

Short Communications

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Notes on the Breeding Behavior of a Philippine Eagle Pair at Mount Sinaka, Central Mindanao

Jayson C. Ibañez,^{1,3} Hector C. Miranda, Jr.,^{1,3,4,6} Gliceria Balaquit-Ibañez,¹
Donald S. Afan,^{1,5} and Robert S. Kennedy²

ABSTRACT.—We documented the breeding behavior and diet of a Philippine Eagle (*Pithecophaga jefferyi*) pair from July 1999 to January 2000 in an isolated forest in Central Mindanao. We observed eight distinct courtship displays and several activity patterns on the nest. Copulation started two months prior to egg laying and continued until the first month of incubation, with a mean of 1.5 copulations per day. Seventy-four percent of the time devoted to incubation was by the female. The incubation period lasted 58 days. Throughout the incubation and early brooding phases the male provided food for the female and the young. Diet consisted of 17 prey items of four vertebrate taxa, mostly mammals, with civet cats (Family Viverridae) and flying lemur (*Cynocephalus volans*) representing the bulk of the diet. Received 30 November 2001, accepted 15 August 2003.

The Philippine Eagle (*Pithecophaga jefferyi*) is one of the most critically endangered birds of prey (Bildstein et al. 1998). It is endemic to the islands of Luzon, Leyte, Samar, and Mindanao of the Philippines. On Mindanao, eagles begin nesting from September to December in habitats ranging from primary lowland forests to highly disturbed woodlands. Recently, efforts were renewed to study the ecology and biology of this highly endangered raptor in an effort to devise management strategies for the long term conservation of the remaining population. An analysis of

the eagles' nesting density suggest that there are about 200 pairs in Mindanao, with each breeding pair occupying about 133 km² (Bueser et al. 2003).

A complete breeding cycle in this species lasts two years, and successful pairs produce a single offspring (Gonzales 1968, Kennedy 1985). Since the detailed work by Kennedy (1977, 1985) on Philippine Eagle nesting biology, there have been few studies on the behavior and ecology of this species. Recently, new information on the eagles' breeding success (Miranda et al. 2000) and nesting density and population estimates for Mindanao Island (Bueser et al. 2003) have been published. This study describes the prey as well as the behavior of a pair of Philippine Eagles nesting in a relict forest in Central Mindanao, Philippines. This initial attempt to quantify activity patterns of a pair in an isolated forest habitat is relevant in the light of continued forest fragmentation in the Philippines, where the behavioral responses of Philippine Eagles to a shrinking habitat remain unknown.

METHODS

We gathered 703 h of behavioral data between July 1999 and January 2000 in Mount Sinaka, Cotabato Province, Philippines. Mount Sinaka (07° 20' N, 125° 12' E) is located in an isolated mountain range (peak at 1,448 m) with 19 km² of relict tropical forest. A nest was found in 1995, and was used during two successful nesting attempts. On 15 June 1999, the female was caught by a farmer and brought to the Philippine Eagle Foundation for rehabilitation. After one week the eagle's right wing was marked by clipping following Young and Kochert (1987), a radio transmitter was installed, and the bird was released the following week. The following month we located the female building a nest

¹ Philippine Eagle Foundation, VAL Learning Village, Ruby St., Marfori Heights Subdiv., Davao City 8000, Philippines.

² Maria Mitchell Assoc., 4 Vestal St., Nantucket, MA 02554, USA.

³ Univ. of the Philippines in Mindanao, Bago Oshiro, Davao City 8000, Philippines.

⁴ Current address: Dept. of Biological Sciences, Univ. of Cincinnati, Cincinnati, OH 45221, USA.

⁵ Current address: Univ. of Santo Thomas, España, Manila 1008, Philippines.

⁶ Corresponding author; e-mail: mirandhc@email.uc.edu

in a tree 200 m away from the old nest. The new nest was in a 29-m White Lauan (*Shorea contorta*, Dipterocarpaceae) tree at 750 m elevation, in an agroforest located on the mountain's western slope. We documented aerial displays and nesting behavior from several blinds located 40–150 m from the nest using 8 × 40 binoculars and a 20–56× spotting scope. We distinguished the female by her wing and by radio tracking. We directly observed and identified prey items delivered to the nest. The egg was laid on 16 November 1999 and hatched after 58 days of incubation. However, the chick died nine days later after three days of stormy weather.

RESULTS AND DISCUSSION

We recorded 118 h of notes on aerial displays, 293 h during nest building and before egg laying, and 292 h during incubation and brooding. We documented courtship behaviors during flight and on the nest. We distinguished four behaviors associated with aerial displays: mutual soaring, dive chase, talon presentation, and territorial flights. Mutual soaring was a circular gliding flight by both birds on thermals with the male usually soaring higher. Dive chases involved a diagonal drop in flight altitude, wings half folded toward the body, with the male trailing in pursuit. A dive chase sometimes was followed by a male talon presentation, which is characterized by a quick extension of the tarsi toward the back of the gliding female. On two occasions the female flipped over and quickly presented her talons. Such mutual talon presentation is known in many species of raptors (Brown and Amadon 1969). Mutual territorial flight behaviors were gliding flights with the male slightly above the leading female. Male courtship acts on the nest included vigorous calling toward the female in a low, horizontal posture (precopulation display), and delivery of prey for the female to consume (courtship feeding; Hatchwell et al. 1999). Food solicitation by the female, a pattern similar to the sexual solicitation display, also was observed. We also noted reciprocal pecking and preening actions directed toward the bill, wings, and other parts of the body of the other bird (allopreening).

We first observed delivery of nest materials on 17 September 1999, and deliveries contin-

ued throughout the study. The male brought more nest materials ($n = 29$ deliveries) than the female ($n = 22$ deliveries) prior to egg laying; the female made more deliveries ($n = 33$) than the male ($n = 7$) during brooding and incubation stages. Nest materials were delivered by both birds 1.7 times/day prior to egg laying, 1.2 times/day during incubation, and 3.0 times/day during brooding. The behavior sequence for nest building was as follows: the bird acquired leafy twigs (fresh or not) or a dried branch, deposited the material around the nest, pressed the materials with the breast, followed slowly by brooding. The mean duration of nest building behavior at the nest (excluding acquisition of materials) prior to egg laying was 5.7 min/day \pm 4.2 SD ($n = 43$).

Copulation occurred on the nest and nearby perches, with or without prior courtship feeding. When prey was delivered to the unattended nest, the male issued loud and prolonged calls that changed into short, high-pitched whines when the female alighted on the nest. Calls became vigorous and gained speed while the male mounted, but gradually waned after copulation. When the male displayed precopulatory behavior without food, he did so in an apparently more submissive and wary manner, walking in a low horizontal posture toward the female and mounting her if she did not exhibit any rejecting behavior (e.g., an erect or threat posture). We observed 27 copulation attempts (25 during courtship, 2 during incubation), for a mean of 1.7 copulations/day between September and December 1999. The duration of copulation from mounting until dismounting lasted a mean of 19 s \pm 3 SD ($n = 6$). In three instances, copulation occurred twice within a period of 30 min, and the maximum number of copulations observed in one day was three. Such copulation rates, which appear more than necessary for fertilization, has been reported in many raptor species (Newton 1979, Pandolfi et al. 1998, Arroyo 1999). Aside from ensuring successful fertilization, frequent copulation also is interpreted as a mechanism to strengthen the pair bond (Newton 1979).

The female performed 74% of the incubation duty (data from 963 instantaneous samples collected at 10-min intervals), but male incubation bouts were longer (the total time

that an adult spent on the nest bowl, sitting or not; male: mean = 3.1 h \pm 1.7 SD, $n = 11$ bouts; female: mean = 1.4 h \pm 0.8 SD, $n = 70$ bouts). Preening, defecation, or nest building by an attending adult commonly ended a bout of incubation. Unlike defecation, which was done only from a different tree, preening was performed also on the nest. When inside the nest bowl, an adult approached the egg with a distinctive gait: flexed toes with claws directed inward and feet leaning sideways. Before the adult sat, the egg was turned by reaching down 2–5 cm ahead of the egg then gently arching its bill toward the belly. While incubating, the adult tugged intermittently at the substrate in front of the egg. The mean time spent away from the nest was 21.0 h \pm 3.8 SD ($n = 5$) for the male and 4.6 h \pm 1.7 SD ($n = 8$) for the female. Turnover of incubation was signaled by calling or by alighting on the nest. The longest period that the egg was left unattended was 102 min. The male performed nighttime incubation on only three occasions, while the female incubated the egg during the rest of the nights throughout the duration of the incubation period.

We did not directly observe hatching, but surmised its occurrence from the behavior of the brooding female. On the morning of 13 January 1999, the female increased her tugging behavior and appeared to be sitting less tightly on the egg. The female turned the egg several times and nibbled frequently at the nesting materials. A few minutes after the chick hatched, the female moved the shell and ate a few pieces. No vocalizations were heard during hatching, but the adults exchanged calls about 3 h after hatching. The first parent-chick interaction consisted of light pecks and brushes by the female soon after the chick was able to raise its head.

Only the female brooded the chick and she spent less time brooding (62% of instantaneous samples, $n = 321$) than incubating (74% of 963 samples). Mean duration of female brooding bouts was 80 min \pm 46 SD ($n = 14$). Although the male did not brood, he attended the nest for a mean duration of 6.7 min \pm 9.7 SD ($n = 9$) when the female was away. The male was absent during the last three days of observation. The chick was left unattended for a maximum period of 232 min on 20 January 2000, eight days into the nest-

ling stage (mean duration = 55.2 min \pm 64.6 SD, $n = 13$). The female alone fed the chick; mean duration of feeding bouts was 13.0 min \pm 6.6 SD ($n = 11$). The first meal was delivered on 15 January 2000, two days after hatching, and consisted of 36 pea-sized bits of rat meat. The chick was fed three times on the third day, three times on the seventh day, and twice on the ninth day.

The male eagle delivered 17 vertebrate prey items to the nest from October 1999 to January 2000: 11 during the courtship period (mean = 0.34 prey/day), 2 during incubation (mean = 0.10 prey/day), and 3 during brooding (mean = 0.50 prey/day). Of the 17 prey items, 16 (94%) were mammals. Prey items included flying lemurs (*Cynocephalus volans*, $n = 7$), civet cats (Family Viverridae, $n = 7$), rice field rats (*Rattus* spp., $n = 2$), and Philippine cobra (*Naja naja*, $n = 1$). Some of the prey items observed in this study also were reported by Kennedy (1985). Contrary to persistent reports by local people, no domestic animals were recorded.

Except for the Philippine cobra, all prey items were mostly gutted and decapitated, with portions of the fur already plucked off. Only the hindquarters of the civet cats were delivered to the nest. All prey appeared fresh, and probably came from new kills. Most of the delivered carcass was consumed, including the tail, bones, nails, and a few internal organs (e.g., kidney, intestine). Portions of prey not eaten immediately were left on the sides of the nest and in most cases were consumed later. On three occasions old prey remains that had not been consumed were removed from the nest. Unlike observations of Harpy Eagles (*Harpia harpyja*) in South and Central America (Alvarez-Cordero 1996, Galletti and de Carvalho 2000), we rarely observed discarded skeletal bones of prey. Although the sample size of prey was small, our observations suggest that studies of the diet of tropical birds of prey such as the Philippine Eagle based solely on prey remains rather than direct observations could underestimate prey species diversity.

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Adoption in the Red-cockaded Woodpecker

James Cox^{1,3} and Phil Spivey²

ABSTRACT.—We observed a young male Red-cockaded Woodpecker (*Picoides borealis*) about 35 days old being fed by adults associated with a neighboring territory. A survey of biologists studying this species revealed similar acts of adoption had been observed elsewhere, but the behavior appeared to be very rare. Adoption generally implies a cost to adults because care is provided to unrelated young, but the situation is complicated in cooperative breeders such as

the Red-cockaded Woodpecker. Adopted birds can help breeding adults raise additional young, and the adopted male we observed remained as a helper in its adopted territory and fed young the following breeding season. *Received 4 December 2002, accepted 12 March 2003.*

¹ Tall Timbers Research Station, 13093 Henry Beadel Rd., Tallahassee, FL 32312, USA.

² Georgia Dept. of Natural Resources, P.O. Box 6385, Thomasville, GA 31758, USA.

³ Corresponding author; e-mail: jcox@ttrs.org

Acts of adoption (parental care of presumably unrelated offspring) have been recorded in <150 species of birds (Evans 1980, Riedman 1982). The behavior occurs with some regularity among species that nest colonially in high densities (Evans 1980), but it also has

been reported in species that maintain larger breeding territories, particularly in association with loss of an adult breeder (Rohwer 1986). Despite its known occurrence among many species, new records of adoption can be noteworthy because they may help elucidate social and reproductive features associated with the behavior (Riedman 1982, Rohwer 1986). In this note we provide the first reports of probable acts of adoption in the Red-cockaded Woodpecker (*Picoides borealis*).

The Red-cockaded Woodpecker is an endangered species (Lennartz and Henry 1985) with a social breeding system (Lennartz et al. 1987, Walters 1990). This species has been the subject of extensive research throughout much of its range (Jackson 1995), but there have been no previous reports of adoption. The information we present stems from field observations in the Red Hills region (84° 18' N, 30° 42' W) of southwestern Georgia (Engstrom and Baker 1995) and a survey of biologists studying this species elsewhere in the southeastern U.S.

We uniquely banded many nestling and adult Red-cockaded Woodpeckers in the Red Hills to monitor the potential effects of translocation (U.S. Fish and Wildlife Service 2000). We banded three nestlings at approximately 6 days of age in May 2001 in territory A. In early June, we observed two of these banded birds (fledglings) in territory A and determined they were males (Jackson 1979). Within an hour of this observation, we observed the third bird banded in territory A (also a male) being fed by an adult in a neighboring territory (territory B). Another fledgling, which we had banded in the nest cavity at territory B, also was observed nearby. We found the adopted fledgling from territory A in territory B on later visits, but none of the fledglings banded in the nest of territory B were observed again.

Adults associated with the two territories were not uniquely banded, so we were not certain that the fledgling from territory A was the only bird that moved into territory B. However, the number of adults associated with each territory was estimated early in the breeding season, and this number had not changed at the time these observations were made (four adults in territory A, three adults in territory B). It is uncommon for new adults

to be accepted quickly by territorial groups (Ligon 1970, Lennartz et al. 1987).

There were other factors that likely contributed to this event. First, the adopted bird was the smallest nestling banded in territory A (29 g compared to 31 and 33 g for the other nestlings). Birds with lower nestling weights are more likely to disperse in response to competition with siblings (Pasinelli and Walters 2002). Second, the distance between territory centers was only 850 m, but a small creek lined with hardwoods (i.e., unsuitable habitat) lay between the territories and may have inhibited return of the dispersing fledgling once it ventured into territory B. Third, and perhaps most important, the adopted bird from territory A was 5–6 days older than the birds banded in territory B. The adopted bird therefore likely was at an advantage in terms of its ability to follow foraging adults and beg for food (Ligon 1970).

We circulated a description of this event to 26 biologists working with woodpeckers elsewhere and asked if any had noted similar behaviors. C. A. Hess (pers. comm.) reported an act of adoption in the Apalachicola National Forest in northern Florida, also during 2001. A banded juvenile moved to an adjacent cluster and was observed being fed by adults from the adopted territory. In this instance, a nesting attempt by the adopting adults failed, so there were no resident fledglings. This event also involved a potential hardwood barrier between territories. J. A. Jackson (pers. comm.) reported observing adoption in populations in Mississippi and South Carolina several years ago. These cases had similarities to the incident we observed, including the thin strand of hardwoods separating clusters and dominance of the adopted bird as a result of hatching asynchrony. J. R. Walters (pers. comm.) reported instances where young birds moved into neighboring territories soon after obtaining independence, but switches by dependent fledglings were very rare; the latter behavior usually was associated with loss of an adult, so the fledgling that moved was not being fed as frequently. As noted, the number of breeding adults did not appear to change during our observations; however, we believe competition with dominant siblings in territory A contributed to the movement of the adopted bird out of its natal territory.

Adoption implies a cost to adult birds because time and energy are spent caring for presumably unrelated individuals (Rohwer 1986, Plissner and Gowaty 1988). There have been refinements to theories concerning the costs and benefits of adoption (Rohwer 1986), but the case of cooperative breeders presents a situation where benefits may accrue for adults that adopt. Young male Red-cockaded Woodpeckers often remain in their natal territories and help raise subsequent broods. Territories with helpers produce more offspring and are more stable than territories lacking helpers (Walters 1990). Helpers also reduce the number of feeding trips that adult breeders make during the nesting period (Khan 1999). These potential benefits were realized in this instance because the adopted male remained in territory B the following year and helped produce three fledgling females. The bird was still in the adopted territory on 1 October 2002 and may have helped produce additional progeny.

Although there are potential benefits associated with adoption, the behavior is rare in Red-cockaded Woodpeckers. Several biologists responding to our query reported observing fledglings in adjacent territories, but most of these were ignored by resident adults. Data from an old growth pine forest (Engstrom and Sanders 1997), which presumably resembles pre-Columbian conditions, suggest woodpecker territories were more tightly aggregated historically. Occasional movements of young among territories could have been more likely under these conditions. Why certain groups adopt wandering fledglings while others ignore these individuals probably is linked to special circumstances that defy generalizations. In addition to some of the circumstances mentioned above (e.g., fledgling interactions, asynchronous hatching, habitat barrier, number of adults, and loss of young), sex-based plumage differences evident in young Red-cockaded Woodpeckers (Hooper et al. 1980, Jackson 1979) would make it easy for adults also to consider the sex of wandering fledglings prior to adoption.

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Intergroup Infanticide in Cooperatively Polyandrous White-winged Trumpeters (*Psophia leucoptera*)

Peter T. Sherman¹

ABSTRACT.—I observed a population of White-winged Trumpeters (*Psophia leucoptera*) in undisturbed lowland moist forest in Peru. During 2,460 h of focal observations, I observed one instance of infanticide that occurred when a permanent group killed the 7-day-old chick of an intruding group that was using a portion of its territory. Trumpeter groups defend large, year round, contiguous territories that barely provide groups with enough food to meet their caloric requirements during the dry season when fruit abundance is low. There may be a selective advantage to such infanticidal behavior if it helps prevent the formation of a new group on a resident group's territory, and the concomitant loss of space that would accompany such an event. *Received 15 November 2003, accepted 11 March 2003.*

Instances of infanticide have been reported for a number of different animal species (Stacey and Edwards 1983, Hausfater and Hrdy 1984, Hiraiwa-Hasegawa 1988). In many of these cases, infanticide was explained as a product of sexual selection in that it creates reproductive opportunities that otherwise would be lacking. One common scenario is that by killing unrelated young, the infanticidal male causes his breeding partner to produce new offspring that he fathers. Infanticide also has been reported in communally breeding groups in which males or females may destroy eggs or kill young of other group members, presumably to increase the odds that the infanticidal individual's offspring will thrive as a result of decreased competition

with other young (Freed 1986, Whitmore 1986, O'Riain et al. 2000, Macedo et al. 2001).

Infanticide also has been reported among colonially nesting birds, where young are killed by neighbors (Fetterolf 1983, Hill et al. 1997). In colonially nesting species where cannibalism does not occur, it has been hypothesized that infanticide may be advantageous in that it prevents misdirected parental care or robbing of food by unrelated chicks (Pierotti and Murphy 1987, Pierotti 1991, Quinn et al. 1994), allows infanticidal individuals to obtain a nesting site that is in short supply (Morris and Chardine 1990, Hotta 1994), or may be a nonadaptive byproduct of aggressive territorial behavior (Hunt and Hunt 1975, Hunt and McLoon 1975).

Although mammals such as chimpanzees (*Pan troglodytes*) have been reported to kill young in other groups in what may be an example of intergroup breeding suppression (Hiraiwa-Hasegawa and Hasegawa 1994), no descriptions of such behaviors have been published for avian species. In this note, I describe an incident in which several members of a group of White-winged Trumpeters (*Psophia leucoptera*) killed the offspring of an intruding group that was breeding on their territory, and discuss whether this behavior might have any adaptive significance.

METHODS

Between 1983 and 1987, I conducted a study on the behavior and ecology of White-winged Trumpeters (Gruiformes, Psophiidae)

¹ Dept. of Biology, Transylvania Univ., Lexington, KY 40508, USA; e-mail: psherman@transy.edu

living in the vicinity of Cocha Cashu Biological Station, in Manu National Park, Peru (11° 51' S, 71° 19' W). The study area was located in undisturbed lowland tropical moist forest (for a detailed description of study site, see Terborgh 1983). During the study I conducted 2,460 h of focal observations on individuals in 7 permanent territorial groups and 10 temporary nonterritorial groups that formed during four breeding seasons. The majority of birds observed were color banded and habituated to humans, allowing me to observe them at distances of ≤ 4 m for entire days. Because trumpeter groups were cohesive and interactions between groups were easily observed, any infanticidal event that occurred during focal observations should have been observed. However, because such events probably occurred infrequently and transpired rapidly, odds were low that an observer would have been present when such an attack took place.

RESULTS AND DISCUSSION

White-winged Trumpeters are cavity nesters. Their chicks are precocial and leave the nesting cavity the day after hatching to travel and forage with their groups on the forest floor. At Cocha Cashu, the majority of trumpeters lived in permanent territorial groups that defended contiguous territories with a mean size of 72 ha (Sherman 1995a). Permanent groups had a cooperatively polyandrous mating system in which multiple adult males mated with a dominant female who laid the only clutch (Eason and Sherman 1995). The mean size of permanent groups was seven, with groups typically consisting of a dominant male and female, beta and gamma adult males, a beta adult female, and the group's offspring that were two years of age or younger. All members of the group helped to feed and protect the group's chicks and guarded them closely until they began to fly at about six weeks of age. Occasionally, temporary nonterritorial groups would form during the breeding season and attempt to nest on a permanent group's territory. These groups had a mean size of three individuals and usually disbanded several months after forming (Sherman 1995a).

During the 1984–1985 breeding season, a temporary group composed of two females

and a male formed on a permanent group's territory and successfully fledged two chicks. Unlike all other temporary groups observed, this group (hereafter referred to as the intruding group) did not disband. During the 1985–1986 breeding season, the intruding group, which now consisted of the original trio, their two offspring, and a new adult male, incubated their clutch in a nesting cavity inside the edge of the permanent group's territory. Four days after the intruding group's chick hatched, the two groups began to interact daily near this nesting cavity. These interactions consisted of the permanent group hearing the intruding group at a distance and responding with 5–10 min of territorial calling, to which the intruding group responded in kind. The groups remained separated by a distance of 70–100 m during these interactions. When trumpeter groups lacked young chicks, permanent groups directly confronted intruders, running toward them and chasing them to the closest territorial boundary (Sherman and Eason 1998). Long distance interactions between groups occurred most often when trumpeter groups had chicks that were unable to fly.

After three days of long distance interaction, five of the seven adults in the permanent group approached the intruding group on the morning of the fourth day. These individuals chased the intruding group, and then the two groups exchanged territorial calls while separated by about 10 m. The intruding group's 7-day-old chick was 90 m from the interaction and was guarded by the group's dominant male and beta female. This chick weighed about 140 g (11% of mean adult weight) and although unable to fly, could run rapidly. I was unable to locate the permanent group's 21-day-old chick and the dominant female and delta male that presumably were guarding it for the duration of the territorial interaction.

After 18 min of interaction, the intruding group's chick started giving repeated severe distress calls, shortly after which two adults gave high intensity alarm calls. The members of the two groups that had been calling ran 90 m to the chick, where three permanent group birds (the dominant male, gamma male, and a subordinate female) were forcefully and repeatedly pecking its chest while it lay on its side on the ground. After giving distress calls for 45 s the intruding group's chick fell silent

and remained motionless. The three permanent group birds continued to repeatedly peck the chick's chest with great force for an additional 75 s. At this time the chick was still breathing but appeared unconscious. For the next 12 min, the permanent group's dominant, beta, and gamma males took turns standing over the chick while the two groups continued to exchange territorial calls. The intruding group then stopped calling and left. When it returned 30 min later, its chick was dead and the members of the permanent group, which were preening 30 m away, chased the group away one last time.

I collected the intruding group's chick at the end of the day and found that its only apparent injury was a puncture wound just below the sternum that was 0.35 cm in diameter. The liver was punctured and a blood clot approximately 1.0 cm in diameter had formed on it. There did not appear to be enough blood on the chick or the ground to indicate that it had bled to death, suggesting that perhaps it died of shock.

The adults' behavior during their attack on the chick was unprecedented. During territorial interactions, trumpeters occasionally engaged in bouts of sparring, during which pairs pecked and kicked at each other but rarely made contact. On those rare occasions when one bird knocked another to the ground, the downed individual would be chased off, not repeatedly attacked. The ganging up of a group of birds on a single individual and the sustained level of aggression during which the chick was repeatedly pecked for 2 min were behaviors that were not seen at any other time during this study.

The hesitancy of groups with young flightless chicks to engage in direct confrontations with other groups suggests that trumpeters may perceive some risk associated with such interactions. The loud territorial calls given during such interactions can be heard by humans more than 300 m away, and are likely to make groups more conspicuous to predators. However, when groups with young chicks interact with other groups, it is not territorial calls that are avoided, but contact with the opposing group.

The proximate cause of the attack could have been the presence of an unfamiliar chick, the incapacitation of an intruding individual,

or some other cue. The adults' aggressive response might be adaptive if it prevented the adoption of an unrelated chick and the resultant cost of misplaced parental care. Instances of infanticide that may be linked to preventing misplaced parental care have been reported for various species in which there are numerous opportunities for dependent young to enter new groups (Pierotti 1991). However, because trumpeter groups occupy such large territories, breed asynchronously during the six-month rainy season, and rarely come into contact with other groups when they have young chicks, the opportunity for chicks to switch between groups is rare. Furthermore, the rapid growth of young chicks and their steady change in plumage make it possible to discriminate individuals that differ in age by only a few days (Sherman 1995b).

The potential benefit of such an attack might be greatest for a permanent trumpeter group that is attempting to prevent a temporary group from becoming established on part of its territory. White-winged Trumpeters are highly frugivorous, with the pulp of fallen fruit providing about 90% of mean daily energy intake. Fruit removal experiments suggest that territory size reflects the area needed for group members to meet their minimum daily caloric requirements during the dry season when fruit abundance is low (Sherman and Eason 1998). A substantial reduction in territory size would lead to the emigration of subordinate adults, who are excluded from limited food resources by dominant individuals, from a permanent group. This would likely result in the continued shrinking and eventual loss of the group's territory as smaller groups are dominated by larger groups during territorial interactions (Sherman 1995a).

The failure of a temporary group to breed successfully may help lead to its disbanding. Four months prior to the attack, a different trio of birds incubated their clutch on the opposite end of the permanent group's territory. The permanent group fought with this trio almost daily, flying up to evict the incubating bird from the nesting cavity and then chasing the group away from the nesting site. The chick that fledged from this group's clutch disappeared for unknown reasons when it was about two weeks old and the group disbanded six weeks later.

Of the 10 temporary groups that formed during four breeding seasons, nine disbanded within 4 months and lacked chicks when they disbanded. Unlike the adults in these groups, no chicks <1 year of age were ever observed to immigrate into new groups or fend for themselves outside a group, and thus available evidence suggests that all nine groups failed to reproduce successfully. A group such as the intruding group that increased its size through successful reproduction and retention of young would have an increased likelihood of being able to establish and defend a new territory. By the end of this study the intruding group had the same mean group size as permanent groups at the study site and had succeeded in taking over about 25% of the permanent group's territory as well as portions of two other groups' territories. An equivalent loss of territory to a second intruding group would likely lead to the collapse of the permanent group unless they were able to acquire additional space from neighboring groups. The infanticidal behavior described here could confer a selective advantage if it helped prevent the breeding and establishment of a temporary group on a permanent group's territory.

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