

The social system of Sharpe's Wren (*Cinnycerthia olivascens*): fluid group composition in a cooperative breeder

El sistema social del cucarachero de Sharpe: fluidez en la composición de grupos en un ave con cría cooperativa.

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Abstract

Cooperatively breeding birds live in groups that normally originate in the retention of offspring, which delay dispersal and stay in the parental territory, helping to raise close kin. Group transfers usually occur when individuals disperse to obtain reproductive positions. Between 1995 and 2000 we studied the social system of Sharpe's Wren (*Cinnycerthia olivascens*) in an Andean forest. Wrens lived all the time in groups of up to seven individuals that maintained year-round, all-purpose territories (mean = 7.6 ha) and raised offspring cooperatively. Each group had only one breeding pair, and produced 1-3 fledglings. Group composition was highly variable. Birds of all age classes frequently joined and abandoned groups. Birds became helpers when joining new groups. In one case a female breeding vacancy was filled by a bird that had joined the group two and a half years earlier. Four focal groups each had up to 20 different, temporary members in three years of observation, and only the breeding pair was permanent. Seven of eight breeding females and one male (of 35 banded adults) had frontal patches and periocular rings of white feathers, suggesting that this characteristic is related to breeding status (but not necessarily age). Groups maintained three or more roosting nests simultaneously and built new nests continuously. Flea infestations may have been a cause of nest abandonment. Fluidity in group membership suggests that benefits of sociality in this species are not related to indirect fitness, nor to direct benefits that hinge on life-long associations between individuals. Instead, group-living may be related to the need to constantly build new, massive nest structures.

Key words: Andes, Colombia, cooperative breeding, helping behavior, social behavior, Troglodytidae.

Resumen

El sistema social del cucarachero de Sharpe: fluidez en la composición de grupos en un ave con cría cooperativa. Las aves que crían cooperativamente viven en grupos que normalmente se originan en la retención de las crías, las cuales difieren su dispersión y se quedan en el territorio natal ayudando a criar parientes cercanos. Las transferencias entre grupos generalmente ocurren cuando los individuos se dispersan para obtener posiciones reproductoras. Entre 1995 y 2000 estudiamos el sistema social del cucarachero de Sharpe (*Cinnycerthia olivascens*) en un bosque de los Andes de Colombia. Estas aves vivieron todo el tiempo en grupos de hasta siete miembros que mantuvieron un territorio todo el año de 7.6 ha en promedio y criaron cooperativamente. Cada grupo tuvo sólo una pareja reproductora y produjo de una a tres crías. El sistema social de estas aves es poco usual pues la composición de los grupos fue altamente variable. Los individuos se movieron continuamente entre grupos y se unieron o abandonaron el grupo en cualquier etapa de su desarrollo (juveniles a adultos). Al unirse a un nuevo grupo los individuos actuaron como ayudantes. En al menos un caso, al desaparecer la hembra reproductora de un grupo, esta posición fue ocupada por una hembra que había inmigrado al grupo dos años y medio antes. En cuatro grupos focales, cada uno tuvo hasta 20 miembros diferentes en tres años de observaciones y sólo la pareja reproductora fue permanente. Siete de ocho hembras reproductoras y un macho (de 35 adultos anillados) tenían parches frontales y anillos perioculares de plumas blancas, lo cual sugiere que esta característica está relacionada con la jerarquía social (pero no necesariamente con la edad). Los grupos mantuvieron tres o más nidos dormitorio simultáneamente y constantemente construyeron nidos adicionales. Los nidos fueron abandonados a menudo por infestaciones de pulgas. La fluidez en la composición de los grupos sugiere que el comportamiento social en esta especie no está relacionado con aptitud indirecta, ni con benefi-

cios directos que dependen de asociaciones a largo plazo entre individuos. La vida en grupo en esta especie puede estar relacionada con la necesidad de estar constantemente construyendo nuevos nidos, los cuales son estructuras masivas.

Palabras clave: Andes, Colombia, cría cooperativa, comportamiento social, Troglodytidae

Introduction

In cooperative breeding systems, birds live in groups and all members of the social unit participate in raising young at a single nest. Groups may be composed of one or more breeding pairs, and one or more non-breeding helpers-at-the-nest. Groups of cooperative breeders are normally family-based (Koenig & Dickinson 2004). Helpers in these groups are usually offspring from previous breeding seasons that delay their own reproduction, staying in the parental territory and assisting breeders in raising related young.

Although cooperative breeding may be a last-resort strategy forced by ecological constraints such as habitat saturation (Koenig & Pitelka 1981, Emlen 1982), staying in the parental territory and helping raise kin may also produce direct and indirect benefits (Stacey & Ligon 1991, Dickinson & Hatchwell 2004, Ekman *et al.* 2004). Direct benefits accrue from increased survivorship related to familiarity with the natal territory, and other benefits of group-living, such as future reciprocity in aid-giving. Indirect benefits derive from indirect fitness gains resulting from increased productivity of related offspring.

In some species of birds, groups may include unrelated individuals that cooperate in raising a single brood (Cockburn 1998). For example, in White-winged Trumpeters (*Psophia leucoptera*), coalitions of unrelated, subordinate males provide food and care to chicks that are the progeny of the dominant female and possibly of several males (Sherman 1995). Subordinate males may transfer to different groups in which they act as helpers, and may return to the original group. Coalitions of unrelated helpers have been described for species



Figure 1. Adult Sharpe's Wren with a frontal patch and periocular ring of white feathers, photographed 20 December 1997 at La Pastora, 2430 m, Central Andes of Colombia. The illustrated bird was the incubating female in group A (Am/Azcl). Photograph by William Beltrán.

such as Riflemen (*Acanthisitta chloris*; Sherley 1990), White-browed Scrubwrens (*Sericornis frontalis*; Magrath & Whittingham 1997) and Carrion Crows (*Corvus corone*; Baglione *et al.* 2002). These cases raise questions related to the possible advantages of helping to raise non-kin (Cockburn 1998). Models show that in some cases recruitment of new individuals into a group (known as group augmentation) increases survival and reproduction and may result in helping behavior (Kokko *et al.* 2001).

In this paper, we describe the social system of Sharpe's Wren (*Cinnycerthia olivascens*, previously a subspecies of the Sepia-brown Wren, *C. peruana*; Brumfield & Remsen 1996). These wrens are known to live in groups and breed cooperatively (Freeman & Greeney 2008), but their social system has not been described in detail. In addition, *Cinnycerthia* spp. have plumage variants, in which some birds exhibit variable patches of white

feathers on their foreheads (Fig. 1), possibly related to dominance hierarchies (Graves 1980, Brumfield & Remsen 1996). We describe the role of white-fronted birds and the dynamics of group composition in a population of these wrens at a cloud forest site in the Central Cordillera of the Colombian Andes.

Study area and methods

The study was conducted at La Pastora (2400-2600 m), an ecotourism facility in Ucumarí Regional Park. This 3,980-ha park is located on the western slope of the Central Cordillera of the Andes of Colombia, Municipality of Pereira. It protects the Otún River watershed between elevations of 1750 and 2600 m. The rain regime in the area is bimodal, with peaks of rain in April and October. Mean annual precipitation for 30 years is 2650 mm. The mean annual precipitation for the 5 years of our study was 2800 mm and varied between 2470 mm in 1997 and 3270 mm in 1999.

The area of La Pastora was cleared for cattle raising in the early 20th century, with native old-growth forest remaining only in some isolated patches on the valley bottom and some inaccessible canyons. In the 1960's a revegetation program was initiated by removing cattle and establishing some Andean alder (*Alnus acuminata*) plantations, whereas other patches were abandoned to natural regeneration at different times (Londoño 1994). Alder is native to the Andes and usually grows in monospecific stands, colonizing disturbed areas. Planted alder stands are overgrown with native vegetation in the understory and edges, and other tree species have reached the canopy but the stands remain dominated by 15-20 m tall alder trees (Murcia 1997). Presently, the study area is a small-scale mosaic of patches smaller than 10 ha, composed of alder stands, early second growth vegetation (5-15 years old) with a thick understory and 5 m tall trees, late second growth (up to 40

years old) with a 15-20 m tall canopy, and small pasture areas with scattered bushes.

Observations were carried out in an area of 100 ha. We started banding wrens with unique color codes in February 1995, but methodical observations were initiated in April 1997 and lasted through May 2000. Between February 1995 and April 1997, we captured birds with mist nets placed at random throughout the study area, and made opportunistic observations each month, mapping the approximate boundaries of the territories of 15 wren groups.

Starting in April 1997, we chose four focal groups (labeled A, F, N and V) for more detailed observations. Each of these four groups was monitored by one observer for four days each month, between 5:30 (when birds left roost nests) and 18:00 (when they retired into roost nests). The observer followed the group in its movements across its territory, noting group composition and behavior. Mist nets were placed intercepting the birds' path in forest edges and early second growth. When one bird was captured it gave alarm calls, which attracted other members of the group to the area. These birds also gave alarm calls and this behavior usually permitted us to capture all or most group members. We used these captures to establish group composition, band unbanded birds, and record molting and brood patches. Between 1997 and 2000, the other 11 groups were followed occasionally. We identified four age classes (fledgling, juvenile, subadult and adult; Table 1) based on recaptures that allowed us recording timing of molting.

Based on a 1995 aerial photograph (scale 1:20,000), we made a map of the study area. We recognized four habitat types used by wrens: (1) alder stands; (2) early secondary growth vegetation; (3) late second growth forest; and (4) pastures. The extent and boundaries of these habitat

Table 1. Description of age classes of Sharpe's Wren in the Central Cordillera of the Colombian Andes. The table shows the duration of the four age classes based on cases of recapture of molting birds. For adult birds, 5 years is the maximum recorded duration.

Age class	Number of cases	Duration (months)	Description
Fledgling	2	2	Gray iris, dark gray head, yellow bill
Juvenile	2	12-17	Gray iris, grayish head, dark maxilla and yellow mandible
Subadult	7	9-16	Brown iris, grayish brown bill with some yellow in base
Adult	6	60	Dark brown iris and black bill; 9 of 35 birds had white frontal patches, 3 also had white tibio-tarsal feathers.

patches were verified on foot. We established territorial limits of the four focal groups by mapping group positions and trajectories, and calculated territory size by the minimum convex polygon method. We measured the percent cover of different vegetation types in each territory on the map with a planimeter. We recorded the number of times a group was observed in each habitat type and tested the hypothesis that the four wren groups used habitat types in proportion to their availability with a *G*-test of independence.

Results

Habitat and group behavior.- We identified 15 wren groups and banded 101 birds in the study area of 100 ha, for an average of 6.7 ha per group and 6.7 birds per group. Groups were cohesive, with members maintaining constant contact through vocalizations, especially when foraging in dense second growth. Groups foraged at forest edges and in understory to mid levels within the forest, moving at a speed of approximately 200 m/h. Wren groups occasionally joined mixed-species flocks passing through their territories.

The four focal groups had a mean (\pm SD) territory size of 7.6 ± 1.2 ha (range 5.9 to 9.2 ha). Groups used the different habitats within territories in pro-

portion to their availability ($G = 8.5$, $df = 6$, $N = 30$ records per group, $P = 0.25$). Territories had on average 60% alder stands, 30% early second growth, 7% late second growth forest, and 3% pasture. Territories overlapped only slightly (<1%). Territorial interactions were observed three times during the study in overlap areas. One pair of birds (later identified as the breeders) of one group initiated territorial defense, with other members joining in a vocal contest and flying around.

All members of the group built and slept together in roost nests. Each group had between one and three alternate roost nests that were used during a given time period. New nests were frequently built using material from old nests. We observed the four focal groups using 34 different roost nests in a period of one year (April 1997-April 1998). Roost nests were used for a mean of 1.2 ± 0.4 months ($N = 9$). On one occasion, we observed group F disassemble a nest in 8 days and use the material to build a new nest a short distance away. Roost nests were usually abandoned because of heavy flea (*Echidnophaga* sp., Pulicidae) infestations.

Occasionally, the group split at dusk and some individuals slept in an alternate nest. Roost nests were supported on crotches of understory shrubs

(Melastomataceae and Solanaceae; mean height \pm SD = 3.7 \pm 1.4 m, N = 34) and were similar to breeding nests but were not used for nesting.

Nesting biology.- We found 12 nests during the study, belonging to the four focal groups and an additional group (AC) that was monitored occasionally (Table 2). The nest was a massive globose structure about 25 cm in diameter, with a downward-sloping entrance tunnel, similar to the nests described by Gochfeld (1979) and Freeman & Greeney (2008) for the Sepia-brown Wren in Peru and Sharpe's Wren in Ecuador, respectively. All breeding nests were built on *Aphelandra acanthus* (Acanthaceae), a spiny shrub.

Access to the incubation chamber was not possible without breaking open the nest. Thus, we could not determine clutch size. The incubation period was approximately 19 days. Four nests failed and produced no fledglings (Table 2). The other eight nests were successful and produced one (one nest), two (six nests) or three (one nest) fledglings.

In three cases that we observed groups building breeding nests for periods of two hours, all members of the group carried material and participated in nest-building. However, in all cases only one individual incubated (presumably the female; Table 2) and was frequently accompanied by her mate when entering the nest. The other members of the group usually stayed away from the nest during incubation. Thus, there was presumably only one breeding pair per group. After eggs hatched, all members fed the young, but their participation was uneven, with the breeding female making up to 50% of all feeding trips (Fig. 2). Nestlings were fed moths, orthopterans, lepidopteran larvae and earthworms (occasional observations). The number of fledglings was not related to group size (r = 0.0001, P > 0.9, N = 8).

Table 2. Identity of incubating female, group size (number of adults, subadults and juveniles), and number of fledglings produced by five groups (four focal and one additional group AC) in 12 nests of Sharpe's Wrens in the Central Andes of Colombia.

Group/Date	Incubating individual	Group size	No. of fledglings
<u>Group V</u>			
Jul/97	Rs+Am/Vcl ^a	7	2
Jan/99	Vcl/Rs	7	2
Oct/99	Vcl/Rs	6	2
<u>Group F</u>			
Jul/97	unbanded ^a	5	0
Mar/99	Fuc/Bla ^a	7	1
May/00	Fuc/Bla ^a	7	3
<u>Group A</u>			
Mar/98	Am/Azcl ^a	5	0
Apr/98	Am/Azcl ^a	5	2
<u>Group AC</u>			
Jan/99	Azcl/Am ^a	7	2
Jan/00	Azcl/Am ^a	6	0
<u>Group N</u>			
Aug/99	unbanded ^a	6	2
Feb/00	Azcl/Na ^a	4	0

^a White fronted bird.

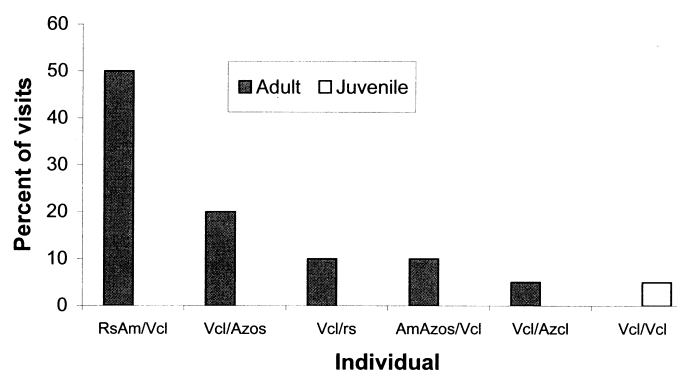


Figure 2. Percent of feeding visits by five individuals (four adults and one juvenile) of Sharpe's Wren at the group V nest in July 1997, in the Central Andes of Colombia. RsAm/Vcl was the breeding female (white-fronted) and Vcl/Azos was the presumed breeding male (20 hours of observation spread throughout 8 days during nestling stage).

Group structure and dynamics.- Group size varied between 4 and 7 individuals in the four focal groups, but their composition was fluid (Fig. 3).

Table 3. Numbers of individuals of different ages moving in and out of groups during three years of observation in four groups of Sharpe's Wren in the Colombian Andes.

Age ^a	Group			
	N	V	F	A
→ J →	2	2	1	1
→ J:SA →		2		
J:SA:A →			1	
J :SA :A	1			
→ SA	1			
SA →			1	
→ SA →		1		2
→ SA :A →			1	
SA :A →	2		1	3
A →	1	4	1	
→ A	1 ^b	1	1	1
→ A →		3		

^a J: juvenile; SA: subadult; A: adult. An arrow before the codes indicates birds joining the group, and after the codes indicates birds abandoning the group. A colon between letter codes indicates molting. Absence of an arrow before codes indicates birds were banded with the group at the beginning of the study, and absence of arrow after the codes indicates that birds were still with the group at end of study.

^b This bird was banded as a juvenile in group V in March 1995; it joined group N in adult plumage with a white frontal patch, in April 1997, and was the incubating female in the February 2000 nest.

Birds of all ages (juveniles, subadults and adults) joined or abandoned groups at different times (Table 3). Birds either joined and stayed in the group for some time and then abandoned the group while in the same age class, or entered, molted to the next age class and either stayed or left. Twenty-six of 50 birds with known histories joined or abandoned groups at some point during the study. The origin or destination of many birds was unknown, but we were able to track movements of some individuals. For example, a juvenile banded on 19 March 1995 in group V, moved as

an adult to group N (two territories away) in April 1997 and then remained with this group at least until August 1999. Another juvenile banded on 26 May 1996 at the periphery of the study area, joined group V as an adult on July 1997 and then remained with this group until September 1999. One bird banded as an adult with group V in July 1997, left this group in November; we lost track of it for some time, but it reappeared in March 1998 with group F. Following is a description of the composition of the four focal groups during the study.

Group V. This group had 20 members over four years, and produced six fledglings during the study (Fig. 3). This group initially had one breeding white-fronted female (Rs+Am/Vcl) which disappeared in mid 1998. This bird was replaced by another adult (Vcl/Rs, not white-fronted) that was with the group from the beginning of the study and became the breeder; this individual was the only permanent member of the group. All others were temporary members: four juveniles joined and abandoned the group (two exited as subadults), and one subadult and three adults joined and abandoned the group at different times (Table 3).

Group A. This group had 10 members over four years, and produced four fledglings during the study (Fig. 3). There was a core pair of breeders with large, yellowish frontal patches. This pair remained in the group throughout our study. Three subadults (banded as members of this group at the beginning of the study), became adults and left; these birds remained with the group for approximately 2 years. Two more subadults joined and left the group at different times (Table 3).

Group F. This group had 11 members, and produced four fledglings during the study (Fig. 3). Only one white-fronted breeding female (Fuc/BlA)

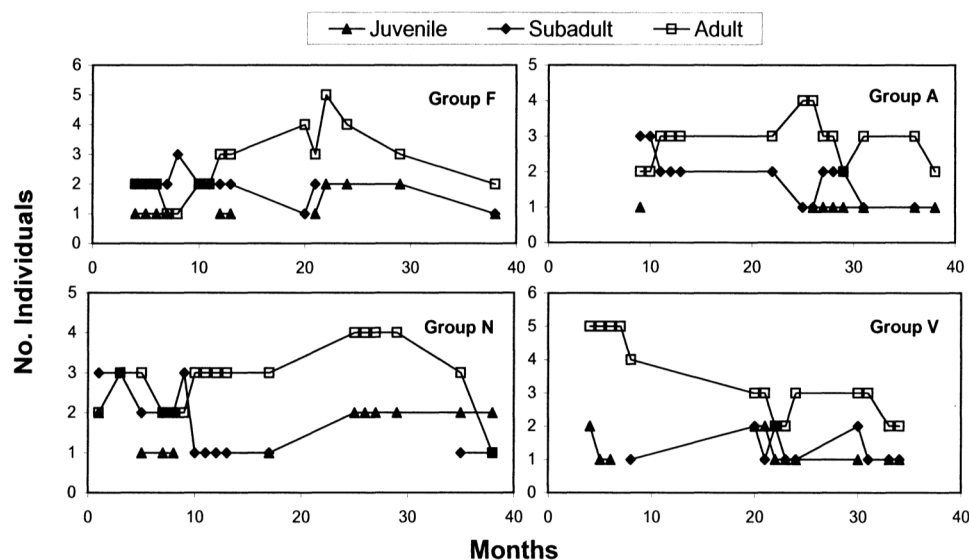


Figure 3. Composition (number of juveniles, subadults and adults) of four focal groups of Sharpe's wrens during three years of observation in the Central Andes of Colombia. Month 1 is April 1997.

was a permanent core member of the group. One juvenile joined and then left the group, and another juvenile (banded with the group at the beginning of the study) molted to subadult and then to adult and then left the group (after 32 months). One subadult that was a member of the group at the beginning of the study, became adult and then left. One adult joined the group and was still with the group at the end of the study (for a permanence of 26 months).

Group N. This group had 14 members over four years, and produced two fledglings during the study (Fig. 3). Only two individuals were permanent group members (throughout the duration of the study). The first one was banded (Azcl/Na) when in juvenile plumage with group V on 19 March 1995, and we found it in adult plumage with a white frontal patch in April 1997; this was the incubating female in the February 2000 nest (Table 2). The second permanent individual was a juvenile that molted into adult plumage. One adult joined the group in October 1997 and remained until the end. Two subadults banded with the group when the study began (April 1997), became

adults and then left; one of them molted into adult plumage in December 1997-January 1998, remained with the group until August 1999, and then moved (as adult) to group V and returned, then moved to group A. Two juveniles joined and abandoned the group at various times.

Discussion

We found that Sharpe's Wrens lived permanently in cooperatively breeding units that collectively defended an all-purpose, year-round territory. Based on the number of fledglings, clutch size was probably two or three eggs, so it is likely that only one female laid eggs and each group had only one breeding pair. All other members of the group were auxiliaries. Territory boundaries were stable throughout the five years of the study. Group membership, however, was fluid, and in some cases the breeding pair comprised the only stable members of the group.

In other cooperative species of wrens (Troglodytidae) such as Stripe-backed (*Campylorhynchus nuchalis*) and Bicolored Wrens

(*C. griseus*), there is one core breeding pair and a variable number of helpers (auxiliaries) (Rabenold 1990). Membership transfers usually occur when there are reproductive vacancies in a group. These vacancies are usually occupied by birds from neighboring groups (Rabenold 1990, Yáber & Rabenold 2002). Incest avoidance is a general phenomenon among cooperative breeders. Therefore, when a breeder dies, other group members of the opposite sex do not become breeders (Haydock *et al.* 1996, Koenig & Haydock 2004). Instead, an outsider fills the position. In the Stripe-backed Wren, dispersal is female-biased and usually results in a lasting change in group membership (Yáber & Rabenold 2002). In a study encompassing 222 social units and 1,599 birds over 21 years, 307 (19%) Stripe-backed Wrens changed group membership within populations (Yáber & Rabenold 2002). Fifty-nine percent of dispersal events were by auxiliaries leaving their natal group and becoming breeders in a neighboring group. Only 15% of dispersal events were of helpers that continued as auxiliaries in their new groups (Yáber & Rabenold 2002).

In Sharpe's Wren, in contrast, 52% of 50 birds with known histories switched groups during three years of observations, sometimes repeatedly moving among groups. For example, one juvenile was recaptured several times during 1997, alternating between groups V and N. Wrens sometimes joined groups for relatively short periods and usually became auxiliaries in the new group. Even adult birds changed groups and became auxiliaries that helped raise young. There may be a large floating population of birds that stay in the neighborhood, moving among groups and continually assessing their options ("stay and foray" strategy; Dickinson & Hatchwell 2004). Female Stripe-backed Wrens scouting for reproductive openings have the ability to discriminate the reproductive potential of groups and compete for reproductive positions in groups with the highest

potential (Zack & Rabenold 1989). Thus, Sharpe's Wrens temporarily joining groups may be assessing their options and the group's potential.

We documented three female reproductive openings during this study. In one case (group N), the female inheriting the reproductive position had immigrated from another group (V) at least three years earlier. In the two other cases (groups V and F), the females inheriting the reproductive vacancy were banded with the group and had been there for at least two and a half years in both cases. They may have immigrated to these groups prior to the beginning of our study.

Our observations indicate that white frontal patches in Sharpe's Wrens are related to breeding status, as predicted by Graves (1980). Seven of eight incubating females had frontal patches. In addition, at least one breeding male (group A) was white-fronted. The breeding pair of group A, which remained throughout the study, had large, yellowish patches. A white frontal patch, however, was not a necessary nor sufficient condition for attaining breeding status, because at least one bird without any white feathers became a breeder, and other non-breeding adults also had white patches. On the other hand, there was no strict relation between a white patch and age, because in at least one case, a subadult acquired a white patch when molting into adult plumage for the first time.

Although we can not rule out indirect fitness benefits, the group fluidity observed in Sharpe's Wrens suggests that kin selection is not a factor conferring an advantage for cooperative breeding, unless the entire population is closely related (Dickinson & Hatchwell 2004). Two alternative explanations (not mutually exclusive) for group-living in Sharpe's Wrens are that 1) there are external constraints such as habitat saturation, or 2) there are direct benefits to sociality. The 15 territories that we mapped were tightly packed, with no un-

used spaces between them, and were stable over 5 years, which could suggest habitat saturation. Our observations, however, indicate that Sharpe's Wrens show plasticity in habitat use. Therefore, habitat saturation does not seem likely, particularly in our study area where an extensive forested landscape mosaic with abundant second growth is available.

The presence of auxiliaries in the 12 nests that we monitored did not increase fledgling productivity in a single Sharpe's Wren nest. It may, however, help the breeders raise several broods, as occurs in Stripe-backed Wrens (Rabenold 1990). Undoubtedly we did not detect all nesting events of the four focal groups during the study, but groups nested throughout the year, including the relatively dry months of July and August, so the breeding season is not restricted. The presence of helpers may permit repeated nesting attempts, or increase the survival of fledglings. Whether auxiliaries help increase long-term productivity in the Sharpe's Wren is unknown.

Group augmentation through recruitment of unrelated individuals (Kokko et al. 2001) may explain group living and helping behavior in Sharpe's Wrens. Direct benefits of sociality may be related to the habit of repeatedly building multiple and massive roost nests, which probably requires cooperation of the entire group. Building multiple nests may be an antipredator strategy, but wrens may be forced to frequently abandon nests because of flea infestations (ironically, with the birds themselves acting as vectors for the fleas, on their own bodies and in recycled material). Because this is a short-term cooperative endeavour presumably with immediate survival benefits, long-term associations between individuals are probably not essential.

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