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Pair Duets in the Yellow-Naped Amazon (Psittaciformes: *Amazona auroalliata*): Responses to Playbacks of Different Dialects

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Abstract

Yellow-naped amazons, *Amazona auroalliata*, have regional dialects in which several functional classes of vocalization, including contact calls and pair duets, change their acoustic structure at the same geographic boundaries. Here we examine the responses of 11 pairs of yellow-naped amazons to playbacks of duets from other pairs nesting near the same roost, other roosts within the same dialect, and roosts in foreign dialect areas. Overall, pairs responded more strongly to duets from their own dialect than to those of the foreign dialect. Pairs responded to both treatments from their own dialect (local same dialect and distant same dialect) with movement towards the broadcasting loudspeaker and more rarely with squeals, a vocalization typically observed only in the context of aggressive chases. These aggressive responses were never observed during playbacks of the foreign dialect treatment or congeneric controls. There were no differences among treatments in the incidence of contact calls or pair duets. A similar pattern of stronger aggressive responses to local than to foreign dialects has been found in a wide range of oscine songbirds. The results of the present experiment suggest that a general function may underlie this behavioral response both in oscines and in other bird taxa with vocal learning.

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Introduction

Among avian taxa, learned vocal dialects are reported in the oscine songbirds (Kroodsma 1982; Catchpole & Slater 1995), the hummingbirds (Snow 1968; Wiley 1971; Baptista & Schumann 1990; Gaunt et al. 1994) and the parrots (Nottebohm

& Nottebohm 1969; Wright 1996). Such dialects are thought to be a product of cultural evolution whereby geographic variation is maintained through the preferential learning of local variants (Mundinger 1982; Slater 1989; Catchpole & Slater 1995). The fitness benefits of such biased learning to the individual remain incompletely understood after several decades of research (reviewed in Krebs & Kroodsma 1980; Mundinger 1982; Baker & Cunningham 1985; Slater 1989; Catchpole & Slater 1995). Songbirds, hummingbirds, and parrots are thought to have independently evolved the capacity for vocal learning (Nottebohm 1972; Kroodsma 1982) and thus offer independent tests of evolutionary hypotheses for the benefits of learning local vocal variants. However, to date, most research has focused on dialects in the oscine songbirds; few published studies describe geographic variation in either parrots or hummingbirds (Kroodsma et al. 1996; but see Snow 1968; Wiley 1971; Gaunt et al. 1994; Wright 1996).

Playback experiments are an important technique for testing the behavioral significance of different acoustic variants to individuals (Falls 1992). Numerous studies of oscine songbirds have compared the responses of territorial males to playbacks of songs from their own dialect vs. those from foreign dialects (reviewed in Petrinovich & Patterson 1981; Baker & Cunningham 1985; Nelson 1998). These studies have generally found that male songbirds respond strongly and aggressively to songs from their own dialect and weakly to those from foreign dialects, although some exceptions have been noted (e.g. Petrinovich & Patterson 1981; Nelson 1998). At present it is unclear whether this general pattern extends to other bird taxa with vocal learning; to our knowledge there are no reported studies examining territorial responses to geographical variants in either hummingbirds or parrots. Such studies are an important first step in understanding the significance of dialects in non-oscine birds and should contribute to a fuller understanding of the importance of vocal dialects in general.

In this paper, we present the results of a playback experiment testing the responses of mated pairs of parrots to dialect-level variation in pair duets. Yellow-naped amazons (*Amazona auropalliata*) in north-western Costa Rica have regional dialects that each encompass several large communal night roosts (Wright 1996). Roosts occur in traditional locations separated by five to 10 km; each roost is attended by 50–300 birds that nest in the surrounding areas. We initially defined dialects by major structural changes in the contact call, the most commonly used call in this species' repertoire (Wright 1996). Subsequently we found that these dialects extended to three other call types in the vocal repertoire (Wright 1997). These vocalizations all exhibit readily discernible shifts in acoustic structure at the same geographic boundaries as the contact call.

One such dialectal vocalization is the pair duet, a complex signal composed of sex-specific notes and contact calls repeated alternately by members of a mated pair. Pairs perform duets near their nests throughout the year and often engage in extended counter-duetting with both neighbors and intruding pairs, suggesting that duets function, in part, for territorial defense (Wright 1997; Wright, unpubl. data). Here we examine the responses of mated pairs of yellow-naped amazons to

duets from other pairs nesting near: (i) the same roost; (ii) other roosts within the same dialect; and (iii) roosts in foreign dialect areas.

Methods

We conducted playbacks with 11 pairs of yellow-naped amazons at their nests, distributed around three traditional night roosts in Guanacaste Province in north-western Costa Rica (Fig. 1). Birds at two of these roosts, Pelon Altura and Horizontes, use the northern dialect; birds at the third, Pelon Bajura, use the southern dialect as defined by Wright (1996). The playbacks took place between Dec. 5 and Dec. 18, 1995, at the end of the rainy season and approximately 1 mo prior to the initiation of egg laying.

We contrasted the responses of nest pairs to duets from three experimental treatments (local same dialect, distant same dialect, foreign dialect) and a control consisting of a duet from a sympatric congener, the white-fronted amazon (*Amazona albifrons*). 'Local same dialect' treatment duets were recorded from pairs nesting within a 3-km radius of the same roost as the test pair but were neither the test pair's own calls nor those of an immediate neighbor. 'Distant same dialect' treatment duets were from pairs nesting near a different roost within the same dialect (a minimum distance of 20 km). 'Foreign dialect' treatment duets were from pairs nesting in a foreign dialect roost area (a minimum distance of 40 km). Pilot tests conducted at nest sites demonstrated that the most dramatic responses by nest pairs consisted of a rapid approach to the loudspeaker and the use of 'squeals', a distinctive, highly aggressive call normally observed only during physical encounters between pairs at nests (Wright and Dorin, unpubl. data). We designed this experiment primarily to test whether the frequency of these short-term aggressive responses varied among treatments.

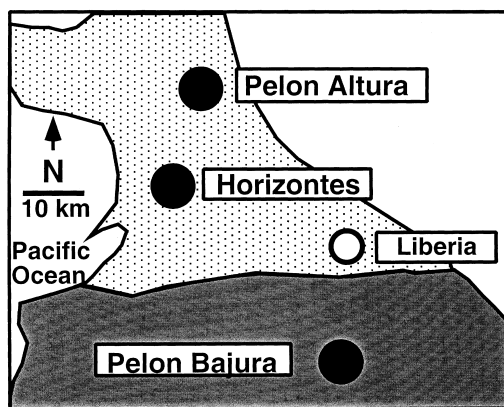
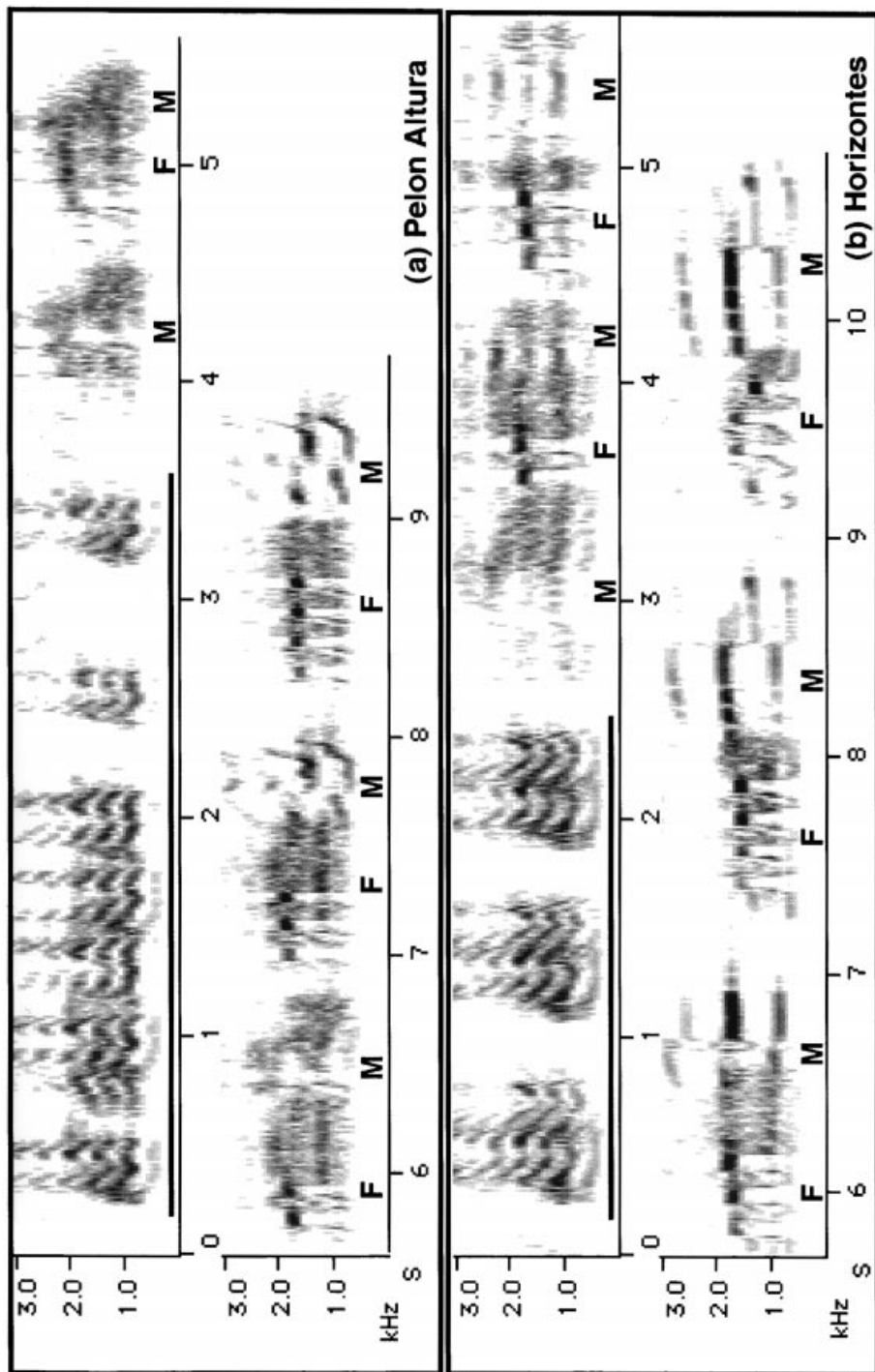


Fig. 1: A map of the three roost sites at which playbacks were conducted in Costa Rica. Liberia, the capital of Guanacaste Province, is shown for reference. Shading on the map shows the extent of the northern (dotted) and southern (grey) dialects



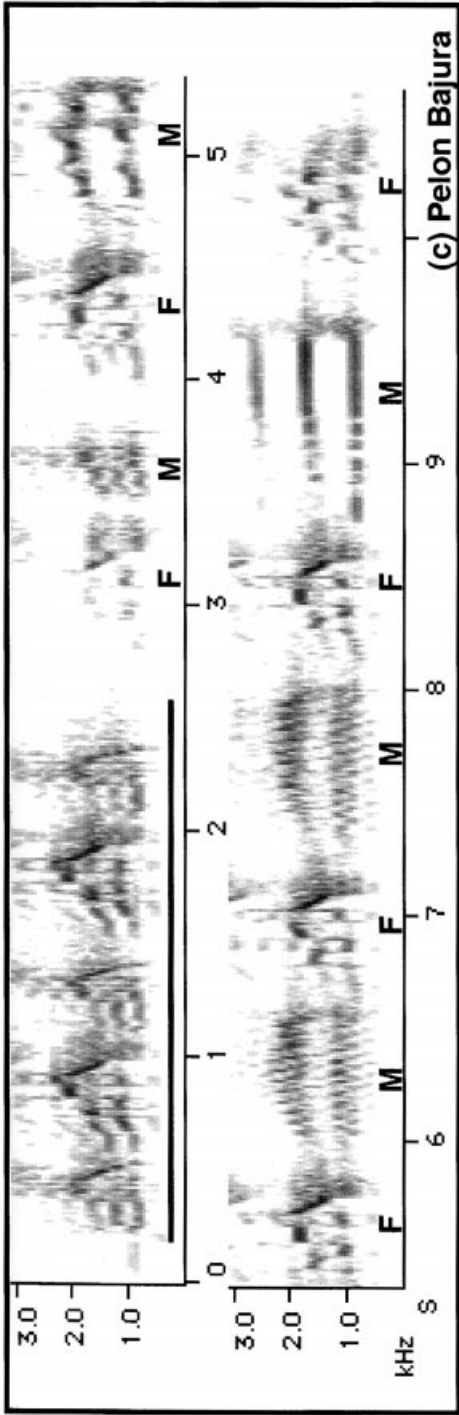


Fig. 2: Representative examples of pair duets used as playback exemplars. Pairs initiate duets with contact calls and then switch to sex-specific notes that are repeated in alternation by the male and female. The contact calls are underlined by a solid bar in each spectrogram, while the sex-specific notes are designated with 'F' for female notes and 'M' for male notes. Both contact calls and sex-specific notes show dialect differences at coincident geographic boundaries. Duets from Pelon Altura and Horizontes are from the northern dialect and the duet from Pelon Bajura is representative of the southern dialect

Playback Stimuli

We recorded duets used as playback stimuli from nest pairs surrounding the three night roosts (Pelon Altura, Horizontes, and Pelon Bajura) during spontaneous calling bouts near their nests (Fig. 2). Duets were recorded at a distance of 30–60 m using a Sennheiser MKH 816P48 microphone powered by a Stewart BPS-1 phantom-power box and fed into the external microphone jack of a Cannon UCS5-A Hi-8 video camera. Calls were band-passed (0.8–6 kHz) by a Krohn-Hite 3500 filter before digitizing at 8 bits and 22 kHz with SoundEdit Pro 1.0 running on a Macintosh Powerbook 180. We edited duets to remove background noise and to control for peak amplitude and total length (mean \pm SD = 10.8 \pm 0.8 s). After digitizing, we saved the duets as Macintosh resource files and inserted each sound into the 'Singit!' interactive playback program (Bradbury & Vehrencamp 1994).

Experimental Design

We selected two duets recorded from the same pair in the same calling bout to use as a combined stimulus for playback presentation. In total we created six such stimuli, one each from two different nest sites near each of the three night roosts. These stimuli were used in a matched reciprocal design (Kroodsma 1989) such that the same stimulus was used in all three experimental treatments, as appropriate at different roosts. For example, a duet stimulus recorded at Pelon Altura would be used as a local same dialect treatment at Pelon Altura, a distant same dialect treatment at Horizontes, and a foreign dialect treatment at Pelon Bajura. Playbacks were presented to two pairs at Pelon Altura, five pairs at Horizontes, and four pairs at Pelon Bajura.

Ideally we would have prepared as many stimuli from each roost as the maximum number of pairs at any one site (e.g. five pairs). However, the logistical difficulties in obtaining sufficient high-quality duet recordings and locating regularly attended nests at several widely separated locations prevented us from obtaining the ideal number of playback stimuli and from balancing the number of pairs among sites or fully blocking the experiment in the distant same dialect treatment. Because of the statistical complications introduced by these factors, we treat n as the total number of pairs tested in each treatment in all statistical analyses rather than the total number of stimuli tested, despite the fact that doing so involves a form of sacrificial pseudo-replication (Hurlbert 1984). We believe the potential for bias introduced by using a reduced number of stimuli relative to numbers of pairs tested is greatly offset by our matched reciprocal design, in which the expected responses to a given stimulus are different when used for each treatment. Furthermore, we did not detect differences among stimuli themselves on any response measure, only differences among the treatments in which stimuli were presented (see Results). We did not use matched sample tests because pairs from the southern dialect were not presented with stimuli representing the distant same dialect treatment.

We created one additional stimulus using duets recorded from a pair of *A. albifrons* to act as a control for the presentation of natural sounds over loud-

speakers near nests. This stimulus was presented to all pairs in the same manner as the experimental treatments.

Playback Presentation

We used an interactive playback presentation designed to mimic natural patterns of counter-duetting in this species, with the goals of preventing rapid habituation to the exemplar calls (Pepperberg 1992) and eliciting more natural responses from pairs (Dabelsteen 1992; Nielsen & Vehrencamp 1995). Each presentation consisted of the first duet in a stimulus, an inter-duet interval of variable length, and the second duet in the stimulus. The length of the inter-duet interval depended on the response of the target pair. If the pair called in response to the first playback duet, then the second duet was played immediately in answer. If this pair did not respond, the second duet was played 30 s after the end of the first, resulting in a maximum duration of 52 s for the presentation of a treatment.

All treatments and the control were presented to nest pairs in a single playback session, with the order of treatments randomized among pairs. Presentation of the first treatment began when the target pair flew to within 300 m of the loudspeaker. Each subsequent presentation began when any overt responses of the pair to the previous one had ended; that is, they were not moving, calling, or displaying (mean interval between the start of each treatment equaled 135 s). Our presentations simulated natural patterns of interactive calling by pairs engaged in counter-duetting; in a sample of 33 duets recorded during spontaneous calling bouts, the median interval between the start of consecutive duets was 60 s and ranged widely, from 9 to 545 s (Wright, unpubl. data). Thus both the interval between the two duets within a treatment stimulus (30 s) and the interval between presentations of different treatments (135 s) lie well within the natural range of duet calling patterns.

Presentation of all treatments within a single session controlled for the possibility that pairs would respond differently on different days due to the presence or absence of other pairs with whom they might engage in counter-duetting. One potential pitfall of presenting the treatments in a single session is that order effects such as habituation or sensitization might outweigh any effects of the treatments, although given that treatment order was randomized between pairs, such order effects would not have created an erroneous effect of treatment. However, we did not detect either sensitization or habituation to the playback stimuli for any response measures (see Results).

Playbacks were broadcast in the early morning or late afternoon from speakers placed in trees located within 50 m of nest trees. We performed playback broadcasts with a Macintosh Powerbook 145B running 'Singit!'. The sound output from this Macintosh was amplified by a battery-powered Fisher PH-W803 cassette player and broadcast by an Anchor Portavox PB-500 loudspeaker suspended 6–12 m high in a tree. Three observers were stationed about 80 m from the loudspeaker. One observer recorded the movements and calling status of the test pair. The second observer ran the playback apparatus. The third recorded the behavior

of the nest pair using the video system previously described. This video-taped record was later used to classify the types of calls uttered by the test pair and to measure the distance of response movements.

Data Analysis

We analyzed two classes of responses by pairs: movements and calling behavior. We scored two measures of movement: (i) the presence or absence of a movement by either member of a pair after either of the two duets in a stimulus; and (ii) the distance from the closest member of the pair to the broadcast loudspeaker at the beginning of the trial minus the distance at the end of the trial. We also scored each trial for the presence or absence of three classes of calls: contact calls, pair duets, and squeals. Differences among treatments were analyzed using non-parametric Kruskal–Wallis tests in STATVIEW (Abacus Concepts 1995) or Fisher's exact tests in SAS, a program which permits the analysis of contingency tables larger than 2×2 (SAS Institute 1996). When we found significant differences in comparisons between all treatments, we used Dunn's method for non-parametric multiple comparisons (Zar 1984) or Fisher's exact tests corrected with the sequential Bonferroni method (Sokal & Rohlf 1995), as appropriate, to identify which pairs of treatments differed significantly.

Pairs never moved or produced aggressive squeals in response to the congeneric control, and they rarely responded to this stimulus with contact calls or duets (Figs 3 and 4). We therefore restricted the analyses of treatment effects to the three treatments of primary interest: local same dialect ($n = 11$); distant same dialect ($n = 7$); and foreign dialect ($n = 11$). Due to unequal sample sizes across treatments

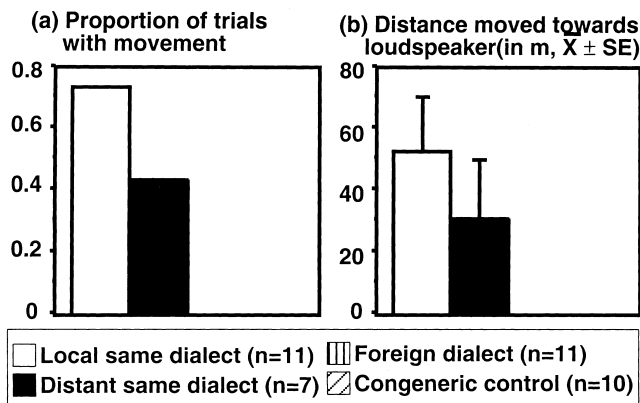


Fig. 3. Measures of movement by pairs in response to the three playback treatments and congeneric control. (a) The proportion of trials in which pairs responded to playbacks with movement. There was no movement in response to the foreign dialect treatment or the congeneric control. (b) The difference between pre-trial and post-trial distance to the loudspeaker in meters ($\bar{x} \pm 1$ SE). All pairs that moved during trials moved towards the loudspeaker

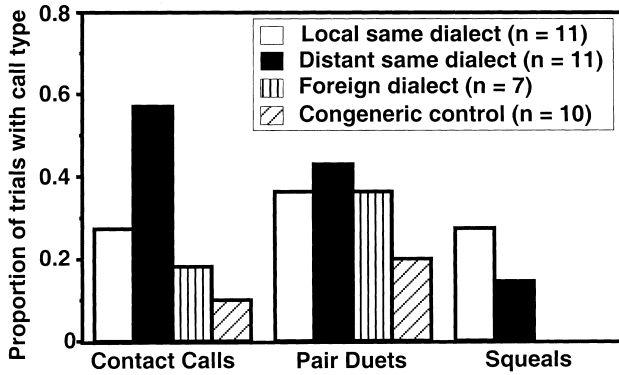


Fig. 4: The proportion of trials of each playback treatment in which the pairs responded with contact calls, pair duets, or squeals. Pairs gave no squeals in response to the foreign dialect treatment or the congeneric control

we give n as the total number of playbacks examined in a particular test; for most cases $n = 29$, except in post-hoc tests and tests for order effects.

Results

Measures of movement revealed a clear difference in response by nest pairs to playbacks of their own vs. foreign dialects (Fig. 3). Pairs moved only in response to duets from their own dialect (73% of local same dialect presentations and 43% of distant same dialect presentations) and never moved in response to the foreign dialect (Fig. 3a, Fisher's exact test, $n = 29$, $p = 0.001$). Post-hoc comparisons of the incidence of movement revealed a significant difference only between the local same dialect and foreign dialect treatments (Fisher's exact test with sequential Bonferroni correction, local same dialect vs. foreign dialect, $n = 22$, corrected $p < 0.05$; local same dialect vs. distant same dialect, $n = 18$, corrected $p > 0.05$; distant same dialect vs. foreign dialect, $n = 18$, corrected $p > 0.05$). In every case that pairs moved in response to calls from their own dialect, they moved towards the loudspeaker and in five of these cases the pair flew from distances of over 100 m from the loudspeaker to within 10 m of it (Fig. 3b). This pattern resulted in a significant difference among treatments in the distance moved during trials (Fig. 3b, Kruskal-Wallis test, $n = 29$, $df = 2$, H corrected for ties = 10.8, tied $p = 0.005$). As with the incidence of movements, post-hoc comparisons revealed a significant difference in movement distance only between the local same dialect and the foreign dialect treatments (Dunn's test, local same dialect vs. foreign dialect, $n = 22$, $df = 1$, $Q = 3.26$, $p < 0.05$; local same dialect vs. distant same dialect: $n = 18$, $df = 1$, $Q = 1.03$, $p > 0.05$; distant same dialect vs. foreign dialect, $n = 18$, $df = 1$, $Q = 1.83$, $p > 0.05$). Similar results (not shown) were obtained by dividing the post-trial distance to the loudspeaker by the pre-trial distance.

Measures of calling by nest pairs did not reveal as clear a pattern in response to different playback treatments. There was no difference among treatments in the incidence of contact calls (Fisher's exact test, $n = 29$, $p = 0.26$), pair duets (Fisher's exact test, $n = 29$, $p = 1.0$), or squeals (Fisher's exact test, $n = 29$, $p = 0.26$). However, it is notable that squeals were given exclusively in response to a pair's own dialect (27% of local same dialect presentations and 14% of distant same dialect presentations) and never in response to foreign dialect or control presentations (Fig. 4, see Fig. 5 for a spectrogram of squeal notes). Pairs that squealed during playback treatments flew to the loudspeaker immediately after playback and appeared to be searching for the source of the calls. Squeals are rarely given by yellow-naped amazons during natural spontaneous behavior (i.e. not during playbacks); they comprised less than 1% of 15 533 calls observed during focal observations conducted in the same areas as these playback experiments (Wright, unpubl. data). These spontaneous squeals occurred only in situations of active aggression between pairs or individuals, further suggesting that their use during playbacks constituted an aggressive response by nest pairs towards duets of their own dialect.

We found no differences in any response measure among the six experimental duet stimuli when responses were combined across all treatments (incidence of movement: Fisher's exact test, $n = 29$, $p = 0.18$; distance moved: Kruskal-Wallis test, $n = 29$, $df = 5$, H corrected for ties = 5.7, tied $p = 0.34$; incidence of squeals: Fisher's exact test, $n = 29$, $p = 0.09$; incidence of contact calls: Fisher's exact test, $n = 29$, $p = 0.76$; incidence of pair duets: Fisher's exact test, $n = 29$, $p = 0.34$). The lack of differences among the six stimuli suggests that responses to the treatments were not biased by the small number of stimuli relative to the number of pairs tested.

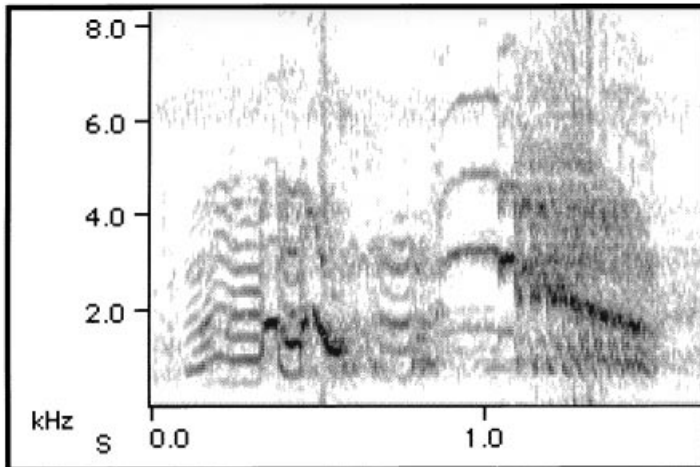


Fig. 5. A spectrogram of two squeal notes given by a pair from Pelon Bajura in the southern dialect in response to a local, same dialect playback treatment

There was no detectable bias in the order of presentation among the experimental treatments and congeneric control (Fisher's exact test, $n = 39$, $p = 0.27$). We also did not detect any difference in response measures between the first presentation in a session and the last, regardless of treatment (incidence of movement: Fisher's exact test, $n = 22$, $p = 1.0$; distance moved: Mann-Whitney U-test, $n = 22$, $p = 0.97$; incidence of squeals: Fisher's exact test, $n = 22$, $p = 1.0$; incidence of contact calls: Fisher's exact test, $n = 22$, $p = 0.64$; incidence of pair duets: Fisher's exact test, $n = 22$, $p = 1.0$). These tests indicate that pairs became neither habituated nor sensitized to playback stimuli during a playback session.

Discussion

Yellow-naped amazon pairs responded more strongly to duets from their own dialect than to those from a foreign dialect. Pairs responded to local duets with movement towards the loudspeaker and, more rarely, with aggressive squeals. These responses were never observed during playbacks of duets from foreign dialects or from a sympatric congener. Responses to duets from distant sites within the same dialect were generally intermediate in strength to responses for local and foreign dialect duets.

These parrots respond to playbacks of different dialects in a manner similar to that described for a wide range of oscine species. Nelson (1998) reviewed results from 11 playback studies on nine species of oscine songbirds and found that territorial males responded more strongly to local songs than to those from foreign dialects in seven of these species. Two other studies reported stronger responses to foreign dialects than to local, and Nelson's own study found no differences in responses to the two types of song (Nelson 1998). However, other studies on the same species have found strongest responses to local songs (Milligan & Verner 1971; Tomback et al. 1983; Thompson Jr & Baker 1993). Thus the general pattern in songbirds, with a few clear exceptions, is for stronger responses by territorial males to local songs than to songs from foreign dialects. Our results extend the generality of this pattern to a second group of birds with vocal dialects.

Two primary hypotheses have been proposed for the general pattern of stronger territorial responses to local than to foreign dialects in songbirds. One hypothesis views this response pattern as a byproduct of species song recognition, in which the songs that elicit the strongest behavioral responses are those that most closely match an individual's internal representation of their species' standard song (Dabelsteen & Pedersen 1992; Lampe & Baker 1994; Nelson 1998). According to this 'recognition' hypothesis, the pattern of weaker behavioral responses to foreign dialects results simply from their acoustical dissimilarity to the local dialect. An underlying assumption of the 'recognition' hypothesis is that songs from the local dialect predominate in the formation of the internal species' standard, to the extent that foreign dialects are not recognized as conspecific (Nelson 1998). This assumption may be less tenable in systems where individuals disperse across dialect boundaries and are exposed to multiple dialects before settlement.

An alternative hypothesis suggests that local dialects elicit stronger behavioral responses because singers of local songs represent a greater threat to territorial ownership than do foreign dialect singers (Rothstein & Fleischer 1987; Temeles 1994). The ability to produce local songs may signal the extent of an individual's experience in an area (Feekees 1977; Rothstein & Fleischer 1987), which in turn may improve its ability to take over a territory (Payne et al. 1988; Beecher et al. 1994). This 'relative threat' hypothesis does not assume limited dispersal of individuals across dialect boundaries, but rather suggests that birds which disperse would be under selection to learn local song types during settlement. Post-dispersal learning occurs in several songbird species (Nelson 1992; Beecher et al. 1994; Bell et al. 1998).

These two hypotheses address different levels of the behavioral response process. The 'recognition' hypothesis is a proximate explanation that focuses on the recognition and classification of playback stimuli; the 'relative threat' hypothesis is an ultimate explanation for why animals differ in response to these stimuli. Distinguishing the relative importance of these two levels is a general problem for field playback experiments (Falls 1992; Weary 1992). In the case of yellow-naped amazons, our playback results do not allow us to distinguish between these two hypotheses, but other evidence suggests that the assumption of low dispersal among dialects, which underlies the 'recognition' hypothesis, is not valid for this species. A recent study of genetic variation in this species revealed high levels of gene flow between the same two dialects treated in this study, indicating that individual dispersal among these dialects is commonplace (Wright and Wilkinson, unpubl. data). The existence of dialects in the face of such gene flow suggests that local vocal types are learned after dispersal, in accordance with the 'relative threat' hypothesis and as found in many songbird species (Nelson 1992; Beecher et al. 1994; Bell et al. 1998). Further study is required to document such learning and to determine whether using duets of the local dialect improves a pair's chances of gaining or retaining a nest site as predicted by the 'relative threat' hypothesis.

In contrast to previous studies in oscines, which used playbacks of male song, our study examined responses to dialect variants in pair duets. By definition, duets are a communication signal jointly produced by the male and female members of a pair and have typically been hypothesized to function either in maintenance of the pair bond or for coordinated defense of a resource (Farabaugh 1982; Arrowood 1988). Our playback results lend support to the coordinated defense hypothesis and suggests that duets in this species are used in the defense of nest sites, much as male song is thought to function in songbirds (Kroodsma & Byers 1991; Catchpole & Slater 1995). We observed aggressive responses by pairs to playbacks of some duets near their nest site; playbacks of conspecific song to male songbirds on their territories typically elicit similar reactions (Kroodsma & Byers 1991; Catchpole & Slater 1995; Stoddard 1996). Other parallels with male song include the conspicuous use of duets by pairs near their nests on a regular basis, and the extensive counter-duetting that occurs between neighboring pairs and between resident and intruding pairs (Wright 1997; Wright unpubl. data). Further playback studies of

parrots using pair duets will yield insight both into the function of duets and the mechanisms responsible for differential responses to dialect variation.

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Literature Cited

- Abacus Concepts 1995: Statview. Abacus Concepts Inc., Berkeley, CA.
- Arrowood, P. C. 1988: Duetting, pair bonding and agonistic display in parakeet pairs. *Behaviour* **106**, 129—157.
- Baker, M. C. & Cunningham, M. A. 1985: The biology of bird-song dialects. *Behav. Brain Sci.* **8**, 85—100.
- Baptista, L. F. & Schumann, K.-L. 1990: Song learning in the Anna hummingbird (*Calypte anna*). *Ethology* **84**, 15—26.
- Beecher, M. D., Campbell, S. E. & Stoddard, P. K. 1994: Correlation of song learning and territory establishment strategies in a songbird. *Proc. Natl. Acad. Sci.* **91**, 1450—1454.
- Bell, D. A., Trail, P. W. & Baptista, L. F. 1998: Song learning and vocal tradition in Nuttall's white-crowned sparrow. *Anim. Behav.* **55**, 939—956.
- Bradbury, J. B. & Vehrencamp, S. L. 1994: Singit!: a program for interactive playback on the Macintosh. *Bioacoustics* **5**, 308—310.
- Catchpole, C. K. & Slater, P. J. B. 1995: *Bird Song: Biological Themes and Variations*. Cambridge Univ. Press, Cambridge.
- Dabelsteen, T. 1992: Interactive playback: a finely tuned response. In: *Playback and Studies of Animal Communication* (McGregor, P. K., ed.). Plenum Press, New York, pp. 97—110.
- Dabelsteen, T. & Pedersen, S. B. 1992: Song features essential for species discrimination and behaviour assessment by male blackbirds (*Turdus merula*). *Behaviour* **121**, 259—287.
- Falls, J. B. 1992: Playbacks: a historical perspective. In: *Playback and Studies of Animal Communication* (McGregor, P. K., ed.). Plenum Press, New York, pp. 11—33.
- Farabaugh, S. M. 1982: The ecological and social significance of duetting. In: *Acoustic Communication in Birds* (Kroodsma, D. E. & Miller, E. H., eds). Academic Press, New York, pp. 85—124.
- Feekes, F. 1977: Colony specific song in *Cacicus cela* (Icteridae, Aves). The password hypothesis. *Ardea* **65**, 197—202.
- Gaunt, S. L. L., Baptista, L. F., Sánchez, J. E. & Hernandez, D. 1994: Song learning as evidenced from song sharing in two hummingbird species (*Colibri coruscans* and *C. thalassinus*). *Auk* **111**, 87—103.
- Hurlbert, S. H. 1984: Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**, 187—211.
- Krebs, J. R. & Kroodsma, D. E. 1980: Repertoires and geographical variation in bird song. *Advance Stud. Behav.* **11**, 143—177.
- Kroodsma, D. E. 1982: Learning and the ontogeny of sound signals in birds. In: *Acoustic Communication in Birds, Volume 2: Song Learning and its Consequences* (Kroodsma, D. E., Miller, E. H. & Ouellet, H., eds). Academic Press, New York, pp. 1—24.
- Kroodsma, D. E. 1989: Suggested experimental designs for song playbacks. *Anim. Behav.* **37**, 600—609.

- Kroodsma, D. E. & Byers, B. E. 1991: The function(s) of bird song. *Am. Zool.* **31**, 318—328.
- Kroodsma, D. E., Vielliard, J. M. E. & Stiles, F. G. 1996: Study of bird sounds in the Neotropics: urgency and opportunity. In: *Ecology and Evolution of Acoustic Communication in Birds* (Kroodsma, D. E. & Miller, E. H., eds). Cornell Univ. Press, Ithaca, pp. 269—281.
- Lampe, H. M. & Baker, M. C. 1994: Behavioural response to song playbacks by male and female white-crowned sparrows of two subspecies. *Bioacoustics* **5**, 171—185.
- Milligan, M. M. & Verner, J. 1971: Inter-population song dialect discrimination in the white-crowned sparrow. *Condor* **73**, 208—213.
- Mundinger, P. C. 1982: Microgeographic and macrogeographic variation in the acquired vocalizations of birds. In: *Acoustic Communication in Birds, Volume 2: Song Learning and its Consequences* (Kroodsma, D. E. & Miller, E. H., eds). Academic Press, San Diego, pp. 147—208.
- Nelson, D. A. 1992: Song overproduction and selective attrition lead to song sharing in the field sparrow (*Spizella pusilla*). *Behav. Ecol. Sociobiol.* **30**, 415—424.
- Nelson, D. A. 1998: Geographic variation in song of Gambel's white-crowned sparrow. *Behaviour* **135**, 321—342.
- Nielsen, B. M. B. & Vehrencamp, S. L. 1995: Responses of song sparrows to song-type matching via interactive playbacks. *Behav. Ecol. Sociobiol.* **37**, 109—117.
- Nottebohm, F. 1972: The origins of vocal learning. *Am. Nat.* **106**, 116—140.
- Nottebohm, F. & Nottebohm, M. 1969: The parrots of Bush Bush. *Anim. Kingdom* **72**, 18—23.
- Payne, R. B., Payne, L. L. & Doehlert, S. M. 1988: Biological and cultural success of song memes in indigo buntings. *Ecology* **69**, 104—117.
- Pepperberg, I. 1992: What studies of learning can teach us about playback design. In: *Playback and Studies of Animal Communication* (McGregor, P. K., ed.). Plenum Press, New York, pp. 47—57.
- Petrinovich, L. & Patterson, T. L. 1981: The responses of white-crowned sparrows to songs of different dialects and subspecies. *Z. Tierpsychol.* **57**, 1—14.
- Rothstein, S. I. & Fleischer, R. C. 1987: Vocal dialects and their possible relation to honest status signalling in the brown-headed cowbird. *Condor* **89**, 1—23.
- SAS Institute, 1996: SAS Software for Mac V6.12. SAS Institute Inc., Cary, N.C.
- Slater, P. J. B. 1989: Bird song learning: causes and consequences. *Ethol. Ecol. Evol.* **1**, 19—46.
- Snow, D. W. 1968: The singing assemblies of little hermits. *Living Bird* **7**, 47—55.
- Sokal, R. R. & Rohlf, F. J. 1995: *Biometry*. W.H. Freeman, New York.
- Stoddard, P. K. 1996: Vocal recognition of neighbors by territorial passerines. In: *Ecology and Evolution of Acoustic Communication in Birds* (Kroodsma, D. E. & Miller, E. H., eds). Cornell Univ. Press, Ithaca, pp. 356—374.
- Temeles, E. J. 1994: The role of neighbors in territorial systems: when are they 'dear enemies'? *Anim. Behav.* **47**, 339—350.
- Thompson, A. D. Jr & Baker, M. C. 1993: Song dialect recognition by male white-crowned sparrows: effects of manipulated song components. *Condor* **93**, 414—421.
- Tomback, D. F., Thompson, D. B. & Baker, M. C. 1983: Dialect discrimination by white-crowned sparrows: reactions to near and distant dialects. *Auk* **100**, 452—460.
- Weary, D. M. 1992: Bird song and operant conditioning: a new tool to investigate song perception. In: *Playback and Studies of Animal Communication* (McGregor, P. K., ed.). Plenum Press, New York, pp. 201—210.
- Wiley, R. H. 1971: Song groups in a singing assembly of little hermits. *Condor* **73**, 28—35.
- Wright, T. F. 1996: Regional dialects in the contact call of a parrot. *Proc. Roy. Soc. (Ser. B)* **263**, 867—872.
- Wright, T. F. 1997: *Vocal communication in the yellow-naped amazon (Amazona auropalliata)*, PhD Dissertation, Univ. of California, San Diego.
- Zar, J. H. 1984: *Biostatistical Analysis*. Prentice Hall, Englewood Cliffs, New Jersey.

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