J. Field Ornithol. 74(2):166–171, 2003

Communication with shared call repertoires in the cooperatively breeding Stripe-backed Wren

J. Jordan Price[1]

Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599 USA

Received 10 October 2001; accepted 23 August 2002

ABSTRACT. Male and female Stripe-backed Wrens (*Campylorhynchus nuchalis*) have repertoires of learned, stereotyped calls that are specific to same-sex relatives in cooperatively breeding family groups. Consequently, they are potential cues for recognizing group membership and sex during social interactions. Here I describe the use of these calls for social communication in this species. Males call much more frequently than females within a group's territory, and dominant birds call more often than subordinates. In playback experiments, males responded to their own-group calls by producing matching call types, and called at relatively high rates following simulated territorial intrusions by neighboring birds. These vocalizations appear to function primarily in maintaining social bonds within a group and in recognizing group identity during interactions with other groups.

SINOPSIS. **Comunicación con repertorio de llamadas compartidas en *Campylorhynchus nuchalis***
La hembra y el macho de *Campylorhynchus nuchalis*, exhiben repertorios de llamadas estereotipadas, que son específicas a relativos del mismo sexo en grupos familiares que se reproducen cooperativamente. Como consecuencia, hay pistas potenciales para reconocer a individuos del grupo y de determinado sexo durante las interacciones sociales. En este trabajo se describe el uso de estas llamadas para la comunicación social en esta especie. Los machos llaman con mayor frecuencia que las hembras, dentro del grupo en el territorio y los individuos dominantes llaman más amenudo que los subordinados. En experimentos con grabaciones, los machos respondieron a las llamadas de individuos de su grupo, produciendo una serie de llamadas que pareaban con las grabadas. Además llamaron con una tasa de mayor frecuencia como respuesta a grabaciones simulando la intrusión al territorio de aves vecinas. Estas vocalizaciones parecen funcionar primordialmente en el mantenimiento del vínculo social dentro de un grupo y en el reconocer la identidad de un grupo durante interacciones con otros grupos.

Key words: *Campylorhynchus nuchalis*, group-specific calls, playback experiment, social communication, song type matching

Much research has focused on the use and functions of learned song in individually territorial songbirds (Catchpole and Slater 1995; Kroodsma and Miller 1982, 1996). Comparatively little is known, however, about vocal communication in birds with more complex social relationships, such as species that breed cooperatively. The Stripe-backed Wren (*Campylorhynchus nuchalis*) is a sexually monomorphic songbird that lives in cooperative family groups on permanent territories in Colombia and Venezuela (Rabenold 1990). Both male and female wrens have repertoires of stereotyped calls, referred to as WAY calls from a passing resemblance to a nasal human voice asking "where are you?," that are shared only among same-sex relatives (Price 1998). Young wrens appear to learn these call repertoires preferentially from older relatives of the same sex within groups. As a consequence, WAY calls provide potential cues for recognizing the sex and the family membership of other birds during interactions between group mates and during encounters between the members of neighboring territories.

Previous playback experiments have demonstrated that Stripe-backed Wrens can discriminate between the WAY calls of different families (Price 1999). These experiments simulated the appearance of callers from different groups and measured responses by subjects that were presumed to reflect aggression toward a potential territorial intruder, such as movement towards the speaker and the performance of territorial duets. The production of WAY calls in response to playback, however, has not been investigated previously. These vocalizations are most often produced outside of aggressive contexts (Price 1998), so calling in response to the calls of oth-

[1] Current address: Department of Biology, St. Mary's College of Maryland, 18952 East Fisher Road, St. Mary's City, Maryland 20686 USA. Email: jjprice@smcm.edu

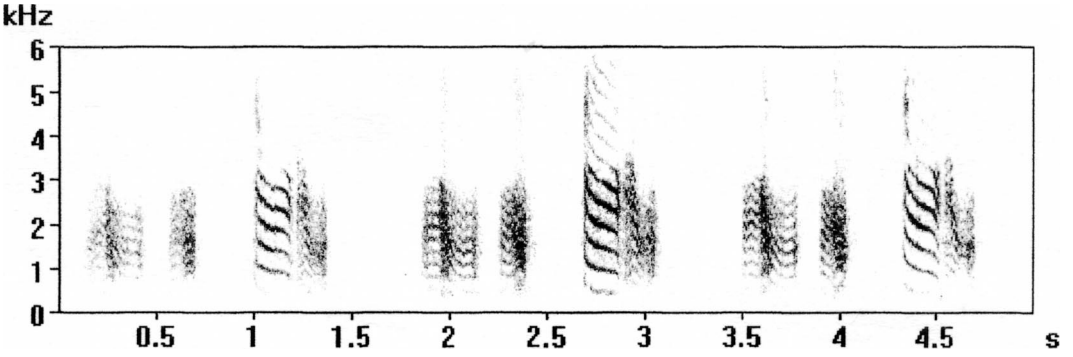

Fig. 1. Spectrogram of a typical WAY call produced by a male Stripe-backed Wren.

er birds is likely to have communicative functions other than territorial defense. In this study I used playback experiments and observations of naturally occurring calling behavior among group members to investigate how WAY calls are used in this species during social interactions.

METHODS

Study population. I studied the vocal behavior of Stripe-backed Wrens at Hato Masaguaral, a large cattle ranch and wildlife reserve located in the seasonally flooded lowlands (llanos) of central Venezuela. The population of wrens on the ranch had been individually marked with colored leg bands and censused annually since 1974. Observed genealogies, as well as DNA fingerprinting (Rabenold et al. 1990), provided data on the family histories and genealogical relationships of nearly all birds in the study area.

Stripe-backed Wrens live in stable social groups of 2 to 14 birds on year-round, communally defended territories with highly traditional boundaries (Rabenold 1990). Groups consist of a principal breeding pair and offspring of preceding years that cooperate in nest maintenance and care of the breeders' young (Rabenold 1985, 1990; Piper 1994). Nonbreeding helpers greatly increase the reproductive success of groups (Rabenold 1984), presumably by defending the nest against predators (Austad and Rabenold 1985). Dispersal from the natal area is highly female-biased (Rabenold 1990; Zack 1990). Nearly all females leave their natal groups as adults to compete for vacant breeding positions in nearby groups (Zack and Rabenold 1989), while males usually remain in their natal groups and form queues to inherit the breeding positions there (Wiley and Rabenold 1984). As a consequence, groups normally consist of patrilineal families that occupy the same territories for generations.

The territorial vocalizations of this species are loud, staccato duets which consist of harsh notes interposed by two or more birds. They are most often performed by the principal breeding pair but can be produced by any male-female combination in a group (Wiley and Wiley 1977). In contrast, WAY calls are of a lower intensity than duets (approximately 12 dB less intense), consist of frequency-modulated harmonics (Fig. 1), and are produced individually by both male and female wrens. Their relatively low sound intensities and complex acoustic structure suggest that WAY calls function primarily for close-range communication rather than long-range territorial advertisement.

Each adult male wren has a stable repertoire of 9 to 19 distinct WAY call types. Young males learn these stereotyped calls from older male relatives with high accuracy. Consequently, male group mates have call repertoires that are nearly identical in acoustic structure (Price 1998). Unrelated males, including members of neighboring groups, almost never share any call types. Adult females have smaller repertoires of three to five distinct WAY call types which are shared only among closely related females. Female calls do not differ in acoustic structure from male WAY calls in any consistent way; nevertheless, call types of females never match those of males in the same group or in any

nearby groups (Price 1998). Thus, WAY call repertoires are specific to same-sex relatives in family groups.

Observations of calling within groups. To compare the rates at which WAY calls are normally produced by different group members, I counted the numbers of these vocalizations heard from individuals within Stripe-backed Wren territories. I observed wren groups daily between 07:00 and 10:00 from 11–20 July 1996. This particular three-hour time window was chosen because (1) it avoided the high noise levels of the early morning, (2) it avoided the period of lower activity in the late morning, and (3) the level of activity in groups appeared to be relatively constant during these hours. For each of 10 groups, I conducted three 30-min observation periods at non-overlapping times on different days, so that I observed each group for a total of 90 min. For each WAY call heard, I recorded the identity, sex, and status (i.e., breeder or helper) of the vocalizing bird. Stripe-backed Wrens are often dispersed while foraging; however, by standing near the center of a group I was able to identify the originators of nearly all vocalizations heard. An entire 30-min observation period was discarded if the originator of any call was not identified.

Calling in response to playback. To investigate the calling behavior of birds in response to the vocalizations of different families, I performed playback experiments using WAY calls from male group mates, neighboring males, and unfamiliar males, presented at two locations in the territory. Female Stripe-backed Wrens are rarely observed producing WAY calls within a group's territory (see below), so only male WAY calls were used as stimuli in this study. Other responses to these playbacks, such as duetting and approaching the speaker by principal pairs, were also measured and have been reported previously (Price 1999).

These experiments were conducted in two parts. Playbacks at the edges of territories were performed 19 June to 22 July 1994 and playbacks near the centers of territories were performed 20 June to 22 July 1995. Environmental conditions did not differ appreciably between years. Eight groups served as subjects in 1994, and eight served as subjects in 1995. Five groups were used both years. All received three different treatments in random order: (1) the principal male's own call (O), (2) an unrelated neighboring principal male's call (N), and (3) an unrelated and unfamiliar, or strange, principal male's call (S) recorded approximately 1 km away. Each treatment consisted of broadcasting a single WAY call five times at 1-min intervals. The WAY calls of male group mates are virtually identical in acoustic structure (Price 1998), so playback of a principal male's own call was intended to simulate calling by any male member of that group. To avoid psuedoreplication, a different individual's call was used for each subject within treatments. Each call was also used in all three treatments each year to control for possible differences between call types. Methods used in constructing the playback tapes and details of the experimental protocol are described in Price (1999).

For each trial, I counted the number of WAY calls produced by group members for 5-min periods before, during, and after playback. For each of these calls I recorded the identity of the caller and whether or not this call type matched the playback call type. To compare responses to the different treatments, the number of calls produced during each 5-min period were compared between treatments with a two tailed Wilcoxon matched-pairs test.

RESULTS

Observations of calling within groups. Stripe-backed Wrens produce WAY calls relatively infrequently during normal activities within the territory (mean = 6.6 calls/h, SE = 1.76, $N = 10$). Territorial duets were heard more than six times more often during the observation periods. Of the WAY calls heard, most were produced by principal males (84.9%), some by male helpers (12.1%), and only a few by principal females (3.0%). No female helpers produced WAY calls during these observations, although calling by such females has been observed on other occasions (Price 1998). Altogether, 97% of the calls heard were produced by males. In groups with more than one male helper, the oldest helper called more than younger males. Group members spent much of their time during these observation periods dispersed throughout the territory. WAY calls by males were sometimes immediately followed by an identical call type produced by a male group mate.

Calling in response to playback. Nearly every WAY call given in response to the six ex-

perimental treatments was produced by a principal male. Only two calls were given by male helpers and no calls were heard from females during these experiments. Thus, only responses by the principal male of each subject group are analyzed here.

For playbacks performed at the edges of territories, comparisons of the three treatments show that principal males called relatively frequently during playback of their own calls (Fig. 2a; O versus N, $P = 0.026$; O versus S, $P = 0.114$; $N = 8$). There were no differences in calling rate among treatments before or after playback. Subjects nearly always responded to playback of their own-group call by immediately producing and repeating the same call type. They never matched the calls of neighbors or strangers.

For playbacks near the centers of territories, comparisons of calling rates before, during, and after the three playback treatments showed that subjects called more frequently during the 5 min following playback of neighbor calls than following playback of both own calls and stranger calls (Fig. 2b; O versus N, $P = 0.050$; N versus S, $P = 0.046$; $N = 8$), which did not differ significantly from each other (O versus S, $P = 0.933$). Again, males frequently responded with matching call types to playback of their own-group call.

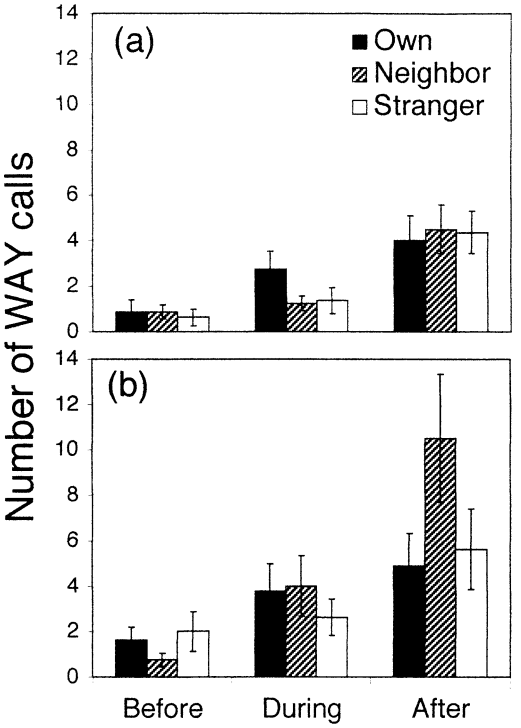

Fig. 2. Mean (±SE) number of WAY calls produced by principal males during 5-min periods before, during, and after playback of the three treatments at the edges of territories (a) and near the centers of territories (b). Males called relatively frequently during playback of their own-group calls near the edge of the territory and after playback of neighbors' calls near the territory center.

DISCUSSION

WAY calls appear to have diverse functions for social communication among Stripe-backed Wrens. For males, observations and playback experiments suggest that these calls are used primarily in communication among group members within the territory and during interactions with neighboring groups at territory boundaries. Wren groups are normally dispersed during much of the day, so WAY calls are probably useful for keeping in contact with one another in the dense foliage typically found in these territories. Contests between neighboring groups can involve many individuals, so these calls probably also provide useful cues for discriminating group mates from other birds. Males' calls appear to function as a form of "group membership badge" for maintaining group solidarity and recognizing group identity during social interactions.

In contrast to males, my results suggest that females rarely use WAY calls during interactions with neighboring birds. A potential explanation for this difference might be found in the pattern of dispersal in this species. Females nearly always disperse from their natal groups to breed in nearby groups when those positions become available (Zack and Rabenold 1989; Zack 1990), while males tend to remain in their natal groups, often for their entire lives (Wiley and Rabenold 1984; Rabenold 1990). Since call repertoires are learned strictly from older relatives of the same sex (Price 1998), females of neighboring groups are more likely to share call types than are males. Thus, males' WAY calls probably provide more reliable cues for recognizing group membership than do females' calls.

Although females occasionally call within their group's territory, long-term observations

indicate that females call most frequently when exploring outside their natal territories and during contests over vacant breeding positions in other groups (Price 1998). These contests can include many dispersing females and usually involve frequent calling by both the female competitors and the resident males. Female relatives sometimes compete in these contests as teams (Zack and Rabenold 1989), and frequent calling could allow them to discriminate relatives from female rivals. WAY calls might also allow wrens to recognize their relatedness to potential mates, and thus avoid close inbreeding, by comparing the call repertoires of these individuals to those of opposite-sex relatives.

Principal males call more frequently than male helpers and dominant helpers call more often than subordinates, which suggests that an individual's calling rate differs according to his social rank in the group. Observations over five years indicate that a male's calling rate typically increases soon after he advances in rank within a group's dominance hierarchy. Calling by females appears to vary with social status in a similar way. Dominant birds of both sexes have been observed interrupting nearby subordinates when they attempt to call, often by vocalizing themselves and sometimes by physically attacking them. WAY calls thus appear to play an important role in maintaining dominance relationships among group members.

In playback experiments performed within Stripe-backed Wren territories, principal males and occasionally male helpers called much more frequently following playback of neighboring males' calls than following the other two treatments. Wrens respond with equal levels of aggression to territorial intrusions by neighbors and strangers (Price 1999); however, the difference in calling behavior to these treatments reported here suggests that familiar intruders are treated differently than unfamiliar ones. Subjects might have called frequently after an intrusion by a neighbor in order to advertise their group membership and thus communicate to a wandering neighbor that he is associating with the wrong group and is in the wrong territory. Naturally occurring boundary incursions among neighboring groups normally involve similarly high rates of WAY calling by males.

Principal males often responded to playback of one of their own calls by immediately producing and then repeating the same call type, especially in response to calls played at the edges of their territories. Male wrens are apparently unable to discriminate their own WAY calls from those of male relatives (Price 1999), so subjects probably perceived these vocalizations as originating from male group mates. Matched counter-calling by principal males in response to the vocalizations of other group members might help to maintain group cohesiveness by signaling to wandering helpers that they are separated from the group or are too close to the boundary of a rival group. Males often call back and forth with matching call types while dispersed within their territory, and such exchanges frequently result in distant birds approaching one another.

Matched counter-calling among male group mates in Stripe-backed Wrens is analogous to the way many songbirds with vocal repertoires often respond to the territorial vocalizations of neighbors by producing a matching song type (Wiley and Wiley 1977; Schroeder and Wiley 1983; Stoddard et al. 1992). Such behavior presumably enables birds to direct these otherwise omnidirectional signals towards specific receivers, rather than indiscriminately to any listeners in the area (Armstrong 1973). Thus, having a repertoire of WAY calls rather than a single group-specific call might enable wrens to interact with specific group mates.

Several other birds that live in groups for at least part of the year are known to develop group-specific vocalizations that are used in maintaining social bonds within flocks and in recognizing social identity during interactions with other flocks (Brown and Farabaugh 1997). Examples include chickadees (*Poecile atricapillus*; Mammen and Nowicki 1981; Nowicki 1989), finches of the subfamily Carduelinae (Mundinger 1970, 1979) and Budgerigars (*Melopsittacus undulatus*; Farabaugh and Dooling 1996; Bartlett and Slater 1999). Group members in these species normally share only one to a few distinctive calls, referred to variously as contact, distance, or flight calls. Stripe-backed Wrens, in contrast, share large repertoires of stereotyped call types which are specific to same-sex relatives in groups. Beyond simply indicating group membership, WAY calls have the potential for communication on more complex levels than possible in the group-specific calls of other species.

ACKNOWLEDGMENTS

I thank R. H. Wiley for encouragement and advice during this work. I also thank D. Kroodsma and several anonymous reviewers for helpful comments on earlier versions of the manuscript. Financial support was provided by Sigma Xi, the Chapman Fund of the American Museum of Natural History, and awards from the University of North Carolina at Chapel Hill. This research would not have been possible without the generosity of Tomás Blohm, owner of Hato Masaguaral.

LITERATURE CITED

ARMSTRONG, E. A. 1973. A study of bird song. Dover, New York.

AUSTAD, S. N., AND K. N. RABENOLD. 1985. Reproductive enhancement by helpers and an experimental inquiry into its mechanism in the Bicolored Wren. Behavioral Ecology and Sociobiology 17: 19–27.

BARTLETT, P., AND P. J. B. SLATER. 1999. The effect of new recruits on the flock-specific call of Budgerigars (*Melopsittacus undulatus*). Ethology, Ecology and Evolution 11: 139–147.

BROWN, E. D., AND S. M. FARABAUGH. 1997. What birds with complex social relationships can tell us about vocal learning: vocal sharing in avian groups. In: Social influences on vocal development (C. T. Snowdon, and M. Hausberger, eds.), pp. 98–127. Cambridge University Press, New York.

CATCHPOLE, C. K., AND P. J. B. SLATER. 1995. Bird song: biological themes and variations. Cambridge University Press, New York.

FARABAUGH, S. M., AND R. J. DOOLING. 1996. Acoustic communication in parrots: laboratory and field studies of Budgerigars, *Melopsittacus undulatus*. In: Ecology and evolution of acoustic communication in birds (D. E. Kroodsma, and E. H. Miller, eds.), pp. 97–117. Cornell University Press, Ithaca, NY.

KROODSMA, D. E., AND E. H. MILLER. 1982. Acoustic communication in birds, vols. 1 and 2. Academic Press, New York.

———, AND ———. 1996. Ecology and evolution of acoustic communication in birds. Cornell University Press, Ithaca, NY.

MAMMEN, D. L., AND S. NOWICKI. 1981. Individual differences and within-flock convergence in chickadee calls. Behavioral Ecology and Sociobiology 9: 179–186.

MUNDINGER, P. C. 1970. Vocal imitation and individual recognition of finch calls. Science 168: 480–482.

———. 1979. Call learning in the Carduelinae: ethological and systematic considerations. Systematic Zoology 28: 270–283.

NOWICKI, S. 1989. Vocal plasticity in captive Black-capped Chickadees: the acoustic basis and rate of call convergence. Animal Behaviour 37: 64–73.

PIPER, W. H. 1994. Courtship, copulation, nesting behavior and brood parasitism in the Venezuelan Stripe-backed Wren. Condor 96: 654–671.

PRICE, J. J. 1998. Family- and sex-specific vocal traditions in a cooperatively breeding songbird. Proceedings of the Royal Society of London B 265: 497–502.

———. 1999. Recognition of family-specific calls in Stripe-backed Wrens. Animal Behaviour 57: 483–492.

RABENOLD, K. N. 1984. Cooperative enhancement of reproductive success in tropical wren societies. Ecology 65: 871–885.

———. 1985. Cooperation in breeding by nonreproductive wrens: kinship, reciprocity, and demography. Behavioral Ecology and Sociobiology 17: 1–17.

———. 1990. *Campylorhynchus* wrens: the ecology of delayed dispersal and cooperation in the Venezuelan savanna. In: Cooperative breeding in birds: long-term studies of ecology and behavior (P. B. Stacey, and W. D. Koenig, eds.), pp. 159–196. Cambridge University Press, New York.

RABENOLD, P. P., K. N. RABENOLD, W. H. PIPER, J. HAYDOCK, AND S. ZACK. 1990. Shared paternity revealed by genetic analysis in cooperatively breeding tropical wrens. Nature 348: 538–540.

SCHROEDER, D. J., AND R. H. WILEY. 1983. Communication with shared song themes in Tufted Titmice. Auk 100: 414–424.

STODDARD, P. K., M. D. BEECHER, S. E. CAMPBELL, AND C. L. HORNING. 1992. Song type matching in the Song Sparrow. Canadian Journal of Zoology 70: 1440–1444.

WILEY, R. H., AND K. N. RABENOLD. 1984. The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. Evolution 38: 609–621.

———, AND M. S. WILEY. 1977. Recognition of neighbors' duets by Stripe-backed Wrens *Campylorhynchus nuchalis*. Behaviour 62: 10–34.

ZACK, S. 1990. Coupling delayed breeding with short distance dispersal in cooperatively breeding birds. Ethology 86: 265–286.

———, AND K. N. RABENOLD. 1989. Assessment, age and proximity in dispersal contests among cooperative wrens: field experiments. Animal Behaviour 38: 235–247.