SHORT COMMUNICATIONS

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CULTURAL DIVERSIFICATION IN THE FLIGHT CALL OF THE RINGNECK PARROT IN WESTERN AUSTRALIA[1]

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Abstract. I investigated geographic variation in a parrot vocalization to obtain an understanding of cultural population differentiation and exchange between hybridizing taxa. The flight calls of Ringneck Parrots (*Barnardius zonarius*) were tape recorded in Western Australia within and outside the zone of overlap and hybridization between the Port Lincoln (*B. z. zonarius*) and Twenty-eight (*B. z. semitorquatus*) subspecies. Measured variables distinguished the Twenty-eight call from those in the overlap populations. Although birds in typical Twenty-eight plumage were present in the overlap zone, no Twenty-eight flight calls were found, suggesting convergence by immigrants. Populations within the hybrid zone also were acoustically differentiated as dialects associated with roosting areas. Observations on the social behavior of the birds indicated that this call functions in coordination of movements of the mated pair. Roost-specific dialects might aid pairs in finding each other in the event of separation during the day's foraging activity.

Key words: Barnardius zonarius, *dialects, flight call, hybrid zone, Ringneck Parrot, social behavior.*

Although parrots are widely known to be vocal learners, field studies of acoustic signals of this group are rare. Dialects, a frequent consequence of vocal learning, have been described in a large number of songbird species (oscine passerines), yet of the 332 parrot species world-wide (Forshaw 1977), in only one case has documentation of vocal dialects been published (Wright 1996). Dialects in two other parrot species are implied in verbal descriptions by Nottebohm and Nottebohm (1969) and Saunders (1983). The cultural differentiation represented by dialects in learned communication signals raises questions about how the geographic differences are established and what, if any, functional significance might be attributed to such cultural markers (Baker and Cunningham 1985).

I studied geographic variation in a vocalization of the Ringneck Parrot, *Barnardius zonarius,* in Western Australia (WA). A morphologically distinct subspecies, the Twenty-eight Parrot (*B. z. semitorquatus*) occupies the southwestern corner of WA, whereas the nominate Port Lincoln Parrot (*B. z. zonarius*) occupies the south central portion of WA and extends eastward into South Australia (Higgens 1999). In a broad zone of overlap and hybridization, including the Perth area and a portion of the wheatbelt region of WA, these two forms occur together with obvious hybrids and backcross phenotypes (Serventy and Whittell 1962, Fisher 1970). In the zone of overlap and hybridization within 50 km of Perth, I identified visually the characteristic plumage phenotypes of both *B. z. semitorquatus* (hereafter *semitorquatus*) and *B. z. zonarius* (hereafter *zonarius*) as well as various intermediate plumages suggesting hybridization.

Naturalists had noticed previously that the "call notes" of *semitorquatus* and *zonarius* sound different (Serventy and Whittell 1962), and field guides mention it as well (Pizzey 1980). Thus, my first objective was to describe differences in these calls of birds in the *semitorquatus* distribution compared to those in the Perth area overlap zone. My second objective was to determine whether the populations exhibited vocal dialects within the overlap zone.

METHODS

STUDY AREAS

From 1 March through 30 May 1999, I tape-recorded vocalizations of the Ringneck Parrot at five sites in Western Australia (Fig. 1). In Perth, I recorded in Kings Park, adjacent to the Swan River, and in Bold Park, 4.8 km northwest of Kings Park. Recordings were also made along a 2-km segment of the Helena Valley Road adjacent to Gooseberry Hill National Park, 21 km west and slightly north of Kings Park, and in Yanchep National Park, 50 km north and slightly west of Kings Park. These four sites will be referred to as the Perth area sites. A fifth recording site was along Donnelly Road and Kevill Road West near Margaret River, approximately 225 km south and somewhat west of Kings Park. The Perth area sites lie within the hybrid zone, whereas the Margaret River site includes only *semitorquatus.*

I also examined a few calls recorded near Greenbushes, WA, 90 km east of Margaret River in the *sem-*

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TABLE 1. Comparison of flight calls ($\bar{x} \pm$ SE) of Ringneck Parrots in the Perth area (n = 16) and at Margaret River (n = 17). Tabled values are measurements taken on seven acoustic variables. Significant overall heterogeneity was found between locations, and all pairwise comparisons for each variable were significantly different.

Variable	Perth Area	Margaret River
1st note frequency range (Hz)	1,243 ± 110	677 ± 34
1st note mid-frequency (Hz)	2,604 ± 49	2,175 ± 23
1st note duration (sec)	0.119 ± 0.006	0.142 ± 0.007
Interval between notes (sec)	0.056 ± 0.004	0.129 ± 0.006
2nd note frequency range (Hz)	618 ± 44	279 ± 38
2nd note mid-frequency (Hz)	2,841 ± 33	2,275 ± 26
2nd note duration (sec)	0.136 ± 0.004	0.161 ± 0.003

itorquatus range (J. Hutchinson, pers. comm.), and near Alice Springs, Northern Territory, east of the hybrid zone within the range of *zonarius*. Neither the Greenbushes nor Alice Springs samples were adequate for statistical analyses.

PLUMAGE VARIATIONS

B. z. zonarius is bright green with a black head, bluing on the cheeks, a bright yellow collar (hence "ringneck"), and a sharply demarked bright-yellow belly. *B. z. semitorquatus* differs in being all-green below and possessing a bright-red frontal band above the beak. This red band is sometimes reduced or absent in females. Intermediate plumages in the hybrid zone were most noticeable in the differing amounts of yellow/green feathering in the belly and in the amounts of red feathering in the frontal band (Higgens 1999). All three classes of plumage were seen in all the Perth area recording sites.

BEHAVIOR AND VOCALIZATIONS

The fundamental year-round social unit of the Ringneck Parrot is the mated pair (Immelmann 1968, Fisher 1970). The pair travels and forages together, but commonly consorts with small numbers of conspecifics in loose and fluid groupings during the day. In the nonbreeding season, for the areas in which I conducted my study, ringnecks usually assembled in traditional roosting areas in the late afternoon. During the day, I was able to follow pairs for considerable time, especially in Kings Park and Bold Park where numerous trails aided my mobility and undergrowth was often sparse enough to allow easy passage. Sometimes such a pair would be alone for an hour or more as they moved about foraging and perching, but eventually they would join a small number of others for a time, and then the group would break up. At the roosting area in the late afternoon, many birds accumulated, spent the night, and ranged outward from the roost area the next morning.

The most common call recorded was termed the flight call because it was produced mainly when one bird of a pair took flight and emitted this call while the other bird followed, itself often calling as well. Sometimes a bird continued uttering the flight call after it landed and was answered by the following bird as it joined the first. The same call was given whether the birds took flight spontaneously (no obvious cause) or if disturbed by human, dog, or automobile and took flight as a result. This call has been referred to by others as a contact call, flight call, or alarm call (Forshaw 1964, Pizzey 1980, Higgens 1999). My observations suggested that this call is a within-pair signal employed in coordinating movements and indicating location if separated, as suggested also by the observations of Immelmann (1968). Random sampling of calls for measurement and inclusion in statistical analysis insured that calls of mated pairs were not both included in the sample, except intentionally to illustrate convergence.

TABLE 2. Comparison of flight calls of Ringneck Parrots recorded at four sites (n = 10 birds each site) in the Perth area. Tabled values are means ± SE of measurements taken on seven acoustic variables. Significant overall heterogeneity was found among populations, and pairwise comparisons[a] revealed significant differences between sites for individual variables.

Variable	Kings Park (KP)	Bold Park (BP)	Helena Valley (HV)	Yanchep (YA)
1st note frequency range (Hz)	1,378 ± 81	1,101 ± 78	926 ± 93	866 ± 57
1st note mid-frequency (Hz)	2,651 ± 29	2,699 ± 47	2,822 ± 70	2,654 ± 43
1st note duration (sec)	0.092 ± 0.004	0.080 ± 0.003	0.106 ± 0.003	0.142 ± 0.003
Interval between notes (sec)	0.041 ± 0.003	0.059 ± 0.004	0.050 ± 0.003	0.072 ± 0.006
2nd note freq. range (Hz)	699 ± 43	585 ± 35	605 ± 25	528 ± 35
2nd note mid-frequency (Hz)	2,963 ± 34	2,875 ± 22	2,884 ± 34	2,882 ± 23
2nd note duration (sec)	0.125 ± 0.002	0.117 ± 0.006	0.133 ± 0.004	0.136 ± 0.004

[a] Significant differences between samples for: 1st note frequency range: KP-BP, KP-HV, BP-YA; 1st note mid-frequency: KP-HV, HV-YA; 1st note duration: KP-HV, KP-YA, BP-HV, BP-YA, HV-YA; Interval between notes: KP-BP, KP-YA, HV-YA; 2nd note frequency range: KP-BP, KP-YA; 2nd note mid-frequency: KP-BP, KP-YA; 2nd note duration: BP-HV, BP-YA.

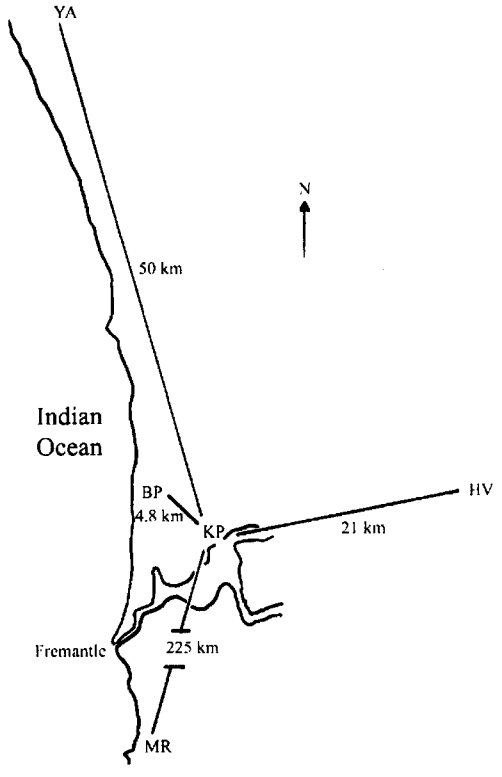

FIGURE 1. Sampling locations of Ringneck Parrot vocalizations in Western Australia. Sites within the zone of overlap and hybridization of *Barnardius zonarius zonarius* and *B. z. semitorquatus* are: KP (Kings Park), BP (Bold Park), HV (Helena Valley), YA (Yanchep). Site MR (Margaret River) is west of the overlap zone and comprises only *B. z. semitorquatus.*

RECORDING AND SPECTROGRAPHIC ANALYSES

Vocalizations were recorded on a Marantz cassette deck (PMD 201) at a tape speed of 4.8 cm sec^{-1} employing a Sennheiser microphone (model ME62) and amplifier mounted in a 45-cm diameter parabolic reflector. Spectrographic analyses were conducted with Kay Elemetrics MultiSpeech and RealTime Spectrogram operating on a computer configured with an audio card and software. Analog-to-digital conversion was 16 bit with a 44.1 kHz sampling rate. Spectrograms were produced with a 512 point (126 Hz) transform and Hamming analysis window. Measurements of frequency and time characteristics of the call were made on the computer screen using the cursor-generated values. Only one call per bird was used in the analysis.

STATISTICAL ANALYSES

All flight calls have two different major notes that occur as a pair. These pairs of notes are most often produced in strings of variable number and at variable rates of delivery. In some populations, a brief note occurs in front of and nearly attached to the first note of the major pair, but not all individuals possess this introductory note. Therefore, all measurements used in statistical analyses were made on the two major notes. This resulted in seven variables: the frequency range, mid-frequency, and duration of each of the two notes, and the interval between them. Multivariate analysis of variance (MANOVA, Harris 1975) was applied to the seven variables. Pairwise comparisons among populations were made for each variable separately by Fisher's LSD, which adjusts for the experimentwise error rate (Carmer and Swanson 1973).

RESULTS

Audible properties of the flight call were easily distinguished between the Perth area ringnecks and those of *semitorquatus* at Margaret River (Fig. 2, 3). Recordings of ringnecks made at Greenbushes, WA, within the distribution of *semitorquatus,* also closely followed the structure of those recorded at Margaret River (Fig. 3, bird A). The different-sounding call of *semitorquatus* is readily discriminated by ear and does not require instrumental analysis for identification by an observer. I spent several hundred hours recording birds of a number of different species in these populations and heard several thousand Ringneck Parrot flight calls. I never heard a *semitorquatus* flight call in the Perth area or a *zonarius* flight call in the Margaret River population. Unpublished sonograms (Rex Buckingham, Bird Observers Club of Australia) of flight calls recorded from ringnecks near Alice Springs, Northern Territory, east of the overlap zone, are similar to ringneck calls from the Perth area.

To examine the statistical differences in the acoustic features of the Perth area birds compared to Margaret River *semitorquatus,* I randomly selected four calls from each of the four Perth area locations to represent a group ($n = 16$) to compare to all the calls recorded at Margaret River ($n = 17$; Table 1). Comparing the Margaret River birds to those of the Perth area for the set of seven variables by MANOVA, the two samples were significantly different (Wilks' lambda = 0.12, $P < 0.001$). Multiple comparisons tests (Fisher's LSD) showed that all seven measured features of these calls differed between the two samples.

In the Perth area samples, I visually identified, and in some cases recorded, birds presenting the full red frontal band and green belly of *semitorquatus.* There also was an abundance of typical *zonarius* plumages as well as those birds with hybrid plumage features. There were, however, no cases of flight calls that corresponded to the acoustic features of the Margaret River birds.

Microgeographic variation occurred in the flight calls in the Perth area samples. I randomly selected 10 calls from each of the four Perth area recording sites. MANOVA results on these samples revealed significant heterogeneity among populations for all seven acoustic variables (Wilks' lambda = 0.04, $P < 0.001$; Table 2). Pairwise comparisons (Fisher's LSD) among populations showed consistent differentiation of the flight call variables, suggesting that each population could be referred to as a different dialect. In addition to the mensural features of the flight calls, certain populations differed in the general shapes of the notes and

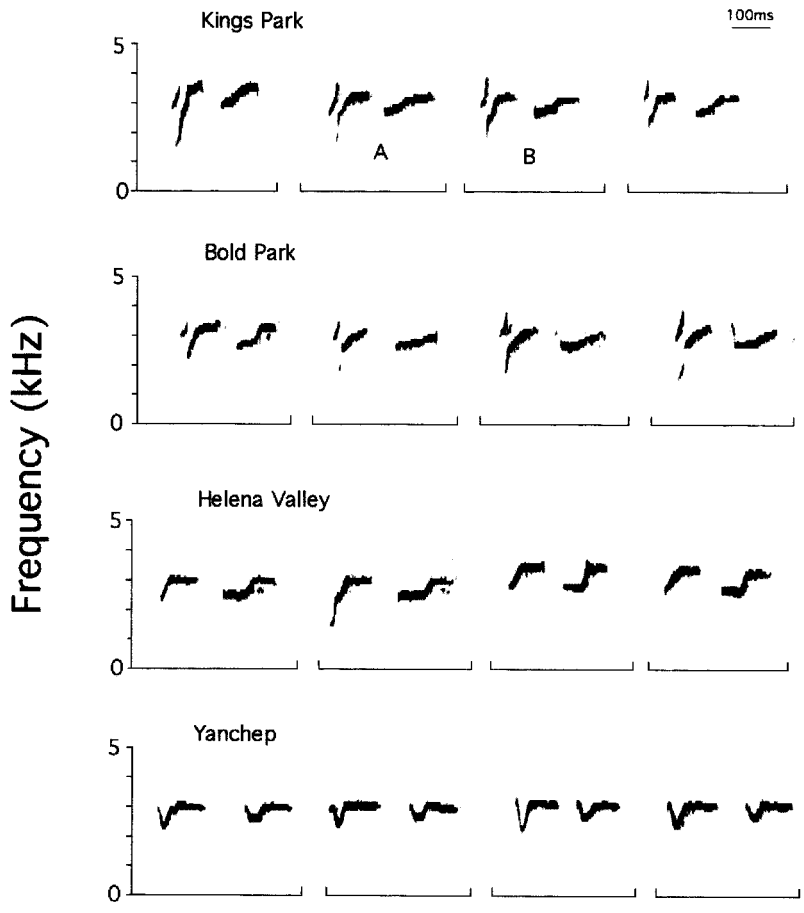

FIGURE 2. Sound spectrograms of flight calls representative of Ringneck Parrots in the Perth area samples. Brackets on the abscissa enclose different individuals. Included are examples from birds from the Yanchep population that were in *B. z. semitorquatus* plumage, the plumage typical of Margaret River ringnecks. Also included are the calls of a mated pair (Kings Park, A and B), indicating convergent features that may imply individual recognition.

in the presence or absence of the introductory note (Fig. 2).

DISCUSSION

The flight calls of *B. z. semitorquatus* at Margaret River and Greenbushes differ from those of birds in the Perth area samples, the latter comprising individuals in *B. z. zonarius* plumage, *semitorquatus* plumage, and hybrids of these two morphs. In addition, there are population differences in acoustic features of the flight calls among the four samples from the Perth area, each sample location corresponding to a major roosting assemblage.

The Margaret River birds are all phenotypically *semitorquatus,* as are other populations of the extreme southwest area (Fisher 1970). They are thought to derive from a late Pliocene or early Pleistocene invasion from the Bassian region of eastern Australia across the southern edge of the continent into the southwest corner of Western Australia (Serventy and Whittell 1962). A period of aridity isolated this population and differentiation occurred over time. These events were followed by moistening of the environment and a second spread of *Barnardius* into Western Australia. Thus ensued secondary contact leading to the existing zone of overlap and hybridization (Serventy and Whittell 1962, Fisher 1970).

Although it is clear that more samples are needed from the entire range of *B. zonarius,* the data are sufficient to raise several questions for further study. Why, for example, do all the birds in the zone of hybridization, at least in the Perth area sites I sampled, possess relatively similar acoustic features distinctly different from those of *semitorquatus*? One possibility is that upon secondary contact, and since then, relatively small numbers of *semitorquatus* dispersed into more dense populations of *zonarius* and altered their vocalizations to converge on the local acoustic features

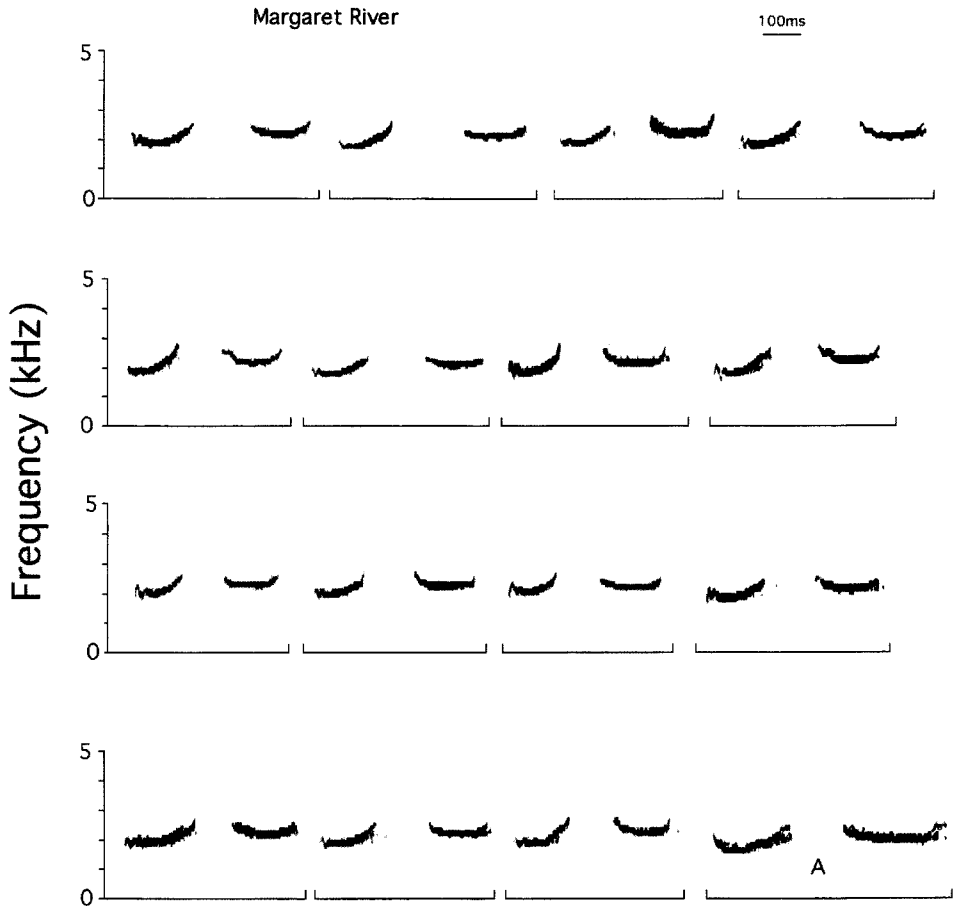

FIGURE 3. Sound spectrograms of flight calls representative of Ringneck Parrots of Margaret River *B. z. semitorquatus*. Bird A, lower right, is from a recording of *B. z. semitorquatus* made by John Hutchinson 90 km east of Margaret River near Greenbushes, Western Australia.

of the flight call encountered there. The characteristic flight call of *semitorquatus* is lost from the hybrid zone even though morphotypes of the subspecies are present in substantial numbers. There may be several contributing factors to such a model of one-way cultural exchange and extinction of the *semitorquatus* form of the flight call in the zone of overlap. First, there may be a semi-permeable habitat barrier that inhibits *zonarius* from entering the range of *semitorquatus* but not vise versa. The western border of the hybrid zone corresponds to a belt of jarrah (*Eucaplytus marginata*) forest mixed with marri (*E. calophylla*), which has been implicated in limiting the westward spread of a number of bird species (Serventy and Whittell 1962). To the west and south is increasingly moist habitat and, correspondingly, an increasing prevalence of the tall forests of karri (*E. diversicolor*). East of the jarrah belt the habitat is more savannah-like, and following the clearing of native vegetation has been turned over to farming, thus constituting the western wheatbelt of Australia. Here, trees of the southwest eucalypt forests are mostly restricted to stream-beds (Seddon 1972). Therefore, the moist and heavily forested habitat of *semitorquatus* may inhibit a westward movement of *zonarius,* but the prevalence of the rich food resources of cereal crops in the wheatbelt may attract *semitorquatus* eastward into the dryer habitat.

In addition, a south-to-north dispersal corridor along the Swan Coastal Plain for *semitorquatus* apparently exists as a consequence of the jarrah, marri, and tuart (*E. gomphocephala*) forest tree species. Tuart, for example, is limited to the Swan Coastal Plain and extends from the Vasse district deep in the distribution of *semitorquatus* to its limits at approximately Yanchep in the north (Seddon 1972). Together with jarrah and marri in the Swan Coastal Plain, these forest species may provide a passageway. This mix of eucalypts is well represented in Kings Park and in Bold Park areas, for example.

A second issue involves the advantages for an immigrant to adopt the flight call features of the local area. A possible advantage of flight call convergence

in local populations, and the consequent geographic differentiation, can be hypothesized by consideration of the use of the flight call in relation to the social structure of these birds. Parrots are typically long-lived with long-term pair bonds, pairs remaining together year round (Saunders 1983, Rowley 1990), and perennial pair bonds in long-lived birds translate into higher reproductive success (Rowley 1983). In Ringneck Parrots, the flight call is the most frequent call produced and is performed in the context of coordinating movements and maintaining pair contact. Birds converge to a night roosting area from which they range out in the morning. In and near the general roosting area are nest sites of some of the pairs, as I judged by occasionally seeing pairs linger in the vicinity of and enter such cavities. All my recording sites were based upon roosting aggregations where I could record birds congregating in the late afternoon and dispersing from the area in the mornings. Movements to and from such roost areas were gradual, which sometimes allowed me to follow pairs and record flight calls when given.

This general description of roosting congregations and daily movements of pairs suggests a possible function of the locale-specific features of the call. If the members of a pair are faithful to a roosting locale but become separated during the day and lose contact with each other while ranging out from the roost area, then following a roost-specific flight call back to the evening aggregation would enable the pair to regain contact. Upon reaching the roosting location there may be a traditional place where the pair spends the night, or they may be able to locate one another from specific and convergent flight call features that are shared by the pair (e.g., Fig. 2, birds A and B; Saunders 1983). Thus, the roost-specific properties (dialect) of flight calls could provide an acoustic map, probably operating in concert with landmarks, which enable a pair to regain their association.

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