



Family- and sex-specific vocal traditions in a cooperatively breeding songbird

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Although songbirds provide well-known examples of cultural transmission of vocalizations, little is known about this process in species that live in stable social groups. Here I describe complex vocal traditions in a cooperatively breeding songbird, the stripe-backed wren (*Campylorhynchus nuchalis*). Repertoires of stereotyped calls were recorded from individually marked males and females in cooperative family groups. Males in the same patriline, whether in the same group or in different groups, had call repertoires that were nearly identical. Females in the same matriline also had identical call repertoires; however, female calls never matched the calls of males in the same group or in any nearby groups. Unrelated birds almost never shared calls. Call repertoires are apparently learned preferentially from same-sex relatives within family groups, so that call traditions separately follow patrilines and matriline. This unique pattern of transmission results in vocal cues that reflect both sex and kinship.

Keywords: *Campylorhynchus nuchalis*; cooperative breeder; cultural transmission; kin recognition; sex-specific vocal development; stripe-backed wren

1. INTRODUCTION

The abilities of songbirds to learn complex vocalizations have made them a model for studies of vocal learning and cultural transmission. The great majority of this research, however, has focused on temperate species, in which learned song is restricted mainly to males and territories are individually defended and often seasonal (reviewed in Catchpole & Slater 1995). These birds most often learn their songs from unrelated neighbours after natal dispersal (Kroodsma 1974; Jenkins 1978; Payne *et al.* 1981; McGregor & Krebs 1982).

Relatively few studies have investigated learned vocal communication in animals with more complex social relationships, such as cooperatively breeding birds. These species typically exhibit delayed dispersal of offspring, cooperative care of young, and cooperative defence of a year-round territory (Brown 1987; Stacey & Koenig 1990). Because offspring often stay in their natal territories to act as helpers, they are exposed to the vocalizations of parents and other close relatives for prolonged periods. Such long-term associations might result in patterns of vocal learning and communication different from those of individually territorial songbirds.

In a number of species, individuals within stable social groups develop shared vocal features that are group-specific (songbirds, Mundinger 1970; Mammen & Nowicki 1981; Trainer 1989; parrots, Farabaugh & Dooling 1996; bats, Boughman 1997; cetaceans, Ford & Fisher 1983; Ford 1991; Strager 1995; Weilgart & Whitehead 1997). In particular, killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) have vocal repertoires specific to matrilineal family groups. Long-term studies of resident populations of killer whales suggest that similarities between these group-specific repertoires reflect

genealogical relationships (Ford 1991). To date, however, similar family-specific vocal traditions have not been documented in other species.

Here, I provide evidence for complex, family-specific call traditions in a cooperatively breeding songbird. Stripe-backed wrens live in stable patrilineal family groups on permanent territories in northern Colombia and Venezuela. Unlike most temperate songbirds, both males and females produce learned vocalizations. Comparing the calls produced by wrens of known genealogy has allowed me to study the cultural transmission of these vocalizations within families.

2. METHODS

(a) *Study population*

I studied a population of stripe-backed wrens at Hato Masagual, a cattle ranch located about 300 km south of Caracas in the seasonally flooded savannah (llanos) of northern Venezuela. This population has been individually marked with coloured leg bands as part of a long-term study of breeding behaviour (Rabenold 1990). Annual censuses and banding of unmarked immigrants and juveniles have provided demographic data on the histories of nearly all the birds in this population since 1976, and recent DNA fingerprinting (Rabenold *et al.* 1990) has confirmed patterns of genealogical relationship.

Stripe-backed wrens breed cooperatively in the patches of deciduous woodlands scattered throughout the ranch. Groups 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 non-breeding helpers, which are nearly always non-dispersing offspring from previous years (Rabenold 1985, 1990; but see Piper *et al.* 1995). All the birds (i.e. 2–14 per group) jointly defend a year-round territory and help raise the young. Females disperse as adults to compete for vacant breeding

positions in nearby groups (Zack & Rabenold 1989). Males usually remain in their natal groups to inherit the breeding positions there (Wiley & Rabenold 1984) or, less often, disperse and attempt to breed outside their natal territories (Zack 1990). A typical group, therefore, consists of males of a single patriline, which remains in the same location for generations, with females joining or leaving the group.

(b) *Vocalizations*

The territorial vocalizations of this species are loud male–female duets, performed mostly by the principal pair (Wiley & Wiley 1977). Individual wrens also produce complex vocalizations (termed WAY calls from an occasional resemblance to the English words ‘where are you?’) which are of a lower intensity than the duets (*ca.* 12 dB less intense) and appear to have a function in close-range communication. Stripe-backed wrens are sexually monomorphic; however, males and females can be discriminated in the field by the context of WAY call production. Males produce the great majority of WAY calls heard within a group’s territory (over 97%), while females call most frequently when exploring outside their natal territories. Because such explorations by females occur infrequently, all of the WAY calls used in this study were recorded from males and females within their groups’ territories.

From 1992 to 1996, I tape-recorded repertoires of WAY calls from 46 principal males, 22 male helpers, and 14 females in 30 groups using a Marantz PMD 221 cassette recorder and an Audio-technica AT815a microphone. I recorded more than 100 calls from each male (mean = 265.6, s.e. = 30.1) to ensure that I had obtained complete repertoires. Females rarely called within a group’s territory, so I recorded far fewer calls from identified females (mean = 9.7, s.e. = 2.9).

(c) *Call classification*

To display the large number of recorded calls, I used a Uniscan II real-time spectrum analyser interfaced with a 68 000 computer to produce black and white spectrograms on a dot-matrix printer (temporal resolution 6.25 ms, frequency resolution 160 Hz). WAY calls were highly stereotyped, so these spectrograms were easily assigned to distinct types based on patterns of acoustic structure. Calls with indistinguishable patterns were catalogued as the same type, while calls with marked differences were classed as different types. Calls that differed in only one or two details were classed as related subtypes.

To evaluate these degrees of similarity, I obtained scores of the similarity of spectrograms from referees with no previous experience with this species’ calls. Five referees judged the similarity of each of 70 randomly assorted pairs of spectrograms in four categories: 20 pairs of the same call type recorded from the same individual (SS); 20 pairs of the same call type recorded from different individuals (SD); 20 pairs of different call types recorded from different individuals (DD); and 10 pairs of related subtypes recorded from different individuals (ST). Scores for similarity ranged from 1 (little similarity) to 5 (essentially identical). I used the average score reported by the referees for each pair of spectrograms to calculate the mean score (\pm s.e.) for each of the four categories. Scores were then compared with a Mann–Whitney *U*-test.

(d) *Calculating call repertoire similarity*

To obtain a quantitative measure of call sharing between individual wrens, I used the number of shared call types and related

subtypes to calculate an index of similarity for each pair of call repertoires. This index was based on Dice’s coefficient of association (Morgan *et al.* 1976; Ford 1991), which normalizes the data to account for differences in repertoire size:

$$\text{call repertoire similarity} = \mathcal{N}_c + \mathcal{N}_s / R$$

where \mathcal{N}_c is the number of identical call types, \mathcal{N}_s is the number of related subtypes, and R is the mean repertoire size of the individuals compared.

By comparing birds within groups, I determined the call repertoire similarity of close relatives. Information about past male and female dispersals also allowed me to compare the repertoires of collateral relatives that were more distantly related than birds within groups. When a female dispersed to become the principal breeder in another group, her descendants were related to her natal group through a common female ancestor. Similarly, when a male dispersed and bred successfully, his descendants were related to his natal group through a common male ancestor. Because these groups consist of stable patrilines, members of separate groups related through a shared male ancestor were patrilineal relatives. I was able to compare the repertoires of some males related through ancestors from several past generations. However, because of the rarity of female calls, females with such distant relatedness were unavailable for comparison.

To determine the repertoire similarity of unrelated neighbours, I compared the calls of principal males that (i) had been neighbours for several years, (ii) shared no known male ancestor, and (iii) were observed to interact vocally during boundary disputes.

3. RESULTS

Calls that I considered to be of the same type were judged to be nearly identical by the referees. The scores revealed that calls of the same type were no more different when produced by different individuals than when produced by the same individual at different times (table 1). Calls that I classified as different types were judged by the referees as having little similarity, and related subtypes were of intermediate similarity.

Each adult male wren had a stable repertoire of 9–19 distinct WAY call types. Males in the same group had call repertoires that were nearly identical in acoustic structure (figure 1), while unrelated neighbouring males rarely shared any call types (Wilcoxon matched-pairs test, two-tailed: $T=0$, $N=27$, $p<0.001$). All male patrilineal relatives, including distant collateral relatives with a common male ancestor, had call repertoires that were remarkably similar (table 2). In contrast, males with a common female ancestor (maternal relatives) almost never shared call types (Mann–Whitney *U*-test: $U=0$, $N_1=56$, $N_2=27$, $p<0.001$). Males shared no more calls with male maternal relatives than with unrelated neighbours (Mann–Whitney *U*-test: $U=279$, $N_1 = N_2=27$, n.s.). Male WAY calls are therefore transmitted strictly along patrilines.

Each adult female had a smaller repertoire of 3–5 distinct WAY call types. Closely related females, whether in the same group or in different groups, had nearly identical repertoires (figure 2), while females without common ancestry never shared call types. Call types of females never matched those of males in the same group or in any

Table 1. Scores (mean \pm s.e.)^a for similarity of pairs of spectrograms in four categories^b

(Calls of the same type were scored as nearly identical in acoustic structure, whether recorded from the same individual (SS) or from different individuals (SD).)

spectrogram pair	score	<i>p</i> (Mann–Whitney <i>U</i> -test)		
		ST	DD	SD
SS	4.39 \pm 0.09	0.003	0.000	0.837
SD	4.37 \pm 0.07	0.002	0.000	
DD	1.72 \pm 0.10	0.000		
ST	3.72 \pm 0.17			

^aScores were on a scale from 1 (little similarity) to 5 (essentially identical).

^bSS, same call type by same individual; SD, same call type by different individuals; DD, different call types by different individuals; and ST, related subtypes by different individuals.

Table 2. Repertoire size, number of shared call types, number of related subtypes, and overall repertoire similarity of males with different genealogical relationships (mean \pm s.e)

(Only patrilineal relatives had similar call repertoires, and this similarity declined slightly with decreasing relatedness.)

relatedness	<i>N</i>	repertoire size	shared call types	related subtypes	repertoire similarity
patrilineal relative					
son	15	11.87 \pm 0.31	11.20 \pm 0.44	0.27 \pm 0.12	0.97 \pm 0.01
brother	17	13.38 \pm 0.42	12.59 \pm 0.55	0.18 \pm 0.09	0.95 \pm 0.01
grandson	2	12.50 \pm 1.44	9.50 \pm 0.50	0.50 \pm 0.50	0.80 \pm 0.00
nephew	16	12.16 \pm 0.29	11.00 \pm 0.47	0.50 \pm 0.18	0.94 \pm 0.02
cousin	2	10.75 \pm 0.75	9.00 \pm 0.00	1.00 \pm 1.00	0.93 \pm 0.06
cousin's son	2	12.50 \pm 0.50	10.50 \pm 1.50	1.00 \pm 1.00	0.92 \pm 0.08
cousin's grandson	2	12.75 \pm 0.48	8.50 \pm 0.50	2.00 \pm 0.00	0.82 \pm 0.02
maternal relative	27	11.94 \pm 0.26	0.89 \pm 0.10	0.07 \pm 0.05	0.08 \pm 0.01
unrelated neighbour	27	12.56 \pm 0.34	0.67 \pm 0.26	0.18 \pm 0.08	0.07 \pm 0.02

nearby groups. Nevertheless, female calls did not differ in acoustic structure from male WAY calls in any consistent way (compare figures 1 and 2). A few females had call types that were very similar to the calls of males in distant groups, so it seems probable that males and females had the capacity to produce any call type.

Comparisons with the repertoires of individuals' fathers and mothers showed that males shared calls only with fathers, while females shared calls only with mothers (table 3). Male and female call repertoires were therefore separately transmitted along sex-specific lines within families.

4. DISCUSSION

Patterns of variation in behavioural traits presumably reflect the underlying mechanisms governing the transmission of these traits. In most songbirds, the existence of shared vocal features within local populations (Mundinger 1982; Baker & Cunningham 1985) or within social groups (Brown & Farabaugh 1997) suggests vocal learning as a likely mechanism of transmission. When vocal features are specific to family lines, however, vocalizations might be (i) learned from relatives or (ii) genetically inherited.

The patterns of repertoire similarity reported here make it likely that stripe-backed wrens' WAY calls are

learned rather than strictly inherited. If they were inherited, an individual's vocalizations should have resembled equally those of both paternal and maternal relatives. In fact, males shared entire repertoires of calls with male patrilineal relatives and shared no more calls with maternal relatives than with unrelated neighbours (table 2). Because males are the homogametic sex in birds, genetic inheritance could not be limited to patrilines. Males' call repertoires thus provide a striking case of sex-specific learning.

Because female WAY calls were so similar to males' in acoustic structure and in patterns of variation, females presumably also acquired their call repertoires by learning. Additional recordings of female WAY calls are needed to confirm this conclusion.

For males, selective learning from same-sex relatives is probably facilitated by the relatively frequent calling of older males. The principal breeding male produces the majority of WAY calls within a group (85%) and is usually the father of juvenile wrens (Rabenold *et al.* 1990; Piper & Slater 1993), so young males hear calls mostly from their father. Few other songbirds regularly learn their father's vocalizations. Those that do normally sing only a single song, for instance various species of Darwin's finches (e.g. *Geospiza conirostris*, *G. fortis* and *G. scandens*; Grant 1984; Grant & Grant 1996) and the zebra finch, *Taeniopygia guttata* (Zann 1990). In contrast, young female

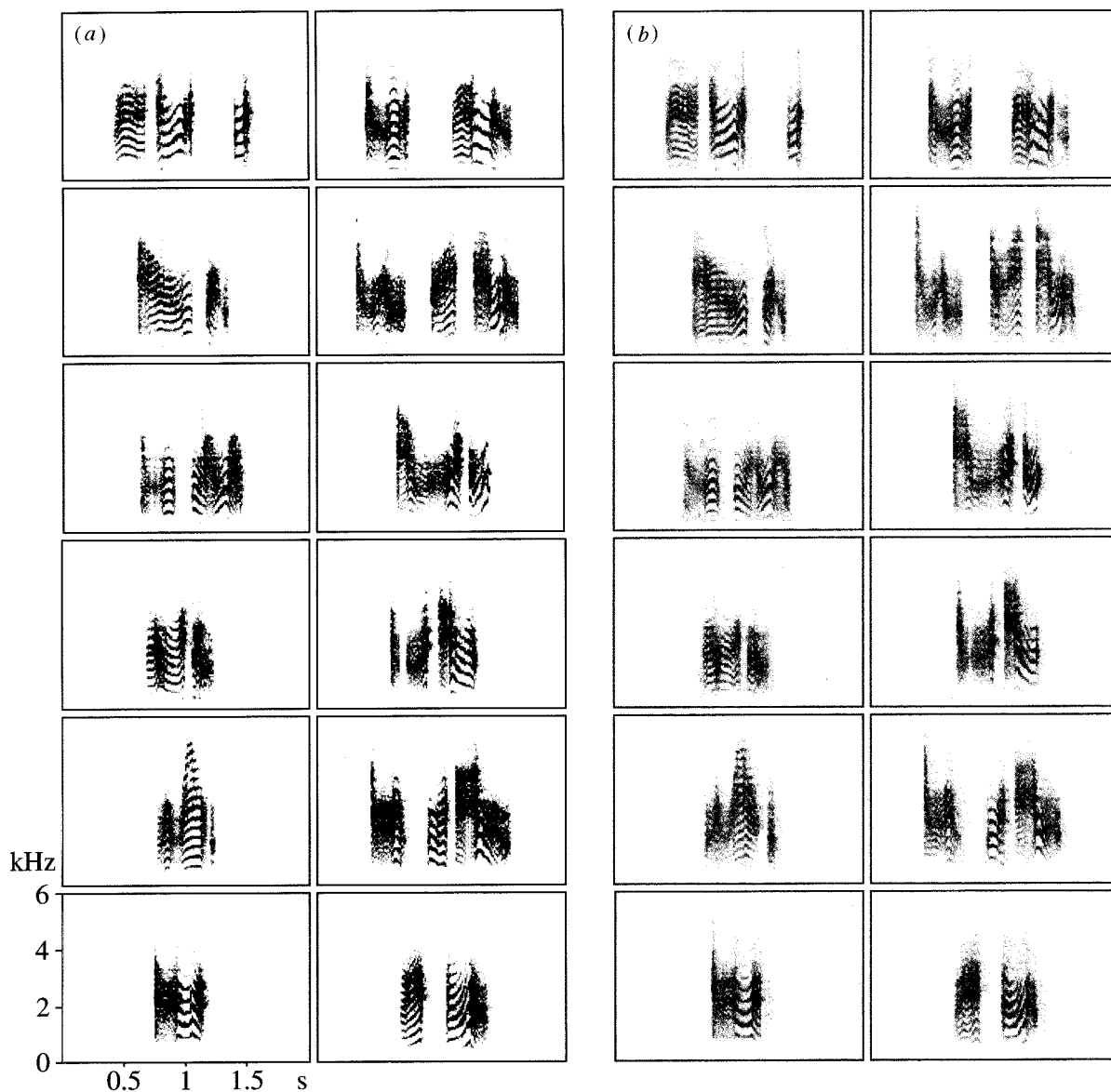


Figure 1. Spectrograms of the complete repertoires of WAY calls recorded from (a) the principal male and (b) a male helper, respectively father and son, from one stripe-backed wren group show the similarities of closely related males' call repertoires. Spectrograms for figures were produced with Avisoft-Sonograph Pro software (sampling frequency 12 000 Hz, FFT-length 256 points) (Raimund Specht, Berlin).

wrens face a difficult task in selectively copying the calls of female relatives. Females rarely call within a group's territory (less than 3% of calls identified), so sex-specific learning cannot be explained simply by the relative frequency of exposure to the calls of older females.

Sex-specific vocal learning occurs in other songbirds in which both sexes produce learned vocalizations. In many duetting species, including stripe-backed wrens, both males and females have distinct sex-specific repertoires of learned vocal phrases which are combined to produce male-female duets (Wiley & Wiley 1977; Farabaugh 1982). Studies of captive birds suggest that, in at least some duetting species, these phrases are learned selectively from same-sex conspecifics (*Laniarius funebris*, Wickler & Sonnenschein 1989; *Thryothorus nigricapillus*, Levin *et al.* 1996). Similarly, in two non-duetting songbirds, Indian hill mynas (*Gracula religiosa*) and common starlings (*Sturnus vulgaris*), males apparently learn songs from males

and females from females (Bertram 1970; Hausberger 1993). The mechanisms of sex-specific learning in these species, however, are not yet fully understood.

Several group-living birds develop group-specific vocal features that change gradually during an individual's lifetime, for instance, chickadees (*Parus atricapillus*; Mammen & Nowicki 1981; Nowicki 1989), yellow-rumped caciques (*Cacicus cela*; Trainer 1989), and budgerigars (*Melopsittacus undulatus*; Farabaugh & Dooling 1996). In contrast, WAY calls are highly stable. I detected no apparent change in the acoustic structure of individual call types during five years of research. Furthermore, comparisons of distant collateral relatives (table 2) showed that male lineages isolated for several generations, and as long as 15 years, retain repertoires that are remarkably similar. Male WAY calls are apparently learned with exceptionally high accuracy. Slight differences in the acoustic structure of relatives' calls (categorized as related subtypes; table 2)

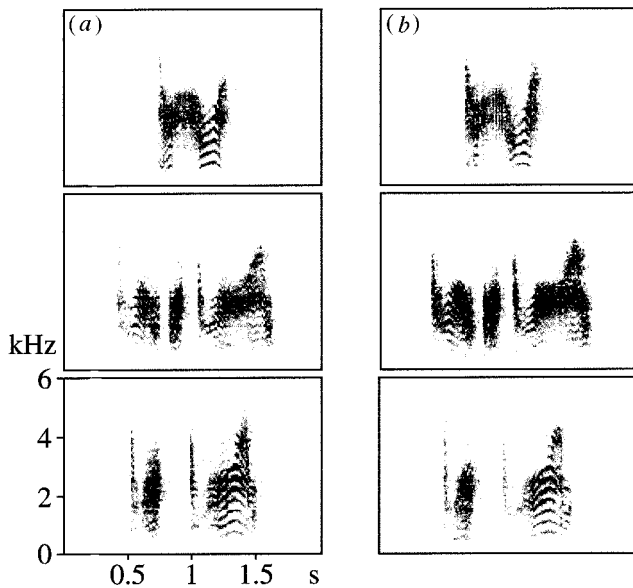


Figure 2. Spectrograms of WAY calls recorded from (a) the principal female and (b) a female helper, respectively mother and daughter, from the same group as in figure 1. Note that the call repertoires of female relatives match each other, but do not match any of the call types of males in the same group.

and occasional call types shared between unrelated neighbours suggest that gradual changes occur within vocal traditions as a result of errors in copying.

Male WAY call repertoires exhibit a pattern of variation more similar to the calls of killer whales than to the songs of other songbirds. This resemblance might be due in part to similar patterns of dispersal and vocal learning. Groups of stripe-backed wrens consist of a patrilineal family from which far fewer males than females disperse (Rabenold 1990; Zack 1990). Many males in fact remain in their natal groups for their entire lives (Wiley & Rabenold 1984). Killer whales live in matrilineal family groups from which no dispersal appears to take place at all (Bigg *et al.* 1990). Both stripe-backed wrens and killer whales have repertoires of highly stereotyped calls that are accurately learned from older relatives within these stable social groups. Consequently, both species exhibit group-specific call repertoires that reflect the genealogical relationships of individuals.

Kin recognition by song is rare in songbirds (McGregor 1989). Males do not normally learn vocalizations from their fathers, so song provides no information about kinship and, in most species, females do not sing. In contrast, stripe-backed wrens develop repertoires of calls which are sex- and family-specific, so vocalizations potentially provide cues indicating both sex and relatedness. It is easy to imagine how such cues might be particularly useful in a sexually monomorphic bird that lives in cooperative family groups.

These calls might allow individuals to avoid infrequent, but potentially deleterious, risks of close incest by comparing the calls of potential mates to those of relatives of the opposite sex. Dispersing females, for example, could avoid mating with males related to their fathers, as suggested for Darwin's finches in which males learn their father's single song (Grant 1984; Grant & Grant 1996). In stripe-backed wrens, short-distance dispersal is likely to

Table 3. Repertoire sizes of males and females and similarities to the repertoires of their fathers and mothers (mean \pm s.e.)^a show that calls were shared only with same-sex parents

sex	<i>N</i>	repertoire size	similarity to father's repertoire	similarity to mother's repertoire
male	8	14.06 \pm 0.54	0.95 \pm 0.02	0.00 \pm 0.00
female ^b	4	3.87 \pm 0.44	0.00 \pm 0.00	0.87 \pm 0.08

^aData include only individuals for which recordings were available for both parents.

^bRepertoire size and similarity between repertoires of females is probably underestimated as a result of the rarity of their calls.

result in significant relatedness between neighbouring groups and might favour special mechanisms for avoiding close inbreeding (Stevens & Wiley 1995).

Much more frequent and potentially greater benefits might come from an ability to recognize the sex and family origins of individuals during contests with other groups. Males might benefit especially in contests with neighbouring groups over territorial boundaries. Dispersing females, on the other hand, could benefit during contests for vacant breeding positions, which often involve competing teams of female relatives (Zack & Rabenold 1989). Both of these situations involve frequent WAY calling, and playback experiments (J. J. Price, unpublished data) show that stripe-backed wrens can recognize the family origins of individual calls.

Stripe-backed wrens probably provide the first recognized example of a bird that regularly learns repertoires of vocalizations from older relatives. Furthermore, these wrens probably provide the first case in which individuals of each sex have been shown to copy preferentially the vocalizations of relatives of the same sex. Future studies of learned vocal communication in other highly social animals might well reveal communication systems that are similarly complex.

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