

Subspecific Divergence in a Loud Call of the Ruffed Lemur (*Varecia variegata*)

JOSEPH M. MACEDONIA AND LINDA L. TAYLOR

Duke University, Department of Anthropology, Durham, North Carolina, Washington University, Department of Anthropology, St. Louis, Missouri

A loud call of the ruffed lemur (*Varecia variegata*) was analyzed for subspecific and gender differences according to four variables: pulse rate, median pulse duration, median high frequency, and median low frequency. These vocalizations of black-and-white and red ruffed lemurs and one hybrid ruffed lemur were recorded at the Duke University Primate Center (Durham, NC). Significant differences were found between subspecies but not between the sexes. Quantitative differences in this loud call of ruffed lemur subspecies indicate that these prosimians exhibit subspeciation trends similar to anthropoid primates for which comparable data exist. Preliminary data are presented that support the hypothesis that the vocalization functions as a terrestrial predator alarm call.

Key words: ruffed lemur, loud call, subspecific divergence, terrestrial predator alarm, *Varecia variegata variegata*, *Varecia variegata rubra*

INTRODUCTION

Specific and subspecific differences in vocalizations have been documented in numerous vertebrate taxa, including frogs, birds, and primates. A positive correlation between color traits (in fur, feathers, beaks, skin, etc.) and specific or subspecific loud calls is a widespread phenomenon [e.g., Mayr, 1970; Zann, 1975; Hodun et al., 1981; Haimoff et al., 1982]. It has been suggested that genetic isolation of populations may be solely responsible for observed correlations between coat color and loud calls [e.g., Marler & Tenaza, 1977; Brockelman, 1978; Lieblich et al, 1980; Brockelman & Gittins, 1984; Geissmann, 1984; Marshall et al, 1984]. Analyses of loud calls have proved useful adjuncts to more traditional forms of taxonomic classification for anthropoid primates [e.g., New World monkeys: Winter et al, 1966; Ploog et al, 1975; Oppenheimer, 1977; Symmes et al, 1979; Hodun et al, 1981; Snowdon & Hodun, 1985; Old World monkeys: Struhsaker, 1970; Marler, 1972; Wilson & Wilson, 1975; Gautier & Gautier, 1977; Waser, 1982; Oates & Trocco, 1983; gibbons: Tenaza, 1975, 1985; Marshall & Marshall, 1976; Haimoff et al, 1982; Brockelman & Gittins, 1984; Creel & Preuschoft, 1984; Geissmann, 1984; Groves, 1984; Haimoff, 1984; Marshall et al, 1984].

Received June 18, 1985; revision accepted August 19, 1985.

Address reprint requests to Joseph M. Macedonia, Duke University Primate Center, 3705 Erwin Rd., Durham, NC 27705.

Black-and-white ruffed lemurs (*Varecia variegata variegata*) inhabit Madagascar's eastern rain forest from the Antainambalana River in the North to an area near the Mananara River in the Southeast. Red ruffed lemurs (*Varecia variegata rubra*) have a restricted distribution, being confined to the Masoala Peninsula east of the Antainambalana River [Tattersall, 1982]. According to Tattersall, a single red-colored form and as many as four racial variations of black-and-white ruffed lemurs are recognized. Like many other primate species and subspecies, *V. v. variegata* and *V. v. rubra* are isolated from one another by a water barrier. However, naturally occurring hybrids have been reported in a region of probable secondary contact between the confluent Antainambalana and Vohimaro Rivers in northeastern Madagascar (based on random sightings and museum skins) [Tattersall, 1982; Buettner-Janusch and Simons, personal communication].

Black-and-white and red ruffed lemurs emit two basic kinds of loud calls. Both calls resemble the loud calls of anthropoid primates in that (1) they may serve several functions; (2) they are "contagious" between groups; and (3) they occur most frequently at dawn and dusk [e.g., Marler, 1969; Gautier & Gautier, 1977; Waser, 1982; Oates & Trocco, 1983].

Our study followed the dichotomous classification scheme for anthropoid primate loud calls proposed by Gautier & Gautier [1977], in which "type 1 loud calls" consist of relatively narrow frequency band pulses that are structurally original between species (or subspecies) and "type 2 loud calls" are relatively wide band pulses that rarely exhibit interspecific structural originality.

The type 2 loud call of the ruffed lemur, termed the "mob roar" [Kress et al, 1978], consists of a series of very wide band roars, punctuated with intermittent high-pitched squeals. This call may serve several functions, including aerial predator alarm and as a startle response to sudden disturbances in the immediate environment [Taylor, 1978; Petter & Charles-Dominique, 1979]. We have observed on several occasions the emission of this call as one component of the male response to female rebuffs during mounting attempts. Unlike most loud calls in anthropoids, there appear to be no gender-specific components of this call (i.e., in *Varecia*, both sexes emit the same calls). In addition, the roaring vocalization exhibits no obvious subspecific differences, as predicted by the Gautiers' model for type 2 loud calls.

Because of pitch and temporal differences apparent to us before beginning the study, we hypothesized that the type 1 loud call produced by this species would, however, exhibit significant variation between the two color variants. This vocalization, referred to here as the "uh-uh-uh..." call [equivalent to the "ko-ko-kie-kie..." call of Petter and Charles-Dominique, 1979:296], consists of a series of rela-

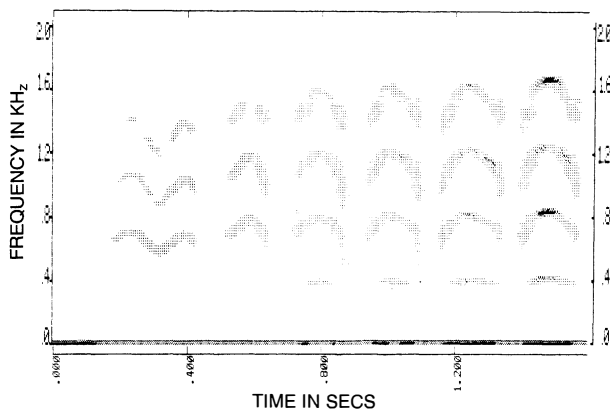


Fig. 1. *V. v. variegata*: Characteristic shape of the fundamental and harmonic frequencies of this subspecies' "uh-uh-uh..." call.

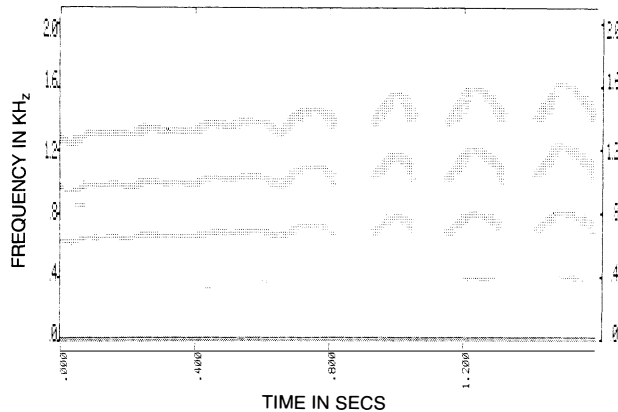


Fig. 2. *V. v. variegata*: Note extended ("uh-----"), common in black-and-white individuals, but never observed in the red ruffed lemurs (*V. v. rubra*).

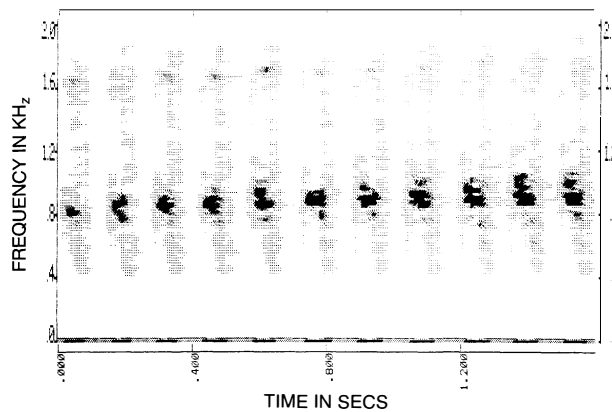


Fig. 3. *V. v. rubra*: Characteristic shape of this subspecies' "uh-uh-uh..." call.

tively narrow band clucking sounds or pulses (e.g., Figs. 1–4). This call has been explained as a spacing mechanism between territorial groups [Petter & Charles-Dominique, 1979]. To date, there are no reports of age/sex class differences in the production of this vocalization. Our observations of the behavior of ruffed lemurs following their occasional sightings of dogs near the DUPC grounds led us to hypothesize that one function of this call was to communicate information about potential terrestrial predators. Data are presented here that support this hypothesis. Additionally, the first quantitative evidence of subspecific differences in a loud call of a prosimian primate is reported.

METHODS

Study Animals

The study animals were 13 adult ruffed lemurs (*Varecia variegata*) housed at the Duke University Primate Center (DUPC, Durham, NC). All lemurs were housed in outdoor enclosures that ranged in size from approximately .24 m³ to 3.4 ha. Eight individuals (four males and four females) were of the black-and-white subspecies (*V. v. variegata*), four individuals (three males and one female) were of the red subspecies (*V. v. rubra*), and one individual was a hybrid female (1/4 *V. v. variegata* × 3/4 *V. v. rubra*). Data on the latter individual are not included in the quantitative analyses except as noted. At the time of recording, the approximate age distribution (in years)

of the study animals was as follows: *V. v. variegata* males: 4–15; females: 3–15; *V. v. rubra*: males: 4–10; female: 4; hybrid: female: 6. All *V. v. variegata* in the study were of the "Type a" classification used by Tattersall [1982:69; Fig. 3.14].

Equipment and Procedure

Vocalizations were recorded with a Sony TCM 5000 EV monaural tape recorder at 1½ ips onto Maxell UDXL-1 normal bias tape. A Sennheiser ME-88 super-cardoid microphone was used throughout. Recordings were made between January and March 1985. A computer keyboard interfaced with a digital real-time audio spectrum analyzer (UniScan II) allowed frequency (± 40 Hz) and time ($\pm .006$ sec) measurements to be made while viewing the monitor screen of the UniScan II. Photographs were taken of the visual displays of each analyzed call to serve as permanent records. Sonograms selected for publication were run on an Epson MX100III dot-matrix printer as direct output from the UniScan II.

Because domestic dogs frequent a dirt road adjacent to the northern perimeter of the DUPC, a leashed dog was presented to all study animals during two sampling sessions in order to clarify the relationship between these dogs and vocalizations emitted by the lemurs. The vocal responses were taped, and other responses were recorded ad libitum.

Analysis and Quantification

During the course of study, observations were focused on two independent variables: (1) subspecies and (2) gender. Because of the possibility that sexual dimorphism in the vocalizations might represent a major source of variation (cf., subspecies), this variable was incorporated into the analyses.

The following parameters were used to quantify the characteristics of individual calls in our sample:

1. Call length
2. Number of pulses, or continuous spectrogram tracings, per call
3. Pulse duration (in seconds) of the first five and last four pulses in each call
4. Highest frequency of the "major energy," or darkest portion of the spectrogram, in each of the nine pulses
5. Lowest frequency of the "major energy" in each of the nine pulses

Thus, each call was examined as a whole, and nine of its individual pulses were examined as well. A total of 105 entire calls were analyzed. Of these, 44 contained at least 9 pulses and/or were sufficiently free from background noise to provide unambiguous data beyond the calculation of pulses per second (pulse rate). Medians and ranges for the number of analyzed calls from individual study animals were as follows: *V. v. variegata* median = 6; range = 1–15; *V. v. rubra* median = 6; range = 2–11; hybrid $n = 12$; males median = 6; range = 2–15; females median = 6; range = 1–12.

Mann-Whitney U tests were performed on the data in order to detect significant differences ($\alpha \leq .05$) between the medians of the two independent variables, gender and subspecies, according to the following four variables:

1. Pulse rate (pulses/sec)
2. Median pulse duration
3. Median high frequency
4. Median low frequency

Nonparametric statistics were chosen because the normality of the data distribution was uncertain.

RESULTS

In general, the red ruffed lemurs showed a greater number of pulses per call (median = 21) and a shorter call duration (median = 2.7 sec) than the black-and-white ruffed lemurs (medians = 17, 3.8 sec). The single hybrid, however, emitted the fewest number of pulses per call (median = 9.5) in the shortest amount of time (median = 2.05 sec).

The statistical results are compared by gender and subspecies for pulse duration and frequency in Tables I and II and for pulse rate in Tables III and IV. No significant differences were found in these variables between males and females. Comparisons between subspecies, on the other hand, revealed some very significant differences.

TABLE I. Mann-Whitney U Tests by Gender: Pulse Duration and Frequency

Variable	Group 1 males (n = 23)	Group 2 females (n = 21)	U	Two-tailed P
Pulse duration (secs)				
Median	.125	.087	164.0	.0683
Range	.043-.206	.062-.188		
High frequency (Hz)				
Median	1,720	1,880	237.0	.9153
Range	1,520-2,040	1,240-2,080		
Low frequency (Hz)				
Median	360	320	235.5	.8843
Range	280-560	280-440		

TABLE II. Mann-Whitney U Tests by Subspecies: Pulse Duration and Frequency

Variable	Group 1 <i>V.v. variegata</i> (n = 29)	Group 2 <i>V.v. rubra</i> (n = 15)	U	Two-tailed P
Pulse duration (sec)				
Median	.144	.075	53.0	< .0001
Range	.063-.206	.043-.100		
High frequency (Hz)				
Median	1,680	1,920	61.5	.0001
Range	1,240-1,920	1,680-2,080		
Low frequency (Hz)				
Median	320	400	136.5	.0384
Range	280-520	320-560		

TABLE III. Mann-Whitney U Tests by Gender: Pulse Rate (in sec)

	Males (n = 61)	Females (n = 44)	U	Two-tailed P
Median	5.432	6.553	1,259.0	.5899
Range	2.105-7.762	2.889-7.397		

TABLE IV. Mann-Whitney U Tests by Subspecies: Pulse Rate (in sec)

	<i>V.v. variegata</i> (n = 64)	<i>V.v. rubra</i> (n = 29)	Hybrid ^a (n = 12)
Median	4.672	7.135	4.401
Range	2.105–6.778	6.179–7.762	3.362–5.097
	U		Two-tailed P
<i>V.v. variegata</i> vs <i>V.v. rubra</i>	31.0		< .0001
<i>V.v. variegata</i> vs hybrid	326.0		.4087
<i>V.v. rubra</i> vs. hybrid	0.0		< .0001

^aHybrid = 1/4 *V.v. variegata* × 3/4 *V.v. rubra*

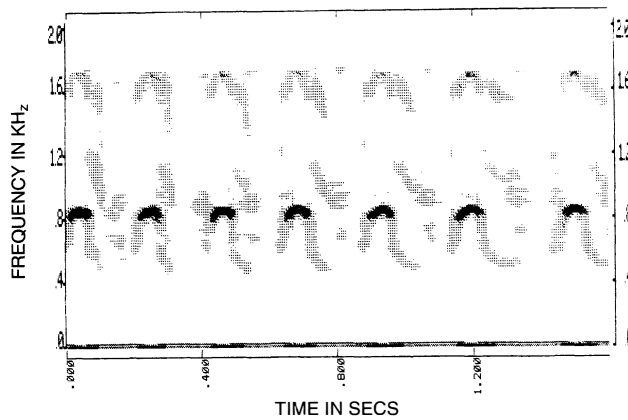


Fig. 4. *V.v. variegata* × *V.v. rubra* hybrid: The shape of this individual's calls differs from those of either parental subspecies.

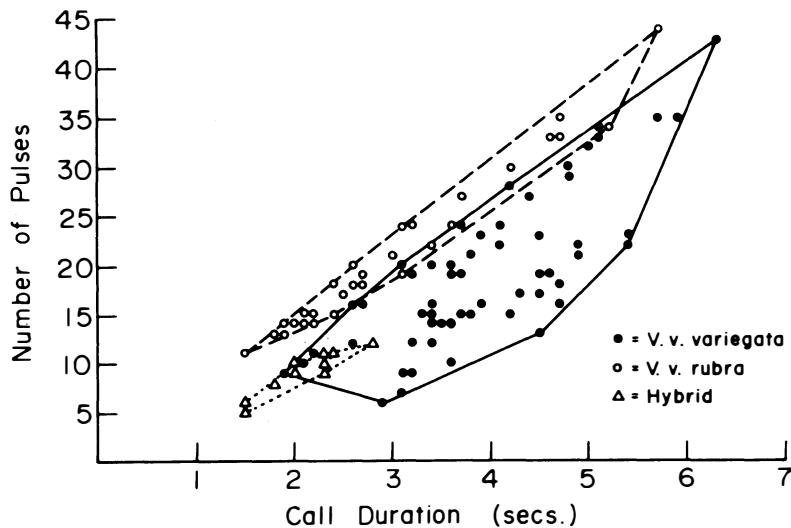


Fig. 5. Plot of the distribution of pulse rate for *V. v. variegata*, *V. v. rubra*, and the hybrid ruffed lemur.

The pulse rate among black-and-white ruffed lemurs was much slower than that among the red ruffed subspecies (4.672 vs 7.135 pulses/second; $U = 31$; $P < .0001$). The median pulse duration of the black-and-white ruffed lemurs was almost twice that of the red ruffed lemurs (0.144 vs 0.075 sec; $U = 53$; $P < .0001$). The median high frequency and the median low frequency of the sampled pulses were consistently lower in the calls emitted by black-and-white individuals than in calls emitted by red individuals (high = 1,860 vs 1,920 Hz; $U = 61$; $P = .0001$; low = 320 vs 400 Hz; $U = 136.5$; $P = .0384$).

When the two subspecies were compared to the hybrid individual (Fig. 4), the pulse rate of the red ruffed lemurs was significantly different from the hybrid (7.135 vs 4.401 pulses/second; $U = 0$; $P < .0001$), but the pulse rate of the black-and-white ruffed lemurs showed no similar degree of difference (4.672 vs 4.401 pulses/second; $U = 326$; $P = .4087$). Because the DUCP population contained only the one hybrid, the sample size was too small to make any other valid comparisons.

There were seven sampling sessions during which a dog was in the immediate vicinity; five were uncontrolled events and two were deliberate presentations. In every instance, adult ruffed lemurs of both sexes responded with the "uh-uh-uh..." vocalization shortly after sighting the dog. No other loud calls were emitted. The response was uniform for both adult males and adult females across subspecies. In most cases, ruffed lemurs in the forested enclosures moved quickly and quietly up into the trees before producing the call. In cages, the lemurs tended to leap to the highest substrate before calling.

DISCUSSION

The data indicated that there were distinct subspecific differences in the "uh-uh-uh..." call of these ruffed lemurs. Pulse rate, pulse duration, and frequency ranges distinguished the two subspecies from one another, supporting our initial hypothesis. The more rapid pulse rate and higher frequencies of the red ruffed form could be detected by the human ear. There was no significant sexual dimorphism in this vocalization.

Although there was some degree of overlap in pulse rate between black-and-white and red ruffed lemurs (Fig. 5), the red form tended to produce more pulses per second. In those anthropoid species that emit loud calls containing pulses, pulse rate has been found to be a strong indicator of phyletic divergence [e.g., Waser, 1982; Oates & Trocco, 1983]. The data presented here indicate that differences in pulse rate may serve to distinguish prosimian subspecies as well.

The range of variation in pulse rate was much greater in the black-and-white ruffed lemurs than in the red ruffed lemurs (Table IV; Fig. 5). Geographical range, and most likely, population size of the black-and-white form greatly exceeds that of the red form [Tattersall, 1982:72; Fig. 3.15]. This difference may account for the greater degree of variation in pulse rate observed in the black-and-white form. It is also possible that differences in the range of variation may reflect vocal idiosyncrasies of the founding members of captive populations. Until data are obtained from the field, however, this point remains conjectural.

Although the hybrid's pulse rate slightly overlapped that of the black-and-white subspecies, there was clearly an area of the distribution that did not fall within the range of either subspecies. Similar phenomena have been reported for hybrid gibbons [Brockelman & Gittins, 1984; Geissmann, 1984 (Fig. 6); Marshall et al, 1984; see also Tenaza, 1985]. Analyses of calls of other hybrid ruffed lemurs may help to resolve this apparent paradox.

Our hypothesis that the "uh-uh-uh..." vocalization is a terrestrial predator alarm call was supported by the following:

1. Terrestrial predator alarm barks were simultaneously produced by other lemur species housed with *Varecia* whenever dogs were visible (e.g., *Lemur catta*). The terrestrial predator alarm bark of ringtailed lemurs clearly differs from the cry elicited from them by avian predators [Jolly, 1966; R. Sussman, personal communication].

2. Whenever adult ruffed lemurs sighted a dog, they moved rapidly to an elevated position in the enclosure *before* responding with the "uh-uh-uh..." call. When calling, adults directed their vocal responses towards the "predator" in view.

3. No other loud calls were ever emitted by adult ruffed lemurs during these episodes.

Because there are no naturally occurring canids on Madagascar, it is likely that the terrestrial alarm call was originally specific to viverrid carnivores, e.g., the fossa (*Cryptoprocta ferox*). Once lemurs were removed from their natural environments, the calls may have been generalized to any potential terrestrial predator, e.g., the domestic dog.

When attempting to determine the functional significance of primate vocalizations, one must consider that the captive setting may distort responses. Therefore, the intergroup spacing function of the "uh-uh-uh..." call, as proposed by Petter and Charles-Dominique [1979], cannot be ruled out. However, we suggest that an important function of this call is to advertise the presence of a potential terrestrial predator.

CONCLUSIONS

1. Significant differences were found between black-and-white and red ruffed lemurs in pulse rate, median pulse duration, median high frequency, and median low frequency of the major energy of the "uh-uh-uh..." loud call.

2. No significant gender differences were found in any of the above variables of the "uh-uh-uh..." loud call.

3. Based on observations of responses to stimuli in random and controlled sessions, a tentative functional designation of terrestrial predator alarm vocalization is suggested for the "uh-uh-uh..." loud call of the ruffed lemur.

ACKNOWLEDGMENTS

The authors thank the DUCP for access to the ruffed lemurs. We are grateful for the cooperation and advice offered by Dr. Elwyn Simons, DUCP Director, Andrea Katz, Dr. Peter Klopfer, and Dr. Jon Pollock. Patricia Wright generously provided the recording equipment. Dr. Haven Wiley allowed us to use his UniScan II, and we are especially indebted to him. We thank the following for reviews of an earlier version of the manuscript: Drs. M.K. Izard, Alison Jolly, Elwyn Simons, Charles Snowdon, and Kenneth Glander. This work was supported by DUCP Discretionary Funds, a Duke University Graduate Fellowship to J.M.M., and a Washington University Graduate Fellowship to L.L.T. SRS Network, Inc. was instrumental in the acquisition of computer hardware.

REFERENCES

- Brockelman, W.Y. Preliminary report on relations between the gibbons *Hylobates lar* and *H. pileatus* in Thailand, pp 315-318 in RECENT ADVANCES IN PRIMATOLOGY, VOL. 3. EVOLUTION. D.J. Chivers; K. Joysey, eds. London, Academic Press, 1978.
- Brockelman, W.Y.; Gittins, S.P. Natural hybridization in the *Hylobates lar* species group: Implications for speciation in gibbons, pp 498-532 in THE LESSER APES: EVOLUTIONARY AND BEHAVIORAL BIOLOGY. H. Preuschoft; D. Chivers; N. Creel; W.Y. Brockelman, eds. Edinburgh, Edinburgh University Press, 1984.

- Creel, N.; Preuschoft, H. Systematics of the lesser apes: A quantitative taxonomic analysis of craniometric and other variables, pp 562-613 in *THE LESSER APES: EVOLUTIONARY AND BEHAVIORAL BIOLOGY*. H. Preuschoft; D. Chivers; N. Creel; W.Y. Brockelman, eds. Edinburgh, Edinburgh University Press, 1984.
- Gautier, J.-P.; Gautier, A. Communication in Old World monkeys, pp 809-964 in *HOW ANIMALS COMMUNICATE*. T.A. Sebeok, ed. Bloomington, Indiana University Press, 1977.
- Geissmann, T. Inheritance of song parameters in the gibbon song, analyzed in 2 hybrid gibbons (*Hylobates pileatus* × *H. lar*). *FOLIA PRIMATOLOGICA* 42:216-235, 1984.
- Groves, C.P. A new look at the taxonomy and phylogeny of the gibbons, pp 542-561 in *THE LESSER APES: EVOLUTIONARY AND BEHAVIORAL BIOLOGY*. H. Preuschoft; D. Chivers; N. Creel; W.Y. Brockelman, eds. Edinburgh, Edinburgh University Press, 1984.
- Haimoff, E.H. Acoustical and organizational features of gibbon songs, pp 333-353 in *THE LESSER APES: EVOLUTIONARY AND BEHAVIORAL BIOLOGY*. H. Preuschoft; D. Chivers; N. Creel; W.Y. Brockelman, eds. Edinburgh, Edinburgh University Press, 1984.
- Haimoff, E.H.; Chivers, D.J.; Gittins, S.P.; Whitten, T. A phylogeny of gibbons (*Hylobates* spp.) based on morphological and behavioral characters. *FOLIA PRIMATOLOGICA* 39:213-237, 1982.
- Hodun, A.; Snowdon, C.T.; Soini, P. Subspecific variation in the long calls of the tamarin, *Saguinus fuscicollis*. *ZEITSCHRIFT FÜR TIERPSYCHOLOGIE, TIERERNAHRUNG UND FUTTERMITTELKUNDE* 57:97-110, 1981.
- Jolly, A. *LEMUR BEHAVIOR*. Chicago, University of Chicago Press, 1966.
- Kress, J.H.; Conley, J.M.; Eaglen, R.H.; Ibanez, A.E. The behavior of *Lemur variegatus* Kerr 1792. *ZEITSCHRIFT FÜR TIERPSYCHOLOGIE TIERERNAHRUNG UND FUTTERMITTELKUNDE* 48:87-99, 1978.
- Lieblich, A.K.; Symmes, D.; Newman, J.D.; Shapiro, M. Development of the isolation peep in laboratory bred squirrel monkeys. *ANIMAL BEHAVIOUR* 28:1-9, 1980.
- Marler, P. *Colobus guereza*: Territoriality and group composition. *SCIENCE* 163:93-95, 1969.
- Marler, P. Vocalizations of East African monkeys: II. Black and white colobus. *BEHAVIOUR* 42:175-197, 1972.
- Marler, P.; Tenaza, R.R. Signaling behavior of apes with special reference to vocalizations, pp 965-1033 in *HOW ANIMALS COMMUNICATE*. T.A. Sebeok, ed. Bloomington, Indiana University Press, 1977.
- Marshall, J.T.; Marshall, E.R. Gibbons and their territorial songs. *SCIENCE* 193:235-237, 1976.
- Marshall, J.T.; Sugardjito, J.; Markaya, M. Gibbons of the lar group: Relations based on voice, pp 532-541 in *THE LESSER APES: EVOLUTIONARY AND BEHAVIORAL BIOLOGY*. H. Preuschoft; D.J. Chivers; N. Creel; W.Y. Brockelman, eds. Edinburgh, Edinburgh University Press, 1984.
- Mayr, E. *POPULATIONS, SPECIES, AND EVOLUTION*. Cambridge, Harvard University Press, 1970.
- Oates, J.F.; Trocco, T.F. Taxonomy and phylogeny of black-and-white colobus monkeys: Inferences from an analysis of loud call variation. *FOLIA PRIMATOLOGICA* 40:83-113, 1983.
- Oppenheimer, J.R. Communications in New World monkeys, pp 851-889 in *HOW ANIMALS COMMUNICATE*. T.A. Sebeok, ed. Bloomington, Indiana University Press, 1977.
- Petter, J.-J.; Charles-Dominique, P. Vocal communication in prosimians, pp 247-305 in *THE STUDY OF PROSIMIAN BEHAVIOR*. G.A. Doyle; R.D. Martin, eds. New York, Academic Press, 1979.
- Ploog, D.; Hupfer, K.; Jurgens, U.; Newman, J.D. Neuroethological studies of vocalization in squirrel monkeys with special reference to genetic differences of calling in two subspecies, in *GROWTH AND DEVELOPMENT OF THE BRAIN*. M.A.B. Brazier, ed. New York, Raven Press, 1975.
- Snowdon, C.T.; Hodun, A. Troop-specific responses to long calls of isolated tamarins (*Saguinus mystax*). *AMERICAN JOURNAL OF PRIMATOLOGY* 8:205-213, 1985.
- Struhsaker, T.T. Phylogenetic implications of some vocalizations of *Cercopithecus* monkeys, pp 365-444 in *OLD WORLD MONKEYS: EVOLUTION, SYSTEMATICS, AND BEHAVIOR*. J.R. Napier; P.H. Napier, eds. New York, Academic Press, 1970.
- Symmes, D.; Newman, J.D.; Talmage-Riggs, G.; Lieblich, A.K. Individuality and stability of isolation peeps in squirrel monkeys. *ANIMAL BEHAVIOUR* 27:1142-1152, 1979.
- Tattersall, I. *THE PRIMATES OF MADAGASCAR*. New York, Columbia University Press, 1982.
- Taylor, L.L. Subspecific differences in vocalizations of *Lemur variegatus*. A paper presented to the meeting of the *AMERICAN SOCIETY OF PRIMATOLOGISTS*, Atlanta, GA, 1978.
- Tenaza, R.R. The functions and taxonomic implications of singing among Kloss gib-

- bons (*Hylobates klossii*) in the Mentawai islands. AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 42:334, 1975.
- Tenaza, R.R. Songs of hybrid gibbons (*Hylobates lar* × *H. muelleri*). AMERICAN JOURNAL OF PRIMATOLOGY 8:249-253, 1985.
- Waser, P.M. The evolution of male loud calls among mangabeys and baboons, pp 117-143 in PRIMATE COMMUNICATION. C.T. Snowdon; C.H. Brown; M.R. Petersen, eds. New York, Cambridge University Press, 1982.
- Wilson, W.L.; Wilson, C.C. Species-specific vocalizations and the determination of phylogenetic affinities of the *Presbytis aygula-megalophos* group in Sumatra, pp 459-463 in CONTEMPORARY PRIMATOLOGY. S. Kondo; M. Kawai; A. Ehara, eds. Basel, Karger, 1975.
- Winter, P.; Ploog, D.; Latta, J. Vocal repertoire of the squirrel monkey (*Saimiri sciureus*), its analysis and significance. EXPERIMENTAL BRAIN RESEARCH 1:359-384, 1966.
- Zann, R. Inter- and intraspecific variation in the calls of three species of grassfinches of the subgenus *Poephila* UNDFUTTERMITTELKUNDE (Gould) (Estrildidae). ZIET-SCHRIFT FÜR TIERPSYCHOLOGIE, TIERERNAHRUNG 39:85-125, 1975.