reduction division[6]. Thus production of sexuals might have taken place through any of the above asexual forms. The detailed cytological studies on the reproductive behaviour will form an interesting pursuit of a hitherto unknown aspect of these aphids under Indian conditions.

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Received 19 October 1992; accepted 5 April 1993

Helpers in cooperatively breeding small green bee-eater (*Merops orientalis*)

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A three-year study of breeding behaviour in the small green bee-eaters (*Merops orientalis*) conducted in and around Bangalore, revealed that in 40% of the nests studied, a solitary helper assisted the breeding pair in nesting activities. In such nests the duration of the nesting was significantly reduced and the number of chicks fledged per nest was significantly higher. It was also observed that nests with helper were more during the season following poor rainfall than those following good rainfall.

OVER 300 species of birds are known to exhibit co-operative breeding behaviour where an auxiliary (non-breeding adult) typically assists the breeding pair in rearing their young[1]. Such a behaviour has been recorded for at least five species in India (Table 1). Such altruism appears, at first sight, to be paradoxical under the Darwinian theory of natural selection. The most important advance to explain such paradoxical behaviour is the theory of inclusive fitness[2]. The central idea in Hamilton's theory is that fitness comes not only from rearing ones' offspring but may also come from caring for ones' genetic relatives. In other words, altruism is not paradoxical since it is nepotistic, i.e. directed preferentially towards genetic relatives[3].

Table 1. Indian birds exhibiting cooperative breedin ;

Name	Source	Year
Chestnutheaded bee-eater *Merops leschenaulti*	Pappanna, per. commun.	1990
Small green bee-eater *Merops orientalis*	This report	1992
Jungle babbler *Turdoides striatus*	Gaston, A. J.[9] Zacharias, V. J.[10]	1976 1978
White-headed babbler *Turdoides affinis*	Zacharias, V. J. and Mathew, D. N.[10] Praveen Karanth, K. and Sridhar, S. unpublished	1978 1990
Pied kingfisher *Ceryle rudis*	Rayer, H. U.[11] Sridhar, S. and Karanth K. P. unpublished	1980 1989

The bee-eaters (family Meropidae) are alert and vivacious birds, distributed in tropical Old World. They specialize in catching bees and related hymenopterans. Of the 24 species of bee-eaters in the world, 11 are reported to exhibit seemingly cooperative breeding behaviour[4]. The small green bee-eater, *Merops orientalis*, has eight races, easily the most geographically variable among bee-eaters with slight plumage variation. They are common in open cultivated fields, nest on face of perpendicular banks of canals and ravines, sandy river banks and sandy bunds and gently sloping bare grounds, around cultivated tracks. The nests are in loose colonies, with a distance between any two nests being more than 10 m. The nesting season around Bangalore is February–August, with peak breeding around April–May. Only one helper is seen with a pair, arriving normally after the completion of nest excavation or beginning of incubation and staying with the breeding pair, even after the chicks have fledged.

A total of 24 pairs were observed for three years (1990 – 92) during breeding months (February to August) at GKVK Campus of the University of Agricultural Sciences, in North Bangalore (13° N 77° E, rainfall 890 mm; altitude 930 m). Three nests were observed daily for 2 h (4.00 PM to 6.00 PM) from the period of nest site selection till the chicks fledged, while the other 21 nests were observed twice a week.

Birds visiting the nest were marked using indelible nontoxic dye for identification. To do this we erected mist net in front of the nests under excavation during night. When the birds leave the burrow or approach the burrow the next morning they became harmlessly entangled in the nets. After taking measurement we put the non-toxic dye (Fevicryl fabric paint), different colours for different individuals caught at each nest. Frequency of food provisioning by individuals (parents and helper) in nests with and without helpers was recorded. Data on each stage of the breeding cycle which included duration of nest digging, incubation, feeding the chicks and feeding the fledglings were also recorded. The average duration of each stage of nest cycle was taken for determining the time spent on primary nesting activities (excavation, incubation and feeding). The peak breeding period was determined by finding out the months in which maximum number of active nests were observed compared to previous months.

Nest digging activity in small green bee-eaters, commenced around mid-February and excavation was completed in 15 to 20 days. A lag period of 5 to 10 days was noticed before egg laying and incubation. The period of

Table 2. Comparison of nests with and without helper

Nests	Predated	Nested	No. of days (analysed)	No. of chicks to fledge	No of chicks hatched	Feeding hatched (freq./h./nest)
Helped	9	0	4	2.25(±1)	6.5(±1)	14 75
Not helped	15	3	5	4.6(±1)	5(±1)	10.50
Mann—Whitney U test to compare nests with and without helper				$P < 0.02$	$P < 0.05$	$P < 0\ 05$

Values in parentheses indicate SD.

incubation varied between 20 and 25 days. The period of feeding the chicks at nest lasted for about 25 days, subsequently the fledglings started emerging.

Nine out of twenty-four (40%) nests were frequented by one helper each, where the helpers normally arrived after the commencement of incubation and assisted in the nesting activities such as incubation, feeding the breeding female, feeding the chicks (for 6 to 7 weeks). The helpers also vocalized with the breeding pairs and chicks.

It was noticed that in the nests with a helper, the nestlings grew rapidly and all the chicks fledged within (2.25 ± 1) days, whereas in an unhelped nest the chicks were at different stages of development; hence the fledging period (the time period between the first and the last chick emerging out of the nest) was significantly higher (4.6 ± 1 days) (Table 2). On an average, the nests with a helper fledged significantly more number of chicks (6.5 ± 1), compared to nests without helpers (5 ± 1) (Table 2). None of the nests helped were predated while 20% of those without helpers suffered predation, this difference is marginally significant (*G*-test of independence, $0.1 > P > 0.05$). The frequency of feeding the newly hatched brood at the nests with helper was significantly higher (14.75 h/nest) compared to the rate in unhelped nest (10.5 h/nest) (Table 2).

The nests initiated following poor monsoon (rainfall < 890 mm) were more likely to receive help compared to nests initiated following good rains (rainfall > 890 mm) ($\chi^2 = 7.8$, $df = 1$, $P < 0.001$) (see Table 3).

In one particular instance, the same individual was seen helping the breeding pair at the same site in two consecutive years (1990 and 1991) thus, suggesting natal philopatry in helpers. In this case the helper was seen preferentially feeding a particular chick after it has fledged from the nest.

Helping increases the number of chicks fledged per nest and decreases the days taken by the chicks to fledge. This is possible because of the increased frequency of food received by the chicks in the nests with helpers. Helpers also reduced the probability of a nest being predated. This is accomplished through increased vigilance of the nest by the frequent presence of one of the three adults in these nests.

The question why the 'helper' should help has been addressed in different ways. One of the arguments is that this happens when the auxiliary has a lower probability of being successful as a breeder[5-8]; that is it is constrained to breed due to prohibitive cost of independent reproduction (ecological constraint model[8]). Such a situation occurs during harsh season (breeding season following poor monsoon) when the insect population is predicted to be low, it then pays to increase ones own fitness by helping a closely related, established pair to reproduce. This is supported by the present work; the frequency of helping was high following a poor monsoon than following good monsoon, the helpers are expected to have a lower probability of success if they attempt to breed on their own following a poor monsoon. Though this report demonstrates that nests receiving help have a higher fitness compared to unhelped nest, more data are required to determine whether helping is directed only towards close relatives.

Table 3. Influence of rainfall on nesting strategy of Bee-eaters

	Poor seasons 1989–90	1990–91	Good season 1991–92	Total
Rainfall (mm)	640	504	1260	
Helped	3	4	2	9
Unhelped	4	3	8	15
Total	7	7	10	24

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ACKNOWLEDGEMENTS. We are grateful to Professors S. T. Emlen of Cornell University, A. Zahavi of Tel Aviv University for their advice, encouragement and constructive comments. We thank B. Mallik and Ganeshaiah, UAS, Bangalore; R. Gadagkar, Anindya Sinha, Milind Watve, IISc, Bangalore for their comments and editing this paper. We are particularly indebted to R.S. Harve and to Late H. B. Papanna for their assistance in our field trips.

Received 2 November 1992, revised accepted 5 May 1993