

Vocal Dialects in the Lesser Spear-Nosed Bat *Phyllostomus discolor*

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In the lesser spear-nosed bat (*Phyllostomus discolor*) pups progressively adapt the structure of their isolation calls by audio-vocal learning to the individually distinct frequency modulation pattern of the maternal directive call. Directive and isolation calls are frequently used during acoustic mother-infant interactions, and both are sinusoidally frequency-modulated signals. The ability of audio-vocal learning is commonly accepted as a prerequisite for language acquisition in humans and for song plasticity in a variety of avian species. As a consequence of vocal plasticity traditions may arise and lead to local dialects in humans and birds. To test whether a similar formation of dialects occurs in *P. discolor* we analyzed the directive calls of two laboratory breeding colonies of these bats with regard to three call characteristics contributing to a mother's "vocal signature" (i.e., the number of frequency minima and maxima per call, the carrier frequency, and the modulation frequency). The geographical origin of one colony is Costa Rica and the other Columbia. As revealed by statistical comparison of group means of the above sound parameters and as further shown by multidimensional scaling techniques, female dialects clearly exist in *P. discolor*.

Audio-vocal learning is most common among oscine birds [1]. Here intraspecific vocal imitation and limited dispersal from the site of imitation often lead to the phenomenon of song dialects or song sharing among

neighboring males [1]. In contrast to songbirds, the ontogeny of mammalian vocalization is thought to be largely under genetic control [2, 3]. Only for a few species, such as humans [4], humpback whales (*Megaptera novaeangliae*) [5], bottle-nosed dolphins (*Tursiops truncatus*) [6, 7], and lesser spear-nosed bats (*P. discolor*) [3, 8], does the modification of call structure through auditory experience seem well established. Despite the obvious absence of vocal plasticity in most nonhuman mammals, geographic [9–11] and colony-specific dialects [12] have been repeatedly described. These findings are complemented by the occurrence of both group- [13] and family-distinctive calls [14, 15] in colonial bats. Evidence that vocal similarities in nonhuman mammals arise through shared genes has been provided for several species. For example, in subterranean mole rats belonging to the *Spalax ehrenbergi* superspecies in Israel it was shown that each out of four chromosomal (i.e., morphologically indistinguishable) species has a vocal dialect significantly different from all others [11]. Further, vocal differences between races or subspecies were noted when comparing populations of deer [16], grey langurs [17], and squirrel monkeys [18]. In contrast with these species, in *P. discolor* isolation calls are modified during ontogeny to match the mother's vocal signature. Since the acquired signature calls obviously remain unchanged in the adult [8], our animal model [19] offers the possibility to study effects of audio-vocal learning on dialect formation in colonies of a terrestrial nonhuman mammal.

Maternal directive calls of "Costa Rican" bats were recorded in a sound-proof and anechoic chamber. The mother was placed on the carpet-covered rear side of a small wire mesh cage (30 × 21 × 20 cm) and her 2- to 3-day old pup was hand-held by the experimenter approximately 1 m apart. Thus infant isolation calls could be used to elicit maternal vocalizations. The recording equipment consisted of a condenser microphone (Brüel & Kjaer, 4135), a preamplifier (Brüel & Kjaer, 2633), a measuring amplifier (Brüel & Kjaer, 2610), and a high-speed tape recorder (Racal, V-Store) operated at 76.2 cm/s (tape: Maxell, HGX-Black). During recordings directive calls were further monitored via an ultrasound detector (Ultra Sound Advice, S-25) and headphone. For sonographic measurements, recordings were fed into a real-time FFT analyzer (Waldmann, Sona-PC) at fourfold reduced speed.

The sinusoidally frequency-modulated directive calls of female *P. discolor* (example in Fig. 1) were characterized as before [3, 8, 19] (scheme in Fig. 2A). On the basis of the calls' fundamental, three parameters were determined: the number of FM peaks (i.e., frequency minima and maxima) per call, the carrier frequency (f_{carrier}), and the modulation frequency (f_{mod}). Since calls may begin variably either with a short upward frequency modulation or somewhere in the following downward modulation (Fig. 2A, dashed area, left) the first frequency minimum was regarded as FM peak 1

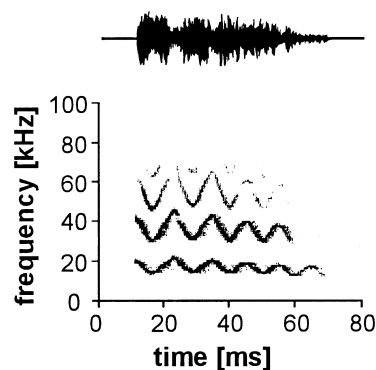


Fig. 1. Directive call of *Phyllostomus discolor*. Above, oscillogram; below, sonogram. The call was uttered from a mother of the "Costa Rican" breeding colony

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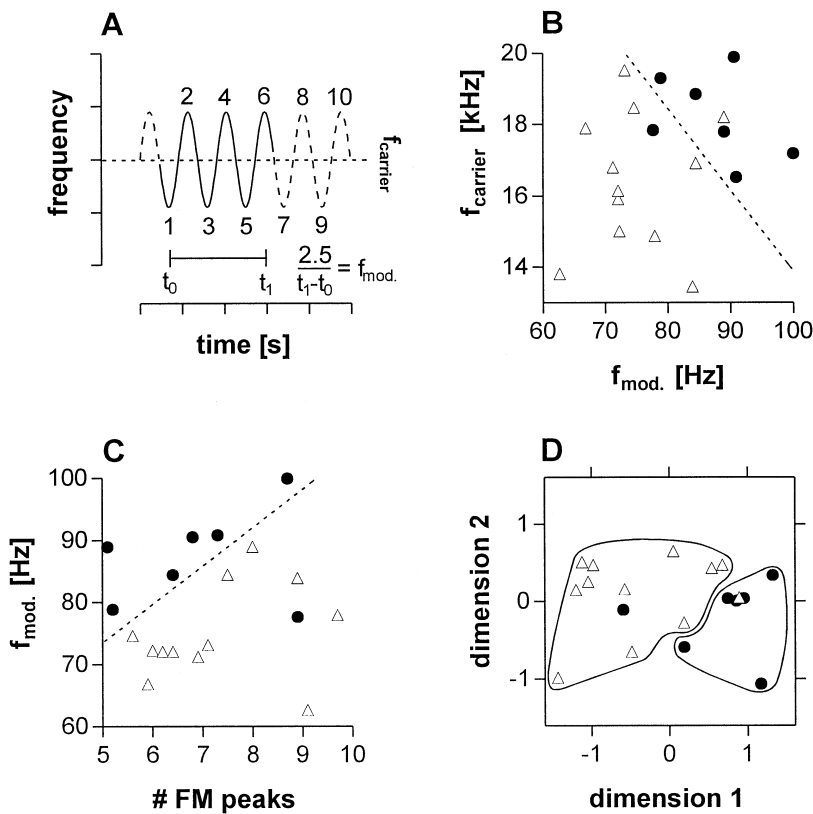


Fig. 2A–D. A) Scheme for the analysis of sinusoidally frequency-modulated communication calls of *P. discolor* (higher harmonics omitted). Three parameters contributing to the mothers' vocal signatures are shown: the number (1–10) of frequency minima and maxima per call (referred to as FM peaks), the carrier frequency (f_{carrier}), and the modulation frequency (f_{mod} ; for details see text). B) Comparison of call characteristics (individual mean values from 19 animals) of “Costa Rican” (Δ) and “Columbian” (\bullet) bats (f_{mod} vs. f_{carrier} ; *dashed line* fitted by eye to indicate separation of groups). C) Comparison based on the number of FM peaks per call and f_{mod} . (*dashed line* as above). D) Two-dimensional spatial representation of call characteristics from MDS analysis. Clusters of “Costa Rican” and “Columbian” bats, respectively, are encircled by *solid lines*. Average distances from population means, based on all three call variables standardized for equal variance, were as follows: 1.45 ± 0.58 and 1.31 ± 0.48 (within groups, “Costa Rica” and “Columbia”); 2.09 ± 0.86 and 2.08 ± 0.50 (between groups)

and further taken as reference value (i.e., t_0) for measuring the duration of 2.5 complete cycles of frequency modulation (t_0 – t_1 interval in Fig. 2 A). This interval was uniformly chosen for calculating the signals' modulation frequency (Hz), given as $2.5/(t_1-t_0)$, since it was the longest one shared by all animals studied. Subsequent to FM peak 6 and the corresponding half cycle of frequency modulation, directive calls may last for a number of FM peaks varying within and between individuals (Fig. 2A, dashed area, right). The carrier frequency of a call (kHz) was determined as the geometrical mean be-

tween average values of successive frequency minima and maxima. As a rule 50 directives were analyzed per bat. In 2 of 12 animals studied only 6 and 12 calls were available, respectively. For a comparison of the directive calls of two colonies of *P. discolor* founded on animals of different geographical origin (i.e., Costa Rica and Columbia), previously obtained data from 7 “Columbian” mothers (20 calls per animal) [8] were reanalyzed following exactly the above procedure. Both bat colonies were housed in different laboratories without acoustic contact to each other. The “Columbian” colony had

been founded almost 10 years and the “Costa Rican” about 4 years prior to recording. Each colony consisted of 50–60 bats, with an almost balanced sex ratio. All females used for the recording of directive calls were adult (i.e., sexually mature and lactating) and of unknown social group or harem affiliation. Further, mothers were included in the study irrespective of whether being wild-caught or captive-born. Within each group (“Costa Rica” $n=12$; “Columbia” $n=7$), the mean carrier frequency, modulation frequency, and number of FM peaks was calculated both for each bat and across animals. Group means, adjusted for unequal sample size, were compared statistically using Student's *t* test (two-tailed, significance level $P < 0.05$) [20]. Individual mean values of carrier frequency, modulation frequency, and number of FM peaks were used to produce a dissimilarity matrix, comparing each mother's vocal signature with that of every other. Multidimensional scaling (MDS; SPSS, SYSTAT 6.0 for Windows) was subsequently applied to place vocal signatures in a space of two dimensions, such that the distances between animals reflect measured dissimilarities [21–23].

Plots of f_{mod} vs. f_{carrier} (Fig. 2B) and of FM peak number vs. f_{mod} (Fig. 2C) revealed marked differences in vocal characteristics between bats from the “Costa Rican” and “Columbian” colony. The two clusters could be distinguished (dashed lines in Fig. 2B, C), with a single misclassification (Fig. 2C) or with one occurring crosswise in each group (Fig. 2B). Directives recorded from “Columbian” bats generally had higher modulation frequencies and higher carrier frequencies than “Costa Rican” bats whereas the scattering of FM peak numbers (Fig. 2C, x-axis) appeared to be quite similar. Group means (“Costa Rica”, $n=12$ bats, vs. “Columbia”, $n=7$) of f_{mod} . (75.44 ± 7.62 vs. 87.34 ± 7.75 Hz) and f_{carrier} (16.41 ± 1.91 vs. 18.21 ± 1.19 kHz) differed significantly ($P < 0.01$, $P < 0.05$) whereas those of FM peak number (7.28 ± 1.38 vs. 6.9 ± 1.5) did not. A similar degree of separation of groups was revealed by multidimensional scaling (Fig. 2D; compare to Fig. 2B,

C) indicating the existence of vocal dialects in female *P. discolor*.

In the related greater spear-nosed bat (*Phyllostomus hastatus*), group-distinctive screech calls have been described recently [13]. In this study [13] the term "group" denotes females taken from the same social group (with or without the harem male) and their descendants. As opposed to the directive calls of *P. discolor* ([3, 8] and present study), screech calls of *P. hastatus* seem to lack an individual vocal signature. Hence, they may give females a means of identifying social group mates but not individuals [13]. Since greater spear-nosed bats display group foraging and cooperative behavior outside the cave [24], the adaptive value of these calls is fairly clear [13]. Generally, however, the existence of individually distinct and group- or colony-specific communication calls in bats is not mutually exclusive, as revealed by the present study. In *P. discolor* a difference in average carrier frequency of calls even larger than the one presently described for bats of different geographic origin (i.e., 2.1 vs. 1.8 kHz) could be produced (*re* an unstimulated control) by hand-rearing of pups and using a call tutor (for details see [3]). Since here [3], both groups of bats (i.e., tutored and control) were taken from a single laboratory breeding colony, and at the end of the study they were further indistinguishable in terms of body weight [25], we are confident that also the reported dialects (present study) resulted predominantly from learning rather than from possible genetic and/or physical differences. Hence the present data on vocal dialects in *P. discolor* offer a very promising perspective for similar studies on a geographical scale, paralleling such studies in songbirds.

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1. Kroodsma DE (1982) Learning and the ontogeny of sound signals in birds. In: Kroodsma DE, Miller EH, Quillet H (eds) Acoustic communication in birds, vol 2. Academic, New York
2. Marler P, Mitani J (1988) Vocal communication in primates and birds: parallels and contrasts. In: Todt D, Goedeckin P, Symmes D (eds) Primate vocal communication. Springer, Berlin Heidelberg New York
3. Esser K-H (1994) Audio-vocal learning in a non-human mammal: the lesser spear-nosed bat *Phyllostomus discolor*. Neuroreport 5:1718–1720
4. Kuhl PK (1989) On babies, birds, modules, and mechanisms: a comparative approach to the acquisition of vocal communication. In: Dooling RJ, Hulse SH (eds) The comparative psychology of audition: perceiving complex sounds. Lawrence Erlbaum Associates, Hillsdale
5. Payne K, Payne R (1985) Large scale changes over 19 years in songs of humpback whales in Bermuda. Z Tierpsychol 68:89–114
6. Caldwell MC, Caldwell DK (1972) Vocal mimicry in the whistle mode by an Atlantic bottlenosed dolphin. Cetology 9:1–8
7. Richards DG, Wolz JP, Herman LM (1984) Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. J Comp Psychol 98:10–28
8. Esser K-H, Schmidt U (1989) Mother-infant communication in the lesser spear-nosed bat *Phyllostomus discolor* (Chiroptera, Phyllostomidae) – evidence for acoustic learning. Ethology 82:156–168
9. Green S (1975) Dialects in Japanese monkeys: vocal learning and cultural transmission of locale-specific vocal behavior? Z Tierpsychol 38:304–314
10. Marshall JT, Marshall ER (1976) Gibbons and their territorial songs. Science 193:235–237
11. Nevo E, Heth G, Beiles A, Frankenberg E (1987) Geographic dialects in blind mole rats: role of vocal communication in active speciation. Proc Natl Acad Sci USA 84:3312–3315
12. Pearl DL, Fenton MB (1996) Can echolocation calls provide information about group identity in the little brown bat (*Myotis lucifugus*)? Can J Zool 74:2184–2192
13. Boughman JW (1997) Greater spear-nosed bats give group-distinctive calls. Behav Ecol Sociobiol 40:61–70
14. Jones G, Ransome RD (1993) Echolocation calls of bats are influenced by maternal effects and change over a lifetime. Proc R Soc Lond B 252:125–128
15. Masters WM, Raver KAS, Kazial KA (1995) Sonar signals of big brown bats, *Eptesicus fuscus*, contain information about individual identity, age and family affiliation. Anim Behav 50:1243–1260
16. Tembrock, G (1965) Untersuchungen zur intraspezifischen Variabilität von Lautäußerungen bei Säugetieren. Z Säugetierk 30:257–273
17. Vogel C (1973) Acoustical communication among free-ranging common Indian langurs (*Presbytis entellus*) in two different habitats of north India. Am J Phys Anthropol 38:469–480
18. Winter P (1969) Dialects in squirrel monkeys: vocalization of the Roman arche type. Folia Primatol 10:216–229
19. Esser K-H (1998) Psychoacoustic studies in neotropical bats. In: Nielzén S, Olsson O (eds) Clinical psychoacoustics. Lund University Press, Lund
20. Sachs L (1992) Angewandte Statistik. Springer, Berlin Heidelberg New York
21. Sparling DW, Williams JD (1978) Multivariate analysis of avian vocalizations. J Theoret Biol 74:83–107
22. Wilkinson L (1996) SYSTAT 6.0 for Windows: statistics. SPSS, Chicago
23. Manabe K, Staddon JER, Cleaveland JM (1997) Control of vocal repertoire by reward in budgerigars (*Melopsittacus undulatus*). J Comp Psychol 111:50–62
24. Wilkinson GS, Boughman JW (1998) Social calls coordinate foraging in greater spear-nosed bats. Anim Behav 55:337–550
25. Esser K-H (1990) Der Einfluss von Lernprozessen auf die ontogenetische Entwicklung sozialer Laute bei der Kleinen Lanzennase *Phyllostomus discolor* (Chiroptera, Phyllostomidae). Thesis, University of Bonn