Published in final edited form as:

Condor. 2008 November ; 110(4): 639–647. doi:10.1525/cond.2008.8609.

LIMITED GEOGRAPHIC VARIATION IN THE VOCALIZATIONS OF THE ENDANGERED THICK-BILLED PARROT: IMPLICATIONS FOR CONSERVATION STRATEGIES

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Abstract

The populations of many species are declining worldwide, and conservation efforts struggle to keep pace with extinction rates. Conservation biologists commonly employ strategies such as translocation and reintroduction, which move individuals of endangered species from one part of their range to another. Because individuals from endangered populations are nonexpendable, identifying any potential barriers to the establishment of viable populations prior to release of individuals should be a priority. This study evaluates the potential for learned communication signals to constrain conservation strategies such as reintroduction in an endangered species, the Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*). We conducted vocal surveys at three geographically distinct breeding populations in the Sierra Madre Occidental of Chihuahua, Mexico. Acoustic analyses utilizing both spectrogram cross-correlations and parameter measurements from spectrograms revealed no significant differences among the three sites in two common call types. Calls did vary among individuals within a site. The apparent lack of significant geographic variation across sampled sites suggests that differences in learned communication signals are unlikely to pose a barrier to the integration of translocated individuals from different populations into newly established populations.

Keywords

contact calls; parrot; reintroduction; *Rhynchopsitta pachyrhyncha*; Thick-billed Parrot; translocation; vocal variation

INTRODUCTION

The increase in the number of species experiencing decreased populations and even extinction over the past century has prompted a growing interest in tactics for species conservation (IUCN 2007). A broad array of strategies has been employed to stem this loss in biodiversity, including translocation and reintroduction (Griffith et al. 1989, Kleiman 1989, Beck et al. 1994). These latter strategies are defined as the intentional movement of individuals from an established wild population or a captive population, respectively, to establish or augment a different population within that species' historical range (Griffith et al. 1989, Kleiman 1989). These population management efforts, however, have met with

limited success (Griffith et al. 1989, Beck et al. 1994). Griffith et al. (1989) found that only 38% of the reintroductions between 1973 and 1986 were successful, while Beck et al. (1994) found that only 11% of 145 reintroductions conducted between 1900 and 1992 succeeded in creating wild populations of 500 or more individuals that were self sustaining. The low success rates of reintroductions cited by both studies suggest that further research identifying potential roadblocks to the establishment of viable new populations should be a conservation priority.

Social behaviors are one factor that could influence translocation success (Brightsmith et al. 2005, Teixeira et al. 2007). Many species depend on interactions with conspecifics for settlement decisions, efficient foraging, access to mates, reduction of energetic costs of movement, and protection from predators (Stamps 2001, Krause and Ruxton 2002). When group membership is exclusive, a newcomer may have difficulty integrating into a new social environment and thus not receive these benefits. Translocations and reintroductions often present new social environments in which a transplanted individual has to interact with completely unknown individuals and social groups. Thus, the stress of forced integration into a new social group could augment the physical stress experienced by animals already searching for new sources of food, water, and shelter (Kikusui et al. 2006, Teixeira et al. 2007). Chronic stress can impair the functioning of multiple physiological systems, resulting in diminished cognitive abilities, reduced growth, suppression of the immune system, and other negative effects (Bergman et al. 2005, Kikusui et al. 2006, Teixeira et al. 2007). The potential negative effects of stressors suggest that careful evaluation of the impact of social behaviors and group membership on individuals moved outside their normal population could improve the success of reintroductions.

A social behavior of potential importance to translocation or reintroduction success is communication via vocal signals. Animal species use vocalizations in a variety of contexts such as defending a territory, finding a mate, or recognizing individuals and group members (Bradbury 2003). In some species, these vocal signals may be learned and may vary among populations due to cultural evolution (Catchpole and Slater 1995). Geographic variation in learned vocalizations has been found in such taxa as songbirds (Marler and Tamura 1962, Nottebohm 1969, Avery and Oring 1977, Briskie 1999, Seibt et al. 2002, Slabbekoorn et al. 2003), cetaceans (Weilgart and Whitehead 1997, Stafford et al. 2001), parrots (Wright 1996, Baker 2000, Bradbury et al. 2001, Bond and Diamond 2005, Kleeman and Gilardi 2005), hummingbirds (Wiley 1971, Gaunt et al. 1994), and bats (Boughman and Wilkinson 1998). This geographic variation is behaviorally salient in many species, with individuals responding differently to vocalizations from their local populations versus those from foreign populations (Petrinovich and Patterson 1981, Nelson 1998, Wright and Dorin 2001). While vocal learning does offer a mechanism by which individuals could eventually match the vocalizations of a new group, there is some evidence that stress can diminish the ability of individuals to learn vocalizations. The nutritional stress hypothesis (Nowicki et al. 1998) proposes that nutritional stress experienced by young birds can, in addition to decreasing overall health and immune function, affect the neural pathways controlling song production and learning if it occurs during critical periods for learning. Studies have now shown that early nutritional stress can reduce song complexity or repertoire size and influence mating success (Nowicki et al. 1998, 2000, Spencer et al. 2003, 2004). While effects of stress on vocal learning abilities have not yet been examined in taxa with adult learning, it is certainly plausible that the stress experienced by individuals moved into new habitats and social groups might reduce their ability to learn new vocalizations, which could in turn pose a barrier to the integration of individuals into new populations during translocations or reintroductions.

The Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*) is an endangered species that inhabits the high-elevation pine forest habitat of the Sierra Madre Occidental in Mexico (Forshaw 1989, Lanning and Shiflett 1983, Snyder et al. 1999). Its decline has been linked primarily to the loss of these high-elevation old-growth forests through extensive logging (Lanning and Shiflett 1983, Snyder et al. 1999, Monterrubio-Rico et al. 2004, 2006). To lesser extents, capture for the pet trade and shooting also may have contributed to population declines; neither of these is thought to threaten current populations (Snyder et al. 1999). Current estimates indicate that there are only 1000–4000 individuals left in the wild in Mexico (BirdLife International 2007). Most breeding is concentrated in three main breeding sites in northwestern Chihuahua: Madera, Tutuaca, and Mesa de las Guacamayas (Enkerlin-Hoeflich et al. 1999, Snyder et al. 1999). Of these sites, Tutuaca is officially protected as a wildlife sanctuary, Madera is in the process of being declared a Natural Protected Area, and Mesa de las Guacamayas is currently protected with a local agreement among the landowners (JC-N, unpubl. data). While these protections partially mitigate the risk posed by logging and forest fires, concerns remain regarding the long-term protection of these breeding sites. These concerns have prompted efforts to introduce individuals into currently unpopulated areas within the historic geographic range of the species (Snyder et al. 1994, 1999). The range of the Thick-billed Parrot historically extended as far north as the pine forests of central Arizona and southern New Mexico (Wetmore 1935, Snyder et al. 1994, 1999). A previous effort to reintroduce Thick-billed Parrots into the Chiricahua Mountains in southern Arizona in the late 1980s was composed primarily of captive-bred individuals; it did not result in a long-term breeding population (Snyder et al. 1994). Current conservation strategies for this species call for translocating wild-caught birds from various breeding populations to the Chiricahua Mountains to establish a new breeding site (R. Valdés-Peña, Tecnológico de Monterrey, and E. Juárez, Arizona Game and Fish Department, pers comm.). In this study, we quantify vocal variation among the three main nesting areas in Mexico to evaluate the potential for cultural differences among populations that might limit the success of translocations.

METHODS

VOCAL SAMPLING

We recorded contact calls of flying and perched Thick-billed Parrots at three different breeding sites (Madera, Tutuaca, and Mesa de las Guacamayas; Fig. 1) in the Sierra Madre Occidental in Chihuahua, Mexico over a two-week period in July 2006. We recorded contact calls in the early morning, when the birds were most active, until midday (06:00–10:00 MDT) and again in the late afternoon until early evening (16:00–19:00). Recorded calls came from breeding birds at or near their nest trees, birds in feeding flocks, and birds in flight. All birds were unmarked. We recorded around a given nest only once to reduce the possibility of recording the same bird twice. We identified two types of contact calls: the bark, a single-note call typically used by birds in flight, and the laugh, a multinote call generally used by perched birds (Fig. 2). We recorded bark calls from five individuals at each of the three breeding sites and recorded laugh calls from 29 different individuals: ten each from Madera and Tutuaca and nine from Mesa de las Guacamayas. Contact calls were recorded using a tripod-mounted Optura60 mini-DV camcorder (Canon U.S.A., Lake Success, New York), or a PMD670 recorder (Marantz America, Mahwah, New Jersey) with a directional ME66 03285 microphone (Sennheiser Electronic, Old Lyme, Connecticut).

ACOUSTIC ANALYSES

Calls recorded on the Marantz PMD670 recorders were saved to internal memory as 16 bit. wav files with a sampling rate of 22.05 kHz or 44.1 kHz then copied onto a PowerBook G4 iMac (Apple Computers, Cupertino, California). Calls recorded on the Canon mini-DV

camcorder were digitized into individual 16-bit .wav files using Raven 1.2.1 sound analysis software (Charif et al. 2004) running on a PowerBook G4 iMac. We randomly selected five contact calls from each individual from among all available high-quality calls (i.e., with low background noise and a high signal-to-noise ratio) for each individual, resulting in sets of 145 laugh calls and 75 bark calls.

Selected calls were then measured via spectrograms created in Raven 1.2.1 with a Hann window size of 1024 samples and 3 dB filter bandwidth of 61.9 Hz, a frequency grid with DFT size of 1024 samples and a 43.1 Hz grid spacing, a time grid with a 512 sample hop size and 90% overlap and averaging of 1 spectrum. For bark calls, we measured seven different time and frequency parameters on the spectrograms in Raven using on-screen cursors (Fig. 2). For the multinode laugh calls, we measured the same seven parameters on the first note for calls with only one note; the first and second notes for two-note calls; the first, second, and last notes for three- and four-note calls; and the first, second, middle, and last notes for calls with five notes or more. Notes were defined as acoustic traces separated by more than 20 msec of silence. All measurements were performed on the second harmonic of each note except for the parameter frequency with maximal energy, which was measured from the entire note.

We also calculated peak spectrogram cross-correlation values between calls. We first equalized the sampling rates of all of the calls to 22.05 kHz using the “resamp” command in SIGNAL 4.03 (Beeman 2004). We then used the CORMAT routine version 2.26 in SIGNAL to perform spectrogram cross correlations using spectrograms with a 512 sample FFT, 100 steps, band pass filtering from 0.5 to 8 kHz, and no frequency shifts or time normalization. We performed separate batch correlations for the complete set of bark calls and a set consisting of the first notes of the laugh calls.

STATISTICAL ANALYSES

We performed nested Analysis of Variance (ANOVA) using JMP 5.1 (SAS Institute 2003) for the seven acoustic parameters for the bark calls and first, second, middle, and last notes of laugh calls. The nested ANOVAs had a fixed effect of site and a random effect of individual nested within site. We set an initial level for statistical significance at $\alpha < 0.05$ and corrected α for multiple tests using a strict Bonferroni correction (Sokal and Rohlf 1995).

We performed principal coordinates analysis (PCO) to visualize the patterns of similarity in the matrices of peak cross-correlation values produced by the spectrogram cross-correlation analysis. We plotted the first two eigenvectors of each PCO plot in two-dimensional space to illustrate trends in the similarity matrix. We also tested for effects of site and individual using standard and partial Mantel tests (Mantel 1967, Smouse et al. 1986) using test matrices with ones for comparisons within a classification (e.g. within the same site or same individual) and zeros for comparisons between classifications. Separate standard and partial Mantel tests were performed between each matrix of similarity values and these test matrices to test for the effects of (a) individuals, and (b) sites controlling for individuals. All of the tests were implemented in the R Package, Version 4.03 (Casgrain and Legendre 2001).

RESULTS

For the bark call, nested ANOVAs performed on seven different time and frequency note parameters (Table 1) showed no significant effect of site before Bonferroni correction (Table 2). Four of the seven parameters (total note duration, initial frequency, final frequency, and highest frequency) showed a significant effect of individuals nested within a

site before Bonferroni correction, but only two note parameters (initial frequency and highest frequency) remained significantly different after the Bonferroni correction (corrected $\alpha = 0.007$).

Results for the nested ANOVA's performed on note parameters of the multi-note laugh calls were similar to those for bark calls (Table 1, 2). Of the seven note parameters measured for the first, second, middle, and last notes of laugh calls, only the time to highest frequency in the second note and total note duration in the last note were significantly different among sites before Bonferroni correction ($\alpha = 0.05$). After Bonferroni correction, no laugh call parameters varied significantly among sites for any of the note types (corrected $\alpha = 0.007$). For the effect of individuals within site, four note parameters (total note duration, initial frequency, final frequency, and highest frequency) were significant for at least one of the four note types before and after Bonferroni correction.

Principal coordinates analysis plots obtained from spectrogram cross correlations showed similar patterns of extensive overlap in the similarity values for calls from different sites for both bark calls and the first note of laugh calls (Fig. 3). When the three sites were examined separately, variation among individuals within each site was apparent for bark calls (Fig. 4), but less so for the first note of laugh calls (not shown). Results from Mantel tests confirmed these patterns (Table 3). For the bark call, a partial Mantel test of call-similarity values on site membership that controlled for the effect of individual identity did find a significant association between call similarity and site membership ($P < 0.007$), but the low Mantel R -value of 0.04 suggested that only a small portion of the variation among the calls was explained by the variation among the sites. In contrast, the Mantel test for bark-call similarity versus individual identity was significant with $R = 0.22$. The first note of laugh calls showed no significant association between call similarity and site membership after controlling for individuals, but did show a significant, albeit weak, association of call similarity with individual identity, with $R = 0.08$ (Table 3).

DISCUSSION

We did not detect significant geographic variation in the vocalizations of the Thick-billed Parrot among the three sites sampled. Neither bark nor laugh calls exhibited strong differences among sites, although both types of calls did exhibit significant differences among individuals within sites. Below, we contrast these results with those found in other species of parrot and discuss the implications for potential translocation programs.

VOCAL VARIATION IN PARROTS

The apparent lack of acoustic differences among populations of the Thick-billed Parrot contrasts to previous results from other parrot species. Studies in the Yellow-naped Amazon (*Amazona auropalliata*; Wright 1996), Ringneck Parrot (*Barnardius zonarius*; Baker 2000), Orange-fronted Conure (*Aratinga canicularis*; Bradbury et al. 2001), Galah (*Eolophus roseicapilla*; Baker 2003), St. Lucia Parrot (*Amazona versicolor*; Kleeman and Gilardi 2005), and Kea (*Nestor notabilis*; Bond and Diamond 2005) have all found evidence of vocal variation among populations. Why might the Thick-billed Parrot be different from all other parrots surveyed to date in this regard?

One reason the Thick-billed Parrot differs from other parrots may lie in the scale of sampling in our study. It is possible that geographic variation exists, or existed previously before range contraction, in the calls of this species, but on a larger scale than the one at which we sampled. This hypothesis is difficult to address, as the three sites sampled are the only major breeding sites known in this species. Furthermore, the distances among the three different breeding populations are large, with about 150 km between the northernmost

breeding population (Mesa de las Guacamayas) and the middle population (Madera), and about another 90 km between Madera and the southernmost population (Tutuaca). These distances are as large as or larger than those typically sampled in other studies of parrot vocal variation. Baker (2003) found geographic variation in contact calls for the Galah at four different sites with an average distance of 45 km between the sites. The three dialects found by Wright (1996) in the contact calls of Yellow-naped Amazons were each 60–120 km in extent along a north-to-south transect. The four main populations of the Orange-fronted Conure sampled by Bradbury et al. (2001) had an average of 63 km between them. Finally, in the four populations of the St. Lucia Parrot found by Kleeman and Gilardi (2005), the average distance between populations was 6 km. The three breeding populations for the Thick-billed Parrot we sampled were an average of 120 km apart. Since the three populations of Thick-billed Parrot had an average distance as far or farther apart than four parrot species that exhibit geographic variation in contact calls, it is safe to conclude that if the Thick-billed Parrot does have vocal variation among some populations, this variation occurs on a larger geographic scale than documented in any other parrot species to date.

A second reason for this difference with other parrots may be the presence of seasonal migration in the Thick-billed Parrot. In contrast to most parrots, the Thick-billed Parrot migrates seasonally from breeding sites in northern Chihuahua to sites farther south in Mexico. Historically, overwintering occurred in Jalisco, Colima, and Michoacan states (Schnell et al. 1974, Villalón 1990, Snyder et al. 1994); the current overwintering sites of the remaining populations are not known. Since migration of the Thick-billed Parrots involves groups of 12 to over 100 (Schnell et al. 1974), and historically, groups as large as 1500 individuals (Wetmore 1935), it is possible that individuals from the different breeding populations intermix during migration. Mixing during migration or on the wintering grounds could reduce vocal differences among populations, particularly if vocalizations help to mediate such social behaviors as flock cohesion during migration, synchronized defense against raptors, the formation of foraging flocks, or sentinel posting during foraging (Lanning and Shiflett 1983, Snyder et al. 1994, 1999, Monterrubio-Rico et al. 2006). Convergence onto a shared group call type has been shown in winter flocks of Black-capped Chickadees (*Parus atricapillus*; Mammen and Nowicki 1981), and has been suggested as one explanation for the formation of dialects in wintering populations of the Bronzed Cowbirds (*Molothrus aeneus*; Warren 2003). If overwintering Thick-Billed Parrots form a single flock, then vocal convergence within this flock could explain the limited variation observed among breeding sites. Locating and protecting the current wintering area or areas of the remaining populations of Thick-Billed Parrots is a critical conservation priority (J. Gilardi, World Parrot Trust, pers. comm.); studies of social interactions in these wintering areas would also be valuable for understanding patterns of vocal variation in this species.

IMPLICATIONS FOR TRANSLOCATION

The low degree of vocal variation detected among the three main breeding populations suggests that population-level differences in communication signals are unlikely to pose a barrier for social assimilation of birds from different areas during translocations. This study, however, did find significant variation among individuals in acoustic structure of both bark and laugh calls. Thick-billed Parrots may use this variation to recognize individuals and mediate behavioral decisions and responses. This recognition process could possibly affect the success of translocations in a negative manner if individuals prefer to associate with known individuals (Kikusui et al. 2006, Teixeira et al. 2007). Playback experiments examining how individuals from one population respond to calls from within the same population and from the other populations could be useful in determining whether birds respond differently to the calls of different individuals and populations. Conservation programs should consider population and individual differences in behavior where such

differences might augment challenges faced by individuals involved in reintroductions or translocations, and work to mitigate these differences where possible.

Acknowledgments

We thank Jose Luis Garcia, Anna Young, and Erin Schirtzinger for assistance in the field, and Mathew Pinch and Georgina Jacquez for performing spectrographic measurements. We also thank Christine Dahlin, Anna Young, Elizabeth Hobson, Kelley Boorman, Alejandro Salinas-Melgoza, and two anonymous reviewers for their useful comments on the manuscript. Research was supported by Conservation Grants from T & E Inc., an Undergraduate Research Initiative Grant from the NMSU Vice Provost for Research, and fellowship support to JEG from the NIH grant MBRS-RISE GM6 1222.

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FIGURE 1.

Map indicating the locations of three main breeding sites of the Thick-billed Parrot in Mexico sampled in July 2006: Mesa de las Guacamayas, Madera, and Tutuaca. Triangles represent the extent of the Sierra Madre Occidental.

FIGURE 2.

Examples of the two types of Thick-billed Parrot contact calls recorded in the Sierra Madre Occidental of Mexico in July, 2006: (A) a multinote laugh call, (B) the first note from the laugh call in (A), and (C) a bark call. The numbers in (B) and (C) represent the measurements taken for each note: 1 = total note duration (sec); 2 = initial frequency (kHz); 3 = final frequency (kHz); 4 = highest frequency (kHz); 5 = frequency of maximal energy (kHz); 6 = time to highest frequency (sec); 7 = time to max frequency (kHz).

FIGURE 3.

Plots of the first two eigenvectors from principal coordinates analysis (PCO) of the matrix of spectrogram cross-correlation values illustrating the extensive overlap in call similarity among sites for (A) bark calls and (B) the first note of laugh calls of the Thick-billed Parrot recorded at the Mesa de las Guacamayas, Madera, and Tutuaca breeding sites in July, 2006.

FIGURE 4.

Plots of the first two eigenvectors from principal coordinates analysis (PCO) of the matrix of spectrogram cross-correlation values for bark calls illustrating the variation among individuals within each of the three breeding sites of the Thick-billed Parrot sampled in the Sierra Madre Occidental of Mexico in July 2006: (A) Mesa de las Guacamayas, (B) Madera, and (C) Tutuaca. In each plot, each point represents a single call, and the five calls of each individual are coded with a different symbol and enclosed in a minimum convex polygon.

Values for seven acoustic parameters of bark and laugh calls of the Thick-billed Parrot averaged over the three breeding sites sampled in the Sierra Madre Occidental of Mexico in July 2006. Values are means $\pm$ SD.

TABLE 1

Parameter	Bark	First note of laugh	Second note of laugh	Middle note of laugh	Last note of laugh
Total note duration (sec)	0.21 $\pm$ 0.04	0.14 $\pm$ 0.02	0.12 $\pm$ 0.02	0.11 $\pm$ 0.01	0.11 $\pm$ 0.02
Initial frequency (kHz)	1.09 $\pm$ 0.26	1.14 $\pm$ 0.24	1.18 $\pm$ 0.21	1.18 $\pm$ 0.19	1.14 $\pm$ 0.25
Final frequency (kHz)	1.50 $\pm$ 0.24	1.26 $\pm$ 0.25	1.22 $\pm$ 0.21	1.22 $\pm$ 0.22	1.10 $\pm$ 0.22
Highest frequency (kHz)	2.27 $\pm$ 0.175	1.56 $\pm$ 0.26	1.51 $\pm$ 0.11	1.50 $\pm$ 0.16	1.38 $\pm$ 0.19
Maximum frequency (kHz)	1.96 $\pm$ 0.24	1.94 $\pm$ 0.49	1.99 $\pm$ 0.48	2.11 $\pm$ 0.48	2.00 $\pm$ 0.62
Time to highest frequency (sec)	0.10 $\pm$ 0.03	0.09 $\pm$ 0.03	0.07 $\pm$ 0.02	0.06 $\pm$ 0.02	0.05 $\pm$ 0.03
Time to max frequency (sec)	0.22 $\pm$ 0.07	0.20 $\pm$ 0.15	0.43 $\pm$ 0.15	1.01 $\pm$ 0.06	1.44 $\pm$ 0.93

TABLE 2

Results of nested ANOVAs for the effect of site and individual nested within site on seven acoustic parameters of bark and laugh calls of the Thick-billed Parrot recorded in the Sierra Madre Occidental of Mexico in July 2006. Asterisks indicate F -values with $P < 0.05$ after Bonferroni correction for multiple tests; df = degrees of freedom for (individual, site).

Test	Parameter	F-value				
		Bark (df = 12,2)	First note of laugh (df = 26,2)	Second note of laugh (df = 25,2)	Middle note of laugh (df = 22,2)	Last note of laugh (df = 26,2)
Effect of site	Total note duration (sec)	0.5	2.5	2.4	0.4	4.6
	Initial frequency (kHz)	3.6	2.5	0.1	2.1	2.1
	Final frequency (kHz)	0.4	2.7	1.8	1.0	3.2
	Highest frequency (kHz)	1.9	1.2	0.1	1.1	0.0
	Maximum frequency (kHz)	0.5	0.1	0.7	0.2	1.2
	Time to highest frequency (sec)	0.8	0.7	4.6	2.5	2.0
Effect of individual	Time to max frequency (sec)	0.5	1.7	0.3	2.3	0.8
	Total note duration (sec)	2.6	1.8	2.2*	1.5	1.3
	Initial frequency (kHz)	3.0*	3.0*	5.1*	6.1*	4.5*
	Final frequency (kHz)	2.6	3.0*	7.5*	4.6*	2.7*
	Highest frequency (kHz)	4.9*	2.6*	4.9*	1.4	2.5*
	Maximum frequency (kHz)	1.4	1.0	1.3	1.3	0.8
	Time to highest frequency (sec)	1.2	1.9	1.3	0.8	1.6
	Time to max frequency (sec)	1.7	1.2	2.0	0.6	1.4

TABLE 3

Values for Mantel correlations between matrices of spectrogram cross-correlation values and matrices of site membership and individual identity for bark calls and the first note of laugh calls of the Thick-billed Parrot recorded in the Sierra Madre Occidental of Mexico in July 2006. Asterisks indicate significance after Bonferroni correction for multiple tests ($\alpha = 0.025$).

Note type	<u>Cross correlation vs. individual</u>		<u>Cross correlation vs. site controlling for individual</u>	
	Mantel <i>R</i>	<i>P</i> -value	Mantel <i>R</i>	<i>P</i> -value
Bark	0.22	0.001*	0.04	0.007*
First note of laughs	0.08	0.001*	0.02	0.04