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Chick growth and prey quality in the European Bee-eater (*Merops apiaster*)

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Abstract. 1. In each of four replicate experiments we fed three groups of bee-eater chicks for 24 h on different diets: bees, dragonflies, and a mixture of the two.

2. Dry weight assimilation efficiency did not differ between treatments and was in the region of 40–50%. Caloric assimilation efficiency was about 60% and did not differ significantly between diets.

3. Mean Growth efficiency (wt. gain/intake) was highest in all four replicates in chicks fed on the mixed diet.

4. When metabolic requirements are taken into account, growth efficiency on the mixed diet varies less with variation in intake than on the two pure diets.

5. The advantage of feeding chicks on a mixed diet may partly explain why parents do not show exclusive preferences for energy-maximising prey types.

Introduction

In this paper we describe an experiment to test whether or not nestling bee-eaters put on more weight per gram of food consumed when fed on a mixed diet than on pure diets of one kind of insect. Our interest in this question arose from tests of energy-maximisation models of foraging. Although these models provide good qualitative accounts of prey choice in many species, including the European bee-eater (Krebs and Avery 1985), predators often show partial preferences where total selectivity is predicted by the models. One of the many possible explanations (Krebs et al. 1983; Krebs and McCleery 1984) for partial preferences is that different prey contain different nutrients so that growth or maintainance is reduced on a pure diet (e.g. Rapport 1980). Although the importance of food quality and chemical defences are widely recognized in the literature on herbivorous and frugivorous animals (e.g. Freeland and Janzen 1974; Owen-Smith and Novellie 1982; Belovsky 1978) it is little studied in insectivorous or carnivorous predators (Greenstone 1979). Three studies of birds feeding on invertebrates have suggested that specific differences in prey quality are important determinants of prey choice, but have not provided direct evidence for the effects of these differences. Royama (1970) explained the tendency of great tits (*Parus major*) to bring spiders to c. 10-day old nestlings in terms of the requirements of nestlings at this age for sulphur-containing amino acids, which are supposedly more abundant in spiders than in lepidopteran larvae, the normal food of great tits. Goss-Custard (1977) found that redshank (*Tringa totanus*) preferred the amphipod *Corophium volutator* to nereid worms even though the latter are energetically more profitable. He suggested that requirements for a nutrient found in the *Corophium* but not in the worms may account for the redshanks' preference; but provided no evidence. Finally Tinbergen (1981), noting that starlings (*Sturnus vulgaris*) preferred to feed their chicks on larvae of the lepidopteran *Cerapteryx* over energetically more profitable tipulid larvae, referred to an observation of Kluijver (1933) that starling chicks fed solely on *Tipula* larvae develop watery faeces and become prone to chilling because of damp plumage.

The European bee-eater in the Camargue, France feeds its chicks largely on two taxonomic groups of prey; Odonata and Hymenoptera. At a nest equipped with an automatic camera in 1982, for example, 46% of prey were dragonflies, 36% were bees ($n=1{,}361$). By dry weight, 85% were dragonflies, 7% bees and no other identified taxon (Orthoptera, Lepidoptera, Hemiptera, Diptera and Coleoptera) accounted for more than 1% of dry weight of the prey (Krebs and Avery unpublished). The dragonfly prey are made up of a small number of genera (primarily *Anax, Aeschna, Orthetrum, Sympetrum* and *Brachytron*) and the Hymenoptera are mainly *Apis* and *Andrena*. Variation in the size of prey brought to the nest can largely be accounted for by a central-place foraging model (Orians and Pearson 1979, Lessells and Stephens 1982) based on the hypothesis of energy-maximising (Krebs and Avery 1985). However, the tendency for parents to bring a mixture of large and small prey when ignoring small ones (bees) would have been energetically more profitable les us to question the validity of the assumption that all prey species are nutritionally equivalent.

We therefore fed experimental groups of chicks for short periods on three diets containing the two main taxa: (a) a pure diet of bees (b) a pure diet of dragonflies and (c) a mixed diet of approximately equal weights of bees and dragonflies. We measured weight gain, amount eaten and faecal production over a 24 h experimental period. The experiment was performed four times with different groups of chicks.

Methods

Chicks

Chicks were taken from nests in 1982 and 1983 at two colonies on the Arles Port-de-Bouc canal under license from CRBPO. The bee-eater is an asynchronous hatching species both within and between broods. There was thus consider-

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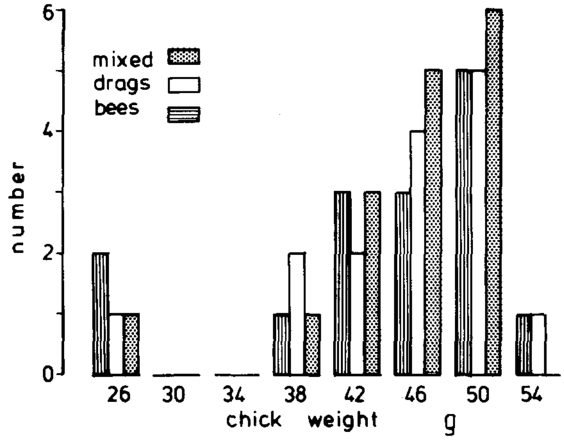


Fig. 1. Size distribution of chicks used in the three experimental treatments

able variation in weight of chicks used in the experiments (Fig. 1). Chicks were assigned to the three treatment groups by mixing broods at random and matching sizes of chicks between treatments. When possible, parents were left with one chick in the nest (observation confirmed that parents always continue to feed a solitary chick) and after the experiment chicks were returned to burrows (and were always fed by adults). A total of 40 chicks from 12 nests were used in the four replicates. In 1983 six chicks were used in two successive experimental replicates, and were assigned to new groups between experiments. In 1982, 11 chicks were used in a pilot study to measure passage time (see below) and 10 of these were then used in the 1982 experiment referred to below.

Prey

The bees, *Apis mellifera* workers, were taken at night from a hive at Tour du Valat, Camargue, France in 1982, and from a hive in Oxford, England in 1983. They were destinged using watchmaker's forceps before feeding them to the chicks. In 1982 about 25% of the bees were *Andrena* spp. captured in a sweep net in alfalfa and clover fields which were habitually used by foraging bee-eaters. The dragonflies in both years were captured at the Arles-Port-de-Bouc canal, another bee-eater foraging site, and primarily belonged to the species *Sympetrum striolatum* with a small proportion of *Crocethemis erythrea* and *Orthetrum cancellatum*. The most effective way to capture dragonflies was to drive a car rapidly along the grass banks separating rice fields, with a sweep net held out of the window at a height of 1 m above the vegetation. With this method it was possible to catch several hundred dragonflies in 0.5 h.

Both prey types were immediately placed in sealed plastic boxes and killed by deep freezing. They were kept frozen until shortly before use and were kept refrigerated between feeds in the course of the experiments. A sample of each prey type used in the experiments was dried at 40° C to a constant weight and subjected to calorimetric estimation in a Phillipson microbomb calorimeter.

Housing the chicks

After assigning them to groups, the chicks were housed in twos in cardboard boxes measuring 25 × 18 × 15 cm. They were kept in twos to aid thermoregulation. During experimental days, when the data on assimilation efficiency were collected (see below), the chicks were kept on dry-weighed pieces of baking foil and absorbent cellulose pads ("Boots cellulose wadding").

Experimental protocol

The procedure for each experimental replicate was as follows. (a) Chicks were fed on their experimental diets for 24–36 h (depending on the time of day they were brought into the laboratory from the field). This was to allow an "equilibration" period on the diets. (b) The experimental day started at 7.00 am. Each chick was weighed on a Mettler top-loading balance and pairs were placed on their weighed foils and pads. They were fed at 45 minute intervals until 7.00 pm and at each feed the number of items fed was recorded. The mixed diet group was fed alternating meals of bees and dragonflies. Some chicks begged readily and were simply fed until satiated at each feed. Other chicks did not beg and were fed by hand similar amounts to those which the begging birds consumed. In the 1983 experiments there were four chicks per treatment, and in 1982 there were four in the mixed group and three in each pure treatment group. The 45 min feeding interval was chosen because it allowed enough time to feed each chick and allow a short gap before the start of the next feed. In the wild, parents at the camera nest referred to earlier fed each chick on average 2.8 times per hour. The mean dry weight of prey given was 137 mgm – yielding a total of 384 mgm/chick/h. In our experimental conditions this would be equivalent to 288 mgm/chick/feed (every 45 min) which is about 10 bees or seven dragonflies. In practice we fed the captive chicks somewhat more than this at each feed ($\bar{x} \pm$ s.e. $= 11.67 \pm 0.3$ for bees and 8.54 ± 0.28 for dragonflies).

At the end of the 12-h feeding period we weighed the chicks and left them over night, weighing them again at 7.00 am the following day. The measurement of weight gain referred to in the results is 24 h weight gain. In a pilot study we measured passage time by feeding the chicks small plastic tags at 7.00 am and at midday. The tags ($n = 24$) were regurgitated, along with chitinous exoskeletons of the insect food, and the mean regurgitation time for the 7.00 am tags was 6 h (no difference between diets). The midday tags were always regurgitated overnight. We therefore concluded that one day's food is processed within 24 h of the start of the day. Any error in this estimate would not affect our results since our animals were equilibrated on the experimental diet before the start of the experiment.

Results

Assimilation efficiency

Table 1 shows the dry weight and caloric assimilation efficiency of chicks on the three diets. For the three 1983 replicates there are more detailed data than for 1982: regurgitated pellets and other excreta were weighed separately, and data for each pair of chicks were kept separate. Since bee-eater chicks regurgitate the exoskeletons of their prey, assimilation efficiency is calculated as:

$$\text{A.E.} = \frac{I-(F+U+P)}{I} \times 100$$

Table 1. Dry-weight assimilation efficiencies of chicks fed on three diets

Treatment	Replicate	Grams eaten	Pellets (g)	Total output ($F+U+P$) (g)	Dry wt Assimilation Efficiency	Caloric Assimilation Efficiency
Bees	1983 I a	9.6837	2.4405	5.39	44.34	55.63
	1983I b	10.3140	3.02	5.88	42.99	53.50
	1983 II a	13.4369	3.3150	6.89	48.72	58.69
	1983 II b	9.1680	3.3680	4.85	47.10	53.91
	1983 III a	11.1162	2.4743	5.946	46.73	57.97
	1983 III b	11.7521	2.6034	6.592	43.90	56.29
	1982[a]	17.721	–	10.681	39.72	–
	$\bar{x}\pm$S.E.				44.79±1.1	56.00±0.86
Mixed	1983 I a	11.314	2.564	5.917	47.70	64.02
	1983 I b	10.293	2.643	5.59	45.69	59.30
	1983 II a	12.486	3.131	8.713	30.22	62.00
	1983 II b	10.123	2.363	4.783	52.75	60.85
	1983 III a	11.157	2.480	6.13	45.06	58.86
	1983III b	11.185	2.964	5.474	51.06	49.92
	1982[a]	26.78	–	14.245	46.81	–
	$\bar{x}\pm$S.E.				45.61+2.8	59.08±2.08
Dragonflies	1983 I a	10.044	2.335	5.15	48.72	63.42
	1983 I b	10.084	3.287	5.63	44.17	58.52
	1983 II a	10.814	3.039	6.64	38.60	56.14
	1983 II b	9.963	2.329	5.46	45.20	66.15
	1983 III a	9.801	2.007	4.67	52.35	66.26
	1983 III b	10.854	2.637	5.87	45.91	61.47
	1982[a]	16.023	–	5.47	65.86	–
	$\bar{x}\pm$S.E.				48.66±3.24	61,99±1.67

[a] 1982 replicates were with 3, 4, and 3 chicks in the groups, pellets were not weighed separately.
In 1983, each group had 2 chicks. ANOVAs for A.E.: Dry weight, $F_{2,18}=0.64$ ($p>0.05$); Calories, $F_{2,15}=3.58$ ($p>0.05$). Values in table 3b were used to calculate caloric A.E. Intake for the mixed diet was a weighted mean.

Where I is intake, F, faeces, U, uric acid, and P, pellets. As Table 1 indicates, there is no significant difference in assimilation efficiency between treatment groups, although dragonflies have a slightly higher mean than bees, and in all cases the mean caloric values (60%) are lower than those given in the literature for insectivorous birds (70–80%). This is presumably because the data in the literature refer to birds fed on insects with soft bodies or on artificial diets with little indigestible material. Pellets account for half the total output of excreta (Table 1) so that caloric assimilation efficiency calculated without pellets is about 80%, closer to the usual figure in the literature. Since it is not possible to separate faeces and uric acid, the estimates of efficiency are probably about 2–5% too low (Drodz 1967).

Growth efficiency

Table 2 shows the growth of chicks (g wet weight) in relation to consumption in g dry weight. The ratio of weight gain/intake is variously referred to in the literature as "feeding efficiency", "efficiency of food utilization", "growth efficiency" and "lipogenic efficiency" (Melnyk and Boshes 1980). We refer to it as "growth efficiency". As indicated in Table 2, there is considerable inter-individual variation in growth efficiency so that in none of the four replicates is there a significant difference between treatments. However, in all replicates, the mixed diet produces the highest mean value: the probability of this happening by chance is 1 in $(3^4)/3=0.037$. We therefore conclude that in spite of considerable variability, chicks on mixed diets tend to grow more efficiently than chicks on pure diets of either prey type. The range of 24 h weight increases we observed in the experiments fell well within the range observed in the wild.

Body weight and amount eaten

Part of the within-group variation is related to body weight. Figure 2a shows that, combining data for all three diets, chicks that were larger at the start of the experiment put on less weight (although they ate more) than chicks who started light. Several explanations of this are possible – for example, older chicks may convert food into more costly material such as protein instead of fat – but at least in part the explanation is that older chicks were given less food than young ones relative to their metabolic requirements. The maintainance requirements of young animals probably increase approximately as a function of body weight$^{0.75}$ (Kleiber 1975). Figure 2b shows that intake/ "metabolic mass' is negatively related to chick weight at the beginning of the experiment. In other words we did not compensate adequately for metabolic mass on feeding the chicks. The effect of variation in corrected intake on growth efficiency is shown in Fig. 2c. For all three diets there is a positive relationship between intake corrected for metabolic mass and growth efficiency, but this relationship

Table 2. "Growth efficiency" (g wt gain/ g dry wt eaten) on three different diets in 4 replicates. Scores are for individual chicks

Treatment	Replicate			
	1983 I	1983 II	1983 III	1982
Bees	−0.263 0.150 0.296 0.199	0.164 0.207 −0.052 0.436	0.180 0.239 0.084 0.068	−0.017 0.232 0.405 –
$\bar{x}$±S.E.	0.096±0.12	0.189±0.1	0.143±0.04	0.207±0.1
Mixed	0.272 0.082 0.130 0.440	0.348 0.276 0.584 0.351	0.112 0.137 0.289 0.314	0.299 0.156 0.455 0.000
$\bar{x}$±S.E.	0.231±0.08	0.391±0.07	0.213±0.05	0.228±0.1
Dragonflies	−0.064 0.525 0.265 −0.156	0.000 −0.017 0.385 0.488	0.269 0.327 0.035 0.068	−0.313 0.018 −0.131 –
	0.143±0.16	0.214±0.13	0.175±0.07	−0.142±0.08

Table 3a. Caloric values, dry wt and wet weights for the prey taxa used in the experiments

Species	Dry wt (mg) (*n*)	Wet weight (*n*) (mg)	Dry weight as % of wet	kJ/g dry wt
Apis mellifera (1982)	31.17±0.8 (25)	102.3 ± 1.74 (25)	30.5	22.44
Apis mellifera (1983)	28.78±0.77 (30)	95.85+ 2.7 (30)	30.0	22.46
Andrena sp.	26.73±0.66 (27)	72.37± 2.2 (49)	36.9	22.17
Sympetrum striolatum (1982)	43.63±0.12 (53)	139.1 ± 6.1 (37)	31.4	21.49
S. striolatum (1983)	40.62±0.8 (30)	116.49± 2.0 (30)	34.9	24.56
Orthetrum cancellatum	151.1 ±7.4 (34)	464.7 ±40.61 (17)	32.5	21.25
Crocothemis erythraea	44.17±5.7 (20)	128.13± 5.83 (34)	34.5	20.41

Regression equations for wet weight against dry weight for the two orders (including all species measured not just those in the table) used in the experiments: Hymenoptera: —wet=2.398 dry +12.93; Odonata: —wet=2.457 dry +32.622

b. Calorific values (kJ/g dry wt) of pellets, and of faeces plus uric acid, produced by chicks fed on different diets

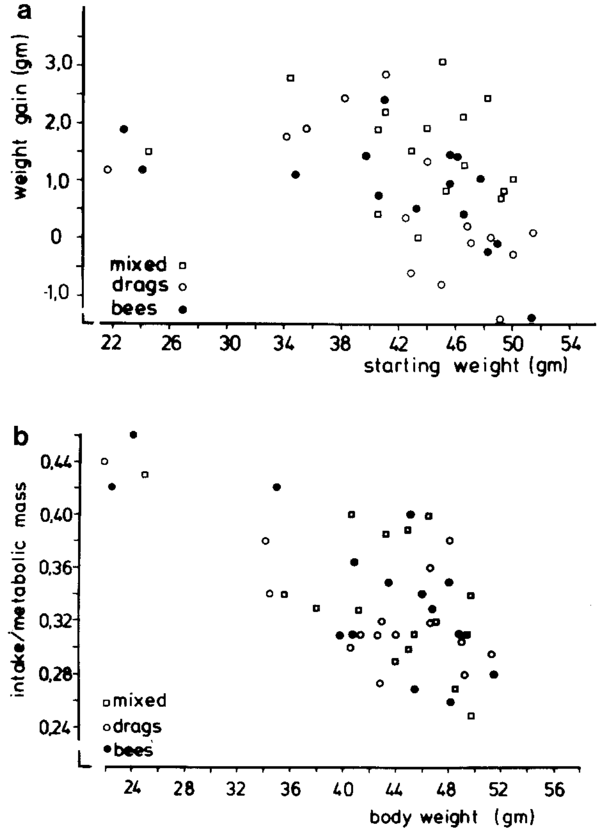
Diet	Pellets	Faeces + Uric acid
Bees	21.60 21.75 21.70	14.77
Dragonflies	20.38 20.35 20.92	15.53 14.49
Mixed	21.08 22.03 21.01	14.89

is not significant for the mixed diet. Three points are worth mentioning. (a) The three regression lines in Fig. 2c do not differ significantly in either slope or elevation, suggesting that the relationship between growth efficiency and corrected intake is similar for all three diets. (b) The mean intake/metabolic mass of the chicks in the three groups were very similar (dry weights, x±s.e.; bees, 0.346±0.059; dragonflies, 0.316±0.047, mixed, 0.348±0.043) did not differ significantly so that our previous result, that growth efficiency is highest on the mixed diet, cannot be an artefact of differences in the amounts the chicks were fed. (c) It is sometimes reported in the literature that growth efficiency decreases with increasing intake over maintainance requirements (eg. Melnyk and Boshes 1980). The fact that the relationships in Fig. 2c have positive slopes suggests that even the birds with high values of intake/mass were not being overfed.

Although variation in intake/mass accounts for some of the within-treatment variance in growth efficiency its effect is not great (33% of the variance for bees, 26% for dragonflies and 5% for mixed). Large variation in growth efficiency has been reported in other studies (eg. Hudson 1983) and may reflect the inadequacy of weight as a measure of growth (Dunn 1975b).

Caloric value and dry weight

Our results have been mainly expressed in terms of dry weight. Table 3a shows that the prey types used in the experiments did not differ appreciably in either caloric value



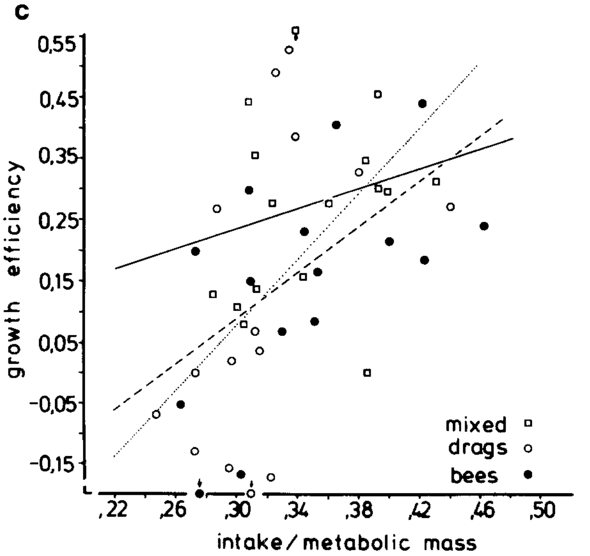


Fig. 2a. 24 h weight gain as a function of starting weight. **b.** Intake/"metabolic mass" (see text) as a function of starting weight. **c.** Growth efficiency in relation to intake/metabolic mass. Correlation coefficients as follows: Bees: 0.58 ($p<0.05$); Dragonflies: 0.57 ($p<0.05$); Mixed: 0.22 ($p<0.10$)

per gram dry weight or in wet weight/dry weight ratio. Similarly the pellets and faeces of the chicks fed on different diets did not differ significantly in caloric value (Table 3b). Our conclusions would not, therefore, be substantially altered by expressing them in terms of calories.

Discussion

Our main results may be summarised as follows (a) dry weight assimilation efficiency of bee-eater chicks is between 40% and 50%. Caloric assimilation efficiency is about 60%. There are no differences between diets. (b) Growth efficiency (24 h weight gain/intake) is consistently higher on mixed diets than on pure diets. (c) On pure diets, growth efficiency is an increasing function of intake relative to metabolic mass (body weight$^{0.75}$) while for the mixed diet there is no significant relationship. From the point of view of the question posed at the start of our study, the demonstration that even over a 24 h period, chicks put on more weight per gram of food delivered to the nest when fed a mixed diet, suggests that one reason why parents do not feed young on pure diets of the two major prey taxa is because of qualitative differences between them. Our study leaves open the nature of these differences, and also the question of whether more extreme differences between experimental groups would emerge in longer term experiments. In demonstrating an advantage of a mixed diet in an insectivorous bird, our results provide experimental evidence for an idea which has been suggested but not tested in previous work (see references cited in Introduction).

The finding that caloric assimilation efficiency of bee-eaters is in the region of 60% rather than the 70–80% values cited in the literature for insectivorous birds (Table 4) is not surprising in view of the fact that bee-eaters feed on

Table 4. Estimate of assimilation efficiency of birds fed on animal food (insects, fish or artificial diets)

Reference	Species	Adult/juv.	Diet	Ass. eff. (%)
Dunn (1975a)	*Phalacrocorax auritus*	Juv.	Fish	79.9–88.1[a]
Al Jaborae (1979)	*Sturnus vulgaris*	Ad.	Chick crumbs and 'sluis'	75
Zimmerman (1965)	*Spiza americana*	Ad.	Chick crumbs	65–75[b]
Kale (1965)	*Telmatodytes palustris*	Ad.	Groundmeat and mealworms	76
Gibb (1957)	*Parus ater*	Ad.	Mixed insects (sweep sample)	76.1
Gibb (1957)	*Parus ater*	Ad.	Mealworms	86.1
Westerterp (1973)	*Sturnus vulgaris*	Juv.	Invertebrates	60–80[c]

[a] Increases with age

[b] Seasonal changes

[c] Decreases with age

large insects with heavy exoskeletons, which are regurgitated by the birds as pellets.

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References

Al Jaborae FF (1979) The influence of diet on the gut morphology of the Starling (*Sturnus vulgaris* L. 1758) D. Phil thesis, Oxford

Belovsky G (1978) Diet optimisation in a generalist herbivore: the moose. Theoret Pop Biol 14:105–134

Drodz A (1967) Food preference, food digestibility and the natural food supply of small rodents. In: Petrusewicz K (ed) Secondary productrivity of terrestrial ecosystems, vol 1. Polish Acad Sci, Warsaw, pp 323–330

Dunn EH (1975a) Caloric intake of nestling double-crested cormorants. Auk 92:553–565

Dunn EH (1975b) Growth, body components and energy contents of nestling double-crested cormorants. Condor 77:431–438

Freeland WS, Janzen DH (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. Am Natur 108:269–289

Gibb J (1957) Food requirements and other observations on captive tits. Bird Study 4:207–215

Goss-Custard J (1977) The energetics of prey selection by redshank *Tringa totana* (L.), in relation to prey density. J Anim Ecol 46:1–19

Greenstone MH (1979) Spider feeding behaviour optimises dietary essential amino acid composition. Nature 282:501–503

Hudson PJ (1983) The variation and synchronisation of daily weight increments of Puffin chicks *Fratercula arctica*. Ibis 125:557–561

Kale HW II (1965) Ecology and bioenergetics of the large-billed marsh wren *Telmatodytes palustris* in Georgia salt marshes. Publ Nuttall Ornith Club 5:1–142

Kleiber M (1975) The fire of life. 2nd edition. Kriege Publishing Co, Huntington N.Y., p 234

Kluijver HN (1933) Bijdrage tot de biologie en de ecologie van de spreeaw (*Sturnus vulgaris vulgaris* L.) gedurende ziju voortpalantingstijd. Pub Plantenzieklenk Dienst Wageningen

Krebs JR, Avery MI (1985) Central-place foraging in a single-prey loader: the European Bee Eater *Merops apiaster*. L. J Anim Ecol (in press)

Krebs JR, McCleery R (1984) Optimisation in behavioural ecology. In: Krebs JR, Davies NB (eds) Behavioural Ecology: an evolutionary approach. Oxford, Blackwells Scientific Publications, pp. 91–121

Krebs JR, Stephens DW, Sutherland WJ (1983) Perspectives in optimal foraging. In: Brush AH and Clark GA jr (eds) Perspectives in Ornithology. Cambridge: Cambridge University Press, pp 165–216

Lessells CM, Stephens DW (1983) Central place foraging: single-prey loaders again. Anim Behav 31:238–243

Melnyk RB, Boshes M (1980) Efficiency of food utilization during body weight gain in Dormice (*Glis glis*). Physiol Behav 24:1017–1021

Owen-Smith N, Novellie P (1982) What should a clever ungulate eat? Am Natur 119:151–178

Rapport DJ (1980) Optimal foraging for complementary resources. Am Natur 116:324–346

Royama T (1970) Factors affecting the hunting behaviour and selection of food by the great tit *Parus major* L. J Anim Ecol 39:619–668

Tinbergen JM (1981) Foraging decisions in Starlings (*Sturnus vulgaris* L.). Ardea 69:1–67

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

Zimmerman JL (1965) Bioenergetics of the dickcissel *Spiza americana*. Physiol Zool 38:370–389

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