GEOGRAPHICAL VARIATION IN THE CONTACT CALLS OF ORANGE-FRONTED PARAKEETS

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ABSTRACT.—We examined patterns of geographic variation in contact calls of Orange-fronted Parakeets (*Aratinga canicularis*) during the nonbreeding season. Calls were recorded throughout the range of that species in Costa Rica. Recordings of wild-caught birds held for one to two weeks indicated that each individual favors one dominant call type and different birds use different favored calls. We used that fact to cull replicate calls from the same individual in field recordings of flocks observed at various locations throughout the sample area. Remaining recordings from a given year were submitted to spectrographic cross-correlation and principal coordinates analysis as described by Cortopassi and Bradbury (2000). Principal coordinates were then correlated with site location using MANOVA. Call durations were also examined for geographical patterns. Like sympatric Yellow-naped Parrots (*Amazona auropalliata*) studied over the same region by Wright (1996), Orange-fronted Parakeets exhibited significant geographic variation but, unlike the larger species, showed no discrete dialect patterns. Call duration varied clinally but with different patterns for the Nicoya Peninsula and the Guanacaste mainland. Two principal coordinates also showed clinal variation even after removing any correlated duration effects. Scale over which local calls were statistically homogeneous was 7–10 km. We compared that figure to home ranges of 18 birds radio-tracked concurrently with call sampling. Both range areas and range lengths were asymptotic after a week of tracking. Asymptotic range lengths were 2–9 km. Scale of movements of birds, at least during that period, was thus similar to distance within which calls tended to be statistically homogeneous. This study and that by Wright show that several well-known patterns of geographical variation seen with passerine song are replicated quite closely in contact calls of parrots, despite the fact that the functions of vocal signals are quite different in the two taxa. *Received 30 August 2000, accepted 24 April 2001.*

VOCAL LEARNING HAS evolved independently several times in birds (Kroodsma 1982). That is reflected in the fact that two of the relevant taxa, parrots and songbirds, use different parts of the syrinx to make their vocal signals (Nottebohm 1976, Gaunt and Gaunt 1985, Suthers et al. 1999) and different parts of their brains to control sound production (Brenowitz 1991, Ball 1994, Striedter 1994, Durand et al. 1997, Jarvis and Mello 2000, Nespor 2000). An obvious question is whether or not the same selective forces have favored vocal learning in those taxa. To answer that question, one needs to know adaptive functions of vocal learning in each group. Whereas songbirds largely use vocal learning for competitive mate attraction, territory defense, and group recognition (Catchpole and Slater 1995), we as yet know little about the function of vocal lability in parrots, and then only for a few species.

In songbirds, vocal learning often results in intraspecific heterogeneity in vocal signal structure. The same passerine may have several different songs that it can sing, and that set may be different from that of other males of the species. In some cases, that variability is itself favored because of social consequences of song selection (e.g. Vehrencamp 2000). In others, selection for local homogeneity coupled with cultural drift between populations may be the source of variation (Lynch 1996). Often, spatial patterns of such variation, including degrees of overlap between repertoires of nearby and distant individuals, provide critical insights into functions of vocal learning (Slater 1989, Lynch 1996). It is with that expectation in mind that we examined geographical variation in contact calls of Orange-Fronted Parakeets (*Aratinga canicularis*).

Typical parrots produce 10–15 distinct call types (Hardy 1963, Brereton and Pidgeon 1966, Noske 1980, Wyndham 1980, Pidgeon 1981, Saunders 1983, Martella and Bucher 1990, Row-

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ley 1990). One of those is very loud, usually produced by both members of a pair in flight, and often exchanged by members of a pair or group when spatially separated but still within earshot. That is usually called the "contact call" (Farabaugh and Dooling 1996). Because it is perhaps the easiest call to record in wild parrots, it is the best known. Wherever they have been examined, contact calls of wild parrots show marked intraspecific variation. Nottebohm (1976, Nottebohm and Nottebohm 1969) noted apparent dialects associated with contact calls of different flocks of Orange-winged Parrot (*Amazona amazonica*). Saunders (1983) reported differences in contact calls of Black Cockatoos (*Calyptorhynchus funereus*) at different night roost sites, and Noske (1980) noticed a similar difference between two night roosts of White Cockatoos (*Cacatua galerita*). The first quantitative study of intraspecific variation in a wild parrot was that of Wright (1996). He mapped contact-call variants of Yellow-naped Parrots (*Amazona auropalliata*) throughout their range in northwestern Costa Rica. He found significant between-individual variation and clear links between call similarity and either social or geographic affiliation. Calls of members of the same pair were more similar to each other than either was to calls of other pairs at the same communal night roost, and calls of members of the same night roost were more similar than those from birds using different night roosts. Most striking was partitioning of the range of that species in Costa Rica into three contiguous but nonoverlapping geographical dialects. Dialects were qualitatively different and boundaries were sharp. Although some birds roosting near to boundaries were able to vocalize in both dialects, they never melded them.

In this paper, we describe geographical variation in contact calls of Orange-fronted Parakeets over the same areas sampled by Wright for sympatric Yellow-naped Parrot call variation. Both species are part of a small assemblage of parrots that occurs throughout dry seasonal forests of western Central America. Although the two species can often be found feeding in adjacent vegetation, they differ markedly in body size, diet, and social dynamics. Parrots have nearly 5 × the mass of parakeets. Whereas Guanacaste parrot populations favor the large fruit and hard nuts of emergent trees (e.g. *Enterolobium*, *Cochlospermum*, and *Quercus*; T. F. Wright pers. comm.), parakeets feed on seeds and pulp of small fruit from a variety of low-lying secondary plant genera such as *Byrsonima*, *Cordia*, *Croton*, and *Bursera* (J. W. Bradbury pers. obs.). Parrots largely forage and move about as single mated pairs even in areas of high population density. Parakeets are much more social during the day than parrots and forage in tightly coordinated flocks that may temporarily fuse with other flocks. Except during nesting, parrots return to the same communal sleeping trees night after night. Those sites are used for decades and are invariably tall trees with skimpy foliage. Night roost staging is noisy and the birds continue making calls and local repositions long after sunset. In contrast, our radio-tracked parakeets rarely sleep in the same tree two nights in a row and typically use trees 2–5 km apart on successive nights. Although they are also highly vocal during staging, they then cache themselves inside the dense canopies of small trees such as *Cochlospermum vitifolium* and remain silent until dawn.

Our goals in this paper are to provide an initial overview of intraspecific variation in contact calls of parakeets and compare any patterns found to those of sympatric Yellow-naped Parrots over the same geographical region. We first captured wild birds and held them in aviaries for one to two weeks to determine number of contact calls per individual and the short-term stability of calls. We then recorded contact calls from wild parakeets along transects in the same study areas sampled by Wright. As a reference scale for geographical variation in contact calls, we radio-tracked individual birds to determine home range dimensions at the same time of year as the recordings. The results paint a markedly different picture of contact call spatial variation from that seen in the parrot study.

METHODS

Study sites.—We recorded Orange-fronted Parakeets at 14 sites throughout the species range in Guanacaste Province of Costa Rica during the early rainy season (June–August) of 1995, 1996, and 1997. Site numbers, site names, and geographical center points for each site are listed below in north-to-south order: (1) Cuajiniquil Junction (10°56.80′N, 85°38.36′W); (2) Pocosol (10°53.42′N, 85°35.97′W); (3) Finca Centeno (10°52.63′N, 85°34.18′W); (4) Fin-

ca Jenny (10°51.71′N, 85°34.51′W); (5) Santa Rosa National Park (10°50.01′N, 85°37.08′W); (6) Hacienda Pelon (10°50.61′N, 85°33.84′W); (7) Quebrada Grande (10°48.95′N, 85°32.28′W); (8) Cañas Dulces (10°42.98′N, 85°30.21′W); (9) Liberia (10°38.65′N, 85°27.52′W); (10) Bagaces (10°31.66′N, 85°17.26′W); (11) Cañas (10°27.28′N, 85°7.66′W); (12) Huacas (10°20.44′N, 85°47.10′W); (13) Hernandez (10° 15.18′N, 85°47.71′W); and (14) Gloria (9°56.852′N, 85°2.42′W). All recordings assigned to a given location were made within 1.5 km of the center point for that site.

We examined geographical variation at three different scales. Recordings of contact calls from eight of the sites in 1995 bracketed the species' range throughout Guanacaste Province (sites 1, 3, 6, 11–14). The two most distant sites were 129 km apart with adjacent clusters of sites separated by 40–60 km. That is our coarse-grained sample. In 1996, we obtained an intermediate-grained sample by recording at eight of the sites along a 67 km mainland transect of the Pan American highway (sites 3, 5–11). Mean distance between all sites was 29 km (range 4–71 km). Adjacent sites were separated by an average 11 km (range 4–22 km). In 1997, we obtained an intensive fine-grained set of recordings from four locations 2–7 km apart centered around the entrance to Santa Rosa National Park (sites 2–6). In each year, all geographical samples were collected within a 45 day period, and the same time of year was used in successive years (mid-June to late July).

Captive studies.—Wild birds were mist-netted at each of four different foraging and night-staging sites within 7 km of the entrance to Santa Rosa National Park. In several cases, members of the same flock were captured simultaneously. Captives were weighed, measured, and marked with numbered metal leg bands provided by park authorities. They were then held in a 4 × 2 × 3 m hardware cloth and wood aviary for 1–2 weeks. A rain shelter was provided on the end opposite to the observation blind and numerous perches were scattered throughout. A platform on one side supplied fresh food and water. The birds were fed fruit of wild plants highly popular with parakeets at that time of year (*Byrsonima crassifolia, Cordia guanacastensis, Croton reflexifolius,* and *Bursera tomentosa*). Some individuals also ate seeds of domesticated guavas. Birds released as groups into the aviary began eating by the second morning and usually maintained weight throughout the week in captivity. Captives vocalized spontaneously from the start allowing for extensive sets of recordings on each bird. Wild parakeets frequently over-flew the aviary stimulating exchanges of contact calls between captives and wild birds. Some wild flocks even landed on the aviary and elicited extensive interactions with captives. Wild birds were all released at their capture sites.

Recording methods.—Contact calls of wild birds were recorded by approaching flocks to within 40 m and recording all vocalizations with Sennheiser MKH 816 P48 directional microphones fed into either SONY DAT-12 or TEAC DA-P20 digital recorders. A concurrent voice track was used to provide annotations on behaviors of the birds, habitats, and geographic locations. The latter were obtained using Scout Global Positioning System (GPS) receivers (Trimble Navigation, Tulsa, Oklahoma). For many sites, samples represent recordings from more than one flock. However, that was not always possible given mobility of the birds and limited off-road access. Captive birds were recorded using the Senneheiser microphones and Canon Hi-8 video cameras. Video tape recordings were used to identify which captive bird made which vocalization.

Sound analyses.—Field and captive recordings were band-pass filtered at 0.1–10 kHz, digitized at 44.1 kHz, and converted into spectrograms using CANARY (Cornell Laboratory of Ornithology, Ithaca, New York) (1996 captive data and all transect samples) or SIGNAL (Engineering Design, Belmont, Massachusetts) (1997 captive data). Spectrograms were generated using a 684 Hz bandwidth, 256 pts/frame, 75% overlap of frames in successive transforms, and a Hanning sampling window. Those settings were found to provide representations of different parts of the call that were stable in either the time or frequency domain across all calls examined. For no two calls was one section seen in the time domain for one call and in the frequency domain for the other. In addition to spectrographic structure, durations were measured for all calls.

Geographical sample selection.—Because we wanted to assess degree to which call-structure variation between sites exceeded that within a site, we needed to ensure that measures of variation within a site were not distorted by including repeat recordings from the same bird. It was usually impossible to identify which bird in a flock produced a given recording. The captive portion of this study showed that wild-caught birds largely produced a single distinctive call type, even when responding to wild over-flying conspecifics. We thus used levels of within-call type variation seen in captives to cull repeats of any call type included within a regional sample of calls. There is a risk that that culling resulted in an underestimate of local homogeneity. We feel that is an acceptable risk, because our null hypothesis is that there is no systematic variation associated with site, and thus our culling makes it more difficult to obtain significant between-site differences. It is also reassuring that very similar fractions of calls in each site were culled using that criterion.

Statistical comparisons.—Call durations from different sites were compared using standard statistical methods. Data were transformed where necessary to ensure homoscedasticity. We compared fine-struc-

tures of calls using spectrographic cross-correlation (SPCC) and principal coordinates analysis (PCO). Details of that combined procedure are outlined in Cortopassi and Bradbury (2000). The advantage of SPCC over discrete measurements on spectrograms is that no *a priori* assumptions need be made about which spectrogram parameters are worthy of measurement. SPCC compares entire spectrograms. The disadvantage is that all differences between two spectrograms have equal weight. PCO helps resolve the latter problem by separating systematic similarities present in sets of spectrograms from random variants and noise. The result of the analysis is a set of parameter values (the principal coordinates) that allow statistical comparisons between calls just as one would undertake with direct measurements.

We used CANARY to create matrices of SPCC similarity coefficients for each set of spectrograms being contrasted. Principle coordinates were then extracted using the R Package (see Acknowledgments). The first five principal coordinates usually captured most of the between-spectrogram variation and thus were used in all statistical tests. We compared the mean principal coordinate values for calls from different captive birds or for calls from different recording sites using standard one-way MANOVA and linear discriminant analysis (LDA) methods (Tabachnick and Fidell 1996). Results of those contrasts were summarized using Wilk's λ, the strength of association parameter, η^2 (roughly equivalent to the r^2 of a regression), the fraction of cases properly assigned to bird or site by LDA after cross-validation, and estimated probability of the result. For the three geographical contrasts, we also show 95% confidence plots for the first two linear combinations of principal coordinates, (called "canonical variates"), that are used by MANOVA and LDA in assessing whether birds or sites are significantly different or not (Johnson 1998). We also performed orthogonal *post hoc* tests to determine which site contrasts contributed most to a significant overall difference among sites. It is known that call durations can affect SPCC values (Cortopassi and Bradbury 2000). Whenever a principal coordinate was correlated with duration, we removed duration effect using regression and repeated the relevant MANOVA and LDA using the residuals. That allowed us to evaluate effect of geographical location on call fine structure independent of call duration. Regressions and MANOVA were performed using the Macintosh program JMP (Version 4, SAS Institute Inc., Cary, North Carolina). LDA and *post hoc* contrasts were performed on SPSS (Version 8, SPSS Inc., Chicago, Illinois).

The spatial scale over which geographic call similarity extended was estimated for our intermediate-grained sample using correlograms (Upton and Fingleton 1985, Legendre and Legendre 1998). Those plots used Moran's I to relate the similarity of call principal coordinates or canonical variates to spatial

proximity of the recording sites. Correlograms were generated using the R Package. Because correlograms compute multiple values of Moran's I, a Bonferroni correction was applied to all significance tests.

Radiotracking.—Radio-tracking was used to estimate home ranges of parakeets during the same period when call transects were sampled. Birds were fitted with a 148 MHz (AVM Instrument Company, Colfax, California) radio-transmitter collar developed especially for this species, and released at the netting site. Maximum battery life for transmitters was limited to 30 days; actual life was shorter because the collars were designed to come off and often did so before the batteries expired. Tracking relied on four-element directional Yagi antennas and either AVM LA-12, Televilt RX900, or Televilt RX8910 (TVP Positioning AB, Lindesberg, Sweden) receivers. Geographic location was obtained using Scout GPS receivers. All radio-tracking was undertaken in the same years and at the same season (mid-June to mid-August) as geographical and captive bird samples were collected.

Home range data were based on daily locations of morning foraging, midday resting, and evening sleeping sites for each tracked individual. Given the topography, signals were not obtained when birds dropped into stream valleys. When signals were lost, we made extensive searches throughout a 20 km area until the signal was regained. Minimum convex polygon and Fourier utilization home range areas were computed using our own program ANTELOPE. (see Acknowledgments). All points were used in computation of polygon ranges; only independent points (Schoener 1981) were used in Fourier computations.

RESULTS

STRUCTURE OF CONTACT CALL

The contact call of this species was first described by Hardy (1963) who called it the "intrapair *chee-chee*" call. It is the loudest vocalization that we have recorded in the parakeet repertoire. Values of 90–95 dB SPL at 2 m are typical. Mean call duration is ~205 ms (range 180–220 ms), within-individual variation is ~5%, and between-individual differences average 11%. Every individual of this species that we have recorded produces that call type and all show the same basic three-segment structure (Fig. 1): a rising harmonic series based on a 0.8–1 kHz fundamental, a subsequent section whose fundamental is frequency modulated stepwise from 3 kHz to and from 5 kHz, and a final descending harmonic series with frequen-
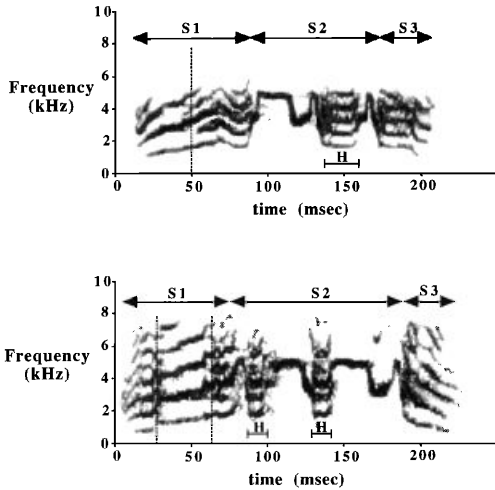
FIG. 1. Spectrograms of Orange-fronted Parakeet contact calls from two different individuals. Arrows and labels (S1, S2, S3) indicate equivalent segments in two calls. Harmonic stacks (H) and mode transitions (vertical dashed lines) are also marked.

cies similar to those in the first part. Short harmonic "stacks" may be inserted into any part of that basic pattern. Calls often have intrinsic noise scattered amid the rich harmonic structure. They can also show sudden discontinuous "mode" jumps in fundamental frequency. Both features may reflect a chaotic sound generation process as seen in Zebra Finches (*Taeniopygia guttata*; Fee et al. 1998).

CAPTIVE RECORDINGS

A total of 20 captives were examined. Eleven birds were netted at two sites in 1996, and eight birds netted at two sites different from the prior year in 1997. All four sites were within 7 km of each other. A stratified random rule was used to pick 20 contact calls from each of the 1996 birds and 40 calls from each of the 1997 ones (except for one bird that was released early because of poor feeding). Stratification broke up the captive period so that different days and different parts of each day were represented in each sample.

Visual inspection of captive-bird spectrograms suggested that each bird had one dominant contact call pattern and that patterns varied between birds. Those impressions were supported by statistical analyses. Comparisons of the first five principle coordinates extracted

from calls showed highly significant between-bird differences for both years (MANOVA: 1996: Wilk's λ = 0.020, η^2 = 78%, P < 0.0001; 1997: Wilk's λ = 0.001, η^2 = 92%, P < 0.0001). LDA classification with cross validation resulted in 79 and 95% correct classifications for the two years, respectively.

Plots of captive birds' calls using the first two canonical variates of the MANOVA showed that each bird's calls tend to cluster in one small region of the overall canonical space and many clusters did not overlap at all (Fig. 2). However, at least half of the birds occasionally produced a call outside of their main cluster of points. We are reasonably sure from our video records that those secondary variants are indeed from the same bird and not sounds assigned to the wrong caller. Thus, many birds can produce more than one call type. However, secondary variants appear to be given rarely, and we relied on that fact to correct for possible repeat recordings of the same individual in our transect data.

GEOGRAPHICAL TRANSECTS

Coarse-grained samples.—In 1995, we divided the entire Costa Rican range of this species into four broad regions and obtained 10 distinct calls per site at one or more sites per region. The northern region sample consisted of 30 calls recorded at three locations within 12 km of each other and centered on the entrance to Santa Rosa National Park (sites 1, 3, and 6). The mid-western region provided 20 calls from two sites near the towns of Huacas (site 12) and Hernandez (site 13), respectively. The center point of that region is 62 km south and west of the northern regional center. The southeastern region provided 10 calls recorded from a single site on the mainland near Cañas (site 11). That region was 67 km south and east of the northern region and 72 km east of the midwestern region. The southern region provided 10 calls recorded near Gloria on the southern tip of the Nicoya Peninsula (site 14). That location is 90 km south and east of the midwestern region center and 56 km south of the southeastern region. Those samples span the region examined by Wright (1996) for Yellow-naped Parrot contact calls.

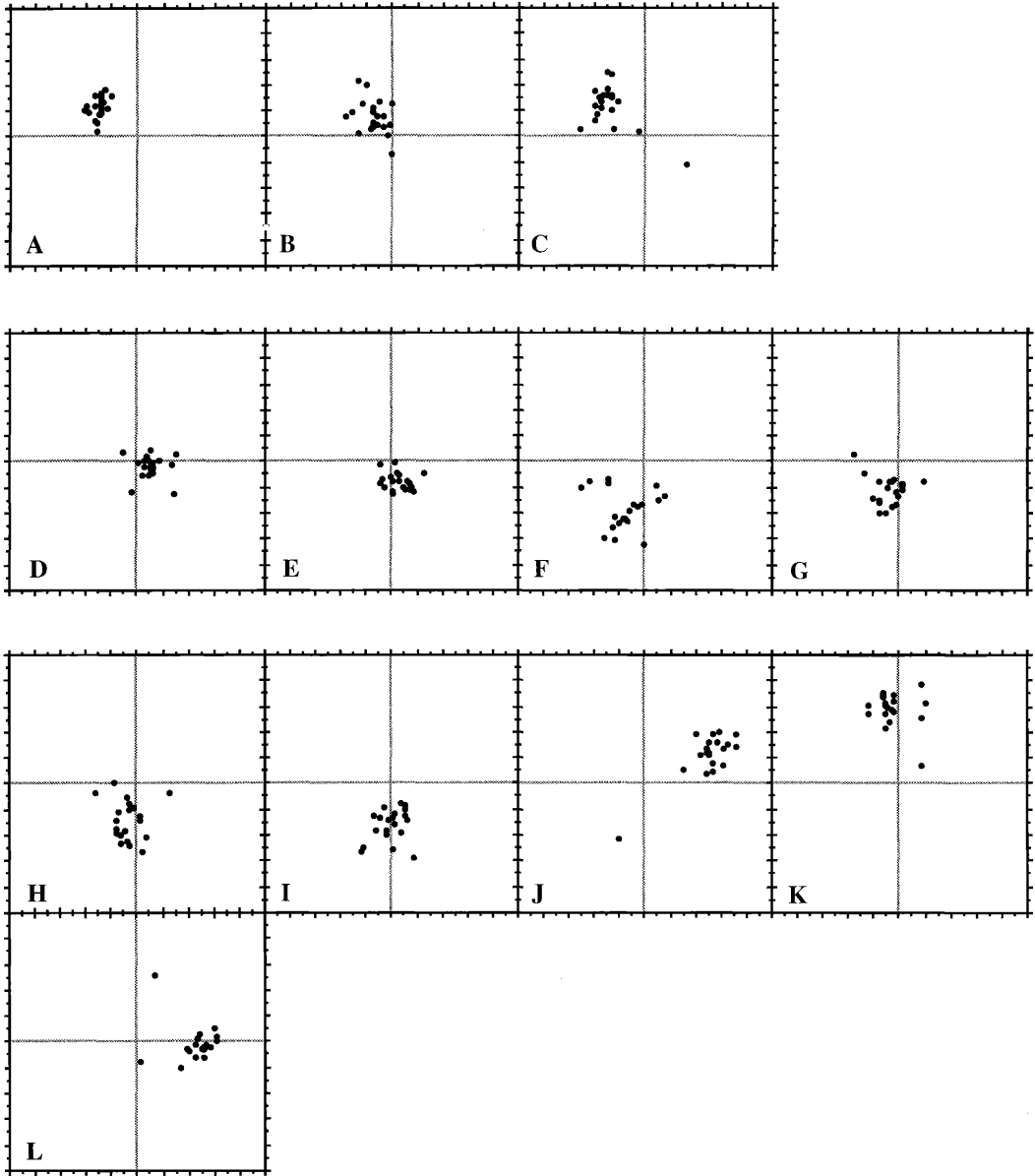Mean call duration was quite variable between regions (CV = 9%). That was partly due

FIG. 2. Within- versus between-individual variation in spectrographic structure of Orange-fronted Parakeet contact calls. Each plot shows 20 calls from a given individual captured in 1996. Axes are first (vertical) and second (horizontal) canonical axes from MANOVA comparisons of call principal coordinate values. All plots are on the same scale with the same origin. Because only two canonical axes are shown, these plots show minimal separation between individual birds. Adding additional axes creates additional separation among the birds in this sample. Birds A–C were netted at the same location. The remaining birds were netted at a second site on two different dates (D–G on first occasion, H–L on second).

to a consistent decrease in call duration along the axis connecting the most northern sites and the southern end of the Nicoya Peninsula (regression of call duration on distance from most northern site: $r = -0.553$, $n = 60$, $P < 0.0001$). A separate gradient in duration along the mainland coast (involving only the southeastern region in this analysis) is described below.
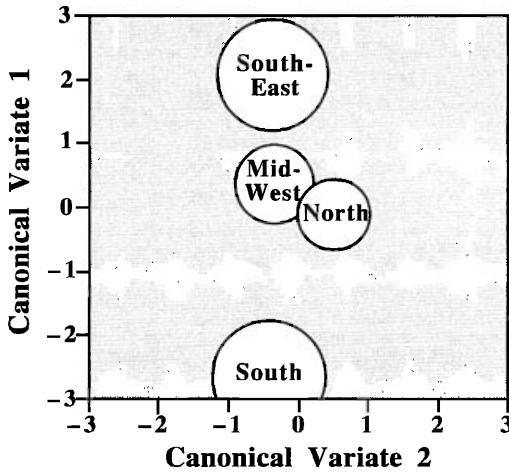
FIG. 3. Geographical variation in contact calls from the coarse-grained transect of 1995. Calls were sampled in four regions bracketing the species' range in Costa Rica. Axes are the first two canonical variates produced using MANOVA of principal coordinates onto region. Each axis is a linear combination of principal coordinates that maximally separates the regions. The first axis provides the best such separation, and the second provides the next best separation after removing the effects of the first axis. Confidence circles (95%) indicate relative amount of within-region variation in call structure. Differences between regions are significant as shown by the minimal overlap of their confidence circles. Both canonical variates in this plot produce significant regional separation ($P = 0.0001$). Southeast region = site 11; mid-west region = sites 12, 13; north region = sites 1, 3, 6; south region = site 14.

The four regions differed significantly in call structure as measured by the first five principal coordinates (MANOVA: Wilk's $\lambda = 0.174$, $\eta^2 = 44\%$, $P < 0.0001$; LDA assignment = 67% correct; Fig. 3). Because of the duration gradient along the Nicoya Peninsula, we repeated analyses with duration effects removed, but differences in call structure between regions remained significant (Wilk's $\lambda = 0.288$, $\eta^2 = 34\%$, $P < 0.0001$; LDA assignment = 57% correct). We used *post hoc* tests to compare contributions of specific regions to the overall result. The southern region differed significantly from the mean of the other three regions (Wilk's $\lambda = 0.390$, $\eta^2 = 61\%$, $P < 0.0001$), the southeastern region differed significantly from the mean of the northern and midwestern regions (Wilk's $\lambda = 0.535$, $\eta^2 = 47\%$, $P < 0.0001$), and the northern and midwestern regions differed signifi-

cantly from each other (Wilk's $\lambda = 0.595$, $\eta^2 = 41\%$, $P < 0.0001$). A repeat analysis with duration-corrected principal coordinate values gave similar results (all $P < 0.0001$; $\eta^2 = 40$–43%).

Intermediate-grained analysis.—In 1996, we collected 71 distinct contact calls from eight different sites (sites 3, 5–11) along a 67 km mainland Guanacaste transect. Six sites provided 10 distinct calls each, one produced six, and the last produced five calls. Distances between adjacent sites varied from 4 to 23 km.

There was again noticeable variation in call duration among the sites (CV = 4.8%). That reflected a consistent gradient running from north to south (regression of duration on the square root of distance from most northern site: $r = 0.422$; $n = 71$, $P = 0.0002$). In contrast to the Nicoya Peninsula gradient, in which more southerly calls were shorter, mainland calls became longer as one moved south.

Despite the shorter average distance between sites in that sample, calls still showed significant intersite differences (Wilk's $\lambda = 0.092$, $\eta^2 = 38\%$, $P < 0.0001$; LDA assignment = 52% correct; Fig. 4). As with the coarse-grained sample, corrections for duration effects did not change that conclusion (Wilk's $\lambda = 0.123$, $\eta^2 = 34\%$, $P < 0.0001$; LDA 42% correct). Of the seven orthogonal *post hoc* tests allowed, five were significant when duration effects were included, and those same five plus one additional contrast were significant when duration effects were removed (Fig. 5). Contrasts that failed to be significant always involved adjacent sample sites.

Several geographical patterns in addition to variation in call durations were observed in that sample. Overall spectrographic structure of calls varied linearly along the north–south axis of the transect (regression of the first MANOVA canonical variate on square-root of distance from northern-most site: $r = -0.712$, $n = 71$; $P < 0.0001$). That result remained significant even if duration effects were removed from principal coordinates before performing the MANOVA ($r = -0.448$, $n = 71$, $P < 0.0001$).

The geographic cline of the first canonical variate implies that calls from adjacent locations are more similar to each other spectrographically than those from more distant sites. To estimate the spatial scale over which call similarity is detectable, we constructed corre-
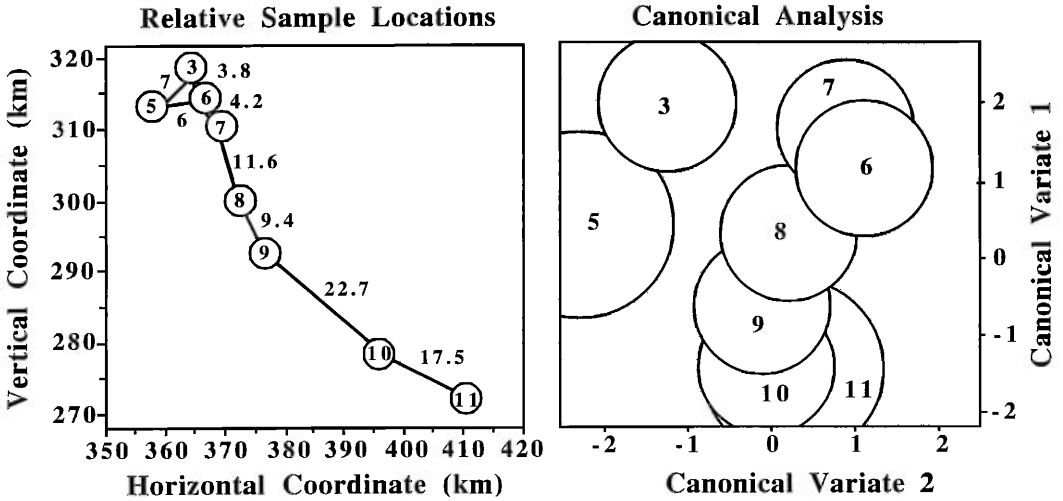
FIG. 4. Geographical variation in contact calls from the intermediate-grained transect of 1996. Left graph shows relative locations and site identification numbers of the eight locations used in this transect. Values next to line segments indicate distances (kilometers) between adjacent sampling sites. Right graph has same format as Figure 3. Note larger confidence circles and greater overlap than for coarse-grained samples. Note also that relative positions of the confidence circles in this graph are largely identical to actual geographical locations of sites shown in the left graph. The major difference is a vertical replacement of site 6 by site 7 in the right-hand graph. Both canonical variates in this plot provide significant site separation ($P < 0.0001$).

lograms for the first two canonical variates and their constituent principal coordinates (Fig. 6). Although several parameters show some positive autocorrelation for very close sites (4 km or less), only the second and third principal co-

Site	Post Hoc Contrast						
Site 3							
Site 5							
Site 6							
Site 7							
Site 8							
Site 9							
Site 10							
Site 11							
Raw Principal Coordinates Analysis							
Wilk's λ:	0.406	0.861	0.857	0.461	0.821	0.799	0.797
η^2 (%):	59	14	14	54	18	20	20
P:	0.000	0.108	0.097	0.000	0.036	0.018	0.017
Duration-Corrected Analysis							
Wilk's λ:	0.512	0.871	0.824	0.497	0.799	0.798	0.818
η^2 (%):	49	13	18	50	20	20	18
P:	0.000	0.139	0.039	0.000	0.019	0.018	0.033

FIG. 5. Within-transect comparisons of call structure for 1996 intermediate-grained sample. Vertical lines indicate sites included in a particular comparison, and horizontal partition indicates how those sites were subdivided into two groups for contrast. Contrast results are summarized below test lines. All *post hoc* tests shown within a box are independent of each other.

ordinates, and the first canonical variate (whose computation weights these two coordinates heavily), showed significant positive autocorrelation for both raw and duration-corrected data. All three variables also showed a rapid drop in spatial autocorrelation by 8 km separation and then a steady slide to significant negative spatial autocorrelation at maximal distances. The other principal coordinates and the second canonical variate showed no consistent changes in autocorrelation over distance.

Fine-grained analysis.—Five locations within 7 km of each other and centered on the entrance to Santa Rosa National Park were used in 1997 for a fine-grained spatial analysis (sites 2–6). Thirty distinct calls were collected for each site. Overall analysis showed some significant site specificity, but with much lower levels of association (η^2) than in the two prior analyses (MANOVA on uncorrected principal coordinates: Wilk's $\lambda = 0.501$, $\eta^2 = 16\%$, $P < 0.0001$; LDA assignment 37% correct; Fig. 7). The repeat analysis with duration-corrected principal coordinates was also significant (Wilk's $\lambda = 0.568$, $\eta^2 = 13\%$, $P < 0.0001$; LDA assignment = 35% correct). Unlike the coarse- and intermediate-grained samples, the *post hoc* contrasts for the fine-grained sample suggested that only
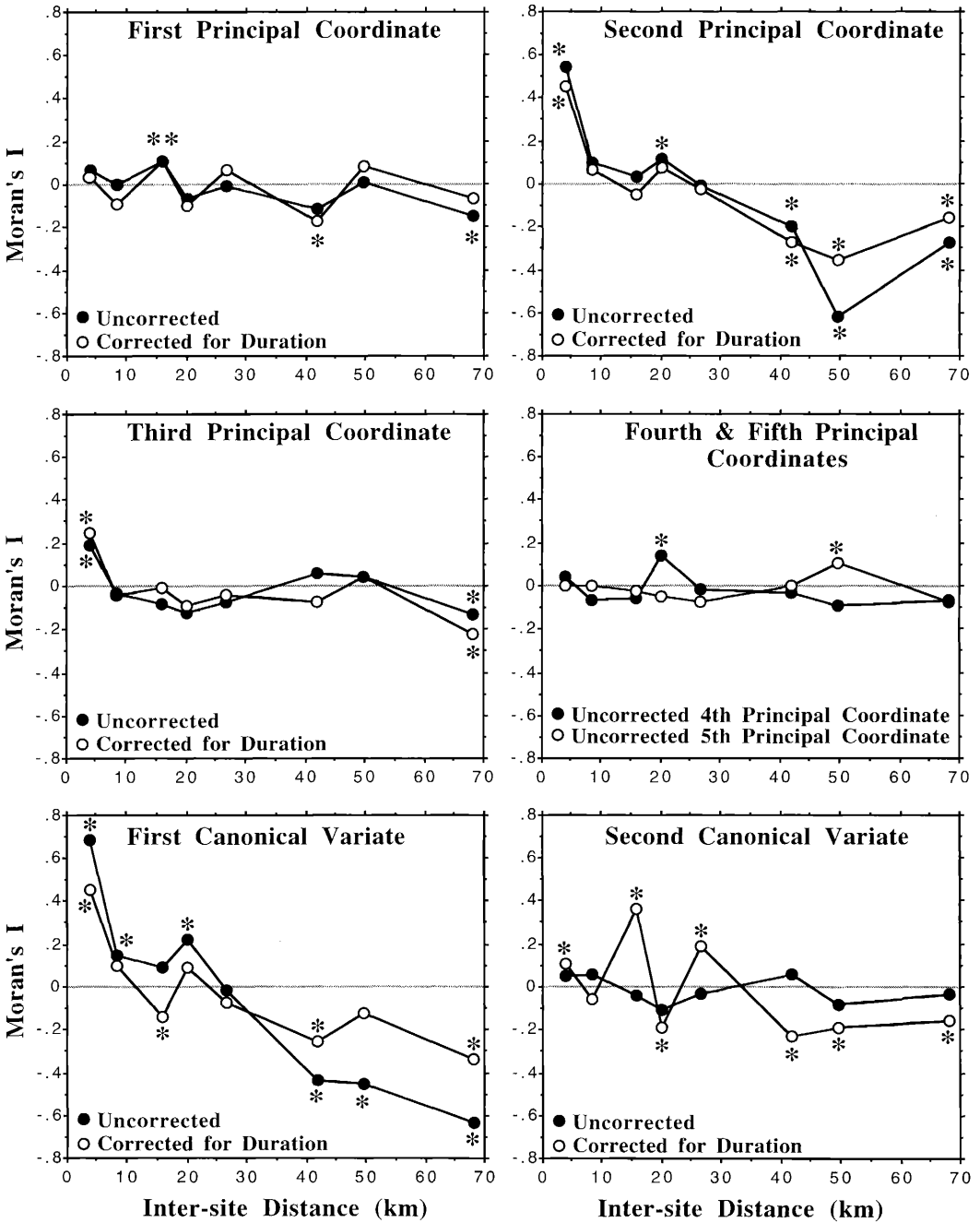
FIG. 6. Fall-off in levels of call similarity with increasing distance between sample sites in 1996. Moran's I is used as the measure of spatial autocorrelation with significant positive values indicating that sites separated by the given range of distances were more similar than expected by chance. Asterisks indicate significant values of I given a Bonferroni criterion probability of 0.00625 (Upton and Fingleton 1985). Where principal coordinates were correlated with call duration, plots for both raw and duration-corrected principal coordinates are given. Plots are also shown for the first two canonical variates both with and without duration corrections.
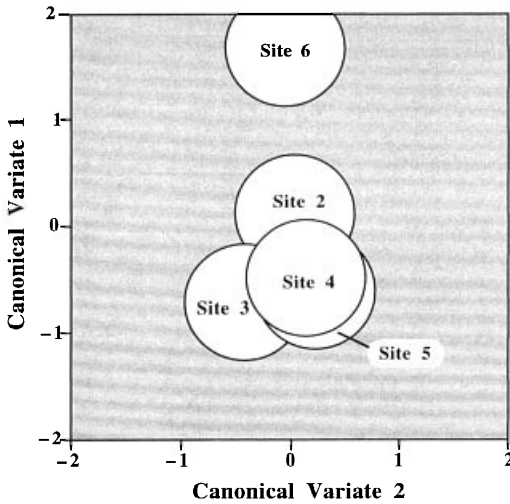
FIG. 7. Geographical variation in contact calls from the fine-grained transect of 1997. Format and axes similar to Figure 3. All sample sites are within 7 km of each other. The first canonical variate provides significant separation of some of the sites ($P < 0.0001$), whereas the second canonical variate does not ($P = 0.282$).

a single outlier site was the source of the significance for the overall test. Of the four independent contrasts possible in that data set, only one was significant for both raw and duration-corrected principal coordinates. That test compared site 6 with the other sites combined (Wilk's $\lambda = 0.578$, $\eta^2 = 42\%$, $P < 0.0001$; duration-corrected MANOVA: Wilk's $\lambda = 0.684$, $\eta^2 = 32\%$, $P < 0.0001$). It is of interest that site 6 differed from the remaining recording locations in that sample by being situated on a plain below the major escarpment on which the other sites are all located. If we discount that single site, then the fine-grained data show that sites 7 km or less apart do not differ significantly in call fine structure.

HOME RANGE ANALYSES

A total of 18 individual parakeets were successfully radio-tracked as part of this study. Radios remained on and working for at least five days for 15 of those birds (mean = 14 days), and 30 or more days for five individuals. Although home ranges were computed by both convex polygon and Fourier methods, results were so similar that we only present the convex polygon data here. Cumulative home ranges

measured by minimum convex polygon methods for birds with five or more days of tracking did not increase significantly with the duration of the tracking period ($r = 0.462$, $n = 15$, $P = 0.084$). Although a trend was apparent, that regression was dominated by a single outlier bird with a final home range 55% larger than that of any other individual in the sample (see Fig. 8, left column, third row). This bird spent the first 11 days at site 5 and then migrated 7 km away where it remained in a second small area near site 3 for the final 21 days. Deleting that bird reduces the correlation significantly ($r = 0.352$, $n = 14$, $P = 0.217$). Average final range area for all 15 birds was 666 ± 700 ha (SD). There was also no significant relationship between range length (maximum distance between any two locations inside the polygon home range area), and duration of sampling for birds with five or more days of tracking records ($r = 0.055$, $n = 15$, $P = 0.843$). Mean range length for the five birds with 30 or more days of tracking was 5.2 km (range 2.2–9.4 km), and that for the 10 birds with 5–16 days of tracking was 5.0 km (range 2.5–7.4 km). There was a trend for larger range lengths to take longer to be achieved, but that was also not significant ($r = 0.517$, $n = 15$, $P = 0.127$). Mean lag before achievement of maximal range length was 15.6 consecutive days (range 2–29 days).

Birds followed in the same and successive years showed extensive overlap in home ranges even after short periods of tracking (Fig. 8). One immediately wonders how much of that overlap might be due to birds moving in the same flock. For each pair of unmated birds radio-tracked concurrently, we computed number of occasions when they were within 100 m of each other during the same 1 h period, and number of occasions when we had sufficient tracking data to know their relative locations. Of the 42 pair-wise comparisons possible, 18 pairs of birds (43%) never used the same sites at the same time, whereas 24 pairs (57%) did so at least once. In the latter group, known birds were found together on average only 16 ± 10% (SD) of the possible occasions. After coming together, birds then separated and 2–15 days might pass before they encountered each other again. An average 54% of the shared sites were foraging locations and the remaining 46% were night roosts or midday resting areas. Thus, the overlap seen does not appear to arise from
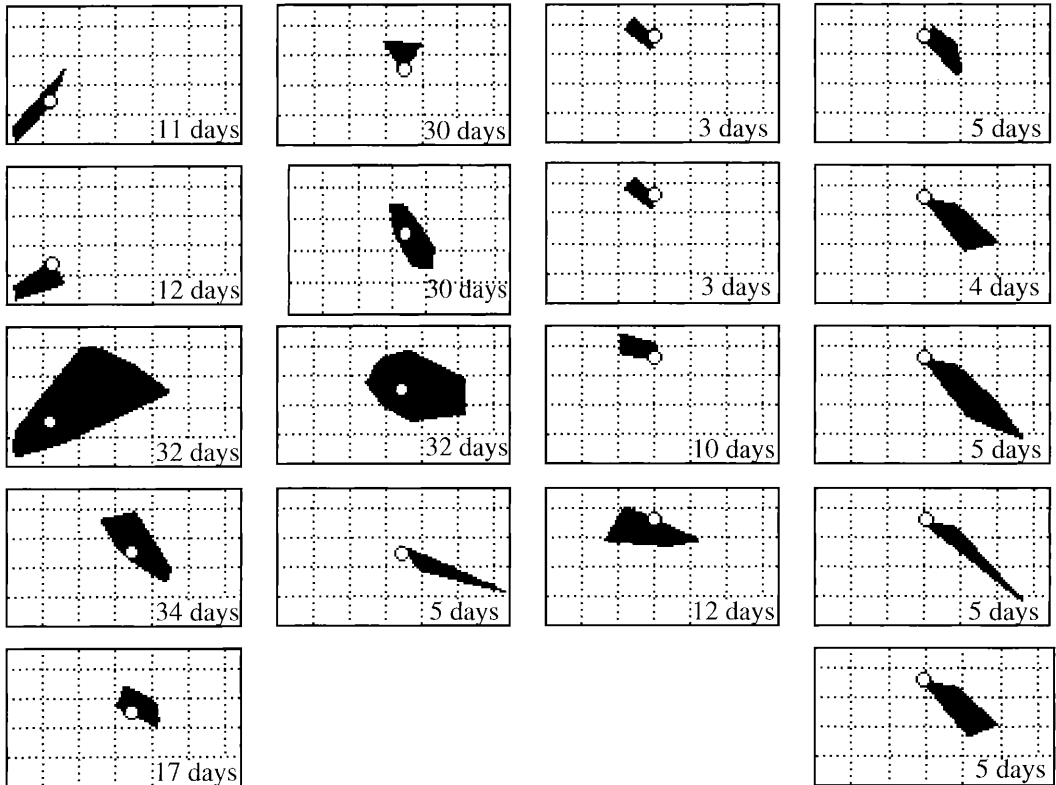
FIG. 8. Minimum convex polygon home range estimates for 18 Orange-fronted Parakeets radio-tracked in the same geographical space. Duration that radio remained on bird and working is indicated in lower right corner of each plot. Grid marks indicate 2 km intervals, and white circles indicate sites of initial capture. Each column groups birds that were followed contemporaneously. First column consists of 1993 samples, second column 1995, third column first half of 1996 season, and last column, last half of 1996 season.

common flock membership of our radio-tracked individuals.

DISCUSSION

Captive recordings.—Each of the 20 captive Orange-fronted Parakeets tended to produce a single contact call type and different birds largely produced different ones. However, like Budgerigars (*Melopsittacus undulatas*; Farabaugh and Dooling 1996), at least half the parakeets occasionally produced contact-call variants unlike their primary call. Unlike captive Budgerigars (Farabaugh et al. 1994, Bartlett and Slater 1999, Hile et al. 2000), we saw no evidence for consistent contact-call convergence by group-mates either among those birds captured at the same time and place, or among those held together in the same aviary. However, it often took several weeks for Budgeri-

gars to show call convergence and we only held birds for at most two weeks. Our studies do not preclude the possibility that wild parakeets change contact calls over longer periods.

Although it remains possible that the secondary contact call variants detected in some birds' repertoires might have been used more often in the wild, we think that is unlikely. Our captives often interacted with wild birds. In addition to daily vocal exchanges between over-flying flocks and captives, some wild flocks descended directly on top of the aviary and spent up to an hour interacting with captives. We often heard much of the normal parakeet repertoire during those exchanges. Despite those interactions, we never detected a shift by any captive away from its current dominant contact call pattern.

The significance of the captive work is that wild-caught birds are likely to use a single con-

tact call type for at least the intervals over which our transect samples were collected. Thus, our geographical samples can be considered "snap-shots" of overall variation at that time. Put another way, it is unlikely given our captive studies that the variation seen in geographical samples confounds geographic and short-term temporal variation. It should largely reflect only the current geographical pattern. As noted above, the observation that parakeets tend to use one dominant contact call type was invoked to cull apparent replicate calls from the same bird from each geographical sample. We did that to ensure that multiple recordings of the same individual did not lower within-site variability in call structure. One consequence is that actual within-site homogeneity may be greater than our samples would indicate.

Geographical variation.—We found significant differences in average contact-call structure for all sites that were at least 7–10 km apart and increasing differences in calls the further apart they were recorded. The minimal site distance for significant divergence was similar whether we examined variation within a transect (Fig. 6), compared MANOVA statistics and canonical plots across transects sampling at different scales (Figs. 3, 4, and 7), or related *post hoc* contrasts to distances between compared sites (Fig. 5). It is probably no accident that distance matches the typical range length of birds radio-tracked at the same time of year. One obvious interpretation is that individual home-range size limits the scale over which forces favoring local call homogeneity can operate.

Several measured call variables showed clinal and continuous variation along transects. Duration varied linearly along a north–south axis but with different gradients for the mainland and the Nicoya Peninsula. The second and third most important variables extracted by principal coordinate analysis from 1996 transect calls, and the canonical variate that was most dependent upon them, all showed steady clines such that differences between calls increased continuously with increasing distance between sampling sites. Those patterns were retained even after removing effects of relevant duration cline. Remaining principal coordinates extracted in that year and their corresponding canonical variate also differed between sites, but those differences were

insensitive to intersite distances. Of considerable interest is that the only geographical patterns seen were continuous rather than discontinuous. Despite sampling parakeets over the same area studied by Wright (1996) for sympatric Yellow-naped Parrots, we found no evidence for the discrete dialects seen in the larger species.

Causes of geographical pattern.—Our work and that of Wright (1996) show that two of the more common patterns of geographical variation in songbirds are replicated quite closely by parrot analogues. Yellow-naped Parrots show discrete dialects with contiguous boundaries (Wright 1996) rather like Corn Buntings (*Emberiza calandra*; McGregor 1980). Orange-fronted parakeets are here seen to produce the nondiscrete and more gradual variation reported for Indigo Buntings (*Passerina cyanea*; Payne 1996) or House Finches (*Carpodacus mexicanus*; Tracy and Baker 1999). What is interesting is that those parallels occur despite overwhelming evidence that respective vocal signals are used for quite different functions in parrots and songbirds. In songbirds, males do the major singing and songs are used to attract females and defend contiguous territorial boundaries against other males. In the two parrot species, pairs remain mated all year, home ranges of many different birds are completely overlapping, and both sexes use calls in hundreds of contexts other than mate selection or nest-site defense. If there are common causes for convergent spatial patterns in parrots and those songbirds, they must exist at some very general level.

There are two steps that presumably occur in generating spatial patterns like those observed here: (1) factors that promote local call homogeneity; and (2) factors that erode or accentuate local effects by mediating what happens to birds at boundaries between different homogeneous areas. Catchpole and Slater (1995) list maintenance of local genetic adaptations, call propagation optimization, founder effects, and social conformity as likely factors favoring local homogeneity in call structure. Wright and Wilkinson (2001) recently showed that there are no genetic differences between Yellow-naped Parrots using different dialects in Costa Rica. Continuous variation of parakeet calls also makes genetic adaptations an unlikely force favoring call convergence. Local adaptations for call propagation seem unlikely given the many

types of forest and open habitat used by a single parakeet flock each day and the similarity of habitats between nearby sites that we show here have different call patterns. Founder effects might explain some of the observed parrot patterns because there has been considerable habitat change in Guanacaste during the last few centuries, and thus opportunities for colonization. However, genetic data cited above indicate that Yellow-naped Parrots regularly migrate across dialect boundaries and yet all birds within a specific area use the same dialect. That means there must be some persistent factors that promote local homogeneity above and beyond periodic extinctions and recolonizations.

That leaves social conformity as the most likely factor favoring local call homogeneity. There are certainly strong indications that such a force may be playing a role in parrots. Captive Budgerigars show contact call convergence when kept in the same flock for extended periods (Brown et al. 1988, Farabaugh et al. 1994; Farabaugh and Dooling 1996, Bartlett and Slater (1999). Spectacled Parrotlets (*Forpus conspicillatus*) use variation in contact calls to discriminate between social associates and kin (Wanker et al. 1996, 1998). Budgerigar pairs show convergence in contact calls over time with males largely copying female patterns (Hile et al. 2000). Wright (1996) also found the highest levels of contact-call convergence when he compared mated pairs of Yellow-naped Parrots. We have not found any evidence for convergence in contact calls of birds captured in the same flock, and radio-tracking data presented here show marked exchanges of individuals between such flocks. That does not rule out social conformity, but suggests that the process in parakeets may be occurring at some level higher than a single mated pair or foraging group. In any case, the current study clearly suggests that identification of any forces favoring vocal conformity in parakeets should be a top priority for subsequent work.

The second set of factors shaping geographical pattern are those that modulate exchanges between adjacent homogeneous units. Our findings that parakeet vocal structure changes continuously over distance and that areas of local homogeneity are roughly commensurate with individual home ranges suggest that local homogeneity plus simple diffusion and drift

models as proposed for songbirds (Lynch 1996) might account for parakeet spatial patterns. Such an explanation will not work for the sympatric Yellow-naped Parrots. Genetic evidence shows that birds cross dialect boundaries often. Some explicit behavioral factors must force those immigrants to acquire the local dialect. Why Orange-fronted Parakeets and Yellow-naped Parrots living in exactly the same habitats should differ so markedly in enforcement of vocal conformity is one of the most interesting questions to come out of this study. It is clearly a second major topic that deserves serious field study and one that is likely to be tied to factors that favor vocal conformity in the first place.

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