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Confirmation of Infanticide in the Communally Breeding Guira Cuckoo

REGINA H. F. MACEDO^{1,3} AND CELINE MELO²

¹Departamento de Zoologia, Universidade de Brasília, 70910-900 Brasília, DF, Brazil; and

²Departamento de Biociências, Curso de Ciências Biológicas, Universidade Federal de Uberlândia, Campus Umarama, 38405-320 Uberlândia, MG, Brazil

The killing of conspecific infants may be common (Hrdy 1979, Sherman 1981, Hrdy and Hausfater 1984, Parmigiani and Vom Saal 1994) but is reported infrequently because the behavior occurs rapidly. In several species of mammals, infanticide has been linked with mate takeover or cases where a new dominant male comes into contact with infants sired by the harem's previous male (Hausfater et al. 1982, Sommer 1994). In birds, infanticide usually has been reported in the context of sibling rivalry (Mock 1984, Fujioka 1985, Drummond et al. 1986, Mock and Forbes 1994), although evidence suggests that the killing of infants also may increase the perpetrator's fitness by decreasing a competitor's reproductive success or enhancing access to a potential mate (Trail et al. 1981, Stephens 1982, Stacey and Edwards 1983, Fujioka 1986).

Guira Cuckoos (*Guira guira*) occur in groups of as many as 26 individuals (Gallardo 1984) and are classified by Brown (1987) as plural breeders with joint nests. During reproductive periods, groups are smaller but still may include as many as 13 adults. Throughout the egg-laying and incubation periods, eggs are commonly tossed out of the nest by group members (Macedo 1992). After chicks hatch, group members do not participate equitably in nestling feeding or nest guarding (Macedo 1994). DNA analysis has shed light on several aspects of group dy-

namics. For example, despite the appearance of social monogamy, the Guira Cuckoo mating system includes polyandry and polygyny (Quinn et al. 1994). Additionally, breeding opportunities may be limited because some group members are excluded from reproduction. Circumstantial evidence has suggested that the killing of newly hatched chicks is a common occurrence and that high chick mortality probably results from infanticide by conspecifics (Macedo and Bianchi 1997b). In this paper, we confirm that infanticide is indeed an important cause of mortality for Guira Cuckoo nestlings, and we speculate about its function as a reproductive strategy.

Methods.—The study was conducted in a suburban area of Brasília, Brazil (15°47'S, 47°56'W; elevation = 1,158 m), from September 1995 to March 1996 and September 1997 to February 1998; these periods coincide with the rainy season in this region. Further description of the study site and vegetation can be found in Macedo (1992). Each active nest was visited daily to check for new eggs, and the ground beneath the nesting tree was searched for vestiges of any eggs or chicks not in the nest. On the first or second days posthatching, each chick received temporary colored leg bands made out of plastic drinking straws, or colored dye marks. Continuous periods of nest observations were conducted primarily during the first week after chicks hatched (the period when nestling disappearance is most prevalent). Group size was estimated by counting the adults around the nest at

³ E-mail: rhmacedo@unb.br

TABLE 1. Fates of eggs and chicks in 15 communal nests of Guira Cuckoos during two nesting seasons. Ranges are in parentheses.

Variable	1995-96	1996-97	$\bar{x} \pm SD$
No. nests monitored	7	8	—
Total eggs laid	65	85	—
Total eggs lost	11	41	—
Total eggs hatched	41	53	—
Total chicks lost	24	30	—
No. eggs laid per nest	9.3 (6 to 13)	10.6 (6 to 21)	10.0 \pm 3.8
No. eggs lost per nest ^a	1.6 (1 to 4)	1.5 (0 to 9)	1.5 \pm 2.3
No. eggs hatched per nest	6.8 (4 to 12)	6.6 (2 to 10)	6.7 \pm 2.7
No. nests with chick losses	6	7	—
No. chicks lost per nest	4.0 (1 to 7)	3.8 (0 to 7)	3.9 \pm 2.5
No. observed infanticides	2	4	—
Overall chicks lost (%)	58.5	56.6	57.5

^a Egg loss from tossing by cuckoos or disappearance with cause unknown.

each visit and during observation periods; three consistent maximum counts were needed before an estimate was considered adequate. Adult group members were captured and color banded whenever possible.

Results.—We monitored 15 successful nests (i.e. at least one chick hatching) from egg laying until at least the eighth day after hatching. The number of eggs laid per nest in both years averaged $10.0 \pm SD$ of 3.8; egg loss per nest averaged 1.5 ± 2.3 (Table 1). Additionally, chicks disappeared from 13 nests ($\bar{x} = 3.9 \pm 2.5$), with more than half of the hatched chicks dying within the first week. Group size averaged 6.4 adults (range 4 to 8) for the seven groups observed. We observed eight infanticides during the study period and had circumstantial evidence for an additional two cases. Below, we detail these 10 cases (nest coding matches other published work), two of which are not included in Table 1 owing to lack of nesting data (nest F1b1).

Infanticide 1, nest A8.2.—On 31 October 1995, at 1115, an adult went to the nest, picked up a two-day-old nestling with its beak, and flew to the ground some 30 m away from the nest tree. Three other adults approached, and for approximately 1 min, they all pecked and pulled on the chick. The nestling was still alive at 1500, at which time it showed no external wounds but was barely moving. The adults did not approach the chick after the initial attack. Group size at this nest was eight adults.

Infanticide 2, nest A8.2.—A second case of infanticide occurred at nest A8.2 at 1205 on the same day, 31 October 1995, when an adult approached the nest, picked up a second nestling, and tossed it over the nest rim. This adult, along with two others, pecked and pulled on the nestling for about 1 min before abandoning it. Upon examination 10 min after the event, the chick was dead and exhibited two abdominal punctures. At 1415, an adult took food to the remaining nestlings and then approached the dead chick, pecked it repeatedly, and tossed it in the air.

Infanticide 3, nest C16.2.—On 13 November 1995, we observed an adult approach the nest at 1235, pick up a live four-day-old nestling, and carry it to the ground about 35 m from the nest tree. It pecked the nestling repeatedly for about 1 min and then left. The chick was examined immediately afterwards and was dead, although without visible external wounds. Group size at this nest was five adults.

Infanticides 4 and 5, nest F1b1.—The infanticide events at this nest occurred on 28 December 1995, when the nestlings were six days old. Our evidence was circumstantial in one case: we found a dead nestling on the ground, about 10 m from the nest, with hematomas around its eyes. We found a live nestling on the ground at 1530, but we did not see it being evicted from the nest. For about 30 min, a group of seven adults vocalized near the nest tree. Gradually, four of them approached the nestling and pecked it violently for a short period of time. At 1800, when the observation period ended, the nestling was alive but motionless. Group size was seven adults.

Infanticide 6, nest B9.1.—At 1025 on 2 October 1997, an adult went to the nest, picked up a three-day-old chick, and carried it to a perch on a fence about 10 m from the nest tree. The chick was alive and moving. Another adult flew from the nest tree and joined the first one. The first adult dropped the chick to the ground, and after about 1 min, both adults flew away from the area. When the chick was inspected about 5 min later, it was dead and showed no external wounds. Group size at this nest was eight adults.

Infanticide 7, nest C16.1.—This episode occurred at 1619 on 8 October 1997. An adult flew to the nest, picked up a one-day-old nestling, and flew to the ground about 10 m from the nest tree. It pecked the chick repeatedly, then picked it up and flew away from the area. Group size at this nest was four adults.

Infanticides 8 and 9, nest B8.2.—At 1250 on 16 November 1997, an adult picked up a live one-day-old nestling and flew to a tree approximately 40 m from the nest. We were unable to determine whether it

dropped the nestling or flew away with it. Later that day, a dead nestling with several head wounds was found at the base of the nest tree. Group size was eight adults.

Infanticide 10, nest D3.2.—On 9 December 1997, a marked adult group member picked up a one-day-old nestling and carried it to a fence about 20 m from the nest. It dropped the chick, retrieved it, and then pecked it occasionally while walking around the area. This adult belonged to a group that nested three times during the rainy season. It was captured and marked during the second nesting event (being described here), when group size was five adults. This adult actively participated in group activities during this nesting bout, such as feeding nestlings and remaining near the nest tree, as well as in the subsequent nesting event. In the nesting bout previous to the one described here (C16.1; group size not estimated), five nestlings vanished within the first week after hatching, and we witnessed one case of infanticide (described above). During the nesting bout following this one (D3.3; group size of five adults, but otherwise not described here), we found one nestling dead inside the nest, without external wounds.

Discussion.—Our observations indicate that infanticide is a common occurrence during reproduction in Guira Cuckoos. More than half of the 54 chicks that hatched died within the following week. These deaths occurred in a sequential fashion at each nest, and the dead nestlings did not exhibit evidence of predation. At least 11% of these deaths occurred as a direct result of adult intervention at nests. This value almost certainly is an underestimate, and we suspect that infanticide is the cause of death for most nestlings.

Our observations suggest that infanticide in Guira Cuckoos occurs in a context somewhat different from that suggested for other group-breeding birds. Most recorded cases of avian infanticide implicate the arrival of an immigrant, for whom the killing of nestlings may result in a breeding opportunity. For example, Stacey and Edwards (1983) reported circumstantial evidence whereby immigrant female Acorn Woodpeckers (*Melanerpes formicivorus*) killed nestlings to obtain a reproductive opportunity within the group and raise their own young. In non-communal species, such as egrets (Fujioka 1986), jacanas (Stephens 1982), and sparrows (Veiga 1993), the behavioral repertoire also includes egg destruction and chick killing during mate-takeover events.

In some (or perhaps all) cases, infanticide in Guira Cuckoos may be perpetrated by accepted group members. Unfortunately, the infanticidal adults, with but one exception, were not marked at the time of their chick-killing behavior. Despite little direct proof, however, several general factors point to the likelihood that infanticidal adults were members of the nesting group. In four of the episodes described,

at least one other adult was in close proximity to the one that evicted the chick, or helped to attack the chick after it had been evicted. We observed no aggression among adults, and it is very unlikely that a group of nonresident individuals could approach the nest and evict chicks without being attacked by the resident group members. In using hand-reared lure birds to capture adult group members (Macedo 1992, 1994), resident birds quickly attacked the strange individual, frequently using alarm vocalizations and aggressive displays. One additional piece of evidence that infanticidal adults are accepted group members comes from observations at nest D3.2. In this nest, the infanticidal adult was marked, and it participated in incubation and chick feeding before and after the infanticide took place. Also, this adult belonged to the group during the nesting bout following the one described. However, we do not exclude the possibility that infanticide is also used by non-group members. Because chicks are not cannibalized after being killed, it is likely that infanticide also functions as a reproductive strategy, perhaps to provoke a nesting failure and force a re-nesting attempt by the group, wherein the infanticidal adult could gain a mating opportunity.

In some of the cases (nos. 1, 2 and 5), multiple adults attacked chicks that had been removed from the nest. One possible interpretation is that all of these adults were infanticidal, and their behavior was due to a lack of breeding opportunity dependent upon group size. However, we do not think that this is a likely explanation. Although nesting attempts may occur with as many as 13 adults, none of the attempts we observed involved groups exceeding eight individuals. It is dubious that in smaller groups the involvement of up to four adults killing a chick qualifies all of them as infanticidal in the specific sense discussed here. Rather, we believe that attacking nestlings that have been removed from the nest may indicate that recognition of a chick as one of the group's offspring does not occur directly, but may be based, instead, on nest-association cues (Sherman 1981). Although this behavior can be considered different from the action of evicting a chick from a nest, this situation clearly demonstrates the capacity of group members to act together during aggressive acts.

Sociality is the result of many conflicting elements through which a point of equilibrium is reached (Emlen 1991). Guira Cuckoo groups fall into the "egalitarian" category proposed by Vehrencamp (1983), whereby all individuals potentially can attain reproductive status. However, the occurrence of infanticide in Guira Cuckoo groups suggests that the objectives of individuals in the group sometimes conflict, and that fitness benefits are not always equal for all individuals during a single reproductive event. In many studies, parental behavior has been associated with gamete contribution (Vehrencamp

1977, Joste et al. 1982, Craig and Jamieson 1985). The lack of a genetic contribution in the brood can result in the absence of parental investment. In the case of Guira Cuckoos, data indicate that some group members are completely excluded from a breeding event (Quinn et al. 1994). This could occur for a number of reasons (e.g. sexual immaturity, lack of copulation opportunities). An adult also could have a low fitness payoff in a particular nesting bout (e.g. a subordinate group member may have all of its early eggs tossed from the nest).

Given these observations, we hypothesize that infanticide in Guira Cuckoos is an alternative reproductive strategy that could benefit several types of individuals: (1) group members who fail to reproduce, and for whom a new breeding opportunity may arise if infanticide decreases the time until a re-nesting attempt is made; (2) non-group members that may gain membership in the next breeding bout by eliminating the communally produced brood; and (3) group members for whom fitness gains potentially are greater in a future nesting attempt than in the current attempt.

An intriguing question raised by these observations concerns the benefits of sociality that would offset the very high reproductive costs represented by egg and chick elimination. The habitat occupied by the study population is not saturated with breeding territories, so sociality probably is not maintained by ecological constraints (Macedo 1992, Macedo and Bianchi 1997a). Potential benefits of sociality in Guira Cuckoos include: (1) increased detection of and defense against predators; (2) improved foraging efficiency through enhanced detection of prey items; (3) increased defense of resources (nesting sites, food, etc.) against conspecifics; (4) better care of nestlings through increased levels of per capita feeding; and (5) higher long-term survival for individuals in groups. Further studies are required to enhance our understanding of the selective pressures that resulted in cooperative as well as contentious behaviors in Guira Cuckoos.

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Consistent Male-biased Seabird Mortality in the Patagonian Toothfish Longline Fishery

PETER G. RYAN¹ AND CHRISTIAN BOIX-HINZEN

Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa

Seabird by-catch from longline fisheries is a global conservation concern. Many thousands of birds are killed each year when they seize bait from longlines and are drowned (Brothers 1991, Alexander et al. 1997). Most of these birds are procellariiforms, which are long-lived species with low reproductive rates and high susceptibility to even small changes in survival rate, especially in adults (Croxall et al. 1990). The estimated effect of the tuna longline fishery in the Southern Ocean during the last 30 years is sufficient to account for observed decreases in breeding numbers of many albatrosses and other procellariiforms (Weimerskirch and Jouventin 1987, Croxall et al. 1990, Gales 1993). More recently, longline fisheries have commenced in the Southern Ocean, notably for Patagonian toothfish (*Dissostichus elegi-*

noides), in waters to the south of the area exploited by the tuna fishery (Cherel et al. 1996, Moreno et al. 1996). Mortality from these fisheries is placing additional pressure on seabirds in the Southern Ocean (Alexander et al. 1997).

Procellariiforms are monogamous (Warham 1990). Consequently, the demographic implications of longline by-catch are exacerbated when mortality is sex biased. Female-biased mortality from longline fisheries has been reported for Wandering Albatrosses (*Diomedea exulans*; Weimerskirch and Jouventin 1987, Croxall and Prince 1990) and Grey Petrels (*Procellaria cinerea*; Bartle 1990, Murray et al. 1993). These biases have been attributed to differences between the sexes in foraging ranges, with females foraging farther north than males and thus spending more time in the waters where tuna longline vessels operate. Here, we report consistent male-biased mortality from the longline fishery for Patagonian toothfish that oper-

¹ E-mail: pryan@botzoo.uct.ac.za