

## SOCIAL ORGANIZATION OF COOPERATIVELY POLYANDROUS WHITE-WINGED TRUMPETERS (*PSOPHIA LEUCOPTERA*)

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**ABSTRACT.**—I observed a population of White-winged Trumpeters (*Psophia leucoptera*) in undisturbed rain forest in Peru for over 2,400 h between 1983 and 1987. At this site, I was able to habituate and band three groups of trumpeters and make occasional observations on four unhabituated groups. The habituated trumpeters lived in cooperatively polyandrous groups that defended large ( $\bar{x} = 72$  ha) permanent territories against conspecifics. The habituated groups always contained a dominant male and female, and usually contained two unrelated subordinate adult males, one unrelated subordinate adult female, and the group's offspring. Only the dominant female contributed eggs to the clutch, and the group's adult males competed to obtain copulations with her. In the habituated groups, the dominant male obtained the majority of the successful copulations with the breeding female during her fertile period, and the beta male obtained a greater number of copulations than the gamma male. Individuals assisted to varying degrees with helping to rear the group's chicks. Subordinate males provided significantly more food to the chicks than the dominant male, and the subordinate female provided significantly less food than the dominant female, while the dominant male and female fed chicks equivalent amounts of food. Offspring usually helped raise one brood of siblings, but both males and females dispersed from their natal group at about two years of age, when they reached sexual maturity. The evolution of cooperative breeding in White-winged Trumpeters appears to be related to the need to defend large permanent territories to provide access to sufficient food during the dry season when resources are scarce. Defense of large territories results in a surplus of adults in the trumpeter population relative to the number of available breeding positions. The low probability of acquiring a breeding position for individuals that remain on their natal territory appears to result in sexually mature offspring dispersing from their natal groups and attempting to join new groups where they have some chance of breeding nonincestuously. The apparent need to have multiple adult males within a group for successful territory defense may explain why unrelated males are accepted into territorial groups, where they are able to copulate surreptitiously with the breeding female. Received 30 July 1993, accepted 21 November 1993.

THE WHITE-WINGED TRUMPETER (*Psophia leucoptera*) is one of three congeners that make up the family Psophiidae. The three trumpeter species occupy mostly allopatric ranges in the lowland rain forests of northern South America (Sibley and Monroe 1990).

The majority of the reports that have been published describing trumpeters' behavior or ecology in the wild have been anecdotal. Several authors described brief observations of alarmed Gray-winged Trumpeter (*Psophia crepitans*) groups (Schomburgk 1848, Beebe and Beebe 1910, Beebe et al. 1917), and Haverschmidt (1968) reported a sighting of an incubating Gray-winged Trumpeter. Willis (1983)

was able to make brief opportunistic observations of Gray-winged Trumpeters feeding at ant swarms, but the birds left as soon as they detected his presence, and Erard et al. (1991) reported on the contents of the digestive tracts of a number of wild Gray-winged Trumpeters.

A recent study of White-winged Trumpeters has provided more detailed information about the ecology and behavior of this species in the wild (Sherman 1991, 1995, Eason and Sherman 1995). In this paper, I report on the social organization and mating system of a population of White-winged Trumpeters, which I observed over a four-year period in southeastern Peru. At this study site, I found that trumpeters lived in cooperatively polyandrous groups (see Faaborg and Patterson 1981) in which all males copulated with a single breeding female and helped rear a single brood.

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## METHODS

I conducted this study on White-winged Trumpeters living near Cocha Cashu Biological Station, in Manu National Park, southeastern Peru ( $11^{\circ}51'S$ ,  $71^{\circ}19'W$ ; for background on the study site and study animals, see Sherman 1995). Three groups of White-winged Trumpeters were habituated and could be followed and observed for entire days at distances of 4 m or less. These groups were designated the house group (HG), north group (NG), and east group (EG). I also observed occasionally four groups that defended territories adjacent to the habituated groups' territories. Individuals in these groups were only partially habituated and were not banded.

Each year, I captured all unbanded juveniles and adults in the habituated groups using a blow gun and tranquilizing darts. All captured birds were weighed, measured, and marked with numbered metal leg bands and unique combinations of colored-plastic leg bands, and then released back into their group. Chicks were caught on their night roost and banded at three to five weeks. I determined the sex of some juvenile birds and most adults 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 distributed over a 23-month period. Further details about methods used to collect data are presented in Results.

## RESULTS

*Social organization.*—At Cocha Cashu, the majority of trumpeters lived in groups that defended permanent territories against conspecific intruders. Territorial groups occupied all habitat types at the study site, and groups' territories were contiguous (Fig. 1). For the three study groups, territory size averaged  $72 \pm SE$  of 8.9 ha (range 58–88 ha). A small proportion of the trumpeters that I observed lived in fugitive pairs or trios that skulked around the study site and were chased off the permanent groups' territories whenever they were encountered (see section on fugitive groups).

Permanent territorial groups consisted of several adult males and females and the group's offspring. Within each group, there was a clear linear dominance hierarchy among adults of each gender, and all adult males were dominant to all adult females. Hereafter, adult males and females are referred to according to their within-gender dominance rank (dominant, beta or gamma individuals). I determined the dominance status of individuals in two ways. First, I recorded which individuals (dominants)

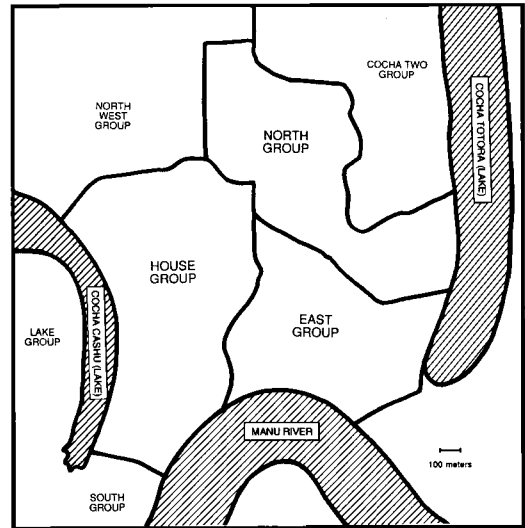


Fig. 1. Territories of White-winged Trumpeter groups in vicinity of Cocha Cashu Biological Station. Complete set of territorial boundaries known only for three habituated study groups (house, north, and east groups).

chased and displaced others (subordinates) during periods of resource scarcity and during the breeding season (see section on mating system). Second, I observed an interaction involving stereotyped behavior that occurred commonly between pairs of trumpeters. During this interaction, the more subordinate of the two birds "wing-spread"; they crouched before the more dominant bird, spread their primary feathers horizontally, and gave a high-pitched twittering call. The more dominant individual frequently responded with a "wing-flick," during which he or she flicked their folded wings forward rapidly, several times in succession.

While a dominant male and female were always present in the three habituated groups, the number of lower-ranking adults varied. Groups usually contained two subordinate adult males (range 1–3) and one subordinate adult female (range 0–2; Fig. 2). The three habituated groups always contained a beta male, although beta males occasionally transferred temporarily into other groups (see section on transfer of adults). The number of offspring averaged  $2.3 \pm 0.19$  (range 0–6,  $n = 65$  modal values calculated monthly for three groups during study) in the habituated groups.

The size of the three study groups averaged  $7.2 \pm 0.22$  ( $n = 65$  modal values calculated

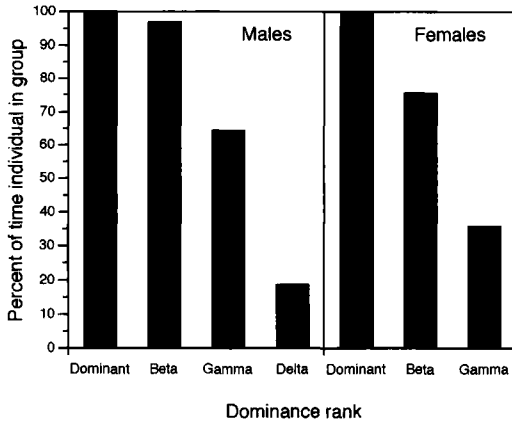


Fig. 2. Percent of time adults of different dominance status present in three habituated groups during 23-month study.

monthly for three groups) and ranged from 4 to 13 individuals (Fig. 3). Group sizes for the four unhabituated permanent groups averaged  $6.4 \pm 0.41$  (range 4–12,  $n = 23$  modal values calculated monthly for four groups during study).

The limited data that I was able to collect suggested that trumpeters' sex ratio at birth was approximately 1:1; four of the eight juvenile trumpeters that I performed laparotomies on were male. I estimated the adult sex ratio by dividing the total number of adult males by the total number of adult females in the three study groups during each month of the study. The average adult sex ratio calculated in this manner was  $1.3:1 \pm 0.06$  ( $n = 26$  monthly sex-ratio values). This may underestimate the total number of adult females in the population because females are not readily accepted into territorial groups (see sections on transfer of adults and fugitive groups).

*Mating system.*—At my study site, White-winged Trumpeter groups were cooperatively polyandrous. Within the habituated groups, the dominant female appeared to be the only individual who contributed eggs to the clutch, and all of the adult males competed with each other to obtain copulations with her. Males began copulating with the dominant female and interrupting each other's copulation attempts about a month before her fertile period began (trumpeter fertile period defined as beginning 13 days before first egg laid and ending 24 h before final egg laid; for detailed description, see Eason and Sherman 1995).

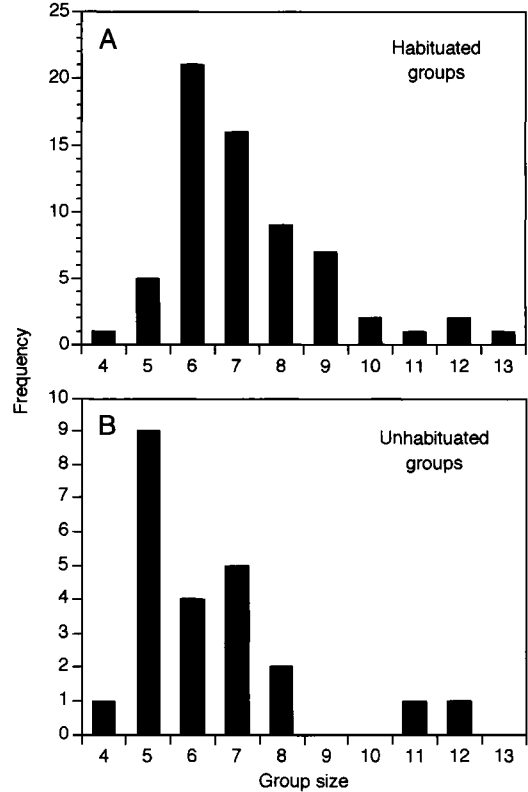


Fig. 3. Group sizes of (A) three habituated groups and (B) four unhabituated groups observed during study. Because group sizes changed when individuals transferred between groups, modal group size was calculated for each group during each month it was observed (for three habituated groups,  $n = 65$  monthly modal values; for four unhabituated groups,  $n = 23$ ). Note that vertical scales differ between panels.

To obtain data on competition between males and on male copulation success, I conducted focal observations on dominant females during the month that preceded their fertile period (detailed data collected for HG and NG for 93.5 h in 1985) and during their fertile period (detailed data collected for HG and NG for 80 h in 1985; data on copulation success only collected for HG for 38 h in 1987). During the month that preceded the fertile period, males interrupted 57% (34 of 60) of each other's copulation attempts, and beta males obtained 50% of the successful copulations, while dominant males obtained 35% and gamma males obtained 15% ( $n = 26$ ; there were never more than three adult males in study groups during two-month period prior to onset of incubation).

During the fertile period, males attempted to

copulate with the breeding female 2.5 times as frequently and guarded her closely, interrupting 90% (115 of 128) of each other's copulation attempts (Eason and Sherman 1995). The breeding female cooperated with all of the subordinate males' copulation attempts during the fertile period ( $n = 40$ ), but was capable of deterring copulations, and walked or flew away from the dominant male as he tried to mount her during 7% (7 of 95) of his copulation attempts. Male copulation success was related positively to male dominance status in both study groups during each of the three different fertile periods when data were collected (Fig. 4). Although sample sizes were too small to detect statistically significant differences in male copulation success within groups, when data from the three groups were combined, there was a significant difference; dominant males obtained the majority (67%) of the successful copulations with the breeding female during her fertile period, with the beta males obtaining 24% and the gamma males 9% of the copulations ( $X^2 = 11.1$ ,  $P < 0.005$ ,  $n = 21$  successful copulations; for more detailed data, see Eason and Sherman 1995).

Subordinate adult females in the focal groups copulated with gamma males and occasionally with sexually mature offspring, but never copulated with higher-ranking males. Subordinate females solicited copulations from beta males, but beta males never attempted to copulate with these females. I only observed a subordinate female solicit a copulation from a dominant male on a single occasion, and this solicitation provoked a severe physical attack, with the dominant male pecking her head multiple times and chasing her. With this single exception, beta and gamma females only solicited copulations from males if they were more than 30 m away from, and out of sight of, the dominant pair.

Even though subordinate adult females obtained some copulations, they did not appear to contribute any eggs to trumpeter groups' clutches. I observed the HG and NG for full days during the period that the dominant female laid her clutch in 1985. Once laying began, I monitored these groups' nesting cavities daily and marked each egg laid so that I could verify that eggs in the clutch were not removed or replaced. In both groups, eggs were laid at regular intervals that corresponded with the laying schedule of the dominant female. In the HG, only a beta female was present, and she did not enter the nesting cavity during the egg-laying

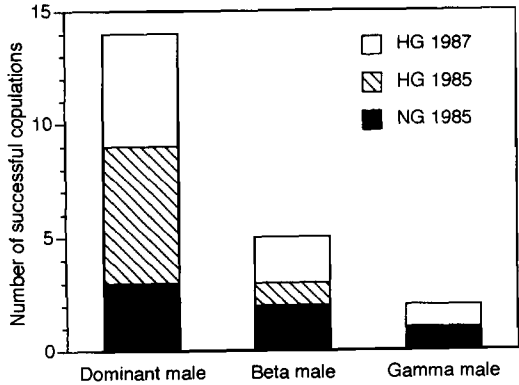


Fig. 4. Number of successful copulations obtained by males of different dominance status during dominant-female's fertile period. Data collected from house group (HG) and north group (NG) during three breeding periods.

period. In the NG, the beta and gamma females each entered the nesting cavity briefly a single time during the laying period, but checking the nesting cavity after each of these visits showed that neither female had laid an egg.

Although I was not able to monitor the study groups' nesting cavities directly during three other breeding seasons, clutch sizes only once exceeded the three eggs laid by the dominant females in 1985, when four chicks hatched from a clutch. The remaining 12 broods that I observed averaged 2.2 chicks (range 1-3). Clutch sizes did not appear to be reduced by females destroying each other's eggs; I never observed dominant or subordinate females attempting to remove eggs from the nesting cavity, and never found eggshell fragments or egg remains below nesting cavities (eggs were too large for adults to carry away from nesting site).

Subordinate adult females also did not appear to be ready physiologically to reproduce at the time that the clutch was laid. Laparotomies performed on four subordinate adult females during the period when their groups' clutch was being incubated showed their ovaries and ova to be undeveloped. Additionally, in two instances when beta females obtained the dominant female's position after the dominant female disappeared during incubation, the former did not begin to lay a clutch for five to nine weeks, even though the dominant male began copulating with them within several days of the dominant female's disappearance. Subordinate females provided little assistance with the

group's chicks (see following section), which also suggests that they were unlikely to have contributed eggs to their group's clutch.

*Helping behavior.*—Individuals in trumpeter groups assisted to varying degrees with territory defense, feeding and protection of chicks, and incubation. All group members participated in territory defense. Territorial fights occurred when two groups encountered each other near a shared territorial boundary, or when one group discovered another intruding on its territory. During fights, all individuals older than three months of age in each group chased and fought briefly with individuals of the same gender in the opposing group. Groups that encountered each other near a shared boundary alternated between bouts of chasing each other and stationary periods where the two groups stood apart and a territorial call was given by adult females, juveniles, and occasionally adult males (for more detail, see Sherman 1995). When intruding groups were encountered on the resident group's territory, the residents chased them to a boundary after which the two groups behaved as described above. Fights between groups lasted anywhere from 10 min to 2 h. It is probable that there was some increased risk of predation or injury to individuals that engaged in fights. I observed several occasions when predators were able to approach fighting groups closely before being detected, although I never observed any adult trumpeters that were injured or captured by predators, or injured by other trumpeters during fights.

All birds in trumpeter groups helped to varying degrees with feeding the group's chicks. Trumpeter chicks were completely dependent on older birds for food for their first three weeks of life and continued to receive more than one-half of their food from older birds until they were more than two months old (Sherman 1995). Group members did not provide equal amounts of food to the chicks; instead, the amount varied depending on the adult's sex and dominance status (Fig. 5A). I conducted focal samples on chicks under three weeks of age in the NG and HG in four different years. In each of these years, there was no significant difference in the number of individual fruit and animal prey fed to the chicks by the dominant male and the dominant female. Each year, the beta male fed chicks significantly more than the dominant male (1983,  $G = 2.43$ ,  $P < 0.05$ ,  $n = 93$ ; 1985,  $G = 36.6$ ,  $P < 0.001$ ,  $n = 89$ ; 1986,  $G = 46.2$ ,  $P <$

$0.001$ ,  $n = 117$ ; 1987,  $G = 80.9$ ,  $P < 0.001$ ,  $n = 204$ ) and the beta female fed chicks significantly less than the dominant female (1983,  $G = 27.6$ ,  $P < 0.001$ ,  $n = 42$ ; 1985,  $G = 9.6$ ,  $P < 0.005$ ,  $n = 22$ ; 1986,  $G = 51.3$ ,  $P < 0.001$ ,  $n = 37$ ; 1987,  $G = 47.1$ ,  $P < 0.001$ ,  $n = 34$ ). The gamma male fed chicks significantly more food than the dominant male during two breeding seasons (1986,  $G = 20.1$ ,  $P < 0.001$ ,  $n = 88$ ; 1987,  $G = 66.0$ ,  $P < 0.001$ ,  $n = 188$ ), but there was no significant difference during the other two years (1983,  $n = 79$ ; 1985,  $n = 42$ ).

For their first couple of months, trumpeter chicks also relied on older birds to detect and deter potential predators (i.e. raptors and felids). Older birds responded to predators by producing alarm calls, approaching the predator, or aggressively defending a chick. These behaviors made the individual producing them conspicuous to the predator and, therefore, should have been associated with an increased risk of injury or death. I observed the study groups with seven different broods, during which I witnessed 19 incidents in which I was able to identify 35 individuals that gave high-intensity alarm calls and/or approached the predator or aggressively defended a chick. The dominant male was most frequently involved in protecting chicks from predators (30% of incidents; Fig. 5B), followed by the subordinate adult males, the dominant female, and offspring (about 15–20% of incidents), with subordinate adult females being least often involved (3% of incidents).

Individuals in trumpeter groups also assisted to varying degrees with incubation. Eggs were incubated by one individual during the afternoon and a different individual overnight and in the morning (Sherman 1995). During 35 days of observation during incubation, the dominant female took 39.4% of the incubation shifts, while the dominant male took 43.7%, the beta male 8.5%, the gamma male 7.0%, and a one-year-old offspring 1.4% (Fig. 5C;  $n = 71$  incubation shifts).

*Dispersal of offspring.*—Trumpeter offspring usually helped raise one brood of siblings before dispersing from their natal groups. Of the 11 young that dispersed during this study, 1 left his natal group before the next year's young hatched, 8 helped with young for one breeding season, and 2 helped for two breeding seasons. Male and female offspring usually dispersed or were expelled from their groups around the time they reached sexual maturity (at about two

years of age; Sherman 1995). Offspring left their natal groups, on average, at  $24.7 \pm 2.40$  months of age ( $n = 6$  offspring for which age and date of dispersal known).

Although my sample size was small, siblings did not appear to disperse from their natal groups together on a regular basis. I was present at the study site when three sets of same-aged siblings dispersed. Of these eight individuals, only two siblings dispersed from their natal group within a few days of each other. The sex of these individuals was not known. One of the other sets of siblings contained two males and a bird of unknown gender, and the other contained two females and a male. All of these individuals dispersed alone, separated from the date of their siblings' dispersal by intervals of one to seven months.

Ten of the 11 offspring that dispersed during my study were assumed to have traveled several kilometers from their natal territories, as they were never sighted again at the study site. Only one bird dispersed a short distance, joining a group whose territory was adjacent to his natal group's territory, where he eventually became the beta male. A twelfth offspring took over the position of beta male in his natal group at 23 months of age, after his mother disappeared and was replaced by the group's beta female. This male remained in his natal group and retained the same dominance status two years later when the study ended.

*Tenure of dominant individuals and adult mortality.*—During the 12 group-years that we collected data on marked individuals in the three study groups, three dominant males and three dominant females lost their breeding positions (Price pers. comm., Sherman 1991). This suggests an average tenure of four years for dominant males and females in permanent territorial groups. I observed the entire tenure of two dominant females (tenure was 2.3 years for one female and 3.0 years for the other) and two dominant males (0.5 years for one male and 1.5 years for the other). Three additional females had retained the dominant position in their groups for more than two years, and two males had been dominant for more than four years at the time that this study ended.

All three replacements of dominant females occurred at the beginning of the breeding season. One dominant female disappeared during the period just before she began to lay her clutch, and the other two disappeared during the in-

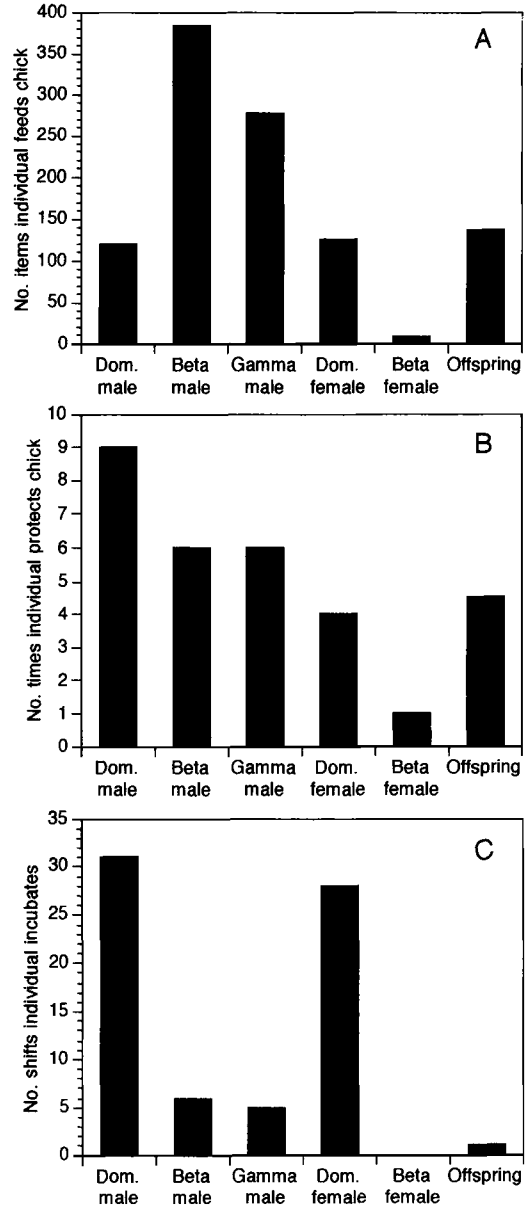


Fig. 5. (A) Number of individual food items fed chicks by different individuals in group during four breeding periods (NG: 1985; HG: 1983, 1986, 1987). (B) Number of times different individuals gave high-intensity alarm calls and/or approached predator or protected chick in group during seven breeding periods. (C) Number of shifts (day or night) different individuals incubated. Data collected during 35 full days of observation (71 incubation shifts) of HG and NG incubating three clutches.

cubation period. It is not known whether these dominant females died or were forced from the group by other individuals. Two of the females were never sited again, but this does not necessarily indicate death, as subordinate females also were seen rarely subsequent to leaving their groups (see following section). All three dominant females that disappeared were replaced by the beta females in their groups.

I have few data concerning the three replacements of dominant males that occurred during this study. One replacement occurred at the beginning of the breeding season, but I observed only the displaced dominant male, and the male who had replaced him, and did not observe the actual interaction that led to the change. The other two replacements occurred while I was away from the study site. Of the three males who were displaced, none were replaced by their offspring. One dominant male was replaced by the male who had been the group's beta male, one was replaced by the group's gamma male, and one was replaced by a male that had not previously belonged to the group. Following their loss of dominance status, one of the displaced dominant males was never seen again and one remained in his original group for a year at the rank of beta male before becoming the dominant male in a different group. The third dominant male, after losing his position in the NG, spent a year in the HG as a gamma male, then became the dominant male in a fugitive breeding group which did breed successfully, and finally became the dominant male in the EG.

I calculated the annual mortality rates of adults by dividing the number of marked individuals that permanently disappeared during a one-year period by the number that were present at the study site at the beginning of the period. For females, I used data only from marked dominant and beta females because gamma females frequently transferred out of territorial groups and were not seen again (see following section). Between 1983 and 1987, the estimated average annual mortality rate of adult females living in territorial groups was 11.9% (eight individuals tracked two to four years for total of 21 adult female-years). I used data from all marked adult males living in territorial groups. Between 1983 and 1987, the estimated average annual mortality rate of adult males living in territorial groups was 2.8% (nine individuals tracked two to four years for total of 31 adult male-years).

*Transfer of adults.*—Subordinate adult male and female trumpeters occasionally transferred out of the three study groups, but exhibited very different patterns of transfer. When females transferred out of their groups, they were often not seen again. I considered an individual to have transferred (as opposed to having become temporarily separated from its group) if the bird remained away for longer than two days. Of the 11 beta and gamma females that transferred out of their groups during this study, 2 later returned and 9 were never seen again. The females that transferred and then returned to their original groups were both beta females. One joined a neighboring territorial group twice (once for five weeks and once for six weeks) during a breeding season when the neighboring group lacked a beta female. The other switched for one week to a fugitive group in which the dominant male copulated with her. Both females regained their beta positions when they rejoined their original groups.

The nine subordinate adult females that transferred out of their groups and were not seen again appeared to have been chased out of their groups. Dominant females and all adult males chased subordinate adult females frequently, especially at the beginning of the breeding season and at the beginning of the dry season when resource abundance decreased (see Sherman 1991). The date of permanent departure was known for six females; three left one to three weeks before the incubation of their group's first clutch began, and three left during the first two months of the dry season (the other three disappeared from their groups during gaps of 10 to 12 months between field seasons). The dominance status of subordinate adult females appeared to be related to their probability of permanently leaving their groups. Beta females in the three focal groups averaged 0.8 permanent departures per group-year, while gamma females averaged 3.3 permanent departures per group-year.

New subordinate adult females that attempted to transfer into the habituated groups were treated aggressively. The nine new females that joined groups while I was at the study site all were attacked and chased repeatedly, principally by the dominant female, but also by the adult males, and traveled and fed separated by about 15 m from the rest of the group for more than a month after they joined. About one-half of the females that joined the habituated groups

did so accompanied by other adult females. Three females joined as a trio, two appeared to be a pair (their entrance into group was separated by two weeks), and four joined unaccompanied by other individuals. During J. Price's studies of the HG and NG, she observed a different trio of females that skulked around these groups' territories, and eventually joined the HG one by one (Price pers. comm.).

In contrast to subordinate adult females, subordinate adult males always transferred into other groups unaccompanied by other individuals. All of the transfers that I observed males make, occurred during territorial fights; the males began the fight in one group, and left the fight with the other group. Additionally, when subordinate adult males transferred out of their groups, they almost always returned. During this study there were 16 instances when subordinate males transferred out of the habituated groups. Fourteen of these males returned to their original group after an average of  $19 \pm 3.1$  days (range 8–40 days,  $n = 11$ ; approximate dates of both departure and return not known for three males). The two subordinate males that did not return both obtained positions of higher dominance status in other territorial groups.

In contrast to subordinate adult females, the dates on which subordinate males transferred out of their groups were spread evenly across all months of the year ( $n = 14$  known departure dates). Seven of the 14 times that subordinate adult males left and returned to their groups, they transferred to unknown locations. Of the remaining seven transfers, four were to another of the habituated permanent groups, where the males entered at equivalent ( $n = 1$ ) or lower ( $n = 3$ ) dominance status. The remaining three transfers were made by gamma males, who temporarily joined a fugitive breeding group that lacked a beta male.

As was the case with subordinate adult females, the dominance status of subordinate adult males was related to the frequency with which they transferred and returned to their groups. Beta males in the three focal groups averaged 1.0 transfer and return per group per year, while gamma males transferred and returned 2.7 times as frequently.

Unlike subordinate adult females, subordinate adult males that transferred into the habituated groups were not treated aggressively. While in the new groups, the transferred males behaved submissively, frequently performing

the wing-spread behavior to the other adult males in the group, and the resident adult males responded by wing-flicking, but did not chase or attack the newly joined males. The newly transferred males traveled and fed near the group's resident males, although more dominant males in the resident group would chase them from limited resources or away from the dominant female if it was during the breeding period.

*Fugitive groups.*—A small proportion of the trumpeter population lived in small, unstable fugitive groups that ranged furtively around the peripheral areas of permanent groups' territories. During this study, I encountered 12 fugitive groups at the study site. They averaged  $2.8 \pm 0.18$  (range 2–4,  $n = 12$ ) individuals and were not territorial. The groups that defended permanent territories chased fugitive groups off their territories whenever they were encountered.

I encountered twice as many fugitive groups during the breeding season as I did during the dry season (sightings multiplied by correction factor to make time I spent at study site during these two seasons equivalent). During the dry season, fugitive groups appeared to be individuals that were unable to join permanent territorial groups. During the breeding season, some fugitive groups did breed; two of nine groups that I encountered had chicks. One trio (two males and a female) hatched a single chick, but it disappeared when about two weeks old and the group disbanded about six weeks later. A pair of trumpeters that I encountered had three chicks, but I did not observe them a second time and do not know what became of them.

None of the fugitive groups remained together for more than four months, with the exception of one trio (the NG's beta male, beta female and an unbanded adult female) that raised a brood of two chicks while I was away from the study site (M. McFarland pers. comm.), and remained together as a group during the following dry season. This fugitive group became a permanent group (the EG) when they succeeded in defending the area in which they bred and foraged against surrounding territorial groups. This area had been part of three other groups' territories, but was little used by these groups as it was located in a seasonally flooded swamp. The EG reproduced successfully during three subsequent breeding seasons, at which time this study ended.



## DISCUSSION

These are the first detailed data obtained on the social organization of any of the three species of *Psophia*, family Psophiidae. At my study site, I found that White-winged Trumpeters lived in cooperatively polyandrous groups that defended large permanent all-purpose territories. Territorial groups occupied all habitat types at the study site and groups' territories were contiguous. In this discussion, I will examine: (1) the reproductive strategies of adult males and females of different dominance ranks; (2) possible reasons why offspring do not remain in their natal groups after they reach sexual maturity; and (3) how trumpeters' unique ecological niche may have promoted the evolution of cooperative polyandry in this species.

*Dominance rank and reproductive strategies.*—The dominant male in territorial groups of White-winged Trumpeters attempted to prevent subordinate adult males from copulating with the dominant female during her fertile period by guarding her closely and by interrupting all copulation attempts made by subordinate males (Eason and Sherman 1995). In this way, trumpeters resemble some of the other species that are cooperatively polyandrous or polygynandrous in that males compete for matings with the breeding female and/or attempt to limit the access of other males to her (Acorn Woodpeckers [*Melanerpes formicivorus*], Mumme et al. 1983, Koenig 1990; Dunnocks [*Prunella modularis*], Davies 1992; Stripe-backed Wrens [*Campylorhynchus nuchalis*], Rabenold et al. 1990, Piper and Slater 1993). In others of these species, however, neither competition between males nor mate guarding has been observed (Dusky Moorhens [*Gallinula tenebrosa*], Garnett 1980; Galapagos Hawks [*Buteo galapagoensis*], Faaborg and Bednarz 1990; Lammergeiers [*Gypaetus barbatus*], Heredia and Donazar 1990; Pukekos [*Porphyrio porphyrio*], Craig and Jamieson 1990; Tasmanian Native Hens [*Tribonyx mortierii*], Maynard Smith and Ridpath 1972; Ridpath 1972; lions [*Panthera leo*], Packer et al. 1988; saddle-back tamarins [*Saguinus fuscicollis*], Terborgh and Goldizen 1985; Goldizen 1989). Reasons for these differences are unclear (Emlen 1991), although the probability that the males in a group are related, or that polyandry will raise their long-term reproductive fitness, may influence whether male-male competition occurs and the degree of such competition (Davies 1991).

In trumpeters, despite extensive mate guarding by the dominant male, subordinate males obtained approximately one-third of all copulations with the breeding female during her fertile period, with beta males copulating almost three times as frequently as gamma males. Such high levels of copulation success for subordinate males have not been observed for other cooperatively polyandrous or polygynandrous species in which male-male competition occurs, perhaps due to the difficulty of observing the surreptitious copulations of subordinate males (see Koenig and Stacey 1990, Rabenold et al. 1990, Piper and Slater 1993). Although genetic data are needed to demonstrate multiple paternity definitively, subordinate males' copulations were not restricted to times when they would be unlikely to fertilize eggs and dominant males appeared unable to decrease the value of these copulations by copulating soon after subordinate males (see Eason and Sherman 1995). In other cooperatively polyandrous or polygynandrous species in which males compete for copulations, genetic-paternity analyses have shown that subordinate males father some offspring (Acorn Woodpeckers [Joste et al. 1985, Mumme et al. 1985], Dunnocks [Burke et al. 1989], Stripe-backed Wrens [Rabenold et al. 1990, Piper and Slater 1993], but also see Gibbs et al. in press).

Subordinate adult male trumpeters appeared to investigate reproductive opportunities in other groups. They transferred into other groups relatively frequently, but always returned to their original group within several weeks unless they obtained a position with a higher dominance rank in a different territorial group. Gamma males transferred almost three times as frequently as beta males (2.7 transfers and returns per group-year compared to 1.0 for beta males), which suggests that transfers may allow males to assess the probability of current or future reproductive opportunities in other groups as dominant or subordinate breeders. This type of social fluidity, in which subordinate males are readily accepted into other groups and readmitted into their own, has not been reported for other cooperatively breeding species.

Although the dominant female was capable of disrupting males' copulation attempts and did so during 7% of the dominant male's attempts to copulate with her during her fertile period, she cooperated with subordinate adult males during all of their copulation attempts

throughout her fertile period. It has been suggested that the amount of help males contribute to rearing young may be related to their probability of paternity, and that breeding females may increase their reproductive success by copulating with all males in their group as equally as possible (Davies 1986, Burke et al. 1989, Koenig 1990, Koenig and Stacey 1990, Davies et al. 1992). Subordinate males did provide a significant amount of help rearing chicks; in each of the four breeding seasons that I collected data, the beta male provided chicks with substantially more food than any other individual in the group, and the gamma male provided chicks with the second greatest amount of food. Whether subordinate males would contribute equivalent amounts of help if they did not obtain any copulations with the dominant female is not known.

In the majority of avian cooperatively breeding species in which more than one potentially breeding female (i.e. adult female unrelated to dominant male[s]) is present within a group, all females contribute to the group's clutch and all help feed the chicks (Acorn woodpeckers, Koenig and Stacey 1990; Groove-billed Anis [*Crotophaga sulcirostris*], Vehrencamp et al. 1986; Dusky Moorhens, Garnett 1980; Pukekos, Craig and Jamieson 1990). In trumpeter groups, however, subordinate adult females did not contribute eggs to their group's clutch and, likewise, these females contributed almost no help rearing the group's chicks. Subordinate adult females were chased frequently by the dominant pair during the month that preceded the laying of the clutch, and sometimes left their groups permanently during this period. Harassment by the dominant male and female probably decreased the ability of subordinate females to breed within the group. Subordinate females never attempted copulations in sight of the dominant pair and frequent harassment may have contributed to their reproductive suppression as evidenced by their undeveloped ovaries and the long delay before subordinate females were able to reproduce after obtaining breeding positions in groups. Reproductive suppression of adult females in cooperatively breeding groups has been reported for a number of mammalian species (see references cited in Macdonald and Moehlman 1982, Wasser and Barash 1983, Creel and Creel 1991), but only for one other cooperatively breeding bird (Stripe-backed Wren; Rabenold 1990, Rabenold et al.

1990). Although subordinate adult female trumpeters appeared unable to breed in territorial groups, the reward to a beta female that remained with a territorial group appeared to be an increased probability of eventually obtaining a breeding position. In the three instances during this study when a group's dominant female disappeared, the group's beta female immediately became the breeder. Gamma females were never observed to rise in dominance status in their groups, and left groups more than four times as frequently as beta females (3.3 permanent departures per group-year for gamma females compared to 0.8 for beta females).

Fugitive groups of two to four trumpeters were capable of raising young successfully, as evidenced by the trio that became the EG. The frequency with which fugitive groups succeeded in raising chicks and the costs associated with breeding in small groups are unknown, so it is not possible to compare the long-term fitness benefits accrued by individuals belonging to permanent territorial groups with those accrued by individuals who attempt to breed in temporary fugitive groups. Individuals breeding in fugitive groups may suffer an increased risk of predation due to small group size, or may have difficulty finding adequate food without continually engaging in fights and being chased off the resident groups' territories on which they are intruding. Such problems may also reduce the probability that fugitive groups' chicks will survive.

*Dispersal of offspring from natal groups.*—Trumpeter offspring contribute substantial help to rearing their siblings, but the majority of male and female offspring disperse or are expelled from their groups around the time they reach sexual maturity at two years of age. They thus differ from the vast majority of species that form stable cooperatively breeding groups, in which grown offspring of one or both sexes delay dispersal and remain on their natal territory until they obtain a breeding position there or on a nearby territory (Emlen and Vehrencamp 1983, Brown 1987, Emlen 1991).

There are several possible explanations for why trumpeters do not remain on their natal territories after they reach sexual maturity. Offspring are unlikely to become breeders if they remain in their natal groups due to inflexible territorial boundaries and the relatively long tenure of the dominant breeding pair. Trumpeters' territories are contiguous and have rel-

atively inflexible boundaries (Sherman 1991) and, thus, there is little possibility for offspring to help enlarge their parents' territory and then "bud off" a breeding territory for themselves (see Woolfenden and Fitzpatrick 1986). A subordinate adult male that remains on his natal territory must wait for his mother to be replaced by a new breeding female before he has the opportunity to breed (White-winged Trumpeters were never observed to copulate incestuously). An adult male that joins a new group, however, has the potential to copulate surreptitiously with an unrelated breeding female. Although adult females are treated aggressively when they transfer into new territorial groups, and are sometimes chased out of these groups, a female that remained on her natal territory would have little chance of ever breeding. For a female to become a breeder on her natal territory, she would have to wait for the dominant male to be replaced (and also the beta and gamma male to avoid completely possibility of incestuous mating) and, subsequently, would have to be able to displace the current breeding female. Likewise, if she waited on her natal territory for a reproductive vacancy to become available on a neighboring territory, she would appear to have little chance of filling this vacancy; in the three instances during this study in which breeding females disappeared, they were always replaced by the beta female in their group. Females that leave their natal groups and succeed in joining and remaining in a territorial group as a beta female have a reasonable chance of eventually becoming the group's breeding female.

A less likely explanation for dispersal of sexually mature offspring is that they may form coalitions that increase their chances of taking over breeding positions in other groups. In lions, male offspring leave their natal groups when they reach sexual maturity and form same-sex coalitions with kin which challenge breeding males in other groups or attempt to establish new groups (Bertram 1975, Bygott et al. 1979, Packer et al. 1988). This seems an unlikely scenario for trumpeters because the majority of trumpeter offspring dispersed from their natal groups solitarily. Additionally, all males that transferred into new groups did so solitarily. Although one-half of the females that transferred into groups did so accompanied by one or two other females, these females were never observed to challenge the resident breeding

female, and did not form any kind of stable association.

*Evolution of cooperative polyandry in White-winged Trumpeters.*—In trumpeter groups, offspring appear to be unlikely to obtain breeding positions by remaining on their natal territories, and unlikely to breed independently due to a shortage of suitable breeding territories. The shortage of breeding habitat in White-winged Trumpeter populations appears to result from the need for trumpeter groups to defend large permanent territories ( $\bar{x} = 72$  ha) to provide them with sufficient quantities of fruit during the dry season when resources are scarce. White-winged Trumpeters depend on the ripe pulp of fallen fruit to provide them with 90% of the calories they ingest daily (Sherman 1991). During the dry season at Cocha Cashu, there is a substantial decrease in the number of trees that produce fruit, and in the overall density of edible fallen fruit (Terborgh 1983, Sherman 1991). Data collected on the daily caloric intake of trumpeters during the dry season showed that there were multiple periods lasting one to three weeks during which dominant individuals in territorial groups were unable to ingest sufficient food to meet their daily energetic requirements. During these periods of resource scarcity, I performed experiments in which I removed daily an amount of fallen fruit from the focal group's territory that was equivalent to the amount of fruit ingested daily by the focal group during a control period that preceded the removal experiment. These removal experiments resulted in a significant decrease in the daily caloric intake of dominant individuals, as they were unable to locate additional fruiting trees either on or off their territories. These results, together with results from other controlled removal experiments during periods when fruit was abundant, indicate that trumpeter territories may need to be large to provide resources adequate to sustain the resident group during seasonal periods of resource scarcity (Sherman 1991, Sherman and Eason in prep.). The defense of large permanent territories appears to result in a surplus of sexually mature trumpeters relative to the number of suitable breeding territories available.

It has been suggested that a lack of suitable breeding territories has acted to promote the evolution of cooperative breeding in the majority of cooperatively breeding species (Brown 1987, Emlen 1982, 1991). Both the habitat-sat-

uration hypothesis (Brown 1969, 1974, Emlen 1982), and the more recent benefits-of-philopatry hypothesis (Stacey and Ligon 1987), suggest that cooperative breeding may result when offspring delay dispersal from their natal group until a breeding position becomes available on a high-quality territory (Emlen 1991). In White-winged Trumpeters, habitat saturation appears to be responsible at least in part for the presence of multiple adults in territorial groups, although trumpeters differ from the majority of cooperative breeders in that these adults are not grown offspring that have delayed dispersal. Trumpeter offspring appear to disperse from their natal territories because they stand little chance of acquiring a breeding position if they remain in their natal group.

Why does the dominant pair of White-winged Trumpeters allow unrelated individuals to join their group? A pair of trumpeters might need to accept additional individuals into their group to defend their territory successfully against larger groups. The initial energetic cost to a dominant pair that allowed a few other individuals into their group might be negligible if the pair was able to exclude the other individuals from limited resources and if the density of edible fruit below most trees during most of the year was greater than the amount needed to meet the energetic needs of the dominant pair. With the number of adults in the population exceeding the number of available breeding positions, however, increasingly large group sizes might be necessary to defend territories successfully against other groups. As group sizes increased, the reproductive success of the dominant pair might begin to decrease due to the energetic costs of competing for limited resources or to kleptogamy. The presence of unrelated subordinate adult males in territorial groups, although potentially costly to the dominant male because of kleptogamy, may also be beneficial due to the apparent advantage of large groups in successful territorial defense. The mass of adult male trumpeters is significantly more than that of adult females (Sherman 1995) and males are dominant to females. This difference in mass and associated dominance play an important role in territorial fights, in which adult males from each group fight each other, and adult females fight adult females. This can be considered to be a type of "prisoner's dilemma," in which per-capita reproductive success is balanced against the need to belong to a group that

is large enough to defend a breeding territory successfully (see Craig 1984, Craig and Jamieson 1990).

In summary, the need for White-winged Trumpeters to defend large permanent territories to provide access to sufficient food resources throughout the year appears to have resulted in a surplus of adults in the trumpeter population relative to the number of available breeding territories. The low probability of acquiring a breeding position for individuals that remain on their natal territory may result in sexually mature offspring dispersing from their natal groups and attempting to join new groups where they have some chance of breeding non-incestuously. Finally, the apparent need to have multiple adult males within a group for successful territory defense may explain why unrelated males are accepted into territorial groups, where they are able to copulate surreptitiously with the breeding female.

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