Recognition of family-specific calls in stripe-backed wrens

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Males of the cooperatively breeding stripe-backed wren, *Campylorhynchus nuchalis*, learn repertoires of stereotyped calls (termed WAY calls) from older male relatives. As a result, these vocalizations are normally specific to patrilineal family groups but are sometimes shared by male relatives in different groups. To determine whether or not this species can recognize the calls of different family groups, I performed playback experiments with individual call types recorded from males of known social and genealogical relationships. Subjects discriminated between the calls of unrelated neighbouring groups and unfamiliar groups, and they discriminated both of these from calls of their own groups. However, subjects failed to distinguish calls of males in other groups from calls of their own groups when these males were members of the same patriline. These results indicate that stripe-backed wrens can discriminate between repertoires of these calls that match or differ from their own. Consequently, they can recognize members of their patriline, not just members of their immediate group. These vocalizations probably provide a useful mechanism for recognizing group membership in this species and might also provide a mechanism for recognizing unfamiliar relatives in other groups.

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Many studies have documented the abilities of songbirds to recognize the territorial songs of male neighbours (Falls 1982; Stoddard 1996) or the calls of parents and offspring within dense colonies (Beecher 1981, 1990; McArthur 1982). Fewer studies have investigated recognition of vocalizations used in other contexts, such as within stable avian social groups. Vocal recognition might be particularly important in group-living species, especially when individuals must coordinate activities with long-term associates in cooperative groups.

Cooperatively breeding birds typically live in stable social groups, in which a breeding pair and one or more nonbreeding helpers cooperate in nest construction, defence of a group territory, and raising the breeders' offspring (Brown 1987; Stacey & Koenig 1990). Groups are normally extended families but can include nonrelatives following replacement of one of the breeders by an unrelated individual (Emlen 1995, 1997). Also, close kin sometimes live in neighbouring groups as a result of short-range natal dispersal (Zack 1990; Stevens & Wiley 1995). Individuals in such social organizations might benefit from an ability to identify relatives, as they could then direct aid preferentially towards close kin and avoid close inbreeding (Hamilton 1964; Holmes & Sherman 1983).

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Most songbirds learn their songs from unrelated territorial neighbours after natal dispersal (Catchpole & Slater 1995; Baptista & Gaunt 1997), so these vocalizations typically provide no information about kin relationships (McGregor 1989). In contrast, cooperative breeders often have delayed natal dispersal and long-term associations between close kin, so young birds have ample opportunity to learn the vocalizations of relatives. I have previously shown that cooperatively breeding stripe-backed wrens, *Campylorhynchus nuchalis*, acquire repertoires of calls from older relatives, apparently through sex-specific learning (Price 1998).

Stripe-backed wrens live in stable patrilineal family groups on permanent territories in Colombia and Venezuela. Males have repertoires of stereotyped calls (known as WAY calls) that are always shared within, but rarely between, patrilines. Call repertoires, therefore, are usually specific to family groups, but in some cases are shared by male relatives in different groups (Price 1998). These calls thus provide potential cues for recognizing close relatives within groups and even distant relatives in other groups.

In this paper, I present an experimental analysis of vocal recognition in this species. I examined whether or not wrens can discriminate between the calls of different families by presenting subjects with single calls recorded from related males in the same group, and from unrelated males living in neighbouring groups and unfamiliar

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groups. I also examined vocal discrimination of individuals within families by presenting subjects with calls recorded from males in the same group and from male relatives living in different groups. Measuring responses to calls recorded from individuals of known genealogy allowed me to test whether or not this species can recognize group members and other kin by their vocalizations.

METHODS

The Study Population

Stripe-backed wrens were studied at Hato Masaguaral, a cattle ranch situated in the seasonally flooded savanna (llanos) of Venezuela about 300 km south of Caracas. This population has been the focus of a long-term study of breeding behaviour (Rabenold 1990) and has been individually marked with coloured leg bands since 1974. Annual censuses, banding of unmarked birds and recent DNA fingerprinting (Rabenold et al. 1990) have provided data on the family histories and genealogical relationships of nearly all birds in this population.

The climate of the llanos is strongly seasonal, with nearly all yearly rainfall occurring during the wet season from May to November. Stripe-backed wrens, like most other birds in the area, breed during the wet season when insects are abundant (Thomas 1979). To take advantage of the increased level of activity during breeding, my study was conducted during the wet seasons (May–August) of 1993–1995.

Groups of stripe-backed wrens consist of a principal male and female, which are generally the sole breeding pair (Rabenold et al. 1990; Piper & Slater 1993), and up to 12 nonbreeding helpers, which aid in nest construction, care of young and defending the year-round, communal territory (Rabenold 1985, 1990; Piper 1994). Helpers are almost always nondispersing offspring from preceding years (for exceptions see Piper et al. 1995) and greatly increase the reproductive success of groups (Rabenold 1984). Nearly all female helpers leave the natal group as adults to compete for breeding vacancies in nearby territories (Zack & Rabenold 1989). Males either remain as helpers to inherit the breeding position in their natal group or, less often, disperse to breed outside the natal territory (Wiley & Rabenold 1984; Zack 1990). The males of a particular group, therefore, are normally members of a single paternal line that occupies the same location for generations.

Vocalizations

Groups of two or more wrens perform loud, staccato duets which appear to serve for territorial advertisement much like the songs of individually territorial songbirds. These vocalizations are performed mostly by the principal pair, but any male–female combination in a group can produce them. Wiley & Wiley (1977) showed that stripe-backed wrens recognize the duets of each of their neighbours; however, discrimination of other types of vocalizations has not been previously tested in this species.

Individual wrens produce repertoires of stereotyped calls, termed WAY calls from an occasional resemblance to the English words 'where are you?', which are of lower intensity than duets and appear to function mostly in close-range communication. Both sexes produce WAY calls; however, males call much more often than females (98.7% of identified calls were recorded from males), and principal breeding males usually call more often than helper males. Therefore, all of the WAY calls used in this study were recorded from principal males.

Each adult male wren has a repertoire of 9–19 distinct types of WAY calls that apparently remain unchanged over an individual's lifetime. These calls are transmitted from older to younger males with high accuracy, so call repertoires are specific to patrilines (Price 1998). Males within family groups have call repertoires that are nearly identical in acoustic structure, while unrelated neighbouring males rarely share any call types. Because males sometimes disperse to attain principal status outside their natal groups (Wiley & Rabenold 1984; Rabenold 1990), different groups sometimes include male relatives that have nearly identical call repertoires. These patrilineally related groups are often neighbours but can be more than a kilometre apart.

Playback Tapes

I tape-recorded the repertoires of WAY calls produced by 15 principal males in 1993 and 19 principal males in 1994 with a Marantz PMD 221 cassette recorder and an Audio-technica AT815a microphone. Examples of calls were randomly selected after checking them for clarity with a Uniscan II real-time spectrum analyser. I then digitized the calls at 16 kHz and 16-bit accuracy on a 68030 Macintosh computer with Audiomedia hardware and software (Digidesign, Palo Alto, California). All calls were adjusted to the same maximal amplitude, then rerecorded on a Marantz PMD 221 cassette recorder to produce the playback tapes. Each tape consisted of 1 min of silence followed by a single WAY call repeated five times at 1-min intervals.

Playback 1: Discrimination Between Family Groups

To test whether stripe-backed wrens discriminate between the WAY calls of different family groups, I compared responses to calls recorded in the subjects' own groups, neighbouring groups and unfamiliar groups. Playback experiments were conducted in two parts: playbacks at the boundaries of territories were performed 19 June–22 July 1994, and playbacks near the centres of territories were performed 20 June–22 July 1995. Environmental and social conditions did not differ appreciably between years. The principal pairs of eight groups served as subjects in 1994, and eight principal pairs served as subjects in 1995. Five pairs were used both years. All subjects received three different treatments in random order: (1) the principal male's own call (O), (2) an unrelated neighbouring principal male's call (N), and (3) an

unfamiliar, or stranger, principal male's call (S) recorded in a group approximately 1 km away. Within each treatment, a different call was used for each subject; however, an attempt was made to use each call in all three treatments, as appropriate, each year to control for differences between call types.

Playback 2: Discrimination Within Patrilines

To test whether stripe-backed wrens discriminate between the WAY calls of individuals within a patriline, I compared responses to the principal male's own call and the same call type by a related principal male in another group. I used calls from principal males that were patrilineal relatives and therefore had similar call repertoires. Most of these related principal males lived in groups within one or two territory diameters of each other, but some were as much as 1 km apart. Preliminary observations of naturally occurring boundary disputes showed that group members normally acted aggressively towards any potential intruders, regardless of whether they were relatives or not. Therefore, if subjects discriminated between individual relatives by their WAY calls, I expected that calls recorded from relatives in other groups would be treated aggressively, while calls recorded in subjects' own groups would elicit little aggression.

These playback experiments were conducted in two parts, concurrently with playback 1. Playbacks at territory boundaries were performed 19 June–22 July 1994, and playbacks at territory centres were performed 20 June–22 July 1995. The principal pairs of six groups served as subjects in 1994, and the principal pairs of seven groups were subjects in 1995. All except one principal pair also served as subjects for playback 1. Subjects received two treatments in random order: (1) the principal male's own call (O) and (2) the same call type by a related principal male (R). A different call was presented to each subject for each treatment; however, each call was used in both treatments during the experiment to control for differences between call types.

Responses of Subjects With and Without Male Helpers

Playback of a principal male's own WAY call, as determined from preliminary experiments, generally elicited little aggression by principal pairs. Males within groups have nearly identical call repertoires; consequently, subjects might have perceived these calls as originating from other male group members. To investigate this possibility, I compared the responses of principal pairs with male helpers to the responses of principal pairs without male helpers to playback of the principal male's own call.

The responses used in this analysis were taken from playback experiments 1 and 2 conducted in 1994 and 1995, and two additional playbacks performed in 1995 on subjects without male helpers. Altogether, nine principal pairs with one or more male helpers and nine principal pairs with no male helpers served as subjects in this comparison. Responses to playbacks at territory bound-

aries and within territories were similar, so they were combined in this analysis.

General Experimental Protocol

All playback trials consisted of broadcasting a single WAY call five times at 1-min intervals, which approximates a high, but realistic, calling rate for a male stripe-backed wren. I broadcast calls on a Marantz PMD cassette recorder connected to a Perma Power S-705 amplifier and a Realistic 5-W speaker (model 40-1244A) on a 5-m lead. To control playback intensity, I matched speaker output to that of naturally calling birds using a Realistic sound-level meter (fast response, C weighting). Calls had a peak intensity of approximately 63.7 dB (SE=0.3 dB) when measured 4 m in front of the speaker or a calling bird.

For the 1994 experiments, the speaker was placed approximately 5 m within the boundary closest to the subjects' neighbour. For the 1995 experiments, the speaker was placed within 10 m of the subject group's nest, usually near the centre of the territory. For all trials, I concealed the speaker in the lower branches of a tree at a height of 1.5–2 m. The same location was used for all treatments to that subject that year. Whenever possible, the speaker was positioned to face the location of the principal pair in the territory.

In each trial, I observed the behaviour of the principal pair during and 10 min after playback. All trials were performed in fair weather between 0700 and 1000 hours to avoid the higher noise levels in the early morning and the period of lower activity in the late morning. I waited until a duet was heard from the principal pair before beginning each trial, which allowed me to determine the initial location of the subjects in the territory and ensured that both members of the principal pair were close to each other. Trials with the same subjects or with immediate neighbours were always conducted at least 3 days apart to avoid any effects of habituation. A trial was aborted if a bird from a neighbouring group came within 10 m of the speaker at any time during the experiment. These manipulations appeared to have no lasting negative influences on the reproductive success of breeding pairs used as subjects.

Response Measures

Playbacks were designed to simulate the appearance of possibly threatening birds at different locations in the territory. I therefore measured several responses assumed to reflect aggression by the subjects: (1) number of duets produced by the principal pair; (2) latency to duet following playback of the first call; (3) total distance flown by the subjects towards the speaker; and (4) total time spent within 10 m of the speaker. For measures 1, 3 and 4, responses both during and 10 min after playback were summed. Preliminary observations of both natural and simulated intrusions showed that a strong response often included the initiation of frequent duets by the principal pair and an immediate approach towards the intruder. The principal male and female were rarely separated by

more than 5 m during these intrusions, so I measured the responses of the pair together.

Statistical Analysis

Because the four response measures were correlated, I used a principal components analysis to extract a single composite measure of response for each treatment (McGregor 1992). To test for differences between treatments, I used the first principal component scores in a Wilcoxon signed-ranks test, two-tailed.

I compared responses of subjects with male helpers to responses of subjects without male helpers by comparing the first principal component scores in a Mann–Whitney U test. I then compared the number of duets produced by the two groups of subjects in a Mann–Whitney U test to determine which subjects responded more strongly.

RESULTS

Playback 1: Discrimination Between Family Groups

Playback at the territory boundary

The subjects consistently showed stronger responses to playback of stranger calls than to either neighbour calls or own calls at territory boundaries (Fig. 1a). The subjects duetted more frequently to stranger calls than to both neighbour calls and the principal males' own calls (Wilcoxon two-tailed signed-ranks test: O versus S, $P<0.05$; N versus S, $P<0.05$). However, the number of duets in response to neighbour calls and own calls did not differ significantly (O versus N, NS). Duetting occurred within 1 min of the start of playback in 20 of the 24 trials. The latency to duet was significantly shorter in response to stranger calls than to own calls (O versus S, $P<0.05$). Neighbour calls elicited an intermediate latency. Differences in the distance flown towards the speaker and the time spent within 10 m of the speaker in response to the three treatments were not significant.

The four responses contributed to the first principal component to different degrees (Table 1). Overall, this principal component explained 51.4% of the total variance in the response measures. The second and third components explained a further 23.7 and 16.0% of the variance, respectively. Only scores on the first component were used for this analysis. Comparisons of these response scores showed that responses to stranger calls differed significantly from responses to own calls and neighbour calls (Wilcoxon two-tailed signed-ranks test: O versus S, $P<0.05$; N versus S, $P<0.05$; Fig. 2a). Responses to own and neighbour calls, however, did not differ significantly (O versus N, NS).

Playback at the territory centre

The subjects showed consistently weaker responses to playback of own calls than to either neighbour calls or stranger calls (Fig. 1b). Unlike their response to playback at the boundary, the subjects responded as strongly to neighbour calls played near the centre of the territory as they did to stranger calls. Principal pairs duetted less
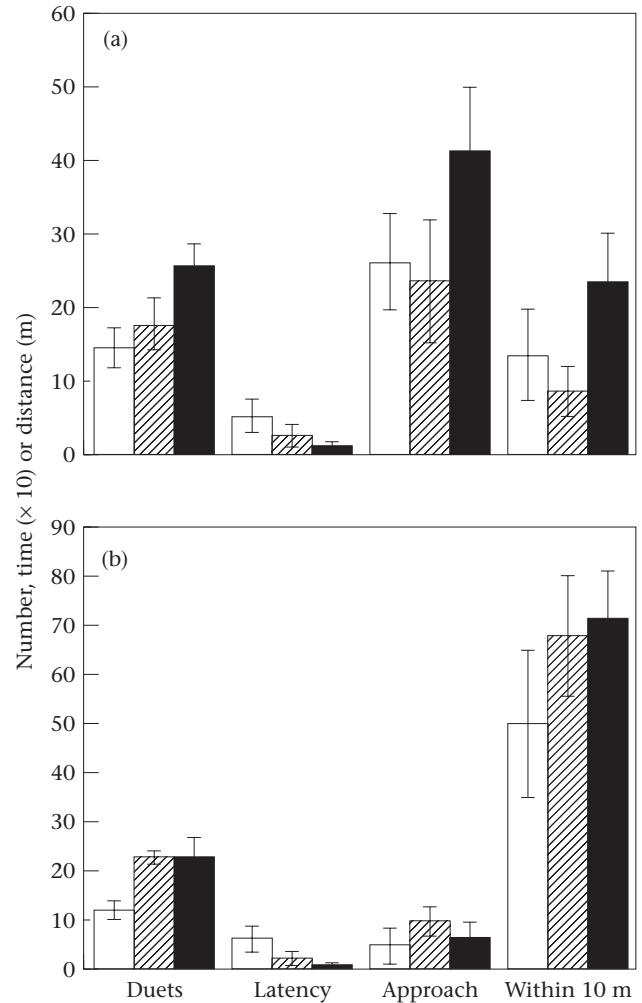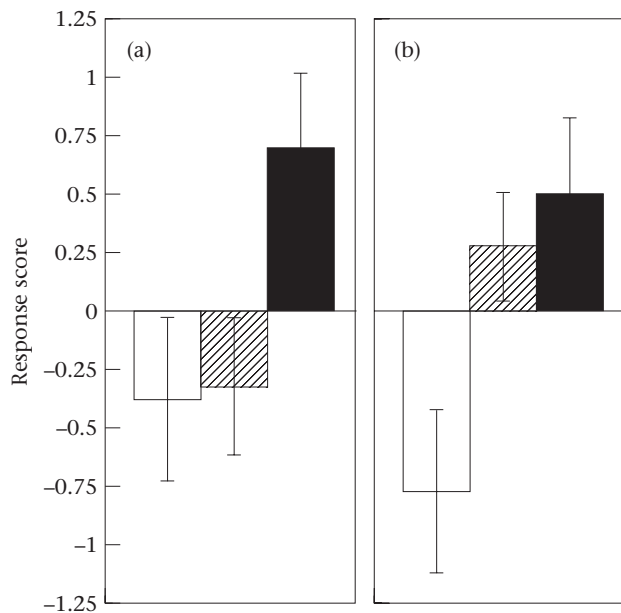

Figure 1. Means (±SE) of responses by principal pairs to own calls (□), neighbour calls (▨) and stranger calls (■) played (a) at territory boundaries and (b) near the centres of territories. Responses are the number of duets (Duets), latency to duet (Latency), distance flown by subjects approaching the speaker (Approach), and time spent within 10 m of the speaker (Within 10 m). A strong response is indicated by a small value for latency to duet and a large value for the other three responses.

frequently to the principal males' own calls than to either neighbour calls or stranger calls (Wilcoxon two-tailed signed-ranks test: O versus N, $P<0.05$; O versus S, $P<0.05$). However, the number of duets in response to neighbour calls and stranger calls did not differ significantly (N versus S, NS). Duetting occurred within 1 min of the start of playback in 19 of the 24 trials. Differences in the latency to duet, distance flown towards the speaker, and time spent within 10 m of the speaker were not significant.

The first principal component explained 39.6% of the total variance in the response measures (Table 1). The second and third components explained a further 28.7 and 18.5% of the variance, respectively. Only scores on the first principal component were compared between treatments. Comparing these scores revealed that both neighbour calls and stranger calls elicited a significantly

Table 1. Loadings of the different response measures on the first (PC1), second (PC2) and third (PC3) principal components for playback of own, neighbour and stranger calls at the boundaries and centres of territories

Location	Response measure	Component loadings		
		PC1	PC2	PC3
Boundary	Number of duets	0.722	0.300	−0.594
	Latency to duet	−0.375	0.904	0.198
	Approach distance	0.861	0.195	0.133
	Time within 10 m	0.808	−0.055	0.481
Centre	Number of duets	0.764	−0.378	0.149
	Latency to duet	−0.725	0.340	0.457
	Approach distance	−0.292	−0.814	0.448
	Time within 10 m	0.624	0.477	0.557

Figure 2. Means (±SE) of the scores on the first principal component of responses to own calls (□), neighbour calls (▨) and stranger calls (■) played (a) at territory boundaries and (b) near the centres of territories.
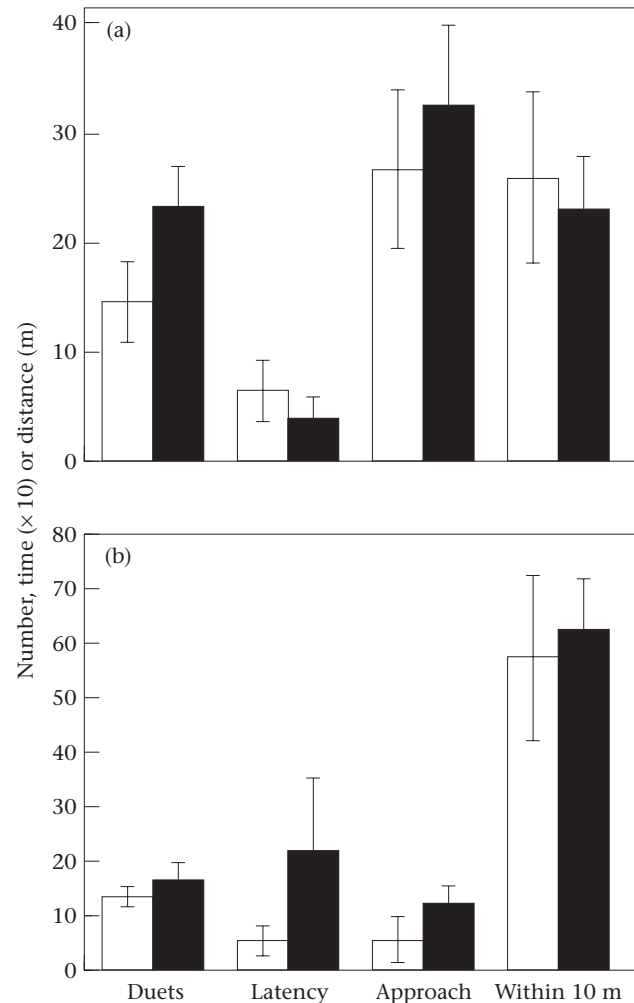

Figure 3. Means (±SE) of responses by principal pairs to principal males' own calls (□) and calls of male relatives in other groups (■) played (a) at territory boundaries and (b) near the centres of territories. Response variables are described in Fig. 1.

greater response than did playback of the principal males' own calls (Wilcoxon two-tailed signed-ranks test: O versus N, $P<0.05$; O versus S, $P<0.05$; Fig. 2b). Responses to neighbour calls and stranger calls, however, did not differ significantly (N versus S, NS).

Playback 2: Discrimination Within Patrilines

Playback at the territory boundary

The subjects responded similarly to playback of the principal male's own call and playback of a patrilineally related principal male's call (Fig. 3a). None of the response measures differed significantly between the two treatments.

The four response variables contributed about equally to the first principal component (Table 2), which explained 52.8% of the total variance in the responses.

The second and third components explained an additional 26.0 and 19.2% of the variance, respectively. A comparison of the scores on the first principal component showed that the subjects' responses did not differ

Table 2. Loadings of the different response measures on the first (PC1), second (PC2) and third (PC3) principal components for playback of the principal male's own call and a related principal male's call at the boundaries and centres of territories

Location	Response measure	Component loadings		
		PC1	PC2	PC3
Boundary	Number of duets	0.512	−0.503	0.696
	Latency to duet	0.658	0.704	0.225
	Approach distance	0.724	−0.512	−0.442
	Time within 10 m	0.944	0.174	−0.196
Centre	Number of duets	−0.875	0.044	0.209
	Latency to duet	0.827	0.223	−0.346
	Approach distance	0.055	0.959	0.265
	Time within 10 m	0.694	−0.285	0.654
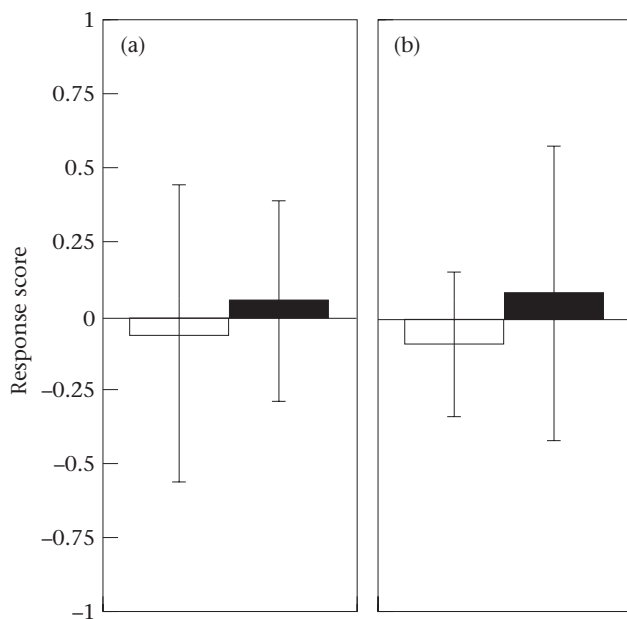
Figure 4. Means (±SE) of the scores on the first principal component of responses to principal males' own calls (□) and calls of male relatives in other groups (■) played (a) at territory boundaries and (b) near the centres of territories.

between the two treatments (Wilcoxon two-tailed signed-ranks test: NS; Fig. 4a).

Playback at the territory centre

Similar to playback at the boundary, playback of both the principal male's own call and a patrilineally related male's call near the centres of territories elicited similar responses (Fig. 3b).

The first principal component explained 48.3% of the variance in the responses (Table 2). The second and third components explained 26.3 and 16.5% of the variance, respectively. A comparison of the first component scores showed that the subjects responded about equally to the two treatments (Wilcoxon two-tailed signed-ranks test: NS; Fig. 4b).

Table 3. Loadings of the different response measures on the first (PC1), second (PC2) and third (PC3) principal components for playback of the principal male's own call to principal pairs with and without male helpers

Response measure	Component loadings		
	PC1	PC2	PC3
Number of duets	−0.858	0.296	0.177
Latency to duet	0.720	−0.287	0.579
Approach distance	−0.654	−0.501	0.501
Time within 10 m	0.152	0.874	0.418

Responses of Subjects With and Without Male Helpers

The response measures contributed to the first principal component to different degrees (Table 3). The first component explained 42.6% of the variance in the responses, while the second and third components explained 29.6 and 19.8% of the variance, respectively. Comparison of the scores on the first principal component showed that the responses of subjects with and without male helpers differed significantly (Mann–Whitney U test: $U=17$, $N_1=N_2=9$, $P<0.05$; Fig. 5). Principal pairs with no male helpers produced significantly more duets than principal pairs with male helpers (Mann–Whitney U test: $U=69$, $N_1=N_2=9$, $P<0.05$; Fig. 6).

DISCUSSION

Recognition of Group Membership

The results indicate that stripe-backed wrens recognize and respond appropriately to the males of different family groups based solely on hearing their WAY calls. Principal pairs responded strongly to calls of unrelated, unfamiliar groups and weakly to calls of their own groups, regardless of speaker location. Calls of unrelated neighbouring groups elicited a weak response when played from the appropriate territorial boundary, but a strong response near the centre of the territory. Thus, subjects showed neighbour–stranger discrimination at
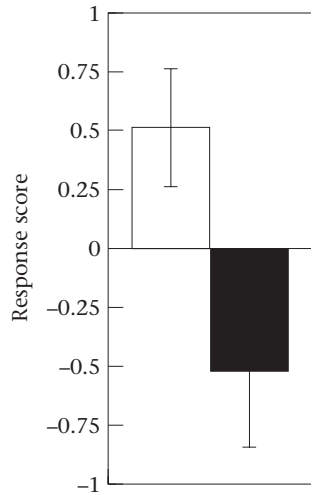
Figure 5. Means (±SE) of the scores on the first principal component of responses by principal pairs with male helpers (□) and without male helpers (■) to playback of the principal male's own call.
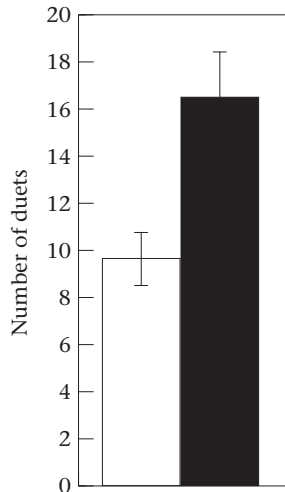

Figure 6. Mean (±SE) number of duets by principal pairs with male helpers (□) and without male helpers (■) in response to playback of the principal male's own call.

territory boundaries, own–neighbour discrimination at territory centres, and own–stranger discrimination at both locations.

Discrimination of neighbours' and strangers' calls is particularly interesting because responses were based on hearing only a single call type from each male's repertoire. Several authors have suggested that the size of a songbird's repertoire might limit the ability of individuals to recognize neighbours, partly because listeners have less exposure to each song type (Kroodsma 1976; Krebs & Kroodsma 1980; Falls 1982). Several other songbirds with moderate to large repertoires are known to recognize neighbours' songs (Brindley 1991; Stoddard et al. 1991; Weary et al. 1992; Godard & Wiley 1995), and stripe-backed wrens, which have repertoires of five or more duet patterns per pair, recognize neighbours' duets (Wiley & Wiley 1977). However, these previous studies measured

responses to territorial vocalizations, which are usually produced more frequently and at higher intensities than are WAY calls. In comparison to territorial duets, WAY calls are produced relatively infrequently (duets are heard more than six times more often within groups) and at relatively low intensities (about 12 dB less intense than duets). Therefore, individual WAY call types are presumably rarely heard outside of a group's territory.

Although stripe-backed wrens hear and remember the WAY calls of neighbours, young males apparently copy the call repertoires of older male relatives rather than neighbouring males (Price 1998). Such selective learning might be facilitated in part by higher exposure to the calls of male groupmates. However, the strong reactions to neighbours' and strangers' calls played within groups' territories suggests an additional explanation. Aggression by older group members to outside calls could provide pressure on young males to accurately copy the calls of their own group. As a consequence, these call repertoires reflect group membership.

In some songbirds and parrots that live in stable, mobile flocks of nonrelatives, flock members develop group-specific contact calls and discriminate these calls from those of other flocks (Mundinger 1970, 1979; Mammen & Nowicki 1981; Nowicki 1983; Farabaugh & Dooling 1996). These flock-specific calls probably aid in the coordination of group movements and maintenance of social bonds during interactions with other flocks (Brown & Farabaugh 1997). In stripe-backed wrens, group-specific calls might be similarly useful for recognizing groupmates during interactions with other groups, such as contests with neighbours over territorial boundaries. Such disputes can include many individuals and usually involve frequent WAY calling.

Recognition of Individuals Within Patrilines

The results suggest that stripe-backed wrens do not distinguish between WAY calls produced by males in the same patriline. Responses to calls recorded from patrilineal relatives in other groups did not differ from responses to calls recorded in subjects' own groups, even though several of these patrilineal relatives lived in distant territories and thus were presumably unfamiliar to the subjects. If subjects had distinguished between these treatments, they should have responded more strongly to the calls of nongroup members.

Males of the same patriline, even distant collateral relatives, have call repertoires that are nearly identical in acoustic structure (Price 1998). Versions of the same call type by male relatives might not differ sufficiently to allow listeners to discriminate between them, as has been suggested for song sparrows, *Melospiza melodia*, which do not discriminate between different males' versions of the same song type (Beecher et al. 1994). WAY calls alone probably provide little information for discriminating between patrilineally related males in different stripe-backed wren groups; however, observations indicate that wrens react aggressively to male relatives in other groups during territorial boundary disputes between related neighbours. In these situations, individuals might use

additional cues for recognizing group membership, such as duet patterns, visual characteristics or location.

Principal pairs generally displayed little aggression to playback of the principal male's own call or the same call type by a male relative. In previous experiments with individually territorial songbirds, responses to playback of a male's own song were difficult to interpret, partly because these birds had never heard their own songs in a natural setting (Weeden & Falls 1959; Brooks & Falls 1975; Searcy et al. 1981). In stripe-backed wrens, territorial groups often include several male relatives that have identical call repertoires, so male wrens frequently hear calls similar to their own. Principal pairs without male helpers responded slightly more strongly than pairs with male helpers, presumably because lone pairs were unaccustomed to hearing the male's calls broadcast from other parts of their territories.

Do Stripe-backed Wrens Use WAY Calls to Recognize Kin Relationships?

Recognition by song has been tested in another cooperative breeder, the splendid fairy wren, *Malurus splendens*, of Australia (Payne et al. 1988). Results of these experiments showed that fairy wrens discriminated between the songs of group members and nongroup members, but did not discriminate between the songs of kin and nonkin in other groups. Payne et al. (1988) therefore suggested that responses in this species were based on social familiarity rather than kin relationships.

In contrast to these previous experiments, results of this study suggest that responses by stripe-backed wrens to WAY calls were at least partly based on kin relationships among callers. Subjects discriminated between groups that included males of separate patrilines, and responded appropriately to their calls based on familiarity and whether or not they were heard from a familiar location. However, subjects did not distinguish between groups that included males of the same patriline, regardless of social familiarity. Thus, stripe-backed wrens only discriminated between calls of different patrilines. Males of different groups are most often members of separate patrilines, so their WAY call repertoires normally provide a useful mechanism for recognizing group membership.

Stripe-backed wrens responded differently to WAY calls recorded from male kin and nonkin in other groups, which suggests that these vocalizations could be used for recognizing unfamiliar male relatives. Female wrens also have repertoires of WAY calls, which they usually produce when exploring outside their natal territories. These calls are similar in acoustic structure to males' calls; however, they are shared only among closely related females (Price 1998). Females' calls thus provide similar cues for recognizing unfamiliar kin.

An ability to recognize unfamiliar relatives would allow wrens to avoid close inbreeding and consequent, potentially deleterious, effects on the survival of future offspring (Brown & Brown 1998; but see Keane et al. 1996). Because natal dispersal by male wrens usually occurs over short distances (Rabenold 1990; Zack 1990), members of neighbouring groups are likely to be significantly related

(Stevens & Wiley 1995). Dispersal by female wrens also occurs over short distances (Zack & Rabenold 1989) and might favour special mechanisms to avoid mating with close relatives.

Individuals could recognize and avoid close kin during breeding dispersal by comparing the WAY calls of potential mates to those of familiar, opposite-sex relatives. This possibility has also been suggested for Darwin's finches in which males learn their father's single song (Grant 1984; Grant & Grant 1996). In these species, females apparently avoid mating with males that have songs similar to their fathers'. In stripe-backed wrens, both sexes might benefit by avoiding individuals with WAY call repertoires similar to opposite-sex relatives. Following the loss of the breeding female in a large, productive group, competitions over the vacant breeding position can include many dispersing females and usually involve frequent WAY calling by both the female competitors and the resident males.

Conclusion

Animals might be expected to recognize kinship in order to direct aid preferentially towards close relatives and to avoid potential risks of close inbreeding (Holmes & Sherman 1983). Stripe-backed wrens live in cooperative groups based on kin relationships, in which many individuals help to raise offspring that are not their own. In addition, during breeding dispersal, individuals must choose mates from among possibilities that include close relatives. The results of this study show that this species is able to discriminate between males of different families by their WAY calls. These vocalizations might therefore be used as cues for recognizing kin relationships among both familiar and unfamiliar birds.

This study provides one of the first cases of a songbird discriminating neighbours from strangers based on vocalizations that function primarily for communication within social groups. Stripe-backed wrens might also provide one of the few examples of a songbird recognizing adult kin by learned vocal cues. In this species, as well as in other species with similar social organization, vocal cues that allow individuals to recognize membership in family groups, as well as to identify kinship within and between groups, would be especially useful for regulating complex social relationships.

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