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CENTRAL PLACE FORAGING IN THE EUROPEAN BEE-EATER, *MEROPS APIASTER*

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SUMMARY

(1) The purpose of this investigation was to discover if variation in the size of prey fed by parent bee-eaters to nestlings could be explained by a model of central-place foraging. The model predicted that selectivity for large prey should increase with distance travelled by the parents from the nest to the feeding site.

(2) Birds were observed by focal-animal sampling to record the search time, pursuit time and handling time of foraging parents. Prey were identified at the moment of capture or as the parent returned to the nest. For each of the main prey types, we estimated dry weight, caloric value and abundance.

(3) Most of the prey brought to the nest were odonates and hymenopterans. For the purpose of testing the model, we divided prey into two classes, big (mainly odonates) and small (mainly bees in 1 year, small odonates in another).

(4) As predicted by the model, there was a decrease in the proportion of items brought to the nest that were small with increasing travel time in 2 years. The model predicted a threshold for dropping small items from the nestling diet, and statistical estimation of a threshold from the observed data by probit analysis showed that in both years the predicted threshold was within two standard errors of the observed. Estimates of relative prey abundance and observations of parents collecting food for themselves showed that differential availability of small prey at different distances from the nest could not account for the size–distance relationship.

INTRODUCTION

The European bee-eater *Merops apiaster* L. feeds its young on large insects which it brings to the nest one at a time. In this paper we test whether variation in the size of prey fed by parents to nestlings can be explained by a model of central-place foraging (Carlsson 1983; Hegner 1982). The model was originally proposed by Orians & Pearson (1979) (see also Schoener 1979), and corrected by Lessells & Stephens (1983). Here we use a simplified algebraic form developed independently by C. M. Lessells (personal communication) and A. I. Houston & J. M. McNamara (personal communication) (see also Carlsson 1983 for a somewhat similar formulation).

The model assumes that the parents maximize rate of delivery of energy (or prey weight) to the nestlings. The parent's foraging time is assumed to consist of the following activities: travel, pursuit and handling, which are taken to be fixed constraints for a particular feeding site or prey type, and search time, which depends on prey abundance and is assumed to be similar in different foraging sites. Prey are characterized by their caloric value or dry weight. The prediction of the model that we test here is that with increasing travel distance

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(time), small prey items should be excluded from the diet of the nestlings: it is not worth returning from distant sites with a small prey. As with optimal diet models in general (e.g. Charnov 1976) the prediction is of a step-wise switch from inclusion to exclusion of a particular size class of prey. The critical travel time for exclusion of the smaller of two size classes of prey can be found as follows:

Let E_i = energy value of prey type i ($i = 1, 2$) ($E_1 > E_2$) (in Joules)
 λ_i = encounter rate with prey type i ($i = 1, 2$)
 h_i = handling and pursuit time for type i (in seconds)
 T = round trip travel time (in seconds)

If the predator brings only one type of prey (the bigger ones) to the nest its rate of energy delivery is:

$$\frac{E_1\lambda_1}{1 + \lambda_1h_1 + \lambda T} \quad (1)$$

While the predator taking both types has a delivery rate:

$$\frac{E_1\lambda_1 + E_2\lambda_2}{1 + \lambda_1h_1 + \lambda_2h_2 + \lambda_1T + \lambda_2T} \quad (2)$$

Therefore the predator should selectively bring large items (type 1) to the nest when (1) > (2), or which by rearranging gives:

$$T_{\text{crit}} = \frac{E_2/\lambda_1 - E_1h_2 + E_2h_1}{(E_1 - E_2)} \quad (3)$$

As in the classical diet models, of which this is a derivative, λ_2 cancels out.

We simplify our analysis by classifying the prey into two types, large and small. By measuring λ_1 , E_1 , E_2 (we use dry weight mg), h_1 and h_2 we are able to predict T_{crit} and compare the prediction with the proportion of prey brought to the nest that are of type 2 (small) for travel times above and below T_{crit} .

METHODS

Study area

The data were collected at two colonies in the Camargue region in Southern France. In 1981 we observed a colony of seven nests in a field called the Ancien Vigne on the Estate of the Station Biologique de la Tour du Valat. The colony was in a ditch in a pasture, surrounded by other pastures, clover and alfalfa fields. The birds fed mainly over the fields or ditches (filled with *Phragmites*) around the field boundaries. In 1982 data were collected at a colony of c. ninety nests in a bank on the east side of the Arles-Port-de-Bouc canal approximately 8 km south of Arles (Mas des Sarcelles). This colony is surrounded by fields of wheat, alfalfa, rice and pasture, with an extensive system of *Phragmites*-filled ditches around the fields.

Birds

Bee-eaters return to the Camargue from their African winter quarters in early May and egg-laying is usually completed by mid-June. We collected data only during the middle to

late nestling stage (15–25 July) (the total nestling period is *c.* 25 days) when nestlings were sufficiently large to eat any size of prey that the adults might bring (unpublished observations). In 1981 all, and in 1982 some of the birds were individually colour marked, by Saflag wing tags in the first year and by painting the tail with acrylic artists' paints in the second year. Birds were captured for marking under CRPBO licence either by means of nest traps inserted into the burrow entrance or by mist nets in front of the nest. By capturing birds only after the start of parental feeding we avoided any problem of desertion.

Observation of time budgets and prey captured

We observed one focal-animal at a time. In 1981 we recorded single individuals for a series of successive foraging round trips from the nest to the feeding grounds and back (Fig. 1) using two observers. One observer sat at the top of a 4 m high tower hide and the other was in a hide 2–4 m from the nest. The first observer timed the sequence of behaviours and the second recorded the prey types brought to the nest by the focal-animal. In 1982 we did not usually follow one individual for a sequence of round trips. Instead we recorded the time budget and prey captured by an individual from the time of its arrival at a feeding site to the return to the nest. To calculate round trip travel time in these observations we simply doubled the homeward trip time.

The definition of feeding sites was usually quite straight forward as the birds tended to fly directly to a particular field or ditch and hunt either by aerial search and pursuit or by perching on a tree or telephone wire to search and flying out in brief sallies to pursue prey.

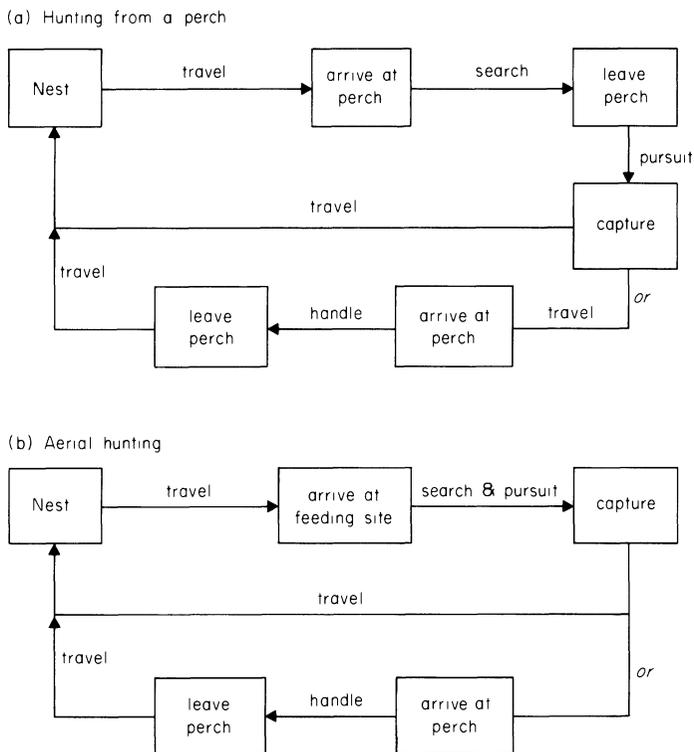


FIG. 1. The sequence of behaviour in foraging trips.

The transition from travel to aerial search was recognizable by a change from direct to irregular, swooping flight.

Prey

Most of the prey captured by bee-eaters in our study area were sufficiently large to be identified simply by observation of the item in the bird's beak. It was often possible to identify prey to genus or species, and almost always to the order. Unidentified prey were classified according to size (small, honey-bee sized; medium, bumblebee sized; large, size of large dragonfly such as *Anax* or large bee such as *Xylocopa*).

In 1982 we used a super-8 movie camera triggered by a microswitch as the parents entered the nest burrow to photograph about 1350 items at a sample nest. These photographs confirmed that no prey other than ones we could identify by eye were brought to the nest in appreciable numbers.

We collected samples of insects, for dry-weighing and bomb calorimetry, by sweep netting. Table 1 shows the number weighed of each species and the dry weight (constant

TABLE 1. Dry weights of prey species (mg). Caloric values measured by bomb calorimetry

Species		\bar{x}	S.E.	<i>n</i>	kJ^{-8} dry weight
Odonata					
<i>Sympetrum striolatum</i> (Charpentier)		43.63	1.23	53	21.49
<i>Sympetrum striolatum</i> (Charpentier)	♀	41.19	1.51	32	
<i>Sympetrum striolatum</i> (Charpentier)	♂	47.35	1.83	21	
<i>Orthetrum cancellatum</i> (Linnaeus)		151.06	7.38	34	21.35
<i>Orthetrum cancellatum</i> (Linnaeus)	♀	156.72	12.36	20	
<i>Orthetrum cancellatum</i> (Linnaeus)	♂	142.89	2.76	14	
<i>Anax parthenope</i> Selys		342.18	24.77	7	
<i>Brachytron pratense</i> (Müller)		189.16	10.17	21	23.95
<i>Brachytron pratense</i> (Müller)	♂	193.73	8.80	16	
<i>Brachytron pratense</i> (Müller)	♀	174.54	34.23	5	
<i>Aeschna isosceles</i> (Müller)		315.38	37.6	4	
<i>Crocothemis erythrea</i> (Brulle)		44.17	56.8	20	20.41
		86.52	2.0	5	
		30.05	1.04	15	
Hymenoptera					
<i>Apis mellifera</i> (worker) Linnaeus		25.04	0.92	21	21.42
<i>Andrena</i> sp 1 Fabricius		26.73	0.66	27	22.17
<i>Andrena</i> sp 2 Fabricius		29.83	0.96	7	
<i>Bombus hortorum</i> (Linnaeus)		78.33	4.96	13	
<i>Bombus agrorum</i> Fabricius		39.7	3.49	12	
<i>Vespa crabro</i> Linnaeus		120.6	—	2	
<i>Xylocopa valga</i> (Gerstaecker)		231.29	9.76	7	21.47
Diptera					
<i>Hybomitra expollicata</i> (Pandellé)		30.45	1.40	3	
<i>Tabanus autumnalis</i> Linnaeus		57.94	2.57	19	
<i>Tabanus bovinus</i> Linnaeus		79.95	8.66	2	
Orthoptera					
<i>Tettigonia viridissima</i> Linnaeus		646.53	161.5	3	
Lepidoptera					
<i>Brintesia circe</i> Fabricius		107.37	15.33	3	
<i>Iphiclides podalirius</i> Linnaeus		107.35	—	2	
<i>Vanessa atalanta</i> (Linnaeus)		107.75	—	2	
<i>Heliothis virescens</i> (Hufnagel)		35.68	4.32	10	
<i>Colias crocea</i> (Geoffroy)		36.48	2.53	8	

TABLE 2. Size classes of insects in 1981 and 1982. Major prey species only listed

Small		Medium		Large	
Species	dry weight (mg)	Species	dry weight (mg)	Species	dry weight (mg)
1981					
<i>Hybomitra expollicata</i>	30.5	<i>Sympetrum striolatum</i>	43.6	<i>Anax parthenope</i>	342.2
<i>Apis mellifera</i> (worker)	25.1	<i>Bombus hortorum</i>	78.3	<i>Aeschna isosceles</i>	315.4
<i>Andrena</i> spp	26.7	<i>Tabanus bovinus</i>	79.9	<i>Brachytron pratense</i>	189.1
<i>Heliothis virescens</i>	35.5	<i>Brintesia circe</i>	107.4	<i>Orthetrum cancellatum</i>	151.1
weighted mean	29.83		60.80		251.8
1982					
<i>Sympetrum striolatum</i>	43.6	<i>Tabanus bovinus</i>	79.9	<i>Anax parthenope</i>	342.2
<i>Sympetrum depressiusculum</i>		<i>Bombus hortorum</i>	78.3	<i>Aeschna isosceles</i>	315.4
<i>Apis mellifera</i>	25.1	<i>Brintesia circe</i>	107.4	<i>Xylocopa vulga</i>	231.3
		<i>Tabanus autumnalis</i>	57.94	<i>Tettigonia viridissima</i>	646.5
weighted mean	41.8		75.5		370.96

weight after drying at 50 °C). For the major prey species we estimated caloric value per gram dry weight using a Phillipson microbomb calorimeter (Table 1). Although bee-eaters take a wide taxonomic range of insects, the bulk of the diet is made up of very few genera. At the camera nest in 1982, for example, over 90% of the dry weight of prey delivered were dragonflies and honeybees (*Apis*). Over 90% of the dragonflies were of three species: *Aeschna isosceles*, *Anax parthenope* and *Orthetrum cancellatum*. It was therefore straightforward to classify all prey captured into three size classes—small, medium and large (Table 2). For the purposes of testing the model, the medium and large classes were combined and the mean weight assigned to the class was weighted by the occurrence of different species in the diet. The smallest size class contained different prey in the 2 years: in 1981 mainly *Apis* and *Andrena* (both Hymenoptera) and in 1982 mainly *Sympetrum striolatum* and *S. depressiusculum* (Odonata). This reflected differences in habitat type and prey availability between the two sites.

Prey abundance

For the purposes of testing the model we estimated the encounter rate with large prey (λ_1) from the time budget records. In addition we estimated prey abundance by direct observation at some sites immediately after taking observations of birds feeding there. These counts served two purposes: (a) they gave a measure of variation in prey abundance between sites that was independent of the birds' behaviour and (b) they allowed us to see if the per cent size distribution of prey potentially available varied between sites. The method we used was analogous to the transect method (Pollard 1977) and involved looking through a pair of 10 × 40 Zeiss Dialyt binoculars focused on an object 15 m away at a height of 1 m and counting all insects flying across the field of view for 5 min. They were classified as bees' *Sympetrum*, butterflies and large dragonflies. This method of assessing insect abundance has three advantages: (a) it is quick; (b) it is likely to incorporate the same biases (greater visibility of big and of flying insects) that would affect foraging bee-eaters; (c) since bee-eaters hunt mainly within 3 m of the ground it samples the appropriate habitat. There was a reasonable correlation between the estimates of two observers collecting data at the same place at the same time (Fig. 2). The two major weaknesses are (a) some prey (e.g. patrolling dragonflies) could be counted more than once in a given sample and (b) when prey such as bees are very abundant, it is hard to count them

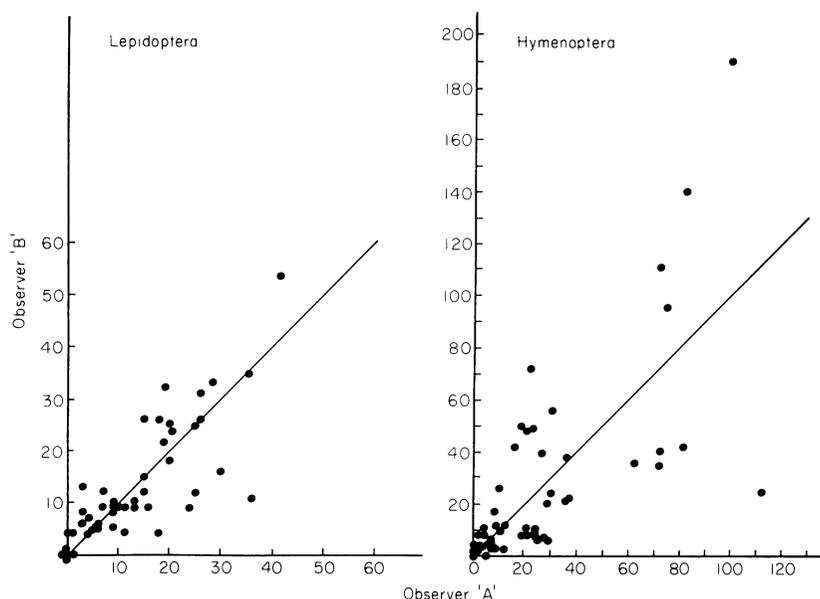


FIG. 2. Scatter plots showing the correlation between insect abundance counts by two observers in the same site at the same time.

accurately. We do not use estimates of insect abundance as absolute measures but only to compare relative values within and between sites. Thus any biases in the method, provided they are consistent, will not seriously affect our interpretation of the data. Below we present two sets of observations which indicate that bee-eaters alter their use of foraging sites in association with changes in abundance assessed by our method, which suggests that we are recording something correlated with availability to the birds.

RESULTS

Insect size-distribution and abundance

Before analysing the size-distance effect in prey brought to the nest, we consider whether differences between feeding sites in prey abundance or size distribution could have influenced the results. In both years at both close and distant sites the majority of potential prey were small (bees in 1981, *Sympetrum* in 1982; see Table 3). Thus any tendency for parents to have selectively brought large prey from distant sites was not accounted for by absence of small items at these sites. The table also shows our estimates of abundance at close and distant sites: in 1981 prey (especially small ones) tended to be more abundant at distant than at close sites, while in 1982 there was no systematic trend with distance. For the purposes of testing the model we assume that abundance did not vary significantly between sites when the birds were using them.

It might be asked why bee-eaters ever fed at distant sites if similar prey abundances could be found close to the colony. In part the answer to this question lies in day-to-day changes in insect abundance due to changes in wind direction or harvesting of crops. Although there may have been relatively small differences between sites when the birds were using them, the birds tended to avoid sites with very low prey abundance on any particular day. In 1981 one of two feeding sites at similar distances from the colony (NE

TABLE 3. Insect abundance (A) and per cent size-distribution at different feeding sites. In both years small prey (bees in 1981, bees and *Sympetrum* in 1982) were the most abundant prey at all sites. Abundance is expressed as $\bar{x} \pm$ S.E. insects min^{-1}

Site	Travel time (s)	Bees		<i>Sympetrum</i>		Butterflies		Large		Number of days	Number of counts
		A	%	A	%	A	%	A	%		
1981											
N	48.5	11.8 ± 4.1	80	0.14 ± 0.5	1	2.9 ± 0.6	19	0.01	0.1	8	32
NE	50.0	7.9 ± 0.8	60	0.05 ± 0.3	0.03	5.3 ± 2.8	39.7	0.0	0.0	8	32
SD	17.3	4.2 ± 1.3	66	0.20 ± 0.1	3	2.0 ± 0.6	31	0.01	0.1	8	32
1982											
E	9.9	0.3 ± 0.1	5	4.1 ± 1.7	81	0.66 ± 0.3	13	0.03	1	7	33
W	11.6	0.14 ± 0.1	4	3.0 ± 1.0	90	0.2 ± 0.1	6	0.0	0.0	3	6
EW	74.3	0.3 ± 0.2	12	2.0 ± 1.1	69	0.5 ± 0.5	18	0.05	2	4	4
SD	95.6	3.5 ± 2.0	29	7.7 ± 1.4	66	0.4 ± 0.3	4	0.02	2	5	6

field) was an alfalfa field. When the alfalfa was cut, both insect abundance and relative visit frequency in NE dramatically decreased (Fig. 3a). In 1982 we compared the proportion of feeding trips that were to closest foraging site (E) with daily variation in insect abundance. With the exception of 1 day, there was a clear association between insect abundance at the closest site and the proportion of trips to the site: when insects were abundant close to the colony the birds tended to feed nearby (Fig. 3b). The main cause of daily variation in insect abundance was windspeed; on days with a strong mistral (northerly wind) there were few insects flying at the exposed close site.

Time budgets

Table 4 shows the estimates of various time budget parameters (Fig. 1) for 1981 and 1982. Travel time is the time from nest to feeding site and return; handling time is the time taken after capture to prepare the food for the young; prey were either handled at the capture site or just before entering the nest, and for many items there was no handling. Pursuit and search make up the rest of the time at the feeding site. If the bird was hunting by aerial gleaning the two could not be separated, but when the birds hunted from a perch pursuit

TABLE 4. Estimate of time budget parameters. The values are $\bar{x} \pm$ S.E. (*n*)

Site	Feeding sites		Prey type	Prey size classes	
	Travel time (s)	λ_1 (prey ^{-m})		Pursuit time (s)	Handling time (s)
1981					
S. Close	0 (247)	0.34 ± 0.07	small	7.0 ± 0.5 (149)	1.78 ± 1.9 (160)
S. Distant	17.3 ± 1.1 (60)	0.33 ± 0.03	medium	5.6 ± 0.9 (12)	14.1 ± 12.4 (12)
S.E.	28.6 ± 1.0 (34)	0.56 ± 0.28	large	3.5 ± 0.5 (2)	13.5 ± 12.5 (5)
N	48.5 ± 3.9 (24)	0.28 ± 0.27			
W	56.0 ± 8.2 (5)				
E	69.4 ± 9.4 (110)	0.48 ± 0.4			
1982					
E	9.9 ± 0.4 (272)	0.2 ± 0.7	Bee (S)	8.1 ± 0.8 (72)	1.1 ± 0.1 (67)
W	11.6 ± 0.4 (272)	0.2 ± 0.1	<i>Sympetrum</i> (S)	10.8 ± 3.5 (21)	1.4 ± 0.5 (267)
EW	74.3 ± 4.0 (37)	0.09 ± 0.1	Bumblebees (M)	14.3 ± 2.6 (6)	1.5 ± 6.8 (21)
SD	95.6 ± 5.9 (36)	0.19 ± 0.1	<i>Xylocopa</i> (L)	9.5 ± 2.3 (6)	32.2 ± 10.0 (9)
WR	40.1 ± 2.2 (18)	0.26 ± 0	Dragonfly (L)	12.3 ± 2.2 (6)	33.0 ± 8.5 (7)

Foraging in the bee-eater

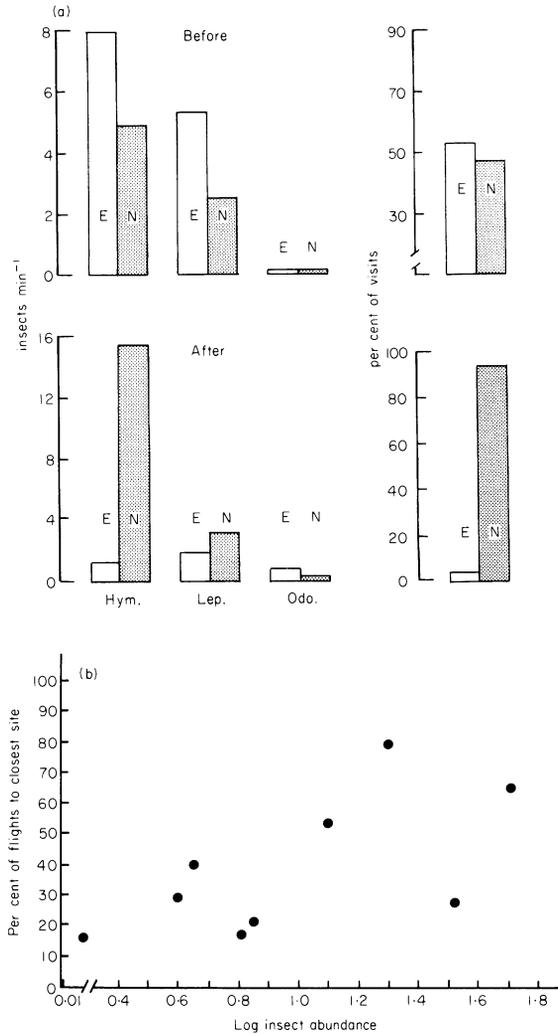


FIG. 3. (a) 1981: per cent of total visits to two neighbouring foraging sites immediately before and after the crop in the NE site (an alfalfa field, labelled E for short on the figure), was cut. Before cutting, the insect abundance was higher in NE than N (left upper panel) and more than half the visits to the two sites were to NE. On the day after cutting both insect abundance and relative use of NE declined dramatically. Hym., Hymenoptera; Lep., Lepidoptera; Odo., Odonata. (b) 1982: per cent of feeding flights that were to the closest site (E) as a function of insect abundance. On each observation day a sample of thirty flights was recorded by each of two observers (total $n = 60$) and insect abundance was measured immediately afterwards. Each dot refers to the average score for a day. ($P < 0.05$, $r_s = 0.6$.)

could be measured as the time from leaving the perch to the moment of prey capture, while search was the time from arriving at the site until the onset of pursuit. The estimates of pursuit time from perch-hunting data were used to calculate (by subtraction) search times for the aerial gleaning forays. To calculate λ_1 we summed the total durations of round trips for each year, subtracted pursuit and handling time for any prey eaten by the bird itself, the pursuit, handling and travelling times for prey taken to the nest. The remaining quantity, total search time, was divided by the total number of type 1 prey taken to give an

average search time per prey: λ_1 is the reciprocal of this value. Thus the search time for small items is included in that for large, i.e. it is assumed that type 1 would always be taken if encountered while searching.

In 1982 we also recorded 'burrow times'—the time spent by the bird in the burrow delivering food to the chicks. In principle, burrow times should be treated as a constraint along with handling, pursuit and travel. A problem is that burrow times were very variable; sometimes the parent remained in the nest for 20 min and we assumed that it was not simply transferring a prey during this time—it was probably brooding the chicks, repairing the burrow or doing some other activity. We therefore consider the appropriate value to take as a constraint is the *minimum* rather than average burrow time. The four prey-distance combinations for which we collected data had minimum values of 0, 1, 1 and 4. We have therefore treated burrow time as negligible and ignored it in our analysis. It is worth noting that had we included burrow time, it would have reduced the predicted value of T_{crit} by about 1 s.

Predicting T_{crit} and testing the prediction

Table 5 gives the values used to calculate T_{crit} in each year. As explained in the Methods section, the mean dry weight of prey type 1 was estimated by taking a mean of the medium and large classes weighted according to their occurrence in the chick's diet. We use dry weight since caloric value per gram dry weight does not vary significantly between prey types (Table 1) and there are no significant differences in assimilation efficiency between bee-eater chicks fed on bees and dragonflies (Krebs & Avery 1984).

The values in Table 5 give the following predictions for $T_{crit}(s)$ see eqn (3).

$$T_{crit} = \frac{(29 \cdot 83 \cdot 60) / 0.35 - 138.5 \cdot 10 + 29 \cdot 83 \cdot 19}{(138.5 - 29 \cdot 83)} = 39.5$$

For 1982:

$$T_{crit} = \frac{(41 \cdot 28 \cdot 60) / 0.19 - 217 \cdot 33 \cdot 12 + 41 \cdot 28 \cdot 20}{(217 \cdot 33 - 41 \cdot 28)} = 63.95$$

(note that the first expression in the top line is multiplied by 60 to convert encounter rates to prey s^{-1}). Below T_{crit} small items should be delivered in proportion to their relative

TABLE 5. Parameter values used in the model for 1981 and 1982

Parameter	Value	Comments
E_1 (1981)	138.5 mg dry weight	Weighted mean of <i>Sympetrum</i> , <i>Bombus</i> , <i>Brintesia</i> , <i>Anax Aeschna</i> , <i>Brachytron</i> , <i>Orthetrum</i>
E_1 (1982)	217.73 mg dry weight	Weighted mean of large tabanids, <i>Bombus</i> , <i>Brintesia</i> , <i>Xylocopa</i> , <i>Aeschna</i>
E_2 (1981)	29.83 mg dry weight	Weighted mean of <i>Apis</i> , <i>Andrena</i> , small tabanids, <i>Heliothis</i>
E_2 (1982)	41.28 mg dry weight	Weighted mean of <i>Sympetrum</i> and <i>Apis</i>
λ_1 (1981)	0.35 min^{-1}	All sites combined
λ_1 (1982)	0.19 min^{-1}	All sites combined
h_1 (1981)	19.0 s	Weighted mean pursuit plus handling time for medium and large prey
h_1 (1982)	20.0 s	Weighted mean pursuit plus handling time for medium and large prey
h_2 (1981)	10.0 s	Weighted mean pursuit plus handling time for small prey
h_2 (1982)	12.0 s	Weighted mean pursuit plus handling time for small prey

E and h were weighted according to frequency of occurrence in diet.

abundance, above T_{crit} they should not be delivered at all. There are two possible ways of estimating the predicted proportion of small items at close sites: from our insect counts and from the relative encounter rates of the birds with type 1 and type 2 prey. We used the former values since this allows our prediction to be independent of the observed captures, although the two methods give quite similar values (80% and 90% type 2 from the insect counts and 85% and 97% from the encounter rates for the 2 years). In both years there is a sigmoid decrease in proportion of small prey brought to the nest (Fig. 4), at short distances the proportion is as predicted from unselective feeding and at long distances it is much lower, but not zero as predicted by the model. (Note that with our observed parameters it never pays to specialize on small items although this is in principle a possible prediction (Orians & Pearson 1979).

The data do not show the predicted step change but this would not be expected for at least two reasons. (a) Data from different days and individuals are combined, and even if

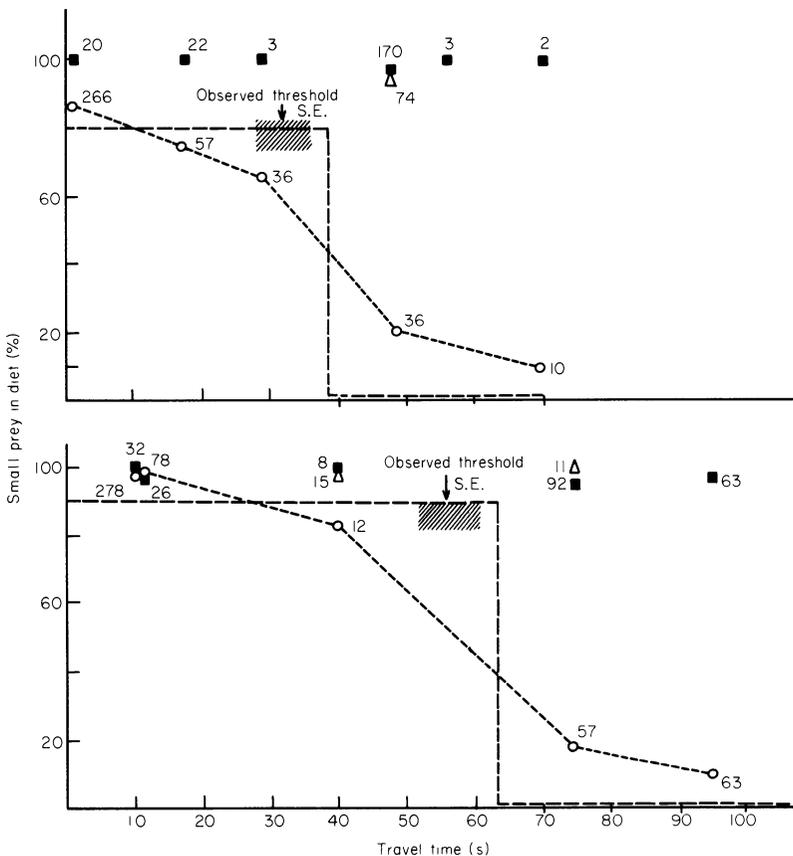


FIG. 4. Predicted percentage of small items brought to the nest (---) as a function of round-trip travel time in 1981 and 1982. T_{crit} calculated according to eqn (3). (O---O), observed percentages (numbers = numbers of prey). Arrow indicates threshold (ED 50) estimated by probit analysis. Shaded area (▨) is standard error of the threshold. For 1981 the probit equation is $y = 1.187 - 0.0354x$, G^2 (d.f. = 3) = 2.88 for goodness of fit. ED50 = 33.5 ± 3.122 (S.E.). For 1982 the eqn is $y = 2.524 - 0.04231x$, G^2 (d.f. = 3) = 3.65 ED50 = 59.6 ± 2.6 . Other data points refer to prey eaten by the parent while foraging (■), and to prey fed to the young after they have fledged and moved to the feeding grounds (△).

one individual on 1 day showed a step change, the average of different thresholds in slightly different places (due to variation in λ_1 and h) would be a sigmoid curve. (b) The prey categories '1' and '2' erected for the purpose of this analysis may not be seen by the birds as two distinct classes, some of our type 1 may be treated as 2 and vice versa. In order to investigate whether the sigmoid pattern in the data could be interpreted in terms of a threshold and if so to identify the threshold position we carried out a probit analysis. Maximum likelihood estimates of the probit transformed percentages were a good fit to a straight line indicating that the data are suitable for probit analysis. The threshold and its standard error for each year is shown in Fig. 4. In both years the predicted threshold is within two standard errors of the probit estimate from the data. Thus the energy-maximising model of eqn (3) predicts both the difference between years and the statistical estimate of the threshold within each year.

Figure 4 also shows data from two other kinds of observation of prey consumption. (a) Parents when feeding themselves ate almost exclusively small items at all distances from the nest, and (b) when the young had just left the nest and were taken by the parents to the feeding sites they were fed mainly small prey regardless of distance from the nest (these data were collected by watching young birds the day after they fledged). These two sets of observations confirm that the size-distance relationship for nestling diet is not due to the absence of available small prey at more distant sites.

The threshold for medium-sized prey.

Equation (3) can be used to calculate the travel time above which it would pay to specialize on large items and ignore medium-sized ones when transporting food to the nest. The values of E and h can be taken directly from Tables 2 and 4, and the value of λ for large items estimated in the way described earlier is $0.09 \text{ prey min}^{-1}$ in both years. The predicted thresholds for 1981 and 1982 respectively are 188.6 and 161.7 s, in excess of any of the observed values. Consistent with this, in 1981 there was no tendency for the ratio of large to medium prey brought to the nest to change with travel time (it was 47:15 for the sum of the three closest sites and 26:11 for the two most distant ones combined). In 1982, however, the ratio of medium to large was more variable. It was 18:0 for the three closest sites, 2:44 for site EW and 20:29 for SD. Thus, contrary to our prediction, there is a suggestion of an increase with distance in the ratio of large to medium. A possible complicating factor in the case of site EW is that on two observation days the birds fed on crickets and other large insects disturbed by a mechanical harvester: thus the high ratio at this site may be an atypical result.

DISCUSSION

Our main conclusion is that the central-place foraging model predicts a distance-related change in proportion of small prey brought to the nestlings which is within the 95% confidence intervals of the statistically estimated change for observations in two different colonies in different years. Two other studies having reported tests of a similar model: Hegner (1982) and Carlsson (1983) were able to show, for *Merops bullocki* and *Lanius collurio* respectively, that a size-distance effect was consistent with the model's predictions. Hegner's results are more directly comparable with ours than are Carlsson's, since the latter study involved simultaneous presentation of prey rather than the sequential encounters assumed in our model. Other studies indicating a possible size-distance relationship include that of Hartwick (1976).

There are a number of factors which analysis has not so far considered, we will now examine some of them.

Energetic costs

As the analyses of Kacelnik (1984), Kacelnik & Houston (1984) and Bryant & Turner (1982) have shown, incorporation of energetic costs (to the parents and/or nestlings) can make substantial differences to the prediction of central-place foraging models. The model we have used can be modified to include a term for average energetic cost per trip to the parent (A. I. Houston & J. M. McNamara personal communication), in which case eqn (3) becomes:

$$T_{\text{crit}} = \frac{E_2/\lambda_1 + E_2h_1 - E_1h_2 + h_2C}{(E_1 - E_2) - C}$$

where C = cost per second \times search time in seconds.

Avery, Krebs & Houston (unpublished) estimate the average metabolic cost for a foraging bee-eater to be 1.5 J s^{-1} which is equivalent to 0.071 mg of prey (Table 1). Using this value to recalculate the values of T_{crit} gives predictions that are about 10 s above those for gross intake. Thus the fit of the model to the data is less good when energy cost is taken into account in this simple way. However a more realistic correction should allow for the difference in energetic cost between activities (Kacelnik & Houston 1984) for which the data are not available.

Classical diet model predictions

Would selectivity be predicted for any of our data by the simple optimal diet equation (Charnov 1976)? The critical value of λ , the encounter rate with the more profitable prey, is given by:

$$\lambda_1 = \frac{E_2}{(E_1h_2 - E_2h_1)}$$

This gives values of λ_1 (prey min^{-1}) of 3.63 and 1.59 for 1981 and 1982 respectively. These are well in excess of any of the observed values, so we conclude that the observed selectivity of parents cannot be explained in terms of simple diet theory and it is therefore likely to be an effect of travel time.

Prey quality

Although the energy-maximizing model gives an adequate description of our data, independent evidence suggests that one of its basic assumptions may in fact be wrong. Krebs & Avery (1984) found that bee-eater chicks tend to put on more weight per gram of food eaten when fed on a mixed diet than when fed on a pure diet of either bees or dragonflies. This suggests that the two main prey types are not perfectly substitutable but that they may contain complementary resources. We have not tested to see if mixtures of different proportions of the two prey result in different growth efficiencies; it is possible that only a small amount of one type is necessary to complement the other. The advantage of a mixed diet would not necessarily conflict with maximizing energy gain by selective foraging on one type on a particular trip if foraging distance varies to include both long and short trips. Thus the model's prediction of T_{crit} is not necessarily altered by a violation of the assumption that prey can be characterized by a simple dimension of quality.

Errors in parameter estimates

The predictions of the model were close to the statistically estimated threshold for small prey, but it should be borne in mind that the parameters on which we based the predictions are subject to quite large estimation errors. For example the values of E_1 and E_2 depend on how accurately the prey are identified and the weight assumed for unidentified prey. In view of these potential inaccuracies, we present a sensitivity analysis of the model in Table 6. It is generally considered that a model is 'sensitive' to variations in its parameters if the percentage change in prediction is at least as great as the percentage change in parameter. In Table 6 we show, by varying each parameter in turn by 15% above and below its estimated value, that the model is sensitive to E_1 , E_2 and λ_1 but not to h_1 and h_2 . Of the first three parameters, the one most likely to be inaccurate is E_1 , since this includes a very wide range of prey sizes. In view of the sensitivity analysis we consider the prediction of a qualitative difference in the position of the threshold for small items between years as possibly a more convincing piece of evidence than the quantitative fit within each year.

TABLE 6. Sensitivity analysis of model parameters. Values of T_{crit} are shown when each parameter in turn is varied by 15% above and below its estimated mean

Parameter	15% below	Estimated mean	15% above
1981			
E_2	30.0	39.5	51.4
E_1	51.4	39.5	32.2
h_1	39.0	39.5	40.6
h_2	41.7	39.5	37.9
λ_1	48.5	39.5	33.4
1982			
E_2	50.1	63.9	77.3
E_1	77.8	63.9	52.0
h_1	63.1	63.9	64.6
h_2	66.3	63.9	61.4
λ_1	76.7	63.9	53.3

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