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Social and Breeding Biology of Bee-eaters in Thailand

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ABSTRACT.—I report on the social and breeding biology of four bee-eater species in Thailand. Little Green Bee-eaters (*Merops orientalis*) breed cooperatively in clusters of overlapping territories. Cooperative breeding units have one to two helpers that join the breeding pair only after incubation has begun. Nests rarely are left unguarded due to threats of predation and possible intraspecific brood parasitism. Males also guard their mates against extrapair copulations. The Blue-tailed Bee-eater (*M. philippinus*) breeds cooperatively and has a complex social system, with evidence suggestive of intraspecific brood parasitism and extrapair copulation. I provide evidence that the Bay-headed Bee-eater (*M. leschenaulti*) breeds cooperatively and report observations of noncooperative breeding at one nest in the Blue-bearded Bee-eater (*Nyctyornis athertoni*).

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The bee-eaters (Aves: Meropidae) are a clade of 26 species with considerable diversity in social and breeding behaviors. This behavioral diversity includes colonial and solitary nesting, migratory and sedentary populations, and cooperative and noncooperative breeding systems. However, for several species data on these behaviors are lacking. These data are crucial for comparative studies concerning the evolution of, and the ecological influences on, bee-eater social system diversity. This paper describes aspects of the social structure and breeding biology of four bee-eater species breeding in Thailand.

The Little Green Bee-eater (*Merops orientalis*) is the most variable species in the family in regard to plumage color and can be subdivided into 6–8 geographically variable races (Fry 1984). Whether this species also shows variation in social and breeding behaviors in populations ranging from western sub-Saharan Africa through the Middle East and Indian subcontinent to south Asia is not known. To address this question, I compare the social system of Little Green Bee-eaters that were studied in Thailand and in India (Sridhar and Karanth 1993). Little information previously was available on the breeding biology of the Blue-tailed Bee-eater (*M. philippinus*), except that it sometimes nests in colonies (Fry et al. 1992). Here I show that this species breeds cooperatively and has a complex social system similar to other colonial bee-eaters. Lastly, I briefly describe the social system of the Bay-headed Bee-eater (*M. leschenaulti*) and the Blue-bearded Bee-eater (*Nyctyornis athertoni*).

METHODS

I made behavioral observations from 12 March through 5 May 1996. I studied Little Green Bee-eaters at Khao Sam Roi Yot National Park (99° 55′ E, 12°

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07′ N; Prachuap Khiri Khan Province; 110 h observation). The study area (0.23 ha) was an open deciduous woodland habitat immediately southwest of the park headquarters. Surrounding areas included open, dry marshlands, prawn farming ponds, mangrove-bordered streams, and open scrub. I studied Blue-tailed (59 h observation) and Bay-headed (11 h observation) bee-eaters on the banks of the Huai Sai Yai, approximately 15 km west-northwest of Ban Nadee (101° 37′ E, 14° 10′ N;, Prachinburi Province). Secondary growth deciduous forest and agricultural fields surrounded the river. I observed nesting Blue-bearded Bee-eaters in a montane evergreen rainforest at Khao Yai National Park (101° 35′ E, 14° 27′ N; Nakhon Ratchasima Province; 4.5 h observation).

I captured Little Green (n = 13) and Blue-tailed (n = 15) bee-eaters using mist nets and I marked individuals with unique combinations of nontoxic paints to allow recognition of individuals. I made behavioral observations of Blue-tailed Bee-eaters from within a blind. I estimated colony size in the Blue-tailed Bee-eaters by repeated censuses of the number of marked and unmarked individuals at the colony. I used the unbiased estimator Petersen method (Krebs 1989) to derive estimates of the colony size. This method estimates the colony size as

$$\hat{N} = \frac{(M + 1)(C + 1)}{R + 1} - 1,$$

where M is the number of individuals marked, C is the total number of individuals censused, and R is the number of marked individuals censused. I also calculated the 95% Poisson confidence limits for colony size (Krebs 1989). I collected 20 30-min focal individual observations of Little Green Bee-eaters from 5 to 10 April to quantify the time individuals showed nest guarding behavior. Nest guarding was identified as being inside the nest or perching ≤10 m and having an unobstructed view of the nest. Cavities at this time contained either completed or initiated clutches. I also recorded the frequency of perch changes, the behaviors associated with perch changes (e.g., flycatching, pursuit of predators, pursuit of conspecifics near nest), and the presence or absence of another bee-eater perched ≤10 m of the nest cavity. I also recorded other behaviors such as copulation and courtship feeding during focal observations. I considered individuals seen copulating and involved in courtship feedings as breeders. I considered individuals that did not copulate, showed submissive behaviors toward breeders (e.g., retreated when challenged for perch position), and brought food to nests as helpers. Species were considered to breed cooperatively if at least one nest had at least one helper. Means are reported with standard error values.

RESULTS

Little Green Bee-eaters.—Little Green Bee-eaters bred in clusters of overlapping home ranges. Breeders actively defended only the area immediately around their nest cavity (2–3 m). I found one cluster of seven nests dug into slightly sloped or flat ground. Mean distance between adjacent active nests in this cluster was 22.9 ± 6.2 m. Several additional unused nest holes were dispersed among those finally chosen for breeding. I found three additional active solitary nests just outside the main cluster of seven nests.

Breeding is quite synchronous among Little Green Bee-eater nests. Excavation of nest cavities was in its final stages or complete by mid-March. Courtship feedings (n = 44) and copulations (n = 14) were seen frequently during mid-March and early April. During five 30-min observation periods of one breeding pair during their laying period, courtship feedings (n = 24) and copulations (n = 7) were seen at a mean rate of 9.6 ± 3.4 and 2.8 ± 0.8 events/h, respectively. During 95% (42/44) of courtship feedings I witnessed, marked males fed only one marked female and marked females were fed by only a single marked male; however, in two groups I saw an extra individual feed the breeding female once. One group was feeding two fledglings on 3 May. On the same date, two nests contained nestlings near fledging age while two others had less developed nestlings. The remaining two nests on the main study area failed before fledging young.

One potential nest predator abundant in the area is the butterfly lizard (*Leiolepis belliana*). During 20 30-min observation periods, bee-eaters directed attacks composed of multiple dives at these lizards on five occasions (0.5 attacks/h). I saw 17 additional bouts of attacks at other times. This antipredator behavior also was directed less frequently toward dogs (n = 2) and a snake (n = 1). Scaly-breasted Munias (*Lonchura punctulata*) and a small, unidentified lizard species did not elicit this antipredator behavior, even when within 1–2 m of the nest. During the periods of egg laying and incubation, individuals spent a significant portion of their time in vegetation ≤10 m from their cavity that gave them clear views of the nest cavity (i.e., nest guarding behavior). I observed five individuals during 20 30-min observations to determine the frequency of this guarding behavior. Individuals spent a mean of 55 ± 8% of their time guarding the nest, with ≥2 individuals guarding 45 ± 8% of the time. Nests were left unguarded for only 18%

± 6% of the time. Males were much more active while guarding than were females, making a mean of 49.6 ± 8.8 perch changes/h versus 18.7 ± 6.2 for females. Most of these movements were associated with flycatching behavior (males: 36.0 ± 8.4 sallies/h; females: 9.3 ± 3.4).

Little Green Bee-eaters breed cooperatively in Thailand. Three or more individuals were associated with four of the seven nests (57%) on the main study site. At one additional nest, the breeding male disappeared during the study and I saw another individual shortly afterward bringing food to this nest. It is unclear whether this individual was a helper or a replacement mate. Two cooperatively breeding groups in the main study site and possibly another group observed on a single occasion outside the study site each contained two helpers. All other cooperative groups had a single helper. I saw helpers associated with breeding pairs only rarely before the onset of incubation. In fact, before egg laying was suspected to be complete, breeding males chased potential helpers from the area of both the nest and breeding female on 11 of 25 (44%) agonistic interactions seen. Eight of these eleven events involved a marked individual that subsequently did become a helper at this nest. The remaining three events involved unmarked individuals at three nests that subsequently also had unmarked helpers. The remaining 14 of 25 agonistic interactions (56%) involved neighboring breeders. Helper duties included mobbing predators, feeding nestlings, feeding fledglings, occasionally feeding the breeding female, and possibly incubation. Helpers contributed significantly to the quantity of food items brought to nestlings. At one nest, I observed the helper bring food items to the nest on seven of twelve occasions.

Blue-tailed Bee-eaters.—Blue-tailed Bee-eaters bred in a dense colony in a sandy riverbank. In the center of the colony, a 130-m^2 vertical area contained 49 nest cavities, 16–19 of which were active. The activity of three cavities was questionable because I saw individuals only perch in the cavity entrance on a few occasions. The remaining cavities were either nests from previous breeding seasons or false nests dug during the 1996 season. Eight additional active nests were located ≤20 m from the main colony. Three estimates of colony size were 38, 43, and 55 individuals (mean of 45.3) with lower and upper 95% Poisson confidence intervals ranging from 16.1–16.7 to 84.8–105.6, respectively.

Excavation of nests dominated colony activity during mid-March, but also occurred during late April at two nests. Birds at most nests made infrequent nest visits (mean of 0.65 ± 0.11 visits/h, 11 nests, 7.5 h observation), suggesting most individuals were incubating during late April. Two groups, however, were feeding nestlings during late April (mean of 2.25 ± 0.33 visits/h, 7.5 h observation). I found an egg in one female, a netting casualty on 27 April, during subsequent specimen preparation. Certain breeders therefore were unsynchronized by at least the length of the incubation period, a period of 19–21 days (Fry et al. 1992, P. F. Coulter and DBB unpubl. data).

Blue-tailed Bee-eaters breed cooperatively in Thailand. I observed at least three birds feed nestlings at eight nests. Helpers could have been present at other active nests and may have escaped detection due to the large number of unmarked individuals. Interactions among individuals in the colony were frequent and suggest a complex social system, similar to that of other colonial bee-eaters (Fry 1972, Emlen and Wrege 1986, Jones et al. 1991, Fry et al. 1992). Intraspecific brood parasitism may occur in this population. I saw three individuals enter at least two active nest cavities and five individuals perched at the entrance of either two or three active cavities each. Individuals vigilantly defended the immediate area around their nests by frequently displacing interloping individuals. Also, I found a cracked bee-eater egg with a small puncture on the ground outside a series of nest cavities from which it apparently had been ejected. These behaviors are consistent with those associated with confirmed brood parasitism in another population of Blue-tailed Bee-eaters (P. F. Coulter and DBB unpubl. data).

Bay-headed and Blue-bearded bee-eaters.—One Bay-headed Bee-eater nest was located on the edge of the Blue-tailed Bee-eater colony, while two others were located 45 m upstream. One nest was only 1 m from a Little Green Bee-eater nest. At least one nest had three individuals bringing food to nestlings during late April. These individuals repeatedly

perched outside the nest cavity, waiting in queue to feed nestlings.

I found a Blue-bearded Bee-eater nest along the orchid waterfall trail in Khao Yai National Park. The nest cavity was dug 1 m high in the side of a small pit. On 30 April, I observed two individuals frequently bringing food to nestlings. I saw no evidence of cooperative breeding at this nest.

DISCUSSION

In most respects the breeding biology of Little Green Bee-eaters in India (*M. o. orientalis*; Sridhar and Karanth 1993) and Thailand (*M. o. ferrugiceps*) were similar. In both areas the species bred cooperatively in small clusters of territories. In India 20–57% of groups had helpers over three years of study, with a mean of 38%. Cooperative breeding was found in four of seven groups in Thailand. In India only a single helper was seen in attendance at each cooperative nest, while in this study two helpers were seen in two of four cooperative groups.

Helpers typically arrived after the start of incubation. Indeed, in this study the behavior of breeding males at early stages of breeding indicated that helpers may have been a threat with regard to extrapair copulation and/or intraspecific brood parasitism. Extrapair individuals that brought food to or simply perched near breeding females were displaced by breeding males, as were individuals who approached the nest cavity.

Two alloparental duties provided by helpers in many cooperative breeding species include feeding young and protecting young from predators (Brown 1987). Helpers in this study delivered a substantial portion of the food items to nestlings, as was the case in India. Little Green Bee-eaters also spent a substantial portion of their time guarding their nests. Frequent diving attacks were directed toward butterfly lizards and other potential predators when they approached the area of the nest cavity. In India, nests with helpers ($n = 9$) experienced no predation, while those without ($n = 15$) suffered 20% predation (Sridhar and Karanth 1993).

Previously, very little information was available on the remaining species studied here. Blue-tailed Bee-eaters were known to nest both solitarily and colonially, with colonies commonly containing 10–30 active nests and occasionally up to hundreds (Fry et al. 1992). The colony studied here was a small colony. This study is the first to document that Blue-tailed Bee-eaters breed cooperatively. This species shows additional similarities to other colonial cooperative breeding bee-eaters: Red-throated (*M. bullocki*), White-fronted (*M. bullockoides*), and European (*M. apiaster*) bee-eaters. Interactions among colonial individuals both within their own and among different breeding groups can be complex and lead to variable patterns of maternity and paternity associated with each nest (Fry 1972, Emlen and Wrege 1986, Jones et al. 1991, Fry et al. 1992). Molecular studies show that behavioral observations alone can lead to large underestimates of the effective rate of extrapair copulations and brood parasitism (Wrege and Emlen 1987). If any evidence of these behaviors exists, then they may be quite common. The behaviors seen in this study are strongly suggestive that extrapair copulation and intraspecific brood parasitism occur in Blue-tailed Bee-eaters.

Concerning the Bay-headed Bee-eater, an unpublished study cited by Sridhar and Karanth (1993) claims that cooperative breeding occurs in India. Blue-bearded Bee-eaters apparently breed only in solitary pairs (Fry 1984, Fry et al. 1992). Observations described here support those conclusions.

It is likely that at least 15 of the 26 species of bee-eaters breed cooperatively (Burt 1996). Some species, such as the Little Green Bee-eater, show slight geographic variation in breeding behavior. As the basic behavioral and natural history data are documented for all bee-eaters, phylogenetically explicit comparative studies will be possible and will lead to an understanding of the patterns of behavioral evolution in this group and the ecological forces that have molded these patterns.

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