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The delivery of surplus prey to the nest by a pair of Bee-eaters (Merops apiaster)

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Observations are presented on the delivery of surplus food to the nest of a pair of Bee-eaters, including the quantity and species composition and size of surplus food items. The delivery of surplus food may be explained by (1) the death of young, (2) the arrival of helpers, (3) increased success of prey capture because of the discovery of a rich food supply nearby, or (4) an aversion of the nestlings to venomous bumble-bees which are fed when other food for the nestlings is unavailable. The delivery of surplus food suggests that the adjustment of food delivery to the nest is not a quick process, and that the adults need a few days to adjust their effort to the requirements of the nestling.

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1. Introduction

Bee-eaters (*Merops apiaster*) are colonial breeders and feed their young with insects (Cramp 1985). Although previous studies reported the composition of nestlings' diet (Korodi-Gál & Libus 1968, Cramp 1985), rate of feeding (Tapfer 1957, Dyer & Demeter 1981) and amount of food delivered (Korodi-Gál & Libus 1968), the delivery of surplus food to the nest, which we describe here, has not been reported before.

In this work we present observations on the delivery of surplus food to the nest of pair of Bee-eaters, including the species composition and size of surplus food items. We suggest some possible hypotheses for explanation of the odd behaviour of one pair studied. The delivery of surplus food suggests that the adjustment of food delivery to the nest is not a quick process, and that the adults need a few days to adjust their effort to the requirements of the nestlings.

2. Material and methods

A single nest was observed for a week in late July of 1984 near the town Kiskunhalas, in southern Hungary. The nest was excavated about 30 cm from the top of an almost vertical dune of firm sand. There were 8 other burrows in the proximity (ca 1-10 m), but only the one studied was inhabited at the time of observation. In previous years all holes had been occupied. Other groups of nest-holes occurred 150-200 m away.

The breeding site was surrounded by farmlands with pastures, orchards, lucerne and clover fields, sunflower and maize fields, and with dunes covered by pines, locust-tree and poplar groves. At the time of observation there were no beehives in the area.

Taxon / time	Bombus terrestris	Bombus lapidarius	Bombus agrorum	Apis mellifera	Vespa spp.	Melolonthioae	Calliptamus italicus	Heteroptera	Total
day 1	60*	3*	2*	3*	2*	3**	4**	2**	79
day 2	22	1	1	–	–	–	–	–	24
day 3	8	1	–	–	–	–	–	–	9
day 4	3	–	–	–	–	–	–	–	3
day 5	1	–	–	–	–	–	–	–	1
day 6	2	–	–	–	–	–	–	–	2
day 7	–	–	–	–	–	–	–	–	0

Tab. 1. The number and composition of surplus prey delivered to the nest by Bee-eaters as a function of time. On the first day fresh and old items were indistinguishable (*), except for some definitely old items (**). The number of items declined during the week (Spearman rank correlation with day one excluded $r=0.943$, $n=6$, $p<0.02$).

The weather was cold and rainy in two days before observation (23-24 July), but in the week of observation the weather conditions were sunny and there was a slow rise in temperature.

On the first visit (25 July), there were several dozen of bumble-bees (Bombus spp.) on the ground directly beneath the burrow, far more than the usual number of items accidentally dropped during feeding. We observed the nest every day for a week, from 14.00-17.00 h. After each observation period we collected the surplus items.

3. Results. Quantity, size and composition of surplus food delivered to nest

On the first day of observation both fresh and old prey items were found beneath the nest (Tab. 1). These could be distinguished because the fresh items were whole, but damaged on their thorax, were sometimes still alive, and were sometimes found in the tunnel burrow. On the other hand, all old prey were dead and some of them were partly covered in sand because of the impact of rain drops on the ground while others had much damaged exoskeletons. However, some of these old items were whole. The number of prey declined during the week (Tab. 1). By far the most common items were *Bombus terrestris* which accounted for 75.9% (n=79) of items on the first day. From the fourth day onwards only that species was found (Tab. 1). Most *Bombus* spp. were small (1.5-2 cm in length, 65.4%, n=104), and only a few were between 2-3 cm (19.2%) or over 3 cm(3-3.5cm, 15.4%).

Our observations were timed to correspond with the previously recorded peak feeding time of Bee-eaters in Hungary (Fintha 1968). The adults delivered prey to the nest at a rate of 50-60 visits/h at the beginning of the week, but at 40-50 visits/h at the end of the week. The visiting rate also decreased slowly within every observation period (Tab. 2). Only adults flew into the study burrow, but they were unmarked, therefore we did not know whether there was a helper among them.

4. Discussion

The following explanation can be suggested for this odd behaviour:

Day hour	1	2	3	4	5	6	7
14-15	60	61	56	49	51	45	48
15-16	51	60	52	50	46	41	42
16-17	55	48	48	46	41	39	43

Tab. 2. The number of visits per hour by adult Bee-eaters. Two ways ANOVA (day: $F=12.61$, $df=6$, $p<0.001$; hour: $F=23.99$, $df=1$, $p<0.001$).

HYPOTHESIS 1: Some or all of the nestlings perished during the two cold rainy days preceding the start of observations. There was a delay before the parents detected this, after which the amount of surplus food delivered to the nest decreased rapidly.

HYPOTHESIS 2: One (or more) failed breeder(s) from the surrounding Bee-eater colonies joined our breeding pair as helper(s), so the provisioning rate of the nestlings increased. The arriving helper was initially frightened of entering the burrow, so it dropped the prey delivered. Later the parents and helper(s) detected the unnecessarily high provisioning rate and delivered less food, so the surplus prey decreased rapidly.

HYPOTHESIS 3: In spite of the rainy and cold weather preceding the first day of observation, the foraging adults of the nest-hole studied discovered a large nest of bumble-bees (*Bombus* spp.) near the burrow, and plundered it over a week. The bumble-bees became much easier to catch during the cold rainy weather before the observations because they were colder so flew more slowly and were less able to evade the Bee-eaters. Later, as the abundant prey source was exhausted, and/or the adults detected the uneaten surplus food they delivered food at a lower rate.

HYPOTHESIS 4: Due to the bad weather the nestlings were provisioned almost exclusively with bumble-bees. The venom of bumble-bees might affect the young adversely, so that the nestlings did not consume all the prey items which were not devenomed, killed and prepared suitably for them by the adults.

HYPOTHESIS 5: A predator (e.g., a snake, weasel) had been seen in or nearby the nest and the adults were frightened of entering the burrow and dropped the prey items delivered below the burrow entrance.

It is difficult to decide unequivocally between these hypotheses. In our opinion they are not mutually exclusive, in fact it is quite likely that two or more are acting at the same time.

HYPOTHESIS 1 is supported by the observation that young Bee-eaters may become lethargic during cold spells and food shortage (Valverde 1953). Chilled and moist young elicit no parental care, and may be pushed aside or even tossed out of the nest (Cramp 1985). Runts are usually left in nest, and the parents continue prey delivery uninterrupted after the death of some nestlings (Glutz & Bauer 1980).

Fintha (1968) noted that nest-holes are generally not dug less than 25-30 cm from the top of banks. Nests dug higher than this often leak, especially if the substrate above the burrow is sandy, leading to the death of nestlings (Fintha 1968). Nest-holes too near the top of banks may also be blocked by the growing roots of plants (e.g., Medicago *Eryngium campestre*), particularly after rain (Fintha 1968). The study nest was in sandy ground and 30 cm from the top of bank, so it may have leaked but we did not find root's mesh blocking the nest.

HYPOTHESIS 2 is possible because non-breeding Bee-eaters may attach themselves (either singly or several together) to breeding pairs as helpers (Lessells 1991). Helpers are tolerated at nest-holes and on territory perches, and help provision the young. They did not arrive until after the brood has hatched. It is not known if they

help the brood in any way other than feeding them (e.g., brooding). Helped broods receive more prey items and the breeding male, but not female, at helped nests delivers food at a lower rate than at unhelped nests. Helpers may start helping at any stage during the nesting periode. The vast majority of helpers are male; male helpers comprise a slightly higher proportion of juveniles than occurs in the breeding population. Birds failing before early-mid June tend to re-nest (early-failed breeders), and those failing after this data to help (late-failed breeders) (Lessells & Krebs 1989).

Our observations were made in the last week of July, so it is likely that failed breeders were around. After the arrival of a helper, an initially surplus delivery of food might be compensated by decreased provisioning by the male.

HYPOTHESIS 3 is supported by the fact that Bee-eaters prefer Hymenoptera. Bumble-bees (*Bombus* spp.) are the most important prey for those living near clover fields and areas with many flowers. The diet often reflects variations in the insect fauna due to seasonal and geographical changes or to weather conditions and temporary and local exploitation of particular species are typical (Cramp 1985). The occurrance of *Bombus* in the diet may be higher during cold rainy weather when almost exclusively *Bombus* spp. fly in the fields (Fintha 1968). However hypothesis 3 would explain only the presence of *Bombus* spp. and not the other prey items.

HYPOTHESIS 4 seems likely, because large or venomous insects are difficult for inexperienced juvenile Bee-eaters to manage (the number of such prey items increases suddenly beneath perches after fledging). Birds show no further interest in prey which has been dropped onto ground (Koenig 1959, Ursprung 1979, Helbig 1982). Inexperienced young birds select large black and yellow insects in preference to plain ones (Ursprung 1979, Cramp 1985). Considerable differences exist between nestling diet and that of the parents at the same time; the young are generally given larger items than the adults consume (Krebs & Avery 1985).

On the basis of the investigations made by Helbig (1982), most preys of Bee-eaters are over 10 mm long, with ca. 28% of them being 5-10 mm, ca. 51% 10-15 mm and ca. 18% 15-20 mm. Compared with this the surplus items delivered (Tab. 1) tend to be larger and perhaps more difficult to handle.

It is unlikely that prey dropped well down the burrow would manage to (regularly) crawl back to the burrow entrance, so most of the prey must have been dropped at the entrance. It is possible that the chicks were of an age when they sat in the burrow entrance, but we could not observe this during the time of observation. So it seems likely that the adults were dropping the prey without entering the burrow. In Bee-eater colonies adults do this if they are reluctant to enter the burrow for some reason, which might be because (Lessells pers. comm.): (a) they are a newly arrived helper, and are reluctant to enter the burrow; (b) the chicks do not make begging calls – when the adult arrives and calls at the nest entrance – because they are satiated (Lessells et al. in press); (c) there is some danger (e.g., a snake near or in the nest).

Chicks reach a maximum weight several days before they leave the nest (Lessells & Avery 1989) and then lose weight before leaving the nest. At this time they feed, and prey can be often found below the nest entrance (Lessells pers. comm.).

5. Conclusions

The food provisioning rate of Bee-eaters is probably determined by three factors: (a) the food requirement of the nestlings

(FRN), (b) the sum of power of food delivery of adults (SPFDA) (parents and helpers) to the nest, and (c) the rate of prey capture (RPC) per bird. If FRN suddenly decreases – due to the death of some nestlings, for example (HYPOTHESIS 1) –, or SPFDA suddenly increases – e.g., due to the arrival of helpers (HYPOTHESIS 2) –, or RPC suddenly increases – due to weather conditions or the discovery of an abundant prey source (HYPOTHESIS 3) – then surplus food may be delivered to the nest for a while until the adults compensate for the change. In HYPOTHESIS 1, the decrease in FRN is compensated by a decrease in SPFDA, in HYPOTHESIS 2 the arrival of helpers is compensated by a decrease in provisioning rate by the breeding male, and in HYPOTHESIS 3 a temporary surplus is alleviated by the gradual exhaustion of the food source.

Recent studies have shown, that there is a trade off between reproductive effort such as feeding young and parental survival (Reid 1987, Nur 1988, Dijkstra et al. 1990). However, our observations suggests that the adjustment of prey delivery to the nest is not an instantaneous process, and that the adults need a few days to adjust their effort to the requirements of the nestlings.

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Összefoglalás

Egy gyurgyalagpár (Merops apiaster) fölös zsákmányhordása

Egy gyurgyalagpár szokatlan viselkedéséről számolunk be, mely abban nyilvánult meg, hogy a felnőtt madarak többlet táplálékot szállítottak a fészekhez. Az el nem fogyasztott fölösleges zsákmány a fészek bejárati nyílásánál halmozódott fel. Beszámolunk a táplálékt öbblet faj és méret szerinti összetételéről valamint mennyiségéről az idő függvényében.

A gyurgyalagok viselkedésökológiájának alapján a következő elképzelhető, egymást ki nem záró hipotéziseket állítottuk fel a zsákmányfölösleg felhalmozódásának magyarázatára: (1) a táplálékigény hirtelen lecsökkenése a fiókák egy részének a fészek beázása következtében való elpusztulása által, (2) a fészekbe hordott táplálékmennyiség ugrásszerű növekedése segítő (helper) gyurgyalag(ok) érkezése és a fiókák etetésébe való bekapcsolódása miatt, (3) a felnőttek zsákmányszerzési hatékonyságának hirtelen növekedése a fészek közelében felfedezett gazdag táplálékforrásnak köszönhetően, (4) a fiókáknak a nagyszámú fullánkos, mérges poszméhtől való idegenkedése, mikor az időjárási körülmények következtében más táplálék nem állt rendelkezésre.

A zsákmánytöbbletnek a fészek környékén megfigyelt felhalmozódásából és időbeli csökkenéséből következtetni lehet a fészekhez való táplálékszállítási folyamat ütemére: a felnőtt gyurgyalagoknak néhány napra van szükségük, hogy a fiókák igényei szerinti mennyiségű táplálékot szállítsanak a fészekbe.

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