	0.004	+0.0001	0.0003	0.0	NS

Figure 4.21: Ash index of Dipper body components as a function of age

(a) Skin and feather
(b) Wings
(c) Legs
(d) Head
(e) Neck
(f) Gizzard and oesophagus
(g) Intestine
(h) Liver
(i) Heart
(j) Lung
(k) Kidney
(l) Body shell
(m) Whole body


(a)
0.1
0.08
0.06
0.04
0.02
5
10
15
20
(b)
0.25
0.20
0.15
0.10
0.05
5
10
15
20
Ash index
(c)
0.25
0.20
0.15
0.10
0.05
5
10
15
20
(d)
0.25
0.20
0.15
0.10
0.05
5
10
15
20
(e)
0.25
0.20
0.15
0.10
0.05
5
10
15
20
(f)
0.15
0.10
0.05
5
10
15
20
Ash index
(g)
0.30
0.25
0.20
0.15
0.10
0.05
5
10
15
20
(h)
0.25
0.20
0.15
0.10
0.05
5
10
15
20
Age (days)


(i)
0.15
0.10
0.05
5
10
15
20
(j)
0.15
0.1
0.05
5
10
15
20
(k)
0.25
0.20
0.15
0.10
0.05
Ash index
5
10
15
20
(l)
0.25
0.20
0.15
0.10
0.05
5
10
15
20
(m)
0.14
0.13
0.12
0.11
0.10
0.09
5
10
15
20
Age (days)

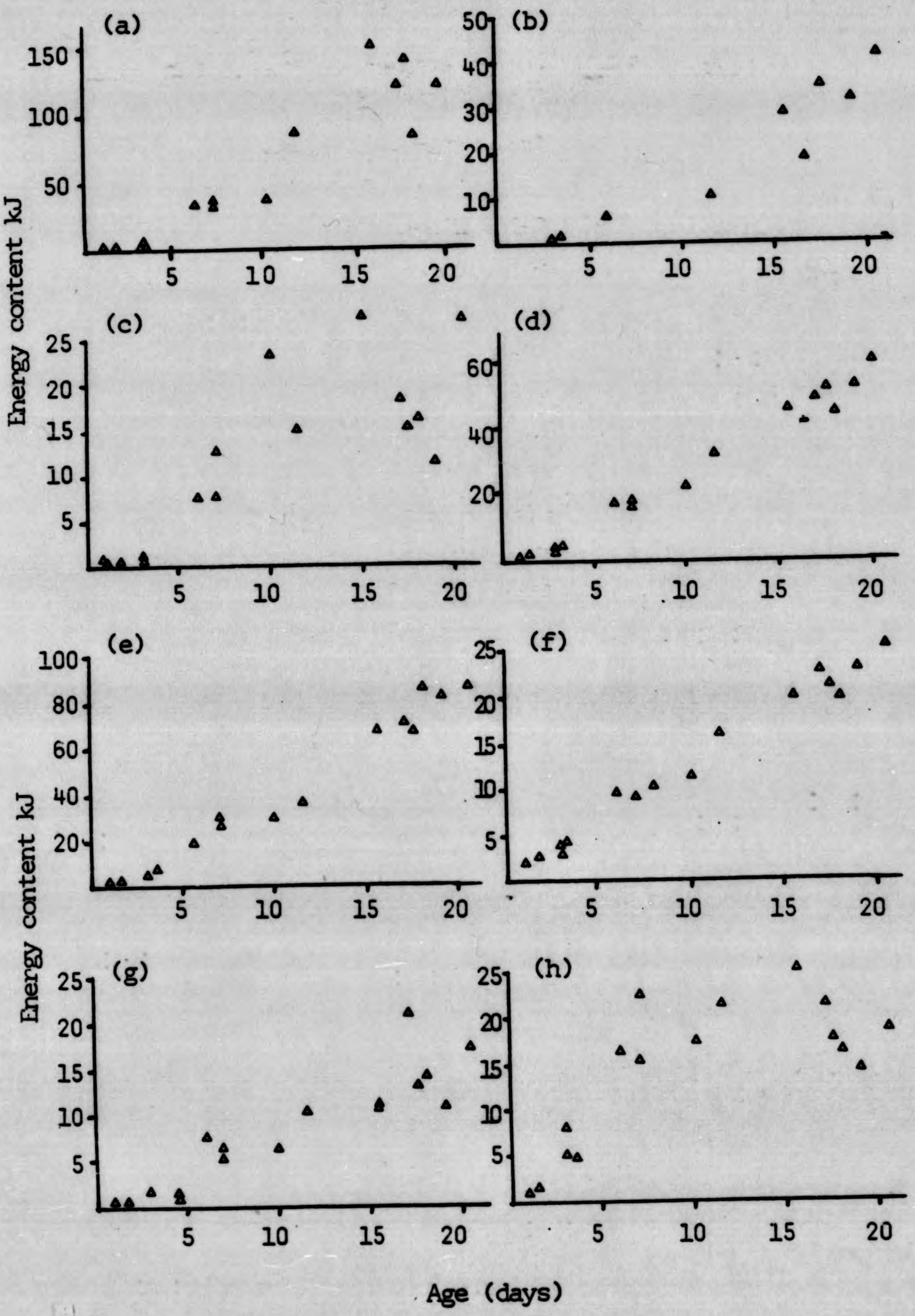
Red-winged Blackbird and comparing his findings to Figure 4.20(m). He states that "the ash index of Red-winged Blackbird nestlings is high initially (13-15 per cent of hatching) and drops to about 10% at five days of age before rising to about 12% by the time of fledging". Austin & Ricklefs (1977) also found this pattern of change in the Cactus Wren, Campylorhynchus brunneicapillus: 10.7% at day 0, decreasing to 6.6% at day four, then increasing to 9.5% at fledging.

4.2.6 The energy content of nestling body components

The energy content of whole body and body components is plotted in Figures 4.23, 4.22. All components continue to increase in energy content until fledging, with the exception of the gizzard, which decreases from about half way through the nestling period. Bryant & Gardiner (1979) found a similar pattern of gizzard energy content change for the House Martin in the only other study that has published data on body component energy content changes with age. The liver energy content increases quickly initially and then levels off, again emphasising early investment of growth in food processing organs. Total energy content increases linearly with age (Figure 4.23). The exponent of the log-log regression (1.27) is lower than that quoted for other species; Barn Swallow 1.65, Cactus Wren 1.39, Rufous-winged Sparrow 1.39 (Austin & Ricklefs, 1977). This is probably due to the fact that Dipper nestlings start with relatively high lipid indices (Figure 4.19), resulting in their high initial energy density

Figure 4.22: Energy content of Dipper body components as a function of age.

(a) Skin and feather
(b) Pectoral muscle
(c) Wings
(d) Legs
(e) Body shell
(f) Head
(g) Neck
(h) Gizzard and oesophagus
(i) Intestine
(j) Liver
(k) Kidneys
(l) Lungs
(m) Heart


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Energy content kJ
Energy content kJ
150
100
50
50
40
30
20
10
25
20
15
10
5
60
40
20
100
80
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25
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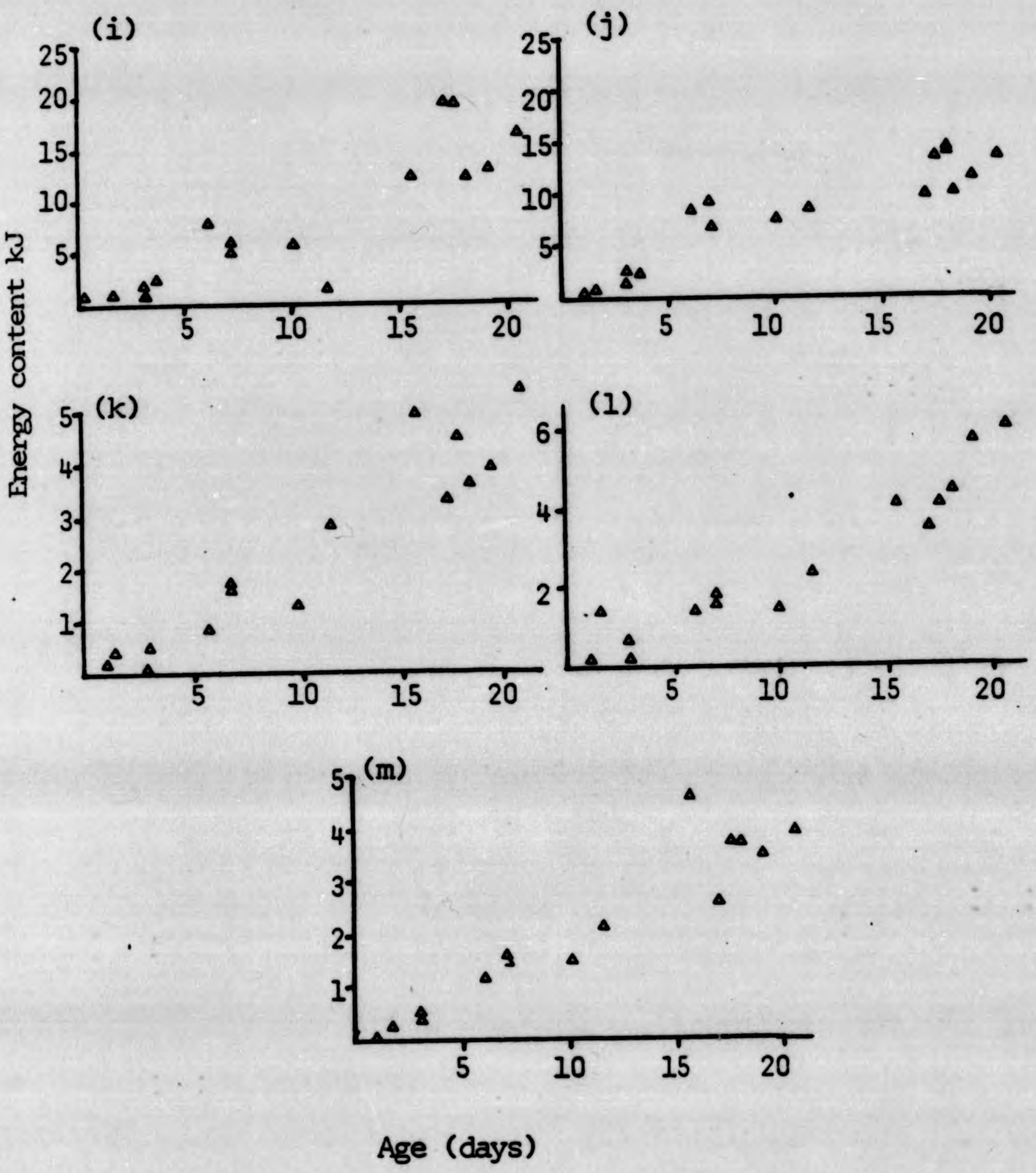
Age (days)


(i)
(j)
(k)
(l)
(m)
Energy content kJ
25
20
15
10
5
6
4
3
2
1
5
10
15
20
Age (days)

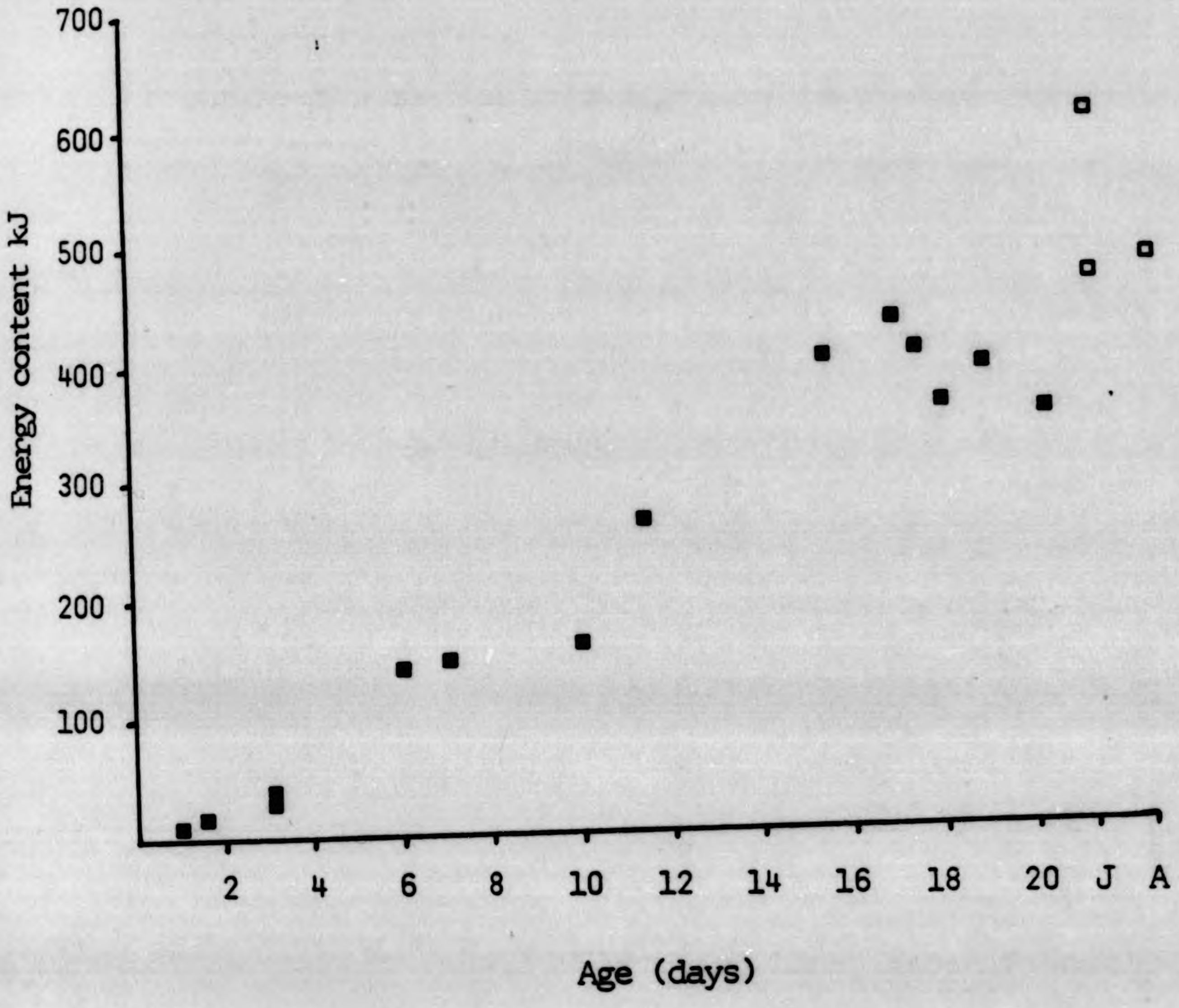


Figure 4.23: Energy content of Dippers as a function of age

(■) Nestlings

(□) Juveniles and adults

The regression equation is:

$\log_e y = 2.30 + 1.27 \log_e x$

$r^2 = 0.98$, $n = 14$, $p < 0.001$

figures of 3.31 kJ g^{-1}, and low slopes of increase in energy density during growth, 3.38 kJ g^{-1} day^{-1} (O'Connor, 1984).

4.3 RESTING METABOLISM OF 'MATURE' DIPPER NESTLINGS

Night-time resting metabolism of well grown (> 12 days) dipper nestlings, able to thermoregulate was measured for brood sizes of 1 - 3 and at three different temperatures; 5°C, 15°C, 25°C. Chamber temperatures of 5°C and 15°C are comparable with field T_a (mean 7.6, range 2.9-14.6°C, n = 36 days observations), whilst field T_a never reached 25°C. The temperatures that nestlings experienced within the nest during periods of inattentiveness in the wild ranged from 12.7-18.7°C (mean = 15.1, n = 11 days observations).

The results of the metabolism study are presented in Table 4.12(a) and Figure 4.24. A two-way analysis of variance (Table 4.12(b)) of resting metabolism against brood-size and temperature was significant (F = 3.03, df 8,26 $p < 0.05$). Nestling metabolic rate tended to decrease with increasing brood-size and temperature. Metabolic rate at 5°C was higher than at 15°C and 20°C across brood-sizes, although single nestlings raised their metabolic rates to a higher level than broods of two or three (Figure 4.24). Single nestlings progressively reduced their metabolic rate as ambient temperature increased. There was no difference between metabolic rate at 15°C and 25°C for broods of two and three although it was lower than at 5°C and comparable to metabolism of a single nestling at 25°C. Huddling thus reduces metabolic costs at low (5°C) temperatures but has less effect at higher

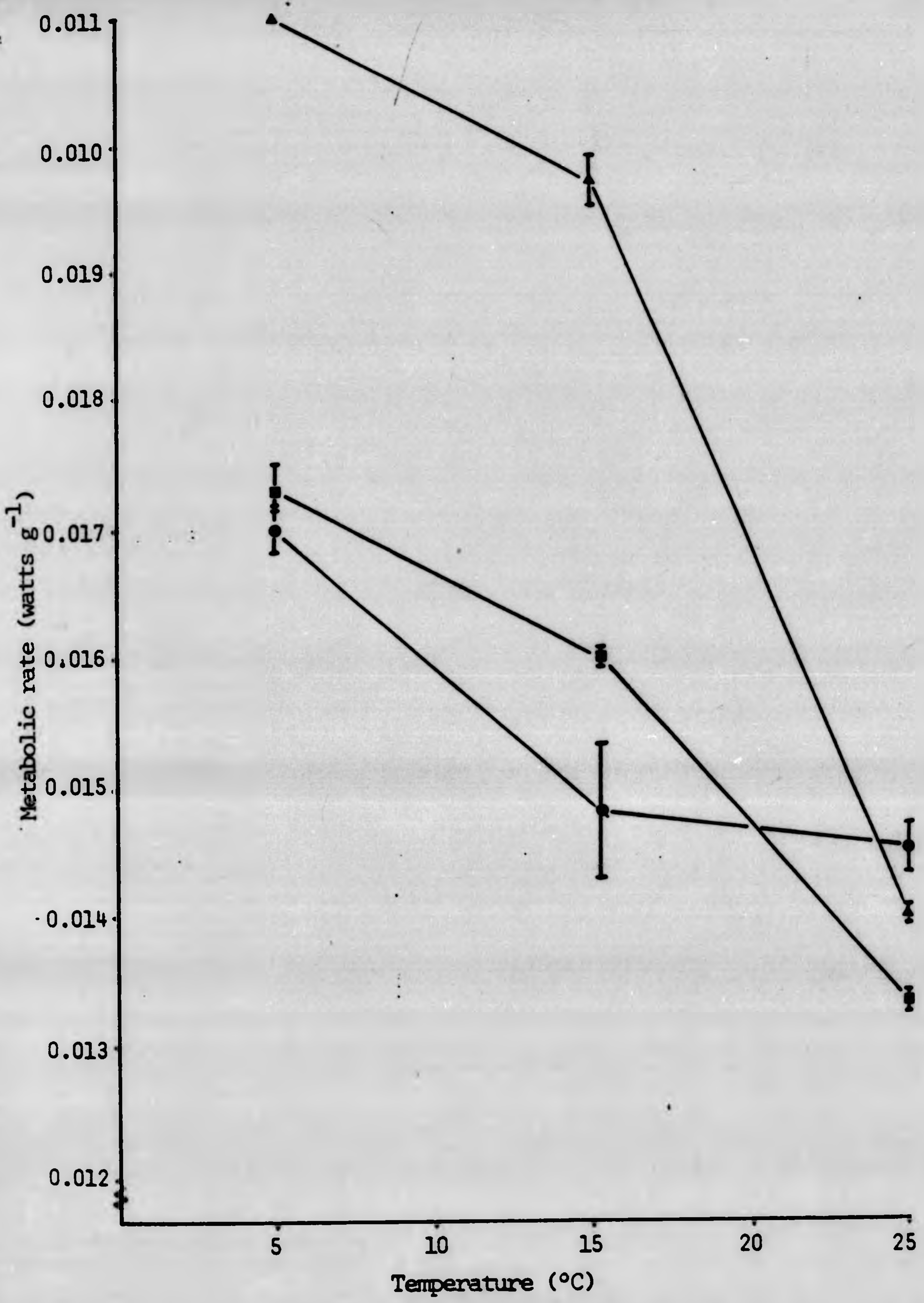


Figure 4.24: Metabolic rate as a function of brood-size and temperature in Dipper nestlings (means ± 1 S.D.)

See also Table 4.12

(▲)	Brood-size 1
(■)	Brood-size 2
(●)	Brood-size 3

TABLE 4.12a: **The mean metabolic rate (± SE) as a function of brood size and temperature in nestling Dippers**

Brood size	Chamber Temperature (°C)	Metabolic rate (Wg^{-1})
1	5	0.0210 ± 0.0000
	15	0.0197 ± 0.0013
	25	0.0140 ± 0.0000
2	5	0.0173 ± 0.0020
	15	0.0160 ± 0.0007
	25	0.0133 ± 0.0010
3	5	0.0170 ± 0.0020
	15	0.0148 ± 0.0005
	25	0.0145 ± 0.0020

Two-way analysis of variance; $F = 3.03$, df 8.26, $p < 0.05$

TABLE 4.12(b): **The effect of broodsize and temperature on resting metabolism in Dipper nestlings, from a two-way analysis of variance**

Source of variation	F	Significance	Degrees of Freedom
Broodsize	4.008	0.036	2
Temperature	3.902	0.039	2
Main effects combined	3.992	0.017	4
Interaction	2.065	0.128	4
Main effects and interaction combined	3.028	0.024	8

temperatures. Huddling in broods of three does not appear to significantly increase savings above broods of two.

4.4 THERMOREGULATION

4.4.1 Model parameters for predicting cooling and reheating rates of Dipper nestlings

Nestling cooling rates were examined in the Dipper in the laboratory and in the field using a portable microprocessor based logging device (Section 3.3.1). Reheating rates were examined in the field only. Rates are expressed as the slope of the fitted $\log_e$ temperature versus time curve which implies a constant proportional change in temperature with time. The slope is the proportion by which initial body temperature drops and can be converted to cooling rate expressed as $°C.°C^{-1}.h^{-1}$ using the equation in Section 4.4.6. All fitted curves were significant at $p < 0.005$.

Several parameters were expected to influence cooling and reheating rates (see Section 4.4.3, 4.4.4). These are presented in Table 4.12(b). The parameters were entered into a stepwise multiple regression analysis using the SPSSX statistical package (Nie et al., 1983). The procedure was halted when the next variable to be entered had a non-significant t-value. It was informative, however, on occasions (see below) to enter variables into the regression that would not have been entered first because of their lower levels of significance. Such variables are hereafter termed 'forced' variables.

TABLE 4.12(c): Model parameters for predicting cooling and reheating rates of Dipper nestlings

BSIZE = Broodsize

BMASS = Brood mass (g)

NMASS = Nestling mass (g)

TIME = Duration of cooling/reheating event (mins)

AGE = Mean age of the brood (days)

RATE = Slope of the $\log_e$ temperature (°C) on time (hours) curve. RATE is synonymous with LCR, FCR and FRR in the text

TA = Ambient temperature (°C)

TB = Initial nestling body (leg-pit) temperature (°C) i.e. immediately prior to cooling or reheating event

TN = Nest temperature (°C)

TBA = TB-TA (°C)

TBN = TB-TN (°C)

TAN = TN-TA (°C)

TBB = K-TB (°C), for reheating only, where K is the mean 'uncooled' nestling body (leg-pit) temperature and is equal to 35.1°C

TBA_i = The temperature gradient between nestling and environment taking into account nest insulation, and is given by $TB-\left(\frac{TAN}{TBN} \times TA\right)$

BSAM = (Brood surface area:mass ratio) x 100

NSAM = (Nestling surface area:mass ratio) x 100

MSAM = Mean surface area:mass ratio, calculated as;

$$\frac{NSAM + (BSAM/BSIZE)}{2}$$

4.4.2 A model of cooling rates of Dipper nestlings in the laboratory

The mean cooling rate of Dipper nestlings in broods of three was;

0.849 ± 0.187 (range = 0.67-1.19, n = 9).

The following variables were entered into a stepwise multiple regression analysis; TA, NMASS, TIME, TB, TBA, BMASS, RATE and BSAM. 93.4% of the variance in cooling rate was explained by the variables NMASS, TA and TB (beta values are 7.68, -5.78 and 3.57 respectively). The relationship (see Table 4.13) is expressed as;

$$\text{Laboratory cooling rate} = 0.56 + (0.051 \times \text{NMASS}) - (0.09 \times \text{TA}) + (0.022 \times \text{TB}) \quad \text{eqn. 4.3}$$

$$F = 23.71, \text{ df } 3, 5, \quad p = 0.0023$$

A matrix of Pearson correlation coefficients is presented in Table 4.14. A number of relationships warrant discussion. Firstly, brood mass is highly correlated with all variables with the exception of TB. This is due in part to chance effects given the low number of broods examined (n = 3), for example the relationship with TA and TBA, since there is no reasonable explanation why brood mass should be correlated with either TA or TBA and brood mass shows no significant relationship with TB. BMASS and NMASS are correlated with each other, because as individual nestlings grow they contribute more towards brood mass, i.e. a brood of heavy individual nestlings will result in a heavy brood mass. Only NMASS is significantly correlated with cooling rate, yet

TABLE 4.13: Step-down multiple regression analysis of factors influencing laboratory cooling rates (LCR) of 7-8 day old Dipper nestlings in broods of three

Independent variable	Partial regression coefficient b	SE of b	Standardised partial regression coefficient Beta	t-value	significance of t
Nestling mass (=NMASS) (g)	0.051	0.007	1.748	7.676	p = 0.0006
Ambient temperature (=TA) (°C)	-0.091	0.016	-1.171	-5.778	p = 0.0022
Body temperature (=TB) (°C)	0.022	0.006	0.636	3.566	p = 0.0161

F = 23.71, df 3,5, p = 0.0022

the positive trend requires explanation, since it implies that bigger nestlings cool more quickly. Also, although not significant, the sign of BMASS correlated with RATE is positive, again at odds with an expected reduction in cooling rate with a reduction in surface area to mass ratio $(\mathrm{NMASS})^{0.67}/\mathrm{NMASS}$).

A discussion of the possible reasons for this apparent anomaly will be deferred until the results for field cooling rate have been presented. Both NMASS and BMASS show positive correlations with TIME (Table 4.14). Since TIME (duration of cooling event) was under experimental control, and NMASS and BMASS are unlikely to be dependent on TIME the positive relationship between TIME and mass is an experimental artifact. It is likely that the experiment was terminated earlier in smaller nestlings so that they would not get too cold, larger nestlings may have been left for longer. As nestlings had been removed from the field for the purpose of the experiment, and were known not to be fully homeothermic, it is possible that considerations of nestling welfare produced the otherwise inexplicable relationships.

4.4.3 A model of cooling rates of Dipper nestlings in the field

The mean cooling rate of Dipper nestlings in their nest in the wild was

0.343 ± 0.281 (range 0.926-0.061, n = 35).

The cooling rate of nestlings aged 7-8.5 days was significantly lower than for nestlings aged 3-4.5 days,

TABLE 4.14: Pearson correlation coefficient matrix of parameters entered into a step-down regression analysis of factors influencing laboratory cooling rate (LCR) of 7-8 day old Dipper nestlings in broods of three (n = 9)

	TA	NMASS	TIME	TB	TBA	BMASS	LCR	BSA
TA	-	0.634*	0.737*	0.161ns	-0.279ns	0.671*	0.039ns	0.647*
NMASS		-	0.941***	-0.478ns	-0.741*	0.945***	0.702*	0.946***
TIME			-	0.466ns	-0.744**	0.996***	0.478ns	0.992***
TB				-	0.903***	-0.533ns	-0.387ns	-0.555ns
TBA					-	0.811**	-0.394ns	-0.822**
BMASS						-	0.519ns	0.999***
LCR							-	0.533ns
BSA								-

Tabulated values are for 'r'. ns = not statistically significant; * = $p < 0.05$;
** = $p < 0.01$; *** = $p < 0.001$

In the text LCR and RATE are synonymous within the context discussed

Figure 4.24(b): Body temperature of Dipper nestlings in the field in relation to parental attentiveness and inattentiveness.

(a) Brood-size = 4, nestling mass = 12.1g, aged 3.5 days

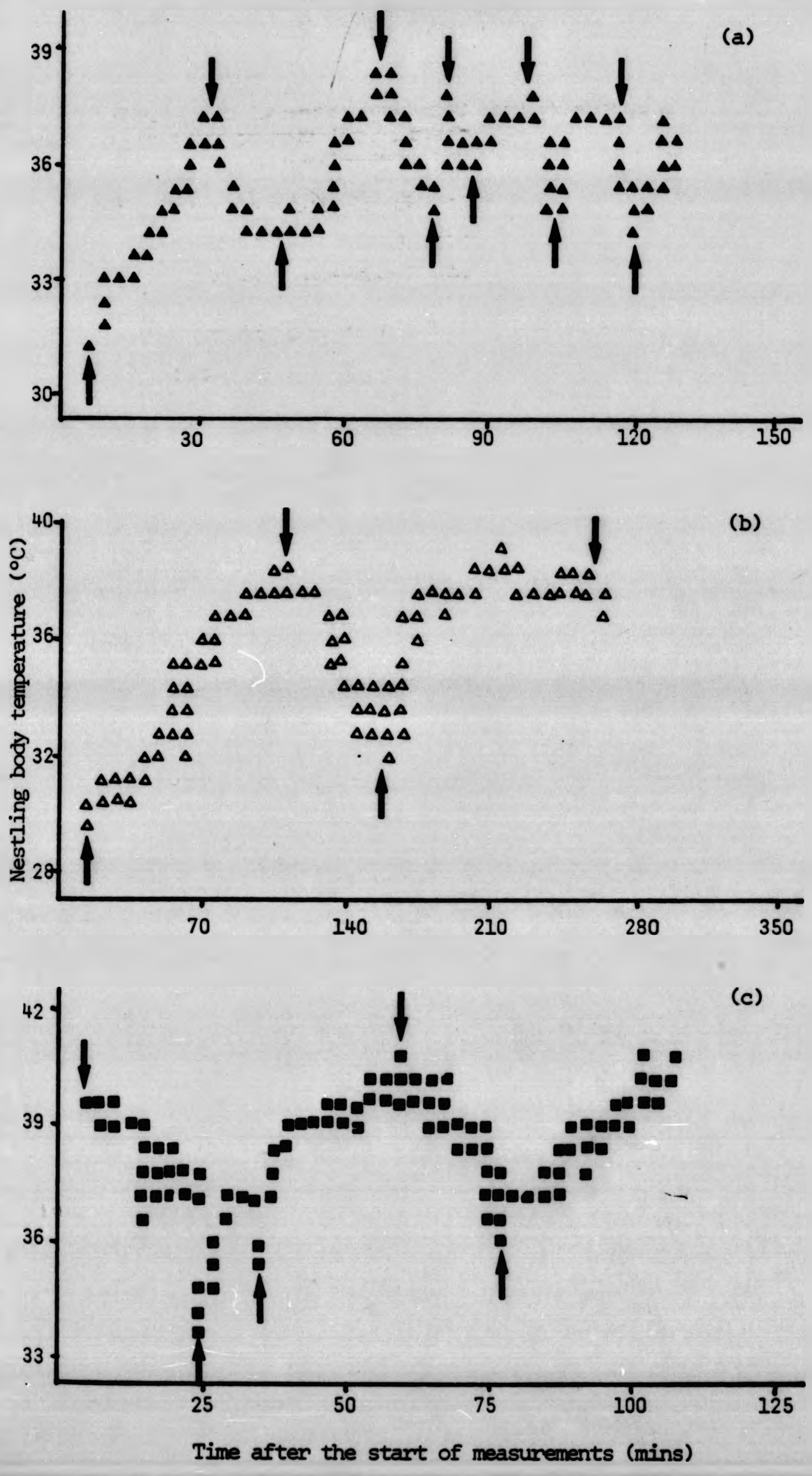
(b) Brood-size = 5, nestling mass = 15.3g, aged 4.0 days

(c) Brood-size = 3, nestling mass = 26.5g, aged 7.5 days

↑ = start of attentive period

↓ = start of inattentive period

3.5 day
4.0 day
7.5 day



the values were 0.170 ± 0.110 and 0.467 ± 0.283 respectively. Since laboratory measurements were made on young aged 7-8.5 days, then nestlings of this age cool on average 5.0 times slower in the wild than in the laboratory at similar nest/chamber temperatures. All of the variables stated above were entered into the multiple regression analysis (with the exception of TBB). The equation explains 61.9% of the variation in field cooling rate (see Table 4.15).

$$\begin{aligned} FCR = -0.68 - (0.17 \times AGE) - (0.26 \times BSIZE) - (0.02 \times TBA) + \\ (0.02 \times BMASS) + (0.1 \times MSAM) \qquad \text{eq. 4.4} \end{aligned}$$

$$F = 9.75,\ df\ 5,\ 30,\ P < 0.0001$$

The positive sign of the BMASS parameter once AGE and BSIZE have been held constant is worthy of comment. Similarly, although it did not significantly increase the fit of the model the next most significant parameter was NMASS which also showed a positive slope. This resembles the laboratory model in which age (7-8.5 days) and brood size (3) were effectively held constant experimentally. MSAM was the least significant parameter included in the model, after both BMASS and AGE, yet Mertens (1977) found excellent agreement between rate of heat loss and an exponent of body mass of 0.613, close to that predicted by considerations of the surface area to mass ratio (i.e. 0.67). This suggests that Dipper nestlings within a brood do not conform to a spherical shape from which the 0.67 exponent is derived (see Chapter 5).

Examination of the Pearson correlation matrix

TABLE 4.15: Step-down multiple regression analysis of factors influencing field cooling rates (FCR) of Dipper nestlings

Independent variable	Partial regression coefficient b	SE of b	Standardised partial regression coefficient Beta	t-value	significance of t
Age (days)	-0.175	0.036	-1.270	-4.94	$p < 0.0001$
Brood size (BSIZE)	-0.264	0.069	-0.916	-3.83	$p = 0.0006$
Temperature gradient between nestling body temperature and ambient temperature (=TBA) (°C)	-0.022	0.006	-0.398	-3.32	$p = 0.0024$
Brood mass (=BMASS) (g)	0.019	0.006	1.127	3.32	$p = 0.0024$
[a]Mean surface area: mass ratio (=MSAM)	0.098	0.039	0.945	2.50	$p = 0.0182$
(cm^2 g^{-1})		$F = 9.75$, df 5,30, $p < 0.0001$			

a See table 4.12c for derivation of MSAM

(Table 4.16) indicates that nestlings with high initial TB are left to cool for longer, and that at low TA nestlings have higher initial TB's suggesting that under low ambient temperatures either brooding is more effective and/or nestlings invest more energy in trying to raise metabolic rate with a subsequent increase in TB. That initial TB is inversely related to cooling rate (FCR) suggests that birds with lower initial TB suffer due to their inability to raise body temperature, a factor which tends to mask temperature gradient effects in which the opposite relationship might be expected. Two further points support this view. The first is that in the laboratory experiments NMASS was the most important variable in explaining variation in cooling rate, and not TA. Secondly the predominance of size related factors (AGE, BSIZE, NMASS, BMASS, etc.) as consistently better predictors of cooling rates than temperature related factors (TA, TB, TBA, etc.) (Table 4.16). This will be further enhanced in the wild by the influence of nest insulation on the temperature gradient between nestling and TA, since the temperature gradient experienced by the nestling is that between itself and nest temperature. Nest temperature averaged 15.1°C and was always about 7.0°C higher than the local ambient temperature during periods of nestling cooling. This suggests TBN would have been a more suitable measure of temperature gradient and that the mean TAN:TBN ratio (TBA_i) is inadequate to compensate for this, explaining the slightly poorer relationship between FCR and TBA_i (Table 4.16).

TABLE 4.16: Pearson correlation coefficient matrix of parameters entered into a step-down multiple regression analysis of factors influencing field cooling rates (FCR) of Dipper nestlings

	AGE	BSIZE	BMASS	NMASS	TA	TB	TIME	TBN	TBA	FCR	BSAM	NSAM	MSAM
AGE	-	-0.84***	0.72***	0.91***	-0.14_{ns}	0.19_{ns}	0.35*	0.49**	0.20_{ns}	-0.53***	-0.68***	-0.86***	-0.79***
BSIZE		-	-0.52**	-0.82***	0.17_{ns}	-0.03_{ns}	-0.11_{ns}	-0.66***	-0.13_{ns}	0.27_{ns}	0.52**	0.82***	0.69***
BMASS			-	0.81***	-0.32*	0.22_{ns}	0.26_{ns}	0.36*	0.33*	-0.31*	-0.99***	-0.86***	-0.92***
NMASS				-	-0.22_{ns}	0.15_{ns}	0.18_{ns}	0.53***	0.23_{ns}	-0.44**	-0.79***	-0.97***	-0.94***
TA					-	-0.33*	0.27_{ns}	-0.72***	-0.83***	0.26_{ns}	0.30*	0.27_{ns}	0.26_{ns}
TB						-	0.30*	0.21_{ns}	0.79***	-0.44**	-0.24_{ns}	-0.16_{ns}	-0.19_{ns}
TIME							-	-0.13_{ns}	0.01_{ns}	-0.26_{ns}	-0.30*	-0.18_{ns}	-0.20_{ns}
TBN								-	0.58***	-0.33*	-0.35*	-0.54***	-0.44**
TBA									-	-0.43**	-0.34*	-0.26_{ns}	-0.28*
FCR										-	0.28*	0.39**	0.39**
BSAM											-	0.85***	0.92***
NSAM												-	0.98***
MSAM													-

Tabulated values are for 'r'. ns = not statistically significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

In the text FCR and RATE are synonymous within the context discussed.

Measurements of FCR show that older nestlings cool slower than younger nestlings (see Section 4.4.2) and for a given age young in larger broods cool more slowly than in smaller broods. Table 4.16 shows that greater brood masses and heavier/larger individual nestlings also cool more slowly, although it is shown that this is largely because of age and not mass effects, since when these are taken into account heavier nestlings/broods cool more quickly.

It could be that heavier nestlings are allowing themselves to cool more quickly in order to dissipate heat although ambient temperatures ($\bar{x}$ = 7.6°C, n = 36) and nest temperatures ($\bar{x}$ = 15.1°C, n = 11) relative to TB ($\bar{x}$ = 35.1°C, n = 35) suggest that this is unlikely.

4.4.4 A model of Dipper nestling reheating rate in the field

The mean reheating rate of Dipper broods in the wild was 0.239 + 0.174 (range 0.2-0.84, n = 42) (units as for cooling rates, Section 4.4.1), somewhat slower than the mean cooling rate; this being reflected in the longer duration of attentive periods (mean 36.9mins, n = 42) when compared with inattentive periods (mean = 17.6mins, n = 35). Examination of the Pearson correlation coefficients (Table 4.18) suggests that nestling age, TA, TBB, TBB and time may play significant rôles in regulating reheating rate, though none explain much of the variation in FRR on their own.

A stepwise multiple regression analysis was performed on these data. The following equation explains

52.8% of the variance (Table 4.17):

$$FRR = -3.67 + (0.1 \times BMASS) + (10.5 \times BSAM) + (0.027 \times TBB) + (0.02 \times TA) \quad \text{eqn. 4.5}$$

$$F = 10.34, \text{ df } 4, 37, \quad p < 0.0001$$

The importance of BMASS and BSAM as predictors of FRR and the absence of age, or individual size effects is in marked contrast to the importance of these parameters as predictors of FCR. This shift in emphasis is presumably due to the lack of rôle for nestlings in their own reheating; the cost being borne by the parent bird. When being brooded nestlings huddle together and hence behave as BMASS rather than as 'constrained' individuals (see Discussion). The lack of age effects suggest that nestlings "switch off" their thermogenesis thereby reducing metabolic costs. This lends support to the 'maximal brooding' model in which the cost of brood thermoregulation is cheaper for a parent, if it broods the young itself, than if the young partially thermoregulate themselves (Section 2.4.3(c)). It is of advantage to the nestlings since their thermoregulation costs are reduced. Although it would seem that mutual benefits are enjoyed by both parent and young, the need to attain homeothermy for independence and the increasing costs of provisioning the brood, force both the parents and brood to incur greater metabolic costs as the brood get older.

The FRR equation more closely resembles that expected from physical factors alone (see Section 2.4.2(a)). Specifically it includes a mass component (BMASS), a surface area component (BSAM), the temperature difference between

TABLE 4.17: Step-down multiple regression analysis of factors influencing field reheating rates (FRR) of Dipper nestlings

Independent variable	Partial regression coefficient b	SE of b	Standardised partial regression coefficient Beta	t-value	significance of t
Brood Mass (=BMASS) (g)	0.015	0.003	1.821	4.471	$p = 0.0001$
Brood Surface Area: Mass Ratio (=BSAM) ($cm^{-2}g$)	10.510	2.814	1.522	3.735	$p = 0.0006$
Normal T_b-cooled T_b (=TBB) (°C)	0.272	0.008	0.405	3.514	$p = 0.0012$
Ambient Temperature (=TA) (°C)	0.019	0.007	0.344	2.996	$p = 0.0049$

TABLE 4.18: Pearson correlation coefficient matrix of parameters entered into a step-down multiple regression analysis of factors influencing field reheating rates (FRR) of Dipper nestlings

	FRR	A	BSIZE	BMASS	NMASS	TA	TB	TIME	TBB	TBN	BSAM	NSAM	MSAM
FRR	-	0.26*	0.09ns	0.24ns	0.17ns	0.35*	0.32*	0.31*	0.32*	0.04ns	-0.10ns	-0.07ns	-0.17ns
A		-	-0.40	0.66***	0.87***	0.03ns	-0.08ns	-0.05ns	0.08ns	0.05ns	-0.65***	-0.78***	-0.49**
BSIZE			-	-0.15ns	-0.46**	0.25ns	0.21ns	-0.07ns	-0.21ns	0.44ns	0.18ns	0.48**	-0.28*
BMASS				-	0.81***	-0.14ns	0.18ns	0.11ns	-0.18ns	0.17ns	-0.96***	-0.78***	-0.85***
NMASS					-	-0.11ns	-0.03ns	0.02ns	0.03ns	-0.03ns	-0.81***	-0.94***	-0.63***
TA						-	-0.01ns	-0.42**	-0.01ns	0.13ns	0.16ns	0.18ns	0.01ns
TB							-	0.16ns	-1.00***	0.90***	-0.16ns	-0.02ns	-0.22ns
TIME								-	-0.16ns	0.40ns	-0.12ns	-0.04ns	-0.04ns
TBB									-	-0.90***	0.16ns	-0.02ns	0.22ns
TBN										-	-0.02ns	0.11ns	-0.05ns
BSAM											-	0.85***	0.88***
NSAM												-	0.64***
MSAM													-

Tabulated values are for 'r'. ns = not statistically significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

In the text FRR and RATE are synonymous within the context discussed.

parent and nestling (effectively TBB) and the temperature difference between nestling and ambient temperature (effectively TA).

The inclusion of time as a fifth parameter in the equation did not significantly increase the fit of the model, although the negative slope of the FRR against TIME relationship both after inclusion of the first four variables, or considering TIME alone, is of interest. This implies that parent birds can make some decisions as to whether they heat the brood up quickly over a short period or more slowly over a longer period of time.

Another possible explanation for an inverse relationship between FRR and TIME is that rapid reheating over a short period may represent reheating rates of nestlings with a lower TB and hence higher TBB. These nestlings would therefore be expected to heat up more quickly even if parental effort were constant. This is because reheating rate is dependent upon the temperature gradient between the parent and nestling, hence a higher TBB will result in quicker heat transfer from considerations of physical factors alone. Indeed in some species a reduction in TB is a specific mechanism for maintaining a greater rate of heat transfer between parent and nestling (O'Connor, 1984). The lack of any significant relationship between TIME and either TBB or TB suggest this is not the case, similarly the maintenance of the negative coefficient of the FRR against TIME relationship after TBB is held constant (equation 4.5) confirms this.

There was some evidence of a thermostatic setting of body temperature with age (O'Connor, 1975) in Dipper nestlings in the wild, but this was not significant between age groups. The mean body temperatures TB of 'young', 'transitional' and 'mature' nestlings were 34.6°C, 35.7°C and 36.6°C respectively (n = 22, 13 and 8 nestling body temperature measurements respectively). The mean TB of nestlings which were still brooded occasionally was 35.0°C(± 2.9), n = 35; appreciably less than the adult range of 38-41°C often quoted (Calder & King, 1974; Ricklefs, 1974) although the values fall within the range of incubation temperatures commonly found in birds (Drent, 1973). It was not possible to measure female body temperature in the field.

4.4.5 Mate Dipper removal and its effect on female brooding behaviour

Female Dipper brooding behaviour was examined in broods of three nestlings when males were present and feeding the young, and when males were removed so that females were forced to both brood and feed the young (Section 3.3.6). Table 4.19 summarizes the behaviour of female Dippers with and without male removal. It can be seen that female Dippers did not leave the brood for significantly longer periods when the male was absent (t = 0.13, n = 18, n.s.). Neither did they brood the young for significantly shorter periods (t = 0.086, n = 20, n.s.), or reheat them at different rates (t = 0.87, n = 15, n.s.). Females did, however, increase their rate of food delivery to the brood to a level that was not

TABLE 4.19: **The brooding behaviour of female Dippers tending broods of three nestlings aged 7.0-8.5 days old, with and without their mates**

	Male present	Male absent
Length of Inattentive period (mins)	[a]19.1 ± 12.6 (n = 24)	28.6 ± 20.4 (n = 22)
Length of Attentive period (mins)	30.3 ± 24.0 (n = 21)	28.9 ± 12.3 (n = 22)
Female [c]feeding rate (feeds h^{-1})	1.2 ± 0.7 (n = 16)	8.8 ± 5.7 (n = 14)
Male feeding rate (feeds h^{-1})	9.1 ± 5.4 (n = 18)	-
[b]Reheating rate	0.131 ± 0.240 (n = 6)	0.230 ± 0.147 (n = 7)

---

[a] All values are means ± 1 standard deviation

[b] Slope of the $\log_e$ temperature (°C) versus time (h) curve

All tests were non-significant, see text

[c] Feeding rate refers to nest visits with food delivered to nestlings

significantly different from the total food delivery to the brood when her mate was present (t = 0.064, n = 25, n.s.). It was not possible to tell whether this additional foraging for the brood resulted in less energy intake for the female, or whether she experienced energy imbalance from increased foraging costs. Clearly these points warrant further investigation.

Feeding rate was calculated for each complete hour of nest observation (Table 4.19) for both males and females. It was not known how long the male spent actually foraging or in other activities when he was away from the nest between feeding visits. Since females spent a significant amount of each brooding the young ($\bar{x}$ 36.9 ± 21.8mins, n = 13), provisioning for the brood was condensed into the relatively short inattentive period. Thus whilst males and females with males removed may have provisioned the young at the same rate, measures of feeding rate alone may underestimate the cost to the female in terms of energy expenditure. Winkel & Winkel (1970) found that female Pied fly catchers forced to provide for the young (7-8 days old) were significantly lighter after a week. There is anecdotal evidence to support the view that female Dippers suffer adverse effects when provisioning broods on their own.

On two occasions one particular male Dipper deserted two different females (1st and 2nd broods) when the chicks were about one week old. Both females continued to provision the brood for about one day and then deserted them, presumably unable or unwilling to incur the additional costs of provisioning the brood. One brood died, the other was 'rescued' by the observer and the young placed in other broods, where all but one survived.

4.4.6 The cost of brooding in the Dipper

The daily cost of brooding for all Dipper nestlings for which cooling rate data had been collected in the field, was calculated using the equation in Section 2.4.2. Field cooling rate (slope of the $\log_e$ temperature change with time, see Section 4.4.1) was converted to $^{\circ}C^{\circ}C^{-1}.h^{-1}$ using the following equation;

$$\text{Cooling rate } (^{\circ}C^{\circ}C^{-1}.h^{-1}) = \frac{T_b \times FCR}{T_b - 15.1} \qquad \text{eqn. 4.6}$$

where T_b is initial nestling body temperature prior to cooling (°C), FCR is the field cooling rate and 15.1 is the mean nest temperature (see Section 3.3.3) measured throughout the study.

The specific heat of nestlings (S) was calculated as;

$$S = 0.91 - 0.0057\ \text{Age} \qquad \text{eqn. 4.7}$$

from carcass analysis data in Section 2.4.2. The time interval (i) over which inattentive periods occurred was taken as the length of the daylight period, 16 hours. From this proportion of time the bird spent brooding was known (Figure 4.28) and entered into the equation. Brooding cost was expressed as Watts, and is calculated for the twenty-four hour day, even though costs of reheating the brood were incurred during daylight hours only. The results for the brooding cost of young nestlings (3.0-5.0 days old) and transition (6.0-8.5 days old), and the mean for all ages, are presented in Table 4.20. The cost of brooding in older birds is less (0.28 Watts) than in young birds (0.635 Watts) even though older birds are left unattended for 82% of daylight hours compared to only 18% in young nestlings. This is due to the reduction in cooling rate caused by partial homeothermy on the part of older nestlings (Figure 2.15(b) and (c)).

The field heat transfer coefficient (h_f) is comparable with h for eggs used in the calculation of incubation costs by Ricklefs (1974) although h_f includes a component of evaporative water loss, whilst Ricklefs' estimates do not. The 'conductance' of altricial clutches in their nests was calculated as 0.989 for the House Wren, 0.906 for the Zebra Finch and 0.744 for the Great Tit, all higher than h_f of nestling Dippers. Brooding costs of young Dippers are higher, however, when expressed as percentage BMR than incubation costs in the House Wren (where T_{na} = 17.1°C was close to the Dipper value of 15.1). The 90.7 per cent BMR cost is still lower than that which would be expected for poikilothermic nestlings, since some degree of homeothermy is present. Considering the large difference between the mass of the brood, however, (58.2g) and the mass of the House Wren clutch (8.2g) brooding costs are still relatively low. Clearly the heat producing capacity of the brood compensates for the higher rates of heat loss expected from considerations of brood mass, and effectively keeps parental brooding costs at a level not dissimilar to

TABLE 4.20: The cost of brooding in the Dipper calculated from field cooling rates for young and transition nestlings

Age	Mean brood mass, W_b (g)	Specific heat of nestlings,s (cal $g^{-1}{}^{o}C^{-1}$)	Cooling rate,r ($^{o}C^{o}C^{-1}h^{-1}$)	Initial body temperature,T_b (^{o}C)	Proportion of time bird spent brooding,c	Field heat transfer co-efficient,h_f^b cal.$g^{-1}{}^{o}C.h^{-1}$	Daily brooding costs (Watts)	(c%BMR)
Young	58.2	0.890	0.808	34.6	0.18	0.719	0.635	90.7%
'Transi-tional'	82.2	0.868	0.303	35.7	0.82	0.263	0.280	40.0%
Mean of all ages	68.1	0.880	0.600	35.1	0.70	0.528	0.480	68.6%

[a] Young = 3-5 days old; transitional = 6-8.5 days old.

[b] For explanation of h_f see Section 2.4.1.

[c] Assumes a female body mass of 57.5g and BMR of 0.70 Watts.

incubation costs. Yet parents also have to provide the brood with energy for their 'contribution' to brood thermoregulation, with the associated extra travelling costs (Section 2.5.2) although this cost is shared by both parents (see Section 4.6 for Dipper nestling thermoregulation costs).

4.4.7 Huddling and the contribution of individual nestlings to brood heat production: A consideration of nestling size

In order to examine the relative contribution of individuals to brood metabolism during huddling in a cold environment it is necessary to separate and measure individual metabolism whilst retaining the effect on that individual, of being in the presence of its warm siblings. Heated dummy nestlings were used to mimic heat production of natural nestlings whilst contributing nothing to 'brood' metabolism.

The metabolic rates of homeothermic Zebra Finch nestlings were measured at a chamber/ambient temperature of 5°C, both in the presence and absence of a heated (40°C) dummy nestling of surface area 16.95 cm^3. The ratio of metabolic rate without a dummy:metabolic rate with a dummy is shown as a function of nestling surface area:mass ratio in Figure 4.25. This suggests that nestlings with large surface area:mass ratio benefit relatively more in terms of thermoregulatory savings from the heated dummy, than do nestlings with smaller surface area to mass ratios. Since nestlings with large surface area:mass ratios tend to be small, it follows that larger nestlings contribute proportionally more to the cost of maintaining homeothermy by huddling than do smaller nestlings.

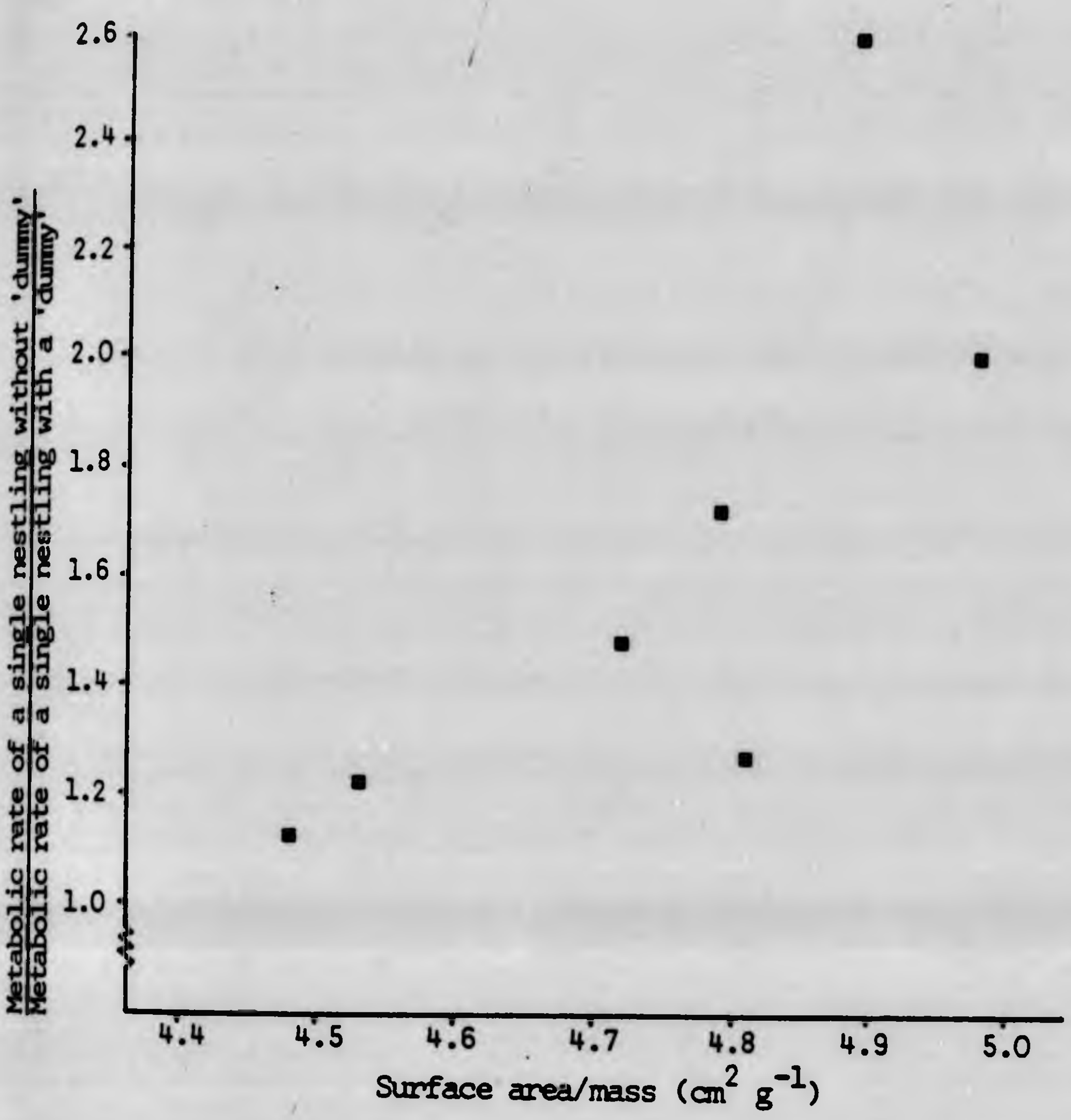


Figure 4.25

Metabolic rate with/without a heated dummy nestling for Zebra Finch nestlings, as a function of nestling surface area/mass ratio

$r = 0.76$, $n = 7$, $p < 0.05$

Surface area calculated as mass$^{0.67}$

Consider the following data on two nestlings huddling together one with a mass of 11.33g, and the other of mass 8.76g. Their respective metabolic rates in the presence of a heated dummy were observed as 0.049 and 0.032 Watts g^{-1}. The pair would be expected to have a mean metabolic rate therefore of 0.0405 Wg^{-1} assuming their body temperatures were 40°C (i.e. if each behaved as the dummy to the other). The heavier nestling therefore contributes 60% of total heat production of the 'brood' (i.e. pair) and the smaller only 40%. Whereas if there were no difference between their contribution each would contribute 50% of the cost. The smaller sibling therefore saves 20% of its own thermoregulatory contribution to brood homeothermy (i.e. 100(1-(40/50))) by virtue of its higher surface area to volume ratio. Whilst sample sizes were far too small to confirm such a relationship, the data demonstrate its potential relative importance. The view that nestlings contribute unequally to the cost of brood thermoregulation during huddling is therefore tentatively supported by these data and suggest that any such effect is in proportion to nestling size. Freed (1981) has shown that older nestlings help out their younger siblings energetically, due to earlier thermoregulation, in the House Wren, _Troglodytes aedon_. Such advantages to younger nestlings may help offset any disadvantages incurred through lower initial hierarchy position (Section 4.11.2), or through smaller size at a given age due to sexual-size dimorphism (see Chapter 5). The latter has been suggested as one way in which the energetic cost of rearing male Yellow-headed Blackbirds, (*Xanthocephalus xanthocephalus*), might be reduced, as females may thermoregulate earlier in this sexually size-dimorphic species (Richter, 1983). This conclusion was however based on considerations of plumage development (Richter, 1983), which is not actually a major factor in the onset of thermoregulation (O'Connor, 1975). Indeed it is more likely that the larger males may help out their sisters energetically, from considerations of nestling size (see this section). This may partly explain why female Dippers (also size-dimorphic) grow more quickly than males (Section 4.1.5, Chapter 5).

4.5 ACTIVITY

A Doppler radar device (Section 3.4.1) was used to quantify nestling activity during metabolism measurements (Sections 3.4.2 and 3.2.1).

4.5.1 The cost of one activity (Doppler) unit

Figure 4.26 shows nestling metabolism as a function of activity (Doppler) units (Section 3.4.2) for a single House Martin nestling. The slope (b) of the regression is therefore the cost of one Doppler activity unit (DAU) and the intercept (a) the metabolic rate at zero activity. Combining the means of a number of replicates for House Martins and Zebra Finches (mean slope t-test, $t = 0.063$, $n = 18$, n.s.), the cost of one DAU was found to be $2.62 \times 10^{-5} \pm 1.21 \times 10^{-5}$ kJ ($n = 13$). The mean daytime resting metabolism at zero activity was 1.94 kJ h^{-1}, compared to a predicted value of 1.28 kJ h^{-1} for adult birds of similar mass (Aschoff & Pohl, 1970), 53% higher.

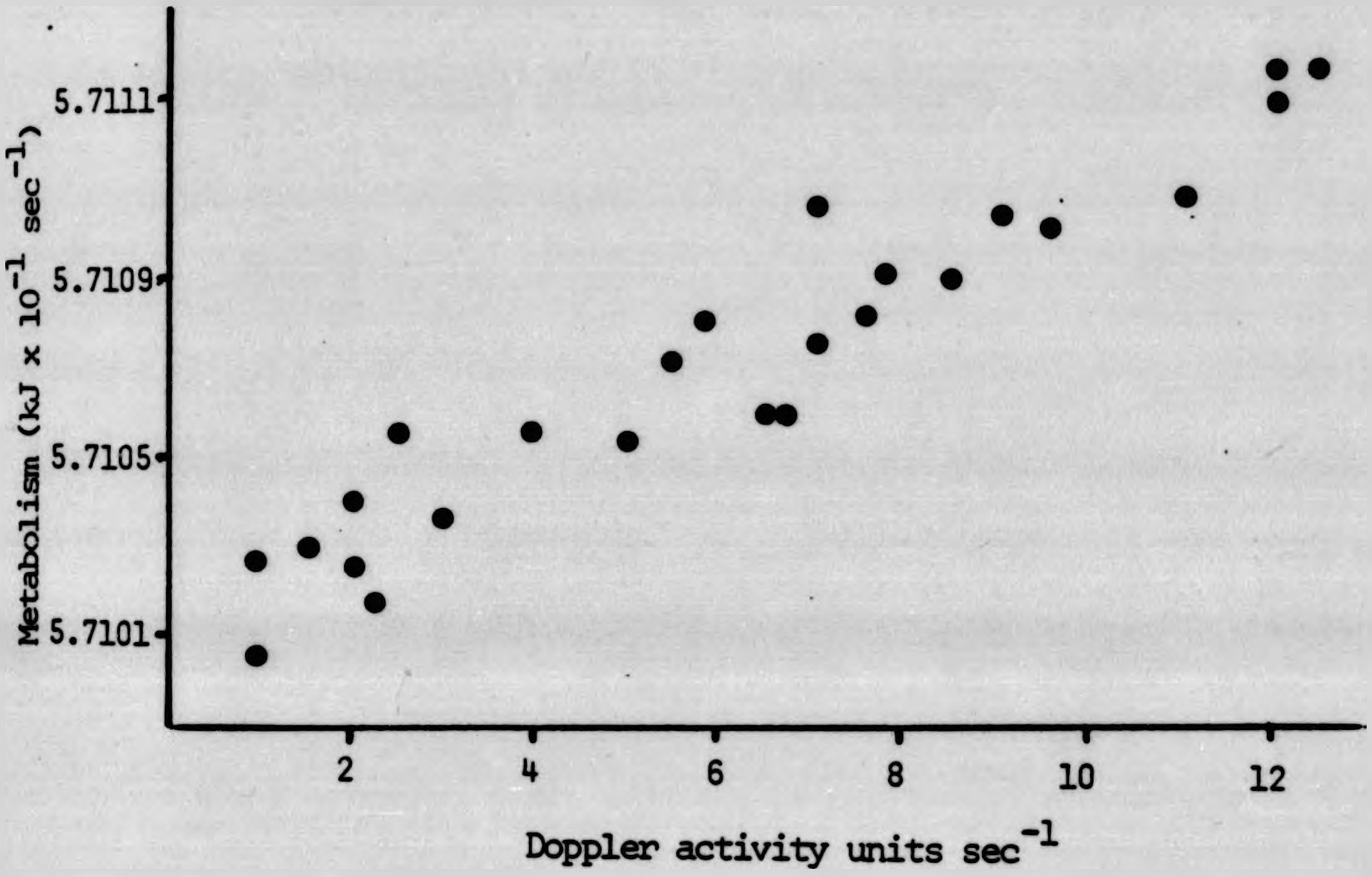


Figure 4.26: An example of the relationship between nestling activity (DAU's.sec^{-1}) and metabolism.

The slope of the line gives the cost of one Doppler activity unit.

The regression equation is:

$y = 0.571 + 0.00001x$, $r^2 = 91.3$

The mean mass of nestlings used for the measure of DAU cost was 14.9 ± 0.15g, n = 13.

The mean duration of begging in hand-reared House Martin chicks was 10.3 seconds (compared to 10.1 seconds for wild birds, Section 4.13). The mean number of DAU's registered during this time was 24.2; or 2.35 DAU sec^{-1}. However, registration of DAU's continued even when begging movements had ceased (Figure 4.27). This was caused by rapid breathing movements of nestlings so when these movements stopped, so also did the registration of DAU's. This is probably explained by the need of nestlings to repay an oxygen debt incurred during an activity, and is therefore an integral part of the cost of that activity. The mean duration of a begging bout, including recovery time was 21.3 seconds, with a mean of 36.4 DAU's registered. If for convenience it is assumed that recovery costs are paid back instantaneously then these can be added to begging costs and the total cost of begging (begging + recovery) recalculated and expressed in terms of the duration of the activity alone. When this is done, the DAU sec^{-1} is found to be 1.5 times higher than when no oxygen debt is taken into account.

DAU's registered during the following activities were therefore multiplied by 1.5 to include recovery costs, and in subsequent discussion DAU refers to these adjusted DAU counts.

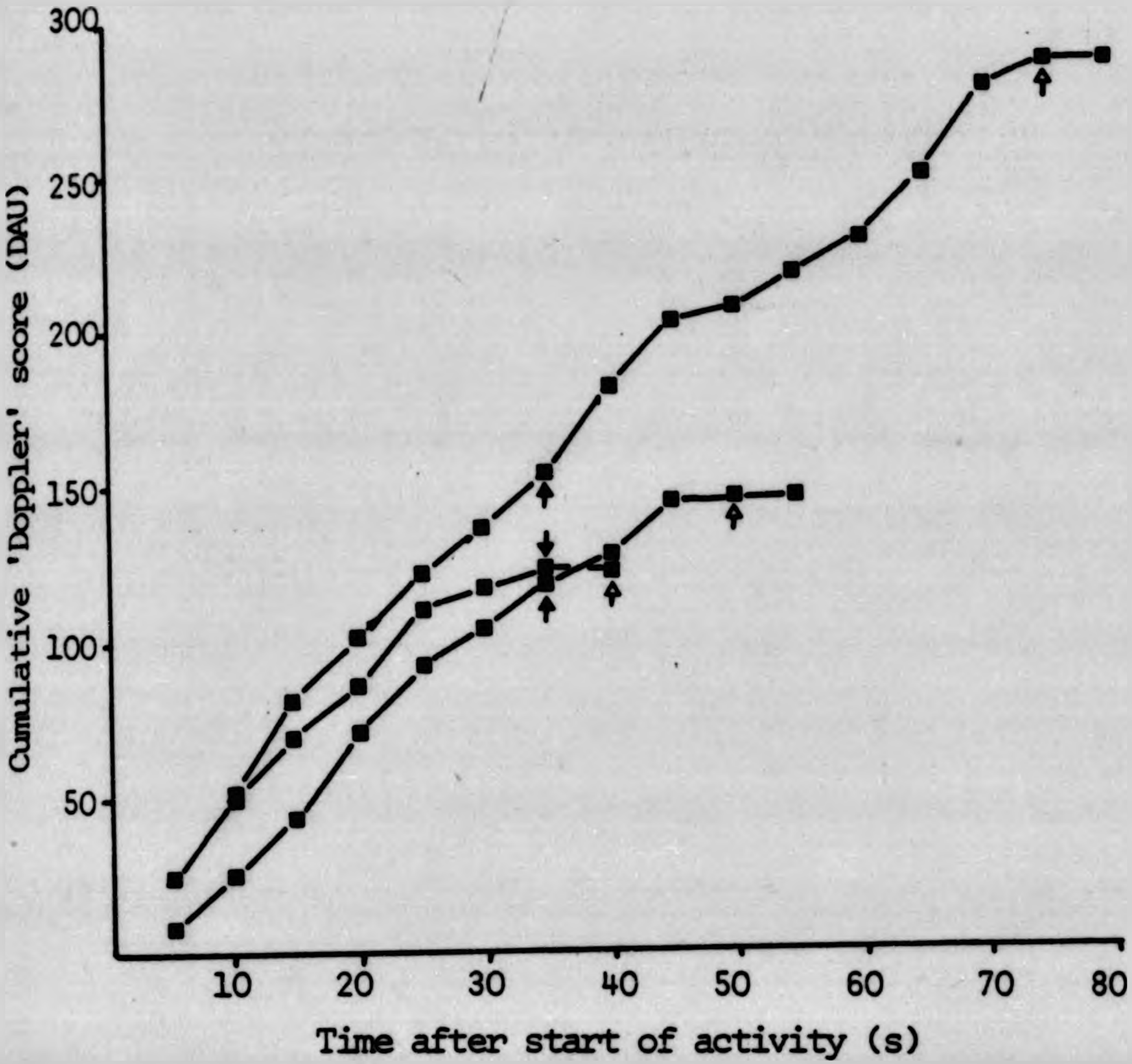


Figure 4.27

Examples of cumulative 'Doppler' score with time after the start of nestling activity.

↑ Activity stops

⇧ Doppler stops registering, i.e. equilibration

(see text for explanation)

4.5.2 Definitions of nestling activities

(a) Begging: For the purpose of this study begging was divided into two types; 'Zebra Finch' begging and 'House Martin' begging. Zebra Finch begging was characterised by weak head waving and no accompanying extension of the neck, rather the head was tilted somewhat to the side. This type of behaviour did not change with an increase in the vocalizations associated with it. House Martin begging was characterised by a rapid extension of the neck on stimulation (see Section 3.7.1) and vigorous head waving, accompanied by vocalisations. Head waving appeared more vigourous when vocalisation volume was louder (pers.obs.).

(b) Feeding: This is defined as the act of removing and swallowing food from the dummy bill. The latter was usually simultaneous with removing food.

(c) Defaecating: This is defined as the movement of the nestling to the edge of the nest, the raising of the posterior during the act of defaecation, and the movement back to its original position within the nest and subsequent 'settling down'.

(d) Scratching: The movement associated with the act of scratching with hind limbs.

(e) Shivering: The movement associated with involuntary contractions of muscles during thermogenesis.

(f) Movement: All other movement not included above. For example, huddling movements, movements to jostle for and maintain favoured positions within the nest for feeding, etc.

4.5.3 The cost of nestling activities

Table 4.21 shows the costs of nestling activities in terms of DAU's, energetic cost (DAU = 2.12×10^{-5} kJ) and the energetic cost expressed as a percentage of BMR for a 14.9g bird (see Section 4.5.1) from the Aschoff & Pohl night-time resting metabolism equation (Section 2.1.2). Since all nestlings studied were of similar mass and age, it was not possible to tell whether activity is a constant proportion of BMR, or if there is a fixed activity cost independent of BMR. The latter would imply disproportionate activity costs with respect to nestling size. The implications of a 'fixed' or 'proportionate' model of activity costs is discussed in Section 4.6 and Chapter 5.

4.6 THE DAILY ENERGY BUDGET OF A NESTLING DIPPER CALCULATED USING THE TIME-ACTIVITY-LABORATORY METHOD

The nestling energy budget was examined in the Dipper in order to calculate daily energy expenditure (DEE) and daily metabolised energy (DME); where DME less DEE is the energy accumulated in tissue during growth (P). DEE can be partitioned into a number of components;

(1) Basal metabolic rate (M), the night-time resting metabolism of nestlings at thermoneutrality;

(2) The cost of biosynthesis (B), which includes both the cost of synthesizing new body tissue (B_n) as well as replacing degraded tissue (B_d);

(3) The energy accumulating as new tissue (P), which may be sub-divided into fat (P_i) and protein (P_p);

(4) Thermoregulation (TR),

TABLE 4.21: The cost of nestling activities for House Martins and Zebra Finches. All figures except begging are for the mean of both species (see below)

Activity	DU s^{-1}	Mean cost of activity		N
		[a] kJ s^{-1}	[b] % BMR	
[c] Zebra Finch begging	3.05	6.47×10^{-5}	24.7	71
[c] House Martin begging	3.53	7.48×10^{-5}	28.5	96
Feeding	6.51	1.38×10^{-4}	52.6	41
Defaecating	5.52	1.17×10^{-4}	44.6	13
Moving	7.25	1.54×10^{-4}	58.7	38
Scratching	3.90	8.27×10^{-5}	31.5	2
Shivering	1.98	4.20×10^{-5}	16.0	3

[a] Using the mean cost of one Doppler activity unit as 2.12×10^{-5} kJ.

[b] BMR refers to that of the mean mass of nestlings tested (= 14.9 ± 0.15), and is calculated using Aschoff & Pohl's daytime resting equation (Section 2.1.2).

[c] $t = 4.63$, df 165, $p < 0.001$. All other t-tests non-significant, therefore data other than begging were combined.

(5) Activity (A);

(6) Alertness (AL) (see below), and

(7) The heat increment of feeding (HIF).

Thus;

$$DME = M + P + B + HIF + A + AL + TR \qquad \text{eqn. 4.8}$$

and

$$DEE = M + B + HIF + A + AL + TR = DME-P \qquad \text{eqn. 4.9}$$

The daily energy budget of a single Dipper in a brood of four was constructed from laboratory data and using published data for calculating components not directly measured (i.e. B, HIF). These components will be dealt with separately and then a comparison made between DEE calculated from these data and DEE measured in the field (hereafter called field energy expenditure, FEE, to distinguish from the laboratory budget) using doubly-labelled water.

4.6.1 Basal metabolic rate (M)

Basal metabolic rate was calculated using the Aschoff & Pohl night-time resting equation (see Section 2.1.2). The masses used for each age of nestling in calculating basal metabolic rate are those for the fitted growth curve (see Section 4.1.1). The change in basal metabolic rate with age is presented in Table 4.24 and Figure 4.33.

4.6.2 Thermoregulation (TR)

Nestlings were assumed to bear thermoregulatory costs only when they were not being brooded (Section 4.4.6). Figure 4.28 shows the hourly percentage time that nestlings were left unattended during daylight hours; the curve is fitted by eye.

Nestlings were brooded at night-time until around day ten (pers.obs.) and it is assumed that this is a result of the nestlings' inability to thermoregulate fully until this time (Figure 4.28). Thereafter nestlings were not brooded during the day or night. Newly hatched nestlings were brooded for about 90% of daylight hours; the female leaving to feed herself (pers.obs.) even though it seems likely that the male also fed her on the nest as well during the first few days of nestling life. Males were observed on occasions giving food to brooding females, but it was not possible to tell whether the female ate the food or distributed it amongst the brood. Such feeding visits by males lasted only a few seconds and were therefore of similar duration to feeding visits by both males and females to 'mature' nestlings (Figure 4.53), suggesting females may have eaten the food themselves.

Female inattentiveness increased sharply between day five and seven, until it was 100% at day ten.

The pattern of changing thermoregulatory capacity of nestlings was assumed to follow the pattern of female attentiveness (Clark, 1984). Hence nestlings bear 100% of their thermoregulatory costs at day ten, 60% at day six, and so on. Thermoregulatory costs not borne by the nestlings were assumed to be borne by the female (Section 4.4). The total cost of thermoregulation during female inattentiveness (see below), was therefore multiplied by the proportion of that cost met by the nestling only (Figure 4.28) to arrive at a nestling's thermoregulation costs (Table 4.24). The light/dark cycle at the time of nesting was taken as approximately 8:16 hours.

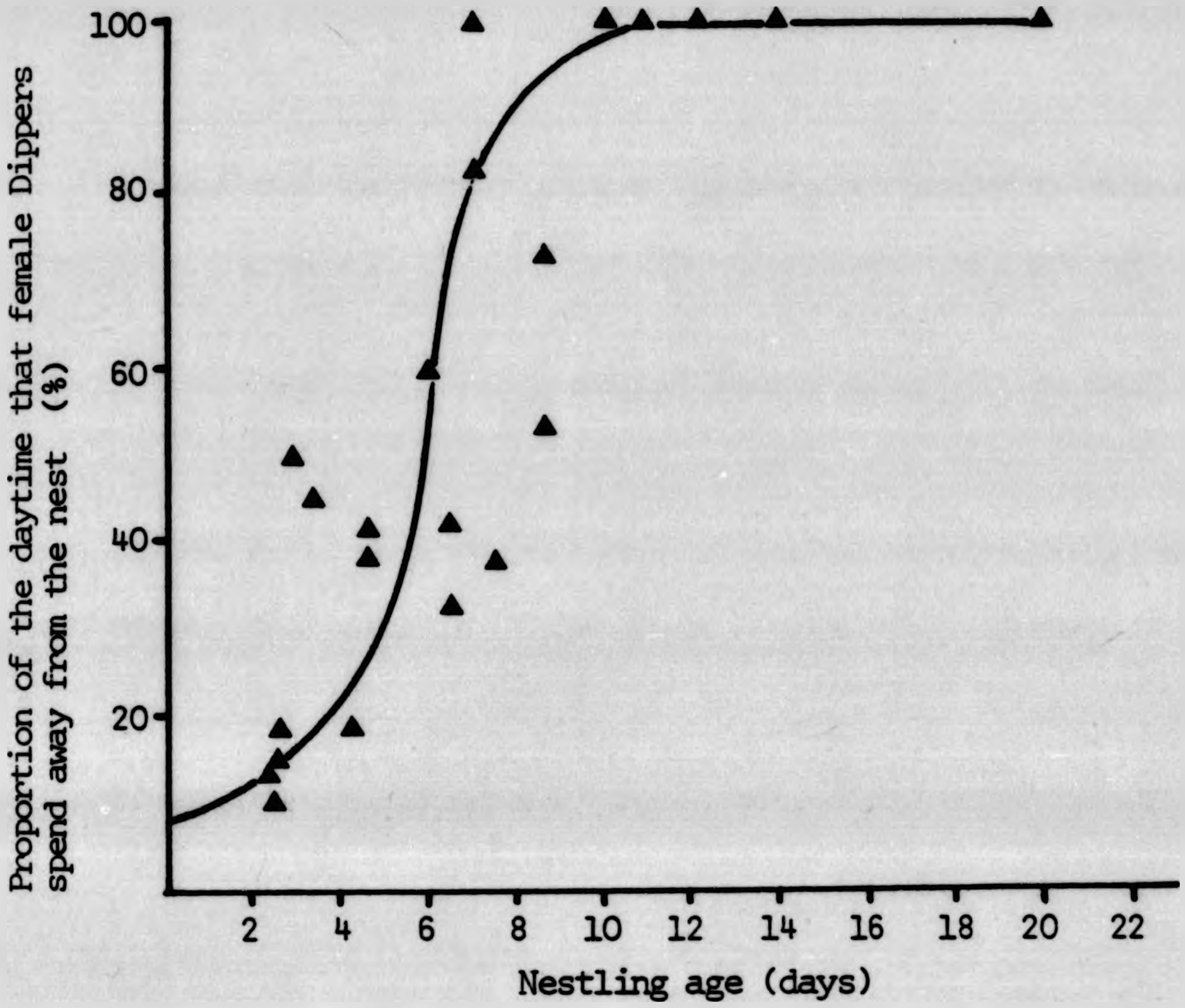


Figure 4.28

Percentage of the 16 hour daylight period spent away from the nest by female Dippers as a function of nestling age. Curve fitted by eye.

The metabolic rate of Dipper nestlings as a function of temperature (enclosed within the nest) was presented in Section 4.3. Metabolic rate was taken as decreasing linearly as a function of ambient temperature (Figure 4.24), and the mean slope of this relationship for brood sizes two and three (see below) was used to calculate metabolic rate of Dipper nestlings at the mean field ambient temperature of 7.6°C (Section 4.4.3). Though the energy budget discussed in this chapter is for a nestling in a brood of four, it is not considered that there will be a significant over-estimate of TR using these data. Firstly, although thermoregulatory costs could be lower for a nestling in a brood of four, due to huddling, this is only likely to be important for mature nestlings during the night-time. Dipper nestlings are constrained in their huddling behaviour during daylight hours (Chapter 5), and are usually only in contact with one or two siblings. Secondly, there is little difference between the metabolic rates of nestlings in broods of two and three (Section 4.3), though they both differ significantly from the single nestling metabolic rates, suggesting further increases in brood-size have a limited effect on TR (Section 4.4).

Using these data, metabolic rate at 7.6°C is 1.35 x basal metabolic rate so the cost of thermoregulation alone is 0.35 x basal metabolic rate. Though resting metabolism in growing nestlings will contain a component of biosynthetic costs of synthesising new tissue (Section 2.1.2), night-time resting measurements were taken from shortly after dusk until just before dawn the next day (Section 3.2.2) to minimise this. It is likely that such biosynthetic costs will be incurred primarily in association with feeding in a similar way to HIF (Calder & King, 1974), thus reducing their contribution to night-time 'resting' metabolism. No mass increase was observed during Dipper nestling metabolism studies. The metabolic rate of Dipper nestlings (Section 4.3) was measured in nestlings greater than fourteen days old only, with a mean mass of 55g. In order therefore to calculate TR in younger nestlings, since the per gram metabolic rate of a bird increases with increasing mass, TR was assumed to change proportionally and calculated as 0.35 x basal metabolic rate for all ages, rather than taking a fixed cost. Using the data in Section 4.3, TR = 0 at 35°C. TR is presented in Table 4.25 and Figure 4.33.

4.6.3 Activity (A)

The cost of specific nestling activities (Section 4.5.3) were applied to Dipper time budget data collected in the field. Definitions of nestling activity are as in Section 4.5.2. The cost of begging used is that for the House Martin, since their begging behaviour, but not that of Zebra Finches, resembles the Dipper.

(i) Unit costs of Activity

The unit cost (kJ sec^{-1}) of activity was calculated in two ways: A single figure of 2.2×10^{-5} kJ DU^{-1} (Section 4.5.1) was used to calculate one set of activity costs and represents activity cost based on a 'fixed unit cost' model.

This implies proportionately increased cost per unit of activity in smaller nestlings. Since the figure of 2.12×10^{-5} kJ DU^{-1} was measured in nestlings of similar mass (though in two different species, Section 4.5.3) it cannot be demonstrated that the cost is indeed fixed for all ages, and an alternative 'proportional unit cost' model may apply. A second set of activity costs was therefore calculated based on the assumption that unit costs are a percentage of basal metabolic rate for each activity type, respectively: 24.7% for begging, 52.6% for feeding, 58.8% for movement and 44.6% for defaecating (Section 4.5.3). Daily activity costs, based on a fixed unit cost (FUC) and proportional unit cost (PUC), together with the mean of the two (MUC) are presented in Table 4.22.

(ii) Begging costs

Dipper nestlings are known to beg at each feeding visit, and also to beg when parents are not present (Section 4.10.2). The ratio of 'feed' begging frequency to 'non-feed' begging frequency is 1:97. At 'non-feed' begging occasions the mean giving-up time (GUT, see Section 4.9.1) is 3.9 seconds. At feeds parental decision time (PDT, Section 4.9.1) is approximately one second. A nestling in a brood of four is assumed to receive one feed every four visits, and to after-beg (ABT, Section 4.9.1) for the duration of the feed unless they themselves are being fed. This view is supported by field recordings of begging behaviour in which vocalizations ceased only after the parent left the nest, although there is no

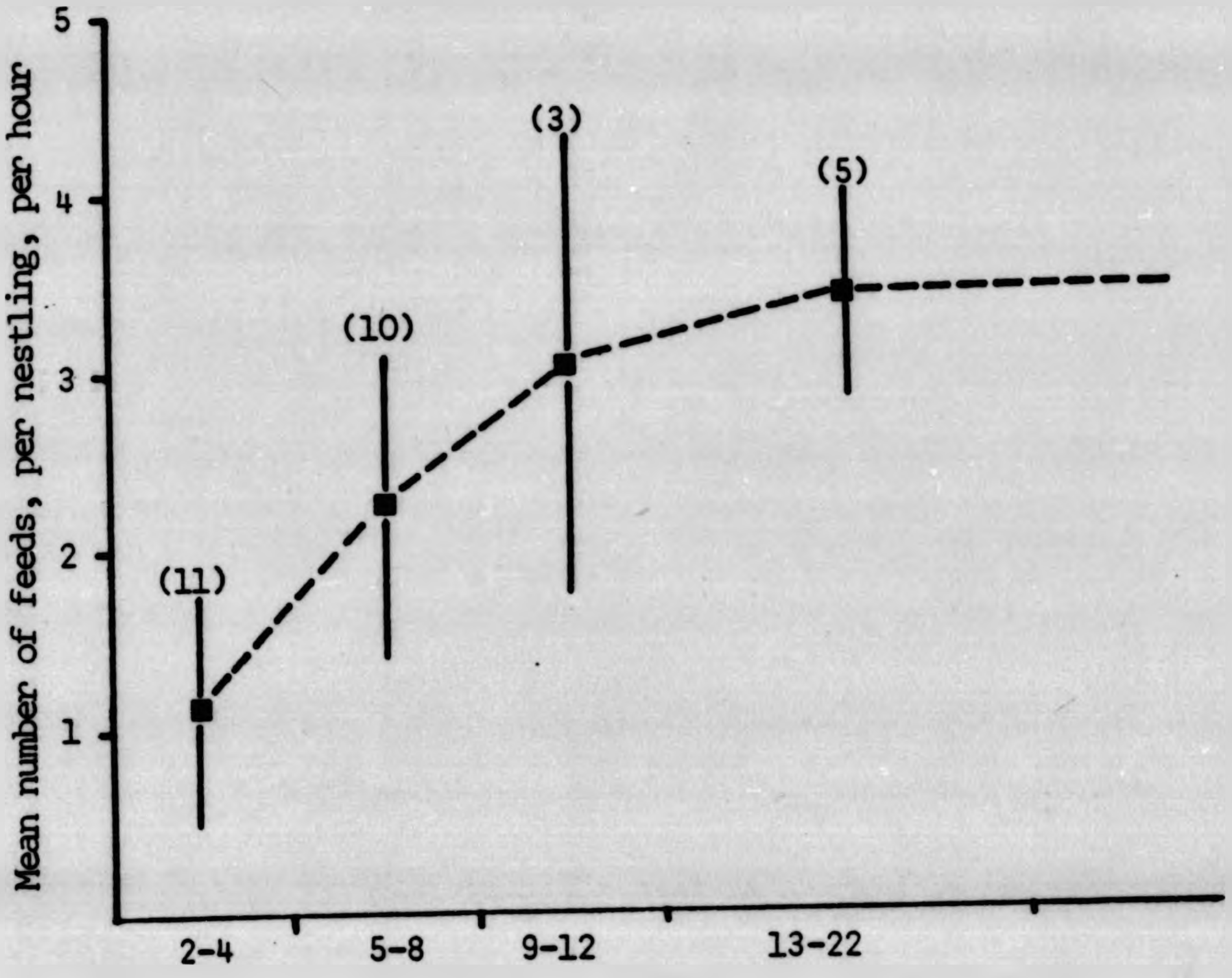


Figure 4.29: Mean feeding frequency of Dipper nestlings as a function of age.

Means ± 1 standard deviation for all brood sizes.

Number of brood days over which data collected in parentheses.

direct evidence to show that all unfed nestlings participated for the entire period. For a single nestling begging costs in a brood of four can be calculated as the sum of the following three behaviours;

'non-feed' begging cost = feed brood frequency x 0.97 x 3.9 x unit cost of begging eqn. 4.10

successful feed begging cost = (feed brood frequency/4) x 1 x unit cost of begging eqn. 4.11

unsuccessful feed begging cost = (feed brood frequency x feed duration/4) x 3 x 1 x unit cost of begging eqn. 4.12

where unit costs are either PUC or FUC. Figure 4.29 shows the mean feed frequency (feeds bird hr^{-1}) for the following age classes; 0-3.9, 4.0-7.9, 8.0-11.9, 12.0-23.0. The brood feed frequency (see above) is therefore four times this figure for a given age. Feed duration (secs) decreases with age (Figure 4.53) and this is allowed for in the above calculations. Begging cost as a percentage of total activity costs for the FUC and PUC models are shown graphically in Figure 4.30.

For the FUC model begging costs initially constitute about 38% of total activity costs, decreasing to about 4% when nestlings are six days old. The PUC model figures for newly hatched young are lower than the FUC model figure at 25%, but decrease to a similar figure of 4%.

The total cost of activity is however over twice as high for the PUC model (Table 4.22) when compared with the FUC model; 78.3 kJ and 36.95 kJ respectively, so that the total begging costs are 1.4 times higher than the PUC model.

TABLE 4.22: The daily activity costs of a Dipper nestling in a brood of four, calculated from proportionate (PUC) and fixed unit cost (FUC) models

Age (days)	[a]Daily activity cost calculated from proportionate unit cost (PUC) (kJ day^{-1})	(% BMR)	Daily activity cost calculated from fixed unit cost (FUC) (kJ day^{-1})	(% BMR)	[b]Mean Daily activity (kJ day^{-1})	% BMR
0	0.00	0.00	0.00	0.00	0.00	0.00
1	0.10	0.7	0.13	0.9	0.115	0.8
2	0.22	1.2	0.26	1.4	0.24	1.3
3	0.30	1.4	0.31	1.4	0.30	1.4
4	0.49	1.9	0.45	1.7	0.47	1.8
5	0.83	2.8	0.66	2.2	0.75	2.5
6	1.84	5.3	1.27	3.7	0.56	3.2
7	3.05	7.9	1.72	4.4	2.39	6.2
8	2.37	7.9	1.89	4.4	2.63	6.2
9	3.75	8.1	1.97	4.3	2.97	6.2
10	4.06	8.3	2.04	4.2	0.05	6.3
11	4.28	8.3	2.04	4.0	3.16	6.2
12	4.42	8.3	2.04	3.8	3.23	6.1
13	4.52	8.3	2.04	3.7	3.28	6.0
14	4.60	8.3	2.04	3.7	3.32	6.0
15	4.66	8.3	2.04	3.6	3.35	6.0
16	4.69	8.2	2.03	3.6	3.36	6.0
17	4.71	8.2	2.02	3.5	3.37	5.9
18	4.72	8.2	2.01	3.5	3.37	5.9
19	4.73	8.2	2.01	3.5	3.37	5.9
20	4.73	8.1	2.00	3.5	3.37	5.9
21	4.73	8.1	2.00	3.4	3.37	5.8
22	4.73	8.1	1.99	3.4	3.37	5.8
23	4.73	8.1	1.99	3.4	3.37	5.8
TOTAL:	78.26	-	36.95	-	57.61	-

a For explanation of PUC and FUC see text

b The mean of columns 2 and 4, and columns 3 and 5 (= MUC, see text).

(iii) Feeding costs

Feeding costs are calculated as;

(Brood feeding frequency x feed duration/4) x
unit cost of feeding eqn. 4.13

Feeding costs constitute approximately twice as much as a proportion of total activity costs for the PUC model compared with the FUC model throughout the nestling period. This is due primarily to the high unit cost of feeding (Section 4.5.3).

(iv) Defaecation costs

Faecal sacs were not removed by the adult at every nest visit in the Dipper (pers.obs.) and observations on hand-reared House Martin nestlings suggest faecal sacs are not produced at every offer of food.

For every two feeds a nestling received it was therefore assumed to defaecate once. Hence, the defaecation cost is calculated as;

(Brood feeding frequency/8) x unit cost of defaecation eqn. 4.14

Whilst faeces are removed from the nest by the parent birds until the young are about four days old, and thereafter the nestlings defaecate out of the nest entrance, observations of very young nestlings of other species shows that the presentation of the faecal sac to the parent still occurs, but that the movement associated with this is reduced (pers.obs.). Since feeding frequency is anyway low in the first few days, no attempt was made to allow for this moderate reduction in defaecation costs, and the full unit cost was applied to all nestling ages. A defaecation was assumed to take ten seconds, a rough average based on hand-reared House Martins. Defaecation costs are similar for both FUC and PUC models.

(v) Movement costs

The mean number of activity units registered per hour for a brood of four House Martin nestlings was 5000 Doppler units (Section 4.5.3) equivalent to 2.87 minutes of movement per nestling per hour. This was assumed to be constant through growth, though the unit cost was calculated from both PUC and FUC models as previously and applied to Dipper nestlings. Movement (Section 4.5.3) was assumed to occur only during periods of inattentiveness by the female (Figure 4.28). The relative importance of the above activities as a percentage of the total activities is presented in Figure 4.30. Movement accounts for the majority of total activity costs, 82.6% and 86.7% for the PUC and FUC models respectively.

Activity costs reach a peak (see Table 4.22, percentage BMR) earlier using the FUC model (day seven) compared with the PUC model (day ten), and decrease to a proportionally lower level. Activity costs drop by 22% of the peak activity cost (as a multiple of BMR) for the FUC model and 3% for the PUC model respectively.

4.6.4 Growth

The amount of energy accumulating as tissue growth was calculated for lipid and protein separately from the

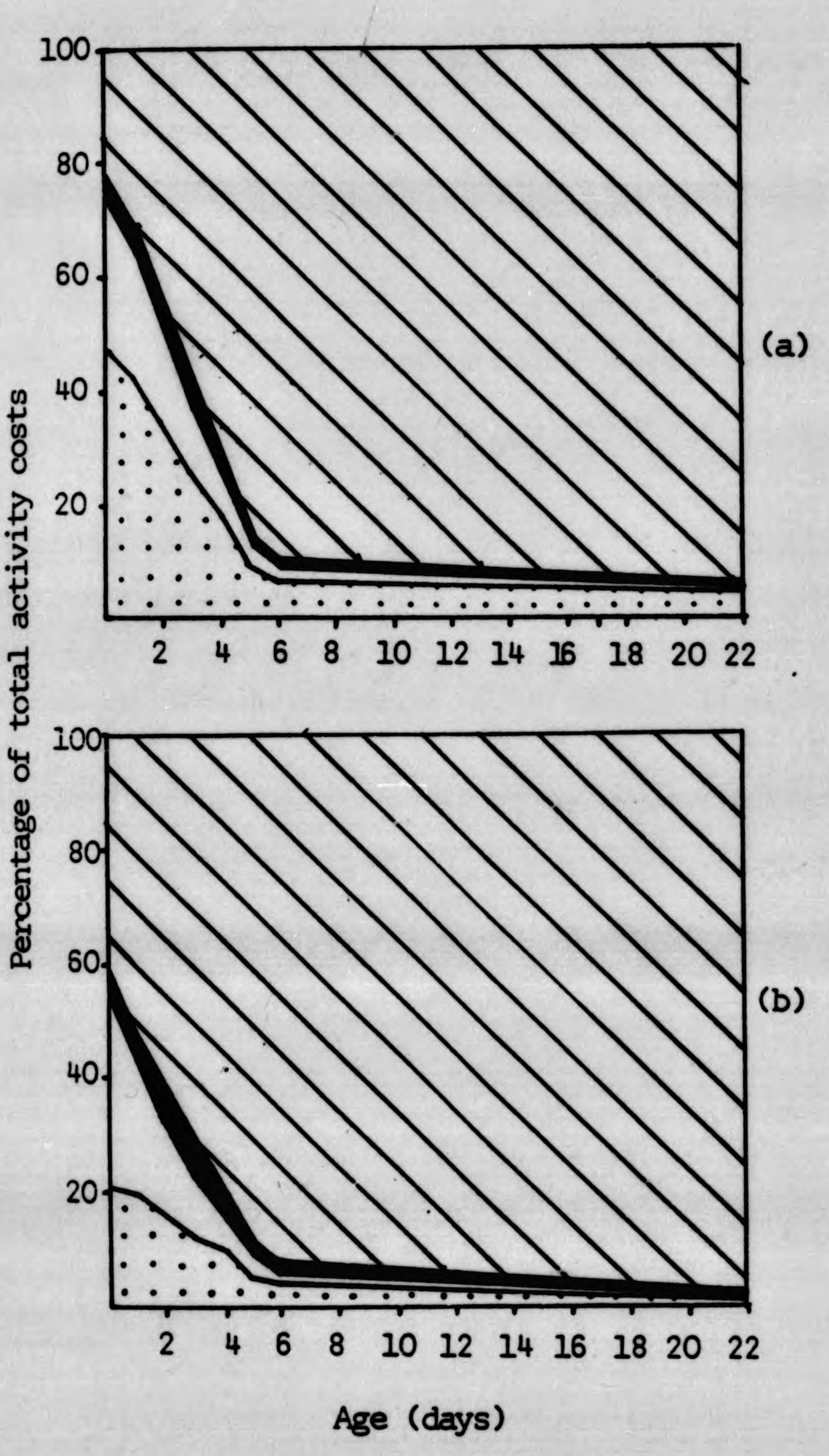


Figure 4.30

Activity costs for nestling Dippers as a function of age calculated using (a) PUC model, and (b) FUC model (see text).

▨	Moving	■	Defaecating
⁙	Begging	☐	Feeding

following two equations derived from Dipper carcass analysis data (Section 4.2.6);

$$PWED = 2.37 + 0.12\ Age \qquad \text{eqn. } 4.14$$

$$LWED = 0.925 + 0.0965\ Age \qquad \text{eqn. } 4.16$$

where PWED and LWED are protein and lipid wet energy densities respectively(kJ g^{-1} wet weight). Daily mass increments from the fitted growth data (Section 4.1.1) were therefore multiplied by the respective equations, and summed to produce figures for the total growth cost (Table 4.23). Protein accounts for 66.8% of total energy accumulated as tissue, and lipid 33.2%. Growth energy reaches a peak at around day seven and eight, shortly after the inflexion of the Dipper growth curve at about 6.5 days (Section 4.1.1).

4.6.5 Biosynthesis (B)

Biosynthesis costs, specifically the cost of producing new tissue (B), were calculated by three methods. Assumptions concerning biosynthetic efficiency previously employed here have been essentially arbitrary, and it was felt that such estimates of biosynthetic cost might be improved. Three models were used to calculate these costs and are presented below.

(a) Biosynthetic efficiency constant with respect to age and lipid:protein ratio

Ricklefs (1974) quoted a figure of 75% biosynthetic efficiency, which has since been used in the construction of DEB from laboratory data (e.g. Williams & Prints, 1986). This cost is assumed to apply across all ages of nestlings and be independent of the relative amount of lipid and protein being produced.

(b) Biosynthetic efficiency constant with respect to age but variable with respect to the lipid:protein ratio

McDonald, Edward and Greenhalgh (1984) calculated the efficiency of lipid and protein production from a consideration of biochemical pathways, and concluded that the efficiencies were 82.6% and 59.8% respectively (based on an amino acid gram molecular weight for the latter of 70). Since the daily increment of lipid and protein was known for Dipper nestlings (see above), the relative amounts of each were allowed for in this calculation, unlike model one (Section 4.6.5(a)). This method assumes no difference in biosynthetic efficiency with age.

(c) Biosynthetic efficiency variable with respect to age and lipid:protein ratio

Wijnandts (1984) calculated the combined cost of growth (P) and biosynthesis in the Long-eared Owl (*Asio otus*) by relating metabolised energy to mass gain in captive reared nestlings of different ages. By extrapolating the curve of mass gain on metabolised energy back to zero, the metabolism at zero growth is obtained (see below). The slope of the curve is thus the cost of mass gain (i.e. P + B). By calculating P for various ages from the equation he provides, and subtracting this from the 'cost factor' (the total cost of mass gain), the cost of biosynthesis remains. That this cost is likely to be exclusively biosynthesis can be demonstrated by examining the remaining components in the nestling energy budget. The only components not included in metabolism at zero growth are growth (P), biosynthesis (B), and HIF. Using a conservative figure for HIF of 20% basal metabolic rate (Kendeigh et al., 1977) and subtracting this and growth (P) from the cost of mass gain in Long-eared Owls shows, (i) that HIF cost alone actually exceeds the total cost of weight gain late in the nestling period, (ii) that if a constant efficiency of biosynthesis (based on model 2, see later) of 66% is assumed and subtracted from the cost of mass gain together with growth (P) then the remaining 'unexplained' cost (presumed to be HIF) actually decreases with age, rather than increasing substantially as would be expected as a greater mass of food is processed. Inclusion of HIF as a component of the cost of mass gain is therefore inconsistent with the observed data, and biosynthetic costs calculated as above are likely to be realistic.

For the Long-eared Owl biosynthetic efficiency is low (38.5%) in one day old nestlings and increases throughout growth to about 66% in 34-35 day nestlings. Moreover, the change in biosynthetic efficiency does not appear to be related to either the lipid energy content/protein energy content ratio (LPR) or the amount of total energy increment daily. In the Dipper LPR increases from 0.38 in seven day old nestlings to 0.60 in twenty-one day old nestlings, but the corresponding change in biosynthetic efficiency is only 2% (i.e. 65% to 67%) when model 2 is applied to Dipper data. Using this model a mean biosynthetic efficiency of 66% is

TABLE 4.23: The daily cost of growth for a Dipper nestling

Age (days)	Energy accumulated in tissue (kJ bird^{-1}) Lipid	Protein	Total	Cost of biosynthesis (kJ bird^{-1}) [a]Method 3	Method 2	Method 1
0	-	-	-	-	-	-
1	2.49	6.54	9.04	11.49	4.92	3.01
2	3.39	8.09	11.48	14.26	6.15	3.83
3	4.55	10.41	14.96	16.64	7.95	4.99
4	5.64	13.19	18.82	19.94	10.05	6.27
5	7.35	15.72	23.07	21.79	12.12	6.46
6	8.39	17.46	25.85	23.12	13.50	8.62
7	9.18	18.63	27.81	25.42	14.45	9.27
8	9.62	19.10	28.72	26.76	14.86	9.09
9	9.70	18.85	28.55	27.60	14.72	8.69
10	9.46	18.03	27.49	26.93	14.11	9.07
11	8.71	16.30	25.01	24.85	12.78	8.34
12	7.98	14.70	22.68	21.65	11.56	7.55
13	7.35	13.82	21.17	20.22	10.84	7.06
14	6.74	12.05	18.79	16.84	9.52	6.27
15	6.27	11.11	17.38	15.06	8.78	5.78
16	5.74	10.06	15.80	12.98	7.98	5.27
17	5.38	9.32	14.70	11.11	7.44	4.91
18	5.25	8.95	14.20	10.30	7.10	4.75
19	5.04	8.59	13.63	9.52	6.85	4.54
20	4.86	8.15	13.01	8.56	6.51	4.34
21	4.63	7.67	12.30	7.70	6.07	4.15
22	4.66	7.70	12.36	7.66	6.10	4.17
23	4.67	7.73	12.40	7.69	6.12	4.19
TOTAL:	147.05	282.17	429.22	388.05	220.48	140.62

For explanation of methods 1-3 used to calculate biosynthesis costs, see text.

found. This figure is practically the same as that found for almost fully grown Long-eared Owl nestlings (and adult females gaining mass) in Wijnandts study. This suggests that McDonald, Edward & Greenhalgh's calculations are based on mature organisms. Wijnandts cost factor for calculating total mass gain cost (growth (P) + Biosynthesis (B)) is shown as a function of the percentage of growth completed in Long-eared Owl nestlings (Figure 4.31). This was then used to calculate biosynthetic costs for the Dipper (see above). A comparison of the three methods is presented in Table 4.23 and Figure 4.32.

The three models for calculating biosynthetic cost yield greatly differing results (Figure 4.32). The total biosynthetic costs for the nestling period for models one to three are; 78.0 kJ, 122.93 kJ and 228.64 kJ respectively. There is nearly a threefold difference in the estimate of biosynthetic costs between the three methods, with important implications for estimating nestling DEB (see Chapter 5). Biosynthetic costs peak at the same time as growth costs and exceed them until day 5 using model three, but are always lower (on a daily basis) using models one and two. Total biosynthetic costs are less than growth costs in all models (Table 4.23).

4.6.6 Alertness (AL)

Resting metabolism is known to vary between night and day (Aschoff & Pohl, 1970), daytime resting metabolism being about one-third higher than night-time resting

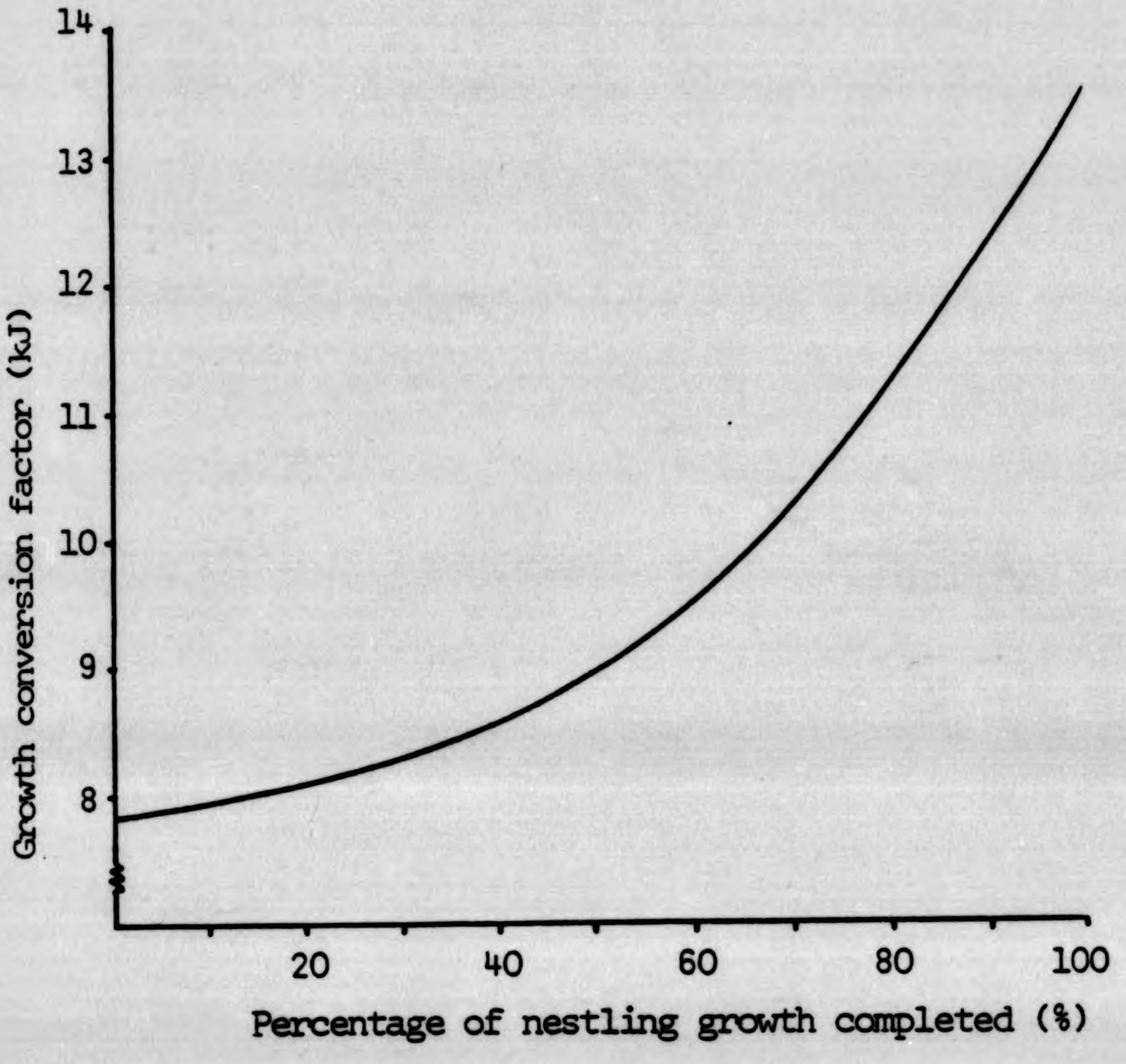


Figure 4.31

Growth conversion factor (after Wijnandts, 1984) for calculating Dipper biosynthesis costs (see text) as a function of the percentage of nestling growth completed

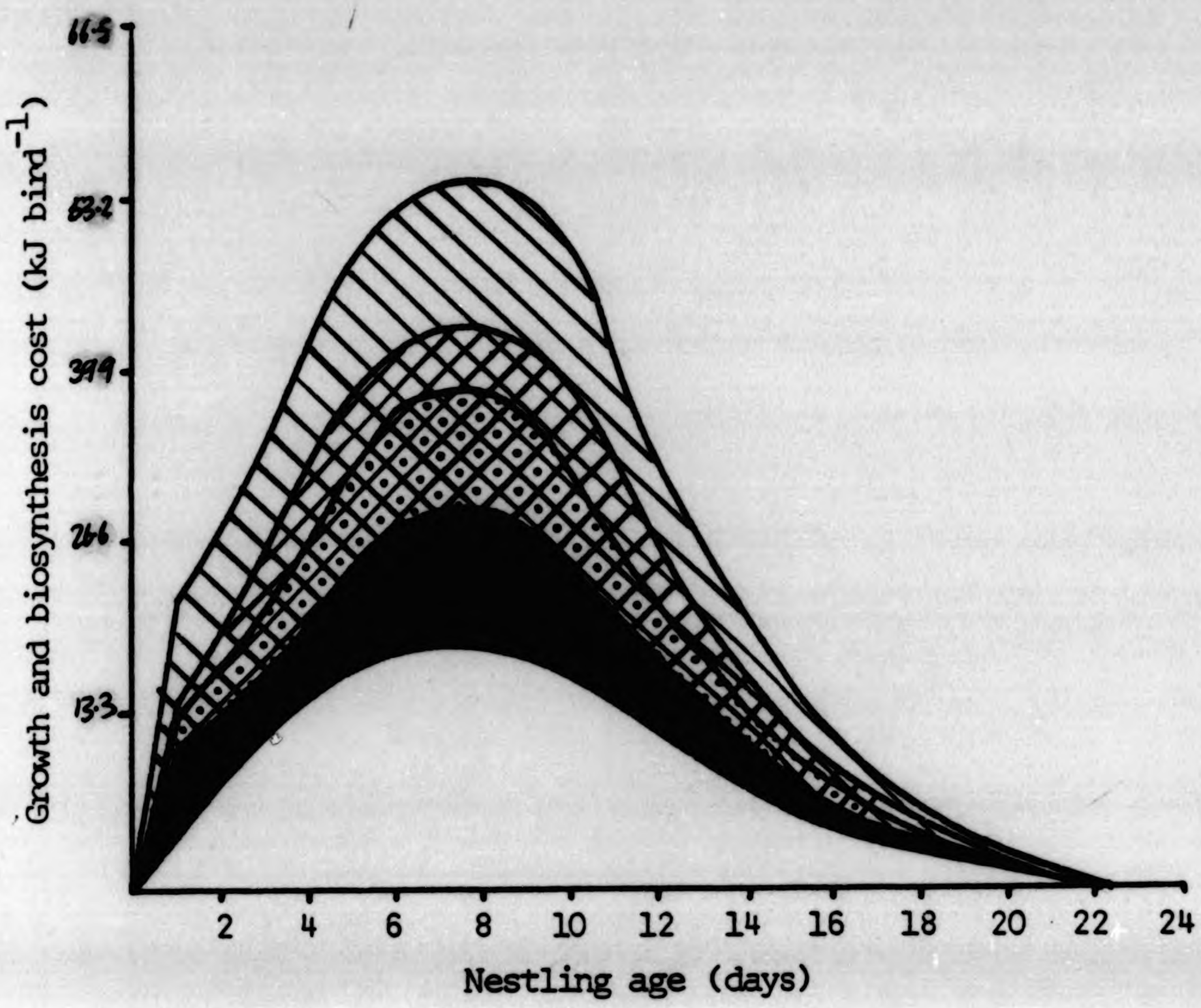


Figure 4.32

The cost of growth and biosynthesis for the Dipper as a function of age

☐ Energy accumulated as protein

■ Energy accumulated as lipid

▧ Biosynthesis cost : method 3

▨ Biosynthesis cost : method 2

⁙ Biosynthesis cost : method 1

metabolism. This difference may be considered as energy used in preparing for muscular activity and increased awareness of surroundings (Kendeigh et al., 1977), and is termed the 'alertness' cost. By definition it cannot be classed as an 'activity' cost per se, but may be added to 'true' activity (A) above for considering the overall cost of activity as generally understood. For clarity the two are treated separately in this study.

4.6.7 The heat increment of feeding (HIF)

Meaningful estimates of HIF in wild birds are difficult to derive since published values for captive birds (mainly domestic fowl) on known diets range from a 20% to 60% elevation of basal metabolic rate (Ricklefs, 1974; Kendeigh et al., 1977). The assumption that HIF (as percentage basal metabolic rate) is independent of temperature is questionable (Kendeigh et al., 1977), so that estimating the proportion of HIF retained at low temperatures for thermoregulation is liable to error. An indirect method for estimating HIF would be that of independently measuring metabolised energy and subtracting the previous components from it, a method used elsewhere to arrive at 'activity' costs (Dunn, 1975; Westerterp, 1973). Metabolic rate at zero activity (Section 4.5.3) was found to be 2.06 x basal metabolic rate in Zebra Finch and House Martin nestlings. Subtracting (P) and (B) for the period of the test (= 0.01 x BMR), and (AL), (=0.35 x BMR) leaves 0.8 x BMR 'unexplained'. Since the activity/metabolism tests were carried out at an ambient temperature of 24°C, a thermoregulatory component must also be subtracted. Thermoregulation costs were not measured for the two species used in the activity/metabolism tests so this cost was predicted using the equation for passerine daytime conductance (heat transfer coefficient) given by Aschoff (1981) (see Section 2.1.5). Nestlings used in the above test were well feathered and homeothermic (see Section 4.5.1).

$$\text{Conductance} = \log 0.857 - 0.463 \log \text{mass} \qquad \text{eqn. } 4.17$$

where conductance is measured in ml $O_2\ g^{-1}.h^{-1}.°C^{-1}$ and mass is in grams. An R.Q.* of 0.86 (see Section 3.2.2) was used for the nestlings. The lower critical temperature was taken to be 29.5°C for a 15g nestling (Figure 2.6). Subtracting the thermoregulation cost then leaves 0.21 x BMR (of the original 2.06) unexplained and attributable to HIF. Although this figure of 21% is within the range of published values it is clearly largely dependent on the accuracy of the thermoregulatory cost estimate. For example if the lower critical temperature was assumed to be 32.6°C then an additional 21% would be taken up by thermoregulation costs leaving HIF as zero. Since it was not possible to demonstrate conclusively a cost of HIF and that it may anyway have substituted a thermoregulatous requirement, this was not included in the Dipper nestling energy budget (Table 4.24 and Figure 4.33).

4.6.8 Daily Energy Expenditure (DEE) and Daily Metabolised Energy (DME)

DEE and DME as a function of age are presented in Table 4.24 and Figure 4.33. They include the cost of activity

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* R.Q. based on measurements of Red-winged Blackbirds of similar mass to Dipper nestlings (Dyer, 1968).

TABLE 4.24: The Daily Energy Budget of a Dipper Nestling

Age (days)	Mass (g)	BMR (kJ bird^{-1})	Growth (kJ bird^{-1})	[a]Bio-synthesis (kJ bird^{-1})	Thermo-regulation (kJ bird^{-1})	[b]Activity (kJ bird^{-1})	'Alertness' (kJ bird^{-1})	D.E.E. (kJ bird^{-1})	D.M.E. (kJ bird^{-1})
0	5.9	11.56	-	-	-	-	4.28	15.84	15.84
1	8.1	14.56	9.04	11.49	-	0.10	5.24	31.39	40.43
2	10.7	17.82	11.48	14.26	0.02	0.22	6.42	38.74	50.22
3	13.9	21.55	14.96	16.64	0.05	0.30	7.54	46.08	61.04
4	17.7	25.68	18.82	19.94	0.17	0.49	8.73	55.01	73.86
5	22.1	30.17	23.07	21.79	0.49	0.83	11.42	73.70	99.55
6	26.7	34.61	25.85	23.12	2.71	1.84	12.82	86.75	114.56
7	31.3	38.84	27.81	25.42	6.62	3.05	9.96	63.24	86.31
8	35.7	42.73	28.72	26.76	8.81	3.37	13.67	95.34	124.06
9	39.7	46.16	28.55	27.60	10.10	3.75	14.77	102.38	130.06
10	43.2	49.08	27.49	26.93	11.34	4.06	15.21	106.62	134.11
11	46.0	51.37	25.01	24.85	11.99	4.28	15.92	108.41	133.42
12	48.2	53.14	22.68	21.65	12.40	4.42	16.47	108.08	130.76
13	50.0	54.57	21.17	20.22	12.73	4.52	16.96	109.00	130.17
14	51.3	55.60	18.79	16.84	12.97	4.60	17.24	107.25	126.04
15	52.3	56.39	17.38	15.06	13.16	4.66	17.48	106.75	124.13
16	53.0	56.93	15.80	12.98	13.28	4.69	17.65	105.53	121.33
17	53.5	57.32	14.70	11.11	13.37	4.71	17.77	104.28	118.98
18	53.9	57.63	14.20	10.30	13.45	4.72	17.86	103.96	118.16
19	54.2	57.87	13.63	9.52	13.50	4.73	17.94	103.56	117.19
20	54.4	58.02	13.01	8.56	13.54	4.73	17.99	102.84	115.85
21	54.5	58.10	12.30	7.70	13.56	4.73	18.01	102.10	114.40
22	54.6	58.17	12.36	7.66	13.58	4.73	18.03	102.17	114.53
23	54.7	58.20	12.40	7.69	13.59	4.73	18.06	102.27	114.67
OTAL:	-	1066.00	429.28	388.05	211.43	78.26	337.44	2081.29	2510.54

[a]Calculated using method 3. [b]Calculated using proportionate unit cost (PUC) model, see Section 4.6.3
The energy budget is based on a single nestling in a brood of four, see Section 4.6

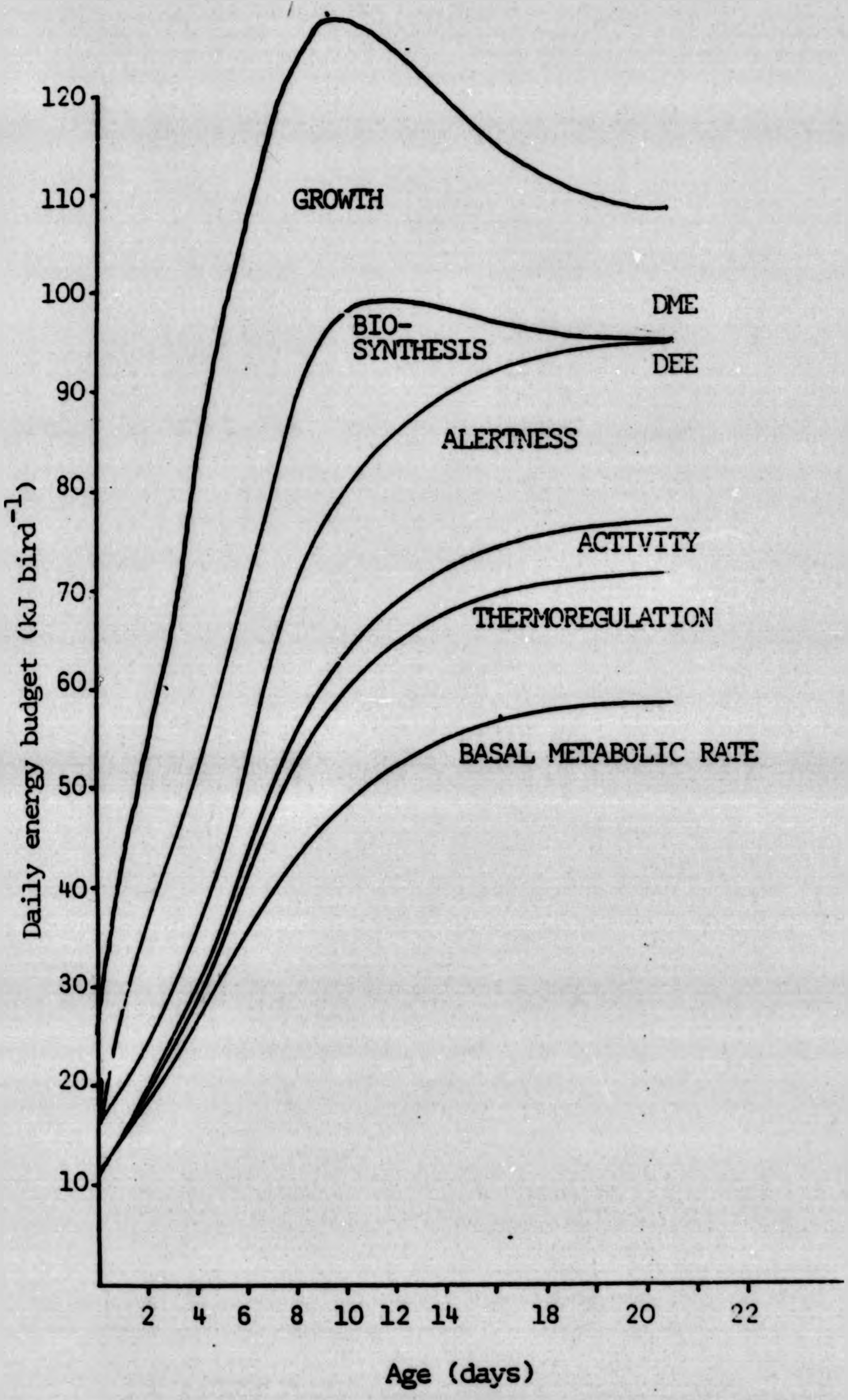


Figure 4.33

The daily energy budget of the nestling Dipper

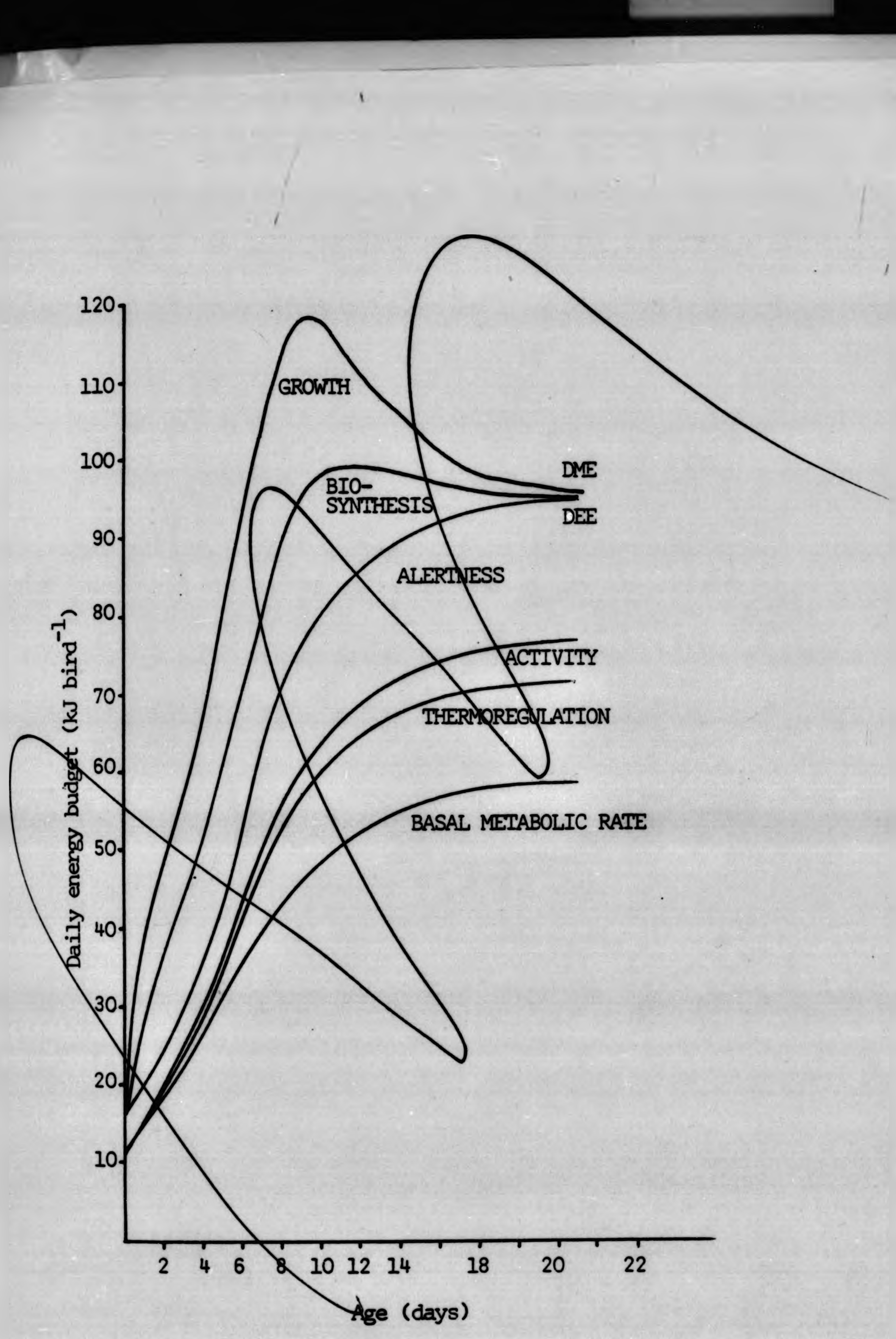


Figure 4.33

The daily energy budget of the nestling Dipper calculated assuming PUC, and biosynthesis using model three. DEE as a multiple of BMR is shown in Table 4.24 and Figure 4.34.

The daily metabolised energy (DME) of Dipper nestlings peaks around day nine (Figure 4.33), primarily due to the peak energy accumulated to growth (P) at this time (Section 4.6.4). Daily energy expenditure (DEE), however, peaked approximately two days later due in part to the reduction in (P) and in part to the increase in alertness, activity and thermoregulation components as nestlings become homeothermic and parental inattentiveness is complete (Figure 4.28). The components contribute the following proportions to the total daily metabolised energy; BMR 42.4%, growth 17.1%, biosynthesis 15.4%, thermoregulation 8.4%, activity 3.1%, alertness 13.4% (activity and alertness combined, see Section 4.6.6 is 16.5%). Basal metabolic rate is therefore the single most costly component, with alertness cost about one-third of BMR. Biosynthesis, growth and thermoregulation are each about one-third of BMR and activity is the least costly component at less than one-tenth BMR. Components are expressed as a percentage of BMR in Figure 4.34, the initial low DEE and DME values are because nestlings have just hatched (i.e. zero days old) and have effectively zero growth and biosynthesis costs, since the first growth increment occurs between day zero and one, and have been wholly assigned to day one costs here. The slight decrease in DME and DEE as a proportion of BMR is due to the decreasing relative costs of biosynthesis and alertness. The patterns of change in components of the

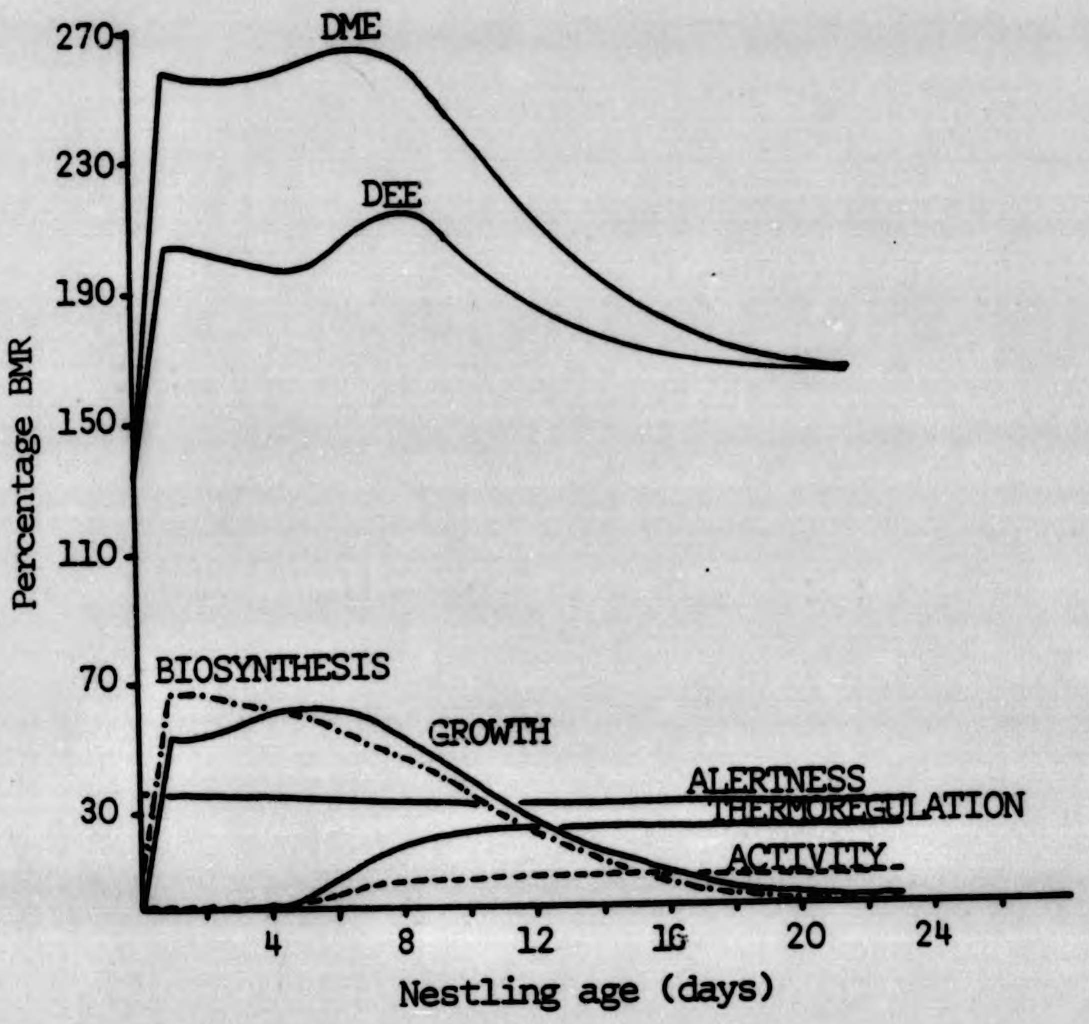


Figure 4.34

Components of the Dipper nestling energy budget expressed as a percentage of BMR

TABLE 4.25: Daily energy expenditure as a multiple of BMR for an eighteen day old Dipper nestling based on the different methods used when calculating activity and biosynthesis costs (see text)

	Biosynthesis Costs		
Activity Costs	Method 1	Method 2	Method 3
Fixed Unit cost	1.72	1.73	1.75
Proportional Unit cost	1.78	1.79	1.80
Mean Unit cost	1.76	1.77	1.78

energy budget is discussed in Chapter 5.

Assumptions concerning which models to use in calculating biosynthesis and activity costs affect the estimate of DEE and DME. Table 4.25 shows this with respect to DEE/BMR for eighteen day old Dipper nestlings for comparison with FEE/BMR (Table 4.26) measured using the doubly-labelled water technique and is discussed in Section 4.7.

4.7 FIELD METABOLIC RATE OF EIGHTEEN DAY NESTLING DIPPERS MEASURED USING THE DOUBLY-LABELLED WATER TECHNIQUE

Field metabolic rate, or field energy expenditure (FEE) was measured in eighteen day Dipper nestlings (n = 8) in the wild (Section 3.5.2). The results for each individual are presented in Table 4.26. Birds were sexed using an earlier version of the equation in Section 4.1.4, so that a sample of four males and four females might be obtained. Subsequent observations caused one male to be re-classified as a female and so the sample presented is for five females and three males. No initial blood samples for female one were obtained for female one, hence the initial isotope concentrations were estimated using the mean values for the per gram isotope loading of individuals injected from the same isotope batch (Ricklefs & Williams, 1984). Since all initial dosages were calculated from the same dosage curve, and body water content was assumed to be a constant 67% (from carcass analysis, Section 4.2), minimal errors should be incurred. FMR was calculated using the following equation:-

TABLE 4.26: A comparison of daily energy expenditure (DEE) measured using the time-activity-laboratory method and field energy expenditure (FEE) measured using the doubly-labelled water method, of eighteen day old Dipper nestlings

Sex	Mass	Brood-size	D.E.E. (kJ bird^{-1}d^{-1})	F.E.E. (kJ bird^{-1}d^{-1})	F.E.E. (kJ g^{-1}d^{-1})	$\frac{FEE}{BMR}$
[a]Female 1	58.6	1	101.7	114.0	1.947	1.86
[b]Female 2	49.6	3.5	90.07	96.3	1.942	1.77
Female 3	54.0	4	95.80	94.0	1.741	1.63
Female 4	54.9	5	96.96	94.5	1.721	1.62
Female 5	58.4	5	101.40	93.1	1.595	1.52
Male 1	64.5	4	108.99	110.4	1.713	1.68
Male 2	54.9	5	96.96	108.5	1.976	1.85
Male 3	57.4	5	100.14	124.4	2.152	2.06

a Initial dosage calculated from mean of other birds

b Brood-size 3.5 since initially brood of 4 but on visit for second blood sample only 3 chicks present

$$FEE = \left[\frac{\bar{N}}{2.08}(K_O - K_D) - 0.015\ K_D\bar{N}\right] Z \qquad \text{eqn. 4.18}$$

where $\bar{N}$ = body water content in mM = mean body mass x 0.67 x 55.56

K_O = Ln (Initial O^{18} excess*)-Ln (final O^{18} excess)/ΔT

K_D = Ln (Initial D excess)-Ln (final D excess)/ΔT

Z = combined factors converting mMol $CO_2.h^{-1}$ to kJ.day using an RQ of 0.86 (see previously).

Comparing FEE of females with brood size showed a highly significant relationship (Figure 4.35). The equation is:

$$♀\ FEE = 117.36 - 5.13\ \text{Brood-size} \quad r^2 = 91.6 \qquad \text{eqn. 4.19}$$

$$F = 32.55,\ df\ 1, 3, \quad p < 0.05.$$

This relationship was very dependent upon female one, as the non-significant relationship when this point is removed demonstrates ($F = 5.99$, d_f 1, 2 n.s.). So whilst it is tempting to infer a reduced cost of FEE with brood size it is clearly unwarranted on the basis of a small sample size, especially as the sexes together show no obvious correlation, although it is known that single nestlings do incur appreciably higher thermoregulatory costs (Section 4.3).

Excluding data for the brood sizes of one and comparing the mean FEE for males and females of similar brood size shows that males have significantly higher FEE costs than females ($t = 4087$, $n = 7$, $p < 0.01$), males averaging 21% higher FEE costs. This is due primarily to the sexual size-dimorphism found in Dipper nestlings (Section 4.1.4),

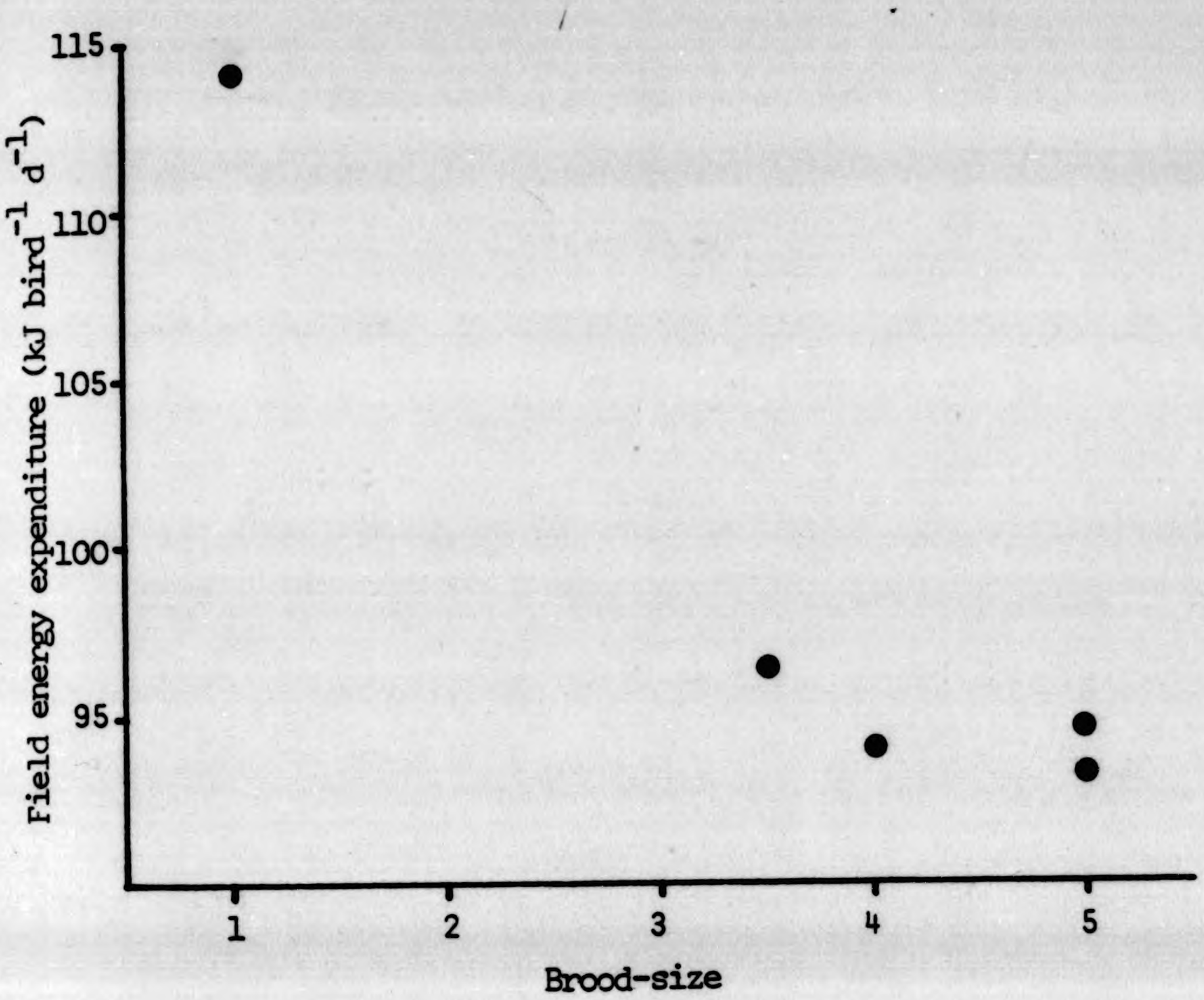


Figure 4.35

Field energy expenditure of 18 day old female Dipper nestlings (measured using the doubly-labelled water method) as a function of brood-size

$r^2 = 0.92$, $n = 5$, $p < 0.05$

for on a per gram basis (FEE kJ g^{-1}, Table 7.5) there is no significant difference between the sexes (t = 1.91, n = 7, n.s.) The mean FEE for males and females was 114.3 and 98.8 kJ.bird.day respectively. If data for brood-size one is excluded, the mean FEE for females is 94.5 kJ.bird.day. FEE of nestlings of both sexes is approximately 1.75 x BMR. By virtue of their lower mass females appear to be less costly to rear than males of this species (see Chapter5).

Table 4.26 also shows data for DEE estimated by the time-activity-laboratory method (see Section 4.6). Whilst DEE was calculated for a nestling in a brood of four, and some error of applying such assumptions to other brood-sizes are expected, it can be seen that the two techniques yield similar results (i.e. within 5.0% of each other). If DEE/BMR is compared with FEE/BMR for brood-size four only, the ratios are 1.660 (using data in Table 4.25) and 1.655 respectively, though it should be noted that all DEE/BMR estimates (Table 4.24) fall within the 95% confidence limits of the brood-size four FEE/BMR figure. These results are discussed in Chapter 5.

PART TWO: HATCHING ASYNCHRONY: IMPLICATIONS FOR NESTLING ENERGETICS

4.8 PEAK LOAD REDUCTION (PLR): A TEST OF THE MODEL

4.8.1 Assimilation efficiency

Six House Martins aged 7-8 days old were hand-reared on a diet of Blowflies (*Calliphora* spp.) imagines to measure nestling apparent assimilation efficiencies (Sections 3.6.2, 3.6.3). The nestlings were kept in two broods. The first was a brood of two taken from a brood of four (and replaced after the experiment). The second was a brood of four taken from two broods and returned to three other broods to make up the broodsizes required for other brood manipulations (Section 3.8).

The dry mass of faeces produced over a twenty-four hour period for each nestling was measured (freeze-drying) and compared with the dry mass of food ingested. The mean water content of the flies used was 70.0±1.8%. "Dry mass" assimilation efficiency was calculated as;

$$\frac{\text{Dry mass of flies ingested}-\text{Dry mass of faeces}}{\text{Dry mass of flies ingested}} \qquad \text{eqn. 4.20}$$

'Dry mass' assimilation efficiency for the six nestlings is presented in Table 4.27. The energy content of House Martin faeces of age 8-16 days is 17.91 kJ g^{-1} (Bryant & Westerterp, 1983) whilst the mean calorific content of aerial insects (chiefly Diptera) has been measured as 22.83 kJ g^{-1} (Turner, 1980). Using these figures 'energy' assimilation efficiencies were calculated by substituting the energy equivalents into the equation above (Table 4.27). The mean 'dry mass' assimilation efficiency was 60.5 ± 3.2 per cent and the 'energy' assimilation efficiency is 69.0 ± 2.5 per cent. These values are similar to those found in other insectivorous species, but differ from Bee-eaters (Krebs & Avery, 1984; Bryant & Bryant, in press). Metabolised energy for the captive birds was therefore calculated from these data as a check that the nestlings were not under-nourished. All nestlings put on mass during the experiment and their metabolised energy was on average 3.4 x Average daily metabolic rate. There is no evidence therefore to suggest nestlings

TABLE 4.27: Energy intake and assimilation efficiency of House Martin nestlings on a diet of *Calliphora* imagines

	Mean nestling mass (g)	Wing (mm)	Food wet mass (g)	Faeces dry mass (g)	Food dry mass (g)	Energy content (kJ)	Assimilation efficiency (kJ) ^{a}I	^{b}II	Metabolised energy (kJ) I	II
	16.9	22.0	17.96	2.295	5.388	123.02	57.4	66.6	71.7	81.9
	18.2	29.1	16.69	2.086	5.007	114.32	58.3	67.3	65.6	76.9
	12.0	22.1	10.42	1.213	3.126	71.37	61.2	69.6	43.7	49.7
	12.1	22.0	10.18	1.171	3.053	69.71	61.6	69.9	42.9	48.7
	17.0	27.9	10.43	1.303	3.129	71.44	58.4	67.3	41.7	48.1
	12.0	21.8	13.69	1.395	4.106	93.75	66.0	73.3	61.9	68.7
mean ± SD	14.7 ± 2.9	24.2 ± 3.4	13.22 ± 3.45	1.577 ± 0.486	3.968 ± 1.036	90.60 ± 23.40	60.5 ± 3.2	69.0 ± 2.5	54.6 ± 13.3	62.3 ± 15.4

a Dry mass assimilation efficiency (I), calculated as $\frac{\text{Dry mass food ingested-Dry mass faeces output}}{\text{Dry mass food ingested}}$

b Energy assimilation efficiency (II), calculated as $\frac{\text{Energy ingested-Energy in faeces}}{\text{Energy ingested}}$, assumes a calorific content for food of 22.833 kJ g^{-1} (Turner, 1980), faeces of 17.91 kJ g^{-1} (Bryant & Westerterp, 1983).

Water content of food was measured as 70.0 ± 1.8%.

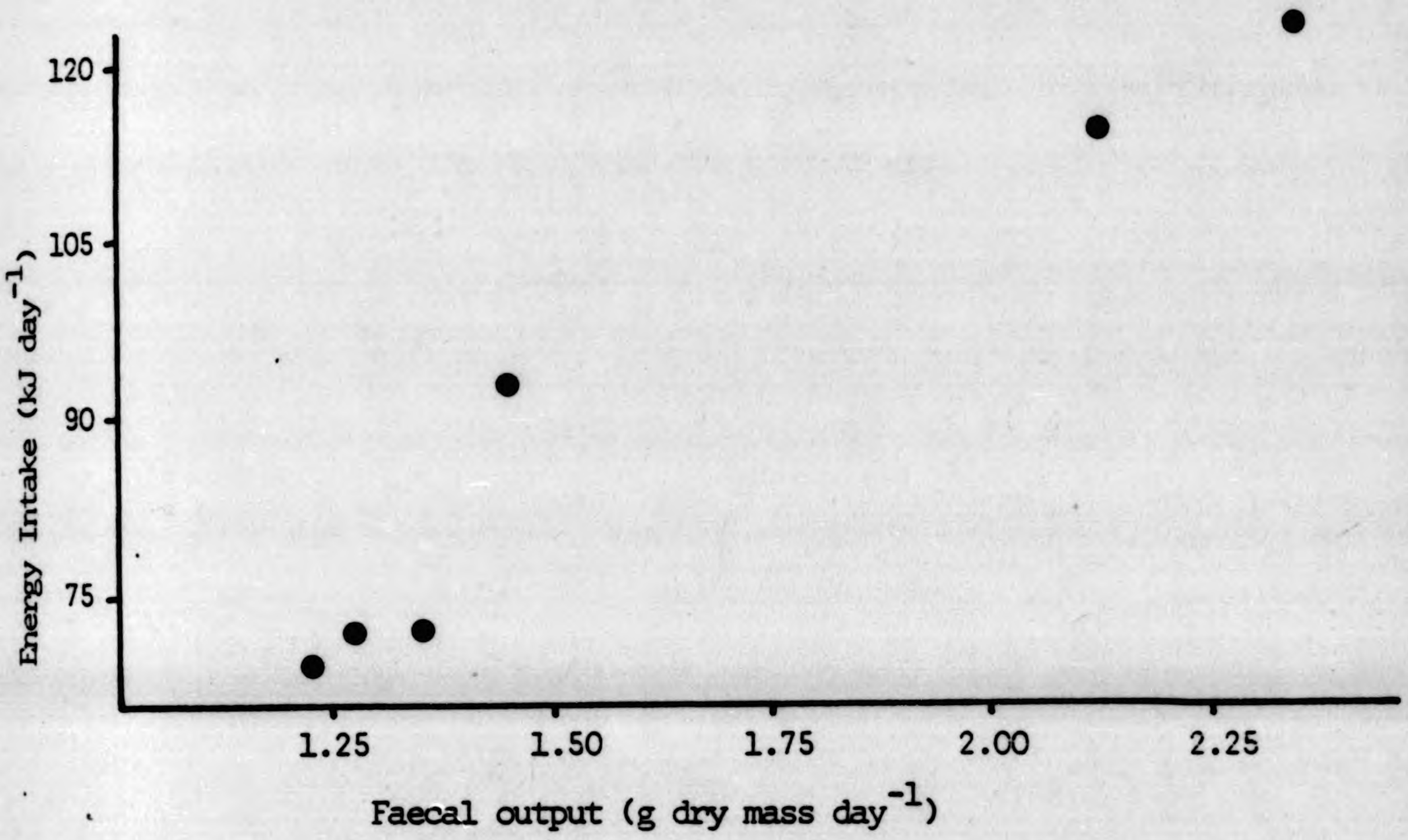


Figure 4.36: Energy intake as a function of dry faecal output for six hand-reared House Martin nestlings (see text).

$r^2 = 0.92$, $n = 6$, $p < 0.05$

were under-nourished. The latter was calculated from Bryant & Gardiner (1979).

Figure 4.36 shows the energy intake of hand-reared House Martin nestlings behaviour is a highly significant function of faecal output (r^2=91.7, $p < 0.001$). Faecal output was therefore considered a suitable measure of energy intake in the House Martin. Evidence for non-linearity is slight and therefore ignored. An assimilation of 69.0% was used to convert faecal output to energy intake for investigating Peak Load reduction (next Section) as follows:-

$$\text{Energy Intake} = \frac{\text{Faecal Dry Mass} \times 17.91}{69.0} \times 100 \qquad \text{eqn. 4.21}$$

where energy intake is in kJ day^{-1}.

4.8.2 Faecal output

Peak Load Reduction (Section 2.2) was investigated in eighteen House Martin broods. The peak energy demand of each brood was measured indirectly by regularly collecting the total faecal output (Section 3.6.1) and converting this to gross energy intake (GEI) from the assimilation efficiency value given for hand-reared nestlings in the previous Section.

Peak faecal output was measured as the mean of three days of highest output, and this figure was used to calculate the mean peak energy demand of the brood ($MPED_B$).

Figure 4.37 (a-c) shows the mean daily faecal output for broods of three to five House Martin nestlings throughout the nestling period. The mean peak faecal outputs are approximately 6.0, 9.5 and 11.0 grams dry mass per brood

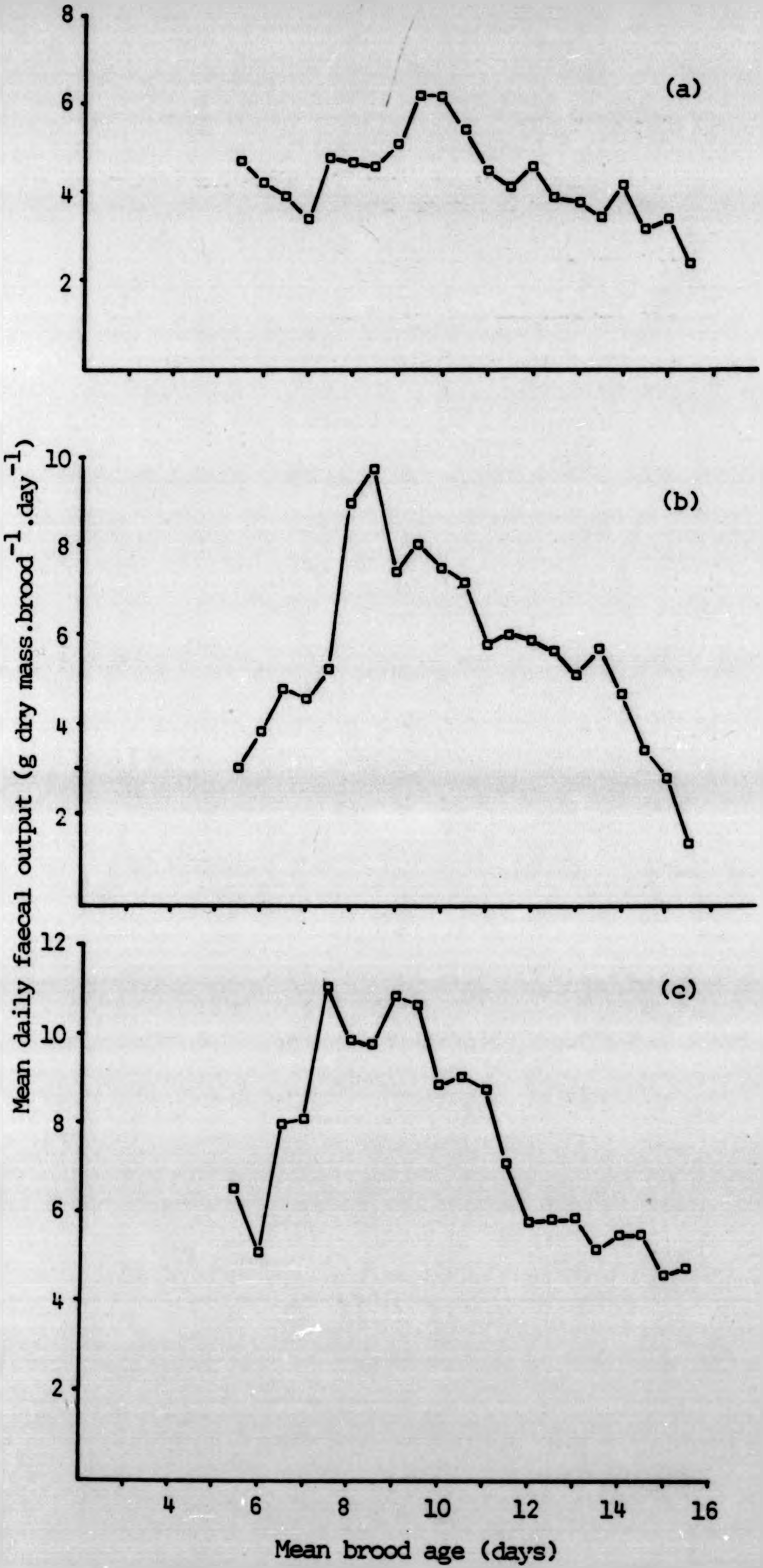
Figure 4.37:

Daily faecal output for House Martin broods as a function of the mean brood age.

(a) Brood size 3 (n = 5)

(b) Brood size 4 (n = 9)

(c) Brood size 5 (n = 3)


(a)
(b)
(c)
Mean daily faecal output (g dry mass.brood^{-1}.day^{-1})
Mean brood age (days)
2
4
6
8
10
12
4
6
8
10
12
14
16

per day, for broods of three to five respectively. The regression of peak faecal output on brood-sizes is significant ($F = 8.46$, $n = 17$, $p < 0.05$) although on a per nestling basis they were not ($F = 1.12$, $n = 17$, n.s.).

4.8.3 Peak Energy Demand

The mean peak faecal output per nestling was used to calculate mean peak energy demand of nestlings ($MPED_n$) and these data were then used to test the model of exponential energy savings through reduced peak energy demand, as asynchrony was increased (Section 2.2). The model predicts that $MPED_n$ should decrease in a curvilinear (concave-up) way with increasing brood-size (Figure 2.8). Figure 4.38 shows $MPED_n$ as a function of asynchrony, measured as the relative difference in hatching mass, RDHM (Section 2.3.3). There is no evidence of a relationship between peak energy demand and hatching asynchrony. Bryant & Gardiner (1979) calculated a small reduction (2.2%) in (GEI) with asynchrony in House Martin broods of four using 'smoothed' data and assigning broods as either asynchronous or synchronous. There are a number of reasons why both of these data suggest that hatching asynchrony did not evolve (at least in this species) primarily as a means of reducing parental costs during peak nestling demand and these will be discussed in Chapter 5.

4.9 COMPETITIVE BEGGING BEHAVIOUR I: A LABORATORY STUDY

4.9.1 Types of Zebra Finch begging behaviour

Nestling begging behaviour was examined in the Zebra Finch (Section 3.7). The following begging behaviours were measured.

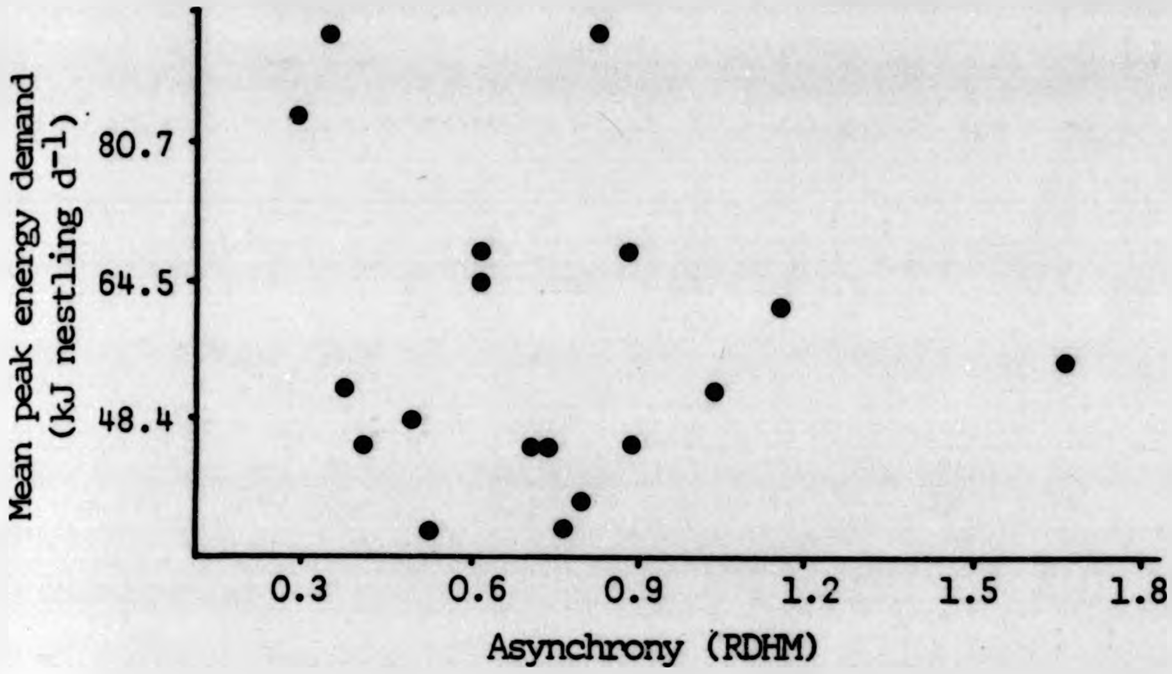


Figure 4.38

The mean peak energy demand of House Martin nestlings as a function of hatching asynchrony for all brood-sizes combined

(D. M. Bryant data, n = 4)

(a) Pre-feed giving-up time (GUT_{pre}), the mean duration of begging (s) in a series of five tests in which nestlings were not offered food (Section 3.7.1) but allowed to beg until they gave up.

(b) Post-feed giving-up time (GUT_{post}), the mean duration of begging (s) in a series of five tests in which nestlings had previously received a single feed at a single profitability; either $F = 0$ or $F = 1$ (Sections 3.7.1, 3.7.2). Nestlings were allowed to continue begging as above.

(c) Handling time (HT), the time taken to remove and swallow food from the dummy bill (Section 3.7.2).

(d) Elevated giving-up time (EGUT), the duration of begging (s) an unfed nestling when its sibling was being fed. The unfed nestling may or may not have received a feed on the previous feeding offer (Section 3.7.1).

(e) Elevated giving-up time/giving-up time (EGUT/GUT), the ratio of EGUT to the mean pre- and post-feed giving-up times (see above). This is a measure of the relative increase in duration of begging during feeding of a sibling.

(f) After-begging (ABT), the duration of begging (s) of a nestling immediately after it has received a feed, and hence after HT.

(g) After-begging/handling time (ABT/HT), this ratio is a measure of the time a nestling will allocate to begging taking into account its previous HT experience.

4.9.2 Zebra Finch begging behaviour in the laboratory

Pre-feed giving-up time (GUT_{pre}) was not found to be significantly different from post-feed giving-up time (GUT_{post}) for either F = 1 or F = 0 (Table 4.28). Comparing GUT_{pre} with the first begging bout immediately after the feed also showed no difference. The data were therefore lumped for subsequent analysis and are referred to as GUT without qualification. Nestlings with lower initial crop-scores (< 4) (Section 3.7.3) did not beg for a significantly different time than more satiated nestlings with higher crop-scores (> 5) (Table 4.28). The presence or absence of a sibling similarly had no apparent effect on the amount of time a nestling would beg without reward.

Neither GUT nor GUT_{pre}/GUT_{post} varied as a function of age. GUT_{pre}/GUT_{post} did not vary when a comparison of means for young chicks (4-6 days) and old chicks (7-9 days) was carried out (Table 4.28). In Zebra Finch nestlings GUT therefore appears to remain fixed at approximately 8.5 seconds ($\bar{x} = 8.4 \pm 0.46$, $n = 110$) under a wide range of treatments.

Handling time and after-begging time (ABT, see below) are presented as a function of nestling age in Figures 4.39 and 4.40. In keeping with previous discussions of nestling size (mass) hierarchies, HT and ABT will be considered further in relation to nestling mass, rather than nestling age (Section 3.7.4). Handling time was found to decrease with mass for both F = 0 and F = 1 (Figures 4.41, 4.42). It had been expected that handling time for F = 0 would be less than the

TABLE 4.28: Giving-up time (GUT) of Zebra Finch nestlings in relation to crop-score, presence or absence of sibling, and food profitability (see Section 3.7.2); and GUT_{pre}/GUT_{post} in relation to nestling age

Variable	Comparison	Mean ± SE	n	t-value	significance
Crop-score	High	10.2 ± 1.88	50	0.115	n.s.
	Low	9.65 ± 1.21	50		
Sibling	Present	10.98 ± 2.00	60	0.325	n.s.
	Absent	9.1 ± 1.25	60		
Feed F = 1	Before	10.48 ± 1.70	75	0.865	n.s.
	After	6.6 ± 1.41	60		
Feed F = 0	Before	6.56 ± 1.42	60	0.357	n.s.
	After	8.30 ± 0.75	55		
Age	[a]Young	2.07 ± 0.47	40	0.299	n.s.
	Old	1.31 ± 0.13	45		

[a] Young = 4-6 days old; Old = 7-9 days old

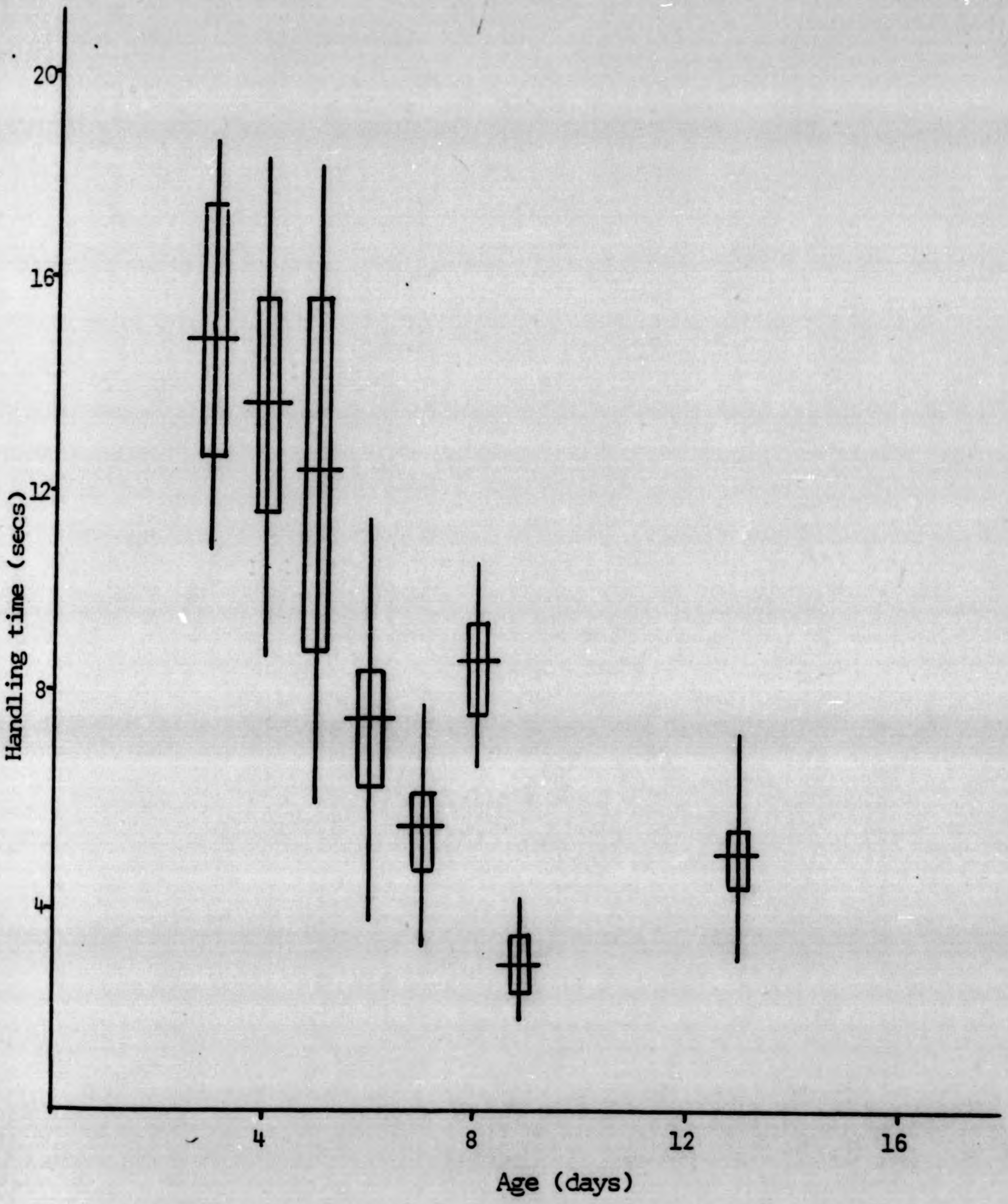


Figure 4.39: Handling time as a function of age in the Zebra Finch. (means, standard deviations and standard errors)

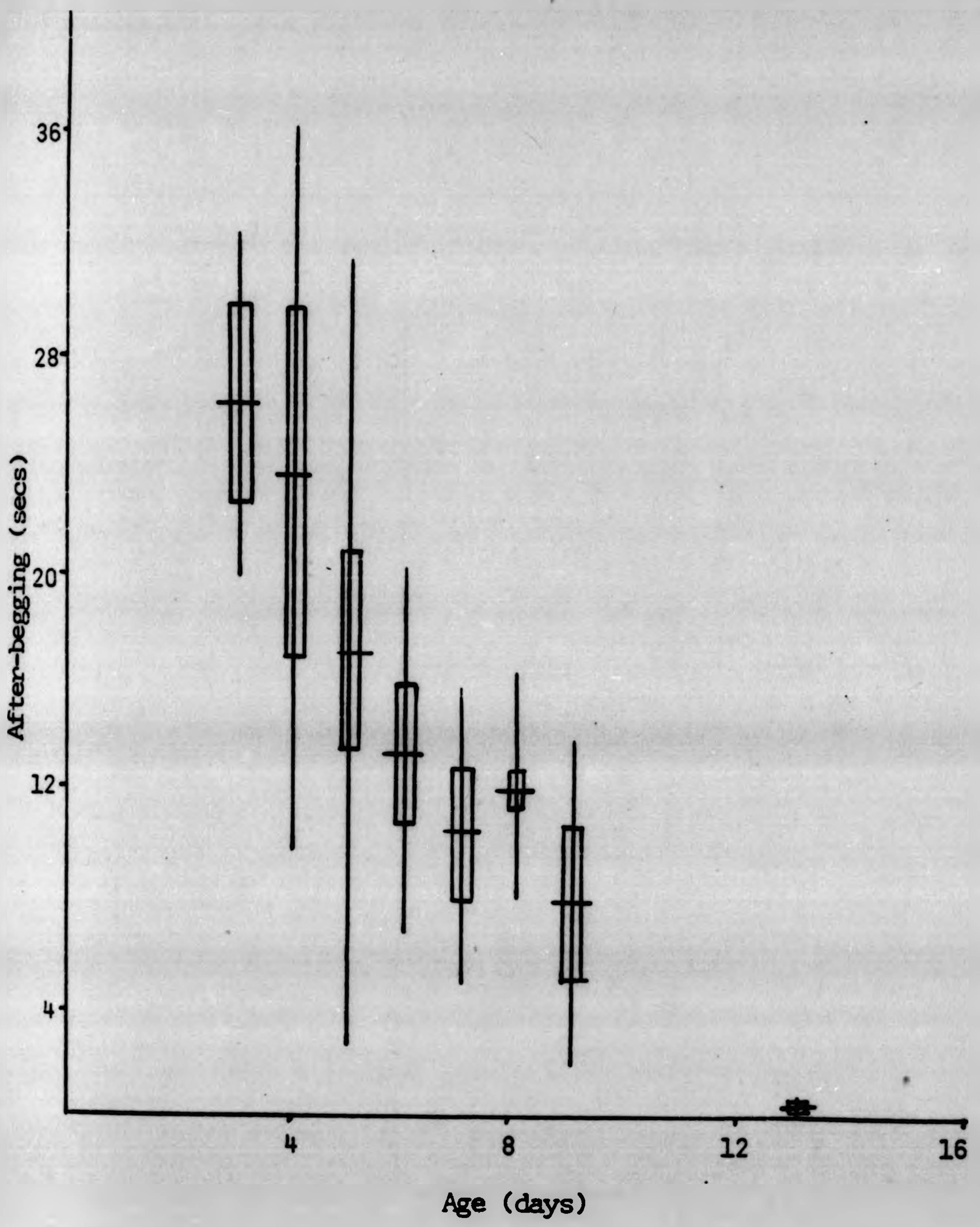


Figure 4.40: After-begging as a function of age in Zebra Finch nestlings.

(means, standard deviations and standard error) handling time for F = 1, yet the reverse was actually found, nestlings taking longer to 'handle' with the dummy bill empty (Table 4.28, 4.29). Paired nestlings had significantly higher handling times than singletons (Tables 4.28 and 4.29). When the data were examined to take into account load size however, it was found that lone nestlings receiving the empty bill (N1:F0), handled for less time than paired nestlings receiving the greater loadsize (N2:F1). This difference was not however significant. The overall relationship between handling time and mass (Section 3.7.4) can be expressed as;

$$\text{Handling Time} = 23.4 - 8.55 \text{ Ln Mass}$$

$$r^2 = 0.523, \; p < 0.001 \qquad \text{eqn. } 4.22$$

In paired nestling treatments it was found that the unfed nestling begged for much longer without reward before giving up ($\bar{x} = 24.5 \pm 1.54$). The sight/sound of its sibling being fed induced it to elevate its begging (= EGUT) above GUT levels, and this difference was significant ($t = 4.84$, $df = 163$, $p < 0.001$). The ratio of EGUT/GUT was not found to vary with either crop-score, mass of unfed nestling, mean brood age, or RDBM (Table 4.30). EGUT and EGUT/GUT therefore appear to be similar in many respects to GUT and GUT_{pre}/GUT_{post}, but at a consistently higher level. In addition to a change in begging behaviour of unfed nestlings in paired treatments, begging behaviour of nestlings receiving food was also found to vary. In both single and paired experiments, immediately after a nestling had finished handling the feed, it began to beg again. This after-begging time (ABT), was found to

TABLE 4.29: Handling-time as a function of $\log_e$ nestling mass in the Zebra Finch

[a] Handling-time (s)	a Intercept	b Slope	r^2	Significance
TOTAL	23.4	-8.55	0.546	$p < 0.001$
F = 1	22.1	-8.17	0.452	$p < 0.001$
F = 0	23.6	-8.30	0.538	$p < 0.001$
Single (N1)	22.7	-8.45	0.521	$p < 0.001$
Pair (N2)	27.5	-10.5	0.523	$p < 0.001$

[a] For explanation of handling-time categories see text

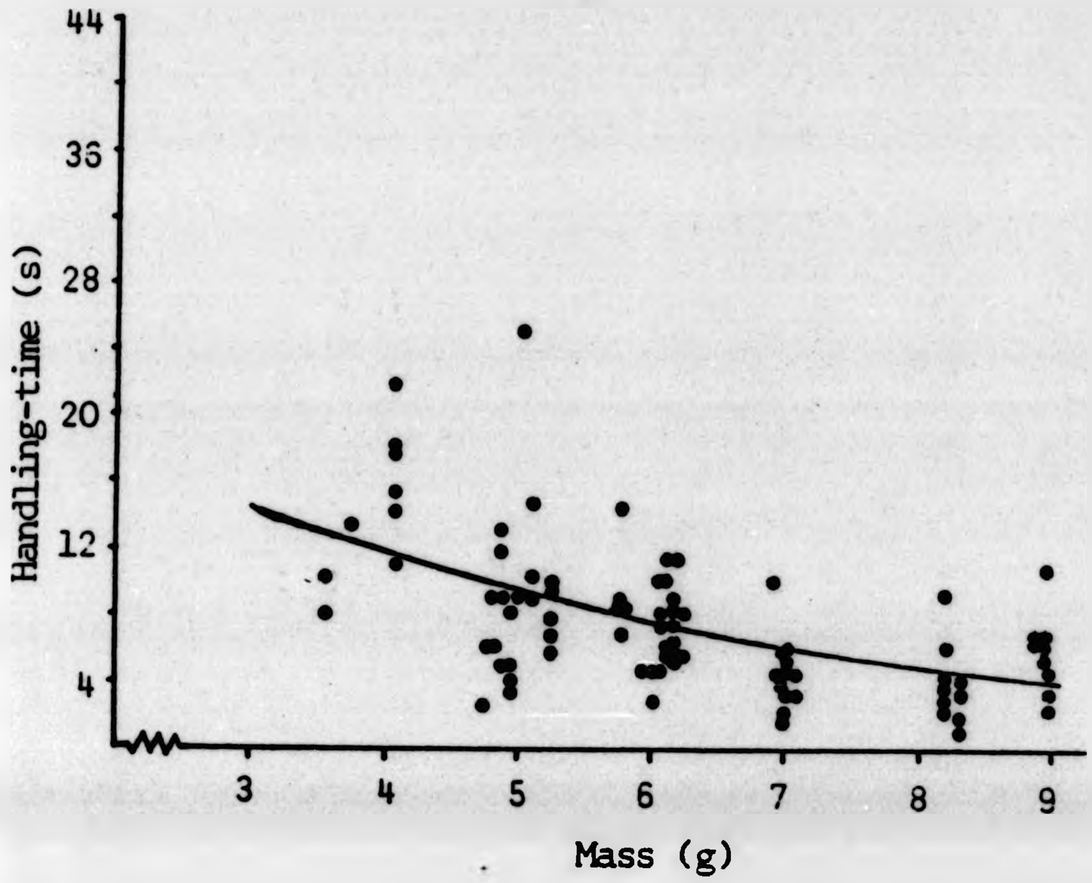


Figure 4.41

Handling-time as a function of nestling mass for Zebra Finches when food profitability is F = 1.

The regression equation,

$$y = 22.1 - 8.17 \log_e x$$

$r^2 = 0.30$, $n = 88$, $p < 0.001$

Standard deviations: $a = 2.44$, $b = 1.34$

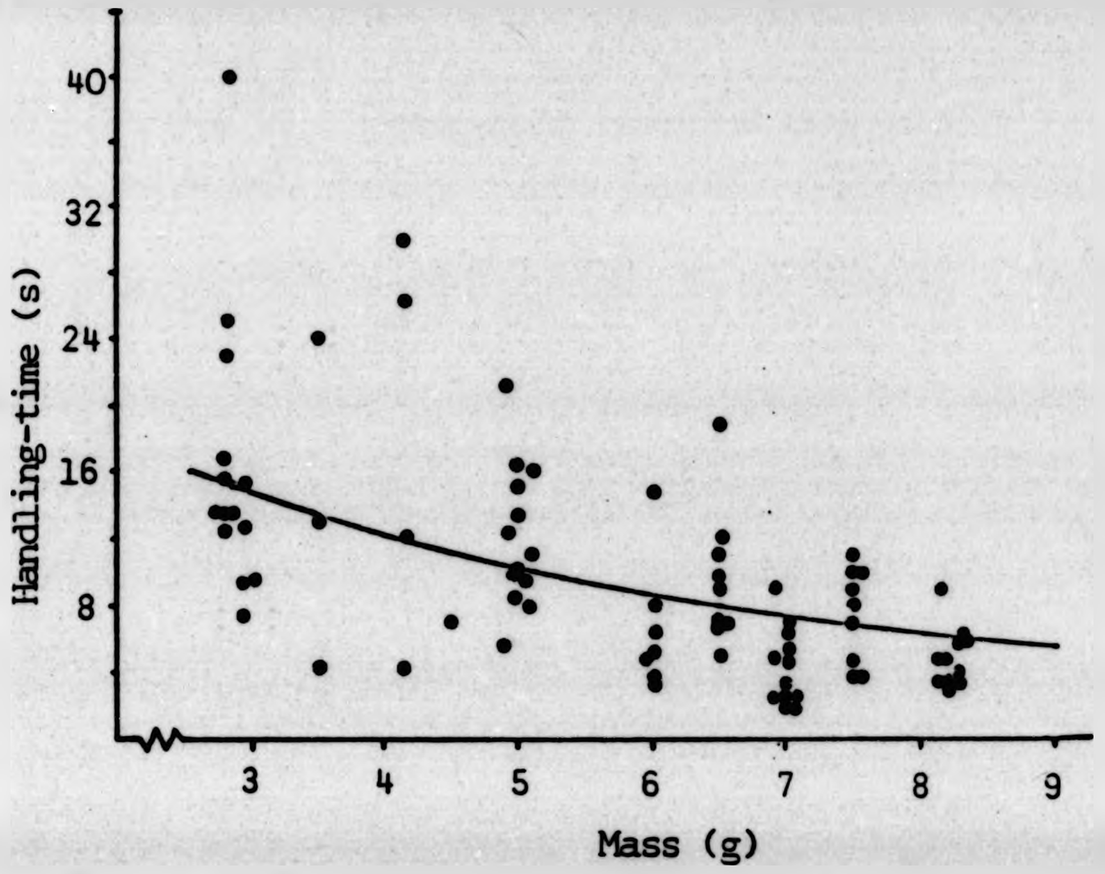


Figure 4.42

Handling-time as a function of nestling mass for Zebra Finch when food profitability is F = 0.

The regression equation,

$$y = 23.6 - 8.3 \log_e x$$

$r^2 = 0.48$, $n = 64$, $p < 0.001$

Standard Deviations: a = 2.30, b = 1.35

TABLE 4.30: Analysis of covariance of handling time versus $\log_e$ nestling mass when; F = 1 and F = 0, and N = 1 and N = 2

Comparison	a Intercepts	b Slopes
F = 1 and F = 0	F = 0.028 n.s.	F = 166.102***
N = 1 and N = 2	F = 1.112 n.s.	F = 118.639***

*** = $p < 0.001$;

n.s. = not statistically significant

Degrees of freedom = 1,164 and 1,81 respectively decrease with age for both F = 0 and F = 1 (Figures 4.43, 4.44) in a similar way to handling time and at a higher level (Table 4.28, 4.31). Nestlings after-begged for longer when F = 1 and when a sibling was present (i.e. paired treatments) and for less time when F = 0 and no sibling was present (Table 4.30).

Analysis of covariance of paired and single treatments splitting F = 1 and F = 0 data showed that N1:F1, N2:F1 and N2:F0 curves were not significantly different from each other and had higher values (ABT_{hi}) than N1:F0 (ABT_{lo}) (Figure 4.45), from which they differed significantly (Tables 4.32, 4.33, Figure 4.46). Moreover ABT_{lo} though resembling the mean handling time curve (Figure 4.46) was significantly different from it (Table 4.33). After-begging is thus markedly different in its relationship to nestling age than either GUT or EGUT. The ratio of ABT/HT was found to decrease with crop-score (Figure 4.47). In other words, hungrier nestlings were after-begging proportionately longer for a given handling time than nestlings with higher crop-scores.

Summary of Zebra Finch begging behaviour

On arrival of a parent bird as inferred from experimental stimulation, nestlings began to beg and continued begging in anticipation of food for on average 8.5 seconds (= GUT). Nestlings that were offered food took a predictable amount of time to handle this food (= HT) and this decreased as they grew. After swallowing, these nestlings began begging again (= ABT) and the duration of this too decreased with age. Lone nestlings receiving food at low profitability

TABLE 4.31: Regression equation parameters for elevated giving-up time (EGUT) as functions of the mass of the unfed sibling, crop-score and mean brood size

EGUT versus:-	a Intercept	b Slope	r^2	significance	df
Mass of unfed sibling	3.01	0.075	0.0	n.s.	47
[a]Crop-score	3.37	0.013	2.0	n.s.	47
Mean brood age	1.25	0.317	1.7	n.s.	34

[a] For derivation of crop-score see Section 3.7.3

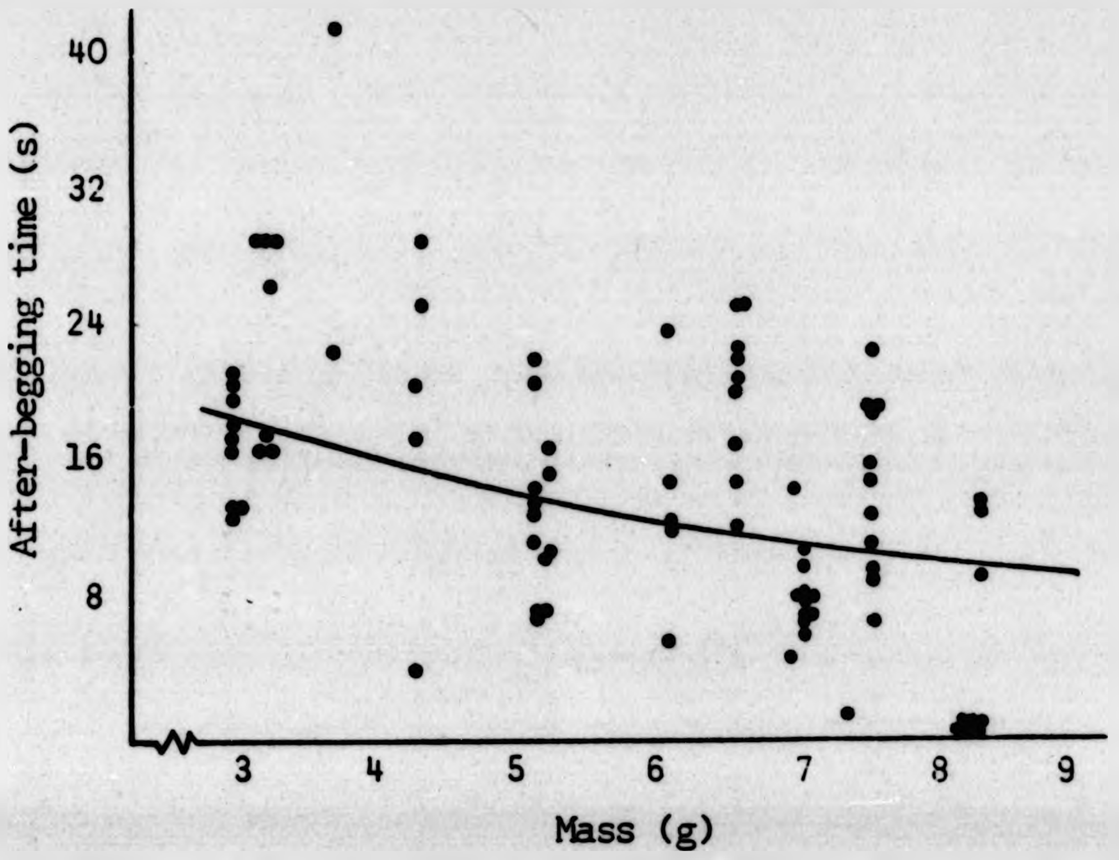


Figure 4.43

After-begging time as a function of mass of nestling Zebra Finches which have received food at profitability F = 0.

The regression equation is,

$$y = 25.8 - 7.26 \log_e x$$

$r^2 = 0.34$, $n = 83$; $p < 0.005$

Standard Deviations: a = 4.03, b = 2.37

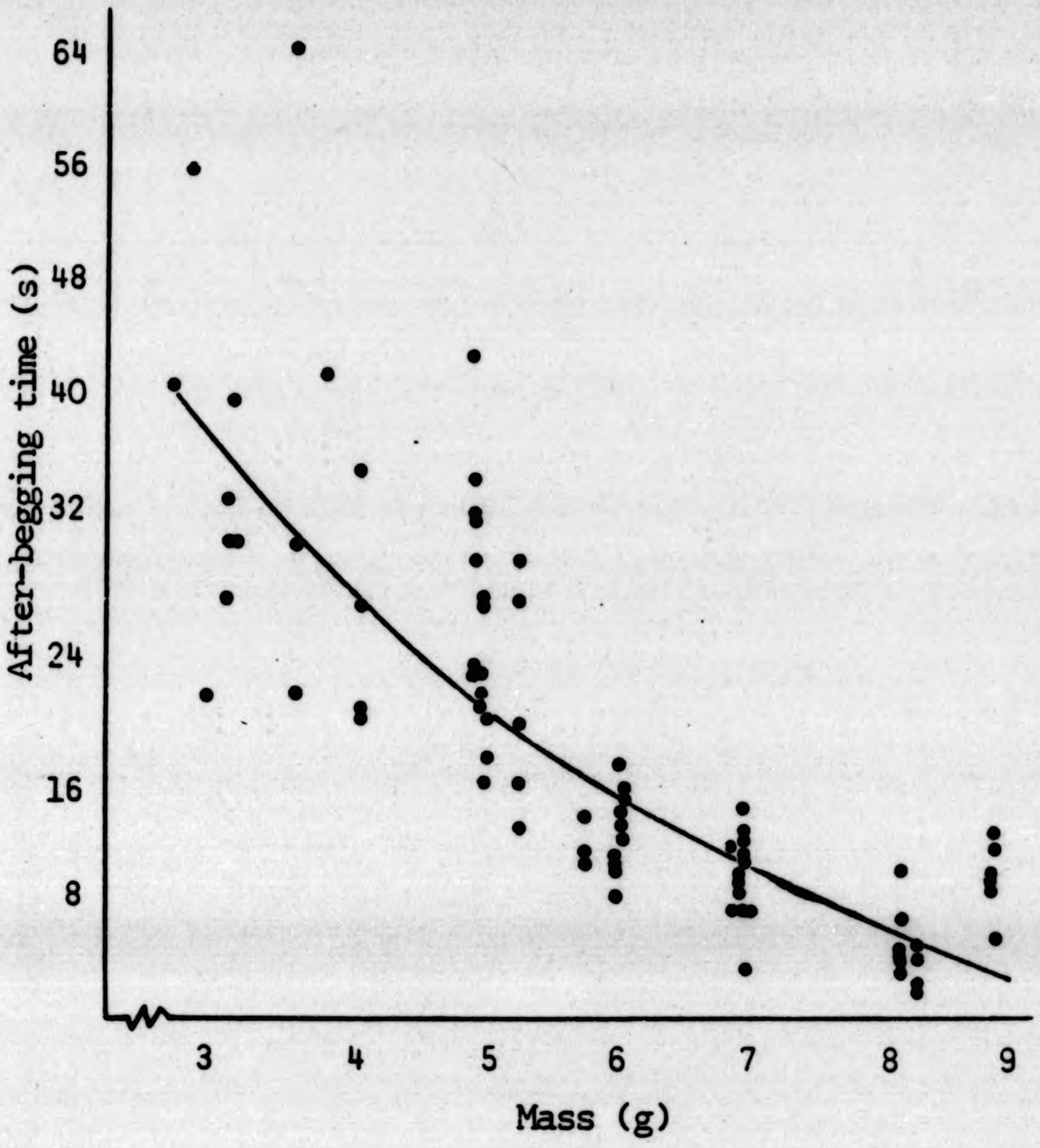


Figure 4.44

After-begging time as a function of mass of nestling in Zebra Finches which received food at profitability F = 1

The regression equation is,

$$y = 66.4 - 29.1 \log_e x$$

$r^2 = 0.47$, $n = 74$, $p < 0.001$

Standard Deviations: a = 6.12, b = 3.38

TABLE 4.32: Regression analysis of ABT against $\log_e$ mass for Zebra Finch nestlings

[1]ABT	a Intercept	b Slope	r^2	Significance
TOTAL	38.7	-14.3	0.483	$p < 0.001$
F = 1	66.4	-29.1	0.688	$p < 0.001$
F = 0	25.8	-7.26	0.339	$p < 0.005$
Single (N1)	33.0	-12.0	0.500	$p < 0.001$
Single (N2)	67.6	-2.87	0.637	$p < 0.001$

---

[1] For explanation of after-begging (ABT) categories see text

TABLE 4.33: Analysis of covariance of after-begging time (ABT) versus $\log_e$ nestling mass when; F = 1 and N = 1 and N = 2, and when F = 0 and N = 2 only. Also ABT when F = 0 and N = 2, and handling time (HT) data combined versus $\log_e$ mass (see text for explanation of categories)

Comparison	a Intercepts	b Slopes
ABT:N2:F=1		
v		
ABT:N1:F=1	F=2.837 n.s.	F=0.558 n.s.
v		
ABT:N2:F=0		
ABT:N1:F=0		
v	-	F=26.248 $P < 0.001$
HT TOTAL		

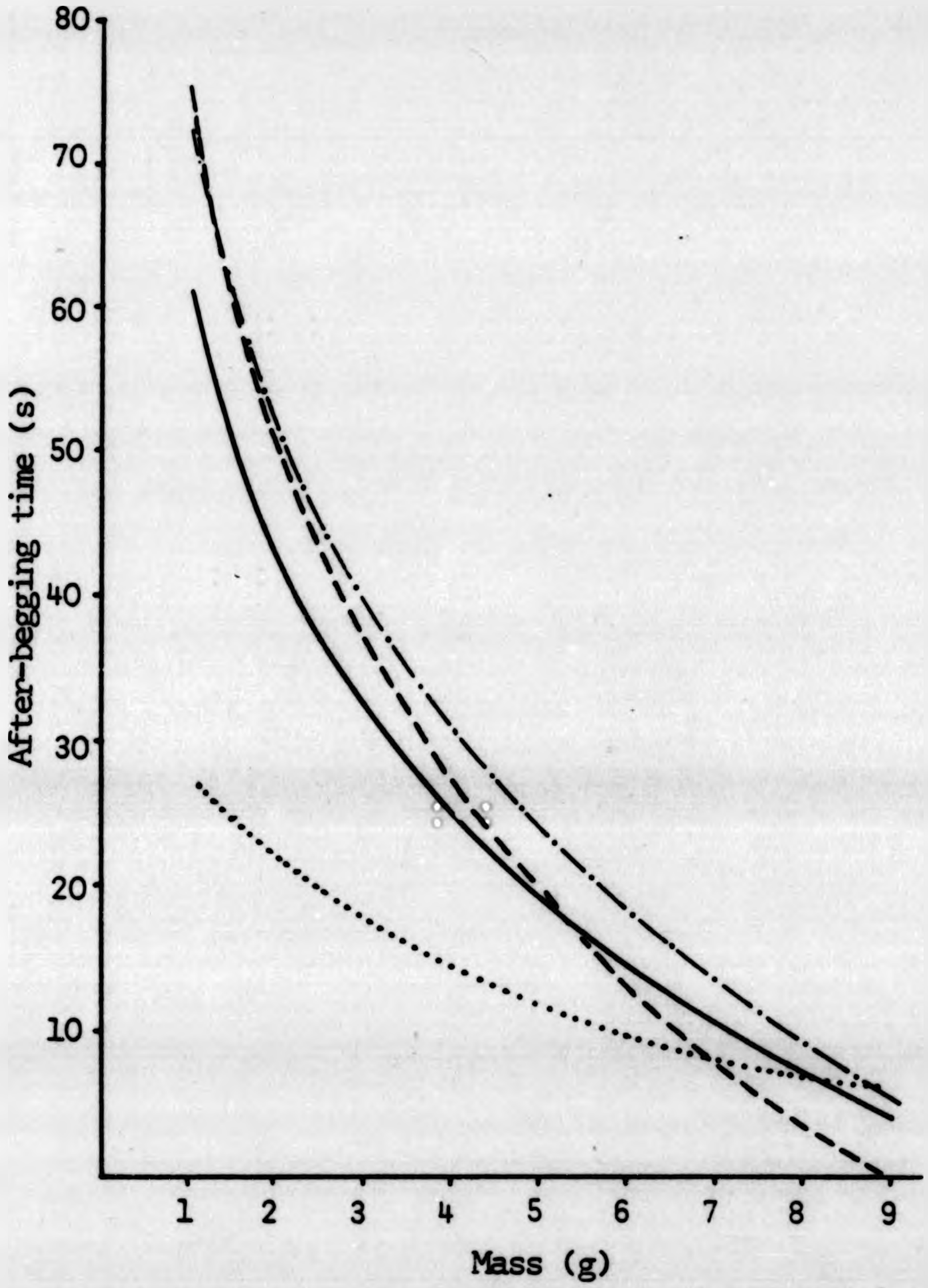


Figure 4.45

After-begging time as a function of nestling mass for the Zebra Finch

N2:F=0 - - - - - - -

N1:F=0 ·············

N2:F=1 —·—·—·—

N1:F=1 ————

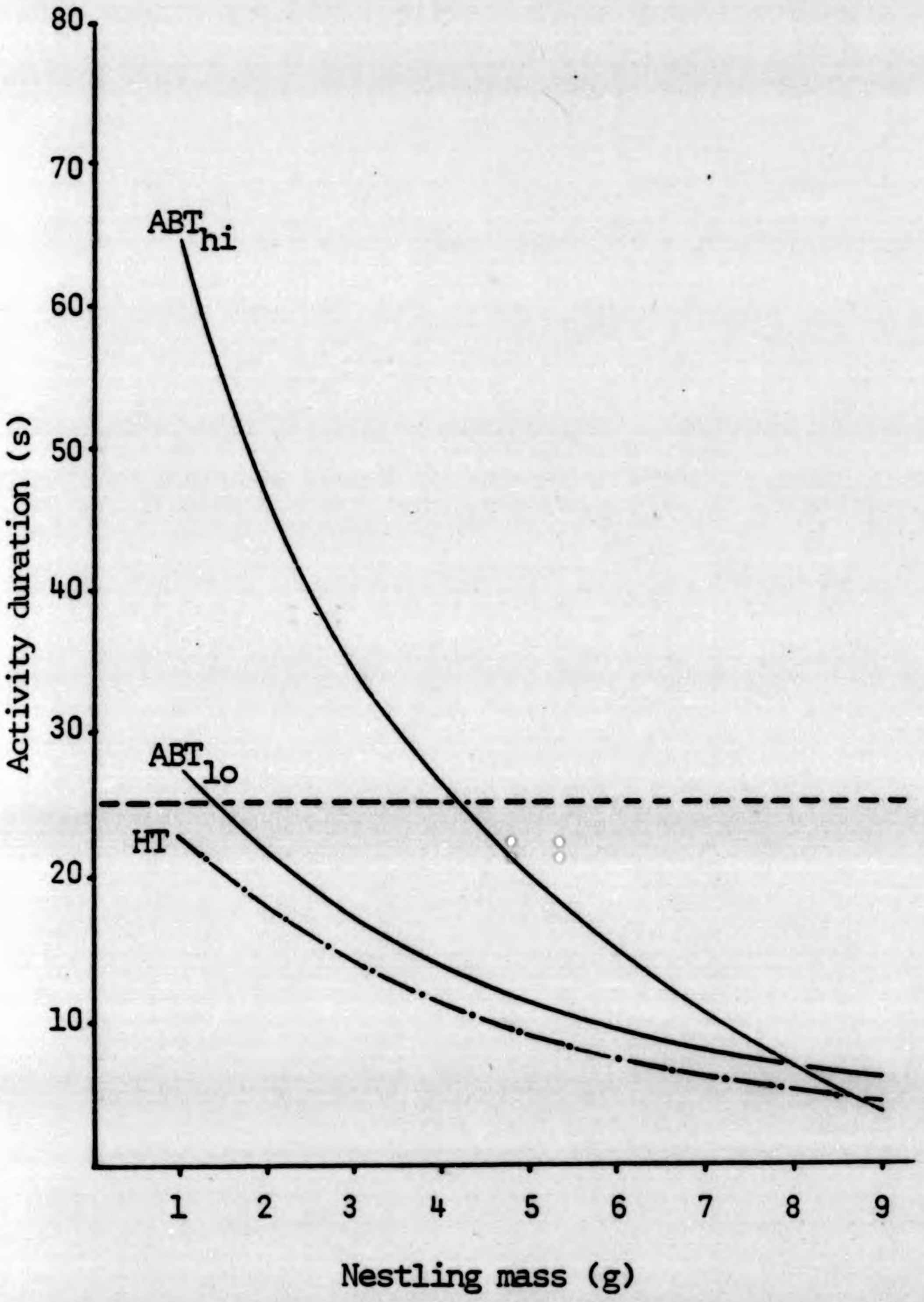


Figure 4.46: Fitted curves of after-begging and handling time as a function of nestling mass in the Zebra Finch.

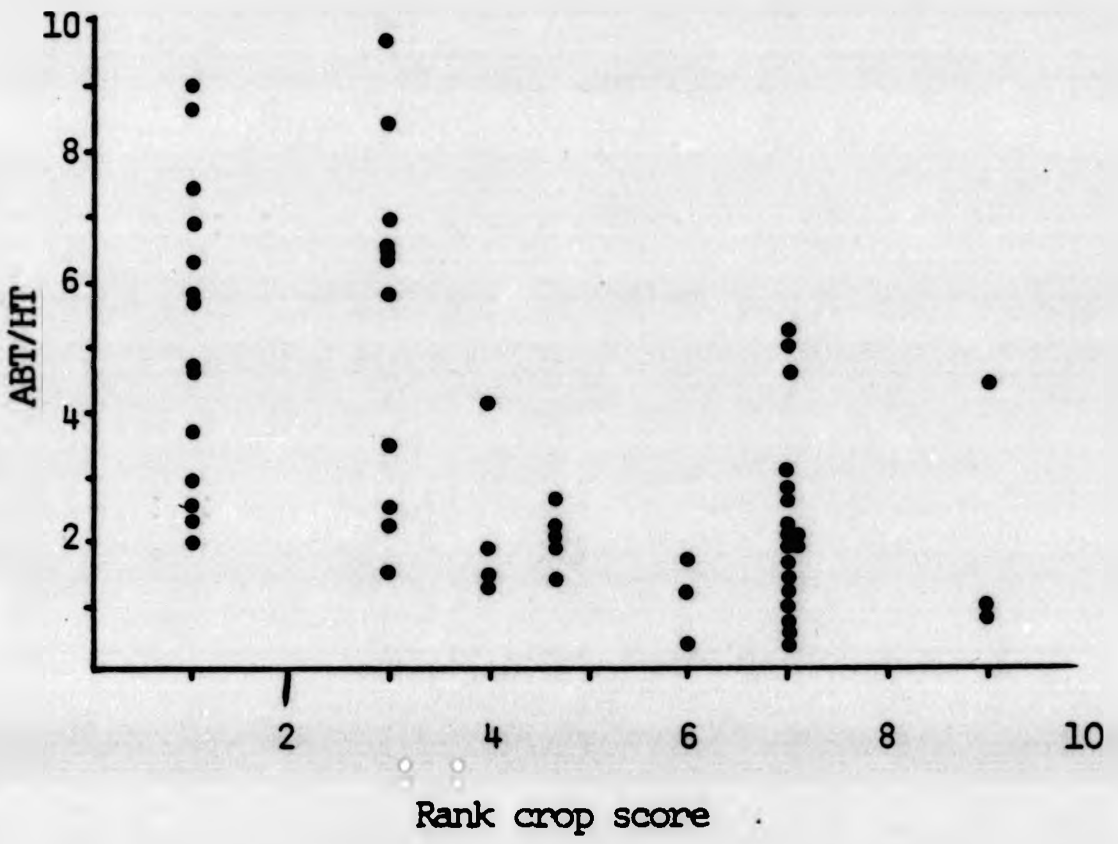


Figure 4.47: After-begging/handling time ratio as a function of hunger level expressed as the rank crop score (see text) for nestling Zebra Finches.

$r = 0.300$, df 58, $p < 0.02$

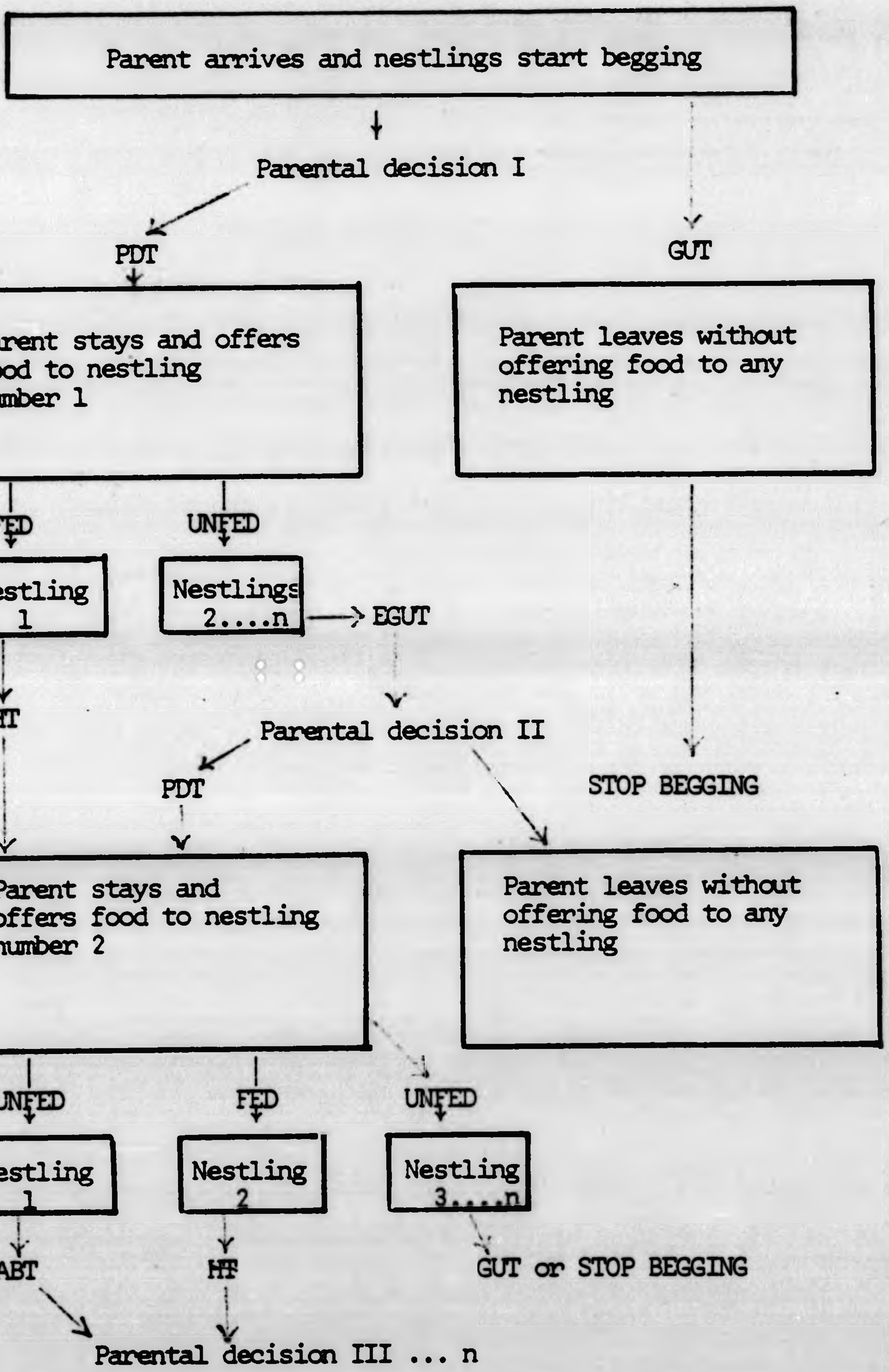


Figure 4.48: Summary of parent/nestling interactions in the Zebra Finch.

——> Behaviour of nestling or parent, see text for explanation of abbreviations

(= N1:F0) begged at a lower level (= ABT_{lo}) than other combination (= ABT_{hi}). In paired treatments unfed siblings elevated their begging to an average of 24.5 seconds (= EGUT), and this was found not to vary with any of the variables measured. The above behaviour is presented diagramatically in Figure 4.48.

4.10 COMPETITIVE BEGGING BEHAVIOUR II: A FIELD STUDY

4.10.1 Types of House Martin begging behaviour

The cost of House Martin begging behaviour (Section 3.4.3) was measured in hand-reared nestlings (Section 3.6.3) and nestlings brought to the laboratory for short periods specifically for this purpose (Section 3.8.3). In the field begging calls were also recorded and begging intensity ranked as either high or low intensity, see below (Section 3.3.1 and 3.8.3).

Begging behaviour was ranked as high, medium or low intensity begging from the tape transcripts, based on two criteria; frequency of 'cheeps' per second, and the volume of the begging calls which generally reflected the number of nestlings participating in the begging bout. Frequency of 'cheeps' was timed with a stopclock, and arbitrarily ranked as follows;

High frequency,	1+ 'cheeps' per second
Medium frequency,	1 'cheep' every 1-2 seconds
Low frequency,	1 'cheep' every 3+ seconds.

Volume of begging calls, were arbitrarily ranked as follows;

High volume,	all nestlings begging
Medium volume,	most nestlings begging
Low volume,	single nestling begging.

In broods of three there was rarely much difficulty in distinguishing the number of nestlings begging; the ranked volume corresponds to three, two and one nestling respectively. In brood size four it was often difficult to distinguish between three and four young begging, so high frequency begging may be overestimated slightly in these broods. The ranked volume therefore corresponds to four, two-three, and one nestling respectively.

The above two ranked scores were combined (see below) to give a single intensity score which was used in subsequent analysis.

High intensity,	high frequency and high/medium volume.
	medium frequency and high volume.
Low intensity,	medium frequency and medium/low volume.
	low frequency and low volume.

High frequency/low volume and low frequency/medium volume were not observed, and hence are not included in the begging intensity ranking.

It was possible to distinguish three types of begging behaviour from the tape transcripts and microprocessor data (Section 3.8.3).

(a) 'Spontaneous' begging by one individual rising in frequency of 'cheeps' noted per second, and not associated with a feeding visit by the parent. This often resulted in other nestlings joining in with begging calls, but the duration of this begging time was generally short and was usually at low, but occasionally medium, intensity. A variety of stimuli induced this type of begging behaviour, e.g. vigorous movement or wing flapping by nestlings within the nest, shadows falling across the nest entrance, mistimed landing at the nest by parent birds with and without food. This type of behaviour was also observed in a Pied Wagtail (Motacilla alba) brood, which spontaneously begged to a Small Tortoiseshell butterfly that alighted on the edge of the nest. Such spontaneous begging is equivalent to the giving-up time (GUT) of Zebra Finch nestlings (Section 4.12.1), and was also noted in the Dipper (Section 4.6).

(b) High intensity feed begging occurred when a parent bird arrived with food. This behaviour was induced by an initial vocalisation by the parent bird and continued until the parent left the nest. It is equivalent to the elevated giving-up time (EGUT) of Zebra Finch nestlings, though it contains a component of after-begging (ABT) by the fed nestling (Section 4.12.1). Since this is always lower than EGUT in duration (Section 4.12.1) it does not affect the estimation of EGUT. High intensity EGUT is referred to below as $EGUT_{hi}$.

(c) Low intensity feed begging was initially stimulated in the same way as $EGUT_{hi}$, but was characterised by repeated vocalisations by the parent bird throughout its duration until the parent left. These persistent parental vocalisations were usually 'echoed' by one or two nestlings. Low intensity feed begging is referred to below as $EGUT_{lo}$.

4.10.2 House Martin begging behaviour in the field

The mean giving-up time (GUT, Section 4.5.2) of Dipper nestlings was 3.9 ± 0.62 seconds (n = 21) and House Martins 10.1 ± 1.58 seconds (n = 22). The latter did not differ significantly from Zebra Finch GUT (t = 0.624, df = 130, n.s.) (Table 4.35). All data hereafter refer to House Martin nestlings unless stated otherwise. GUT did not vary with either mean wing-length of the brood (as an index of brood age), RDBM, or brood-size (Table 4.34).

Nestlings were found to beg for longer when siblings were being fed, as was found in the Zebra Finch, and the mean EGUT measured in the field was 38.2 ± 5.7 seconds (n = 70). This corresponds to 3.73 x GUT, compared to 2.92 x GUT in the Zebra Finch. EGUT is positively correlated with GUT (Figure 4.49), and decreases significantly with age as indicated by the mean wing-length of the brood (Table 4.34).

EGUT was ranked as high intensity begging ($EGUT_{hi}$) or low intensity begging ($EGUT_{lo}$) (Section 3.8.3). $EGUT_{hi}$ was significantly correlated with nestling age (Figure 4.50, Table 4.34), but $EGUT_{lo}$ showed no such relationship ($r^2 = 0.0$, n = 14, n.s.). $EGUT_{hi}$ and $EGUT_{lo}$ appeared to be positively related (Figure 4.51), but this was not significant. The proportion of low intensity begging visits did not vary with age (Figure 4.52).

TABLE 4.34: Correlation matrix of begging behaviour in 10-21 day old House Martin nestlings, with respect to broodsize (BS), the relative difference in hatching mass (RDHM, see Section 2.3.3), mean wing-length of the brood ($\bar{x}$WNG) and GUT

	BS	RDHM (g)	$\bar{x}$WNG (mm)	GUT (s)
GUT (s)	0.26	0.0	0.0	-
EGUT (s)	0.34	0.0	-0.46	0.74**
EGUT$_{HI}$ (s)	-	0.0	-0.87***	-
EGUT$_{LO}$ (s)	-	0.12	0.0	-

EGUT = Elevated giving-up time (Section 4.5.2)

GUT = Giving-up time (Section 4.5.2)

*** = $p < 0.001$, ** = $p < 0.005$

TABLE 4.35: The mean duration of begging activities in some passerine nestlings

Activity	Species	Mean ± SE (secs)	n
[a]Giving-up Time (GUT)	Zebra Finch	8.4 ± 0.62	110
	House Martin	10.1 ± 1.58	22
	Dipper	3.9 ± 0.46	21
Elevated Giving-up Time (EGUT)	Zebra Finch	24.5 ± 2.7	96
	House Martin	38.2 ± 5.7	70

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[a] Definitions of begging behaviours are as given in Section 4.5.2

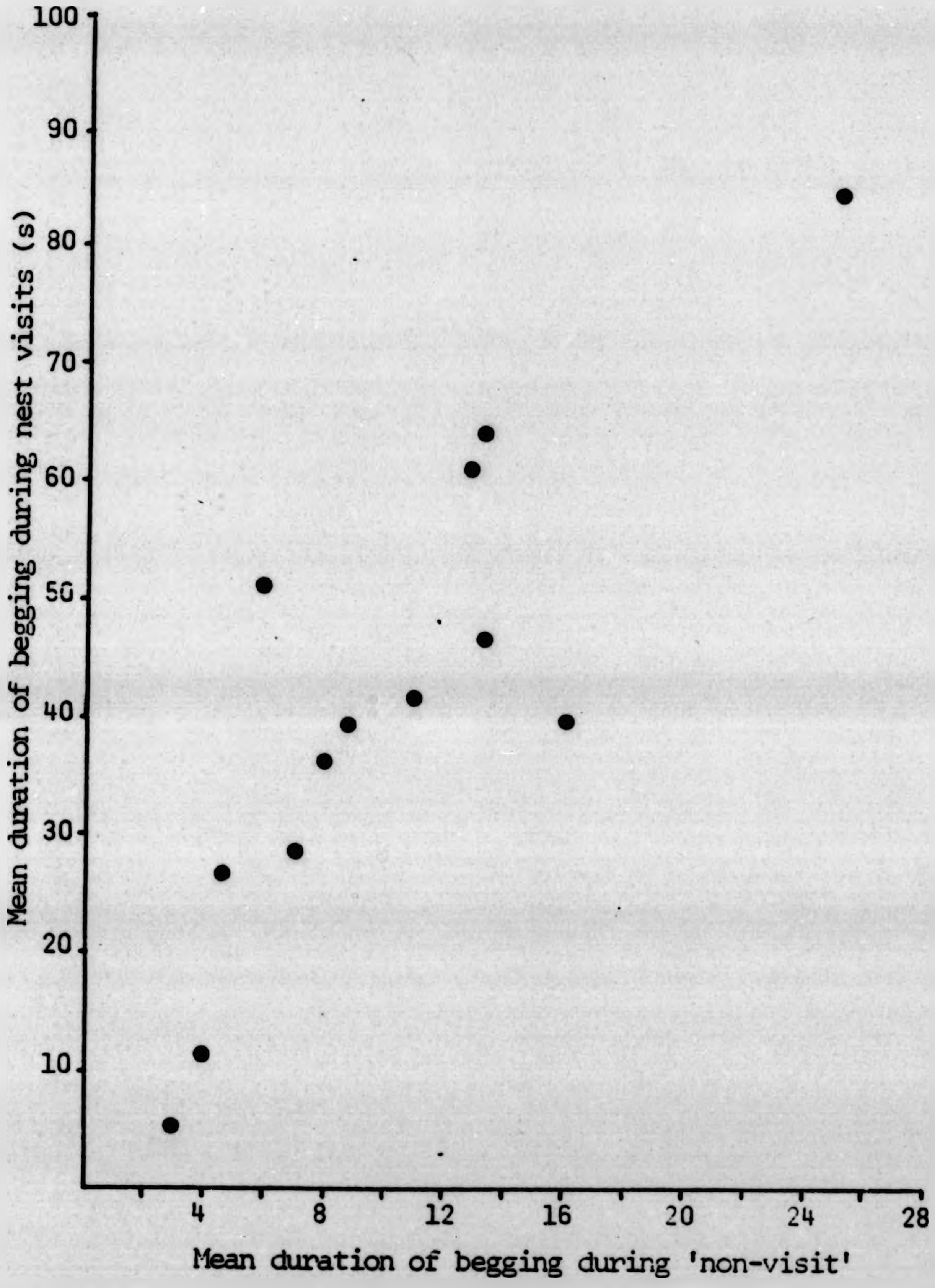


Figure 4.49: Relationship between nest 'visit' and 'non-visit' begging bout duration in the House Martin.

$r = 0.829$, $n = 13$, $p < 0.05$

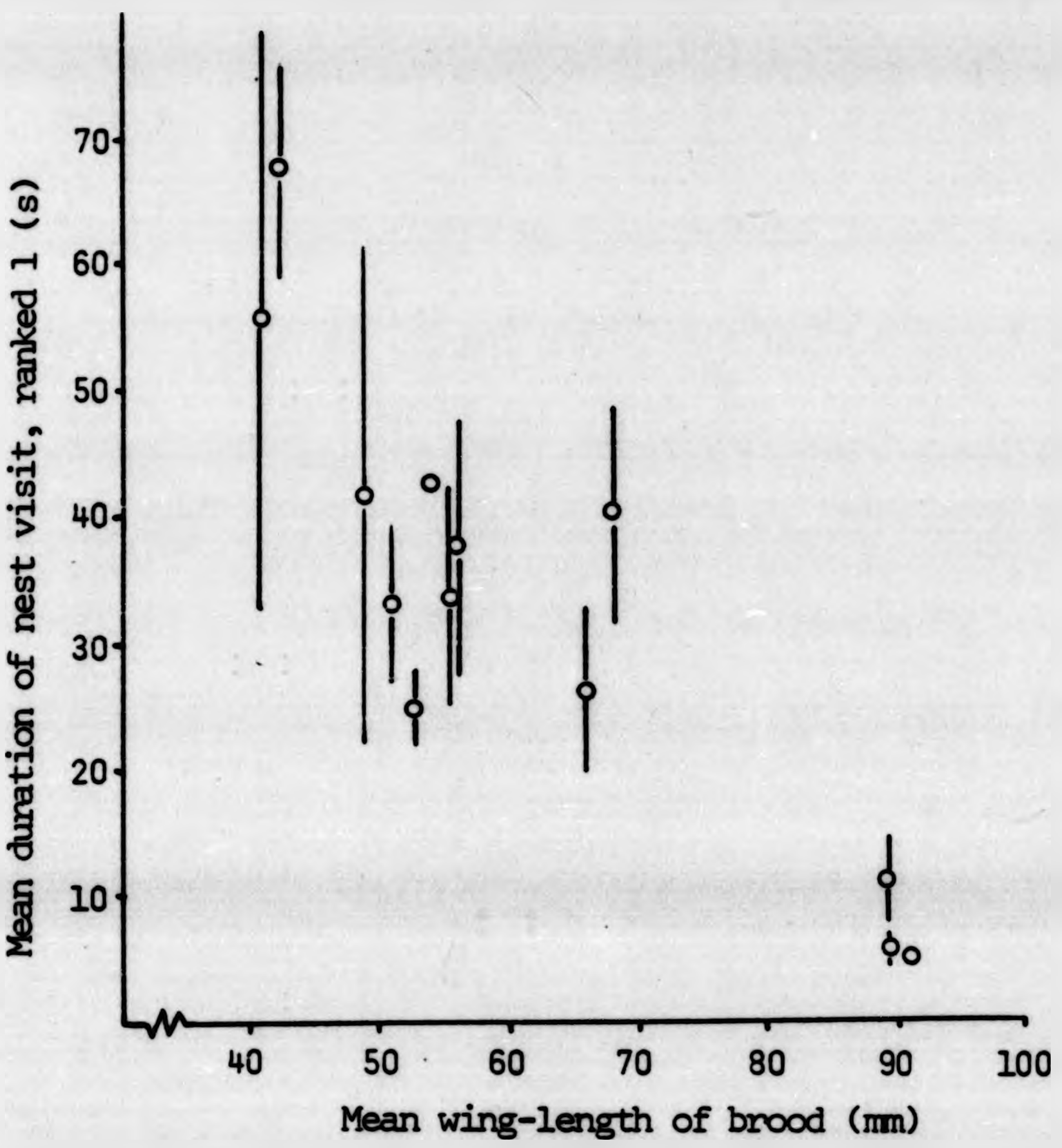
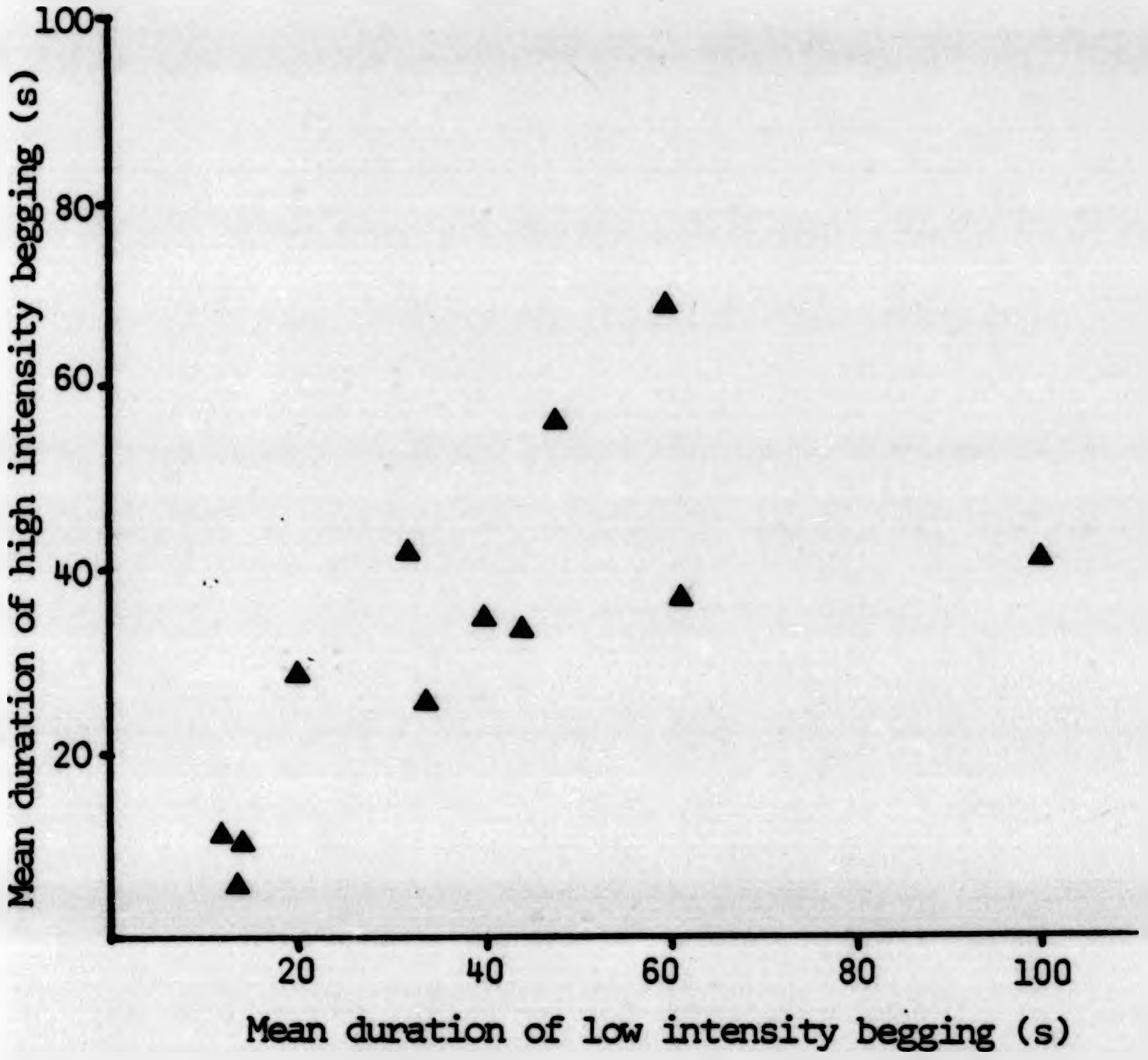


Figure 4.50: The relationship of the mean duration of each nest visit, ranked one (see text) with the age of the brood, expressed as mean wing-length. Diagram shows means ± 1SE.

The regression equation for the means is:-

$x = 93.0-0.991y$, $n = 13$, $p < 0.001$

Data are for the House Martin



<u>Figure 4.51</u>: The relationship of high intensity begging to low intensity begging in the House Martin.

$r = 0.46$, $n = 11$, $p < 0.1$

It was not possible to measure handling time in House Martins in the field, but data for the Dipper (Figure 4.53) bear a close resemblance to the form of the handling time curve for the Zebra Finch studies (Figures 4.42, 4.43, 4.46). After-begging was found to occur in hand-reared House Martins (Figures 4.42(a-c)), the duration of which varied with handling time (Figure 4.55). Nestlings after-begged less when food profitability was low, $F = 0$ (Figure 4.54(c)), than when it was high, $F = 1$ (Figure 4.54(b)) and this difference was significant ($\chi^2 = 25.5$, df = 10, $p < 0.001$).

When the relationship of after-begging to handling time was compared in the House Martin and Zebra Finch using analysis of covariance and standardised units (Sokal & Rohlf, 1969; Figure 4.56) it was found that the slopes did not differ significantly ($F = 0.073$, df = 1, 201, n.s.). There is good agreement between laboratory begging behaviour measurements and measurements in the field. These results are discussed in Chapter 8.

4.10.3 A test of the reduced sibling rivalry model on the House Martin

The reduced sibling rivalry model (Section 2.3) was tested by comparing the amount of time and energy expended in competitive begging behaviour (Section 4.5) with the degree of hatching asynchrony within the brood, measured as the relative difference in hatching mass, RDHM (Section 2.3.3). Field begging data were collected as previously (see above) for thirteen House Martin broods of three to four young which included both manipulated and unmanipulated broods. Measurements

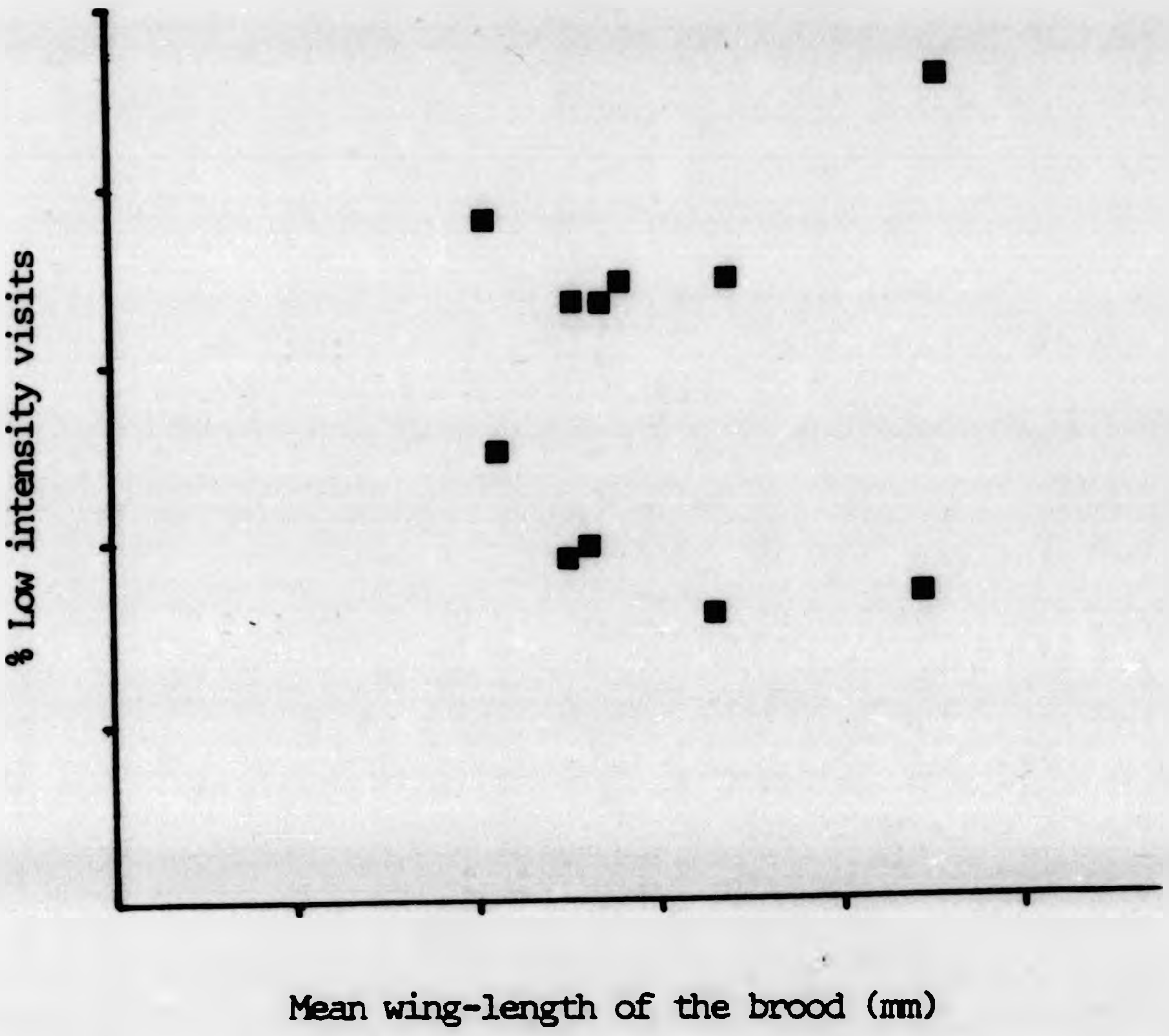


Figure 4.52: The relationship of the percentage of low intensity begging visits with nestling age in the House Martin, expressed as the mean-winglength of the brood.

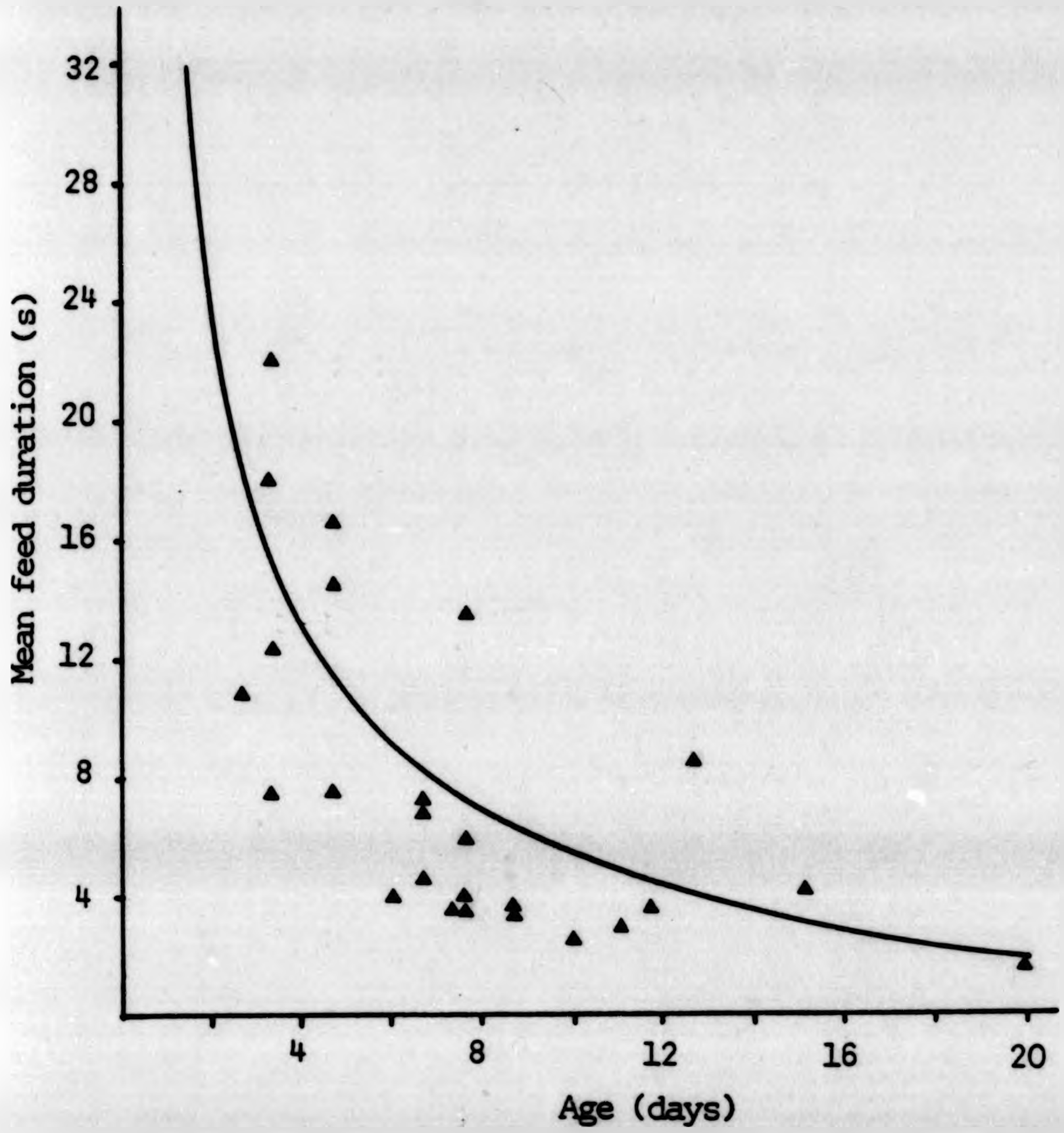


Figure 4.53: The mean duration of feeding visits to Dipper nestlings, as a function of nestling age. Curve fitted by eye.

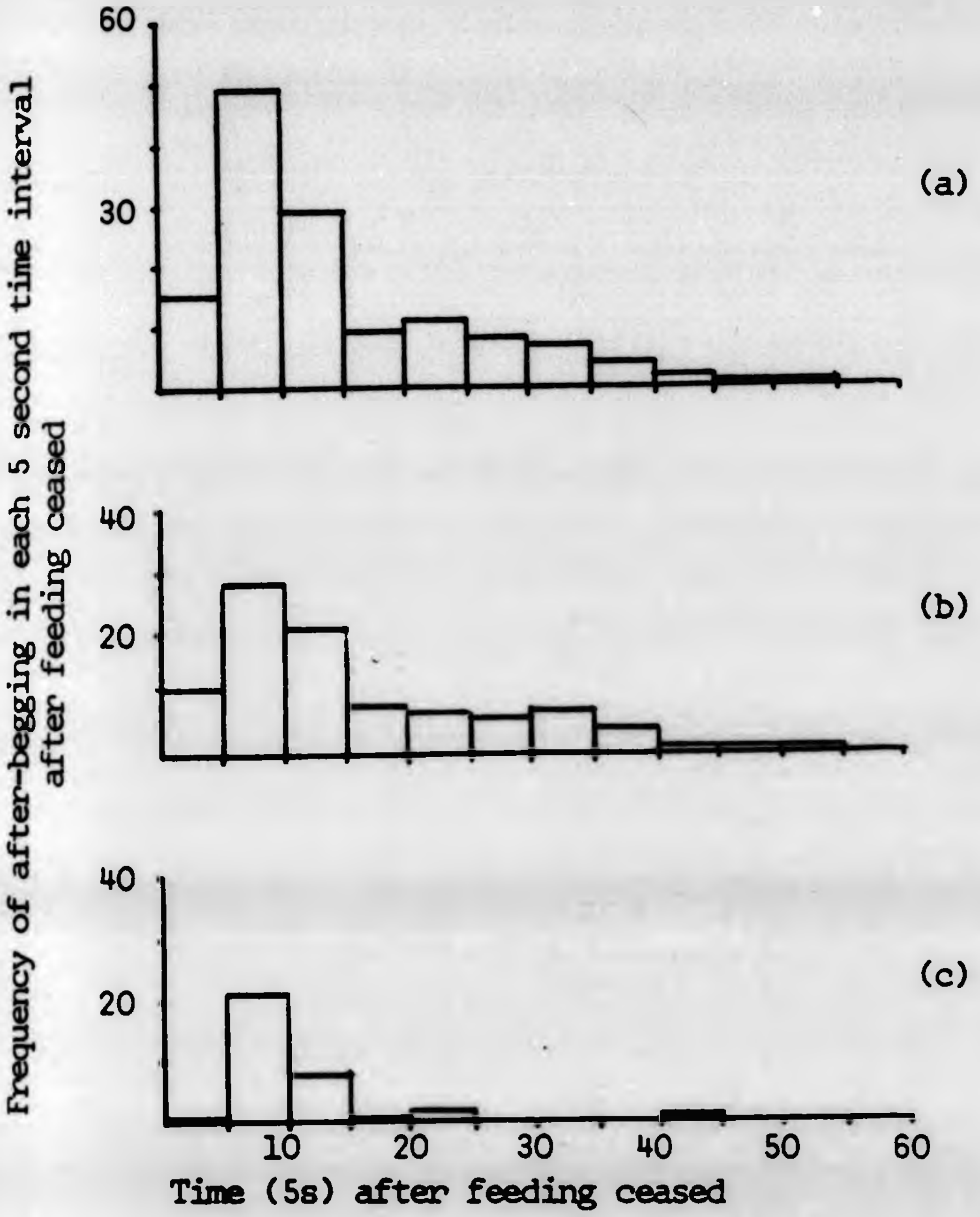


Figure 4.54:

Frequency of after-begging per 5 second interval after cessation of feeding for House Martin nestlings in the laboratory.

(a) All data (i.e. F = 1 and F = 0).

(b) After feeding when F = 1 (see text).

(c) After feeding when F = 0 (see text).

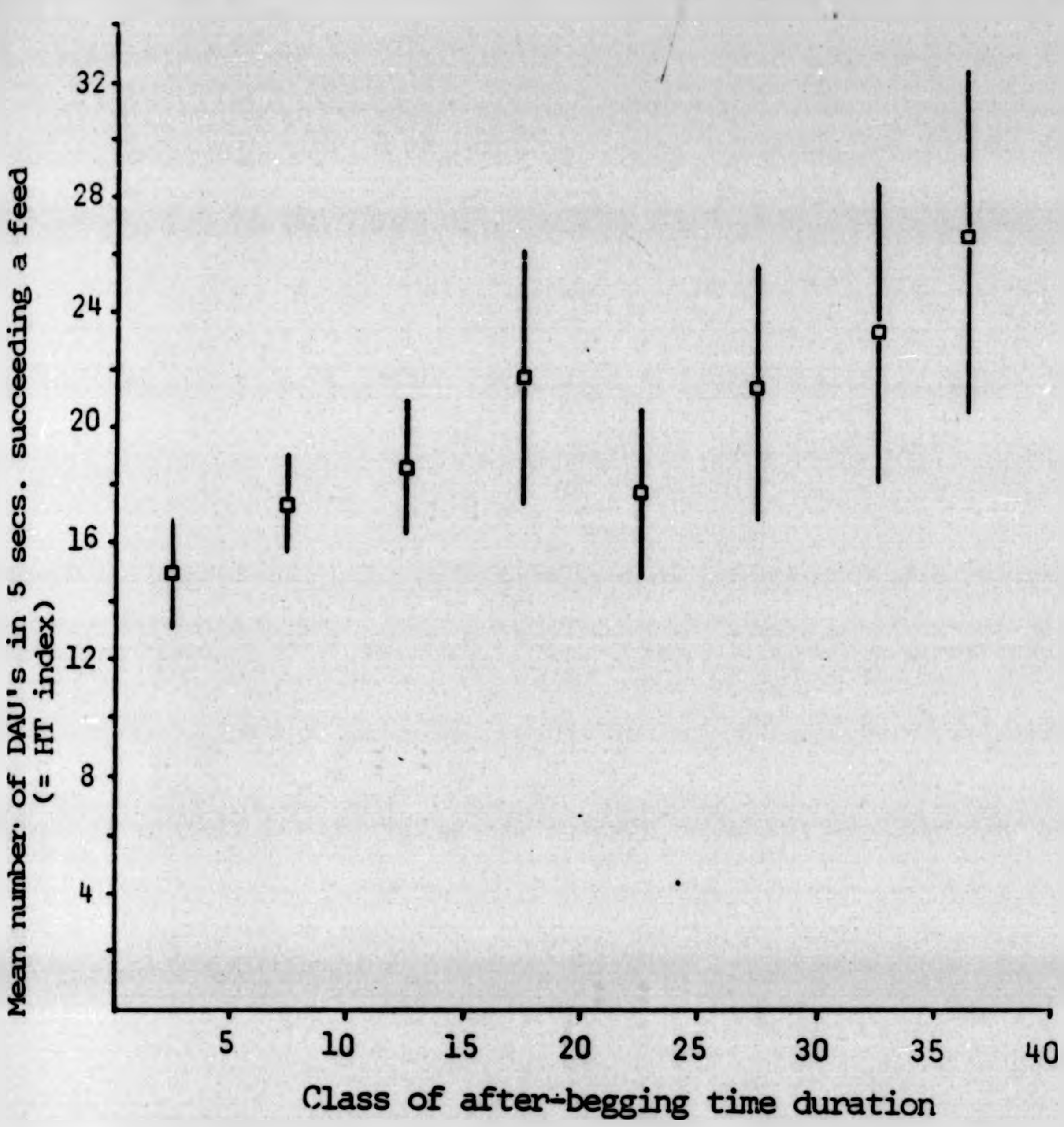


Figure 4.55:

Mean number of Doppler activity units (DAU's) accumulated in the 5 second time intervals immediately succeeding a feeding attempt, as an index of handling time (HT), as a function of after-begging time. The latter is expressed as the 5 second period in which no further DAU's were accumulated (see text for discussion). Bars represent S.D's.

The regression equation is:-

$$y = 4.65 + 0.801x, n = 92, p < 0.001$$

Data are for the House Martin.

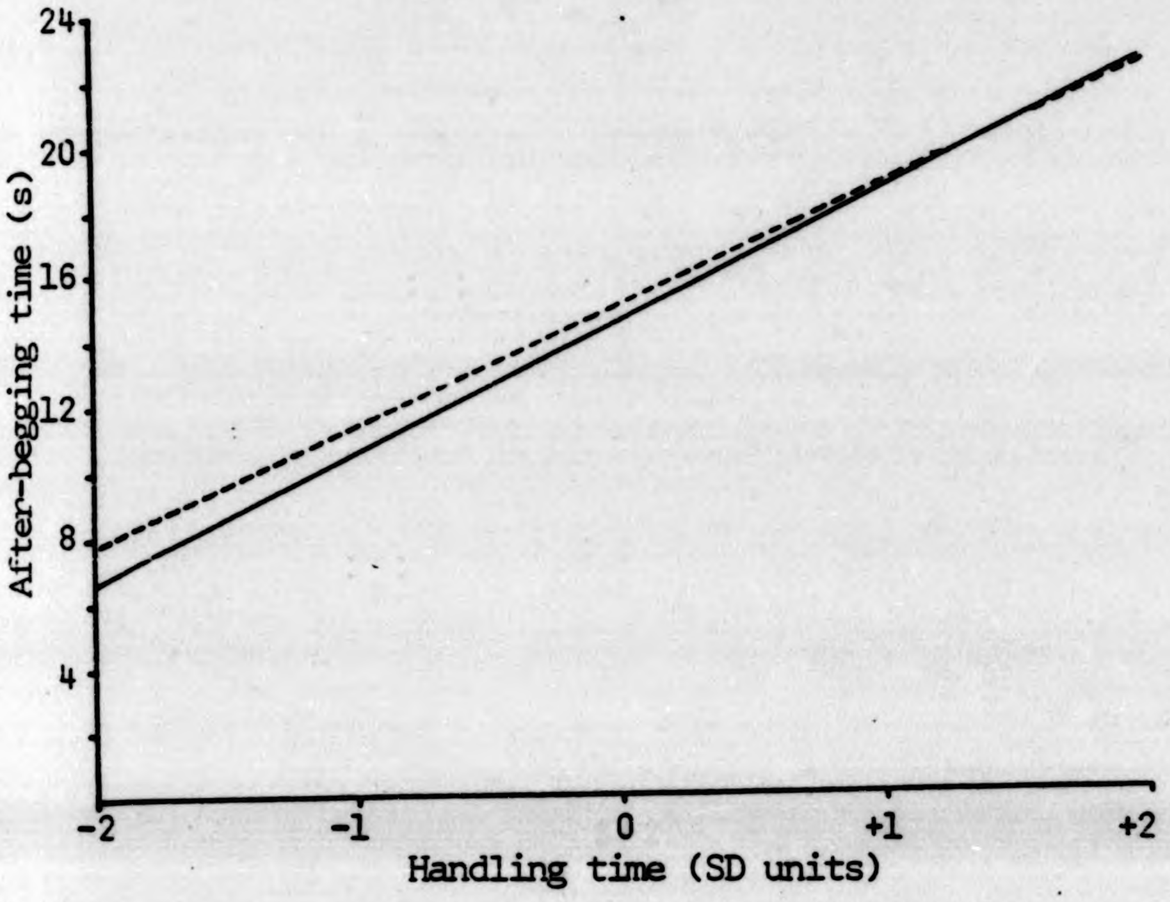


Figure 4.56:

The relationship of after-begging time, to handling time (measured in standard deviation units, see text).

House Martin ----, regression is,

$$x = 14.9 + 3.61y, n = 84, p < 0.005$$

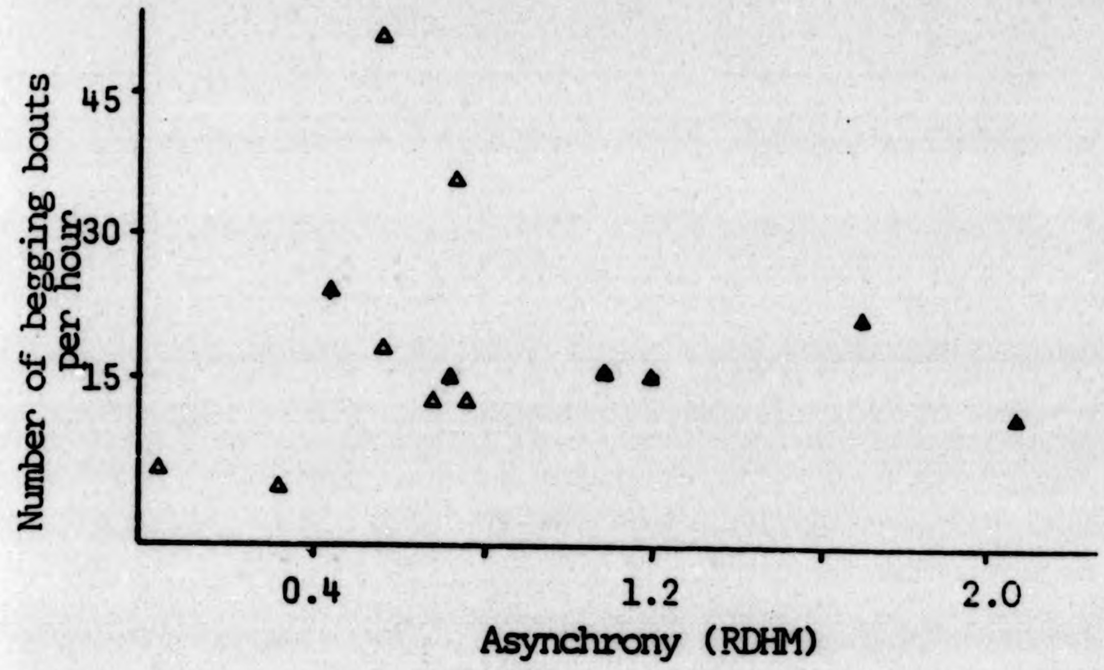
Zebra Finch ———, regression is,

$$x = 14.5 + 3.92y, n = 115, p < 0.001$$

were made over the period of highest brood energy demand and nestling peak mass, between days ten and twenty-one inclusive. The RSR model predicts a progressive reduction in competitive energy expenditure with increasing asynchrony, to a minimum, and then CEE is expected to rise again (Section 2.3.4). The pattern of changing CEE with asynchrony may be reflected in several measurements of nestling begging behaviour. One way in which nestlings might reduce CEE is to reduce the frequency of begging bouts with asynchrony (Figure 4.57), but there is no evidence of such a relationship. The mean duration of begging bouts might be regarded as a more accurate measure of CEE, and this is shown as a function of asynchrony in Figure 4.58. There is however, no evidence to support the RSR model from these data. Nestlings not only beg at feed times, but also when the parent is absent (Section 4.6). A reduction in the ratio of productive begging (i.e. when the parent arrives with food) to unproductive begging (i.e. when the parent is absent) may be an alternative method of reducing CEE. Figure 4.59 shows this, but again no significant relationship is demonstrable. Begging efficiency, the number of begging bouts/number of feeds delivered to the nest also shows no relationship (Figure 4.60). Begging intensity was ranked as either high or low (see Section 4.10.1). A decrease in the proportion of high intensity begging bouts with asynchrony would be consistent with the RSR model, yet this was not found (Figure 4.61). No measure of nestling begging behaviour therefore, was found to confirm the proposed mechanism of reduced sibling rivalry in House Martin broods.

Assumption (v) of the RSR model (Section 2.3.2) is that nestling competitive costs are energetically expensive. The cost of begging in the House Martin was presented earlier (Section 4.5.3). The activity costs measured in the laboratory were applied to begging data collected in the field (see above) and the daily cost of nestling activities calculated for a single House Martin nestling, of mean mass 14.9 grams, and in a brood of four. This mass of nestling was chosen since it is equal to the mean mass of nestlings used to calculate activity costs (Section 4.5.3) and it is not known whether activity costs are 'fixed' or 'proportionate' (Section 4.6). Using this mass for calculating daily costs will therefore not be affected by assumptions regarding the validity of 'fixed' or 'proportionate' models of activity cost.

It was assumed that a nestling received on average one feed from four parental visits, and defaecated every other feed. Feeding rates were calculated from field begging data presented above (see also Section 3.8.3). The nestling was assumed to after-beg in the manner discussed in Section 4.9.1, and elevate its giving-up time (EGUT) similarly. It was also assumed that this nestling would incur begging costs at the mean level experienced by the birds which were examined in the field, although a bird of this mass will tend to be younger. The costs presented should therefore be regarded as the maximum cost a bird of this size will incur. The mean ABT was calculated for the mean handling time presented in Figure 4.56 (i.e. HT = 0 SD units). HT was not measured directly in the laboratory for House Martin nestlings. Since EGUT approximates



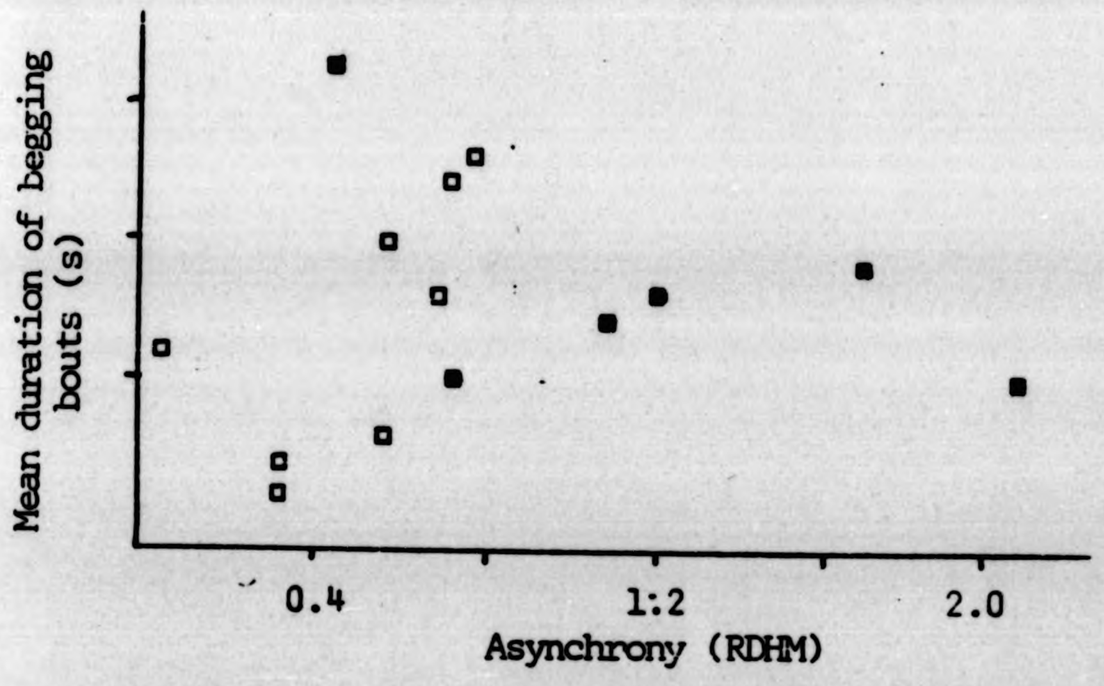
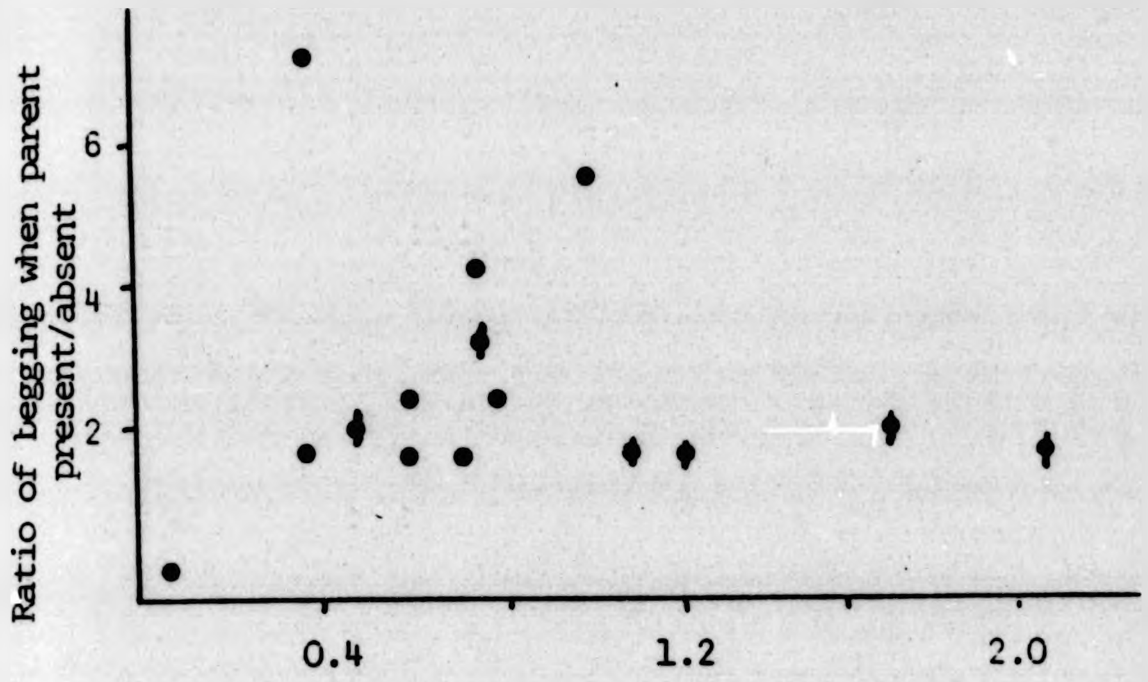
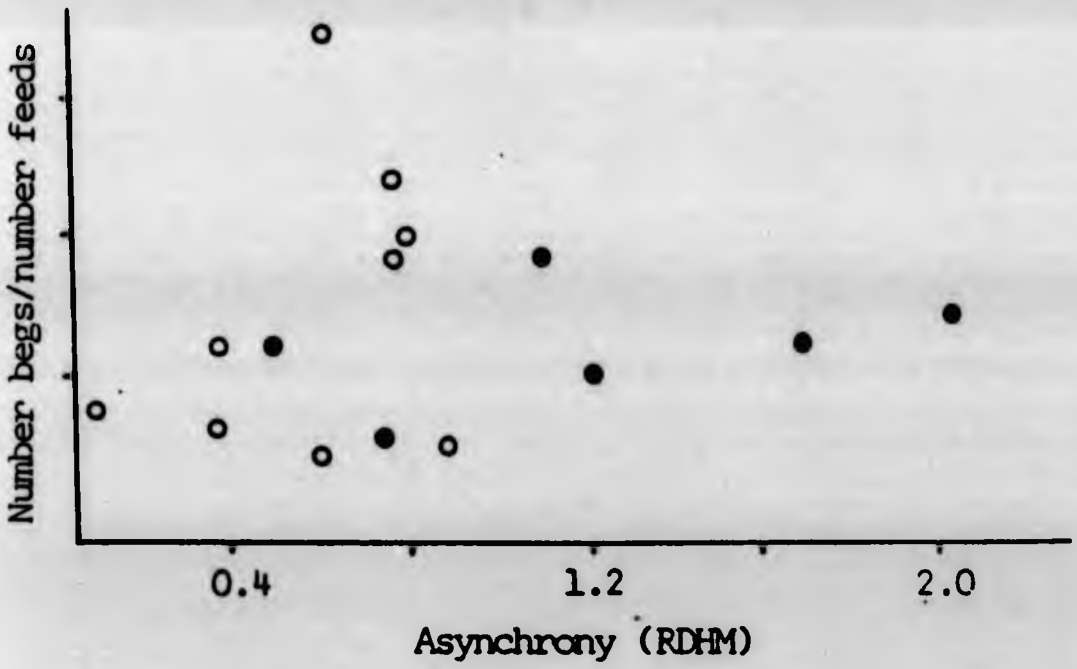


Figure 4.57 (top): Frequency of begging bouts in the House Martin as a function of hatching asynchrony.

Figure 4.58 (bottom): Mean duration of begging bouts in the House Martin as a function of hatching asynchrony.

Solid symbols manipulated broods





<u>Figure 4.59</u> (top): Ratio of begging bouts when parent present to when the parent is absent for the House Martin, as a function of hatching asynchrony.

<u>Figure 4.60</u> (bottom): Ratio of number of begging bouts to the number of feeding visits, during the entire observation period (see text), as a function of hatching asynchrony for the House Martin.

Manipulated broods: Top ◆ bottom ●

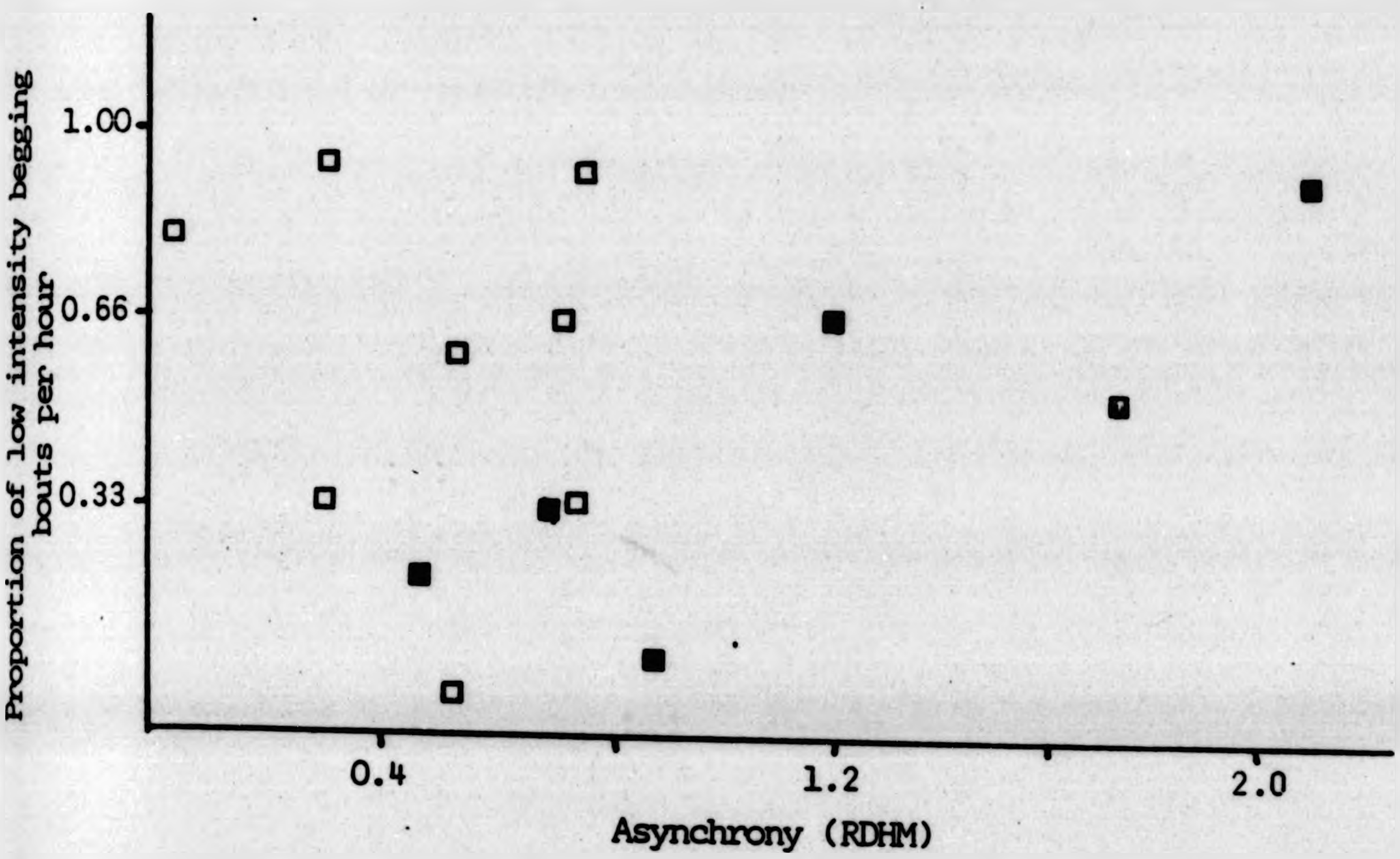


Figure 4.61: The proportion of low intensity begging bouts per hour, as a function of hatching asynchrony in the House Martin.

Solid symbols manipulated broods

to the duration of a feeding visit (see above), and a nestling is either being fed during this visit or is begging (Section 4.9.2), by subtracting ABT of the fed nestling from EGUT will leave the time it spends actually feeding (i.e. HT = EGUT-ABT). Moving costs are the same as presented in Section 3.4.3.

Table 4.36 shows the cost of the above activities. The total activity cost is only 0.104 kJ h^{-1}, or 1.248 kJ day^{-1}, assuming a 12:12 hour diurnal cycle (see Section 4.6). This daily cost is equivalent to 5.5% BMR, calculated from Aschoff & Pohl (1970). All begging behaviours combined (GUT, EGUT, ABT) account for 56.7% of the total activity cost, handling food 14.4% and moving 26.0%. The final 2.9% is defaecation costs. Comparing the costs of the different begging behaviours as a percentage of total begging costs, shows that EGUT is most expensive (67.8%), followed by GUT (23.7%), and ABT (8.5%). So whilst begging costs form a large proportion of total activity costs in the House Martin (but see Section 4.6), these costs are much smaller as a proportion of the total DEB than previously assumed (Section 2.1.4). Though costs are low, and there is no evidence to support the RSR model, there is evidence to show that nestlings modify their begging behaviour (see above), and that this may itself lead to energy savings. This will be discussed in Chapter 5.

4.11 FURTHER CONSIDERATIONS OF THE RSR MODEL

The RSR model (Section 2.3) predicts conditions that must be met if RSR is important (Section 2.3), briefly; that disparity in nestling size should be optimized and

TABLE 4.36: The daily activity cost of a single 14.9g House Martin nestling in a brood of four

Activity	Frequency (Activity h^{-1})	Mean Activity Duration (s)	Mean time Spent in Activity ($s.h^{-1}$)	Energy (kJ h^{-1})	Percentage of total Activity Cost (%)
[a]GUT	18.0	10.1	182	0.014	13.5
EGUT	14.1	38.2	538	0.40	38.4
[b]ABT	4.7	14.4	68	0.005	4.8
[c]HT	4.7	23.8	112	0.015	14.4
Defaecating	2.8	10.0	23	0.003	2.9
Moving	-	-	172	0.027	26.0
TOTAL	-	-	1095	0.104	100.0

[a] For definitions of begging behaviour see Section 4.5.2

[b,c] For calculation of ABT and HT see text

maintained throughout growth, that competitive costs are substantial and that savings from RSR should be allocated to some component of fitness. The cost of competition is discussed in Sections 4.10 and 4.11, the other two points will be dealt with here.

4.11.1 Peak mass and hatching asynchrony

It was suggested in Section 2.3 that energy saved from reduced competition might be reallocated to growth in nestling House Martins, leading to some measure of nestling growth increasing with increasing asynchrony, peaking at an optimum and then declining again (Figure 2.11). House Martin nestlings grow quickly in the first two weeks and reach peak body mass at about 16 days (Bryant & Gardiner, 1979) thereafter they undergo a period of mass recession, associated with a decrease in water content, and feather growth (specifically wing and tail) in common with a number of species (Ricklefs, 1968; Turner & Bryant, 1979) (Figures 4.65(a-f)). Peak mass may be used as an index of nestling quality; poorly nourished young having lower peak masses than well-nourished young. If savings from RSR were reallocated to growth, for example progressively laying down greater fat reserves (Section 2.3.5), then this could be reflected in a higher peak mass. Peak mass (taken as the mean of the three days of greatest mass) was measured in 157 House Martin nestlings from 37 broods, both natural and experimentally manipulated. Table 4.37 shows the mean peak mass and asynchrony (RDHM) for brood-sizes two to five. The mean peak mass in broods of three and four were not significantly different ($t = 0.06$, $n = 21$, n.s.) and were

Figure 4.62:

Nestling mean peak mass as a function of hatching asynchrony, measured as the relative difference in hatching mass (RDHM), for House Martin broods.

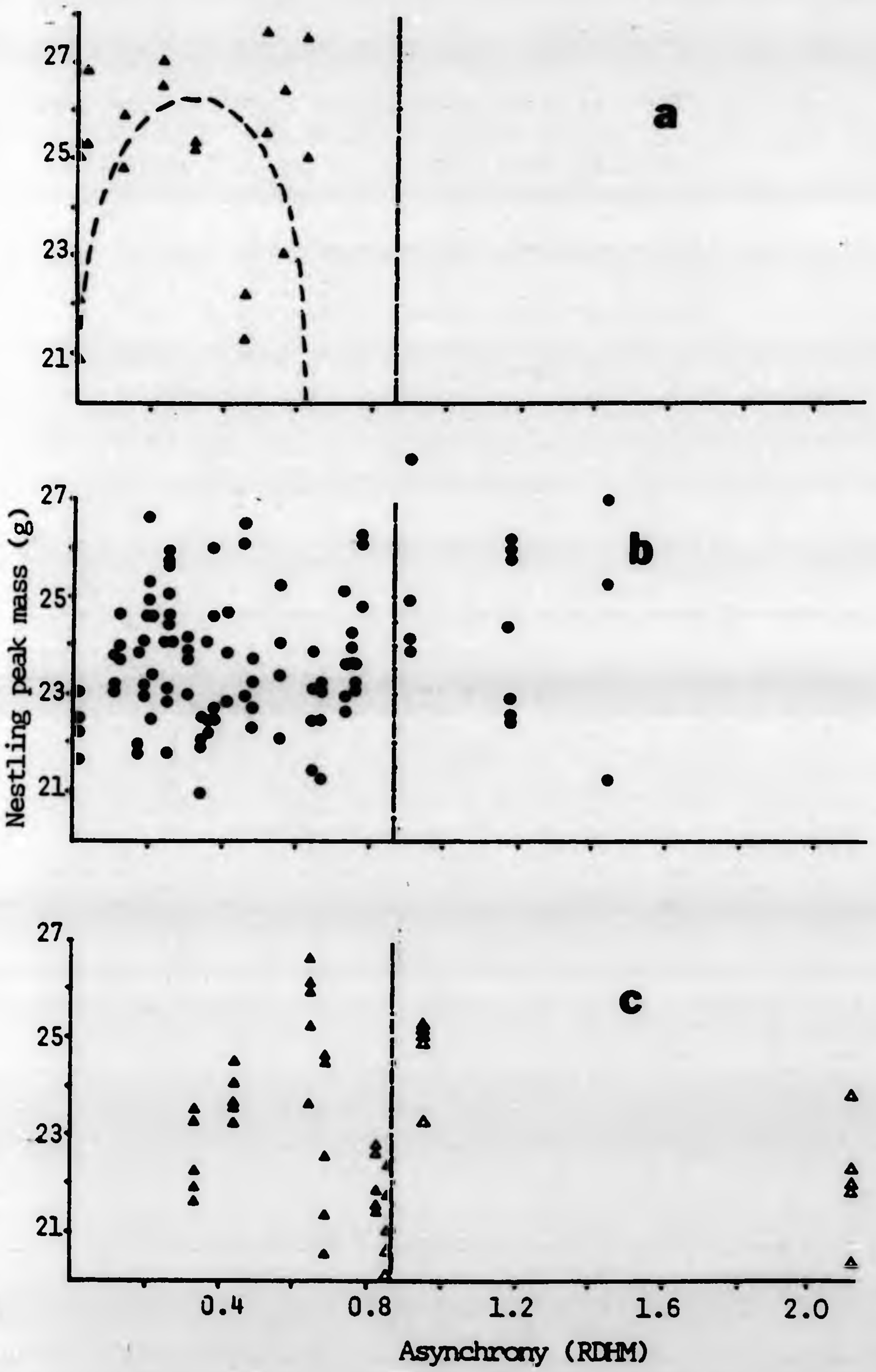
(a) Brood-size 2. Dashed line is fitted curve (see text for explanation)

(b) Brood-size 3 and 4 data combined.

(c) Brood-size 5.

-·-·- Maximum degree of asynchrony found in unmanipulated House Martin broods.

(Refer to text)



a
b
c
27
25
23
21
Nestling peak mass (g)
0.4
0.8
1.2
1.6
2.0
Asynchrony (RDHM)

therefore combined for subsequent analysis. The mean peak mass of broods of two is significantly higher than broods of three and four ($t = 2.57$, $n = 117$, $p < 0.02$) which are in turn higher than broods of five ($t = 2.35$, $n = 137$, $p < 0.02$). The mean hatching asynchrony increases with brood-size (Table 4.37). The difference in mean hatching asynchrony between brood-sizes two and three and brood-size five were statistically significant, t-tests on other pairs of brood-sizes were not ($t = 2.66$, $n = 16$, $p < 0.01$ and $t = 3.42$, $n = 17$, $p < 0.01$). Figure 4.62 (a-c) shows nestling peak mass as a function of hatching asynchrony (RDHM) for brood-sizes of two, three to four and five.

If these graphs are compared with that of the model for RSR (Figure 2.10), we find no similarity with the possible exception of broodsize two. The quadratic term of a second order polynomial regression was significant ($r^2 = 0.86$, $F = 11.01$, df 1, 9, $p < 0.05$). Given the small sample size and lack of any highly asynchronous brood data for brood-size two, however, it provides only weak support for the model. Also, if RSR is important then there is no reason to assume that this will not occur in all brood-sizes which is not the case.

RSR does not appear to determine the pattern of peak mass observed and therefore the Peak Load Reduction hypothesis will now be considered. If the mean peak mass of nestlings in highly asynchronous broods (right of dashed line, Figure 4.62) with that of moderately asynchronous broods (left of dashed

TABLE 4.37: **Mean (± SD) hatching asynchrony (expressed as RDHM, Section 2.3.3) and mean peak mass of House Martin nestlings as a function of brood size**

Brood size	Mean peak mass (g)	^an	RDHM	^bn
2	24.92 ± 1.39	20	0.300 ± 0.25	10
3	23.78 ± 1.48	45	0.275 ± 0.19	11
4	23.74 ± 1.40	52	0.417 ± 0.19	10
5	22.96 ± 1.80	40	0.628 ± 0.21	6

^an = number of nestlings

^bn = number of broods

Data for 18 broods from D. M. Bryant

line, Figure 4.62) in broods of three/four highly asynchronous broods have a significantly higher mean peak mass ($t = 2.15$, df 108, $p < 0.05$), although the difference is small, 24.65 and 23.76 grams respectively (= nearly one gram of extra fat). This slight increase was not apparent in broods of five ($t = 0.688$, df 39, n.s.). If this slightly higher mean peak mass in highly asynchronous broods of three and four were accepted, it would require a 54% increase over the maximum asynchrony found in natural broods, to produce the observed 3.7% increase in peak mass. The mean asynchrony of the highly manipulated broods was 1.176, equivalent to a hatching spread of four days. If savings from PLR are reallocated to growth in the manner proposed for RSR, the predicted mass increase may be calculated (Section 2.3.5).

Predicted PLR savings increase linearly (Figure 2.9) over the range of asynchrony values found in unmanipulated House Martin broods (Figure 4.62 (b)), and are consistent with a slight trend of increasing peak mass with asynchrony (shown in Figure 4.62 (b)) although this was not significant.

Using the theoretical DEB, a brood of four would save 0.22 Watts brood^{-1} from PLR if hatching was spread over four days (Figure 2.9). This is equivalent to 6.33 kJ per nestling per day, or the equivalent of 0.66g of additional fat, an increase of 2.8% over moderately asynchronous broods. Considering the differences that will occur between the theoretical DEB and actual House Martin DEB's, the figure is consistent with that found. In summary, there does not appear to be any evidence to support the view that RSR, resulting in increased peak nestling mass at some optimal asynchrony, occurs in House Martins. The differences in peak mass between highly and moderately asynchronous broods of three and four, although significant is small, and consistent with predicted savings from peak load reduction using the theoretical DEB. The latter would however require that parents allocate any saving accrued into producing bigger chicks and there is no direct evidence for this.

4.11.2 Hierarchy stability and the flexibility of House Martin growth

Central to the hypothesis of RSR is that bigger differences in nestling size produced by asynchrony result in less competition. If this is the case then natural selection should favour the maintenance of size differences between individuals either throughout growth, or until a fixed dominance hierarchy is established, which will then remain constant even though size differences may cease to be maintained (Section 2.3.2), with associated benefits to the highest ranked members. Examination of the size hierarchies within House Martin broods show that the relative difference in body mass (RDBM) is not maintained, but declines (Figure 4.63). Moreover, by about eleven days RDBM is similar for all broods irrespective of initial RDBM.

The House Martin growth curve may be approximated by a logistic curve until peak mass is reached. If nestlings hatch asynchronously then the growth curves do not 'coincide'; they progress 'out of phase'. Since daily mass increments

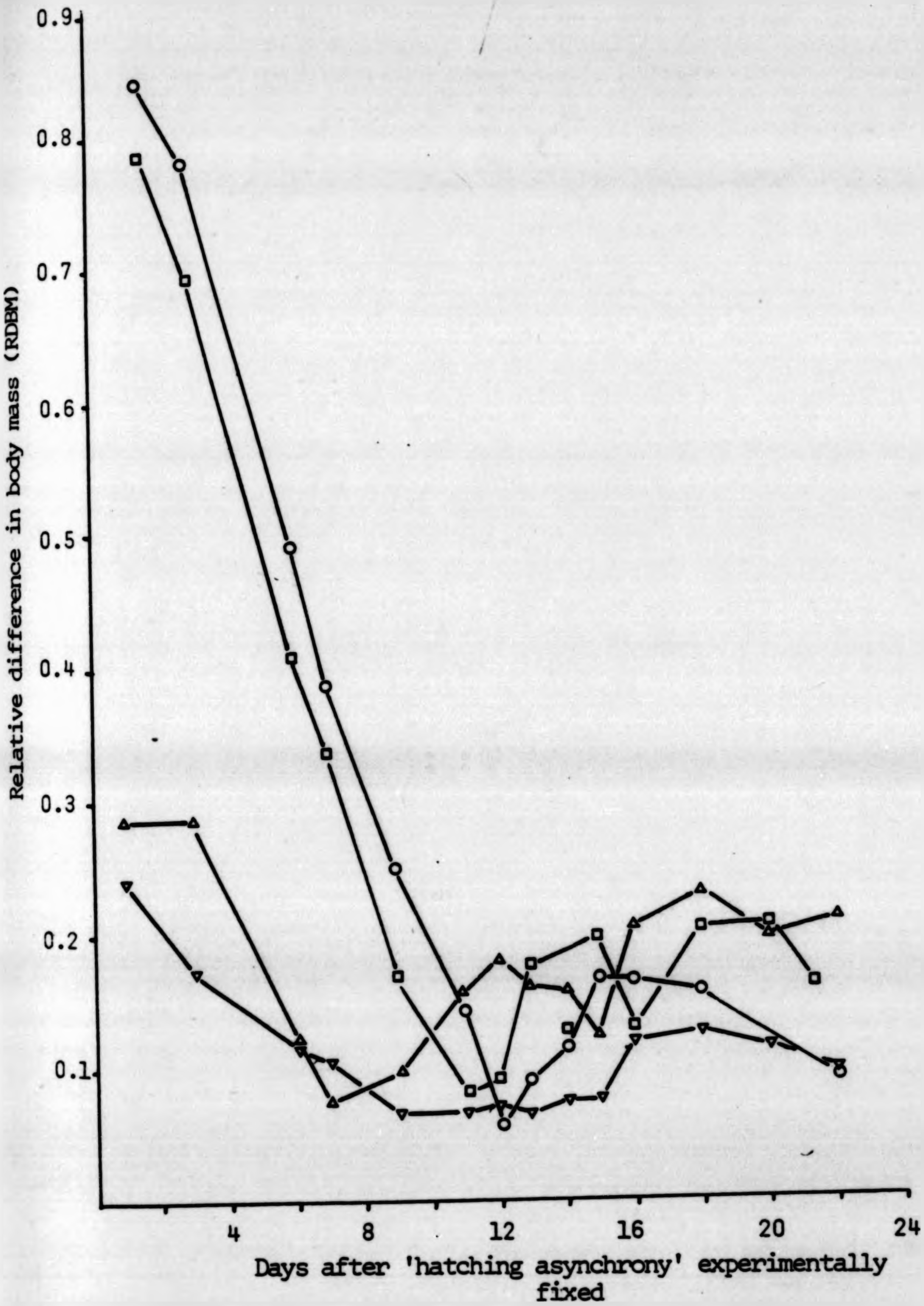


Figure 4.63: RDBM as a function of age in the House Martin

○ , □ Asynchronous broods

Δ , ∇ Synchronous broods

increase until mid-growth and then decrease, individuals within a brood that hatch first will reach the inflexion point of their growth curve first and thereafter although still increasing in mass, will be doing so at a decellerating rate, whilst their late hatched siblings may be increasing in mass at a progressively greater rate (i.e. before their own inflexion point is reached). The relative difference in body mass will therefore decline in the manner shown (Figure 4.63). The initial drop in RDBM is therefore not due to mass recession, although after the first nestling has reached peak mass a slight reduction in RDBM may be attributable to this factor. As each nestling reaches peak mass and begins to undergo mass recession RDBM increases slightly again (Figure 4.63). Decreasing RDBM is not inconsistent with the establishment of a persistent dominance hierarchy during early growth, provided that the size difference remains reasonably large during this period for the reasons given in Section 2.3.2. The period over which mass difference should remain high during early growth will of course also be affected by how long it takes nestlings to establish their position within the hierarchy. Suppose that a fixed hierarchy is established in the first days after the brood has hatched so that in a brood of two the largest sibling consistently gets a greater proportion of the food brought to the nest and continues to grow more quickly than its smaller sibling. The pattern of growth shown in Figure 4.64(a) might then apply. Note that even though the growth curves are parallel, RDBM as a measure

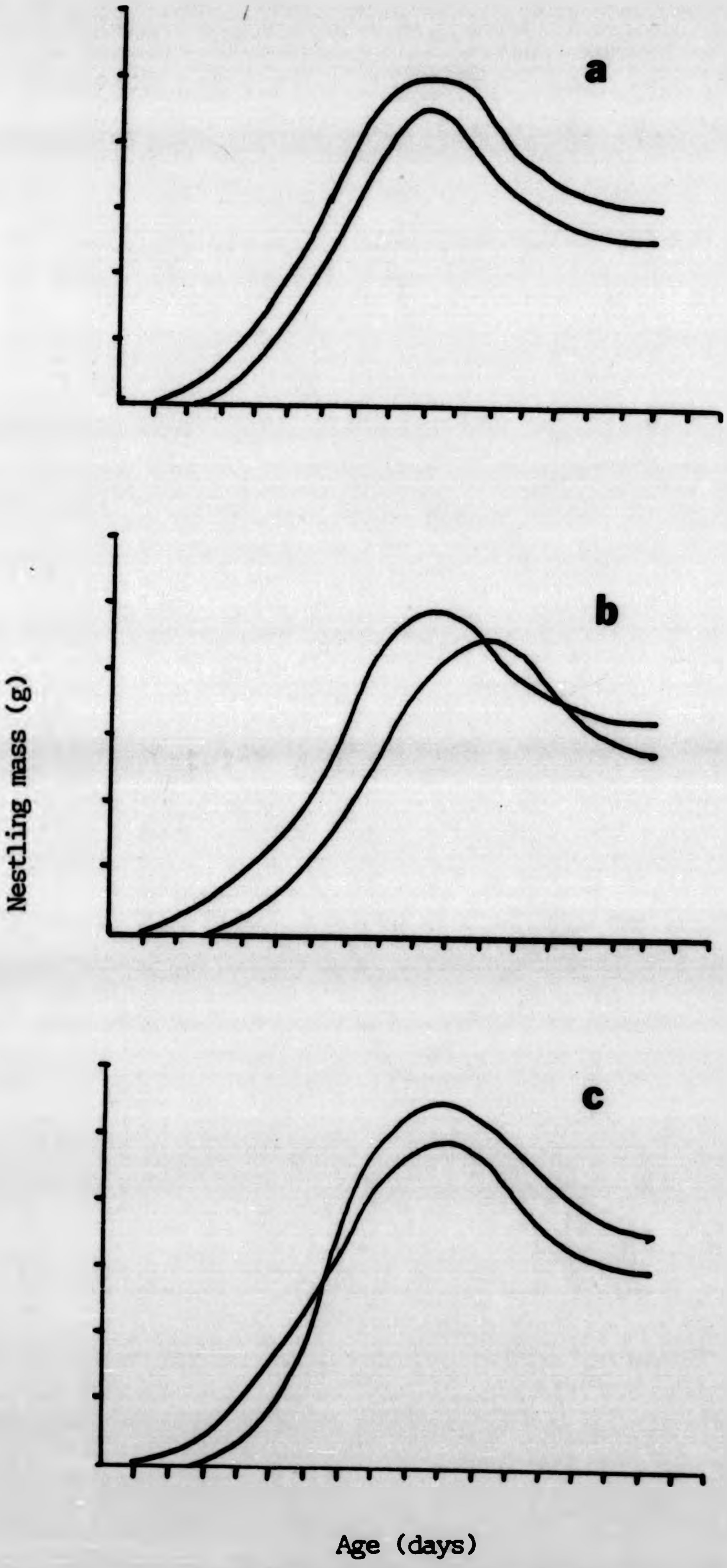


Figure 4.64: Models of nestling growth showing the potential for hierarchy instability (see text).

of proportionate size differences will still decline with age as shown previously. Due to the mass recession shown in House Martins, however, it is possible that there will be a time when the last hatched (and hence lowest ranked member of the brood) is actually heavier than its elder sibling (Figure 4.65(b)). Even so this size difference would be short-lived hence the youngest chick eventually returns to being the lightest. Neither of these patterns is inconsistent with the maintenance of a persistent dominance hierarchy, by initial large differences in nestling mass. In Figure 4.65(c) however, the lowest ranked nestling achieves a greater peak mass than the first ranked nestling.

The hypothesis that asynchrony evolved as a means of establishing size differences to reduce competitive costs is inconsistent with these data, since the lowest ranked siblings competitive ability appears to be independent of the size hierarchy. Such instability within nestling hierarchies is common amongst House Martins, and Figures 4.65(a-f) show examples of how hierarchies may change. Figure 4.65(a) shows a synchronously hatched brood of five in which the original hierarchy is reversed completely. This is an extreme example but noteworthy in that it might be interpreted as supporting the view that asynchrony is required to ensure that hierarchies are maintained, in accordance with the BSR hypothesis, since synchrony does not result in maintenance of the hierarchy in this example.

Figure 4.65(b) is an asynchronous brood of three

Figure 4.65:

Individual nestling growth curves for House Martins showing the flexibility of growth and instability of nestling hierarchies.

(a) 'Synchronous' brood of 5. IHS = 1.0

(b) 'Asynchronous' brood of 3. IHS = 0.0

(c) 'Asynchronous' brood of 4. IHS = 0.83

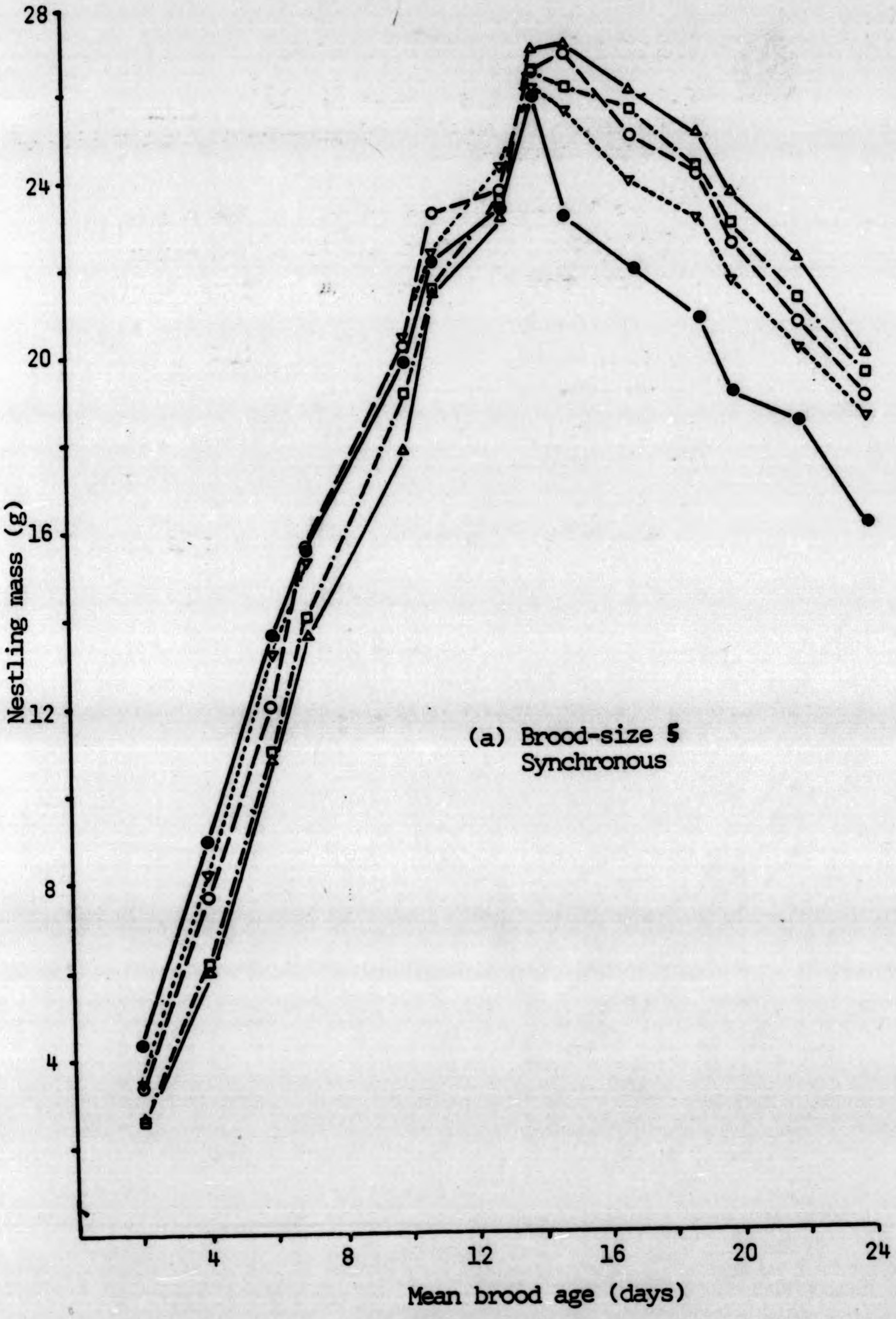
(d) 'Asynchronous' brood of 3. IHS = 0.33

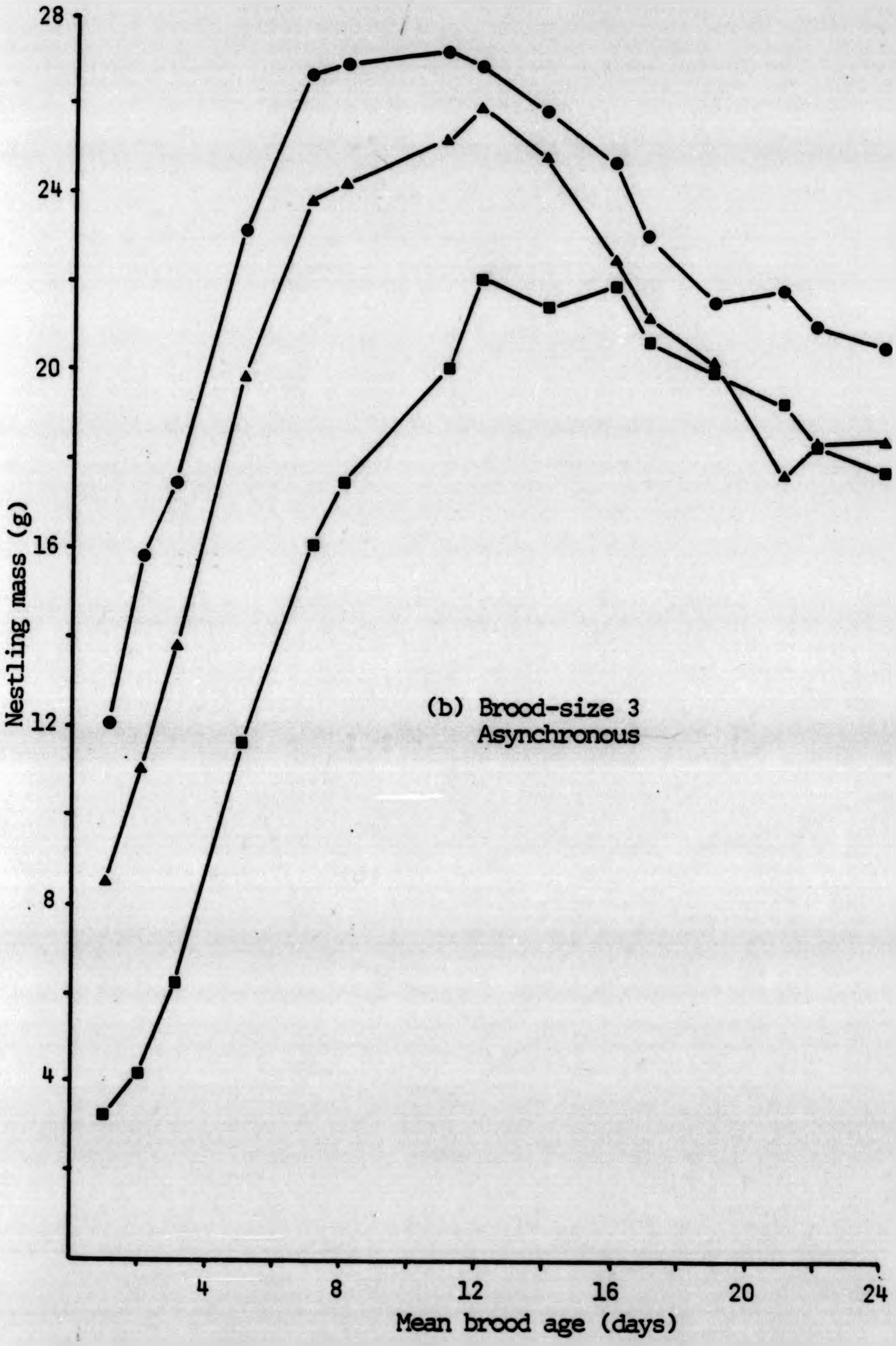
(two nestlings ranked equally, initially as 1, and finally as 2).

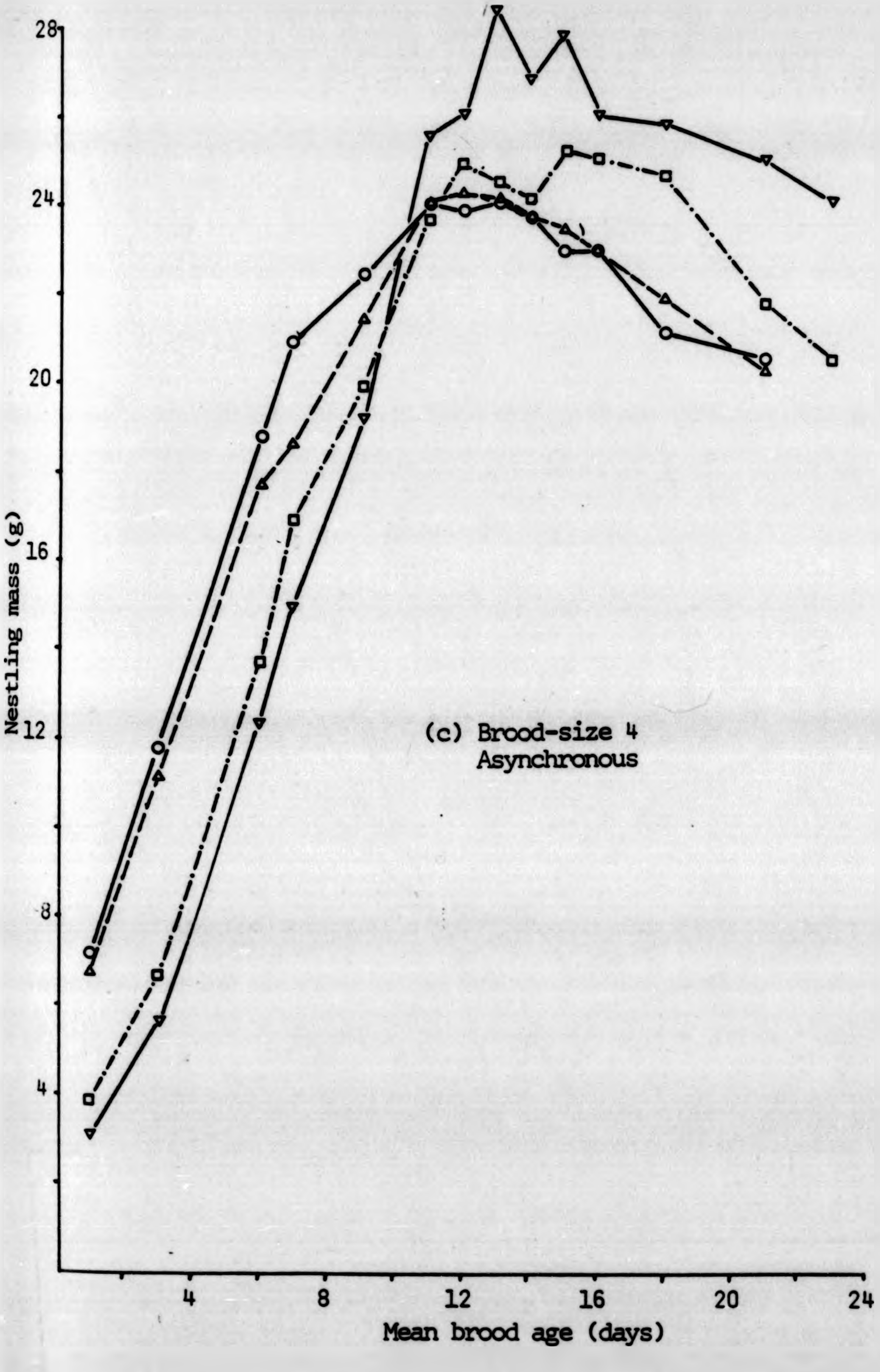
(e) 'Synchronous' brood of 3. IHS = 0.17

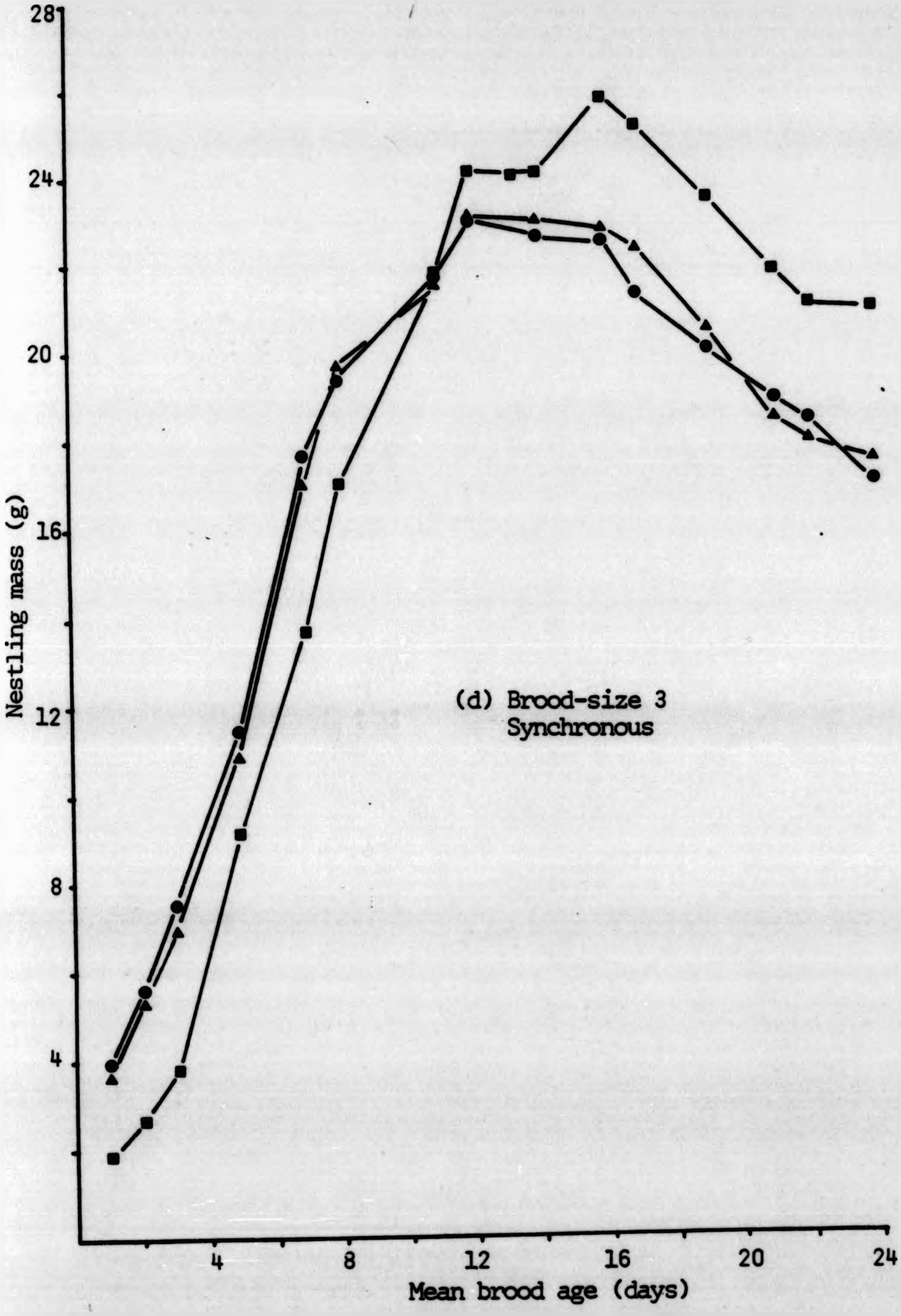
(f) 'Synchronous' brood of 4. IHS = 0.17

(three nestlings initially ranked equally as 1, and two nestlings finally ranked equally as 2).

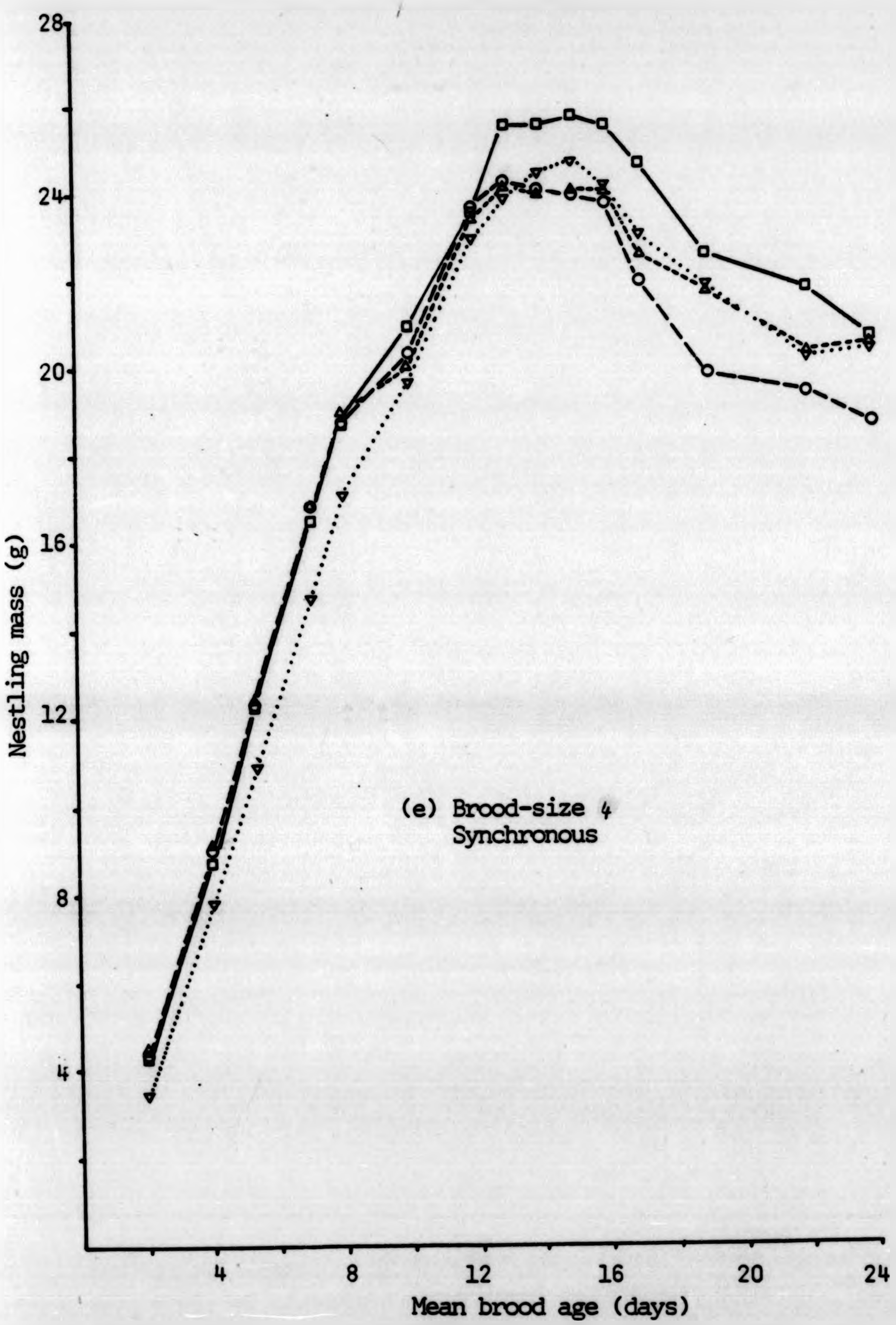

28
24
20
16
12
8
4
Nestling mass (g)
4
8
12
16
20
24
Mean brood age (days)
(a) Brood-size 5
Synchronous

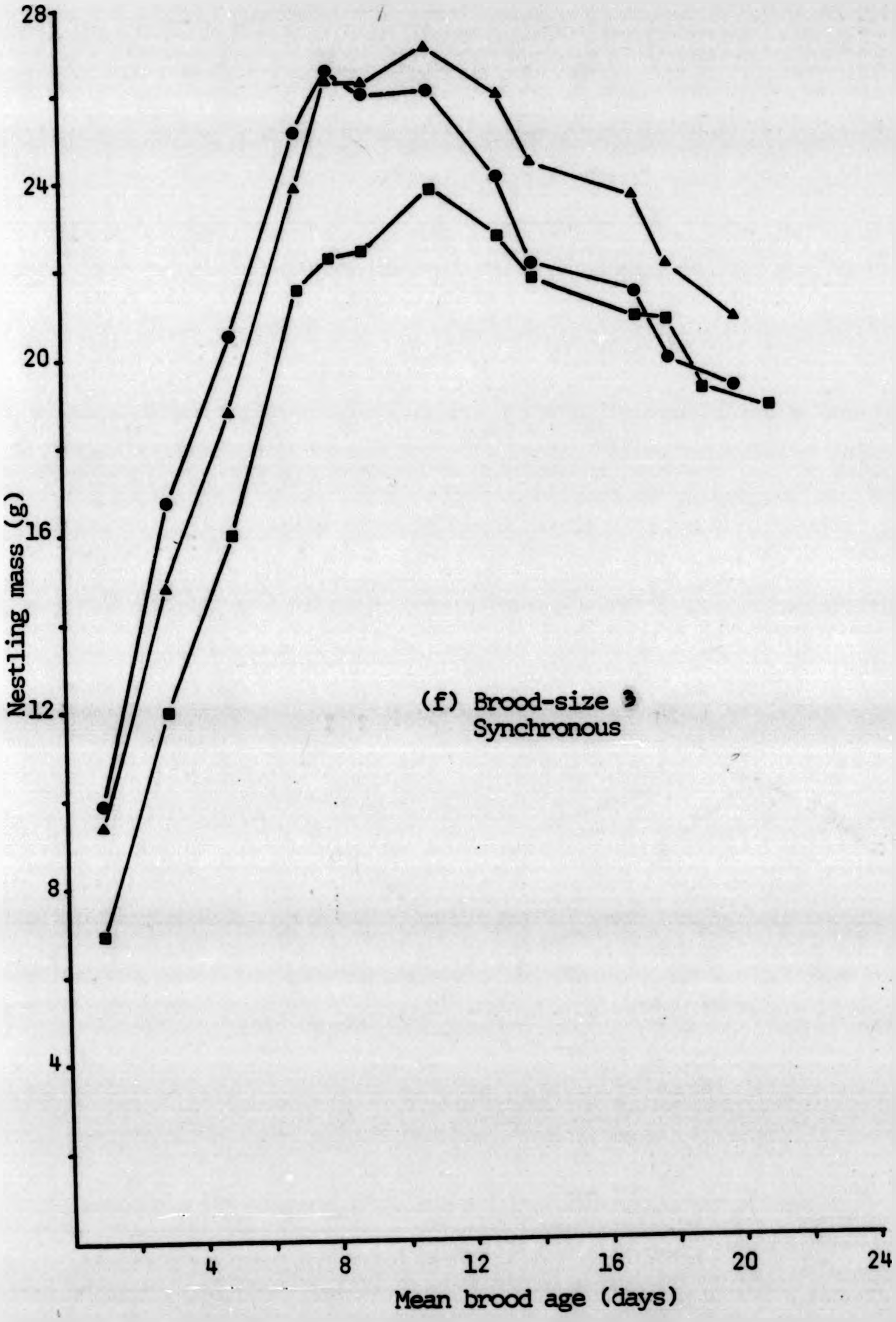

(b) Brood-size 3
Asynchronous
Nestling mass (g)
Mean brood age (days)
28
24
20
16
12
8
4
4
8
12
16
20
24


(c) Brood-size 4
Asynchronous
Nestling mass (g)
28
24
20
16
12
8
4
Mean brood age (days)
4
8
12
16
20
24



28
24
20
16
12
8
4
Nestling mass (g)
(d) Brood-size 3
Synchronous
4
8
12
16
20
24
Mean brood age (days)


28
24
20
16
12
8
4
Nestling mass (g)
(e) Brood-size 4
Synchronous
4
8
12
16
20
24
Mean brood age (days)


28
24
20
16
12
8
4
Nestling mass (g)
(f) Brood-size 3
Synchronous
4
8
12
16
20
24
Mean brood age (days)

and may be viewed as the classic hierarchy type that lends support to the RSR hypothesis (see Figure 4.65(a)). In this example, hatching asynchrony was artificially high (> 4 days) and it is the only example of its type found amongst 28 House Martin broods (see below). Figures 4.65(c) and (d) are for natural asynchronous broods of four and three respectively. In both cases the smallest nestling eventually becomes the largest. Figure 4.65(e) is a synchronous brood of three in which the smallest nestling remains the smallest, but the second ranked sibling, eventually peaks at a higher mass than its larger sibling. It also demonstrates that a high degree of asynchrony is not necessary to ensure that the smallest sibling remains the smallest. Finally, Figure 4.65(f) shows a synchronous brood of four in which the third size ranked individual peaked at an appreciably higher mass and remained heavier, even though the initial size difference between the top three ranked individuals was very small, and similar peak masses might be expected on this basis. To consider further the occurrence of permanent hierarchy shifts within House Martin broods, an Index of Hierarchy Stability was calculated as:-

$$\frac{2 \times \text{Number of growth curve crossovers}}{(\text{Broodsize}-1) \times \text{Broodsize}} = \frac{C_n}{C_{max}} \qquad \text{eqn. } 4.23$$

where the number of crossovers is established by joining the curves between a nestling's initial mass ranking and its final mass ranking allowing for age differences. Figure 4.66 shows the calculation of C_n and C_{max} for a

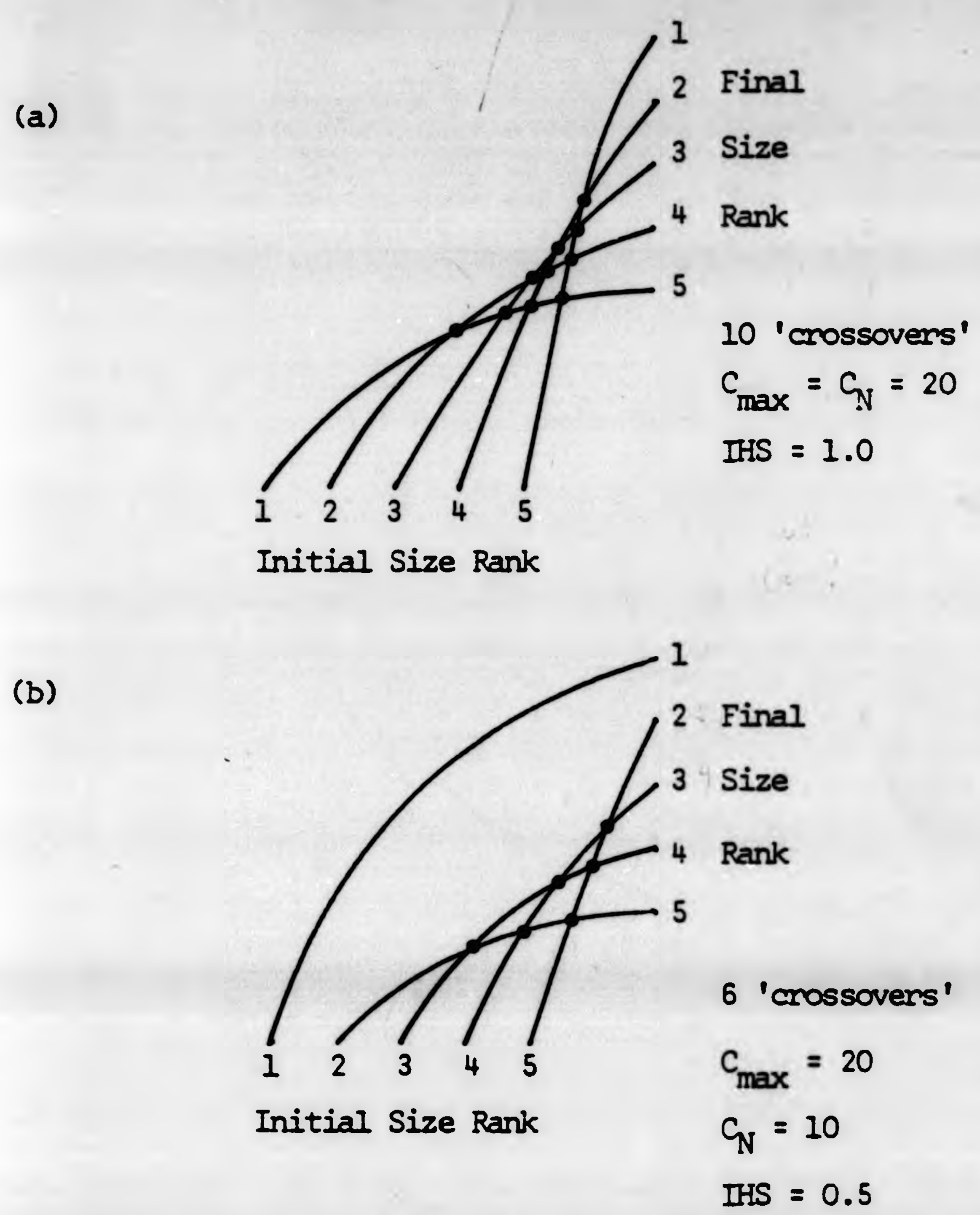


Figure 4.66: Calculating the index of hierarchy stability (IHS) from initial and final size ranking.

(a) Maximum possible number of crossovers ($C_{max} \div C_N$) i.e. complete hierarchy reversal

(b) Half the maximum number of crossovers (C_N), partial hierarchy instability hypothetical hierarchy. So where IHS = 0, there is no change in hierarchy, and where IHS = 1 there is complete reversal of the hierarchy with intermediate values representing a degree of change between individuals (see Figures 4.65(a-f).

In 28 House Martin broods in which it was possible to measure IHS, only 11% of the hierarchies remained stable (IHS = 0). Of the remaining 89%, 68% showed some permanent change in hierarchy structure, (IHS = 0.16-0.88) and 21% showed complete hierarchy reversal (IHS = 1.0) of the 68% that showed some permanent hierarchy change 43% resulted in the initially highest ranked individual being superseded by lower ranked siblings and 14% of these became the lowest ranked individuals. Table 4.38 summarizes these results. In broods which showed partial hierarchy changes (IHS = 0.1-0.9) figures are presented with respect to the effect of the change in position of the highest ranked individual, rather than as ranked indices. This is because each IHS value represents several different combinations of hierarchy change, and does not specifically identify cases where the highest ranked individual was superseded by lower ranked individuals (Table 4.38). Thus IHS is useful for general comparison between species, brood-sizes, etc., but since there is such a large number of possible combinations of hierarchy change it is more informative to discuss specific combinations separately.

The only instances (n = 3) in which hierarchies were maintained was in the highly asynchronous brood shown in

TABLE 4.38: The proportion of House Martin broods showing permanent changes in mass hierarchy within the brood (n = 28)

Hierarchy change		Percentage occurrence
(i)	No change (IHS = 0.0)	11%
(ii)	Partial change (IHS = 0.1-0.9)	
	(a) Highest ranked individual not superseded by lower ranked individuals	25%
	(b) Highest ranked individual [3]superseded by lower ranked individual (s), but not all of them	29%
	(c) Highest ranked individual superseded by all lower ranked individuals	14%
(iii)	[2]Complete change (IHS = 1.0)	21%
	TOTAL	100%

---

[1] See text for explanation of derivation of IHS

[2] Complete changes from the point of view of the highest ranked individual is as in (ii(b))

[3] 'superseded' refers to the difference in initial and final size rankings

Figure 4.65(b) and in two broods of two. Since the number of suitable broods of two was small (n = 4) it is possible that hierarchy stability may be more common in this brood size. Yet no examples of hierarchy stability was found in the House Martin broods of 3 - 5 (with the exception of the above manipulated brood) and this begs the question, do initially lower ranked siblings in broods of three or more young in fact gain some advantage from their higher ranked siblings which enables them to peak at a higher mass and remain heavier? O'Connor (1975b) demonstrated that later-hatched young received more visits than did their earlier hatched siblings in the Blue Tit, thus enabling them to grow more quickly. Although this may occur also in the House Martin it is unlikely that this alone could explain hierarchy instability. Firstly there is no evidence to suggest that any advantage to early growth in the late-hatched young is maintained throughout growth in either the Blue Tit or House Martin, and it is more likely that limited early growth benefits might serve to narrow the size gap between individuals rather than produce changes in hierarchy. Secondly, if late-hatched nestlings had such a consistent advantage then one might expect the last hatched young to consistently increase its size rank, which does not occur. Finally, egg size effects were not controlled in this study and so differences in growth due to hatching mass variation cannot be ruled out. Indeed the data on IHS are entirely consistent with that which one might expect from differences in egg mass. House Martins do not show any pattern of changing egg mass with laying sequence

(Bryant, 1975b, 1978b), so that the lightest egg may hatch first and the heaviest last. It has been shown for a number of species that heavier eggs produce heavier chicks (Bryant, 1978; Davis, 1975; Parsons, 1970; Schifferli, 1973) and that heavier hatchlings produce heavier fledglings with subsequent increased probability of survival (Horsfall, Lundburgh & Vaisanen, 1979) although not in House Martins (Bryant, 1978). If hatching mass in the House Martin is therefore independent of hatching order, nestling peak mass would be expected to reflect this initial hatching mass and not hatching order and so any given combination of hierarchy crossovers should occur with equal probability. For example, there are only two outcomes with respect to nestling hierarchy in a brood of two; maintenance or reversal. They would be expected to occur equally if hatching mass (and hence peak mass) is independent of hatching order. Of the four broods examined two had an IHS of 0, and two had an IHS of 1. For broods of three, four and five there are six, twelve and twenty possible combinations of hierarchy changes respectively. Sample sizes for IHS measurements were eleven, seven and six broods for the respective broodsizes and so, on the basis of such a small number of broods, it would not necessarily be expected that hierarchy maintenance in the larger brood sizes would be detected.

To summarise, the instability of hierarchies in House Martins is consistent with a model of peak mass independent of hatching order. Examination of the literature shows that hierarchy instability occurs in other species; Black Vultures, Coragyps atratus (McHargue, 1981); European Robin, Erithacus rubecula (Lack & Silva, 1949); Willow Warbler, Phylloscopus trochilus, Reed Warbler, Acrocephalus scirpeus, and Great Reed Warbler, Acrocephalus arundinaceus (Dyrcz, 1974). The importance of understanding changes in hierarchy will be further discussed in Chapter 5, with respect to the rôle of hatching asynchrony.

4.12 PREMATURE FLEDGING IN THE DIPPER

Dipper nestlings are capable of swimming and diving long before they can fly (as early as day 12, pers. obs., Shaw, 1978), and are able to continue development out of the nest if forced to fledge early. Data regarding the survival of prematurely fledged young are scarce, yet important, as there is evidence that in the Dipper differential growth occurs to maximize the chances of survival of prematurely fledged young (Section 5.1). For selection to favour such an adaptive strategy there must be significant mortality of nestlings that are unable to fledge early, and evidence that prematurely fledged young are able to survive and recruit into the adult population.

Table 4.39 shows data for prematurely fledged young which were subsequently either caught or sighted after they had become independent of their parents. The data, though very few, demonstrate the ability of prematurely fledged nestlings to continue growth outside of the nest, and enter the adult population.

TABLE 4.39: Survival of prematurely fledged Dipper nestlings observed after independence from parents

Age at fledging	Time between fledging and last sighting	Source
[a] 14 days	2 weeks	This study
[b] 14 days	Several months	Balát, 1964
[a] 16 days	3 weeks	This study
16 days	3 months	" "
17 days	3 months	S. Newton, pers.comm.
17 days	12 months	This study
[c] 17 days	20 months	" "

a Observed being fed by the parent after fledging

b Two birds from one brood

c Known to have subsequently bred

Three main factors may be responsible for nestling mortality that would provide selective pressure for premature fledging in the Dipper; human disturbance, predators and flooding. The latter two together account for 38.0% of nest failures (Shaw, 1978). Flooding is the single most important natural cause of nest failure (19.6%), and is even likely to be underestimated. This is because Shaw's figures were based on analysis of BTO nest record cards, which tend to be biased towards easily surveyed bridge nest sites, which are relatively secure compared with more natural sites. If egg stealing by humans is not included in the above considerations of nest failure causes, flooding and non-human predation account for a minimum of 54.5% of all nest failures. The ability to fledge early, whilst perhaps reducing the chances of brood survival, will however increase the likelihood of at least some young surviving, and thus may be selected for.

The ability to jump out of the nest, and climb out of the water once the immediate danger has been avoided, seems likely to be enhanced by well developed tarsi (Section 5.1). Dipper nestlings usually combine swimming on the surface with intermittent diving once they have left the nest, before climbing on to the river bank or a low rock ledge down stream (pers.obs.).

Though nestlings tend to use their wings when diving, surface swimming involves primarily the use of the feet (pers.obs.). This is also true of adults (Glutz & Bauer, 1985). Nestlings also appear to initially avoid deep pools once fledged and remain near shallow rocky areas of river, where they can scramble over the rocks and surface swim (pers.obs.). One nestling that jumped from the nest at 16 days into a deep pool, surface swam for a while, but drowned during its first dive, perhaps due to strong undercurrents. Dipper nestlings, though, are capable of surviving leaps into very fast flowing water. One 14-day old individual having disappeared beneath the 'white water' at the bottom of a 1.5 metre waterfall below its nest, was found unharmed an hour later on the river bank downstream (see also legend, Table 4.39). The water below the nest however was relatively shallow. Dipper nestlings have been observed apparently attempting to self-feed as early as 17 days old, though parents continue to deliver food to fledged young (pers.obs.). It is not known in what way the allocation of parental care varies during post-fledging in prematurely fledged young compared with nestlings that fledge at around 23 days. Adaptations to surviving premature fledging are discussed in Section 5.1.

CHAPTER FIVE

DISCUSSION

PART I: THE NESTLING ENERGY BUDGET

5.1 DIFFERENTIAL GROWTH AND BODY COMPOSITION IN THE DIPPER

Differential growth involves the allocation of limited resources to those tissues and organs of greatest current need. This necessarily involves trade-offs, since energy and materials diverted to specific organ growth result in deficits to other tissues, resulting in slower growth of the latter. In the short-term therefore certain tissues must pay the cost of slower growth, though in the longer term the overall benefits of such an adaptive strategy are realised by the organism as a whole. The relationship of this differential growth to nestling developmental strategy has been investigated in only a few species (Bryant & Gardiner, 1979; O'Connor, 1975; 1977; 1978; Ricklefs, 1975; 1979; Tatner, 1984). Differing patterns of growth have been identified between modes of development (i.e. precocial, semi-precocial, altricial; Ricklefs, 1979) and more importantly within a given mode, for example amongst altricial species (O'Connor, 1977; 1978). Dipper nestling development is characterized by two factors which have not been significant in previous studies; premature fledging (Section 4.12) and sexual size-dimorphism (Sections 4.1.4, 4.1.5). The latter will be discussed in Section 5.2. Differential growth and premature fledging will be discussed here.

A number of adaptations which facilitate rapid early growth ensure that nestlings are relatively 'mature' midway through the growth period, so that if premature fledging is necessary the chances of nestling survival are enhanced.

Bill morphology in nestling birds is different from that of adult birds (O'Connor, 1977; Royama, 1966; this study), and in the Dipper may be divided into two types. In the first phase of bill growth, bill shape is likely to be governed by the need to provide a large target area to stimulate parents. During this phase mouth target area (MTA, Section 4.1.2) is circular and is referred to hereafter as MTAI. In phase two, the bill gradually changes in shape to the adult diamond shape (MTAII, Section 4.1.2), to enable the transition to self-feeding in fledged young.

Phase I of Dipper bill growth is characterised by an increase in both gape-width and bill-length (Section 4.1.2, Figures 4.8-4.11) such that MTAI continues to increase in size until day twelve. MTAI then decreases in size as the fleshy bill cushion atrophies. Since MTA changes shape to MTAII as the nestling grows, the shape of MTAI does not accurately reflect bill shape during the second phase of bill growth. MTAII (and that of the parent bill) conversely, describes well the shape of MTA during the second phase of bill growth but not the first phase. Figure 5.1 shows MTA calculated for both the 'circular' (MTAI) and 'diamond' (MTAII) shapes, as a function of age in the Dipper (see also Figures 4.8, 4.9; Section 4.1.2).

MTAI allows a larger target area for the parent, compared with MTAII up until day twelve when the two curves cross. This shape of mouth is likely to be beneficial to

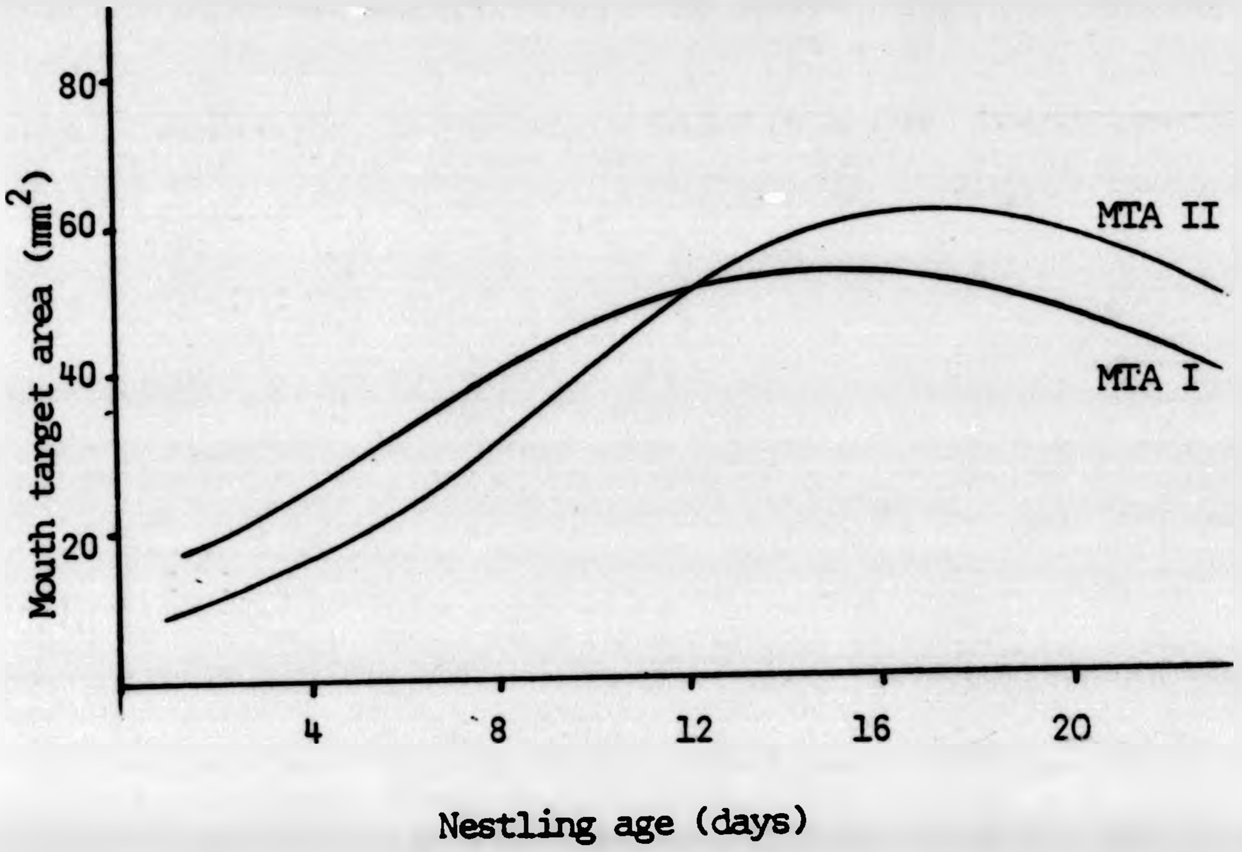


Figure 5.1: Change in mouth target area as a function of age in the Dipper

MTA I = circular mouth shape

MTA II = diamond mouth shape

nestlings during early growth for a number of reasons. Firstly, it provides greater visual stimulation to the parent because of the larger target area. Secondly, it reduces the likelihood of food boluses being accidentally dropped by nestlings, during the stage when nestlings are least coordinated, particularly during the first few days after hatching. Thirdly, it allows nestlings to handle larger food boluses than would be possible if the mouth was diamond shaped (i.e. MTAII), since MTA is larger for MTAI.

The change in bill shape during phase two can also be viewed as adaptive for two reasons. After day twelve changing bill shape to MTAII ensures that mouth target area remains large (Figure 5.1), rather than decreasing which would happen if mouth shape remained circular (MTAI) due to the reduction in gape-width (Figure 4.5; Section 4.1.2). Also, change in bill shape to that of the adult occurs during the period when young can prematurely fledge, rather than later in the nestling period, or earlier which would involve a lower MTA during the period of peak energy demand (see below). Days 12-23 may represent the minimum time necessary to effect a change in bill shape to that of the adult, and may equally explain why the change in shape (MTAI → MTAII) does not occur later in the nestling period without the need to involve adaptive arguments with respect to premature fledging. It appears, however, that change in bill shape (and hence reduction in MTA) is deferred until after the period of peak nestling energy demand (day 9.0, Table 5.1), thus reducing foraging costs to the parent, since fewer feeding trips will be necessary to provide a given amount of food.

TABLE 5.1: A summary of the timing of some developmental stages during Dipper nestling growth

	Developmental Stage	Age (days)
(i)	Peak RLDM of Gizzard	6.0
(ii)	[a]Main insulating feather tracts 'split'	6.0
(iii)	Maximum growth rate of body mass	6.5
(iv)	Peak daily metabolised energy (DME)	9.0
(v)	Growth rate of body-length begins to slow down	10.0
(vi)	[b]Full homeothermy attained	10.0
(vii)	Peak daily energy expenditure (DEE)	11.0
(viii)	Tarsus growth complete	12.0
(ix)	Mouth target area (MTAI) reaches a peak	12.0
(x)	[c]Peak nestling mass	17.0

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[a] primarily back feathers

[b] mean for all brood sizes estimated from parental inattentiveness patterns (Section 4.6.2)

[c] nestling mass reaches an asymptote earlier than this (Section 4.1.1) but mass recession starts about day 17.

Other structures associated with procurement of food show rapid early development and may be viewed as adaptations to permit maximum rate and efficiency of energy intake and processing. Body-length growth is a crude indicator of how far a nestling can stretch its neck to receive food (Section 4.1). Body-length growth begins to slow down at day ten (Table 5.1) having increased linearly thereto, so that approximately 90% of body length growth has occurred before day twelve. Tarsus-length similarly shows an early linear increase, whilst the leg as a whole (measured as LDM) grows more quickly than the rest of the body (Section 4.2.2). Early growth of the legs has been found in other species (Austin & Ricklefs, 1977; O'Connor, 1977), and is important both for thermogenesis through shivering and attaining and maintaining feeding positions within the nest (Rydén & Bengtsson, 1980; Werschkul, 1979; Calder & King, 1974; Marsh, 1979; O'Connor, 1975), the former being partly responsible for the attainment of homeothermy by day ten (Table 5.1). Hence nestlings, that fledge prematurely are capable of independent thermoregulation.

The growth of food processing organs undergoes early development and maturation which coincides with the maximum rate of mass growth. The relative lean dry mass (RLDM) of the gizzard peaks at day six and then starts to decline (Section 4.2.2). A similar pattern has been observed in the House Martin (Bryant & Gardiner, 1979). The RLDM of the liver is high initially and decreases in relative size during growth, whilst both liver and intestine have lower water contents than the body as a whole (Section 4.2.4) reflecting their early maturation.

The large relative size of the head is one notable adaptation for food procurement since it includes the main trophic structure (O'Connor, 1984) though the head's initial large size may also reflect the need to provide strong protection for the well developed brain (Portmann, 1955). There may also be an adaptive conflict in having a large head, since it represents an area of high vascularization and heat loss (Marsh, 1979). Differential growth of feather tracts appear to partly compensate for this: feathers on the head 'prick' through the skin first (Section 4.1.3) and pins split early. Head feathers, however, grew slower than other insulating feather tracts (Section 4.1.3), but since the head decreases in size relative to the rest of the body, rapid continued growth of feathers becomes less important. Conversely, the emphasis on heat loss shifts from the head, to the rest of the body (notably the exposed back) which does not decrease in relative size as growth continues (Sections 4.2.2, 4.4). Energy for feather growth is therefore apparently transferred to allow rapid growth of the main insulating feather tracts on the back. The back feathers grow the quickest of all the insulating feather tracts (Section 4.1.3). At approximately 7-8 days Dipper nestlings therefore have a well established insulating layer of feathers on their dorsal surface. Nonetheless, larger nestlings tend to cool more quickly than smaller nestlings of similar age (Sections 4.4.2, 4.4.3). This would appear to be due to heat loss through the primary and secondary pins (see Section 5.3), which prick through the skin at about 5.5 days, but the feathers do not split from their pins until about 8.5 days (Section 4.1.3). Early pricking of primary and secondary feather pins may therefore represent a trade-off, since these feathers have eventually to achieve the greatest length. Early pricking of the feather pins may thus be necessary to allow sufficient time for the flight feathers to grow. The rapid growth of these feathers lend support to this view (Section 4.1.3).

Dipper nestlings have high lipid indices compared with some other species (O'Connor, 1977; 1984), and even from a young age, lipid indices are substantially similar to adult/juvenile lipid indices (Section 4.2.1). Nestlings that fledge prematurely therefore have significant energy reserves to utilise during the period in which energy demand is likely to be highest. Nestling lipid index gradually increases during growth so that young that fledge at around 23 days have lipid indices of about twice that of adults/juveniles. This may be an adaptive strategy since Dippers may nest as early as February in the study area, when ambient temperatures are still low and snowfall and frosts still occur. Thermoregulation costs of newly fledged Dippers are therefore likely to increase considerably, especially during the day, since they may return to the nest to roost at night (Shaw, 1979; pers.obs.).

Tarsal growth is complete by day 12 (Section 4.1.1), the earliest age nestlings were known to jump from the nest, whilst wing growth is only about 90% complete at 23 days. Growth of legs at the apparent expense of the wings can be viewed as an adaptation ultimately to favour efficient early locomotion in prematurely fledged young (see Section 4.12). This appears to be one of several adaptations for early growth allowing young to fledge prematurely if necessary, and yet in a relatively mature state. Since growth differs between the sexes in the Dipper (Section 4.1.5), differences in developmental strategy and nestling energetics may be expected. This is considered in the next section.

5.2 SEX-SPECIFIC ENERGETICS AND GROWTH DYNAMICS IN THE DIPPER

Adult Dippers are sexually size-dimorphic, males averaging larger than females (Anderson & Wester, 1971). In this study adult males were 20% heavier than females and had 20% greater wing-length. This size dimorphism was evident among nestlings (Section 4.1.5), and was reflected in the greater field energy expenditure of eighteen day old male nestlings compared to females (Section 4.7).

Whilst male nestlings average 11% heavier than female nestlings at fledging (Section 4.1.5), their daily field energy expenditure (FEE) was 21% higher than females (Section 4.7). Nonetheless the apparently high FEE is explained almost entirely by the lower mass difference, since this difference is primarily due to the associated increased metabolic costs as a result of greater body mass. This view is supported by the energy budget data presented in Section 4.6, in which an increase of 11% body mass produces a 20.7% increase in daily energy expenditure, in good agreement with that found in the field.

That the greater energy demand of male offspring is explained by the mass difference between the sexes has also been demonstrated for the sexually size-dimorphic Red-winged Blackbird (Agelaius phoeniceus), in which the higher male field metabolic rate was reflected in body size differences (Fiala & Congdon, 1983). Both studies thus show there is a greater cost of rearing males than females in such size-dimorphic species.

Sex ratio theory (Fisher, 1930) predicts that at the termination of parental care, equal total expenditure of energy, time or some other measure of parental investment should have occurred for both sexes within the brood. Such equality of investment may thus be expected to produce a sex ratio of one. Unequal investment on the sexes, as implied in the Dipper, may therefore be expected to produce a primary sex ratio skewed in favour of the least costly sex, i.e. females. Of the nestlings it was possible to sex pre-fledging, 37 were females and 32 were males, producing a sex ratio (♀/♂) of 1.16, apparently skewed in favour of females, although not significantly so ($\chi^2 = 0.362$, $n = 69$, ns). Discriminant analysis showed that females were more reliably sexed than males (Section 4.1.4) which may explain the greater number of females in the sample, due to the possible inclusion of small males.

Given that the Dipper appears to show both unequal energy expenditure on the sexes and a primary sex ratio not different from unity, some explanation is required. One explanation may be that the high energy demand of male offspring does not necessarily represent an unequal investment between the sexes by the parents. In other words, the energetic cost of rearing a particular sex may not reflect the reproductive cost to the parent. This may be because the effect of higher energy expenditure by the parent on future reproductive attempts is small, for example if parents can compensate for increased demand by adjusting their foraging behaviour. Another explanation is that there is differential mortality between the sexes during the nestling stage, biased against the more costly males, which tends to even out the extra cost of rearing male offspring.

Slagsvold et al. (1986) identify three possible mechanisms which may bring such differential mortality about:-

(1) Parents distribute food more or less equally among all nestlings, irrespective of sex, but the higher energy demand of the offspring of one sex (in the Dipper, males) renders them more susceptible to starvation;

(2) Sibling competition, e.g. males fighting and injuring each other more than females;

(3) When parents cannot adequately feed the whole brood, they preferentially feed the less expensive sex, in the case of the Dipper, females.

The latter necessarily implies sex recognition by the parent. Hypotheses 1 and 2 are variations on the brood reduction theme (see also Section 5.12), and all three hypotheses are concerned with partial brood loss. Three more hypotheses may be added:-

(4) Females may be more able to avoid predation or flooding by premature fledging than males (Section 5.1), and once fledged have greater probability of survival;

(5) Dipper adult males may selectively feed female nestlings in order to reduce the likelihood of future competition from male offspring (Harper, 1985). Males of the species tending to be more philopatric than females, as in many bird species (Greenwood, 1980);

(6) Both parents invest more in the dispersive sex (in the Dipper, females, S. Newton, pers.comm.), resulting in greater likelihood of starvation or other mortality of males. This is similar to (3) but should occur irrespective of food availability.

Since no data are available on food distribution amongst brood members by each parent, and causes of nestling mortality are often difficult to assess with certainty, evidence for the hypotheses is indirect though suggestive.

Are male offspring more susceptible to starvation within the nest? Partial brood loss consistent with starvation of individuals was uncommon in this study. Of the 63 broods for which young were known to fledge, only six suffered loss of a single nestling, and one brood of six suffered the loss of two nestlings, prior to twelve days of age, at which time nestlings could fledge prematurely. In each case young were missing from the nest on a subsequent visit by the observer, and so no details are available as to the cause of death, or likely sex of the individuals. Shaw (1978) examined the incidence of total brood loss and partial brood loss in a much larger sample of Dipper nests (n = 455) and found that of the young that hatched, 4.6% were lost through partial brood loss, whilst over twice as many were lost through whole brood loss (11.4%). There was no evidence to suggest partial brood loss was due to starvation. If feeding of nestlings were entirely at random (e.g. Reed, 1981) as proposed by hypothesis (1) then male mass might be expected to show a greater variance than female mass, since in times of food shortage males may suffer under-nourishment. Richter (1983) found that the variance in male mass was greater than the variance in female mass in the Yellow-headed Blackbird. (He also presented data for three other sexually size-dimorphic species in which the larger sex showed greater variation in mass than the smaller sex; Red-winged Blackbird, Common Grackle, and European Sparrowhawk). The variance in male mass in the Dipper was not significantly different from the variance in female mass (F = 1.56, df15,18 ns) for days twelve to twenty-one, though the number of sexed nestlings for which comparable growth data were available was small (n = 35). The misclassification of small males as females during 'Discriminant' analysis (Section 4.1.4) may perhaps be interpreted as suggesting males suffer more in times of food shortage than females. Large females, presumably those well nourished, were never classified as males (Section 4.1.4). The limited evidence available therefore suggests that whilst males may possibly suffer from undernourishment more frequently than females differential mortality through preferential starvation of males is likely to be uncommon.

Fighting between nestlings, as proposed by hypothesis (2) was never observed in the Dipper. No Dipper nestlings showed any signs of physical injury, or bald patches of feathers consistent with sibling fighting. Thus there is no support for hypothesis (2).

Preferential feeding of females is predicted by hypotheses (3), (5) and (6) though the reasons for it occurring are different. Hypothesis (3) specifically infers selective starvation of males (see also hypothesis (1)) which I have suggested is uncommon in the Dipper. None of the three hypotheses is however inconsistent with higher mortality of males predicted by hypothesis (4). Indeed the data suggest that differences in energy allocation to growth between the sexes, and not provisioning rates, are likely to explain the proportionately faster growth of females. This is because males grow more quickly in absolute mass terms and hence must receive proportionately more food than their sisters. There were too few carcases available however to test differential investment to early maturation of organs adapted for premature fledging, in females. Preferential feeding of females is thus not necessarily inferred by these data. If males were to preferentially feed females as proposed by hypothesis (5), then it might be expected that adult females would compensate for this by preferentially feeding male young. Since it is the male that primarily feeds the young until they become fully homeothermic (pers.obs.) it seems unlikely that the female could compensate for this initially biased investment in female offspring. This view appears to be supported by the observation that males and females do not appear to differ markedly in their provisioning rates to mature young in this species (pers.obs.). Initial investment in early organ maturation by female offspring may be further aided by the ability of the more rapidly developing females to outcompete their brothers, and thus secure further shares of food brought to the nest. Conversely, the larger size of male nestlings may mean that they occupy higher positions within the nestling hierarchy and so offset any increased mobility of their sisters. There was no sex-specific difference in either body-length or mouth target area, as indices of competitive ability (see Table 5.2).

Since total brood loss is more common than partial brood loss (see earlier this Section), and premature fledging appears to be an adaptation to avoid this (Section 5.1), then the more rapid development of female young would speed up the time at which they could leave the nest. Their more rapidly developing tarsi, and greater completion of adult growth, would also improve their chances of survival over their less

TABLE 5.2: Male and Female Dipper nestling body measurements as functions of age and mass respectively. a and b are regression constants.

	Age			Mass		
	Intercept a	Slope b	r^2	Intercept a	Slope b	r^2
Female						
[a]Mouth Target Area (mm^2)	12.3	0.74	84.8	11.0	0.24	90.5
[b]Body-length (mm)	57.8	6.02	92.4	57.1	1.48	95.2
Male						
Bill-length (mm)	12.7	0.74	83.5	11.0	0.23	94.0
Body-length (mm)	58.1	6.00	92.6	56.7	1.43	95.2

All regressions were significant at $p < 0.001$

a Mouth Target Area; n = 139 females and n = 99 males

b Body-length; n = 126 females and n = 76 males.

All regressions were for the linear phase of body component growth, see Figures Section 4.1.

'mature' brothers, as predicted by hypothesis (4). The advanced growth of females is unlikely to be an adaptation solely to produce differential mortality of males, but more likely to be a beneficial consequence of the need for early maturity for dispersal. Male offspring conversely have more to gain by investing energy into mass gain (increasing body size) at the expense of maturity, since dominance in males is likely to be size related, in part, and the males do not disperse widely.

To summarize: it seems probable that the higher energy demand of male offspring in the Dipper does involve unequal investment by parents in favour of males. This appears to be offset by differential mortality of male offspring due to a lower ability to avoid predation and/or the consequences of flooding. This is likely to be as a direct result of preferential feeding by males of female nestlings, though the underlying reason behind this has yet to be identified. Additional starvation mortality of males may occur, though this is likely to be less important than predation and flooding mortality.

5.3 THE FAILURE OF THE 0.67 EXPONENT TO EXPLAIN HEAT LOSS IN DIPPER NESTLINGS

Heavier Dipper nestlings cool more quickly than lighter Dipper nestlings of a similar age (Sections 4.4.2, 4.4.3) at odds with that predicted from considerations of mass:surface area effect based on the 0.67 exponent (Calder & King, 1974). This suggests that Dipper nestlings within a brood do not have the properties of a sphere. Mertens (1969), however, found a very strong relationship between log (brood mass) and log (brood heat production) in Great Tit broods at 12°C, with an exponent of 0.672. There are behavioural and nest structure differences between these two species however, which may account for this. Great Tits have large broods (mean broodsize = 7.5; Perrins, 1979) whilst Dippers have much smaller broods (mean broodsize = 3.2, this study), the former lending itself to more efficient huddling. There is also little room for moving away from siblings to increase convective heat loss in large broods confined within closed nest structures, such as the Great Tit. Indeed hyperthermia was found to be more of a problem than hypothermia in some large Great Tit broods (Mertens, 1977a). Dipper nestlings conversely show no signs of hyperthermia in the birds studied, even in older nestlings (> 12 days old). Great Tits are thus forced by their large broodsize and enclosed nest to behave as a single brood mass, even if this is sometimes detrimental. In Dipper nestling huddling behaviour is constrained by other factors which will be discussed below.

5.3.1 'Constrained' and 'unconstrained' huddling

Great Tits are fed from within the nest at all ages, with only a limited directional component to feeding site (i.e. parents do not feed from one direction only). Faecal sacs are removed by the parent birds (Perrins, 1979). There is thus no conflict between positioning to obtain feeds (or to defaecate) and huddling to reduce heat loss. Dipper nestlings (and House Martin nestlings) however, are constrained in their huddling behaviour by the directional nature of the feeding offers (Figure 5.2(a)). A trade-off exists between

Figure 5.2: Huddling positions of Dipper nestlings

(a) The most common position in 7.0-8.5 day old Dipper nestlings in the field (brood-size 3)

(b) Huddling in young nestlings (≤ 3.5 days) in the field, and 7.0-8.5 day old nestlings in the laboratory

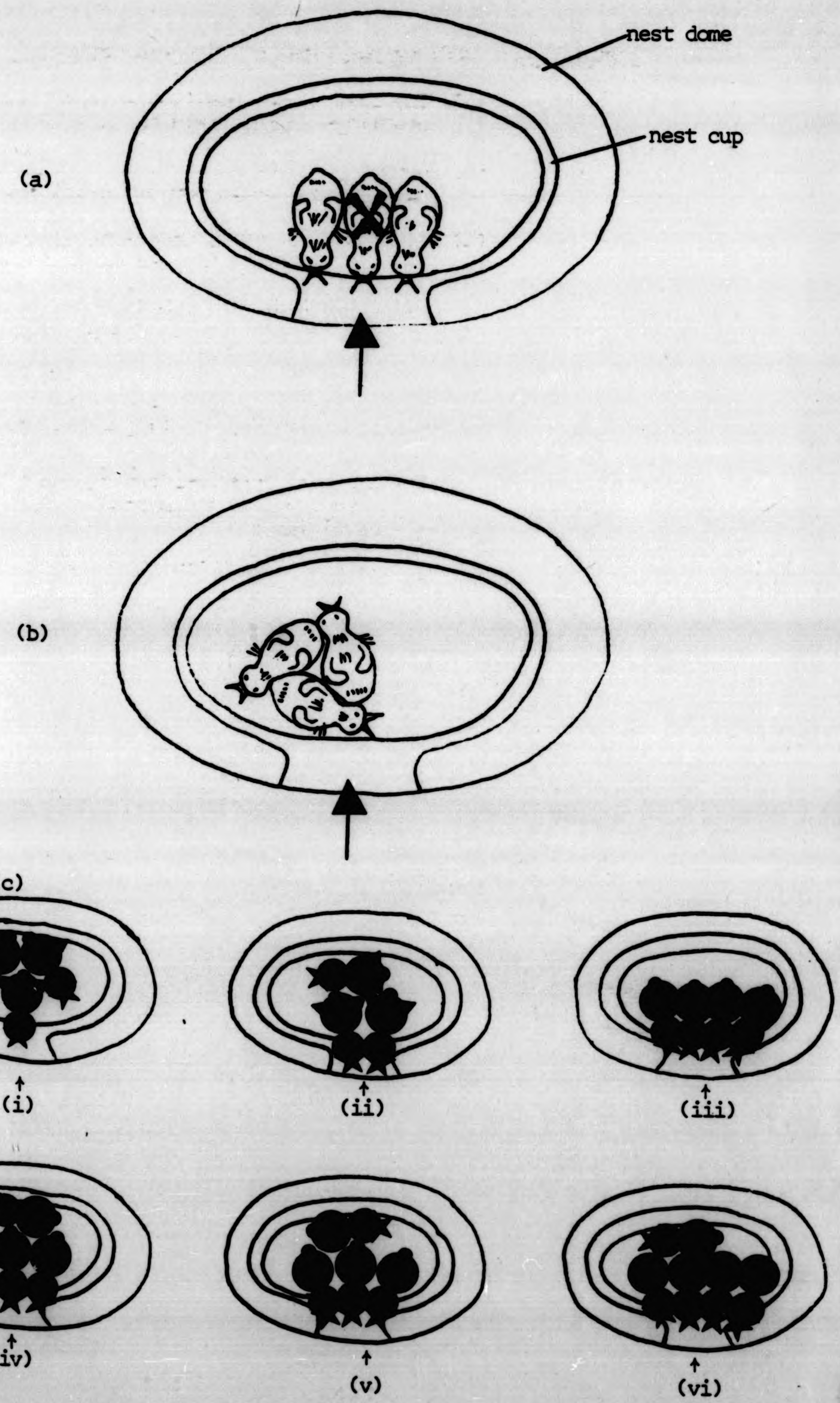
(c) (i) and (ii) Other positions observed in 7.0-8.5 day old Dippers in broods of three

(iii) and (iv) The two commonest positions in 7.0-8.5 day old Dippers in broods of four

(v) and (vi) The two commonest positions in 7.0-8.5 day old Dippers in broods of five

X = position that combines the most huddling benefits with the need to maintain a forward position for obtaining food

↑ = direction from which food is delivered to the brood


nest dome
nest cup
(a)
(b)
(c)
(i)
(ii)
(iii)
(iv)
(v)
(vi)

the best nest position with respect to reducing cooling rate (i.e. in an effective huddle; Figure 5.2(b)) and the best position with respect to receiving a high proportion of feeds (i.e. at the front of the nest; Figure 5.2(a)). In the latter, nest position X would be the energetically preferred position, since it combines huddling with a central position for feeding. This might be expected to produce competition for this favoured nest position, with associated movement of nestlings further reducing the time spent in an effective huddle. Bryant & Gardiner (1979) attributed an increase in the metabolic rate of House Martin nestlings in broods of three to this factor. In addition, Dipper nestlings defaecate out of the nest entrance from about five days onwards (pers.obs.), unlike Great Tits, exposing themselves to further cooling. The high relative humidity outside of Dipper nests will again increase cooling rate of nestlings, since it will reduce the insulative capacity of the nest material (Section 2.5.1).

In the laboratory cooling rate experiments, when there was no constraint on feeding positions, Dipper nestlings assumed positions within the artificial nest as in Figure 5.2(b). This position was, however, only assumed by small nestlings in the field (approximately ≤ 3.5 days old). These were fed within the nest, rather than from the nest hole, and also had their faeces removed by the parent (pers.obs.) and at this age, the pattern of behaviour thus resembled that found in Great Tit broods. The difference between these two types of behaviour, ≥ 3.5d Dippers in the field, Great Tit nestlings of all ages, and Dippers in the laboratory compared with Dipper nestlings ≥ 3.5 days old in the field, may be called 'unconstrained' and 'constrained' huddling, respectively. Thus wild Dipper nestlings may be regarded as essentially 'constrained' huddlers, whilst Great Tits are 'unconstrained' huddlers. The characteristics of these two huddling types are summarized in Table 5.3.

Since the previous arguments of huddling constraints could equally apply to all nestlings of ≥ 3.5 days old, then a positive relationship between age and field cooling rate would be expected due to the greater mobility of older nestlings and hence reduced huddling. Indeed, if brood mass or nestling mass (BMASS, NMASS; Section 4.4.1) are entered as 'forced' variables (Section 4.4.1) into the regression analysis of field cooling rate, ahead of age, such a positive relationship is found. Dipper nestlings are thus inefficient huddlers, and spend substantial amounts of time in little contact with their siblings. This partly explains why the 0.67 exponent of heat loss on brood mass does not hold for the Dipper.

5.3.2 Feather growth and heat loss in the Dipper

Feather growth results in a greatly increased surface area during transition to homeothermy, resulting in a potentially large source of heat loss. Larger nestlings show more advanced feather growth than smaller nestlings (Section 4.1.3) and this is more closely related to mass than age. This is because (a) nestlings of the same age will often have different masses due to the relative inaccuracy of the age estimate (Section 4.1.1) (± 0.5 days), compared with nestling mass

TABLE 5.3: The differences between 'constrained' and 'unconstrained' huddling broods in accounting for the failure of the 0.67 exponent of brood mass, to explain cooling rates of Dipper nestlings

Brood Factors	Unconstrained	Constrained
(i) Brood-size	Large - little opportunity for movement within the nest. Heat dissipation slow.	Small - greater opportunity for movement. Heat dissipation rapid.
(ii) Feeding position of nestling	Non-directional or limited directional component.	Directional. Young need to face nest entrance to be 'first in the queue'.
(iii) Defaecation	Parents remove faeces up until nestlings are near to fledging.	Nestlings defaecate out of the nest from a young age.
(iv) Nestling age effects	No differences between ages in the above parameters	Nestlings ≤ 3.5d, behave as unconstrained huddlers. Nestlings ≥ 3.5d, behave as constrained huddlers.
(v) Removal of constraint in previously 'constrained' birds	-	Behave as unconstrained huddlers.

measurements (± 0.1g), and (b) because growth of individual body components are related to growth of the whole body (Section 4.2). O'Connor (1975) demonstrated that the stage of plumage development was not correlated with metabolic heat production in three altricial nestling species. Hence feather growth is viewed as a mechanism for reducing thermoregulatory costs once established. This being so it may be expected that larger nestlings with their associated advanced feather growth will cool more slowly for given age; the converse of what is seen (earlier this Section). Feather pins however, have both a rich blood supply, and a large surface area, and represent a significant source of heat loss until a sufficient length of feather has 'split' from the feather pin (Section 4.1.3). This violates the assumption that the brood (or individual nestling) approximates a sphere, and on which assumption surface area is predicted from body mass. In the Dipper, between ages six to eight days old the maximum amount of exposed feather pins are present, particularly on the wings (Section 4.1.3), with little if any insulation from feather tufts. Thus, for the majority of nestlings examined in the field, any reduction in cooling rate possible from feather insulation is of limited value until the 'transition' stage is complete. Thus the combination of greatly increased surface area and reduced huddling efficiency (Section 5.3.1) appear to explain the relationship between size/age and cooling rate found in Dipper nestlings.

5.4 FACTORS INFLUENCING PARENTAL BROODING BEHAVIOUR IN THE DIPPER

Parent birds must make decisions between keeping the brood warm and self-feeding (Section 2.4.3). Usually there is a gradual reduction in the amount of time adults spend brooding the young, until brooding ceases. The proximate causes of reduced brooding with increased nestling age have yet to be conclusively identified. Some possible causes will be discussed here.

Parent birds not only have to decide when and how often to leave the brood unattended, but how long to stay away. Three models of female Dipper inattentiveness were introduced in Section 2.4.3. The 'net energy gain' model (Section 2.4.3(a)) was found to overestimate the optimal inattentiveness of incubating Swallows (Jones, 1985). The 'minimal nestling temperature' model (Section 2.4.3(b)) and the 'maximal brooding time' model (Section 2.4.3(c)) incorporate two possible additional constraints which may account for the apparent failure of the 'net energy gain' model to predict female inattentiveness. This will be discussed in Section 5.4.2. The proximate causes of female inattentiveness will be discussed below.

5.4.1 Proximate causes of female inattentiveness in brooding birds

Many studies on female inattentiveness patterns have been concerned with incubating birds (Davis et al., 1984; Haftorn & Reinertsen, 1985; Jones, 1985; Morton & Pereyc, 1985). Proximate causes affecting these patterns are likely to be similar for brooding adults. A clutch of eggs, however, provides a relatively stable energetic reference point on which the female may base decisions regarding inattentiveness. Environmental conditions alone are thus likely to be of primary importance in regulating incubating behaviour. A brood of nestlings, however, generates additional factors since the cost of reheating the brood (Section 4.4.6), the broods ability for thermogenesis (Section 4.4.3) and brood energy requirements (Section 4.6) all change as nestlings grow. Brooding birds are thus subject to a wider range of energetic demands than incubating birds, and may thus provide some insight into decision making in the latter.

Three hypotheses may explain when, and how often a parent bird becomes inattentive:-

(1) Nestling homeothermic capacity increases;

(2) Increased energy demand as nestlings grow, necessitating increased time to feed the young;

(3) Greater difficulty of the brooding bird to maintain energy balance during short inattentive periods.

Note that hypotheses (2) and (3) differ in that the proximate factor for brooding is chick hunger level in hypothesis (2) and parent hunger in hypothesis (3).

For hypothesis (1) to hold, adults must be able to assess nestling homeothermic capacity and respond accordingly. One way in which this may be done is by sensing nestling body temperature. Indirect evidence for sensory perception of egg temperature in the Village Weaver (Ploceus cucullatus) via the brood patch has been suggested by increased inattentiveness in birds which had their brood patch anaesthetised (White & Kinney, 1974). White & Kinney (1974) suggest that inattentiveness is cued by the use of a 'release temperature' (for the Village Weaver, 37°C) at which point the bird leaves the nest. This hypothesis could equally apply to nestlings. As nestlings begin to thermoregulate for themselves, this is mirrored by a progressive increase in body temperature (Section 4.4.4; e.g. Dawson et al., 1976; Marsh, 1979; O'Connor, 1975; 1978), thus change in body temperature (T_b) also parallels change in attentiveness, i.e. as body temperature increase, inattentiveness also increases. Davis et al. (1984) artificially cooled eggs of the Savannah Sparrow and found female attentiveness increased. The reverse was found when the eggs were artificially warmed.

That birds sense nestling T_b and adjust attentiveness was shown in Section 4.4.3. Dipper nestlings with higher T_b were left for longer and cooled more slowly. This was not a result of higher ambient temperatures, since nestling T_b was negatively correlated with ambient temperature, suggesting parents may have additionally invested more in heating the brood when T_a was low. There were insufficient data available to test this in the Dipper, although there was evidence that parents could vary the rate of reheating the brood.

Clark (1984) related the homeothermic capacity of Starling nestlings, measured in the laboratory, to field data on attentiveness patterns. She found that parents altered the proportion of time they brooded young in response to homeothermic capacity of nestlings rather than age or brood-size, per se.

Johnson & Best (1982) found the amount of brooding in the Gray Catbird (Dumtella carolinensis), was negatively correlated with nestling age, brood-size and ambient temperature (T_a). Alternatively parents could reheat the brood for longer but not at an increased rate. Davis et al. (1984) found that attentive periods lengthened on cool days in incubating Savannah Sparrows, lending support to this view. An alternative explanation of prolonged attentiveness may be that by having a few long attentive periods, particularly on cool days, adults may reduce their reheating costs, as well as obtaining shelter in the nest. Two other pieces of evidence lend support to the view that parent birds judge egg and nestling temperature and adjust attentiveness accordingly. Firstly it has been found that for the normal development of embryos, eggs must be maintained above a threshold temperature of about 25°C (Kendeigh et al., 1977). Sensory perception of egg temperature would therefore be selected for in order to avoid loss of the clutch through chilling. Morton & Pereyc (1985) found that eggs were kept above 25°C for 92.2% of daylight hours, and 99.9% of the night-time in the Dusky Flycatcher (Empidonax oberholseri). Secondly, ambient temperature does not parallel the progressive change in brooding behaviour of nestlings as they get older, suggesting the relationship between attentiveness and T_a observed in some species (e.g. Johnson & Best, 1982) is an indirect one, and more likely sensed through egg/nestling temperature.

There is some evidence that adjustment of attentiveness in response to nestling/egg temperature is only part of the explanation of proximate causes of attentiveness in incubating/brooding birds. Clark (1984) found that brooding still occurred in Starlings in which the nest box was heated to regulate nestling thermoregulation costs. Female Dippers did not alter their attentiveness patterns, or reheat nestlings at different rates when males were removed despite an inferred additional cost to the female (Section 4.4.6). Davis et al. found that Savannah Sparrows continued to incubate even when egg temperature is held at 40°C (see earlier this Section) and implied that other factors might play a rôle. Haftorn (1981) suggests that incubating birds have a natural rhythm of attentiveness which can only be adjusted within certain limits in response to ambient conditions. One possible cause of this rhythm may be an alternation between the drive to incubate (or brood) and the drive to self-feed (Kendeigh, 1952). This is broadly similar to hypothesis (3) (see earlier this Section). Wittenberger (1982), however, found that female Bobolinks (Dolichonyx oryzivorous) actually increased their brooding of nestlings when food was scarce and weather was poor, presumably at the expense of self-maintenance and at odds with Kendeigh (1952).

Jones (1985) found that female Swallows returned to incubate earlier than predicted from considerations of maximizing net energy gain, suggesting that brooding to a degree took precedence over self maintenance.

In general, there is little support for the view that the brooding adult's hunger level is the primary proximate cause of inattentiveness, although the hypothesis is intuitively attractive.

Hypothesis (2) (earlier this Section) can hardly apply to incubating birds, in which attentiveness rhythms have been proposed (Davis et al., 1984; Haftorn, 1981). Johnson & Best (1982) suggest that in Gray Catbird, female attentiveness may be reduced in larger broods because of the higher total energy demand of the brood. Larger broods, however, effectively thermoregulate sooner, and so their data are also consistent with hypothesis (1).

Clark (1984) was able to demonstrate that Starling nestlings in heated and unheated nest boxes did not receive different frequencies of feeding visits, despite inferred differences in nestling hunger level due to the reduced energy demand of young in heated nest boxes. Dipper females were able to compensate for the absence of experimentally removed males when feeding young (Section 4.4.6) by increasing their feeding rate to the nestlings without affecting attentiveness patterns, at least in the short term.

To summarise it seems likely that the proximate causes regulating attentiveness in incubating birds is carried through to the brooding phase. This is supported by evidence of attentiveness adjustment in response to both nestling and egg temperature, and the lack of evidence for nestling food demand *per se* as an important factor. The latter would be obviously inapplicable to attentiveness in incubating birds lending further support to this view. Evidence for an internal attentiveness rhythm as suggested for incubating birds is at present lacking for the brooding phase, although it is implied by some of the data discussed. Yet further work is needed to identify the driving mechanism of any attentiveness rhythm, before brooding adult hunger level is dismissed as a possible candidate.

5.4.2 Factors regulating optimal inattentiveness in the Dipper

Both the 'minimal nestling temperature' model (MNT) and the 'maximal brooding time' model (MBT) (see earlier this Section) predict that parents should spend longer periods away from the young (a) as the nestlings get older, (b) in larger brood-sizes, due to the earlier onset of effective thermoregulation, and (c) when ambient temperatures are high, since this will affect nestling T_b (Section 5.4.1). Whilst away parents should seek to maximize net energy gain in accordance with the model proposed by Jones (1985) (see Section 2.4.3(a)). Female attentiveness did show a positive relationship with nestling age, brood-size and T_a (Section 4.4.3), although the relationship with brood-size was not significant when considered alone, suggesting it to be less important than nestling age. Nestling age was the most significant factor influencing cooling rate in Dipper nestlings (Section 4.4.3), followed by brood-size and the temperature difference between nestlings (T_b) and T_a.

The two models differ in their predictions of how female inattentiveness should be related to the minimal nestling body temperature (T_{bmin}) (Section 2.4.3). The MNT model predicts attentiveness to be independent of T_{bmin}, whilst the MBT model predicts a negative correlation between inattentiveness and T_{bmin}. Figure 5.3 shows T_{bmin} in relation to duration of the bouts of inattentiveness in the Dipper. There is no significant relationship ($F = 3.26$, df 1,33, ns) suggesting MNT to be a more realistic model, though the evidence is weak. The variance in T_{bmin} (6.76) is however greater than might have been expected if parents were staying away as long as possible until nestlings had cooled to a theoretical minimal threshold temperature. This threshold temperature may be similar to that suggested for eggs, approximately 25.0°C (Kendeigh et al., 1977). Figure 5.3 shows that in all but one case nestling T_{bmin} remained greater than 25.0°C, implying the presence of some threshold temperature. Nonetheless, parent birds appear to be returning to brood much earlier than predicted by the model, i.e. at values of T_{bmin} much greater than 25.0°C. Indeed the mean T_{bmin} was found to be 31.4 ± 2.6°C. There are several possible explanations for parents returning before the presumed minimal threshold temperature is reached. The time taken for a female Dipper to maximize net energy gain (Jones, 1985) may be shorter than

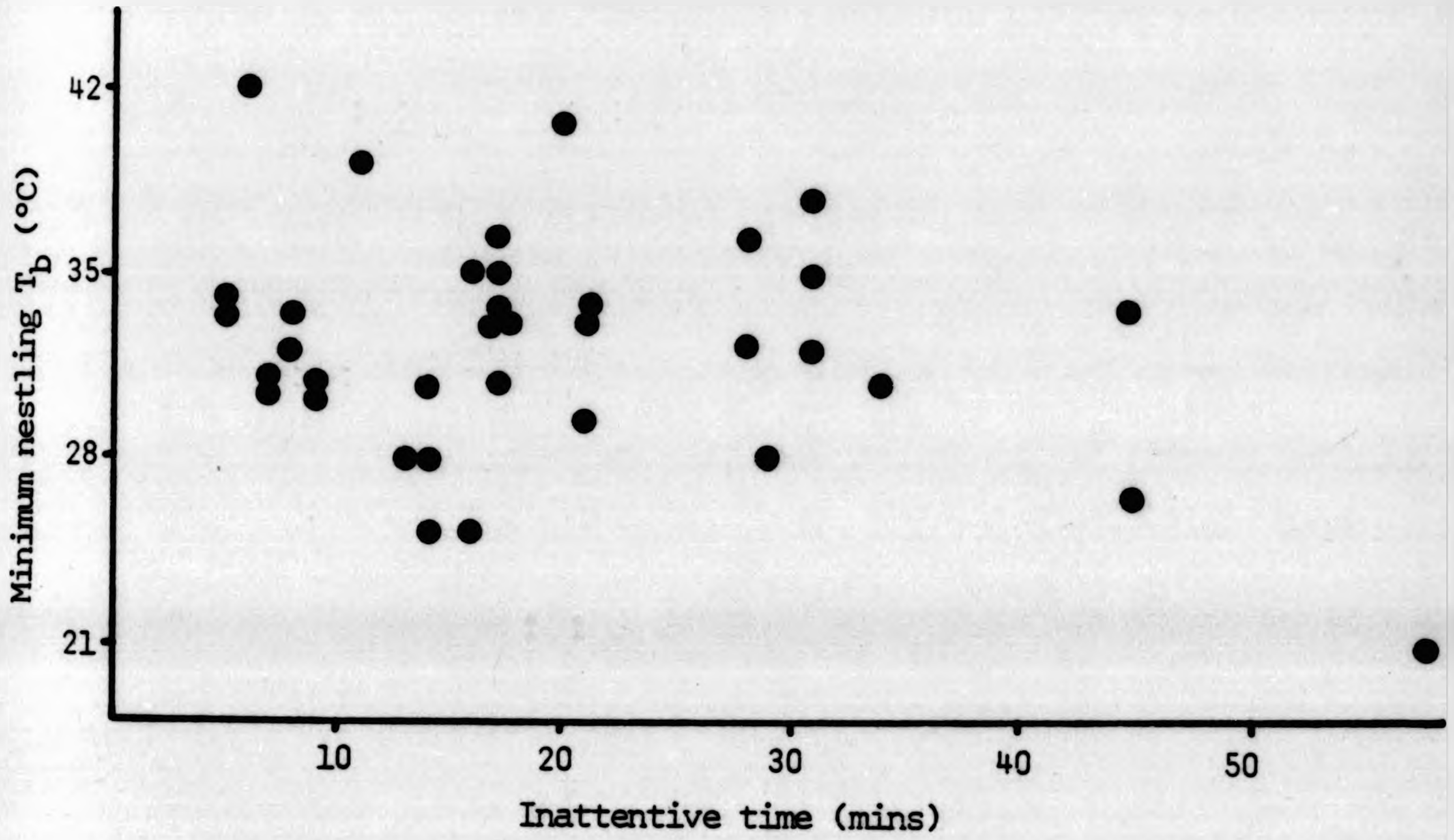


Figure 5.3: Minimal nestling body temperature (T_{bmin}) as a function of female inattentive time in the Dipper.

the time taken for nestlings to cool to minimal threshold temperature. Parents may therefore return earlier than expected. There are several reasons why this time is likely to be shorter in the Dipper. Firstly, the Dipper's food supply is predictable, birds often returning to the same feeding site for long periods during nestling rearing (pers.obs.). Secondly, Dipper foraging is likely to be less costly than the aerial foraging of Swallows, upon which Jones (1985) based his (79) net energy gain model. Thirdly, Dipper nests are well insulated, which may reduce brooding/incubation costs below those of the Swallow, although the sheltered position of many Swallow nests (for example in farm buildings) may offset some of the difference. Finally as nestlings get older the brooding cost to the female decreases due to partial homeothermy of the brood (Section 4.4.6), and hence the time needed to regain energy used for brooding will also decrease.

Another explanation may be that parent birds are not sensing nestling T_b *per se* to decide adjustments in inattentiveness, but the amount of energy they have to invest in reheating the brood at a given time. This will itself partly depend on nestling T_b prior to reheating (Section 4.4.4), and will partly be responsible for changes in T_b subsequent to reheating. Parents would still be able to assess nestling homeothermic capacity even though nestlings 'switch off' thermogenesis during brooding. The difference between adult T_b and nestling T_b will be a function of nestling homeothermy, and would affect reheating costs. The large variation in

T_{bmin} may thus represent the inaccuracy with which T_b reflects reheating costs.

An alternative explanation may be that the MNT model and the MBT model are not mutually exclusive, but represent two aspects of a more complex decision making model. Parent birds may therefore have their maximum inattentive period set by considerations of minimal nestling temperature, but as the brood becomes homeothermic and this maximum period increases, indirect parental cost (e.g. travelling cost, Section 2.4.3(c)) also increases. The optimal inattentive period with respect to net energy gain will therefore decrease. Since nestlings are left to cool for less time than predicted by considerations of a minimal threshold temperature, their T_{bmin} will be higher than this minimal nestling temperature threshold. There are several lines of support for this hypothesis in the Dipper.

(i) Nestlings with higher T_b (and hence more advanced homeothermy) are left unattended for longer (see previous Section);

(ii) Nestlings are however rarely left long enough for body temperature to drop below a theoretical minimum threshold temperature of 25°C based on considerations of egg development;

(iii) Parents often return earlier than $T_{bmin} = 25.0°C$;

(iv) Dipper nestlings appear to switch off their own thermogenesis when the parent bird returns to brood (Section 4.4.4) consistent with the maximal brooding model.

Additional variation in the length of the inattentive period may arise as a result of any attentiveness rhythm (see previous Section), so that birds neither stay away for extremely long periods or extremely short periods, even if ambient conditions dictate that they should. Further experimental work is needed before the mechanism by which adult birds assess nestling homeothermic capacity is fully understood.

5.5 NESTLING ACTIVITY COSTS

5.5.1 A comparison of activity costs in the Dipper and House Martin

Nestling activity costs have often been assumed to be high in the past (Section 2.1.4). Measurements of activity costs in this study, however, have shown this assumption to be incorrect (Sections 4.5, 4.6.3, 4.10.3), the error apparently being due to the non-inclusion of biosynthesis and 'alertness' components in previous energy budgets (Section 4.6).

Nestling energy expenditure on activity (as expressed by % BMR, Figure 4.34) as a function of nestling age follows that presented for the Double Crested Cormorant (Dunn, 1980), and that used in Section 2.1.4, although the absolute values are much smaller. Energy expenditure for nestling competition appears to vary between the species in this study. Table 5.4 shows the proportion of energy expenditure for each nestling activity component as a percentage of the total, for the House Martin data presented earlier (Table 4.36) and Dipper nestlings of a comparable stage of

TABLE 5.4: A comparison of activity costs in the Dipper and House Martin: Proportions of total activity costs

	Dipper activity costs			House Martin activity costs	
	[a]PUC	FUC	MUC	[b]PUC/FUC	[c]HM/Dipper
Proportion of total activity costs (%)					
Defaecation	2.4	2.4	2.4	2.9	x 1.2
Feeding	2.8	2.8	2.8	14.4	x 5.1
Begging	7.3	5.3	6.3	56.7	x 9.0
Movement	87.5	89.5	88.5	26.0	x 0.3

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[a] PUC = Proportionate unit activity cost,
FUC = Fixed unit activity cost,
MUC = Mean unit activity cost (Section 4.6.3(a))

[b] PUC/FUC = activity cost for a 14.9g House Martin, independent of either PUC or FUC models (Section 4.5.1)

[c] House Martin/Dipper MUC estimate

development (see legend, Table 5.4). Movement costs predominate in the Dipper whilst begging costs predominate in the House Martin. It may be that most of the movement costs were associated with jostling to maintain favoured nest positions for feeding, and should hence be regarded as competitive costs in addition to begging. Total competitive costs would then be similar, for the Dipper, 94.8%, and for the House Martin, 82.7%.

Movement was not examined in this study of birds in the field. Reed (1981), however, noted that shifting of nestling position in the Song Sparrow occurred usually during and immediately after a feeding visit, and was in response to a loss of position during acts such as defaecation. A large part of any movement costs was therefore likely to have been included within the begging costs previously measured (Section 4.5.3). Thus whilst there may be a small additional 'movement' component to competitive costs it is unlikely to be dominant, particularly in the House Martin where begging costs were over twice as high as total movement costs.

Both Dippers and House Martins are 'constrained' huddlers (see Section 5.3), and thus may be expected to show similar responses with respect to shifting positions within the nest. If movement costs were associated with this then costs between the two species ought to be similar. House Martins expend nine times more energy begging than the Dipper (based on the mean unit cost model (MUC) (see Section 4.6.3(a)), and five times as much energy feeding. This suggests that feeding frequency in House Martin broods is higher than in Dipper broods. The House Martin broods at the age examined received an average 18 feeds per hour (Table 4.36), whilst the Dipper broods received 9 feeds per hour (Figure 4.29). House Martin energy expenditure on begging and feeding might therefore have been expected to be approximately double that of the Dipper. Table 5.5 shows that total daily activity costs for the House Martin, expressed as % BMR is 1.3-1.6 times that of the Dipper, less than expected from feeding frequency considerations alone. This is probably due to the higher cost of nestling movement in the Dipper (Section 4.5.3), offsetting begging costs in the House Martin. This implies differences between species in competitive energy expenditure, on a per feed or per visit basis. Nonetheless, the range of daily activity costs for the two species (Table 5.5) are broadly similar; 2.9-9.7 % BMR for the Dipper and 5.5-11.0 % BMR for the House Martin. Peak daily activity cost in the Dipper is a little higher, 4.4-12.4 % BMR, whilst total activity cost for the whole nestling period is 3.5-10.4 % BMR, suggesting that an average activity cost of about 8% BMR may be realistic across species. A reduction in nestling activity costs (or indeed of any DEE component cost) may be of direct benefit to nestlings since it would allow more efficient utilization of energy resources and perhaps allow a greater allocation to growth, thus reducing the nestling period. This may also be of benefit to the parents, particularly in larger broods, since activity costs are to some extent dependent on feeding frequency which increases in larger broods (see above).

TABLE 5.5: A comparison of activity costs expressed as % BMR calculated using adult (BMR_{ad} - see legend) and wet energy density corrected BMR equations (BMR_{wed} - see page 190) for the Dipper and House Martin

	Dipper Unit Costs			House Martin Unit Costs
	[a]'Proportionate'	'Fixed'	'Mean'	'Mean'
(i)				
Peak activity cost				
BMR_{ad}	8.3	4.4	6.4	-
BMR_{wed}	12.4	6.3	9.4	-
(ii)				
Total activity cost				
BMR_{ad}	7.3	3.5	5.4	-
BMR_{wed}	10.4	4.9	7.7	-
(iii)				
Activity costs one-quarter of the way through the nestling period				
BMR_{ad}	4.0	2.9	3.5	5.5
BMR_{wed}	9.7	6.7	8.2	11.0

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[a] For explanation of 'proportionate', 'fixed' and 'mean' unit activity costs see page 99.

WED corrections for the House Martin from Bryant & Gardiner, 1979.

This will be discussed in Section 5.7. The question of whether nestlings can and do reduce their activity costs will be dealt with now.

5.5.2 Do nestlings minimize their activity costs?

Reduced sibling rivalry is proposed as one mechanism for utilizing a resource more efficiently by not wasting energy on sibling-sibling competition (Hahn, 1981). A model of reduced sibling rivalry (RSR, Section 2.3) was tested in two ways; directly and indirectly. The direct method involved the measurement of begging behaviour and its associated energetic cost in the House Martin, with changing asynchrony (Section 2.3.4, 4.10). The indirect method involved the measurement of nestling growth to test if reallocation of savings predicted from the model (Section 2.3.4) were reflected in the peak mass of House Martin nestlings (Section 2.3.5, 4.11.1). Both methods showed independently that there was no reduction in sibling rivalry in association with hatching asynchrony, in this species. This may be because these are associated costs with reducing sibling rivalry which outweigh potential benefits through small energy savings, or because reduced sibling rivalry is independent of hatching asynchrony. This will be discussed in detail in Section 5.10.

The begging behaviour of House Martins in the field was found to be very similar to laboratory studies of begging behaviour in the Zebra Finch (Section 4.9). Since it was however possible to examine Zebra Finch behaviour in more detail, this will be discussed with regard to reducing begging costs in the next Section.

5.6 REDUCING BEGGING COSTS: A DETAILED ANALYSIS OF THE ZEBRA FINCH

Zebra Finch begging behaviour may be divided into three sections; pre-feed behaviour, feed behaviour and post-feed behaviour. These will be discussed in turn.

5.6.1 Behaviour of Zebra Finch nestlings prior to a feed being offered

If nestlings simply beg for a duration (Giving-up time = GUT) directly proportional to their hunger level, then one could predict that this GUT should decrease as satiation is neared, or by analogy for the next feed, and that this reduction ought to be proportional to the size of that feed. However, GUT does not vary for either feed size when compared before and after a feed, neither is it correlated with hunger level as measured by crop-score (Table 4.28). Comparison of high and low crop-scores also show no such relationship. Whilst it is true that a single feed is unlikely to satiate a nestling it is also probable that even if a chick were sensitive to such small changes in hunger level, a flexible response with respect to GUT would be of limited value.

In the artificial laboratory system, nestlings were not offered food until they had given up begging. GUT thus represents the maximum time a nestling is prepared to spend begging without getting a reward. In practice the parent usually spends a few seconds deciding which chick to feed (Parental Decision Time = PDT), and chicks rarely reach their giving up time before this. Since GUT is effectively 'cut short' by the parent, chicks will gain no advantage in a flexible reduction of GUT. A fixed cut off point is of advantage though when one considers begging without parents being present at the nest. In House Martins the mean number of begging events for each feeding visit is 2.72 ± 0.44 (n = 14) and in Dippers 1.97 ± 0.81 (n = 6), where n is the mean taken over each day's observations. Since PDT is much less than GUT the question arises as to why GUT is not shorter. Nestlings sometimes refuse food offered by a parent, in which case it is usually offered to another nestling thus effectively increasing PDT. Since parents only feed young which are begging, a higher GUT might therefore be regarded as an example of nestlings 'bet-hedging'. An alternative explanation may be that nestlings have to learn to reduce GUT by experience. A non-significant regression of GUT on age, however, suggests no such effect (Section 4.9.2).

In Zebra Finches GUT remains fixed at approximately 8.5 seconds and there is no difference between brood-sizes (i.e. one and two), whereas an increased investment in begging prior to feeding might have been expected with brood-size 2 since the number of siblings competing is increasing.

Once food has been allocated to an individual, nestlings may be conveniently divided into two categories; fed and unfed. Begging behaviour differs in these two categories.

5.6.2 Behaviour of nestlings receiving food

Handling time (HT) as expected varied with age (Figures 4.39, 4.41, 4.42), but surprisingly HT when F = 0 was greater than when F = 1. This might be explained by the artificial nature of the F = 0 treatment in which birds may have continued 'handling' the dummy bill, confused by the expectation of a reward that never came. In the same way that nestlings beg for a certain amount of time before giving up (GUT) when they are not offered a feed, HT when F = 0 is the equivalent time for handling without reward; a 'handling' GUT. Nestlings in pairs took longer over handling food than those alone. A possible explanation of this may be interference caused by either parental distraction through conflicting vocalisation cues by the nestling sibs, or by jostling by the latter. The mechanism would appear to be nestling mediated however, (since parental distraction was controlled for in the experiments by having an artificial parent), and may be viewed as analogous to increased vigilance observed in some birds when foraging in the presence of kleptoparasitic species. In this case, increased vigilance results in less efficient foraging behaviour. There is no evidence to suggest that unfed nestlings respond differentially to the variation in HT of their fed sibs (see below). A fixed response, in terms of competitive interference through begging behaviour, is not however inconsistent with the above hypothesis, provided that unfed nestlings beg for a sufficiently long time, and that this always exceeds HT. For a mechanism of interference to operate it is not necessary for unfed nestlings to actually intimidate their fed sib, since it is the fed sibs expectation of events that will be likely to underly its behaviour.

5.6.3 Behaviour of nestlings not receiving food

A number of hypotheses may be put forward to predict how nestlings not receiving food should behave once the parent has allocated food to one of their siblings.

Hypothesis 1: Stop begging immediately, since wasteful expenditure of energy without possibility of returns is disadvantageous;

Hypothesis 2: Continue begging until fed or until the parent leaves the nest;

Hypothesis 3: Continue begging until a threshold point is reached which itself is fixed by considerations of position within the brood hierarchy, or the Reduced Sibling Rivalry hypothesis (Section 2.3);

Hypothesis 4: Continue begging for a variable period in direct response to the behaviour of the fed nestling;

Hypothesis 5: Continue begging for as long as is energetically profitable, i.e. until expectation of benefit = cost of begging for that benefit;

Hypothesis 6: Continue begging for a fixed time period before giving up.

These six hypotheses will be considered in turn.

Hypothesis 1:

This hypothesis does not hold widely since in all but two cases (n = 53) nestlings begged for much longer when a sibling was being fed ($\bar{x} = 24.5 \pm 1.54$s). The degree to which begging was elevated, does not vary with age, crop-score, mass of unfed nestling or relative difference in body mass (RDBM).

The occurrence of continued begging by an unfed nestling after its sibling has been fed, and its elevated level both require explanation. Firstly, continued begging will ensure that the parent receives the correct cues regarding the hunger level of the brood (see above). Secondly, Zebra Finches regularly split the food brought to the nest, and to dependent fledged young between different young; up to ten times in the latter case (pers.obs.). Zebra Finches are therefore regarded as 'splitters' as opposed to 'lumpers', which do not generally split between individuals the food brought to the young (e.g. Great Tit).

Hypothesis 2:

Continuing to beg until fed or until the parent leaves the nest would be an energetically more expensive strategy than hypothesis 1. Since nestling handling time varies, the amount of time that a parent spends at the nest during a feeding bout will also vary. There is a reasonably fixed elevated giving up time (EGUT, Section 4.9.2). However, suggesting that nestlings do not continue to beg as expected by this hypothesis.

Hypothesis 3:

The reduced sibling rivalry hypothesis (Section 2.3) predicts that competitive energy expenditure (CEE, in this case the amount of begging), should decrease to a minimum and then increase again (Figure 2.10) with increasing relative size difference between nestlings. The relative difference in body mass (RDBM) was calculated for pairs of Zebra Finch nestlings.

The degree of elevation of begging (EGUT/GUT) is shown as a function of RDBM in Table 4.30, and there is no evidence to support hypothesis 3.

Hypothesis 4:

Parents only offer food regularly to nestlings that beg for it. The time taken by a parent in deciding which nestling to feed (PDT) is usually short (about 1 second or less (pers.obs.) on the Dipper and House Martin). Handling time, however, is variable in Zebra Finch nestlings (notably with respect to age). An unfed nestling which stopped begging once the parent had allocated the first food 'split' to its sibling and then waited until the feed had finished before starting to beg again, as predicted by this hypothesis, would run the risk of being too slow to react to the cessation of feeding, and not be begging during the short PDT. This would be a particular problem for young nestlings with no or limited visual cues and possible conflicting auditory cues from unfed siblings. The relatively constant values for EGUT lend support to this view and are inconsistent with hypothesis 4.

Hypothesis 5:

The relatively constant values of the elevated giving up time are consistent with this hypothesis provided that the mean 'split' energy content is reasonably constant. The fixed EGUT observed would then be equal to the energetic equivalent (taking into account assimilation efficiency) of the mean 'split' mass. Whilst it was not possible to test this directly, it seems likely that nestlings would have evolved to maximise net energy gain at each feed. If feed ('split') size was indeed relatively constant then a reduction in begging costs would be the logical mechanism for bringing this about, yet there is no evidence of a reduction in EGUT in relation to any of the parameters examined (see Section 4.9.2). Similarly, there is no evidence to suggest that the energy content of a particular load size brought to the nest is constant (Carlson, 1983; Carlson & Moreno, 1983; Turner, 1980).

Hypothesis 6:

The fixed nature of EGUT (see above) and the apparent inability of nestlings to reduce their begging based on cues from their fed siblings (see above, and Section 4.9.2) are consistent with this hypothesis. Unfed Zebra Finch nestlings therefore beg for a fixed time period before giving up.

5.6.4 The behaviour of nestlings after having received food

As shown previously, nestlings began to beg again immediately after receiving a feed, and this after-begging decreased with age in a similar way to handling time. Thus nestlings that have been fed reduce their contribution to the begging of the brood. Two points, however, are worthy of comment. Firstly, why did the fed nestling not cease begging altogether? Secondly, why does after-begging decrease in a similar way to handling time with age? It may be that most information on the mean hunger level of the brood is given by nestlings during and after a feed. For example, since parental decision time before a feed is short (see above), the amount of information that a parent would receive in this time alone may be small. An alternative or complementary explanation could be that since Zebra Finches split food between young at feeds, after-begging could be a means of securing an extra feed in a similar way to EGUT.

Neither of these explanations however explain the pattern of change of after-begging with age. Suppose a nestling receives a feed, it then begins after-begging, whilst one of its siblings receives a second 'split' of the food brought by the parent. Since after-begging is on average of longer duration than handling time (Section 4.9.2), the first fed nestling will be assured of begging when the parent offers the third 'split' as will those nestlings which elevate their begging (EGUT). However, if the parent were to leave without offering a second or third 'split', or does not offer it to the after-begging nestling, then it would have wasted less energy in begging than its elevated begging sibs (Section 4.9.2). The change in after-begging with age may therefore be explained by the fed sibling adjusting its begging effort to a little over the duration of its own handling time. It therefore seems to use its own experience of handling time to estimate the handling time of its siblings.

There is some evidence that Zebra Finch nestlings may make decisions about how long to after-beg not only on the basis of their own experience of handling time, but possibly with respect to profitability of food ingested. There appear to be two levels of after-begging (Section 4.9.2) with little gradation, corresponding to high and low food profitabilities offered i.e. F = 0 and F = 1. This appears to hold for single nestlings, but pairs of nestlings after-beg at the higher level only.

House Martins also appear to adjust after-begging in response to their experience of handling time (Section 4.10.2), and yet are not generally regarded as load 'splitters'. They do, however, split boluses brought to the young early in the growth period but this ceases after about a week (D. M. Bryant, pers.com.), yet older young still after-beg. It is likely therefore that a component of the after-begging behaviour is to contribute to communication of the mean brood hunger level to the parent.

5.7 THE DAILY ENERGY BUDGET: POTENTIAL ERRORS IN ESTIMATING DAILY ENERGY EXPENDITURE BY THE TAL METHOD

The daily energy budget (DEB) of the Dipper was constructed from laboratory and field data, and from published data for components not directly measured (Section 4.6). Comparisons of a number of estimates of daily energy expenditure (DEE), based on different models of activity, biosynthesis and 'resting' metabolic costs (Section 4.6.3, 4.6.5) all showed good agreement with the energy expenditure of 18 day old Dipper nestlings measured directly in the field (FEE), using the doubly-labelled water method (Section 4.7).

Since FEE was however only measured at one nestling age, the accuracy of the TAL method in estimating DEE for the whole nestling period should be considered. In addition, assumptions regarding DEB component costs vary greatly between studies (see later this section for nestling DEB references). To what extent errors in these assumptions affect the accuracy of predicting DEB is not known. This will now be examined for the Dipper, with reference to the total current nestling DEB data available for altricial birds.

Kendeigh et al. (1977) constructed a predictive equation for calculating the nestling DEB. Kendeigh et al. used the term DEB to represent daily metabolised energy. In subsequent discussion however DEB will be used for broad discussion of the nestling's daily energy budget in terms of its components and DME will be used specifically to discuss the daily energy expenditure (DEE) plus that energy accumulated as tissue during growth (P) (see also Section 4.6).

The equation presented by Kendeigh et al. was based on only two species; the House Sparrow, Passer domesticus (using data from Blem, 1975) and the Black-bellied Tree Duck, Dendrocygna autumnalis (using data from Cain, 1976). Drent & Daan (1980) subsequently published data for eight altricial species (including Blem's data for the House Sparrow), but provide no equation for these data. The original Kendeigh equation is:-

$$\text{DME (kJ.d}^{-1}\text{)} = 5.660 \text{ mass (g)}^{0.814} \qquad \text{eqn. 5.1}$$

Data are now available for a total of fifteen altricial and semi-altricial species, and these are presented in Figure 5.4. Some of these data include thermoregulation (TR) costs, others do not, and some are not specified. Two equations were

Figure 5.4: The relationship of daily metabolised energy (DME) to nestling mass for 15 altricial species. Symbols are as follows:-

(i) Nestling mass 0-50 grams

† △ Savannah Sparrow, *Passerculus sandwichensis* (William & Prints, 1986)

† ▲ Red-winged Blackbird, *Agelaius phoeniceus* (Fiala & Congdon, 1983)

▽ Willow Warbler, *Phylloscopus trochilus* (Tiainen, 1983)

* ▼ White-bellied Swiftlet, *Collocalia esculenta* (Bryant & Hails, 1983)

* ○ House Sparrow, *Passer domesticus* (Blem, 1975)

● House Martin, *Delichon urbica* (Bryant & Gardiner, 1979)

* □ Pacific Swallow, *Hirundo tahitica* (Bryant & Hails, 1983)

* ■ Blue-throated Bee-Eater, *Merops viridis* Bryant & Hails, 1983)

†† ◆ Red-backed Shrike, *Lanius collurio* (Diehl & Myrcha, 1973)

(ii) Nestling mass 50-100 grams

† ◇ Dipper, *Cinclus cinclus* (this study)

▼ Starling, *Sturnus vulgaris* (Westerterp, 1973)

(iii) Nestling mass 100+ grams

□ Herring Gull, *Larus argentatus* (Dunn, 1980)

● Double Crested Cormorant, *Phalacrocorax auritus* (Dunn, 1980)

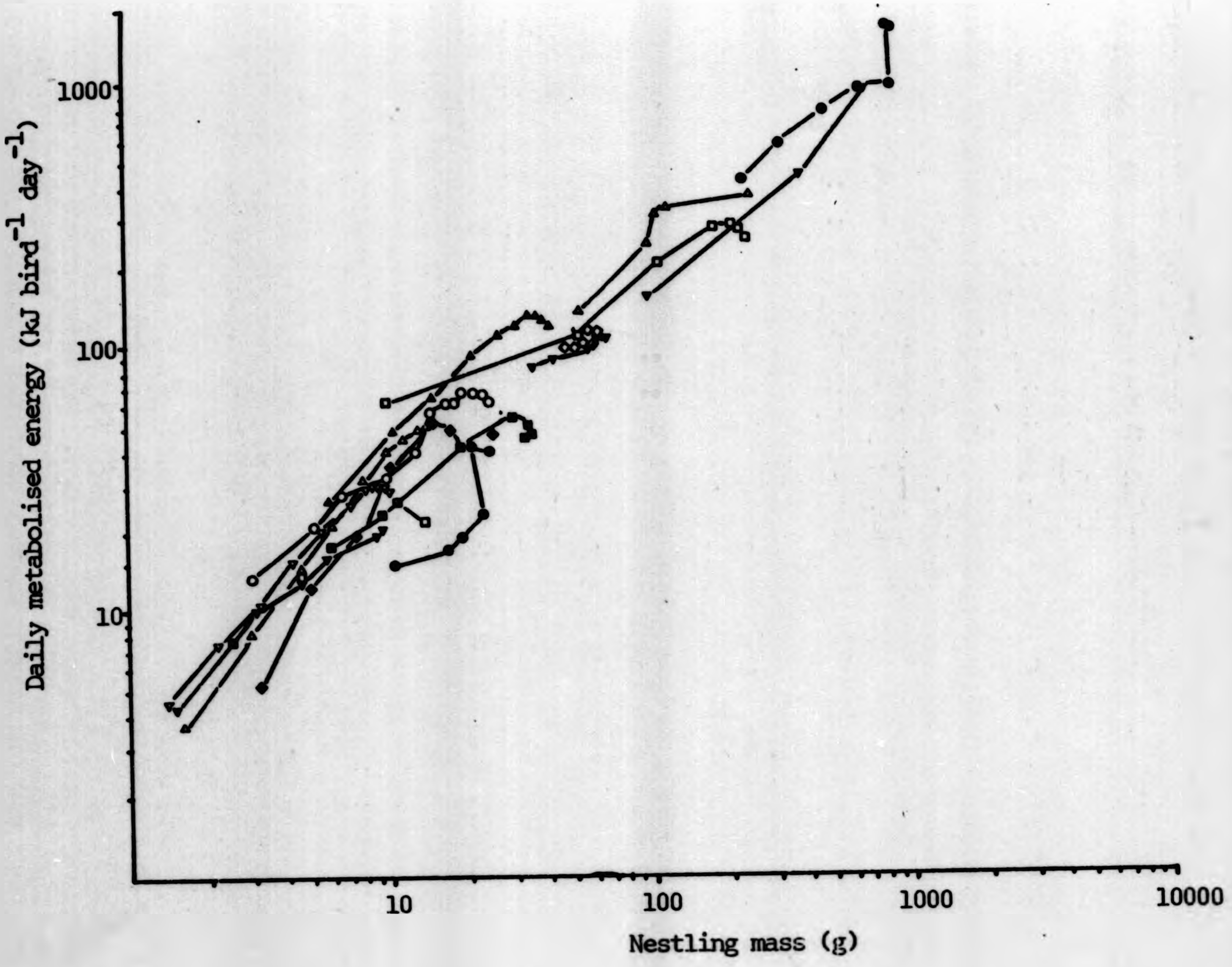
†† ▼ Pigeon Guillemot, *Cephus columba* (Koelink, 1972)

△ Long-eared Owl, *Asio otus* (Wijnandts, 1984)

* Excludes thermoregulation

† Measured using doubly-labelled water

†† Not known if thermoregulation costs included


Daily metabolised energy (kJ bird^{-1} day^{-1})
1000
100
10
10
100
1000
10000
Nestling mass (g)

therefore constructed. One only used data for species in which TR costs were known to have been included. The other included data for those studies in which TR costs were known to have been - excluded by the experimental design used; subtracted from DME during this analysis using TR costs presented in the original published material; or unimportant because of high ambient temperature (e.g. Bryant et al., 1983) (see legend, Figure 5.4, for those species included in each analysis). The two equations are:-

$$\mathrm{DME} = 4.256\ \mathrm{mass}^{0.825} \qquad r^2 = 93.8 \qquad \text{eqn. 5.2}$$

$$\mathrm{DME\text{-}TR} = 4.055\ \mathrm{mass}^{0.811} \qquad r^2 = 97.1 \qquad \text{eqn. 5.3}$$

(units are as in equation 5.1, as are all subsequent units used).

Less of the variance about the regression line is explained by mass in equation 5.2 suggesting variation in TR costs may have only a small effect on estimates of DME. Either brood-size (range 1-4) or environmental conditions, or both, however, varied in the studies examined and so greater error in DME estimate is to be expected on these grounds alone; the error is however small (r^2 of 94 and 97 respectively). Equation 5.3 resembles Kendeigh et al. (1977) original equation (though the intercept is somewhat lower) which also did not include TR costs. Inclusion of three species in which it was not known to what extent (if at all) TR costs had been included in DME estimates ($\mathrm{DME}_{\mathrm{additional}}$) (Diehl & Myrcha, 1973; Koelink, 1972; Kushlan, 1977) had little effect on the goodness of fit of the equations (see below), but increased estimates of slope and reduced estimates of intercept in both cases:-

$$DME_{additional} = 3.199\ mass^{0.888} \quad r^2 = 94.6 \quad \text{eqn. } 5.4$$

$$DME\text{-}TR_{additional} = 3.793\ mass^{0.837} \quad r^2 = 96.5 \quad \text{eqn. } 5.5$$

Equations 5.2 and 5.3 will be used in subsequent discussion since the nature of the data are known. Equation 5.2 was used to predict DME for Dipper nestlings in which FEE had been measured (Section 4.7); this is presented in Table 5.6. The equation tended to overestimate DME for the Dipper by an average 5% for eighteen day old young, even though the Dipper DEB was calculated using an RQ of 0.86 (Section 4.6, 4.7) whilst equation 5.2 was calculated from data using RQ's of 0.72-0.75. The overestimate is likely to be due to the very small growth costs in mature nestlings (Section 4.6.4) which results in a levelling off of log DME as a function of log mass (see Figure 5.4 also). In other words, DME of older nestlings tended to deviate from the linear relationship described by the equations.

Allometric equations were calculated for Dipper DME, using the various models previously discussed (Section 4.6), for comparison with equation 5.2, in order to assess the possible errors in each model. These equations are plotted as the log-log relationship of nestling DME versus mass in Figures 5.5-5.7. The effect of each component on the estimate of Dipper DME (i.e. the similarity between 'observed' DME and

TABLE 5.6: Predicted and observed DME for eighteen day old Dipper nestlings

	Females					Males			Mean ± SD sexes combined
	1	2	3	4	5	1	2	3	
Nestling mass (g)	58.6	49.6	54.0	54.9	58.4	64.5	54.9	57.4	56.5 ± 4.3
Predicted DME[a] (kJ day^{-1})	116.2	100.6	108.3	109.8	115.9	126.3	109.8	114.2	112.6 ± 7.5
Observed DME[b] (kJ day^{-1})	116.8	99.14	96.8	97.3	95.9	113.2	111.3	127.2	107.2 ± 11.6
Observed/ predicted percentage	100.5	98.5	89.4	88.6	82.7	89.6	101.4	111.4	95.3 ± 9.3

[a] Calculated from equation 5.2

[b] FEE (Table 4.26) + 2.84 kJ (i.e. P for 18 day old nestlings, Table 4.23)

'expected' DME curves, the latter calculated from equation 5.2) is discussed below.

5.7.1 Thermoregulation (TR)

Figure 5.5 shows Dipper DME (dashed line) calculated with TR costs included (Figure 5.5(a)) and excluded (Figure 5.5(b)), compared with equations 5.2 and equation 5.3 (solid lines) respectively. If TR costs have a large effect on the accuracy of predicting DME, then observed DME would be expected to more closely resemble equation 5.3 (Figure 5.5(b)), whilst if TR costs were not important no such relationship would be expected. Both figures show that Dipper DME is progressively higher in smaller nestlings, compared with that expected. Since the magnitude of the observed overestimate is similar in both cases (i.e. with or without TR costs included), TR appears to be unimportant in affecting the accuracy of DME estimates. Further support for this view is discussed in Section 5.8. Both Dipper equations do however provide reasonable estimates of DME in nestlings of around 50.0-65.0 grams, thus confirming the conclusions in Section 4.7.

5.7.2 Activity and Biosynthesis

Figure 5.6(a) shows Dipper DME calculated using a fixed unit cost (FUC) activity model (Section 4.6.3(a)) and three models for calculating biosynthesis costs; Model 3 (after Wijnandts, Section 4.6.5(c), curve A), Model 2 (after Greenalgh et al., Section 4.6.5(b), curve B), and Model 1 (after Ricklefs, Section 4.6.5(a), curve C). Figure 5.6(b) shows the corresponding biosynthesis models but using a

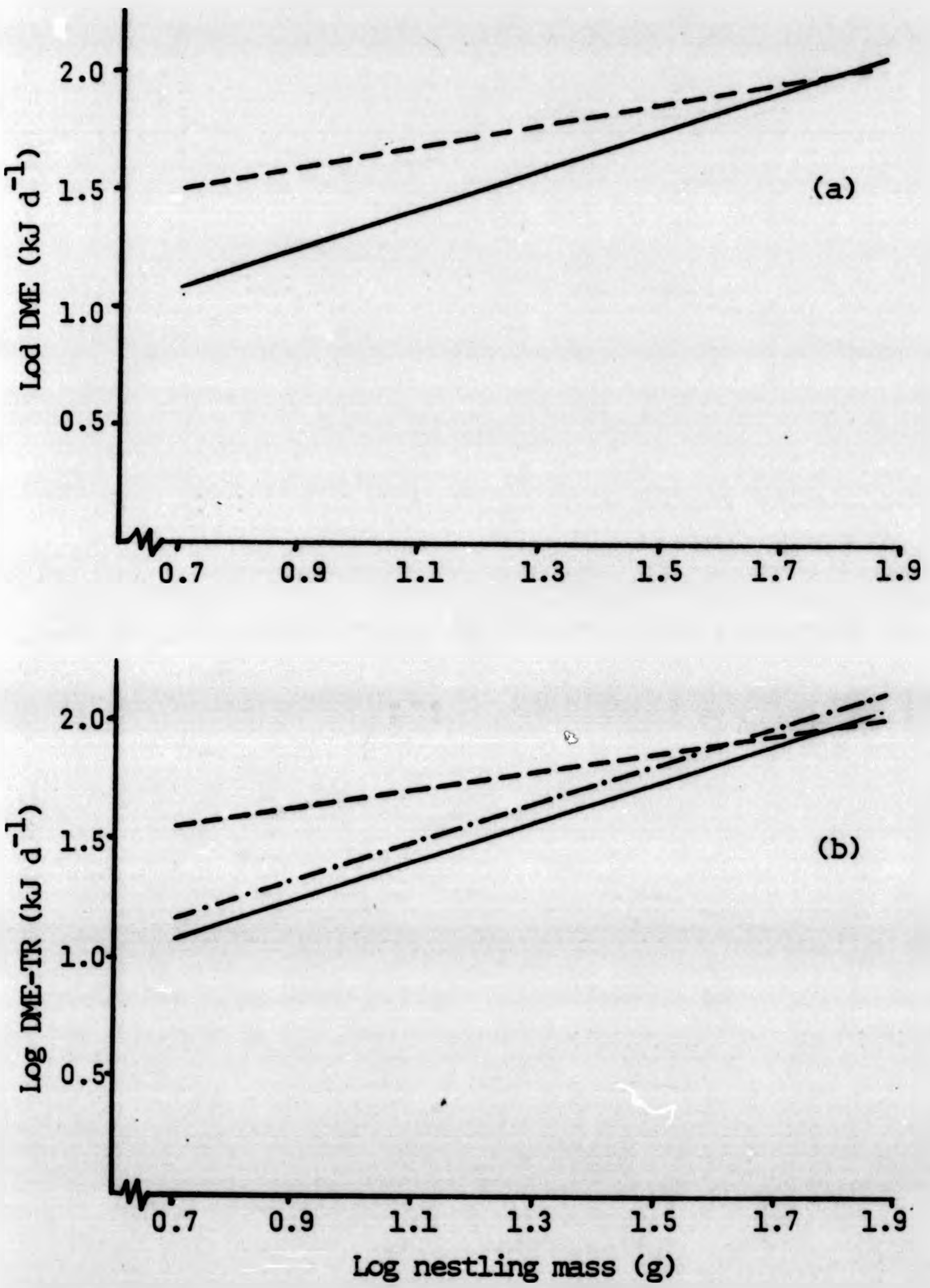


Figure 5.5:

(a) Daily metabolised energy including TR costs as a function of nestling mass

(b) Daily metabolised energy excluding TR costs as a function of nestling mass

Dipper – – – –

15 altricial species ————

Kendeigh et al., 1977 —·—·—·—

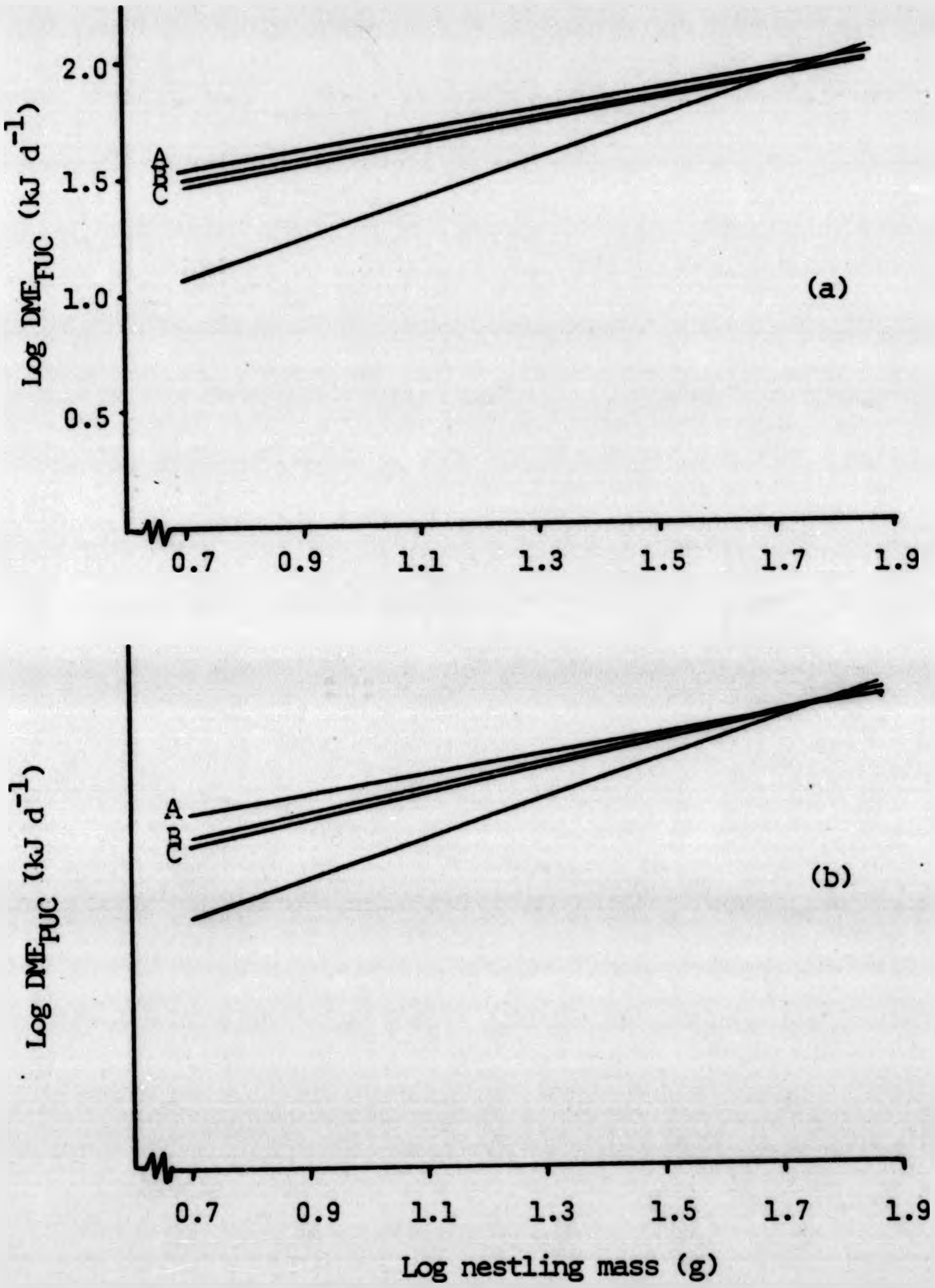


Figure 5.6: Daily metabolised energy as a function of nestling mass.

(a) FUC activity model, and three biosynthesis models (see below)

(b) PUC activity model, and three biosynthesis models (see below)

A = Biosynthesis model 3)
B = Biosynthesis model 2) see text
C = Biosynthesis model 1)

proportionate unit cost (PUC) activity model (Section 4.6.3(a)). Using the FUC model, the various estimates of biosynthesis costs are very similar and have little effect in reducing the error in observed DME estimates of younger nestlings. The PUC model and biosynthesis model 3 (curve A, Figure 5.6(b)) is essentially the same as a mean of the FUC/biosynthesis curves presented in Figure 5.6(a). Biosynthesis models 2 and 1 slightly reduce the error in observed DME, but insufficiently to explain all of the error. Both activity and biosynthesis estimates therefore have little effect on estimates of DME.

5.7.3 Growth

Growth energy (strictly P; see Section 4.6.4) was measured accurately by carcass analysis (Section 4.2). Large over-estimates of this component are therefore unlikely. Some error may arise in measurements on very small nestlings due to the tiny size of individual body components and the possibility of some water uptake by freeze-dried tissue at weighing (see Section 3.1.3). This is only likely to be a source of error in nestlings of less than three days old. In older nestlings all body components were of sufficient size for water uptake by the tissue to be negligible. Growth is therefore unlikely to contribute much to errors in calculating DME.

5.7.4 BMR and 'alertness'

The single component which contributes most to the DEB is BMR (in the Dipper, 49.3%; based on Aschoff & Pohl, 1970) and may be regarded as a suitable candidate for contributing to the error in observed DME estimates. 'Alertness', the day-time additional 'resting' metabolism cost (Section 4.6.6) contributes 15.6% to the total Dipper DME, whilst all other components together account for only 35.0% of total DME (Section 4.6). Metabolism in nestlings may be over-estimated because of differences in body composition between adults (on which the Aschoff & Pohl equations are based, Section 2.1.1) and nestlings (Section 4.2). The proportion of metabolising tissue is lower in nestlings than in adult birds of similar mass, due partly to the greater water content of nestlings (Sections 4.2.1, 4.2.4). There are also differences in energy density of nestling tissue compared to that of adults (Section 4.2.1). Both energy density and the proportion of metabolising tissue (as indicated by dry mass, or lean dry mass) increase as nestlings grow, approaching adult levels in older nestlings (Section 4.2). This is consistent with the trend in the error noted when estimating DME in the Dipper. Increases in mass specific metabolism have been found for a number of nestling species (Mertens, 1977(a); Reyer & Westerterp, 1985; Wijnandts, 1984; Williams & Prints, 1985), though Myrcha et al. (1973) found it decreased in the House Sparrow. Other studies have found no detectable trend in mass specific metabolism (Marsh, 1979; O'Connor, 1975(c)). Given, however, the mass specific differences in body composition found in the majority of nestling energetics studies (Section 4.2, Appendix I), mass specific metabolism differences between nestlings (particularly very young nestlings) and adults are likely to be the rule. Wet energy density (WED) and lean dry mass (LDM) change with age in the Dipper as described by the equations in Section 4.2.1. Since BMR, 'alertness' and thermoregulation were calculated from equations for adult birds, the ratio of either WED or LDM in the nestling at a given age to that of the adult may be used to take into account the lower proportion of metabolising tissue in nestlings, and thereby adjust these components of the energy budget to more realistic nestling values by, for example:-

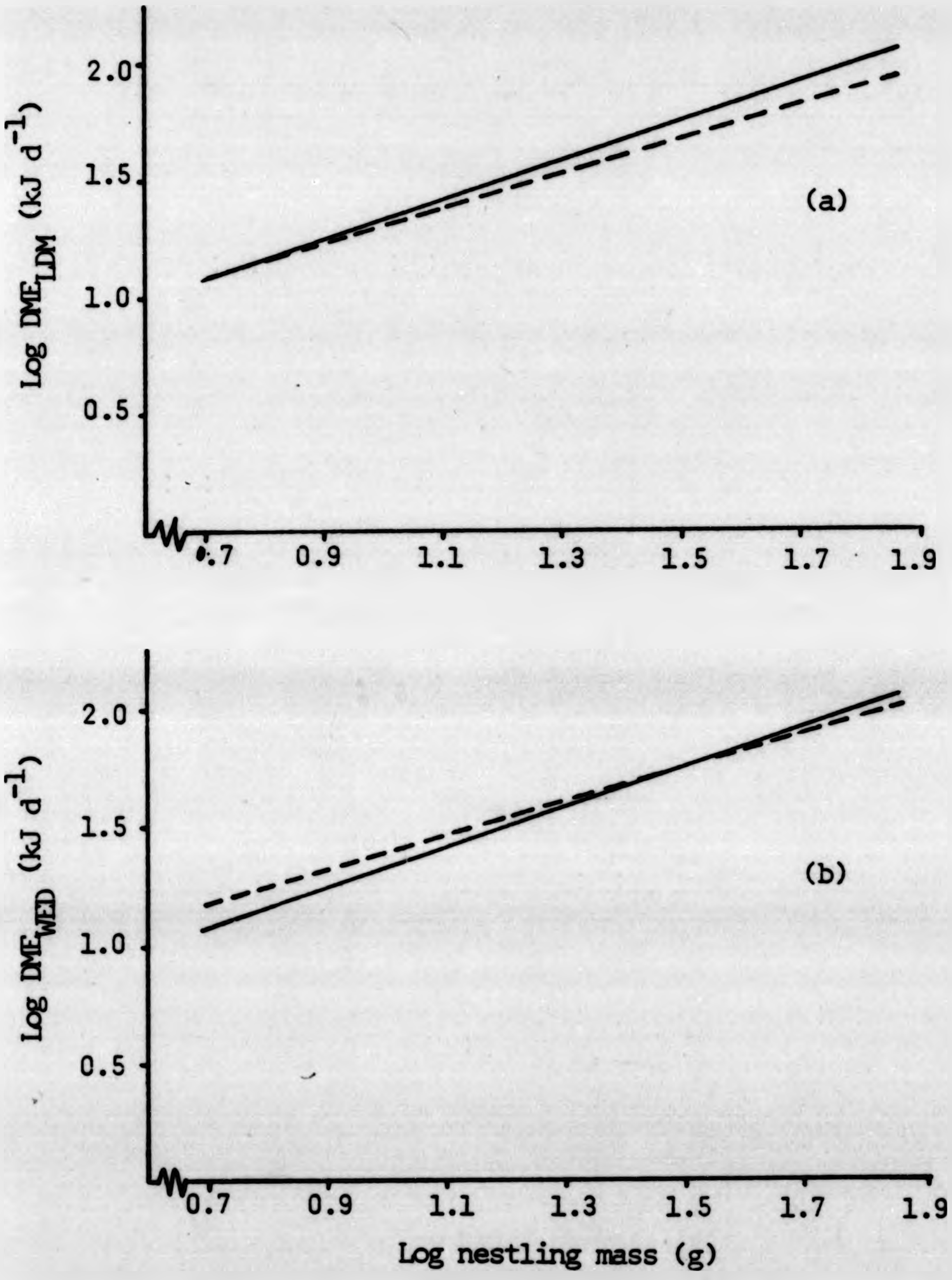
$$\text{DME}_{\text{adjusted}} = \frac{\text{WED}_{\text{nestling}} \times \text{wet mass}}{\text{WED}_{\text{adult}}} \qquad \text{eqn. 5.6}$$

WED correction will tend to underestimate slightly DME since it over-emphasises the lipid component (with its low metabolic rate) of nestling tissue. An LDM correction conversely will tend to overestimate DME slightly, since it assumes all extracted lipid is in the form of storage components. Figures 5.7(a) and (b) show Dipper DME 'corrected' using LDM and WED respectively. It can be seen that this reduces the error in the observed DME considerably, such that the Dipper DME curves and the curve predicted by equation 5.2 are similar.

Inclusion of the Dipper DEB (corrected by WED) into equation 5.2 yields a new equation:-

$$\text{DME} = 3.78 \text{ mass}^{0.833} \qquad r^2\ 93.1 \qquad \text{eqn. 5.7}$$

The corrected Dipper DEB thus has a negligible effect on the goodness of fit of the regression (i.e. r^2 = 93.1 as opposed



<u>Figure 5.7</u>: DME as a function of nestling mass.
(a) LDM adjusted DME)
) see text
(b) WED adjusted DME)

Dipper - - - -
15 altricial species ———

to the original $r^2 = 93.8$; equation 5.2) suggesting that the previous error in observed DME was due almost entirely to the use of adult metabolism equations in calculating nestling metabolism.

This conclusion could be of some value if a general equation for nestling WED or LDM as a function of the proportion of growth completed could be extracted from a review of the literature. This could then be used to calculate nestling metabolism by correcting metabolism predicted by existing adult metabolism equations. Nestling energy budgets could then be constructed with some confidence for any altricial species of any age for which nestling mass as a function of age was known. Unfortunately the necessary data needed to construct such equations are rarely published.

A revised energy budget for the Dipper is presented in Table 5.7, taking into account the mass specific metabolism differences between small nestlings and adults. It is constructed using the mean of WED and LDM adjusted values for BMR, 'alertness' and thermoregulation, for each nestling age, and using the data presented in Table 4.25, Section 4.6.

Comparing Table 5.7 with Table 4.25 shows that recalculation of the components mentioned above, whilst altering absolute values has little effect on the relative importance of each component expressed as a percentage of total DME, although BMR is substantially lower than in the previous energy budget (Section 4.6). Conclusions drawn from the uncorrected budget (Section 4.6) are thus unlikely to be significantly invalidated by omission of the correction factor.

TABLE 5.7: Energy budget for the Dipper taking into account mass specific metabolism differences between nestlings and adults (see text)

Mass (g)	BMR (kJ bird^{-1})	Growth (kJ bird^{-1})	Thermo-regulation (kJ bird^{-1})	'Alertness' (kJ bird^{-1})	Activity (kJ bird^{-1})	Bio-synthesis (kJ bird^{-1})	DEE (kJ bird^{-1})	DME (kJ bird^{-1})
5.9	2.400		0.000	0.890	0.00		3.290	3.290
8.1	3.475	9.04	0.000	1.250	0.10	11.49	16.315	25.355
10.7	4.800	11.48	0.005	1.730	0.22	14.26	21.015	32.495
13.9	6.480	14.96	0.015	2.270	0.30	16.64	25.705	40.665
17.7	8.520	18.82	0.055	2.895	0.49	19.94	31.900	50.720
22.1	10.945	23.07	0.180	3.615	0.83	21.79	37.36	60.480
26.7	13.630	25.85	1.065	4.500	1.84	23.12	44.155	70.005
31.3	16.505	27.81	2.815	5.450	3.05	25.42	53.240	81.050
35.7	19.485	28.72	4.020	6.235	3.37	26.76	59.870	88.590
39.7	22.485	28.55	4.920	7.195	3.75	27.60	65.950	94.500
43.2	25.430	27.49	5.875	7.880	4.06	26.93	70.195	97.665
46.0	28.210	25.01	6.585	8.740	4.28	24.85	72.665	97.625
48.2	30.830	22.68	7.195	9.555	4.42	21.65	73.650	96.330
50.0	33.360	21.17	7.780	10.365	4.52	20.22	76.245	97.415
51.3	35.715	18.79	8.335	11.075	4.60	16.84	76.565	95.355
52.3	37.975	17.38	8.860	11.770	4.66	15.06	78.325	95.705
53.0	41.870	15.80	9.765	12.985	4.69	12.98	82.290	98.090
53.5	43.945	14.70	10.250	13.620	4.71	11.11	83.635	98.335
53.9	45.970	14.20	10.730	14.245	4.72	10.30	85.965	100.165
54.2	47.960	13.63	11.185	14.865	4.73	9.52	88.260	101.890
54.4	49.890	13.01	11.645	15.465	4.73	8.56	90.290	103.300
54.5	51.760	12.30	12.080	16.045	4.73	7.70	92.315	104.615
54.6	53.625	12.36	12.520	16.620	4.73	7.66	95.155	107.515
54.7	55.465	12.40	12.950	17.210	4.73	7.69	98.155	110.445
TOTALS:	690.68	429.22	148.77	316.04	78.26	388.05	1530.070	1951.899

TABLE 5.8: A comparison of Dipper energy budget components expressed as % total daily metabolised energy (DME) for adjusted and unadjusted DME (see text) over all ages

Component	DME[a] adjusted	DME[b] unadjusted	Difference between adjusted & unadjusted
BMR	34.9	42.4	- 7.5
Growth	21.6	17.1	+ 4.5
Thermoregulation	7.5	8.4	- 0.9
'Alertness'	16.0	13.4	+ 2.6
Activity	3.9	3.1	+ 0.8
Biosynthesis	19.6	15.4	+ 4.2

a See text and Table 5.7

b See Section 4.6.8

5.8 THE DAILY ENERGY BUDGET: CONSIDERATIONS OF BROOD ENERGY DEMAND

Nestlings in larger brood-sizes receive on average less feeding visits than nestlings in smaller brood-sizes (Best, 1977; Bryant, 1978; Bryant & Westerterp, 1983; Hails & Bryant, 1979; Lack, 1966; Perrins, 1970; Royama, 1966; Seel, 1960; Section 4.6.3(c)). Daily metabolised energy (DME) has been found to be lower in larger brood-sizes than in smaller broodsizes (Bryant & Gardiner, 1979; Bryant & Westerterp, 1983; Westerterp et al., 1982). Two possible explanations have been put forward to account for these observations. Firstly, nestlings in larger broods require less energy due to reduced thermoregulation costs through huddling (Mertens, 1969, 1977; Royama, 1966). Secondly, parent birds have some optimal working capacity (Drent & Daan, 1980; von Haartman, 1954; Royama, 1966) at which level they are unable to sustain work for long periods without detriment to survival chances (Reyer & Westerterp, 1985; Royama, 1966), and hence lifetime reproductive success. These two hypotheses will be considered in turn.

5.8.1 Do nestlings in larger broods require less energy because of reduced thermoregulation costs?

Nestlings in large broods do have lower thermoregulatory costs than smaller broods (Mertens 1969; 1977; Section 4.3) and this is reflected in the earlier onset of effective homeothermy (Dunn, 1976; 1979) in larger broods. Hails & Bryant (1979) found that in the House Martin feeding rate was proportional to brood mass raised to the 2/3 power, consistent with the hypothesis of reduced thermoregulatory costs due to reduced surface area:mass ratio in larger broods (Mertens, 1969). There is evidence, however, to suggest that such energy savings in larger broods are too small to account for the observed reduction in DME of nestlings. Reduced costs may be explained in another way.

Nestlings in larger broods tend to be lighter than nestlings in smaller broods (see references earlier in this Section), and this has been shown to result in reduced survival (Nur, 1984; Perrins, 1979). Birds of smaller mass have lower metabolic requirements (Aschoff & Pohl, 1970; Kendeigh et al., 1977; Lasiewski & Dawson, 1967) of which thermoregulation is only one component (Dunn, 1980; Section 4.6). For example, BMR and 'alertness' (Sections 4.6.1, 4.6.6) account for 65% of the Dipper energy budget, hence any reduction in mass will effect DME via these components considerably more so than thermoregulation which is only about 10% of the total energy budget. Drent & Daan (1980) found DME to be highly correlated with the maximum growth rate ($g.d^{-1}$) in 8 atricial nestlings lending support to this view. The age of the onset of endothermy is also highly correlated with nestling growth rate, in this case K in the logistic equation (Dunn, 1975), while the majority of thermoregulation costs are not incurred until after the maximum growth rate has been reached (Dunn, 1980; Section 4.6).

The equation of DME as a function of nestling mass presented in the previous section (equation 5.2 was calculated for species in which the data were taken from brood-sizes 1 to 5, with little apparent effect on the variance about the regression line ($r^2 = 0.97$) suggesting thermoregulation to be unimportant in affecting nestling DME. This may explain Hails & Bryant's (1979) observations, since it was brood mass not brood-size that was the important factor related to frequency of feeding visits in the House Martin. Elsewhere Bryant & Gardiner (1979) conclude that huddling had a small impact upon brood demands, whereas requirements for individual growth, maintenance metabolism, and different numbers of nestlings is of greater importance. Nur (1984) concludes that thermoregulation costs decrease as brood-size increases only up until a certain point and thereafter, larger brood-sizes do not experience reduced thermoregulation costs, but still receive reduced food levels.

Clark (1982) demonstrated that frequency of feeding visits and fledging mass in the Starling were similar for broods from heated nest boxes and natural broods, lending support to the view that thermoregulation costs are of little importance to nestling energy demand. Reduced thermoregulation costs may be offset in larger brood-sizes in a number of ways. The earlier reduction in parental brooding in larger broods may result in greater indirect cost to the parent of maintaining brood homeothermy by increasing travelling costs (see 'maximal brooding time' model, Section 2.4.3(c), Section 5.4).

Increased nestling competition for the most energetically profitable nest position (Section 5.4) may explain the higher DME of House Martin broods of three compared with other brood-sizes thus negating the effect of huddling (Bryant & Gardiner, 1979). Deterioration of nest insulation due to trampling and faecal contamination have been put forward to explain the higher gross energy intake of Starling broods of seven, compared with broods of five (Westerterp et al., 1982).

A consistent reduction in thermoregulation costs of larger broods does not therefore explain the reduced frequency of feeding visits to, and reduced DME in large brood-sizes.

5.8.2 Do nestlings in larger broods receive less energy because of constraints on the parents ability to provision the brood?

Parents rearing larger broods appear unable to adequately nourish their young and this may lead to reduced survival amongst light nestlings (Section 5.7.1). This seems to be due to an inability of the parent birds to increase food delivery to a sufficient level. In the House Sparrow, both males and females increase the rate of provisioning the brood, but females more so than males during the late nestling period. Nonetheless nestlings in larger broods were underweight (Seel, 1966). A similar pattern has been observed in the Field Sparrow (Spizella pusula; Best, 1975). In House Martin broods which were experimentally enlarged from brood-size 3 to 7, feeding rate per brood was reduced by 22% and faecal output (reflecting DME; Section 4.8.2) was reduced by 32% (Hails & Bryant, 1979). Reduced feeding frequency may be offset by increased load size or energy content of the prey (van Balen, 1973; Bryant & Gardiner, 1979; Westerterp, 1973). Additionally, assimilation efficiency could be greater in larger broods (Bryant & Gardiner, 1979) although this is insufficient to prevent lower fledging masses in the House Martin. Energy delivery to the brood is not, however, an accurate estimate of parental workload (Bryant & Westerterp, 1983). In order to assess the constraints on the parents ability to provision different brood-sizes, some measure of energy expenditure of adult birds is required. The doubly-labelled water technique (see Section 3.5.2) has provided the opportunity to examine this in a number of species. Measurements of DEE in adults feeding nestlings has suggested an upper limit of sustainable workload of approximately 4.0 x BMR (Drent & Daan, 1980). This appears to be confirmed by a number of studies (Bryant & Westerterp, 1983; Hails & Bryant, 1979; Reyer and Westerterp, 1985; Ricklefs & Williams, 1984; Utter, 1971; Utter & LeFebvre, 1973; Wijnandts, 1980; Williams & Nagy, 1985), which could limit the parents ability to provision large broods. There is also evidence, however, that parents are able to nourish larger broods and remain within this threshold.

Ricklefs & Williams (1984) found no significant differences between DEE of adult Starlings provisioning different brood-sizes (where brood-sizes ranged from 3 to 7, and involved a 50% increase in brood mass). Williams & Nagy (1985) found no significant difference in adult DEE in Savannah Sparrows rearing broods of 2 or 3. The most informative study to date, however, is for the House Martin (Bryant & Westerterp, 1983) and shows that for a brood-size range of 1 to 8, and a corresponding 560% increase in brood DME, adult birds only increase their DEE by 16.1%. This is equivalent to a 0.028% increase in adult DEE per 1% increase in brood DME. In the above study DME of the brood was calculated indirectly from faecal output (see also Section 4.8) and took into account the reduced body mass of nestlings in larger brood-sizes (Bryant & Gardiner, 1979), DME calculated from faecal output was similar to the equation produced by Kendeigh et al. (Bryant & Westerterp, 1983; Section 5.6, equation 5.B).

DME required for broods of five House Martins was found to be 276.4 kJ d^{-1} or 138.2 kJ d^{-1} from each adult, assuming an equal share in brood provisioning (Bryant & Westerterp, 1980). The equivalent figure using Kendeigh et al. equation was 124.8 kJ d^{-1} for each adult. Nestlings in large broods tend, however, to be undernourished in some species, or likely to be more susceptible to undernourishment. Nonetheless the cost of adequately nourishing the brood may be very small. This can be demonstrated using the House Martin as a model, and using fitted growth data for different brood-sizes. Whilst House Martins are an example of one species in which consistent undernourishment of naturally large broods is not demonstrable (Bryant, 1975), the data show that mass differences between nestlings, of an order observed in other species, results in little additional energy expenditure by the parent.

Nestlings in broods of five tend to weigh on average 20.1g on day 10, just prior to peak energy demand (Bryant & Gardiner, 1979). If all nestlings were as well nourished as a nestling in a brood of one (i.e. 23.2g, for the same age) brood DME would be 135.6 $kJ.d^{-1}.adult^{-1}$, an increase of 8.7% DME. The corresponding increase in adult DEE necessary to allow adequate nourishment of a brood of 5 House Martins is only therefore 0.25%, or an increase from 99.29 $kJ.day^{-1}.adult^{-1}$ (Bryant & Westerterp, 1983) to 99.54 $kJ.day^{-1}.adult^{-1}$. Furthermore, adults could remain in net energy balance (Bryant & Westerterp, 1983; Table 6).

Adult birds should therefore be able to adequately nourish their young without energy inbalance, or resorting to use of their own body reserves. Why then are large broods undernourished? An explanation could be that energy requirements per nestling actually increase with increasing brood-size, rather than decreasing because of reduced thermoregulation costs. One component of the DEB that increases with increasing brood-size is activity costs, specifically begging behaviour and associated movement within the nest (Section 4.6.3, 4.10). For example, although the cost of begging for a single House Martin chick in a brood of four is only about 3.0% BMR on average, the cost to the parent would be four times this. Indeed, since nestlings beg on each visit, irrespective of whether they are fed, and the number of nest visits increases proportionately with brood-size then begging costs of the brood would increase exponentially. Accelerating activity costs might therefore be expected to negate savings from thermoregulation costs via huddling, and perhaps lead to a more or less linear increase in DME costs as a function of brood-size. Energy savings from huddling, and begging costs for the Great Tit and Blue Tit respectively, were calculated using the data presented in Table 5.9. Brood metabolism including thermoregulation costs were calculated for all brood-sizes between and including the mean and maximum brood-sizes observed (Table 5.9), using the following equations:-

$$\text{Great Tit metabolism} = 6.320 \text{ brood mass}^{0.672} \qquad \text{eqn. 5.8}$$

$$\text{Blue Tit metabolism} = 6.340 \text{ brood mass}^{0.750} \qquad \text{eqn. 5.9}$$

where metabolism ($\dot{m}_b$) is in $kJ \cdot brood^{-1} \cdot day^{-1}$ and brood mass is in grams (Mertens, 1969; O'Connor, 1975). The RQ used for both equations is 0.71.

In order to assess thermoregulatory savings in larger brood-sizes and test whether activity costs do indeed exceed savings, thermoregulation costs in the absence of huddling need to be calculated. By assuming all nestlings within a brood behave as discrete individuals and do not huddle, brood metabolism costs would be equal to:-

$$\text{Brood metabolism} = \text{Single nestling metabolism} \times \text{broodsize} \qquad \text{eqn. 5.10}$$

However this method is likely to grossly overestimate potential savings since brood-sizes of one are very uncommon in the species considered here and are likely to be the result of partial clutch or brood loss. Since it is nestlings in larger than average brood-sizes which tend to be undernourished, a more

TABLE 5.9: Variables used in calculating thermoregulation and begging costs in average sized and 1.5-average sized broods of Blue Tits and Great Tits

Variable	Blue Tit	Great Tit
Mean brood-size	[a] 10.0	[b] 8.0
Age of nestling (days)	[c] 11.5	[d] 13.0
Ambient temperature (°C)	[c] 15.0	[d] 12.0
Mean nestling mass (g)		
(i) Mean brood-size	[a] 9.9	[d] 15.0
(ii) 1.5 x Mean brood-size	9.5	12.7
Brood mass (g)		
(i) Mean brood-size	99.0	120.0
(ii) 1.5 x mean brood-size	142.5	152.4
Feeding frequency (feeds $brood^{-1}$ day^{-1})		
(i) Mean brood-size	[e] 740	[d] 375
(ii) 1.5 x mean brood-size	[e] 1072	[d] 575

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a Nur, 1984(a)

b Perrins & Moss, 1975

c O'Connor, 1975

d Royama, 1966

e Nur, 1984(b)

useful estimate of thermoregulatory costs can be derived by brood comparison with the average brood-size. To derive predicted metabolic costs, assuming no additional benefits from huddling in larger than average brood-sizes, the mass specific metabolism of the mean brood-size was used:-

$$M_p = M_{sm} \times W_b \qquad \text{eqn. 5.11}$$

where M_p is the predicted brood metabolic cost including thermoregulation (eqns. 5.8 & 5.9); M_{sm} is the mass specific metabolism of the mean brood-size; and W_b is the brood mass of the larger than average brood-sizes. The latter were calculated to include the progressive reduction in mass of individual nestlings found in large broods of the two species. Thermoregulation savings (TR_s) are thus calculated as:-

$$TR_s = M_p - M_b \qquad \text{eqn. 5.12}$$

where M_p and M_b are the predicted and observed brood metabolism respectively (see equations 5.11 and 5.8, 5.9), and expressed as $kJ.brood^{-1}.day^{-1}$.

Begging costs were calculated assuming a one, five or ten second begging duration per nest visit, and a unit cost of 7.48×10^{-5} kJ.sec^{-1} (Section 4.5.3). All nestlings were assumed to beg at each nest visit. Nestlings were also assumed to beg between nest visits as found in the House Martin and the Dipper (Sections 4.6, 4.10). Begging costs were therefore multiplied by 1.97, the ratio of 'begging between' to 'begging during' nest visits found in the Dipper (Section 4.10). Feeding frequencies for the Great Tit were calculated from

Royama (1966) and for the Blue Tit from Nur (1984). Calculations are for 11.5 day old Blue Tits and 13.0 day old Great Tits (Table 5.9). Ambient temperatures are those used in calculating equations 5.8 and 5.9 (see Mertens, 1969; O'Connor, 1975). Figures 5.8 and 5.9 show that begging costs do negate thermoregulation savings, and may exceed them, under some circumstances. The relationship is clearly sensitive to ambient temperature; an increase in ambient temperature of 3.0°C (Figures 5.8 and 5.9) results in thermoregulation savings being exceeded by begging costs in all but the largest brood-size at 15°C for the Blue Tit (given a ten second begging duration). If a begging duration of five seconds is considered this leads to a reduction in TR savings of 33.0% for the Great Tit and 47.4% for the Blue Tit based on the largest brood-size. The reduction in TR savings increases as brood-size decreases. Since ambient temperatures are often likely to be higher than 12-15°C during the Spring and Summer in Britain, and parents may still brood nestlings at the ages used in these calculations (Mertens, 1969) TR savings may be overestimated. Additionally, nestlings do not thermoregulate fully until well grown; prior to this begging costs will exceed TR savings more often. A begging duration of ten seconds may be a realistic mean for all nestling ages since beg duration is initially much higher in the species examined during this study (Sections 4.9, 4.10), and may be longer than 10 seconds in some species even during the latter half of the nestling period (Section 4.10). Figures 5.8 and 5.9 thus show (a) that activity, specifically begging costs, may play an important rôle in modifying brood

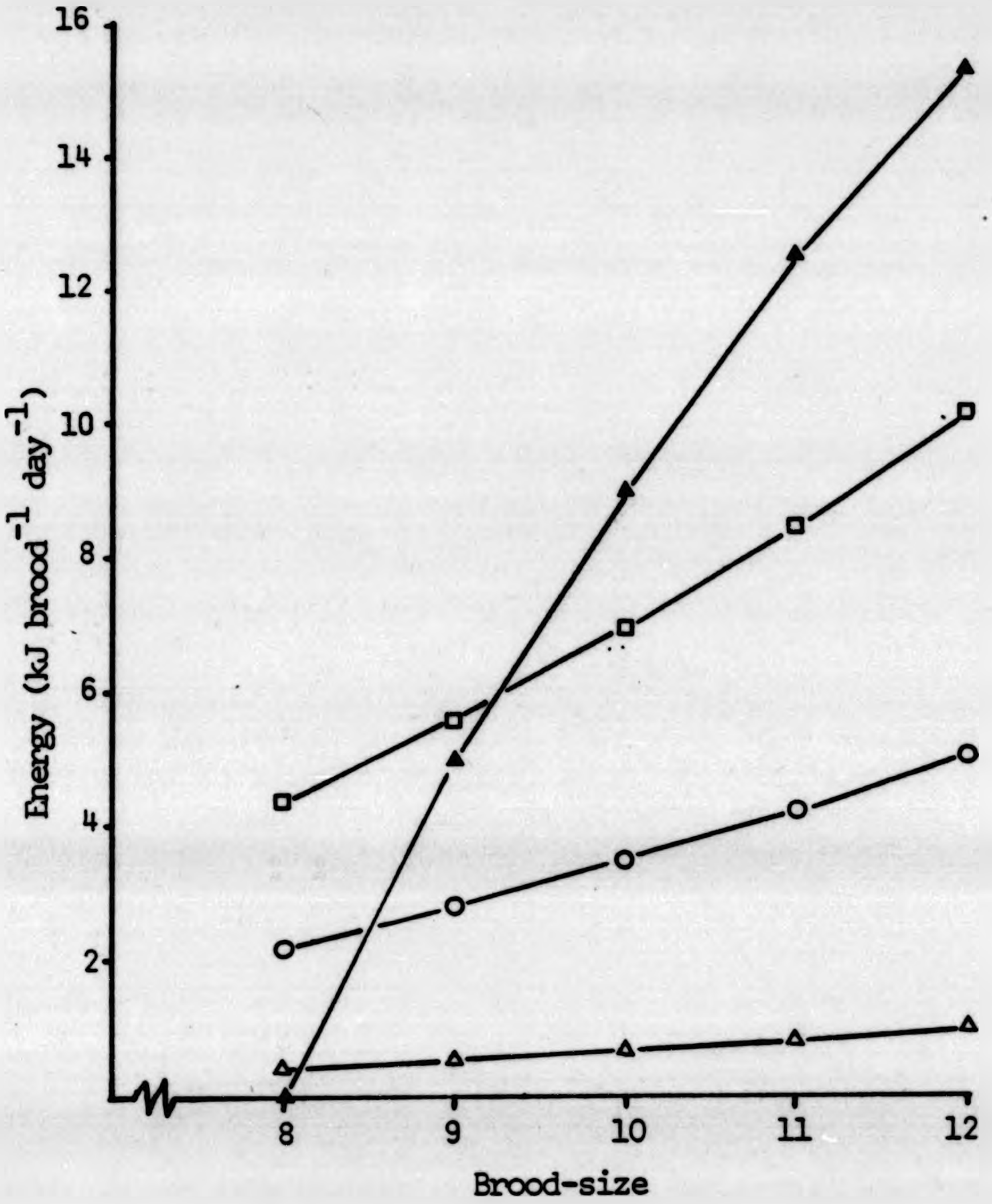

Figure 5.8: Comparison of benefits through reduced thermoregulation costs via huddling at 12°C, and costs of nestling begging behaviour for the Great Tit (see Table 5 as a function of brood-size.

Thermoregulation savings. ▲

Begging costs assuming a begging duration of:

One second △

Five seconds ○

Ten seconds □

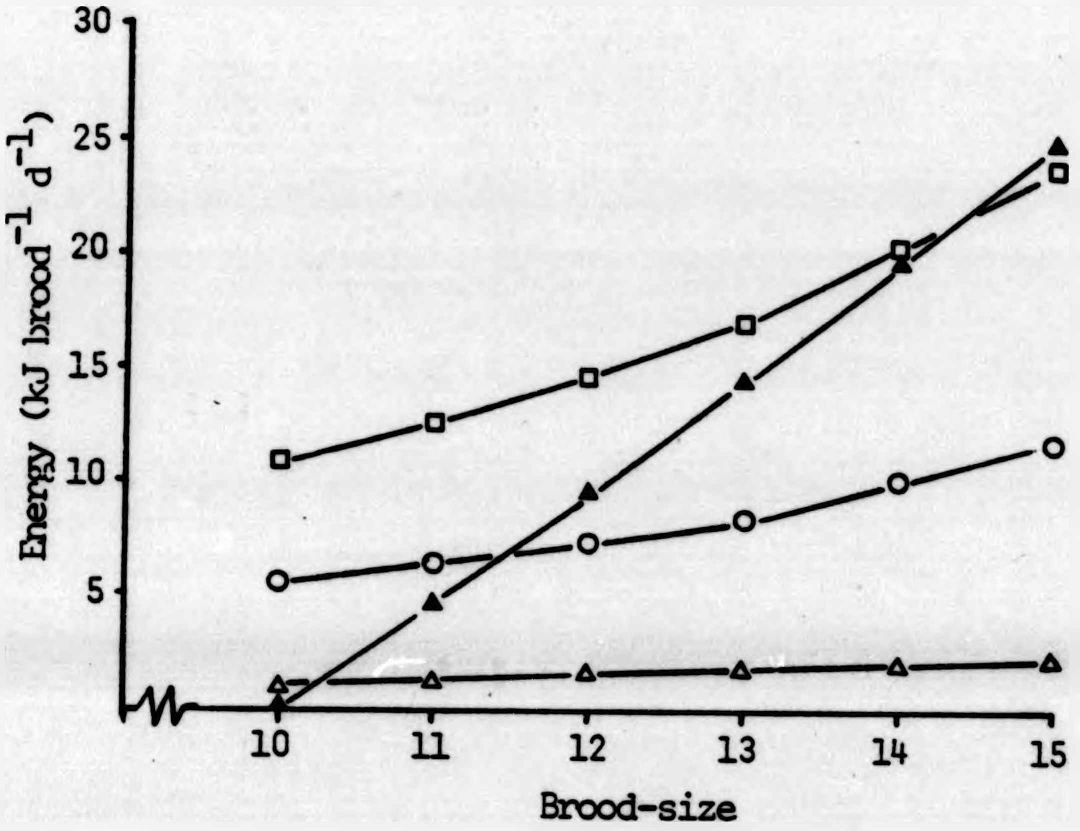

Figure 5.9: Comparison of benefits through reduced thermoregulation costs via huddling at 15°C, and costs of nestling begging behaviour for the Blue Tit (see Table 5.) as a function of brood-size.

Thermoregulation savings. ▲

Begging costs assuming a begging duration of:

- One second △
- Five seconds ○
- Ten seconds □

energetics in larger than average brood-sizes, and (b) that larger than average brood-sizes should be relatively economic to rear on a per nestling basis since TR savings tend to exceed begging costs in these brood-sizes. In conclusion, accelerating activity costs do not appear to explain why young in larger brood-sizes are undernourished.

In some species which have very large brood-sizes even the most common or most productive brood-sizes may show apparent undernourishment of the young. Nur (1984(b)) found this to be the case for the Blue Tit, and interpreted it as the result of a decision by the female not to adequately nourish the brood, based on her own probability of survival. Nur demonstrated that female Blue Tits incur progressive mass losses as a result of increasing their feeding frequency to larger brood-sizes. Elsewhere he showed that lighter females have lower survival probabilities (Nur, 1984(c)) and views feeding frequency to be optimized through a trade-off of parental versus nestling survival. The feasibility of his model does however depend to what extent costs to the adults are related to feeding frequency. For example, although mass loss of females was a linear function of feeding frequency, survival differences were only demonstrable above and below a 'threshold' mass of 10.6g. Heavier females may therefore be able to lose mass without affecting their survival (Jones, 1985). Also, since male Blue Tits suffer no apparent differences in survival as a function of feeding frequency (Nur, 1984(b)), it is unclear why males do not compensate for any reduced feeding by the females. By increasing their own feeding rates males would increase their fitness by producing heavier nestlings with subsequently better chances of survival (Nur, 1984(a)). In view of this the question of undernourishment among large altricial broods remains unresolved.

PART II: HATCHING ASYNCHRONY: IMPLICATIONS FOR NESTLING ENERGETICS

Hatching asynchrony is a widespread phenomenon amongst bird species. It is facilitated by starting incubation prior to completion of the clutch, so that the young may hatch some days apart (Lack, 1954; 1968). It is commonly assumed that such a hatching pattern has an ultimate, adaptive, value (Slagsvold, 1986). A number of hypotheses have been presented to explain its occurrence (Clark & Wilson, 1981; Hahn, 1981; Hussel, 1972; Lack, 1954; O'Connor, 1978).

Recently, however, the basic assumption of an adaptive value to hatching asynchrony has been questioned (Mead & Morton, 1985). Most attention has been focused on two hypotheses to explain hatching asynchrony, (i) the nest failure hypothesis (Clark & Wilson, 1981), and (ii) brood reduction (Lack, 1954; 1968). This study has further considered two more possible explanations of hatching asynchrony, (iii) the peak load reduction hypothesis (Bryant & Gardiner, 1979; Hussel, 1972) (Sections 2.2, 4.8), and (iv) the reduced sibling rivalry hypothesis (Hahn, 1981; Hamilton, 1964) (Sections 2.3, 4.10, 4.11). Many assumptions regarding the latter are pertinent to considerations of brood reduction (see Section 5.11), and so hypotheses (iii) and (iv) are considered first.

5.9 PEAK LOAD REDUCTION

The assumption that the spread of hatching results in an equivalent spread in the peak energy demand curves have not been demonstrated for any species (see also Figures

4.65(a-f)). Data were presented in Section 4.8 which failed to show any trend in the mean peak energy demand of nestlings ($MPED_n$) in relation to asynchrony. This was contrary to small predicted savings from the peak load reduction model, and from calculations based on the House Martin DME estimates (Bryant & Gardiner, 1979). This discrepancy will now be discussed.

Nestling energy demand is in part related to nestling growth (Section 4.6), indeed it is the growth and biosynthetic component of the nestling energy budget which is primarily responsible for the peaked shape of the DME curve (Figure 4.64). This holds for species that undergo mass recession (e.g. House Martin, Delichon urbica) as well as species which do not (e.g. Cactus Wren (Campylorhynchus brunneicapillus) contrary to what is sometimes assumed (Mead & Morton, 1985). Species which undergo mass recession will tend however to have "sharper" peaks to their's. DME curves and thus peak load reduction may be envisaged as producing greater potential benefits in such species. Nonetheless estimates of savings from peak load reduction, taking this into account, do not produce widely differing results, and savings in both cases are small (Section 4.8.2).

For the spread in peak energy demand to reflect the time between the first and subsequent hatchings, growth rate of the first and later hatched nestlings should be similar, and yet the peak mass of later hatched nestlings was often higher than their earlier hatched siblings (Section 4.11.2), reflecting their faster growth. This acts to reduce the spread of the peak energy demand. It is possible, however, that benefits only accrue when food conditions are poor. In poor weather the last chick may grow more slowly so that its peak demand curve lags behind that of its more well nourished siblings, whereas in good conditions any tendency for synchrony of peak demand curves may be encouraged because parents can adequately provision the brood, and the nestling period would be completed more quickly. However, asynchrony of peak demand curves under poor conditions would be as a result of the slower growth of some nestlings, and not hatching asynchrony *per se*. There is evidence to suggest that a marked hatching asynchrony is not necessary to promote slow growth in later hatched young (see Sections 5.10, 5.12).

Nestling energy demand curves should be relatively stable, if asynchrony evolved for the purpose of peak load reduction and PLR was to be found in all broods and all conditions. Stability means not only similar growth rates (see above) but that the energy demand curve should be free of large unpredictable irregularities which could often smother the benefits of asynchrony. This might be expected for species which exploit predictable food resources.

House Martins, on the other hand, exploit unpredictably occurring patches of food resource (aerial insects), the abundance of which is influenced by weather conditions (Bryant, 1975; Jones, 1985; Turner, 1980), which results in very irregular growth of the level of individual broods. This may disrupt the synchrony of hatching spread and spread of peak energy demand.

Variation in peak energy demand can be extreme, for example in two broods of four House Martins, of similar asynchrony (RDHM 0.843 and 0.784), the mean peak energy usage by individuals was 44.6 and 89.0 kJ day^{-1}, the latter being similar to energy usage usually found in broods of five. Since energy intake can vary so greatly, even with similar asynchrony, and in such an apparently unpredictable way, asynchrony is unlikely to have evolved primarily as a means of reducing parental costs. Such an 'investment' in asynchrony for the purpose of small energy savings from peak load reduction could easily be negated by a change in weather conditions.

It was found in House Martins, that very asynchronous broods (manipulated experimentally) had significantly higher peak masses than moderately asynchronous natural broods. This was only found in brood-sizes of three and four and the increase in peak mass was only 0.89 grams. If this was a result of reallocation to nestling growth of savings from peak load reduction then a much greater degree of asynchrony would be expected to occur in House Martin broods (Section 4.11.1). Reallocation of energy savings to nestling growth would also require that nestlings could induce the parents to continue working at their original level, and presumably risk a reduction in fitness (see Section 5.8). There is no evidence to suggest this occurs.

If peak load reduction evolved for the reason discussed above then it should also be most easily detected in broods of five, which was not the case. It therefore seems most likely that hatching asynchrony, although on occasions possibly conferring energy savings through peak load reduction, did not evolve primarily for this purpose.

5.10 REDUCED SIBLING RIVALRY

A model of reduced sibling rivalry (RSR, Section 2.3) was tested by direct (Sections 2.3.4, 4.10) and indirect methods (Sections 2.3.5, 4.11.1). Both methods showed independently that a reduction in sibling rivalry in association with hatching asynchrony was not demonstrable in the House Martin. There are a number of possible explanations for this:-

(1) Sibling rivalry is not primarily facilitated through begging behaviour;

(2) Sibling rivalry is independent of hatching asynchrony;

(3) Reduced sibling rivalry is unimportant because there are associated costs which outweigh potential benefits.

These will be discussed in turn.

5.10.1 Is sibling rivalry facilitated by means other than begging behaviour?

Jostling to maintain favoured nest positions for feeding may be an alternative or complementary way in which sibling rivalry is brought about. This would be more analogous to the fighting seen in raptors and Ardeids. There was no evidence however to suggest that a significant 'movement' cost was excluded by analysis of begging behaviour alone in the House Martin (Section 5.5.1), since shifting in nestling position within the nest is anyway likely to occur during begging bouts (Reed, 1981).

5.10.2 Is sibling rivalry independent of hatching asynchrony?

This question can be restated as a number of separate questions. Firstly, is hatching asynchrony necessary to produce mass hierarchies within broods? Mass hierarchies may develop even when differences in hatching are small in House Martin broods (Section 4.11.2). A hatching spread of twelve to twenty-four hours may occur even when incubation commences with the last egg (Clark & Wilson, 1981), and this is sufficient to allow brood reduction within a number of species (Gibbons, 1987; Ligon, 1970; Poole, 1979; Ricklefs, 1965). In some species parents can effectively cause dominance hierarchies by preferential feeding, independent of nestling size (e.g. Coots, *Fulica atra*, Horsfall, 1984b). Hatching asynchrony is not therefore necessary to produce mass hierarchies. Mass hierarchies are, however, common within altricial broods and may still be important in regulating sibling rivalry. Does position within such mass hierarchies result in permanent dominance within the nest for the larger individuals? Significant correlations have been shown between nestling mass and 'size' in House Martins (O'Connor, 1975), yet changes within the mass hierarchy are common in this species (Section 4.11.2). Whilst it cannot be proven that changes in mass hierarchy are reflected by parallel changes in dominance, the data in Section 4.11.2 does show that any benefits associated with such dominance, were it to remain fixed, do not confer persistent advantages to the highest ranked siblings. Conversely, other studies have found irreversible mass related dominance (Groves, 1984; Meyburg, 1974; Ricklefs & Hainsworth, 1967). In species in which siblings physically attack each other (e.g. raptors, Ardeids) such irreversible dominance is likely to be the rule: For example, in the Cattle Egret, dominance rank is decided by fighting and was not found to be correlated with either growth rate or winning ratios in food contests (Fujioka, 1985b). In species which do not fight however the establishment and maintenance of permanent dominance hierarchies may be less common. In such species hierarchy maintenance requires preferential feeding of some individuals by the parent. The cost of feeding nestlings lower in the hierarchy however may not be as great as in those species which fight (see Brood Reduction below), thus the selective pressure to feed the largest nestling and maintain a hierarchy may also be less. Support for this view may be found from a number of studies of nestling feeding behaviour.

Parents of species in which siblings do not fight do not consistently feed the largest nestling as is often stated (O'Connor, 1984). Food may be offered to the smallest sibling preferentially (pers.obs., Clark & Stamp, unpublished); the 'hungriest' chick (Skutch, 1976); at random (Reed, 1981); to a specific sex of nestling (Harper, 1985; Horsfall, 1984b); to nestlings specific to a particular parent (Smith, 1978);

or to the most mobile nestling (Bengtsson & Ryden, 1983). In the latter case this was also the smallest nestling, as demonstrated in the Fieldfare. In such 'non-aggressive' species, therefore, dominance hierarchies may persist, change or not exist at all. Reduced sibling rivalry facilitated by differences in nestling mass cannot therefore be demonstrated conclusively for any species. If it occurs there is evidence to suggest that it is unlikely to exert a strong selective pressure on either nestlings (see Section 5.8) or parents; this is discussed further below.

5.10.3 Do the costs of reduced sibling rivalry outweigh the benefits?

There are two reasons why this may indeed be the case. Firstly, any potential saving from reducing sibling rivalry would be small (Section 5.5), and likely to be overriden by similar factors to those affecting Peak Load Reduction (see previous Section). Even so, benefits although small would be selected for if they increased fitness (Section 5.5, 5.6). Secondly, there may be associated costs with reduced sibling rivalry which outweigh any potential benefits. These have received little attention in past studies (e.g. Hahn, 1981). In those altricial nestlings which do not fight, reduced sibling rivalry is mediated through begging behaviour (Section 2.3.1, earlier this Section), thus reduced rivalry results in reduced begging. Von Haartman (1949) showed that feeding rate in the Pied Flycatcher (<u>Ficedula hypoleuca</u>) was governed by the amount of begging that occurs. Thus, when recorded begging calls are played during feeding visits, parents increase their food delivery rate (Bengtsson & Ryden, 1983; Reyer & Westerterp, 1985). A reduction in begging due to reduced sibling rivalry would therefore lead to a reduction in parental delivery rate. No reduction in food delivery rate was observed in Great Tit broods in which mass differences between nestlings were manipulated to be large (Bengtsson & Ryden, 1983) suggesting there were no benefits from reduced sibling rivalry. There is evidence however from other studies, that birds in artificially synchronized broods may beg more than birds in asynchronous broods under similar food conditions. Fujioka (1985b) found that begging was greater in artificially synchronized broods of the Cattle Egret compared with naturally asynchronous nests. This resulted in more food being brought to the nest in the first part of the nestling period, although delivery rates were similar thereafter. The growth of chicks in such synchronous nests was almost as fast as first hatched chicks in asynchronous control broods. Since increased begging in synchronous broods appears to benefit these broods through increased food delivery, asynchrony would appear to involve a cost rather than a benefit (see Section 5.13). Does greater begging in synchronous broods mean greater sibling rivalry? Not necessarily, if begging frequency of a nestling on average reflects its DME curve, i.e. if begging is dependent on requirement, then nestlings that hatch synchronously may have synchronous peak begging curves in a similar way to the DME curves of the Peak Load Reduction model. A greater level of begging for a given age will therefore occur in more synchronous broods, other factors being equal, with no need to invoke more intense competition as an explanation. Fujioka (1985a) found that begging frequency in the Cattle Egret rose to a peak at about two-thirds of the way through the nestling period and then declined. This is consistent with pattern of DME change with age found in many species. (There are no figures published for the change in DME with age for this species).

To summarize; hatching asynchrony is not necessary to produce mass hierarchies within altricial species. Mass hierarchies, if they occur, do not consistently confer advantages to the largest nestlings, and there is little evidence to support the view that sibling rivalry is mediated by differential begging of high and low ranked nestlings. If sibling rivalry is important, and there is no evidence to suggest that it is, the associated costs of reduced food delivery by the parents (because of reduced begging) may outweigh benefits through energetic savings from this reduced begging which is relatively cheap. There is therefore little support for the view that hatching asynchrony evolved to reduce conflict among nestlings and to allow a more efficient utilization of energy resources.

5.11 THE NEST FAILURE HYPOTHESIS

The nest failure hypothesis and brood reduction hypothesis came to quite different conclusions regarding the adaptive significance of hatching asynchrony. The nest failure hypothesis views brood reduction as a necessary cost of hatching asynchrony evolved to minimize total nest failure through predation (Clark & Wilson, 1981). This view has been criticized by Richter (1982) who argued that such a cost was unreasonably high to have allowed selection of hatching asynchrony for any other reason than brood reduction. This was subsequently challenged by Hussel (1985a) who showed a number of disimilarities between the assumptions of Clark & Wilson's model and Richter's critique.

Clark & Wilson begin by assuming no partial mortality occurs within the nest, and that the survival probability of nestlings (P2) is less than that of eggs (P1) and, also, that P2 is constant. Therefore the total number of offspring W(m) produced in any one nestling attempt, as a function of asynchrony, is given by

$$W(m) = P_1[(m-1)t_1 + t_2]P_2t_3(m + \sum_{i}^{N-m} P_2{}^{it_1})$$

where

N = clutch size

m = egg at which incubation starts (m = 1 and m = N correspond to complete asynchrony and synchrony, respectively)

t_1 = laying interval (days between laying of successive eggs)

t_2 = incubation period for a single egg (days)

t_3 = nestling period for a single chick (days)

P_1 = daily probability of survival of nest contents from the start of incubation to first hatch

P_2 = daily probability of survival from first hatch to first fledge.

Although the model is simplistic in that it only considers two survivorship values (Hussel, 1985b; Slagsvold, 1986) addition of further survivorship values does not affect the predictions of the model (Clark & Wilson, 1981; Hussel, 1985b).

The model predicts that when total nest failure is high due to predation, asynchrony should be favoured, since it speeds up the time at which the first chick fledges. Also, when nest predation is concentrated in the nestling stage as opposed to egg stage of the nesting attempt, synchrony should be favoured since it reduces the time during which young are in the nest. This differential mortality between egg and nestling stage, Clark & Wilson call the nest-failure ratio (NFR) and is given by:-

$$NFR = (1 - P_2)(1 - P_1)$$

Thus the nest failure model predicts a trade-off between asynchrony favoured by total nest failure and synchrony favoured by high NFR. They demonstrated that it was the latter that was most important in regulating optimal asynchrony, and that an NFR of > 5.4 was needed to favour total synchrony. Thus, when the probability of nest failure is high, females should commence incubation prior to completion of the clutch. The model was tested with data from 87 altricial species of bird, and Clark & Wilson conclude that "... the distribution and frequency of asynchronous hatching corresponds well to the general predictions of the nest-failure model", and "... in most cases hatching asynchrony is determined by selective pressures which have little to do with brood reduction".

Does their model explain hatching asynchrony in the House Martin? It follows from the assumptions and the model, that asynchronous species such as the House Martin (Bryant, 1975b; 1978a; Section 4.11.1) are those in which total nest failure is high. No nest predation was observed during this study, and nest predation is generally rare in this species (Bryant, 1978b), a fact in common with some other hirundines (D. M. Bryant, pers.comm.). Occasional predation of House Martins may occur by Corvids, though there is no reason to suppose that this is concentrated in either egg or nestling stages of the nesting period. Species with low NFR's (this is not necessarily the same as high total nest failure as implied by the model) should tend to be asynchronous. The House Martin with an NFR close to one, should therefore commence incubation when $m = 1$ (Clark & Wilson, 1981) i.e. on the first egg. House Martins commence incubation when $m \geqslant 2$ (Table 1, Clark & Wilson, 1981; Bryant, 1975b). Slagsvold (1984b) analysed intraclutch variation in egg size and concluded that species which adopt the "brood-survival strategy" (nest failure model) should lay relatively heavy final eggs, whilst those adopting the brood-reduction strategy should lay relatively small final eggs. House Martins show no consistent pattern of egg size with laying order (Bryant, 1975b; 1978b) although embryo size did decrease with laying order (1975); the latter is not consistent with the nest failure model.

Hussell (1985b) applied the nest-failure model to Snow Bunting data. He found the model only predicted a small increase in productivity of optimally asynchronous broods compared with synchronous ones (1.5% and 2.4% increase in productivity in clutches of 5 and 6 respectively). In all cases the mean observed asynchrony was slightly less than predicted, though the variation was large. He concluded that the increasing asynchrony found with increasing brood-size tended to lend support to the nest-failure model. House Martins also show an increase in asynchrony with brood-size (Section 4.11.1, Bryant 1978a), but experience negligible nest predation. Clearly the nest failure model does not explain all these patterns.

There are a number of criticisms of the nest failure model.

5.11.1 Is the relevant daily survival probability included in the model?

The nest failure model implies independence of young at fledging, and that any consideration of minimizing loss of the brood from predation by adaptive hatching asynchrony, does not apply to fledged young. Yet in most altricial species parents continue to feed the young out of the nest for a period of time until independence is reached (Davies, 1978; O'Connor, 1984). Furthermore, the period when nestlings leave the nest is often the time at which predation risk is highest (Perrins, 1979). It is difficult to support the view that a period of high potential nestling loss, during which young are still dependent upon their parents, is not an important source of brood/nestling mortality which should also be encompassed by the model. Perhaps the most relevant survival probability is that between fledging and independence. Independence is however difficult to define, since parents gradually become 'mean' towards their offspring (Davies, 1978). The survival probability which would be theoretically appropriate, that of survival between the first and last young to become independent, may be, practically, unmeasurable. Survival between fledging and independence may therefore be a more suitable probability to use. If such a probability of survival (P_4) is relatively low, then this will tend to raise the NFR (see below).

5.11.2 Is the estimation of nest-failure ratio accurate?

The nest failure model predicts that synchrony should be favoured only when NFR $\geq$ 5.4. Absolute synchrony (or zero difference in hatching mass) is unlikely to occur regularly simply because of the variation in egg mass within clutches (Slagsvold et al., 1984) which will affect hatching mass. Eggs of differing mass/size tend to have slightly different incubation times (i.e. t_2 is variable), smaller eggs taking a little less time to incubate (Bryant, 1975b). This assumes that the heat transferred to the eggs via the brood patch is equal for all eggs. It is unlikely especially in large clutches that this will be the case, and is the likely reason for egg turning in many species (Ricklefs, 1974). The threshold of 5.4 is therefore likely to be unrealistically high. NFR's for most species tend to be less than 3.0 (Clark & Wilson, 1981; Table 1). These values may be under-estimated, therefore biasing them towards favouring asynchrony, for two reasons. Firstly, the exclusion of a potentially high source of nestling mortality (P_4), underestimates the nestling component of NFR (see above). Secondly, total loss of eggs from nests which may be recorded as predation events can occur by other means, for example human predation (unlikely to affect the nestling stage), removal of damaged or infertile eggs by the parent, or even whole clutches of viable eggs after bad weather (O'Connor, 1979), or possibly after nest parasitism. Estimation of the egg component of NFR is therefore open to errors which may overestimate its importance. This may be one reason why species tended to be more synchronous than predicted by the model (Clark & Wilson, 1981).

5.11.3 Do values of D confirm the predictions of the nest-failure model?

Slagsvold et al. (1984b) used the deviation of the last laid eggs size (D) from the mean of the rest of the clutch to examine predictions regarding brood reduction and nest-failure hypotheses. Positive values of D should correspond to species which have evolved a high degree of asynchrony in response to a high risk of total nest failure or low NFR, since this will tend to offset the cost of losing young through non-adaptive brood reduction (Clark & Wilson, 1981).

Of the 67 species examined, there are corresponding NFR and total nest failure data for only 7 species, these are presented in Table 5.10. Though the sample is very small there is no consistent pattern that gives support to the nest failure model.

5.11.4 Is the use of 'm' as a measure of asynchrony valid?

The use of 'm', the egg on which incubation commences has been criticised, as a measure of hatching

TABLE 5.10: The relationship of the deviation of final egg size (D) from the rest of the clutch (Slagsvold et al., 1984) to the nest failure ratio and percentage of total nest failure (Clark & Wilson, 1981)

	Nest Failure Ratio	Total Nest Failure %	D	
			[b]predicted sign	observed sign
Apus apus	[a]1.00	low	+	[c]- and +
Apus melba	[a]1.00	low	+	-
Hirundo rustica	0.11	low	+	+
Troglodytes aedon	0.34	-	-	+
Sturnus vulgaris	1.61	low	-	-
Passer domesticus	1.37	37%	+	-
Quiscalus quiscula	1.72	42%	+	+

a Almost nil predation due to nest-site security, therefore assumes P1 = P2

b Sign predicted on the basis of NFR and/or TNF. High TNF/low NFR = t; Low TNF/high NFR = -. See text for explanation.

c Values in Slagsvold et al. are for three estimates from O'Connor (1979). Two are positive (one just so) and one is negative.

asynchrony, since it is automatically biased against small clutch sizes which can never obtain a markedly asynchronous score (Slagsvold, 1986). Another criticism is the inconsistency with which 'm' reflects hatching spread (see previously). It is hatching spread on which the nest failure model is based and yet it is 'm' on which Clark & Wilson base their conclusions, (Figure 6, Clark & Wilson, 1981). Their data (Table 1) were re-analysed using hatching spread instead of m, and compared with NFR for species given.

There was no significant difference between NFR in species in which young hatched < 24 hours apart ($n = 8$), compared with those in which the young hatched 24-48 hours apart ($n = 10$); Mann-Whitney U-test, $Z = 0.11$, $p > 0.1$. It was not possible to compare species in which hatching spread was greater than 48 hours for two reasons. Firstly, with the exception of the Scarlet Flycatcher (Pyrocephalus rubinus) for all species in which NFR is high (i.e. > 1.8) no data were available on hatching spread. Secondly, with the exception of the Cactus Wren for all species in which hatching spread was particularly high (≥ 72 hours), no data were available on hatching spread. My analysis did not include species for which hatching spread and NFR were measured in different studies (e.g. Lapland Longspur, Calcarius lapponicus) as these parameters often varied considerably between studies, especially the latter. The significance is however likely to be even less if these species were included, since several had both high hatching spread and high NFR values (e.g. Snow bunting, Lapland Longspur).

5.11.5 Is asynchronous fledging advantageous?

Asynchronous fledging of the young, as implied by the model, may be a disadvantage for two reasons. Firstly, a rapid transition of feeding young in the nest to feeding young out of the nest may benefit both parent and young. For example during three hours of observations on one Dipper brood, the single fledged youngster was not fed, though it begged twice as often as its sibs still within the nest, which were provisioned as usual by both parents (pers.obs.).

Secondly, if predation of newly fledged young is high, then synchronous fledging (and by implication, more synchronous hatching) might be favoured as a mechanism to 'swamp' predators. If synchronous fledging is advantageous it might be expected that late-hatched young would fledge earlier than expected. Highly asynchronous manipulated House Martin broods (five day age difference) fledged over two-three days (pers.obs.). The lightest or last-hatched young in Tree Swallow broods fledge significantly earlier than expected (Zach, 1982), suggesting asynchronous fledging is not adaptive.

The view that hatching asynchrony is an adaptation to reduce nest failure, does not hold for the House Martin. It is more likely that hatching asynchrony is determined by selective pressures that have little to do with nest-failure. (113)

5.12 BROOD REDUCTION

Hatching asynchrony has been interpreted as an adaptation by adult birds to adjust their brood-size under conditions of unpredictable food shortage, by selectively starving the later hatched young (Lack, 1954; 1968; O'Connor, 1978c). Evidence for brood reduction as an adaptive strategy, however, remains largely circumstantial (Hahn, 1981). Hatching asynchrony and brood reduction have been inexorably linked since Lack first proposed this hypothesis yet two separate questions are outstanding.

(1) Is hatching asynchrony necessary for brood reduction to operate?

(2) Is brood reduction adaptive?

These questions will be dealt with in turn.

5.12.1 Is hatching asynchrony necessary for brood reduction to operate?

The mechanism that is envisaged as affecting brood reduction is a size hierarchy within the brood. Size hierarchy formation has been discussed in relation to sibling rivalry, and it has been shown that only small differences in the size of individuals is necessary to produce such hierarchies (Section 5.10) and these may not be permanent or confer persistent advantages to the highest ranked individuals, particularly in 'non-aggressive' species. The evidence suggests that brood reduction can and does occur in synchronous broods (as predicted by O'Connor, 1978c).

Gibbons (1987) found that 80% of chick mortality was due to starvation in both asynchronous and artificially synchronized broods of the Jackdaw (Corvus monedula). Hahn (1981) found no significant difference between partial brood loss and complete nest failure (assumed to be through starvation), between naturally asynchronous and artificially synchronized broods in the Laughing Gull. Brood reduction has been reported in experimentally synchronized broods of the White-bellied Swiftlet (D. M. Bryant, pers.comm.) in Blue-eyed Shags (Phalacrocorax atriceps, Shaw, 1985), in synchronous broods of the Curved-billed Thrasher (Toxostoma curvirostre, Ricklefs, 1965), and the Red-cockaded Woodpecker (Picoides borealis, Ligon, 1970).

Much attention has focussed on the relevance of the size of the last laid egg in considerations of brood reduction (Howe, 1976; 1978; O'Connor, 1978c; Clark & Wilson, 1981; Slagsvold et al., 1982). A large last egg has been alternatively viewed as supporting brood reduction (Howe, 1976) or refuting it (Clark & Wilson, 1981); whilst small last eggs are generally seen as an adaptation to increase size differences between individuals and hence support the brood reduction hypothesis (O'Connor, 1978c; Parsons, 1975; Slagsvold et al., 1984). Others have shown that egg size difference and trends with laying sequence are not consistent between years for a given species (Slagsvold et al., 1984; Mead & Morton, 1986). Smaller eggs produce slower growing young in the Great Tit (Schifferli, 1973), thus increasing size differences between siblings. Ricklefs (1982) found no evidence to support the view that growth rate varied between synchronous and asynchronous broods. Thus hatching asynchrony is not a prerequisite for brood reduction.

There is some evidence however that in broods in which size hierarchies are more marked brood reduction is facilitated more quickly. Edwards & Collopy (1983) found that in raptors obligate fratricide was characterized by a small increase in hatching spread and a two to four times increase in the difference in egg size between first and second laid eggs (approximately 12-13% mean percentage volume difference), when compared with faculatively fratricidal species. This suggests that egg size effects are more important than hatching asynchrony per se. In 'non-aggressive' species however similar and even greater mean percentage egg volume differences occur without obligate fratricide. For example, mean percentage egg volume differences from data presented by Slagsvold et al. (1984) for clutches of two, yield 11.6% for the House Sparrow and 45.4% for the Common Swift.

Hatching spread was found to be the most important factor affecting the relative difference in hatching mass in the House Martin (Bryant, 1978a), followed by food abundance at the time of laying, yet this was not due to differences in egg size. Gibbons (1987) found that in asynchronous broods, late hatched young died at an earlier age than in artificially synchronous broods; similar results have been found in the Fieldfare (Slagsvold, 1982).

Thus there is no consistent evidence to suggest that hatching asynchrony is more important than egg size effects in regulating the effectiveness of any supposed brood-reduction strategy. Is brood reduction then adaptive?

A number of assumptions are inherent in the idea of an adaptive value to brood reduction:-

(1) Brood reduction operates under conditions of food shortage when parents are unable to provision all of the brood (Lack, 1954);

(2) Parents allow selective starvation of the nestling in which least energy has been invested; usually the last hatched and smallest nestling;

(3) Such starvation results in increased reproductive success for parents operating brood reduction when compared with parents that do not operate brood reduction under similar food conditions.

These assumptions will be considered in turn.

5.12.2 Brood reduction and food shortage: Is there a link?

In the House Martin there is no evidence that the frequency of asynchronous hatching is correlated with direct measures of food supply nor any parameters that might indicate a deteriorating food supply, such as the progressive decline in clutch size, increased mortality amongst second broods, and failure of many pairs to attempt second broods at all (Bryant, 1975b). Conversely there is evidence that brood reduction might be maladaptive in this species. 17% of broods suffered death of the smallest chick although there was an adequate food supply. Of these 71% were from broods in which the relative difference in hatching mass was high and the remaining 29% from more synchronously hatching broods

(Bryant, 1975b). The breeding success of the Great Tit and Pied-flycatcher, Ficedula hypoleuca, was reduced to a greater degree in spruce-alder woodland than in rich deciduous woodland when hatching spread was experimentally increased, contrary to the prediction of the brood reduction hypothesis (Slagsvold, 1985).

Studies of Ardeids in which brood reduction is common suggest that parental inability to provision the brood is not linked with brood reduction. Mock (1985) showed that in fourteen of the seventeen Great Egret broods studied, brood reduction occurred, resulting in the loss of 26.5% of nestlings. Hand reared nestlings however given an unlimited food supply still fought suggesting that neither the hunger level of the largest sibling (O'Connor, 1978c) nor the food supply *per se* effects brood reduction. Similar results have been shown in Great Blue Herons fostered by Great Egrets (Mock, 1984), and in the Little Blue Heron (Werschkul, 1979). This suggests that it is the inability of parents to distribute food evenly amongst the brood, that regulates brood reduction.

Fujioka (1985a) found that no nestlings starved in artificially synchronized broods of the Cattle Egret, compared with asynchronous broods (where starvation was found) under similar food conditions, suggesting poor food supply is not the reason for brood reduction in this species. Braun & Hunt (1983) concluded that brood-reduction in Black-legged Kittiwakes, Rissa tridactyla, is related to the amount of food that chicks receive. Whilst the implication of the Kittiwake study was that food abundance determined the probability of brood reduction, the precise wording of their conclusion may be nearer the truth (see below).

5.12.3 Are small late-hatched young selectively starved?

I could only find evidence in one species that chick survival might be affected by the parents deliberately regulating food distribution between the young. In the Common Coot, *Fulica atra*, parents regulate which chicks accompany them on foraging trips and therefore actively maintain feeding differences within the brood (Horsfall, 1984b). This is viewed as a mechanism by which adults may preferentially feed chicks of the opposite sex (particularly by adult males) as a mechanism for reducing potential competitors for mates. There was no evidence to show that preferential feeding occurred during the period of chick mortality. Within the nest, though, this period is short.

There is more evidence to suggest it is the oldest siblings which regulate the occurrence of brood reduction. In 'aggressive' species such as raptors, Ardeids and some species of Bee-eater, older nestlings physically attack the smaller nestling and prevent access to food brought by the parents (Bryant, pers.comm.; Edwards & Collopy, 1983; Fujioka, 1985a; 1985b; Meyburg, 1974; Mock, 1984; 1985; O'Connor, 1978c; Ploger & Mock, 1986; Werschkul, 1979). In 'non-aggressive' species evidence that elder nestlings actually prevent access to food is lacking. In the Black-legged Kittiwake death of second hatched chicks does not directly result from reduced access to food (Braun & Hunt, 1983). In this species the smallest chick is forced from the nest by its bigger sibling and dies from exposure or starvation. In the Herring Gull, Laughing Gull and Blue-eyed Shag it appears that the smaller chick cannot compete effectively with its larger sibling (Hahn, 1981; Parsons, 1975; Shaw, 1985). Death of the smallest nestling due to overcrowding or trampling by larger siblings has been reported for a number of species (Holcombe, 1969; Rowan, 1967; Snow & Snow, 1973), and suggested as a possible factor in others (Slagsvold, 1982; 1985).

Accidental chilling of small young may be another explanation if parental brooding is inefficient, large siblings being more likely to obtain energetically advantageous positions within a huddle of chicks, and smaller nestlings forced to take positions around the edges of the huddle.

There is therefore evidence that in 'aggressive' species the smallest young are selectively starved, though in 'non-aggressive' species this has not been convincingly demonstrated.

The stage for brood reduction is theoretically set by the parent via either hatching asynchrony, or egg size, or both (O'Connor, 1978c), and brood reduction is viewed as an adaptive strategy whereby a parent increases its reproductive success. Is parental behaviour after hatching consistent with this hypothesis? Horsfall (1985b) asks the question "... do the parents reinforce sibling inequalities or attempt to negate them?" The decision as to whether or not a parent can successfully rear its brood must be made by that parent since it alone is sampling the environment with respect to food. If brood reduction is adaptive then parents should not persistently negate sibling inequalities. In some species, however, parents do attempt to prevent fights between siblings through brooding (Ingram, 1959; 1962; Meyburg, 1974; Proctor, 1975) although this may not be successful (Edwards & Collopy, 1983). In other 'aggressive' species no attempt is made by the parent to regulate sibling aggression (Edwards & Collopy, 1983; Fujioka, 1985b; Steyn, 1973).

Howe (1976) suggested that increasing egg mass with laying sequence was a means by which Common Grackles could 'insure' against brood reduction occurring too early. Conversely there is no evidence that parents actively reinforce sibling inequalities by ceasing to feed the smallest chick. This would be most effective if parents were to reduce their brood quickly and effeciently without wasting energy on feeding young which are doomed to die. This is one of the many paradoxes of the brood reduction hypothesis. It is assumed that parents would not let the smallest young die through starvation or physical attack from elder siblings if it were not in the parents interests to do so (Edwards & Collopy, 1983; Howe, 1978). A failure to negate sibling inequalities does not necessarily imply parental consent as suggested above. By preferentially feeding the largest sibling a parent may reduce the number of attacks on the smaller sibling and thus improve its survival chances in cases where sibling competition involves physical attacks.

Although, as stated above, in some species fighting still occurs when the eldest sibling is well fed. If a nestling were to effectively blackmail its parent by threatening to reduce parental fitness through siblicide (O'Connor, 1978c) then it would be in both the parents and eldest chicks interest to feed it first. This may explain why there is such a lack of evidence that late-hatched nestlings are selectively starved in 'non-aggressive' species since siblicide has not been demonstrated in such cases. Brown & Hunt (1983) suggest that replete chicks may be less aggressive in the Black-legged Kittiwake lending support to this view. Hence the original implication in the brood reduction hypothesis proposed by Lack (1954), that of a passive mechanism of selective starvation brought about solely by size differences within the brood, and which can be negated in times of food abundance, is not supported by detailed evidence from the literature.

Patterns of brood-reduction are not consistent between 'non-aggressive' species, and mechanisms which may bring this about have yet to be proven. In 'aggressive' species however there is strong evidence to support the view that it is the larger nestlings that determine brood reduction, but it is unclear if this is in the interest of the parent or not since parents seem regularly to attempt to reduce sibling conflict within some species. The adaptive significance of brood reduction thus remains unproven, by these data. The only way in which this may be conclusively demonstrated is if the lifetime reproductive success of brood reducing parents is significantly higher than non-brood reducing parents under similar conditions.

This is considered below.

5.12.4 Is the reproductive success of brood-reducing parents higher than non-brood reducing parents under similar conditions?

Few studies have sought to answer this question, Hahn (1981) compared the reproductive success of parent Laughing Gulls rearing asynchronous and artificially synchronous broods, and concluded that "... data on parental reproductive success confirmed Lack's hypothesis that staggered hatching of the brood would allow parents to fledge more offspring on average than would synchronous hatching". Her data are discussed below since it is the most direct attempt to demonstrate the adaptive significance of brood reduction to date.

The average fledging rate of parents with asynchronously hatching broods was significantly higher than those with synchronously hatching broods, thus indeed appearing to confirm Lack's hypothesis. The higher fledging rate in asynchronous broods however, was largely due to the higher proportion of full broods fledged, i.e. those in which no brood reduction had occurred. Hahn acknowledges that this is a 'major source of the difference between groups', but contends that brood reduction is only activated in broods where parents cannot rear all of the young. The capability to increase reproductive success will be reflected only in the relative frequency with which asynchronous broods salvage partial broods and avert complete nest failure. The rationale behind this explanation is sound, however Hahn's data do not support her conclusions for several reasons. Firstly, the number of pairs fledging full broods in the study is the only significant source of difference between the groups. Neither partial broods raised nor those in which complete nest failure occurred were significantly different (Hahn, 1981, Table 1). Yet Hahn presents as evidence (Table II) in support of her view that synchronous nests have twice as many nest failures. By the same token, however, synchronous broods have 1.5 times as many partial broods reared, at odds with the brood reduction hypothesis. The ratio of partial broods reared to complete nest failure is higher in asynchronous broods, but is this relevant? Complete nest failure can be caused by factors other than death of the brood through starvation due to food shortage as proposed by the brood reduction hypothesis. For example, desertion due to disturbance could be one important source of error in this measurement. Partial brood failure is more consistent with death through starvation, though not conclusively so (see Section 5.12.3). It only requires one less complete brood failure in Hahn's synchronous broods for the two ratios to be almost identical. On the basis of such a small sample size such conclusions cannot be justified.

There are other inconsistences with the brood reduction hypothesis. The proportion of third chicks fledging in the Laughing Gull was similar for synchronous and asynchronous broods (62.5 and 54.2% respectively). Mortality of the first hatched chicks occurred in partial loss broods, 6.3% for asynchronous and 23.5% for synchronous broods. Nestlings therefore did not consistently die in the order predicted by the brood reduction hypothesis, i.e. smallest first.

Survival of the third-hatched chicks in the Cattle Egret (Bulbulcus ibis) was not significantly different from first or second hatched chicks, despite losing more fights and receiving less food than their siblings (Ploger & Mock, 1986). Asynchronous and artificially synchronous broods of the Jackdaw did not differ in the number of chicks fledged, or mass, wing-length or tarsus length at 26 days of age (Gibbons, 1987). Artificially synchronized broods of the White-bellied Swiftlet fledged almost twice as many full broods 42%, compared with naturally asynchronous broods 23%, and artificially asynchronous broods 7% (Bryant, pers.comm.). Nor was there a difference in the quality of nestlings from synchronous and naturally asynchronous broods as indicated by fledging mass.

In enlarged Fieldfare broods, when only small age differences existed amongst hatchlings, their survival rate was higher than that of enlarged asynchronous broods (Slagsvold, 1982).

A study of the Blue-eyed Shag has shown that in a sample of artificially synchronized broods, chick survival was as high as normal asynchronously hatching broods, but there were more cases of total brood loss (Shaw, 1985). Total brood loss was found to be high in the House Sparrow even though it shows hatching asynchronous which supposedly favours brood reduction and thus avoids total brood loss (Clark & Wilson, 1981). There was no significant difference in survival of fledged young to eighty days old in broods of Magpies which had brood reduced young replaced with live young of similar age, when compared with control broods in which young were not replaced, and a third group in which nestlings were artificially brood reduced (Husby, 1986). Almost twice as many fifth-hatched young survived in synchronous broods (19.4%) compared with asynchronous broods (11.5%) in the Common Grackle (Howe, 1976).

These studies show that parents can fledge more young by synchronously hatching their broods than by asynchronously hatching them and apparently suffering a cost through brood reduction.

There is a possible explanation that could account for the apparent maladaptive nestling mortality due to hatching asynchrony. Egg-dumping has been reported in some species (e.g. Bertram, 1980; Bryant, pers.comm., Møller, 1987; Yom-Tov et al., 1974) and may be more widespread than previously thought due to difficulties in detecting dumped eggs. If egg dumping was found to be common amongst altricial birds, brood reduction might be an adaptation to protect against this. The powerful new tool of 'DNA fingerprinting' may be one way in which this could be examined (Jeffreys et al., 1985a,b) by looking at the identity of brood reduced individuals, or 'runts' and seeing if they are more likely to be 'dumped' young. This technique has the advantage over enzyme polymorphism studies in that individual-specific 'fingerprints' may be detected (Hill, 1987). Though initially used primarily on humans it has recently been applied to wild birds (Burke & Buford, 1987; Wetton et al., 1987). Wetton et al. (1987) were able to detect mixed parentage among nestling House Sparrows by this method, and identify male House Sparrows engaged in extra-pair copulations by "finger-printing" colony members.

To summarize:-

(1) Brood reduction occurs in even-aged and uneven-aged broods, although the latter may speed up the death of the smallest chick;

(2) There is no evidence that hatching asynchrony is necessary to produce brood reduction;

(3) The available evidence shows that brood reduction occurs independently of food availability for the brood, and that young may die when food remains abundant;

(4) Little evidence exists to demonstrate a mechanism of selective starvation in 'non-aggressive' species, i.e. those in which sibling rivalry is mediated through begging behaviour alone.

(5) Selective starvation is common in 'aggressive' species (e.g. raptors, Ardeids) and is primarily determined by aggressive behaviour of early-hatched siblings over later-hatched siblings and not by selective feeding by the parents;

(6) There is some evidence to suggest that parents attempt to counteract this behaviour but that it is not generally successful;

(7) There is no evidence to support the view that brood reduction results in a greater reproductive success in any particular breeding season;

(8) There is evidence to suggest brood reduction may incur a cost and is likely to be maladaptive;

(9) There appears to be distinct advantages to be gained through synchronously rather than asynchronously hatching broods and these will be discussed further below.

5.13 HATCHING ASYNCHRONY: COST OR BENEFIT?

The previous discussions on the evolution of hatching asynchrony in birds has shown that there is no evidence to confirm the view that hatching asynchrony is adaptive. There is evidence, however, to suggest that birds should tend to be as synchronous as possible in hatching their broods, since advantages do seem to be demonstrated in these instances (see above).

Why then do many atricial birds not commence incubation on the last egg? There are possibly two further explanations which should be considered in subsequent studies on birds. The first is that hatching asynchrony is an incidental rather than selected trait (Mead & Morton, 1985). The second is that reproductive fitness of a female (and perhaps her mate) is likely to be correlated with longevity. Hence any factor which results in a high probability of female mortality would be selected against; selection against female mortality is thus likely to be greater than from losing the odd nestling (or brood) through hatching asynchrony.

It is possible that egg carrying females are more vulnerable to predation, or other mortality out of the nest, although as far as I am aware this has not been demonstrated. Whilst if this does occur, it may be advantageous for birds to be on the nest, it does not explain why they commence incubation before the last egg is laid, since birds can attend the nest without incubating. There are a number of factors which may select for early nest attendance. Guarding against predators in large species (Slagsvold et al., 1984), preventing the stealing of nest material (Blaker, 1969), prevention of egg freezing (Hussell, 1972), or overheating (Maclean, 1967); or even preventing destruction of eggs by potentially polyandrous males (Davies, 1985). None of these factors explain the lack of early incubation in most species.

It would therefore appear that a view of hatching asynchrony as an incidental trait may be a realistic alternative to current adaptive hypothesis. Mead & Morton (1985) suggest a hormonal hypothesis for hatching asynchrony. They provide some evidence that a single hormone possibly prolactin, is responsible for both the inhibition of ovulation and the initiation of incubation. Egg production and hatching asynchrony are thus envisaged as varying in response to the rate of prolactin synthesis and release. The hypothesis predicts that most birds should commence incubation on the penultimate egg, a fact already confirmed for passerines (Clark & Wilson, 1981; Smith, 1983). Consideration of hatching asynchrony in this study did not find support for current adaptive hypotheses, but rather lend support to the view that hatching asynchrony is an incidental trait, and one in which costs may outweigh benefits.

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APPENDICES

APPENDIX I

Energetics of nestling growth: Data available and sources

(a) Species for which water index or water content data are available and sources

(i) Water index of whole bird v. age

Starling, *Sturnus vulgaris*	Ricklefs, 1979
Common Tern, *Sterna hirundo*	Ricklefs & White, 1981
Japanese Quail, *Coturnixc.japonica*	Brisbin et al., 1973
Wood Duck, *Aix sponsa*	Clay et al., 1979
Double Crested Cormorant, *Phalacrocorax auritus*	Dunn, 1975
Sooty Tern, *Sterna fuscata*	Ricklefs & White, 1981
Rufous-winged Sparrow, *Aimophila carpalis*	Austin & Ricklefs, 1977
Cactus Wren, *Campylorhynchus brunneicapillus*	Austin & Ricklefs, 1977
House Martin, *Delichon urbica*	Bryant & Gardiner, 1979
Barn Swallow, *Hirundo rustica*	Ricklefs, 1967
Red-winged Blackbird, *Agelaeus phoenicius*	Ricklefs, 1967
Sand Martin, *Riparia riparia*	Jones, 1985
Herring Gull, *Larus argentatus*	Dunn & Brisbin, 1980
White-bellied Swiftlet, *Collacalia esculenta*	Bryant & Hails, 1983
Blue-throated Bee-Eater, *Merops viridis*	Bryant & Hails, 1983
Pacific Swallow, *Hirundo tahitica*	Bryant & Hails, 1983
Magpie, *Pica pica*	Tatner, 1984
Dipper, *Cinclus cinclus*	This study

(ii) Water index of major body components

Sooty Tern	Ricklefs & White, 1981
Common Tern	Ricklefs & White, 1981
Rufous-winged Sparrow	Austin & Ricklefs, 1977
Red-winged Blackbird	Ricklefs, 1967
Canvasback, *Aythya valisena*	Lightbody & Ankey, 1984
Lesser Scaup, *Aythya affinis*	Lightbody & Ankey, 1984

(a)(ii) continued...

Blue Tit, *Parus caeruleus*	O'Connor, 1977
House Sparrow, *Passer domesticus*	O'Connor, 1977
House Martin, *Delichon urbica*	O'Connor, 1977
Northern Gannet, *Sula bassana*	Ricklefs et al., 1984

(iii) Water index at hatching only

Leach's Storm-Petrel *Oceanodroma leucorhoa*	Ricklefs et al., 1980
Sooty Tern	Ricklefs, 1981
Common Tern	Ricklefs, 1981
Starling	Ricklefs, 1979
Japanese Quail	Ricklefs, 1979

(iv) Water content of whole bird

Blue Tit	O'Connor, 1977
House Sparrow	O'Connor, 1977
House Martin	O'Connor, 1977
White-bellied Swiftlet	Bryant & Hails, 1983
Blue-throated Bee-Eater	Bryant & Hails, 1983
Pacific Swallow	Bryant & Hails, 1983
Starling	Westerterp, 1973
Northern Gannet	Ricklefs et al., 1984
Dipper	This study

(b) Species for which lipid index or lipid content data are available and sources

(i) Lipid index of whole bird v. age

Sand Martin	Turner & Bryant, 1979
Wood Duck	Clay et al., 1979
Double Crested Cormorant	Dunn, 1975
Japanese Quail	Brisbin & Tally, 1973
House Martin	Bryant & Gardiner, 1979
Barn Swallow	Ricklefs, 1967
Red-winged Blackbird	Ricklefs, 1967
Herring Gull	Dunn, 1980
White-bellied Swiftlet	Bryant & Hails, 1983
Blue-throated Bee-Eater	Bryant & Hails, 1983
Pacific Swallow	Bryant & Hails, 1983

(b)(i) continued...

House Martin	O'Connor, 1977
House Sparrow	O'Connor, 1977
Blue Tit	O'Connor, 1977
Magpie	Tatner, 1984
Dipper	This study

(ii) Lipid content of whole bird v. age

Blue Tit	O'Connor, 1977
House Sparrow	O'Connor, 1977
House Martin	O'Connor, 1977
Barn Swallow	Ricklefs, 1967
Red-winged Blackbird	Ricklefs, 1967
Rufous-winged Sparrow	Austin & Ricklefs, 1977
Common Tern	Ricklefs & White, 1981
Sooty Tern	Ricklefs & White, 1981
Leach's Storm-Petrel	Ricklefs & White, 1981

(c) Species for which non-lipid data are available and sources

References refer to lean dry mass unless asterixed which refers to lean wet mass.

(i) Non-lipid content of whole bird v. age

Japanese Quail	Ricklefs, 1979
Starling	Ricklefs, 1979
Common Tern	Ricklefs & White, 1981
Sooty Tern	Ricklefs & White, 1981
*Leach's Storm-Petrel	Ricklefs et al., 1980
Rufous-winged Sparrow	Austin & Ricklefs, 1977
White-bellied Swiftlet	Bryant & Hails, 1983
Blue-throated Bee-Eater	Bryant & Hails, 1983
Pacific Swallow	Bryant & Hails, 1983
Sand Martin	Jones, 1985
House Martin	O'Connor, 1977
House Sparrow	O'Connor, 1977
Blue Tit	O'Connor, 1977
Magpie	Tatner, 1984
*Northern Gannet	Ricklefs et al., 1984
Dipper	This study

(d) Species for which energy content or energy density data are available and sources

(i) Wet energy density v. age

White-bellied Swiftlet	Bryant & Hails, 1983
Blue-throated Bee-Eater	Bryant & Hails, 1983
Pacific Swallow	Bryant & Hails, 1983
Barn Swallow	Ricklefs, 1967
House Martin	Bryant & Gardiner, 1979
Rufous-winged Sparrow	Austin & Ricklefs, 1977
Red-winged Blackbird	Ricklefs, 1967
Starling	Westerterp, 1973
Herring Gull	Dunn & Brisbin, 1980
Japanese Quail	Brisbin & Tally, 1973
Double Crested Cormorant	Dunn, 1975
Wood Duck	Clay et al., 1979
Dipper	This study

(ii) Dry energy density v. age

House Martin	Bryant & Gardiner, 1979
Starling	Westerterp, 1973
Double Crested Cormorant	Dunn, 1975
Dipper	This study

(iii) Energy content v. age

House Martin	Bryant & Gardiner, 1979
Barn Swallow	Austin & Ricklefs, 1977
Cactus Wren	Austin & Ricklefs, 1977
Red-backed Shrike, *Lanius collurio*	Austin & Ricklefs, 1977
House Sparrow	Austin & Ricklefs, 1977
Rufous-winged Sparrow	Austin & Ricklefs, 1977
Red-winged Blackbird	Austin & Ricklefs, 1977
Dipper	This study

APPENDIX II

Software for the microprocessor system. This is primarily in BBC 'Basic' with minor alterations to allow compatability with the 'Eurocube' BBC card. The latter was the main microcomputer component and is essentially a BBC computer without the keyboard. The program reads thermistor signals via a 12 bit A-D converter and stores all data in a 32K memory card fitted with 'CMOS' RAM chips, to increase field usage time. The initial machine code section of programme logs the data against a real-time clock on another card within the microprocessor. Lines 10-2420 control the record mode whilst lines 2430-2860 control replay mode and sends the data to a DEC VAXA mainframe computer.

```
10     PORTA=&FE01
20     DDRA=&FE03
30     ?DDRA=16
40     ?PORTA=16
50     SW=?PORTA
60     SW=SW AND 8
70     IF SW=0 GOTO 2430
80     IRQ2V=&0206
90     OLD2V=&3FF7
100    Time=&3FF0
110    ?(Time)=0
120    ?(Time+1)=0
130    ?(Time+2)=0
140    VIA=&FE00
150    P%=&3E00
160    FOR PASS=0 TO 2
170    COPT PASS
180    .Clk
190    PHA
200    CLC
210    INC Time
220    LDA Time
230    CMP #100
240    BCC OUT
250    LDA #0
260    STA Time
270    INC Time+1
280    CLC
290    LDA Time+1
300    CMP #100
310    BCC OUT
320    LDA #0
330    STA Time+1
340    INC Time+2
350    .OUT LDA &FE04
360    PLA
370    RTI
380    .Stclk SEI
390    LDA IRQ2V
400    STA OLD2V
410    LDA IRQ2V+1
420    STA OLD2V+1
430    LDA #Clk MOD 256:STA IRQ2V
440    LDA #Clk DIV 256:STA IRQ2V+1
450    LDA #&FF
460    STA VIA+&02
470    STA VIA
480    LDA #&C0
490    STA VIA+&0B
500    LDA #&7F
510    STA VIA&0D
520    STA VIA+&0E
530    LDA #&C0
540    STA VIA+&0E
```

```
550   LDA #&10
560   STA VIA+&04
570   LDA #&27
580   STA VIA+05
590   CLI
600   RTS
610   .Stpclk SEI
620   LDA OLD2V
630   STA IRQ2V
640   LDA OLD2V+1
650   STA IRQ2V+1
660   LDA #&7F
670   STA VIA+&0D
680   STA VIA+&0E
690   LDA #&00
700   STA VIA+&0B
710   CLI
720   RTS
730   ]
740   NEXT PASS
750   M=0
760   F=0
770   SW2=0
780   BASE=&0800
790   MIN=44
800   CALLStclk
810   AT=?(Time+1)+(100*?(Time+2))
815   CT=AT DIV 60
820   BT=AT MOD 60
825   PRINT"TIME="CT"MINS",BT"SECS"
830   PROCSWCH
840   DEF PROCTEMP
850   PRINT"TEMP"
860   @%=&00020103
870   CH=0:PROCAD(CH):PROCMEM
880   CH=1:PROCAD(CH):PROCMEM
890   CH=2:PROCAD(CH):PROCMEM
900   CH=3:PROCAD(CH):PROCMEM
910   CH=4:PROCAD(CH):PROCMEM
920   CH=5:PROCAD(CH):PROCMEM
930   CH=6:PROCAD(CH):PROCMEM
935   PROCEOF
940   ENDPROC
950   DEF PROCAD(CH)
960   ?&DC0E=&7F
970   ?&DC0C=&00
980   ?&DC03=%FF
990   ?&DC02=&FF
1000  ?&DC00=&F5
1010  ?&DC01=(CH)
1020  ?&DC00=&F1
1030  ?&DC00=&F5
1040  ?&DC03=&00
1050  ?&DC00=&F7
```

```
1060  ?&DC00=&F3
1070  MSB%=?&DC0F
1080  ?&DC00=&FB
1090  LSB%=?&DC0F
1100  ?&DC00=&F5
1110  ?&DC03=&FF
1120  LSB%=(LSB% AND 240)DIV 16
1130  Z=(MSB%*16)+LSB%
1140  V=(Z*10)/4095
1150  T=0.517+(13.9664*V)-(0.3298*V^2)+(0.4554*V^3)
1160  PRINTT
1170  ENDPROC
1180  DEF PROCMEM
1190  ?(BASE)=MSB%
1200  BASE=BASE+1
1210
1220  IF (BASE)=&2000 THEN PROCRESET
1230  IF (BASE)=&8000 THEN GOTO 1580
1240  ?(BASE)=LSB%
1250  BASE=BASE+1
1260  IF (BASE)=&2000 THEN PROCRESET
1270  IF (BASE)=&8000 THEN GOTO 1580
1280  ENDPROC
1290  DEF PROCSWCHMEM
1300  ?(BASE)=255
1310  BASE=BASE+1
1320  PRINT"MARKER IS 255"
1330  IF (BASE)=&2000 THEN PROCRESET
1340  IF (BASE)=&8000 THEN GOTO 1580
1350  ?(BASE)=SW
1360  BASE=BASE+1
1370  IF (BASE)=&2000 THEN PROCRESET
1380  IF (BASE)=&8000 THEN GOTO 1580
1390  ENDPROC
1400  DEF PROCTIME
1401  AT=?(Time+1)+(100*?(Time+2))
1402  BT=AT MOD 60
1403  CT=AT DIV 60
1410  ?(BASE)=CT
1420  BASE=BASE+1
1430  IF (BASE)=&2000 THEN PROCRESET
1440  IF (BASE)=&8000 THEN GOTO 1580
1450  ?(BASE)=BT
1460  BASE=BASE+1
1470  IF (BASE)=&2000 THEN PROCRESET
1480  IF (BASE)=&8000 THEN GOTO 1580
1490  @%=&00020003
1500  PRINT"TIME="CT"MINS",BT"SECS"
1570  ENDPROC
1580  ?PORTA=0
1590  CALL Stpclk
1600  END
1610  DEF PROCRESET
1620  BASE=&4000
```

```
1630  PRINT "CHECK"
1640  ENDPROC
1650  DEF PROCTEN
1660  THERM=T
1670  PRINT"THERM="THERM
1680  GRND=?(Time+1)+(100*?(Time+2))
1690  CURRENT=?(Time+1)+(100*?(Time+2))
1700  SW=?PORTA
1710  SW=SW AND 7
1720  SW1=SW EOR 7
1730  IF SW2=SW1 THEN GOTO 1770
1740  PROCSWCHMEM
1750  PROCPRNT
1760  SW2=SW1
1770  IF CURRENT=GRND +15 THEN PROCNOB ELSE GOTO 1690
1780  SW=?PORTA
1790  SW=SW AND 7
1800  SW=SW EOR 7
1810  IF SW=0 THEN GOTO 1860
1820  IF SW=1 THEN GOTO 1860
1830  IF SW=2 THEN GOTO 1860
1840  IF SW=3 THEN GOTO 1860
1850  GOTO 1680
1860  IF NOT (T<THERM) THEN GOTO 1880
1870  GOTO 1680
1880  PRINT"EXIT PROCTEN"
1890  ENDPROC
1900  DEF PROCSWCH
1910  SW=?PORTA
1920  SW=SW AND 7
1930  SW1=SW EOR 7
1940  IFSW2=SW1 THEN GOTO 1910
1950  PROCSWCHMEM
1960  PROCSTATUS
1970  SW2=SW1
1980  GOTO1910
1990  ENDPROC
2000  DEF PROCSTATUS
2010  IF SW1=0 PRINT"NO BEG   M.IN   F.IN"
2020  IF SW1=0 PROCTIME:PROCTEMP
2030  IF SW1=1 PRINT"   BEG   M.IN   F.IN"
2040  IF SW1=1 PROCTIME:PROCTEMP
2050  IF SW1=2 PRINT"NO BEG   M.OUT  F.IN"
2060  IF SW1=2 PROCTIME:PROCTEMP
2070  IF SW1=3 PRINT"   BEG   M.OUT  F.IN"
2080  IF SW1=3 PROCTIME:PROCTEMP
2090  IF SW1=4 PRINT"NO BEG   M.IN   F.OUT"
2100  IF SW1=4 PROCTIME:PROCTEMP
2110  IF SW1=5 PRINT"   BEG   M.IN   F.OUT"
2120  IF SW1=5 PROCTIME:PROCTEMP
2130  IF SW1=6 PRINT"NO BEG   M.OUT  F.OUT"
2140  IF SW1=6 PROCTIME:PROCTEMP:PROCTEN
2150  IF SW1=7 PRINT"   BEG   M.OUT  F.OUT"
2160  IF SW1=7 PROCTIME:PROCTEMP:PROCTEN
2170  ENDPROC
```

```
2180  DEF PROCPRNT
2190  IF SW1=0 PRINT"NO  BEG   M.IN   F.IN"
2200  IF SW1=0 PROCTIME:PROCTEMP
2210  IF SW1=1 PRINT"    BEG   M.IN   F.IN"
2220  IF SW1=1 PROCTIME:PROCTEMP
2230  IF SW1=2 PRINT"NO  BEG   M.OUT  F.IN"
2240  IF SW1=2 PROCTIME:PROCTEMP
2250  IF SW1=3 PRINT"    BEG   M.OUT  F.IN"
2260  IF SW1=3 PROCTIME:PROCTEMP
2270  IF SW1=4 PRINT"NO  BEG   M.IN   F.OUT"
2280  IF SW1=4 PROCTIME:PROCTEMP
2290  IF SW1=5 PRINT"    BEG   M.IN   F.IN"
2300  IF SW1=5 PROCTIME:PROCTEMP
2310  IF SW1=6 PRINT"NO  BEG   M.OUT  F.OUT"
2320  IF SW1=6 PROCTIME:PROCTEMP
2330  IF SW1=7 PRINT"    BEG   M.OUT  F.OUT"
2340  IF SW1=7 PROCTIME:PROCTEMP
2350  ENDPROC
2360  DEF PROCNOB
2370  SW=?PORTA
2380  SW=SW AND 7
2390  SW1=SW EOR 7
2400  PROCSWCHMEM
2410  PROCPRNT
2420  ENDPROC
2430  @%=&00020103
2440  BASE=&0800
2450  M=?(BASE)
2460  PRINTM
2470  IF M=255 GOTO 2480 ELSE GOTO 2730
2480  PROCINC
2490  SW=?(BASE)
2500  PRINTSW
2510  PROCINC
2520  CT=?(BASE)
2530  PRINTCT
2540  PROCINC
2550  BT=?(BASE)
2560  PRINTBT
2570  PROCINC
2610  FOR K=1 TO 7
2620  MSB%=?(BASE)
2630  PROCINC
2640  LSB%=?(BASE)
2650  PROCINC
2660  LSB%=(LSB% AND 240)DIV 16
2670  Z=(MSB%*16)+LSB%
2680  V=(Z*10)/4095
2690  IF K=1 THEN T=47.4-(37.4*V)+(12.2*V^2)
2691  IF K=2 THEN T=-7.21+(9.67*V)+(0.318*V^2)
2692  IF K=3 THEN T=8.02+(2.55*V)+(1.37*V^2)
2693  IF K=4 THEN T=8.04+(2.26*V)+(1.42*V^2)
2694  IF K=5 THEN T=8.05+(2.46*V)+(1.47*V^2)
2695  IF K=6 THEN T=8.24+(1.98*V)+(1.40*V^2)
2696  IF K=7 THEN T=7.98+(2.80*V)+(2*V^2)
```

```
2700  PRINTT
2710  NEXT K
2711  G=?(BASE)
2712  IF G=250 GOTO 2745
2720  GOTO 2450
2730  PRINT"ERROR"
2740  END
2745  PRINT"END OF FILE"
2746  END
2750  ENDPROC
2760  DEF PROCINC
2770  BASE=BASE+1
2780  IF (BASE)=&2000 THEN BASE=&4000
2790  IF (BASE)=&4000 THEN PRINT"RESET"
2800  IF (BASE)=&8000 THEN GOTO 2820
2810  ENDPROC
2820  PRINT"MEMORY FULL!"
2830  END
2840  DEF PROCEOF
2850  ?(BASE)=250
2860  ENDPROC
```