

Intraspecific Variation in the Vocalizations and Hand Pad Morphology of Southern Lesser Bush Babies (*Galago moholi*): A Comparison with *G. senegalensis*

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Previous studies have shown the taxonomic value of vocal repertoires and hand (volar) pad characteristics in the classification of cryptic nocturnal primates such as bush babies. However, no study included quantitative comparisons within the geographical range of any one species. We investigated levels of intraspecific variation in calls and hand pad characteristics of the southern lesser bush baby (Galago moholi), using the northern lesser bush baby (Galago senegalensis) for interspecific comparisons. Examination of calls recorded from different regions along a transect of 1500 km across southern Africa revealed low levels of intraspecific variation in Galago moholi, whereas comparisons with homologous call-types in G. senegalensis revealed them to be significantly different. Volar pad measurements across the ranges of both species also showed low levels of intraspecific variation and relatively high interspecific variation. These findings demonstrate that vocal and volar pad characteristics can be used as consistent measures of difference between species that look almost identical. These methods provide a practical means of distinguishing between cryptic species, whether in the field, in captivity, or, in the case of volar pads, of preserved specimens.

KEY WORDS: galago; taxonomy; vocalization; morphology; zoogeography.

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INTRODUCTION

The taxonomic status of bush babies (or galagos), a nocturnal prosimian group from Africa (Order Primates; Subfamily Galagoninae; nomenclature according to Jenkins, 1987), has long been contentious because of considerable similarities among species. Studies of behavior, genetics and comparative morphology have begun to disentangle the confusion surrounding specific identity. Indeed, the number of species described within this group has increased from 6 (Hill, 1953) to 17–18 (Bearder, 1999; Kingdon, 1997). Current studies predict that this number will continue to increase as more is discovered about these cryptic primates.

Bioacoustic studies of wild and captive populations have shown that calls provide strong indications of the existence of separate species. For example, several morphologically similar galago populations exhibit distinctive loud calls. Qualitative differences in vocal repertoires and acoustic differences in homologous calls suggested that both the southern lesser and the northern lesser bush babies (along with thick-tailed greater Garnett's greater bush babies) are different species (Zimmermann *et al.*, 1988; Zimmermann, 1990; Masters, 1991; Bearder *et al.*, 1995). Studies of reproductive behavior, genetics, and male genital morphology have lent further credence to such findings (Dixon, 1989; Zimmermann, 1989; Izard and Nash, 1989; Bayes, 1998; Anderson, 1998). Hand (volar) pads have also proven to be very useful taxonomically. For example, differences between some or all pads—all galago species possess four interdigital pads and a single thenar pad—has allowed for reassessment of several closely related galago populations (Anderson, 1999). We examined volar pads because they are present in many museum specimens. While the use of other morphological characters, such as penile morphologies (Anderson, 2000), would have been useful, the low numbers of preserved penes precluded their use.

The majority of studies utilizing these approaches were focused on gross specific differences based upon wild and captive specimens from a limited number of geographical areas. Although results from previous studies indicate that even closely related species can be distinguished, the true nature of intraspecific variation across the entire geographic range of any one species remains unknown.

We address the validity of using comparisons by examining intraspecific variability in the three loudest vocalizations of the repertoire—loud calls—and in volar pad morphology in a very well-established species—the southern lesser or mohol bush baby (*Galago moholi*, A. Smith, 1839), which range southward from Tanzania over a wide area of southern Africa. Recordings of vocalizations from widely spaced free-ranging populations, along with data on volar pad morphology taken from galagos in the same

regions housed in museum collections, have allowed for quantification of variability in specimens across southern Africa. We compared the results with measurements obtained from *Galago senegalensis*, which replaces *G. moholi* northward from Tanzania to Senegal.

METHODS

Field Recordings of Vocalizations

Details of the location and numbers of individuals recorded and the call types analyzed are in Table I. Recorded calls of *G. moholi* are from 7 sites covering the majority of their known range in South Africa, Botswana, and Namibia (Fig. 1 and Table I). Sites 1, 2, 3, and 4 are in more northwesterly locations (1, Waterburg Plateau, Namibia; 2, Maun, Botswana; 3, Western Caprivi, Okovango River, Botswana; 4, Hippo Lodge, Zambesi River, Katima Mulilo, Botswana). The remaining sites (5, 6, and 7) are in more southeasterly locations (5, Naboomspruit, South Africa; 6, Nylsvley, South Africa; 7, Kempiana, eastern Transvaal). Locations were clustered into NW and SE areas respectively to accommodate for later representation of variability of calls within *G. moholi*. This was necessary as we could not record the respective loud calls in all investigated populations, e.g., no bark at site 7, no whistle at sites 2 and 7, no yap at sites 3 and 5 (Tables I and II).

Bearder made all recordings at site numbers 1–5 in 1998 and sites 6

Table I. Location of individuals recorded and calls analyzed for the populations of *Galago moholi* and *G. senegalensis*^a

Species	Location	Site name	N/n		
			Bark	Whistle	Yap
<i>Galago moholi</i>	Northwest	Waterberg Plateau, Namibia	1/10	3/65	3/70
		Maun, Botswana	2/20	—	2/60
		Okavango River, Botswana	3/30	2/40	—
		Hippo Lodge, Zambesi	2/20	2/40	2/60
	Southeast	Naboomspruit, South Africa	2/20	3/34	—
		Nylsvley, South Africa	5/50	5/60	5/66
		Kempiana, Eastern Transvaal	—	—	3/50
			Wool	Tjong	Fwa
<i>Galago senegalensis</i>	Kenya	Galana Ranch, Kenya	5/50	4/50	3/60
		Tana River, Kenya	1/10	2/25	3/35

^aN, number of individuals; n, number of units measured. The nomenclature of call types follows Zimmermann *et al.* (1988).



Fig. 1. Map showing locations of sites where vocalizations were recorded (*G. moholi*: 1-7 and *G. senegalensis*: 8 and 9) and where hand pads were measured (*G. moholi*: A-F and *G. senegalensis*: G-L) in Africa. (1) Waterburg Plateau, Namibia; (2) Maun, Botswana; (3) western Caprivi, Okovango River, Botswana; (4) Hippo Lodge, Zambesi River, Katima Mulilo, Botswana; (5) Naboomspruit, South Africa; (6) Nylsvley, South Africa; (7) Kempiana eastern Transvaal; (8) Galana Ranch, Kenya; (9) Garisse, Kenya. (A) Swartbois drift, Namibia; (B) Nata, Botswana; (C) Kasimpa, Zambia; southeast locations: (D) Rustenburg, South Africa; (E) Acornhoek, South Africa; (F) western Mozambique; (G) Bakal, Senegal; (H) Ejura, Ghana; (I) Kaduna, Nigeria; (J) northern Cameroon; (K) Dolo, Ethiopia; (L) Kalongoli, Uganda; (M) Naru Moru, Kenya.

Table II. Ranges of call characteristics measured in each call type in populations of *Galago moholi* and *G. senegalensis*^a

Species	Location	Site name	Call type						
			Bark		Whistle		Yap		
			Units per phrase (s)	Interphrase interval (s)	Fundamental frequency (kHz)	Unit length (s)	Fundamental frequency (kHz)	Unit length (s)	
<i>Galago moholi</i>	Northwest	Waterberg Plateau, Namibia	1-2	1.20-1.62	1.29-2.02	0.3	-0.6	0.86-1.34	0.04-0.07
		Maun, Botswana	1-2	1.07-1.66	—	—	—	0.94-1.36	0.04-0.06
		Okavango River, Botswana	1-2	1.21-1.86	1.38-2.20	0.43-0.7	—	—	—
	Southeast	Hippo Lodge, Zambesi	1-2	1.16-1.59	0.86-1.89	0.3	-0.65	1.16-1.34	0.05-0.09
		Lilongwe, Malawi	1-2	1.09-1.62	1.03-1.77	0.29-0.89	—	—	—
		Nylsvley, South Africa	1-3	1.15-1.98	1.29-2.41	0.31-0.58	—	0.89-1.39	0.06-0.09
Kempiana, Eastern Transvaal	—	—	—	—	—	0.95-1.33	0.05-0.08		
<i>Galago senegalensis</i>	Kenya	Galana Ranch, Kenya	1	0.66-0.77	0.47-0.56	0.20-0.42	—	0.62-0.98	0.10-0.15
		Tana River, Kenya	1	0.67-0.88	0.39-0.52	0.29-0.43	—	0.72-0.88	0.15-0.23

^aNumbers are lower and upper values in each case.

and 7 during 1977. From the repertoire of calls recorded, we selected 3 for analysis—barks, whistles, and yaps—since they were the loudest and most common calls heard. Together they constitute vocal profile (Bearder *et al.*, 1995).

The calls of *Galago senegalensis* were available from 2 sites in Kenya: (8 and 9 in Fig. 1), recorded by T. Butynski in 1994 and 1995. They include 3 call types that appear to be homologous with the loud calls of *G. moholi*: wools, tjongs, and fwas (Zimmermann *et al.*, 1998).

Bearder and coworkers located galagos via detection of eyeshine using 4.5-V Petzl zoom headband flashlights with halogen bulbs and followed them at close quarters (5–10 m) for as long as possible while recording all their vocalizations. Alternatively, they approached calling subjects to ≤ 10 m to ensure good-quality recordings and to prevent the same individual being mistaken as two galagos. They used a Sony professional cassette recorder (WM-D6C) (frequency response: 40–15,000 Hz) with a Sennheiser MKH 816T directional microphone (frequency response: 40–20,000 Hz) at sites 1–4; a Uher 4000 Report-L reel-to-reel tape recorder (frequency response: 20–25,000 Hz) with a Uher M514 microphone (frequency response: 35–20,000 Hz) at sites 5–7; and a Sony professional cassette recorder (frequency response: as above) with Beyer Dynamic directional microphone (frequency response: 50–18,000 Hz) at sites 8 and 9. Data on the behavioral context of each call were collected simultaneously by an observer who was not involved in recording calls via event *ad libitum* sampling and continuous (all occurrences) recording techniques (Martin and Bateson, 1986) via a 6-V Mag-lite flashlight and Bushnell 4 \times 42 Natureview binoculars. Calls were displayed and measured via Avisoft Sonogram Pro 2, a sound analysis program for IBM-compatible personal computers running Windows 3.1 (Raimund Specht, Berlin).

The frequency resolution was 43 Hz (FFT length 512; 50% overlap; Hamming window) with an analog-to-digital rate of 22,050 Hz.

Analyses of Vocal Patterns

The call parameters for comparison are (1) units per phrase and (2) interphrase interval for barks of *Galago moholi* and wools of *G. senegalensis*, and (3) unit length and (4) fundamental frequency for whistles and yaps of *G. moholi* and tjongs and fwas of *G. senegalensis* (Table 1; Zimmermann *et al.*, 1988). We selected parameters with respect to the temporal pattern of each recorded call.

The components are (Figs. 2a and 2b) unit: the basic element of a call that is represented as a continuous tracing along the temporal axis of the

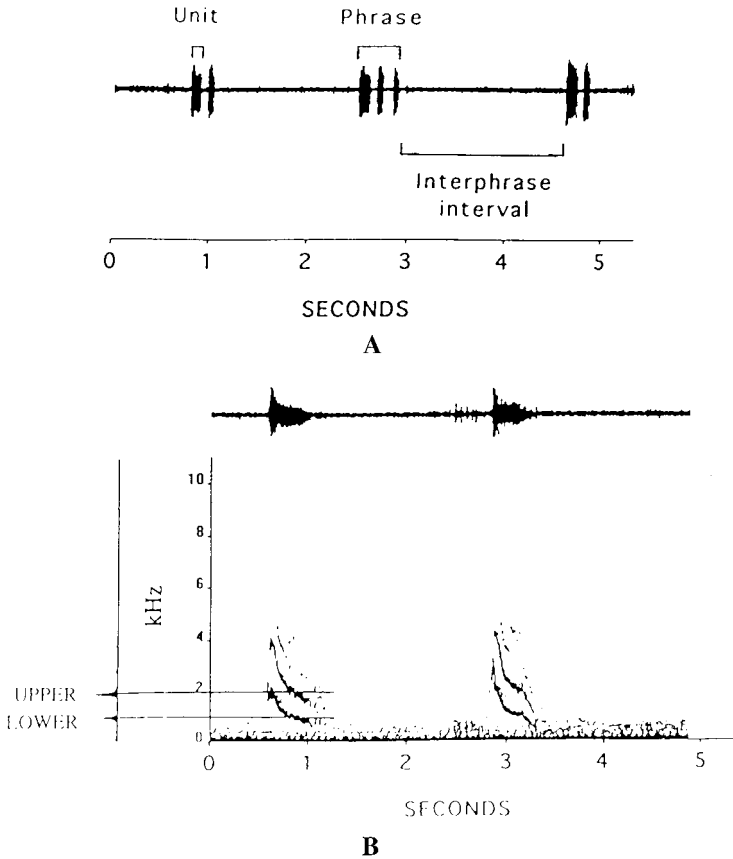


Fig. 2. (a) Oscillogram of a yap call of *G. moholi* to show how each vocalization is divisible into units, phrases, and interphrase intervals. (b) Sonogram of a whistle (frequency-modulated call) of *G. moholi* to show how fundamental frequency is measured. Upper and lower cursors are marked and a midpoint value taken.

sonogram; phrase: a unit or group of units that is repeated within a single bout of calling; interphrase interval: time interval between two consecutive phrases; and fundamental frequency: measured from the lowest harmonic of each unit (kHz). Where the lowest harmonic was frequency-modulated, we calculated the fundamental frequency as the midpoint between maximum and minimum frequency (Fig. 2b).

We compared each call measurement for *G. moholi* (10–25 units were measured per subject per characteristic) via an analysis of variance (ANOVA) in order to assess the level of intraspecific variation of call

characteristics between populations across the range of the species. Because several calls could not be recorded in all locations (no bark at site 7; no whistle at sites 2 and 7; no yap at sites 3 and 5: Tables I and II), we represented sites used in the analysis as either northwestern or southeastern in the results.

Having established levels of intraspecific variation for *Galago moholi*, we compared characteristics of individual calls (bark, whistle, and yap) with the homologous vocalizations of *G. senegalensis* (wool, tjong, and fwa) to establish levels of population specificity and taxonomic specificity. We used a nested ANOVA (in order to partition the variance between species and populations) and, where there were significant differences between call characters, we assessed them via post hoc Newman–Keuls pair-tests. We used the SPSS PC 5.0 (DOS) statistical package for IBM-compatible personal computers for all analyses.

Measurements of Volar Pad Morphology

We measured the volar pads of 37 preserved specimens of *Galago moholi* from the collection at the Transvaal Museum in Pretoria, South Africa, representing 7 areas: (A) Swartbois drift, Namibia; (B) Nata, Botswana; (C) Kasimpa, Zambia; (D) Rustenburg, South Africa; (E) Acornhoek, South Africa; (F) western Mozambique (Fig. 1 and Table I). Thirty-three specimens of *Galago senegalensis* were available from the Natural History Museum, London, and we also examined 17 live subjects in an illegal shipment from Cameroon to Amsterdam. The specimens and subjects originated from 7 sites: (G) Bakal, Senegal; (H) Ejura, Ghana; (I) Kaduna, Nigeria; (J) northern Cameroon; (K) Dolo, Ethiopia; (L) Kalongoli, Uganda; (M) Naru moru, Kenya (Fig. 1 and Table I).

We recorded images of the volar pads (Fig. 3) via a Hi-8 video camera and digitized them using an Apple Macintosh Power PC with a digital image grabber board. All images are of the right hand and include a scale for calibration. We measured individual pad areas via NIH Image, an image analysis program for the Apple Macintosh (Anderson, 1999). We also, compared the volar pad measurements of the preserved specimens to those of the live subjects of *Galago senegalensis* to ascertain whether preservation had affected the sizes of the volar pads.

Analyses of Volar Pad Morphologies

We corrected measurements of pad areas for body weight to facilitate allometric comparisons, thus ensuring that any difference was not due to

i. FACE MASK

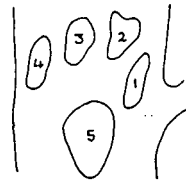
(a) *Galago moholi*



(b) *Galago senegalensis*



ii. HAND PADS



iii. OSCILLOGRAMS AND SONOGRAMS

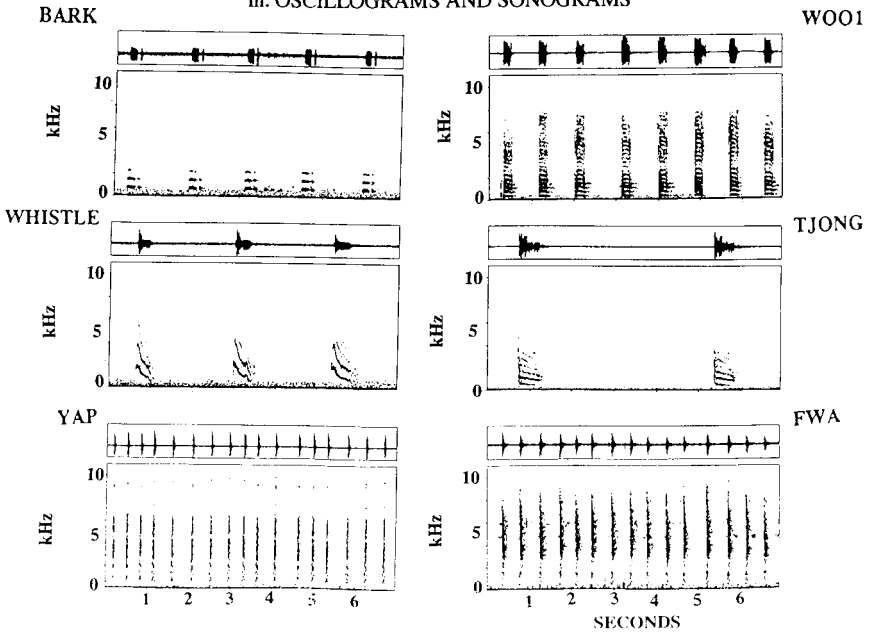


Fig. 3. Qualitative differences between (a) *G. moholi* and (b) *G. senegalensis* in facial appearance, hand pad morphology, and temporal structure of calls.

variations in body size. We used an indirect measurement of body weight—head–body length—in all cases because body weights were not available for many of the museum specimens. We plotted the log of the square root of mean pad area against the log of head–body length, fitted a major-axis regression line to all the data sets, and calculated pad size residuals. Having controlled for body size, we analyzed the pad size residuals to ascertain levels of intraspecific variation across the populations of *Galago moholi* via an ANOVA. We also performed analogous measurements and subsequent statistical analyses of volar pads in *Galago senegalensis*. When the ANOVA showed significant differences in pad characteristics, we assessed them via post hoc Newman–Keuls pair-tests.

Having established levels of intra-specific variation for both species types, we compared pad size residuals of *G. moholi* and *G. senegalensis* to establish levels of interspecific variation. Via a nested ANOVA we made comparisons in order to partition the variance between species and populations and, when there were significant differences between pad size residuals, we assessed them using post hoc Newman–Keuls pair-tests. We conducted all analyses via the SPSS PC 5.0 (DOS) statistical package for IBM-compatible personal computers.

RESULTS

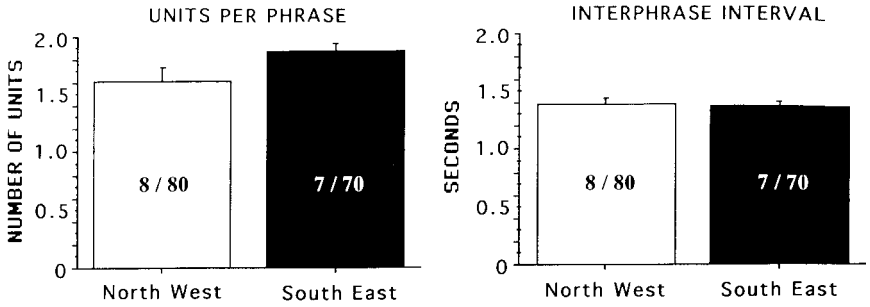
Vocalizations: Intraspecific Variation in *Galago moholi*

An ANOVA using quantified call characteristics—units per phrase and interphrase interval for barks and unit length and fundamental frequency for whistles and yaps, each selected with respect to the temporal pattern of each call—revealed no significant difference between populations across all sites in the geographic range. It follows that there is no difference between northwestern and southeastern locations in South Africa, Botswana, and Namibia (Fig. 4). Numbers of galagos and units measured at each site that we used to assess interpopulation variability are in Table I. The range of call parameters is in Table II. Intraspecific variation of all call characteristics is very low across the entire geographic distribution of *Galago moholi*. No single call characteristic belonging to any one call type differs significantly between individuals of any population across the range.

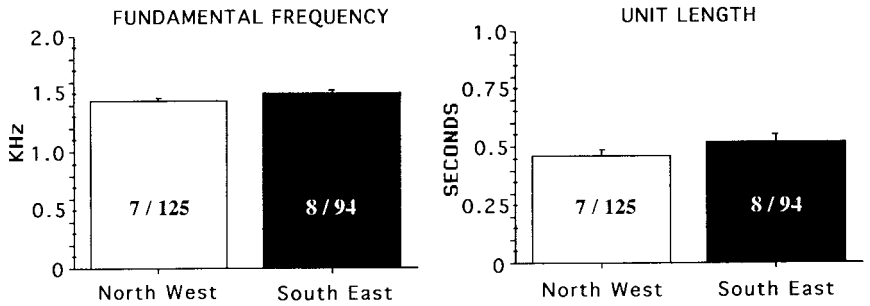
Vocalizations: Interspecific Comparisons

A subsequent nested ANOVA comparing characteristics of homologous calls of *Galago moholi* and *G. senegalensis*—bark vs. woo 1 using

Bark Calls



Whistle calls



Yap calls

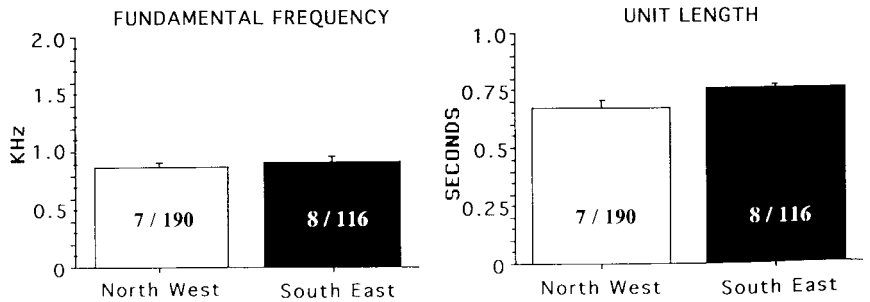


Fig. 4. Quantitative measurements of call structures (barks, whistles, and yaps) in free-ranging *G. moholi* in northwestern (□) and southeastern (■) parts of the species distribution range. Data are means and standard errors; bars show N/n , where N = number of specimens and n = number of units measured.

units per phrase and interphrase intervals; whistle vs. tjong and yap vs. fwa using unit lengths and fundamental frequency—across all sites sampled shows that significant differences occur between populations resulting from differences between species ($F = 137.24$, $p < 0.001$). Post hoc Newman–Keuls comparisons indicate that all homologous calls are significantly different from each other ($p < 0.001$) (Fig. 5). The interspecific variation of each respective call characteristic is significantly higher than that observed intraspecifically in the case of *Galago moholi*.

Volar Hand Pads: Intraspecific Comparisons

Initial observations of the volar pads of *Galago moholi* at the different sites across Africa (Fig. 1) revealed very little qualitative or quantitative difference in terms of individual pad shape and size. Comparisons of preserved and live specimens also revealed no marked differences in volar pads. All four interdigital pads are similar in size across all specimens, while the fifth (thenar) pad is uniformly larger. The volar pads of *Galago senegalensis* from different geographical regions exhibited similarly low levels of variation to those of *G. moholi*.

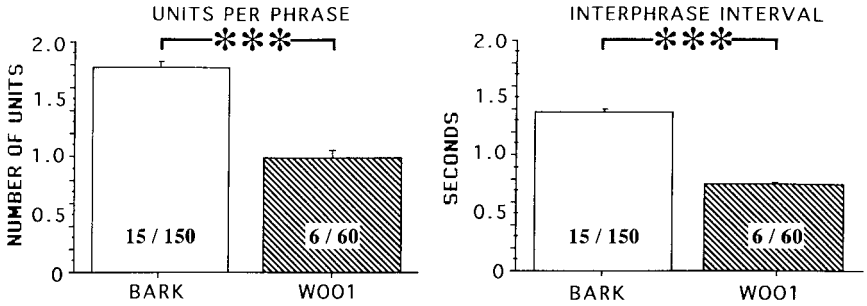
An ANOVA for all pads, using means of pad size residuals, revealed no significant difference between populations within the geographic range of *Galago moholi* (Table III). Intraspecific variation of pad size is very low across their overall geographic distribution. No individual pad of any specimen of *Galago moholi* differed from the same pad of another, after controlling for body weight.

A further ANOVA, using means of pad size residuals for all pads measured, similarly revealed no significant difference between populations of *Galago senegalensis* (Table III). As with *Galago moholi*, no single pad of any *G. senegalensis* differed from the same pad of another, after controlling for body weight.

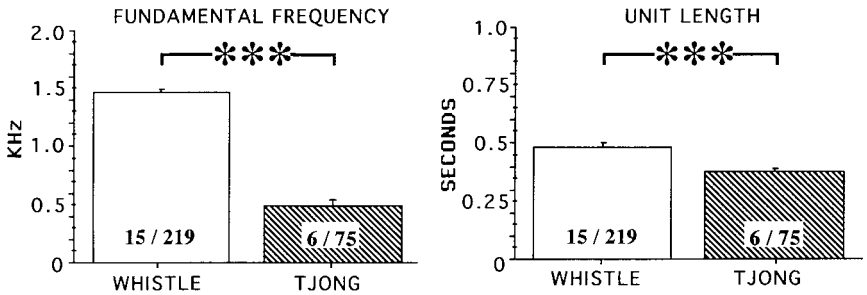
Volar Hand Pads: Interspecific Comparisons

Individual pad shape, size, and distribution across the palm clearly differ between *Galago moholi* and *G. senegalensis* (Fig. 3). A nested ANOVA across the two species using the means of pad size residuals revealed significant differences between populations, which resulted from differences between the two species ($F = 5.89$, $p < 0.001$). Post hoc Newman–Keuls pairwise comparisons indicated that there is no significant difference between the residuals of interdigital pads 1, 2, and 3 of *Galago*

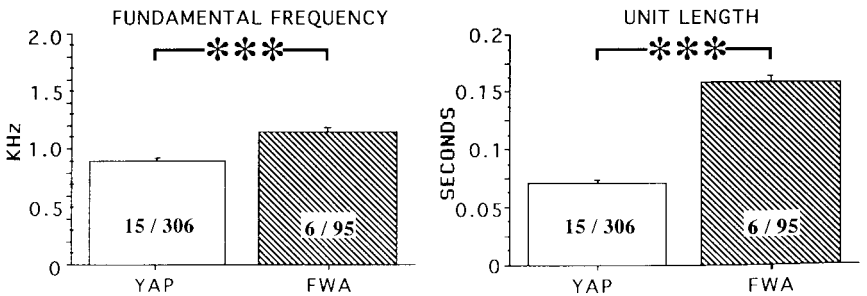
Bark vs Woo1 Calls



Whistle vs Tjong calls



Yap vs fwa calls



*** = $p < 0.0001$

Fig. 5. Quantitative comparisons of homologous calls in free-ranging *G. moholi* (□) and *G. senegalensis* (▨). Data are means and standard errors; bars show N/n , where N = number of specimens and n = number of units measured.

Table III. Volar pad sizes at six different sites across the ranges of *Galago moholi* and *G. senegalensis*^a

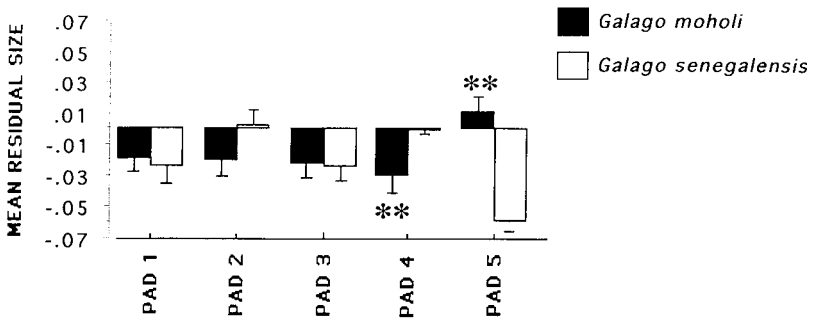
Species	Site sampled	Volar pad number				
		1	2	3	4	5
<i>Galago moholi</i>	Swartbois, Namibia (6)	-0.024 ± 0.009	-0.020 ± 0.010	-0.028 ± 0.012	-0.029 ± 0.011	0.010 ± 0.006
	Nata, Botswana (7)	-0.023 ± 0.011	-0.021 ± 0.010	-0.025 ± 0.010	-0.032 ± 0.010	0.011 ± 0.005
	Kasimpa, Zambia (4)	-0.019 ± 0.009	-0.017 ± 0.008	-0.020 ± 0.009	-0.024 ± 0.008	0.008 ± 0.005
	Rustenburg, South Africa (7)	-0.013 ± 0.007	-0.014 ± 0.009	-0.018 ± 0.009	-0.019 ± 0.009	0.006 ± 0.003
	Acornhoek, South Africa (8)	-0.016 ± 0.007	-0.014 ± 0.008	-0.014 ± 0.006	-0.021 ± 0.009	0.004 ± 0.002
Western Mozambique (5)	-0.010 ± 0.006	-0.017 ± 0.008	-0.015 ± 0.009	-0.019 ± 0.007	0.007 ± 0.003	
<i>Galago senegalensis</i>	Bakal, Senegal (6)	-0.019 ± 0.009	0.0036 ± 0.01	-0.026 ± 0.008	-0.0018 ± 0.012	-0.06 ± 0.009
	Ejura, Ghana (7)	-0.023 ± 0.009	0.0032 ± 0.0012	-0.026 ± 0.009	-0.0019 ± 0.0009	-0.058 ± 0.009
	Kaduna, Nigeria (8)	-0.026 ± 0.008	0.0031 ± 0.0015	-0.030 ± 0.01	-0.0019 ± 0.001	-0.064 ± 0.008
	Dolo, Ethiopia (6)	-0.022 ± 0.011	0.0026 ± 0.0015	-0.031 ± 0.01	-0.0025 ± 0.0009	-0.062 ± 0.01
	Kalongoli, Uganda (7)	-0.030 ± 0.009	0.0030 ± 0.001	-0.020 ± 0.01	-0.002 ± 0.0009	-0.054 ± 0.01
Naru Moru, Kenya (6)	-0.025 ± 0.01	0.0025 ± 0.001	-0.023 ± 0.009	-0.0019 ± 0.001	-0.062 ± 0.009	

^aData are the means ± SEM residuals of volar pad sizes at each site. The number of specimens measured at each site is given in parentheses.

moholi and *G. senegalensis*. However, the two species showed highly significant differences when the residuals of interdigital pad 4 and thenar pad 5 were compared ($p < 0.01$: both cases; Fig. 6). Accordingly, interspecific variations in pad are significantly greater than the intraspecific variations across the ranges of both *Galago moholi* and *G. senegalensis*.

DISCUSSION

Confusion over the true taxonomic status of galagos has been compounded by repeated misidentification of specimens in wild populations and museum collections. This has been primarily due to the use of inadequate morphological indicators, such as skeletal measurements and pelage coloration, which failed to reveal the true extent of speciation within the group. Additionally, differences in the vocalizations of wild populations have only been considered using qualitative comparisons (Bearder *et al.*, 1995). Previously, quantitative laboratory studies and preliminary field studies have addressed the issue of intraspecific variation in the vocalizations and certain morphologies of galagos (Zimmermann, 1985, 1990; Masters, 1985, 1991; Zimmermann *et al.*, 1988). However, the degree of intraspecific variability in vocalizations or in morphological traits, such as the volar pads in free-ranging galagos, had not been measured. We have quantified vocalizations and volar pad morphologies across the geographical range of a widely



PADS 1, 2 AND 3: NOT SIGNIFICANTLY DIFFERENT: $p > 0.05$

PAD4, PAD 5: ** = $p < 0.01$

Fig. 6. Quantitative comparisons of mean residual pad size in *G. moholi* (■) and *G. senegalensis* (□). Data are means and standard errors; *G. moholi*: $N = 37$; *G. senegalensis*: $N = 50$.

distributed galago species (*Galago moholi*) and compared them to those of a closely-related species (*G. senegalensis*).

The structure of any one call type in a nocturnal primate can vary in four main ways: (1) between species, (2) between populations of a species (dialects), (3) between individuals, and (4) within individuals, e.g., in relation to mood. Moreover, different individuals may give different call types, e.g., males/females, adults/infants, or the calls may be seasonal, e.g., mating calls. Therefore, if calls are to be used to identify a species it is important to examine the possible effects of the other causes of variation. Similarly, when using morphological traits to assess specific status, it is necessary to choose characteristics that remain conservative. We have demonstrated that certain call parameters and volar pad structures are highly conserved across the geographical range of *Galago moholi*, which allows them to be clearly distinguished from *G. senegalensis*, which at first sight seem to be physically identical in gross anatomical characteristics.

Previous studies showed that all the loud calls of *Galago moholi* and *G. senegalensis* are given by both males and females and they are not restricted to any one season such as the time of mating (Zimmermann *et al.*, 1988). Calls vary in relation to changes in mood and individual differences in voice, but the effects appear to be relatively minor, e.g., pitch, volume, and speed of repetition. It unknown whether differences in dialect exist in galagos or, indeed, what parts of their vocal repertoire might be concerned in dialectic variation. However, Zimmermann (1989) demonstrated that certain calls display relatively high levels of intraspecific variation, e.g., noisy calls that indicate agonism, alarm or attention seeking, while others are much less variable, e.g., advertising calls. Dialectic and conservative calls have also been observed in other primates by Mitani and Stuht (1998), in song birds by Catchpole and Slater (1985), and, in amphibians by Halliday and Adler (1986). The usefulness of vocal analyses in the resolution of taxonomic problems therefore relies upon the discrimination of different calls or call characteristics. Our study reveals that certain vocalizations exhibit low intraspecific variation in certain parameters across the geographical range of *Galago moholi* and yet are strikingly divergent from the homologous calls of *G. senegalensis*. These findings apply to the units per phrase and interphrase intervals of barks, and the unit lengths and fundamental frequencies of whistles and yaps in *Galago moholi*, when compared to homologous calls in *G. senegalensis*: units per phrase and interphrase intervals: wool; unit lengths and fundamental frequency: tjong and fwa. Our results support the conclusion that *Galago moholi* and *G. senegalensis* are indeed separate species (Zimmermann *et al.*, 1988; Zimmermann, 1989, 1990; Nash *et al.*, 1989), rather than being subspecies of *G. senegalensis* (Schwartz, 1931). The consistency of interspecific differences across the

distribution of both galago species also suggests that our techniques can be used for specific determination in other galagos.

The choice of call parameters is often constrained by the practical difficulties of making recordings in the field. Factors such as weather conditions, air temperature, and distance of the caller from the microphone will affect the quality of recordings and reduce the reliability of detailed analysis. But similar problems face the animals if they are to communicate effectively at a distance and it might be expected that loud calls are strongly selected to be relatively unambiguous. Our study confirms that this is true for certain call characteristics of *Galago moholi* and it is likely that they will be valuable for distinguishing among galago species in general.

The species-specificity of calls is thought to relate to recognition between members of the same species as part of a specific-mate recognition system (SMRS) which, in turn, forms part of a shared fertilization system (Paterson, 1985). If a population becomes physically isolated and local variations in calls and other aspects of the SMRS become fixed over time, this may explain the emergence of a new species. It may follow that unique combinations of loud calls—vocal profiles—may be species-specific. Conversely, as long as gene flow continues between populations, stabilizing selection will tend to prevent aspects of the SMRS from diverging. Such processes fit well with the results of our study. *Galago moholi* has a more-or-less continuous distribution across a vast area of southern Africa, and characteristics of their calls remain conservative between widely distributed populations (≥ 1500 km). *Galago senegalensis* utilizes similar habitats but has a more northerly distribution across Africa, and their calls, while recognizably similar to those of the former species, are measurably different. However, the relationship between these two allopatric species in areas where their ranges converge has yet to be explored.

Analyses of volar pads in both *Galago moholi* and *G. senegalensis* also reveal low levels of variation within species and significant differences between them, and they, too, provide a useful means of separating cryptic species. Penile morphology is also strongly diagnostic for galago species (Dixon, 1989; Anderson, 2000), but we used hand pads since they are present in both sexes and can usually be measured from museum specimens, whereas the male genitalia are often lost during the process of preparing skins.

Differences in the hand pad characteristics between the two species mainly involved interdigital pad 4 and thenar pad 5. Although genetic drift may be involved in the divergence between the two species, it is also necessary to consider the possible functional significance of the observed differences in volar pad morphology. The relative shape and size of each pad is thought to be associated with arboreal locomotion, with each pad

serving to obtain grip—the degree of interlocking with the surface of the substrate—and adhesion: the elasticity of each pad's surface (Cartmill, 1974). Accordingly, pad characteristics may correlate with the grasping pattern of each galago and the type of support it regularly uses. All galagos exhibit a relatively simple prehensile pattern, so it seems likely that varying degrees of friction required for adhering to the available supports may be the main cause of specific adaptations (Cartmill, 1979). Both *Galago moholi* and *G. senegalensis* occupy similar woodland/savanna habitats, and the possibility that they use different kinds of support, or use different grips, remains to be demonstrated. Further detailed studies of hand function and behavioral ecology in free-ranging galagos are required to identify selective forces responsible for the evolution of differences in hand pad morphology.

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