BREEDING BIOLOGY OF WHITE-WINGED TRUMPETERS (*PSOPHIA LEUCOPTERA*) IN PERU

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ABSTRACT.—I studied the breeding biology of a population of White-winged Trumpeters (*Psophia leucoptera*) in undisturbed lowland rain forest in Manu National Park, southeastern Peru. At this study site, it was possible to habituate trumpeters to humans, allowing groups to be followed and observed at distances of a few meters for entire days. I found that White-winged Trumpeters lived in cooperatively polyandrous groups of 4 to 13 individuals that defended permanent year-round territories. Clutches that averaged three eggs were laid by the dominant female on the floor of elevated cavities in trees. Eggs were incubated for about four weeks, primarily by the group's dominant male and female. Chicks hatched around the end of October at the beginning of the rainy season. If at least one of the brood survived, a subsequent clutch was not laid until the following breeding season. Predation on eggs and chick mortality resulted in an average of 1.6 young per group-year surviving to adulthood. White-winged Trumpeter chicks were precocial and left the nesting cavity the day after they hatched, able to walk and climb. Chicks were dependent on older birds to provide them with all of their food for over three weeks and were still receiving more than one-half of their food from adults at two months. Trumpeters reached sexual maturity at about two years of age, at which time both male and female offspring dispersed from their natal groups. *Received 3 June 1993, accepted 24 October 1993.*

THE FAMILY PSOPHIIDAE (order Gruiformes) includes three species: the White-winged Trumpeter (*Psophia leucoptera*), the Gray-winged Trumpeter (*P. crepitans*), and the Green-winged Trumpeter (*P. viridis*). Little is known about any of the trumpeters, which are hen-sized terrestrial birds found primarily in the rain forests of the Amazon and Orinoco basins (Sibley and Monroe 1990). Published information on the breeding biology of wild trumpeters consists principally of observations that local people offered to turn-of-the-century naturalists, and these reports are anecdotal and frequently contradictory. For example, wild Gray-winged Trumpeters have been reported to nest on the ground, in the branches of trees, in nesting cavities in trees, and in the crowns of palm trees (Schomburgk 1848, Lloyd 1897, Penard and Penard 1908, Beebe and Beebe 1910, Chubb 1916, Beebe et al. 1917). Clutch sizes of 2 to more than 10 white, green or blue eggs have been reported (Lloyd 1897, Penard and Penard 1908, Beebe and Beebe 1910, Chubb 1916, Beebe et al. 1917). Furthermore, it has been suggested that this species nests colonially, with five to six pairs building nests in adjacent trees (Beebe et al. 1917), and that the birds nest communally, with all females in the group laying eggs in a single nest (Lloyd 1897).

In this paper I describe the breeding biology

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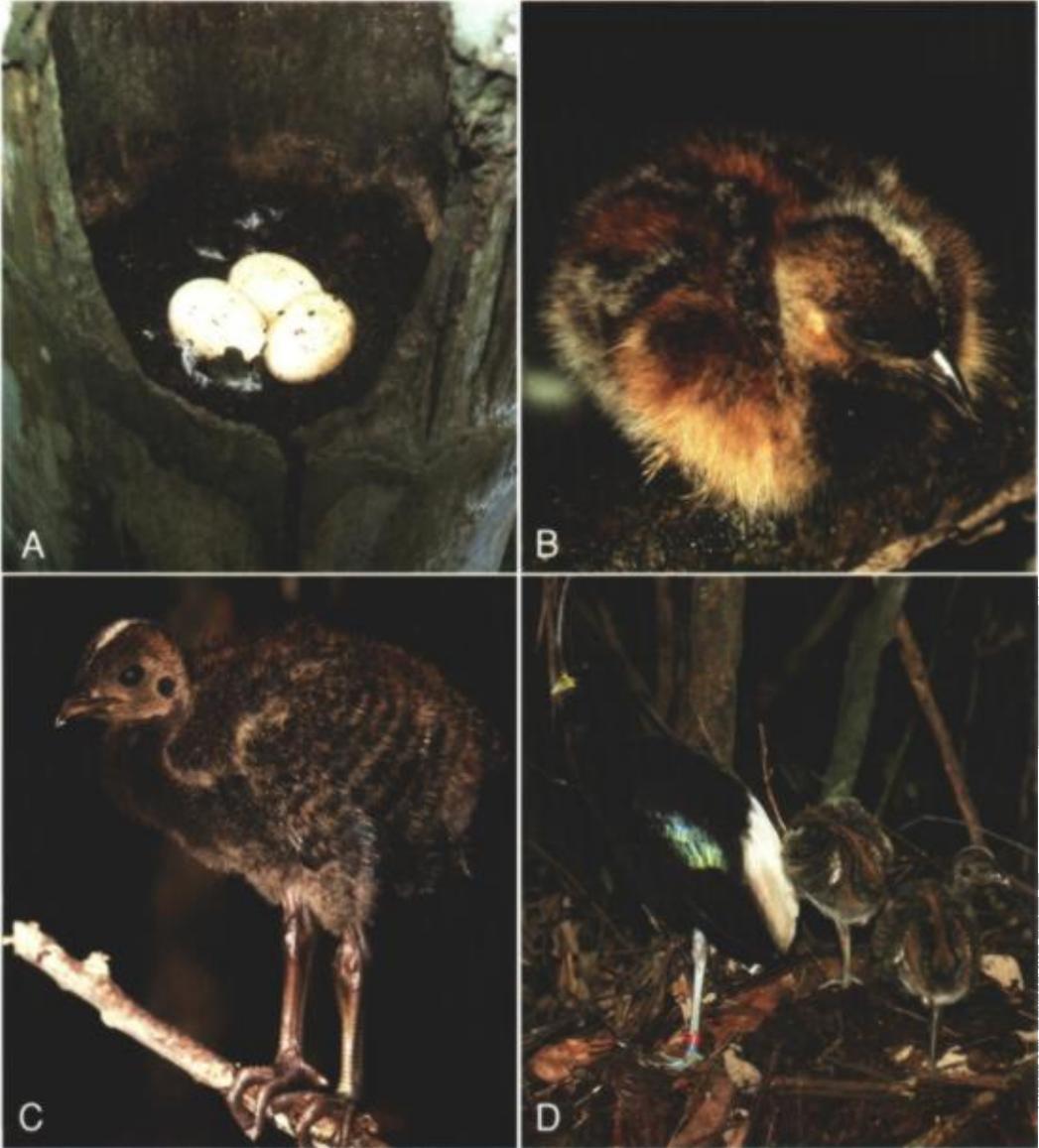
FRONTISPIECE.   (A) Undisturbed White-winged Trumpeter eggs in enclosed nesting cavity in trunk of palm tree (*Iriartia ventricosa*). (B) Down-covered White-winged Trumpeter chick 24 h after hatching. (C) White-winged Trumpeter chick about two weeks after hatching. When wings are in resting position, they largely obscure down-covered back and sides. (D) Adult male and 22-day-old White-winged Trumpeter chicks. Chicks' off-white secondary feathers are visible. By five weeks of age, these feathers will form patch similar to rump patch of adults.

TABLE 1. Mass (in grams) of different individual adult male and female White-winged Trumpeters and 8- to 15-month-old birds of both sexes. All adults were at least two years of age.

	n	$\bar{x} \pm$ SE (range)
Adult males	7	1,378 $\pm$ 22.5 (1,280–1,440)
Adult females	9	1,256 $\pm$ 15.3 (1,180–1,320)
8–15 months old	21	1,160 $\pm$ 13.2 (1,031–1,255)

of White-winged Trumpeters, which I observed during four breeding seasons in Manu National Park, southeastern Peru. There I observed several groups of marked and habituated individuals, which could be followed and observed for entire days.

METHODS

I conducted this study on White-winged Trumpeters living in the vicinity of Cocha Cashu Biological Station, in Manu National Park, southeastern Peru (11°51'S, 71°19'W). The habitat of the study area consists of undisturbed lowland tropical moist forest (for detailed description of study site, see Terborgh 1983).

The three permanent groups of White-winged Trumpeters observed were designated as the house group (HG), north group (NG), and east group (EG). These groups were habituated and could be followed and observed for entire days at distances of 4 m or less. I also was able to observe occasionally four permanent groups that defended territories adjacent to the habituated groups' territories. Each year, I captured, measured, and banded all unbanded birds in the three habituated groups; 46 birds were banded during the study. I determined the sex of some juvenile birds and most adult birds by laparotomy or by observing copulations.

Between 1983 and 1987, I observed the habituated trumpeter groups for partial or full days for a total of 2,460 h spread over a 23-month period, which included four different breeding seasons. Further details on the methods used to collect data are presented in the appropriate sections in Results.

RESULTS

White-winged Trumpeters are monomorphic in their plumage, but are slightly sexually dimorphic in size, males weighing about 10% more than females (Student's t-test, $t = 4.63, P < 0.001$; Table 1). White-winged Trumpeters are nonmigratory and are primarily terrestrial. They do all of their traveling and foraging on the forest floor, and fly up into trees to roost, nest, and escape terrestrial predators. Ripe fallen fruits account for 90% of White-winged Trumpeters' diet (all seeds are defecated undigested), with leaf-litter arthropods and small vertebrates supplying the remainder (Sherman 1991).

Mating system.—At Cocha Cashu, most trumpeters lived in groups that defended permanent territories against conspecific intruders. The average group size for the seven groups at the study site was 7.0 $\pm$ SE of 0.20 individuals (range 4–13; see Sherman 1995). Within each group, there was a clear linear dominance hierarchy among adults of each gender. Groups consisted of a dominant male and female, their offspring under the age of two years, and usually a beta and gamma adult male, and a beta adult female (for more detail on group composition and how dominance status was determined, see Sherman 1995).

All of the habituated trumpeter groups had a cooperatively polyandrous mating system; only the dominant female contributed eggs to the clutch, and all adult males in the group copulated with her and helped raise the brood. During the dominant female's fertile period, competition between males to obtain copulations with her was intense and the dominant male obtained the majority of the successful copulations (Eason and Sherman 1995, Sherman 1995).

Annual breeding cycle.—Cocha Cashu has a distinct annual pattern of precipitation, with a dry season generally from May through October and a rainy season from November through April. Trumpeters began incubating their first clutch during the last two weeks in September or during October ($n = 9$), and the eggs hatched around the beginning of the rainy season. If the first nesting attempt was successful, a subsequent clutch was not laid until the following breeding season.

The beginning of the breeding season was signaled by several changes in trumpeters' behavior: (1) investigation of nesting cavities increased; (2) copulation attempts and male competition for copulations both increased; and (3) males began to provide food to the breeding female. Each breeding season the dominant pair of each focal group investigated 10 to 12 different nesting cavities on their territory (see section on nesting sites). Investigation of different nesting cavities began about two months before the breeding female's fertile period and increased in frequency until the clutch began to be laid (Fig. 1A). About a week before the
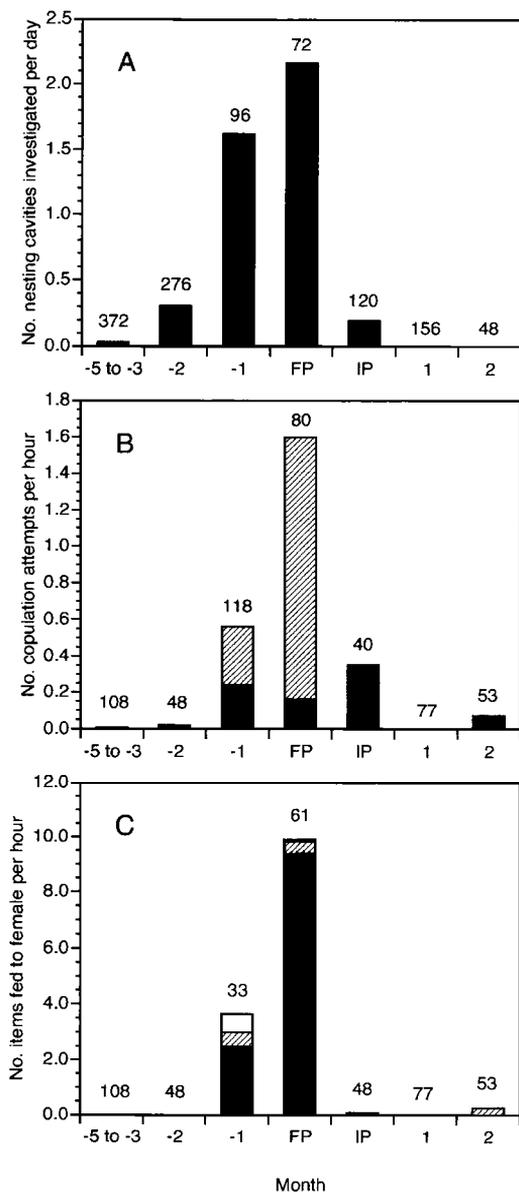
Fig. 1. **(A)** Average number of different nesting cavities investigated per day by dominant pair of trumpeters. Repeat visits to same nesting cavity on same day counted as single investigation. **(B)** Average number of copulation attempts that were successful (solid bars) or that were not successful because of interruptions by other males (hatched bars). **(C)** Average number of food items fed to breeding female by groups' dominant male (solid bars), beta male (hatched bars), and gamma male (open bars; no other individuals fed dominant female). Negative numbers on horizontal scale represent 30-day periods (months) before fertile period began. FP indicates 16-day fertile period and IP the 28-day incubation period. Positive

clutch was laid, the dominant pair began to focus their attention on a single nesting cavity. This cavity was visited one to three times daily, but other cavities continued to be visited until the female laid the first egg in the focal cavity.

Copulations began to increase in frequency about one month before the breeding female's fertile period. At the beginning of this month, males copulated infrequently and did not interrupt each other's copulations. As the month proceeded, copulation frequency began to increase, and males interfered increasingly with each other's copulation attempts. During the fertile period, both male copulation attempts and interference reached their peak (Fig. 1B; see Eason and Sherman 1995, Sherman 1995). During incubation, while the dominant male was incubating, the breeding female solicited copulations from subordinate males, and the subordinate males copulated after each solicitation. After the clutch hatched, however, solicitations and copulations occurred infrequently.

About a month before the fertile period began, males started offering fruit and arthropods to the breeding female. The dominant male contributed about two-thirds of the food items provided to the female, and the beta and gamma males each provided about one-half of the remainder (Fig. 1C). During the fertile period, the number of food items provided to the female almost tripled, and the dominant male was responsible for 95% of this provisioning. During incubation, and after the clutch hatched, males offered food to the breeding female infrequently.

Mating behavior.—Trumpeters' copulation attempts were generally preceded by a short period of solicitation, at least when the mating pair were not disturbed by other individuals. The solicitation was usually initiated by the female, who crouched at about two-thirds her normal height, partially extended her head and neck horizontally, and presented her rump to the male. She then shifted her head laterally from side to side, lifting first one foot and then the other a few centimeters at about 1-s intervals. If the male did not approach her while she

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numbers represent months after chicks hatched. Value above bar is number of hours data collected during period.

was soliciting, she occasionally gave a soft, repetitive, medium-pitched call, *e-e-e-e-e-e-e-e-e-e-e-e*.

A male usually responded to a female's solicitation by approaching and then stopping when he was about 5 cm behind the female. Frequently, the male would not mount immediately, but instead would extend his neck vertically, and walk behind the female in complete or partial circles. As the male circled, the female pivoted, keeping close to the male while continuing to solicit him. During solicitations, the dominant male frequently gave a call similar to the female's solicitation call; this call was not given by subordinate males. Among undisturbed pairs, periods of precopulatory solicitation ranged generally from 3 to 20 s, although solicitations occasionally lasted several minutes.

During copulation attempts, the female spread her wings slightly as the male stepped onto her back. The female then lifted her tail and elevated her rump, and the male lowered his cloaca until it was in contact with the female's cloaca. During copulations, the male pressed his cloaca firmly against the female's cloaca for 3 to 5 s while twitching his tail laterally back and forth. While the male copulated, the female would often give a quiet, high-pitched twittering call that lasted about 1 s.

In general accounts of the family Psophiidae, all three trumpeter species are reported to engage in noisy and acrobatic courtship dances (Gilliard 1958, Austin 1961, Rutgers and Norris 1970, Sick 1972, Johnsgard 1983), and to gather in large flocks at the beginning of the breeding season to perform courtship displays (Colston 1985). I never observed such behavior in the context of courtship, although I observed many copulations. Courtship dance as described by these authors, however, matches perfectly the actions and behavior that I observed during play within trumpeter groups and fighting between groups.

Within-group play is common throughout the year and can involve one to several birds, or the whole group. During play, trumpeters flap their wings, jump into the air, and run in short bursts, with their heads lowered, their wings arched slightly above their backs, and their flight feathers fanned down covering their sides. Mixed in with the above behavior are short bouts of play attacks directed at objects like leaves or branches. During these bouts, trumpeters alternate between pecking and kicking forward at the object, like a fighting cock. When more than one bird plays, the birds involved usually alternate between attacking objects by themselves, and chasing after each other with heads lowered and wings back-arched. Two birds will often face off, stretch their necks, and alternate pecking at each other without making contact, followed by more running and chasing.

Fights occurred when two groups encountered each other near a shared territorial boundary, or when one group encountered another intruding on its territory. Fights lasted anywhere from 10 min to approximately 2 h and occurred throughout the year, although they occurred more frequently during the dry season (May through October), when the abundance of fruit and arthropods eaten by trumpeters declined (Sherman 1991). During fights, the same behaviors observed during play were directed aggressively by all members of each group at individuals of the same gender in the opposing group. Individual trumpeters would chase after each other with heads lowered and wings back-arched. Individuals that caught up to birds they were chasing would peck at them, which sometimes led to brief bouts of fighting in which the two birds pecked and kicked at each other while jumping into the air and flapping their wings.

Bouts of chasing alternated with stationary periods when the two groups stood 10 to 30 m apart and gave loud, booming calls, *o-o-o-o-ooooooo*, a descending series of three to five staccato notes followed by a descending resonant vibrato. These calls were given primarily by females and juveniles, although adult males also occasionally joined in. The calls carried a great distance (audible at 300 m) and were used primarily during territorial interactions.

Nesting sites.—White-winged Trumpeters laid their eggs in elevated cavities in trees, using only preexisting cavities. The nesting cavity was prepared by the dominant male or female, who cleaned the cavity floor by kicking out or tossing out debris. Trumpeters did not build a nest, instead laying their eggs directly on the nesting cavity floor.

I marked and measured 12 nesting cavities on the HG territory (10 inspected by dominant pair and 2 used for incubation), 10 nesting cavities on the NG territory (7 inspected and 3 used for incubation), and 1 nesting cavity on the EG territory (used for incubation; I conducted a limited number of observations on the EG dur-

ing the preincubation period). All but 2 of the 23 nesting locations inspected by the dominant pair were hollowed-out portions of tree trunks. The two exceptions were cavitylike spaces formed where the main tree trunk split into two halves. Both of these locations had high walls on the sides and back, but no roof. Five cavities inspected and two used to incubate eggs were in elevated bulges in the trunks of one species of palm tree (*Iriartia ventricosa*). The remaining 16 cavities were in a variety of different tree species. I never observed trumpeters competing for access to any of these nesting cavities with other species.

Nesting cavities used to incubate eggs had an average height of 11.0 ± 0.82 m ($n = 6$, range 7.6–12.8 m). Cavities inspected by birds but not used averaged 11.0 ± 0.81 m in height ($n = 14$; three could not be relocated for measurements), and all but three fell within the range of heights given above (exceptions were 3.7, 15.2, and 16.8 m above ground).

I used a climbing rope to investigate four cavities in which trumpeters incubated eggs. Each of these cavities had an internal diameter of about 30 cm. The cavities' floors were either flat or slightly concave and consisted of a thin layer of well-packed, decayed wood overlying a more solid base. The lips of the cavity entrances were about 1 to 2 cm higher than the cavity floors. It is probably necessary for the entrance to the nesting cavity to have a shallow lip, or no lip at all, if the chicks are to fledge successfully (see section on fledging).

Eggs.—Trumpeter eggs were white, and the shell texture was similar to that of chickens' eggs (see Frontispiece). Their average mass was 83 g, about 6% of the mass of the female that laid them (Table 2).

While laying their clutch, dominant females entered the nesting cavity daily, but laid eggs every other day (for two groups, nesting cavities were monitored daily in 1985 during egg laying). On both laying and nonlaying days, visits usually occurred after 1400 (9 of 10) and lasted about 2 h ($\bar{x} = 111 \pm 10.3$ min, $n = 10$). Occasionally, during the laying period, the female entered the nesting cavity in the afternoon and remained inside overnight (three of nine times).

The average clutch size, based on a small sample size ($n = 4$), was 3.0 (range 2–4). When I monitored nest holes in 1985, the HG and NG dominant females each laid a total of three eggs.

TABLE 2. Mass and size of freshly laid White-winged Trumpeter eggs. Eggs were first clutches laid by breeding female in each of three focal groups in 1985, and are listed in order in which they were laid. Clutches are complete for HG and NG; it is not known if EG female laid more than two eggs.

	Mass (g)	Length (mm)	Width (mm)
House group (HG)			
Egg 1	89.7	69.4	48.9
Egg 2	89.7	67.6	49.3
Egg 3	82.2	67.8	47.4
$\bar{x} \pm$ SE	87.2 ± 2.50	68.3 ± 0.57	48.5 ± 0.58
North group (NG)			
Egg 1	82.7	62.5	48.7
Egg 2	83.7	61.9	49.4
Egg 3	83.2	63.0	48.8
$\bar{x} \pm$ SE	83.2 ± 0.29	62.5 ± 0.32	49.0 ± 0.22
East group (EG)			
Egg 1	78.7	60.0	49.5
Egg 2	75.7	62.8	48.0
$\bar{x} \pm$ SE	77.2 ± 1.50	61.4 ± 1.40	48.7 ± 0.75

I did not look into nesting cavities in other years, but observed one group of two chicks and another of four chicks leaving their nesting chambers the day after they hatched.

In 10 additional cases I observed trumpeter groups with chicks three weeks of age or younger. The number of chicks seen with these groups averaged 2.1 ± 0.34 (range 1–3). Egg loss and chick mortality, however, make it difficult to estimate clutch size based on the number of chicks first seen with a group.

Incubation.—Incubation began the day after the final egg was laid and lasted 23 to 29 days ($n = 4$). All eggs within a clutch hatched simultaneously. For two clutches, I was present both on the day when incubation began and the day when the chicks hatched. In each case, chicks were heard peeping inside the nesting cavity in the late afternoon on the 29th day of incubation and left the nesting cavity the next day (see next section). I was able to estimate an incubation length of 23 to 26 days for two other clutches. In each instance, I observed when incubation began and then encountered the group shortly after the chicks hatched.

Incubation duties were shared primarily by the dominant male and female (83.1% of incubation shifts; $n = 71$), although the beta and gamma males also incubated (see Sherman 1995). There were two incubation shifts; the dominant female usually incubated from dusk until early
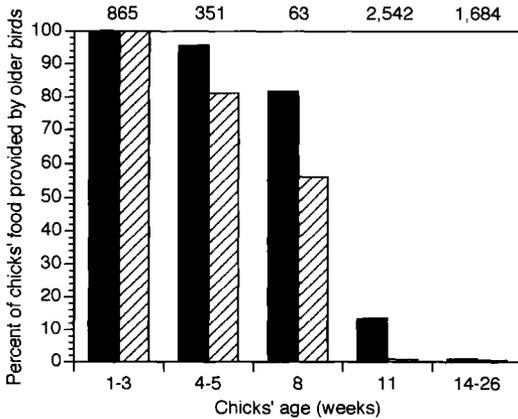
Fig. 2. Proportion of arthropods (solid bars) and fruit (hatched bars) provided to chicks of different age by older individuals in their groups. Data grouped by chick age (e.g. 1–3 weeks = chicks between 1–21 days of age). Data groups are discontinuous because information collected irregularly for older chicks. Values at top of diagram indicate total number of food items that I observed fed to or ingested independently by chicks in each age category.

morning, and the dominant male incubated from late morning until dusk. Eggs usually remained covered except for brief periods during incubation shift exchanges.

In the NG, the male relieved the female, on average, at 1000 (SE = 6 min, $n = 9$; data from 1987) and spent an average of 7.8 ± 0.15 h incubating ($n = 6$). In the HG, the male took over incubation from the female, on average, at 1215 (SE = 26 min, $n = 13$; data from 1983 and 1987 for same individual) and incubated for an average of 4.9 ± 0.41 h ($n = 10$). The NG and HG breeding females took over incubation from males between 1715 and 1745 ($n = 23$).

During the day, the group remained away from the nesting cavity, returning only when an exchange of incubating individuals occurred. The individual that had been incubating would then join the group and forage for the 4 to 8 h available before returning to incubate.

Fledging.—Chicks left the nesting cavity the morning after they hatched without adult assistance. While the entire group called from the ground, each chick climbed onto the ledge of the nesting cavity one at a time and then jumped to the ground. After landing, each chick sat motionless for 4 to 5 s before standing up and walking off. All chicks left the nesting cavity

within an hour after the adult group members had flown down from their night roost. Within 30 min after the last chick had jumped to the ground, the group began to travel away from the nesting site.

Trumpeter chicks were precocial; they left the nesting cavity the day after they hatched covered with down, with open eyes, and able to walk, run and climb (see Frontispiece). Although newly hatched trumpeter chicks would peck at the ground, they did not pick up anything edible and were completely dependent upon older birds to provide them with food for over three weeks. Fruit and arthropods were provided by all of the older birds in the group, with the exception of the subordinate adult female(s), who rarely fed the chicks (Sherman 1995). Beginning at about four weeks of age, chicks began to feed themselves about 5% of the arthropods and about 20% of the fruit that they ingested daily. As the chicks grew older, the proportion of food that they obtained themselves increased steadily and, by three months of age, chicks were feeding almost completely independently (Fig. 2).

Nesting success and fledgling survivorship.—I observed the focal groups incubating 10 clutches; 6 produced at least one chick and the remainder did not produce any. I was not able to determine exactly what caused nest failure; there never were eggshell fragments or chick remains below nesting cavities, and there were no remains inside three nesting cavities investigated after the entire clutch disappeared. Primates and snakes are the only predators at the study site that would be able to remove intact eggs from the nesting cavity and, thus, were presumed to be responsible for egg loss.

During four breeding seasons, the three focal groups averaged 1.6 ± 0.33 (range 0–3, $n = 13$) young per year that survived to adulthood. Chicks appeared to be at greatest risk during their first month of life. Of the 12 newly hatched chicks that I observed in the focal groups, 5 (42%) disappeared at ages ranging from 1 to 30 days, and the remainder survived until adulthood, at which time they dispersed and were not seen again. A 1-day-old chick and a 14-day-old chick were assumed to have been eaten by predators, as they disappeared from their roosts overnight, and a 7-day-old chick was pecked to death by the adults of a neighboring group during a territorial fight. The cause of death of the remaining two chicks was not known. It is prob-

able that chicks had a higher mortality rate than observed; because I was present when only six of these chicks left the nesting cavity and encountered the other six within a week of their hatching, some newly hatched chicks may have died before I first encountered their group.

Although chicks attacked each other, pecking forcefully at each other's heads, adults always intervened rapidly, pecking at the chicks' backs and pulling the chicks away from each other before any injury was sustained. Sibling aggression began the day the chicks left the nesting cavity, but decreased in frequency over the first three weeks of the chicks' lives. Adults continued to separate chicks during bouts of sibling aggression until chicks reached about two months of age, when chicks were better able to escape or defend themselves, and aggressive incidents between siblings decreased.

Chicks were probably most vulnerable to attack or predation before they could fly. During the day, young chicks relied on adults for protection during threatening circumstances. At night, chicks were unprotected, as they roosted alone and close to the ground. Trumpeters did not appear to see well in the dark, and adults at night never moved from their 8- to 15-m-high roost. Before they could fly, chicks reached their night roost by climbing diagonal trunks of small trees or lianas. For the first three weeks, chicks roosted 1 to 2 m above the ground ($n = 8$) and, for about the next three weeks, roost heights increased to 3 to 5 m ($n = 4$). By six weeks of age, chicks began to be able to fly short distances and were able to reach roost heights of 7 to 9 m, close to the rest of the group.

Renesting.—If the first nesting attempt was successful, the breeding female did not lay a subsequent clutch until the following breeding season. If the nest failed or the chick(s) died after hatching, up to two additional clutches were laid in a given breeding season. Groups with chicks born from late clutches were observed three times during this study. Based on the size and appearance of the chicks, I estimated that they came from eggs that were laid in March or the first half of April.

I was able to observe renesting following the failure of three clutches. In one instance, the breeding female began laying the subsequent clutch in the same nesting cavity 28 days after the first clutch disappeared. In the other two cases, the breeding females disappeared at the same time as the clutches were abandoned; one

female was never seen again, and one rejoined the same group as a lower ranking female a year later. After both disappearances, the groups' beta females became dominant breeders; one laid a subsequent clutch 36 days, and the other 64 days, after the previous clutch was abandoned.

In cases where chicks disappeared after leaving the nesting cavity, the breeding female laid another clutch only if all of the chicks in the current brood were lost. In three of the five cases in which a chick disappeared, the chick was the group's only offspring, and the breeding female produced another clutch during the same breeding season. In the other two instances when chicks disappeared, at least one of their siblings survived, and the female did not produce another clutch until the subsequent breeding season.

Chick development.—When they hatched, trumpeter chicks were covered with a thick russet down, with the exception of their off-white underside and a black bib that covered their throat and the upper part of their chest (see Frontispiece). Four white stripes with black borders ran lengthwise along their backs, and a single white stripe with black borders and a thin black center, bisected their crown, beginning at the rear of the upper mandible and ending at the base of the neck. The bill and legs of chicks ranged in color from dark gray to black.

By the time the chicks reached 10 days of age, the sheaths of their black primaries were becoming visible and the natal down on their wings was beginning to be replaced by black contour feathers with about 1 to 2 mm of brown at their distal tips (see Frontispiece). By five weeks of age, the chicks' wings and flight feathers had grown sufficiently to cover the natal down remaining on their sides and backs, and their secondaries formed an off-white rump patch similar to adults. By six weeks, the chicks' flight feathers were sufficiently developed to allow them to fly short distances (about 2 m). By nine weeks, iridescent feathers similar to those present on adults were becoming visible on the chicks' wings and necks. Plumage development has not been described previously for White-winged Trumpeters, but is very similar to that described for Gray-winged Trumpeters (Beebe et al. 1917, Horning et al. 1988).

By three months, White-winged Trumpeter chicks looked like small adults, although the contour feathers on their body differed slightly from adults in that they still retained the dark
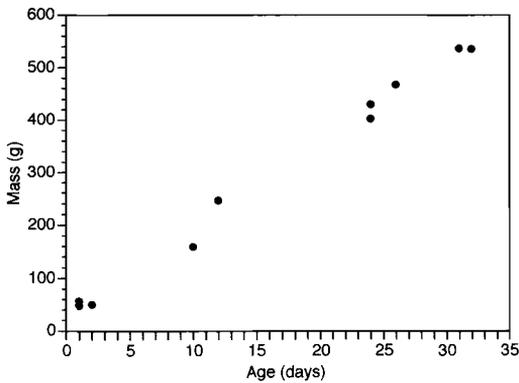
Fig. 3. Increase in mass of wild White-winged Trumpeter chicks during first 32 days after hatching. Measurements taken from 12 chicks in early morning before they left their roost. Four one-day-old chicks had masses that ranged from 49 to 59 g.

brown edging at the distal tip, instead of being completely black. Juveniles retained their brown-tipped contour feathers until they molted into the adult plumage at about one year of age. After they molted, juveniles could not be distinguished visually from adults, although they did not reach their full adult mass until they were about two years old.

The average mass of trumpeter chicks was 53 ± 2.4 g ($n = 4$) the day they left the nesting cavity, and their mass increased steadily during their first month (Fig. 3). I was not able to weigh juveniles again until they had reached at least 8 months of age, when their growth had greatly slowed; the mass of birds between 8 and 15 months of age was on average 1,160 g (Table 1), about 90% of the average mass of adults. I found no difference in the masses of males and females of equivalent ages for the eight juveniles sexed by laparotomy.

Male trumpeters appeared to reach sexual maturity at around two years of age. One-year-old males did not engage in sexual behavior and never showed any response if females solicited copulations from them, but two-year-old males showed typical precopulatory behavior and readily copulated with unrelated adult females during the breeding season. I do not know definitely when female trumpeters reached sexual maturity because they never solicited copulations while in their natal groups. Both male and female offspring dispersed from their natal groups around the time they reached two years of age (see Sherman 1995).

DISCUSSION

My data suggest that the breeding biology of trumpeters is quite different from other members of the Gruiformes. This is not particularly surprising because Gruiformes is a diverse order with families that share few breeding characteristics, with the exception that the majority of species have precocial young.

The extreme difficulty of observing trumpeters in the field has prevented scientists from being able to collect much data on the biology of wild psophiids. My observations on White-winged Trumpeters suggest that much of the anecdotal information published previously about trumpeters is likely to be inaccurate.

Most of the information available about the breeding biology of wild trumpeters consists of descriptions of nests and eggs, which are frequently contradictory. Wild Gray-winged Trumpeters have been reported to nest in a variety of locations (Schomburgk 1848, Lloyd 1897, Penard and Penard 1908, Beebe and Beebe 1910, Chubb 1916, Beebe et al. 1917), and to construct nests made of leaves or twigs (Lloyd 1897, Beebe and Beebe 1910, Beebe et al. 1917). This variability in nest location and nest type for Gray-winged Trumpeters has probably resulted from some cases of mistakenly identifying nests of other birds as belonging to trumpeters. For example, several reports described blue or green eggs found in the nests of Gray-winged Trumpeters (Lloyd 1897, Beebe and Beebe 1910, Chubb 1916), whereas all eggs laid by Gray-winged Trumpeters in captivity have been white (Haverschmidt 1968, Horning et al. 1988).

At my study site, White-winged Trumpeters only nested in elevated cavities in trees. They did not build a nest, but instead removed any loose debris present in the nesting cavity and laid their eggs directly on its floor. More recent observations of Gray-winged Trumpeters suggest that their nesting behavior is quite similar to that of White-winged Trumpeters. Haverschmidt (1968) reported that an incubating Gray-winged Trumpeter was observed in a large hollow in a tree, but that no further particulars were known. Gray-winged Trumpeters that have nested in captivity at five different zoos did not build nests and removed all nesting material and debris from the cavitylike spaces where they laid their clutches (Horning et al. 1988). Clutch sizes, laying interval, and incubation period also appeared to be approximately the same for

White- and Gray-winged trumpeters (Horning et al. 1988). The only information reported on the breeding biology of Green-winged Trumpeters is that their incubation period was 27 days in captivity (Anonymous 1981).

In a number of general references, trumpeters have been described to engage in courtship behavior involving cranelike dancing, noisy strutting, and acrobatic leaps (Gilliard 1958, Austin 1961, Rutgers and Norris 1970, Sick 1972, Johnsgard 1983, Colston 1985). Although White-winged Trumpeters engaged in brief bouts of ritualized precopulatory behavior, I never observed acrobatic displays in the context of courtship. These accounts, however, accurately describe the behavior of White-winged Trumpeters engaged in play within groups or territorial fights between groups. Territorial interactions between groups are one of the few behaviors of untame trumpeters that can be observed in the field, and this may account for the frequency with which accounts of "courtship dancing" have been reported.

Descriptions of the mating system of wild trumpeters are extremely scant and consist only of brief accounts. The mating system of Gray-winged Trumpeters was described to Lloyd (1897) by his local assistants as being communal, with all females in the group laying eggs in a single nest on the ground, whereas Beebe et al. (1917) were told that Gray-winged Trumpeters nested colonially, with five to six pairs building nests in adjacent trees. At my study site, I found that White-winged Trumpeters lived in cooperatively polyandrous groups (see Faaborg and Patterson 1981) in which the dominant, beta, and gamma males copulated with a single breeding female, and helped rear a single brood (Sherman 1995).

Cooperative polyandry is rare and has been documented for only a small number of avian species through genetic analysis of paternity (Dunnocks [*Prunella modularis*], Burke et al. 1989; Stripe-backed Wrens [*Campylorhynchus nuchalis*], Rabenold et al. 1990, Piper and Slater 1993; Tasmanian Native Hens [*Tribonyx mortierii*], Gibbs et al. in press), or observation of copulations by more than one male (Galapagos Hawks [*Buteo galapagoensis*], Faaborg et al. 1980, Faaborg 1986; Lammergeiers [*Gypaetus barbatus*], Heredia and Donázar 1990; Egyptian Vultures [*Neophron percnopterus*]; Tella 1993). Two additional species (Black Tit [*Parus niger*]; Tarboton 1981; Brown Skua [*Catharacta lonnbergi*], Young

1978, Millar et al. 1992) also appear to form cooperatively polyandrous groups, but copulations have not been observed, and paternity analyses have not been conducted.

Among the better studied cooperatively polyandrous species are Dunnocks, Stripe-backed Wrens, Galapagos Hawks, and Tasmanian Native Hens. As is the case for the majority of avian cooperative breeders (Brown 1987, Emlen 1991), cooperatively polyandrous species (with the exception of Dunnocks) inhabit areas where there is a shortage of suitable breeding habitat, which results in the number of adults in the population exceeding the number of breeding positions available. The specific selective pressures that have led to the evolution of cooperative polyandry, however, are not always clear, and appear to differ from one species to another.

In Dunnocks, cooperative polyandry appears to occur as a result of the inability of the dominant male in a group to maintain exclusive reproductive access to the breeding female. In Dunnock groups, males compete to obtain copulations with the breeding female, who gains fitness benefits in the form of increased help with rearing chicks by copulating with all males in the group (Davies 1992). Similarly, in cooperatively polyandrous groups of Stripe-backed Wrens, the dominant male, in spite of guarding the breeding female and behaving aggressively towards subordinate males, was unable to prevent subordinate males from siring about one-half of the clutch (Rabenold et al. 1990, Piper and Slater 1993).

In contrast, in Galapagos Hawks and Tasmanian Native Hens, males do not appear to compete for copulations. Faaborg (1986) proposed that cooperative polyandry may have evolved in Galapagos Hawks because of the need for multiple males to cooperate to obtain and defend a territory where they will experience substantially greater survivorship than they would if they remained living among a non-territorial flock. For Tasmanian Native Hens, Maynard Smith and Ridpath (1972) suggested that kin selection may have been responsible for the evolution of mate sharing by brothers, although other selective factors such as a shortage of suitable breeding habitat probably also have had a significant effect on the evolution of cooperative polyandry in this species (Brown 1987, Gibbs et al. in press).

The occurrence of cooperative polyandry in White-winged Trumpeters appears to be related

to the need for trumpeter groups to contain multiple adult males for successful territory defense (Sherman 1995). Because trumpeter offspring disperse from their natal group at sexual maturity, trumpeters must accept unrelated adult males into their group in order to achieve an adequately sized group for territorial defense.

Although all three trumpeter species are not currently considered to be endangered, their future status remains uncertain. Trumpeter groups appear to require large territories and depend on monkeys and other arboreal frugivores to knock ripe fruit to the ground (Sherman 1991). As hunting and deforestation increase, trumpeters will suffer adverse effects both indirectly and directly. At present, trumpeters are uncommon near human settlements. They are an attractive prey item for humans because they live in groups, are relatively large, and are easy to hunt because the birds approach imitations of their territorial call or respond by calling, allowing them to be attracted during the day or located on their roost at night. I hope that my study will provide a more accurate picture of the breeding biology of trumpeters and, thereby, contribute to their conservation in the wild and in captivity.

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