'Boom' call variation in Cercopithecus mona as a possible proxy for genetic relatedness

Thesis

Presented in partial fulfillment of the requirement for the degree master of arts in the Graduate School of The Ohio State University.

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2015

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The mona monkey population on the island of Grenada was introduced over 350 years ago during the trans-Atlantic slave trade. The source population in Africa has yet been determined. Variation in vocal ability is traditionally argued to be primarily genetic with minimal plasticity due to learned variations. If true, then similarities in vocal behaviors among populations can be used as a proxy for genetic material to estimate relatedness. I tested whether acoustic similarities in loud calls could help ascertain from which mainland African population the Grenadian *Cercopithecus mona* originated.

*Cercopithecus mona* is one of nine guenon species known to emit loud call vocalizations known as 'boom' calls. In *C. mona*, these calls occur at low frequencies (Hz). They are also audibly short, tonal, double-phased calls. Booms are typically produced as responses to perceived threats, for territorial defense, or to initiate group movement. The lead males of mixed sex groups always give the boom calls. Boom call duration and bandwidth were analyzed in 18 boom calls from two *Cercopithecus mona* populations in Nigeria. They were then compared with previously analyzed calls recorded in Cameroon (n=19), Benin (n=17), and on Grenada (n=16). Boom calls from Nigeria had an average bandwidth of 358 Hz (range ~ 118-774 Hz), and duration of 121 ms. They are most similar to calls recorded in Cameroon. Calls from Benin and Grenada are distinctly similar, further supporting the hypothesis that mona monkeys on Grenada are descendants of a population from Benin.

To my parents, Mark and Sara Werling for their unending support in all of my endeavors,

## Acknowledgements

I wish to thank the members of my committee for their feedback and support with this project. I would also like to thank the Governments of Grenada, Nigeria and Cameroon, and the Office National du Bois and Mission Forestier Allemand du GTZ in Benin. I especially thank Thomas Struhsaker for granting access to boom calls from Cameroon, Reiko Matsuda Goodwin for access to the boom calls from Benin, Mary Glenn and Keith Bensen for access to calls from Grenada, and Carrie Vath and Fatsuma Olaleru for granting me access to recordings made in Nigeria. I also thank Matthew Medler and the Cornell Lab of Ornithology, Yoon Kim, Mark Hubbe, Rebekah Dickens, Amy Remer, Kena Worsham, May Patiño, as well as the many assistants who helped in the field. I am grateful to Ken Ayoob, the HSU College of Arts, Humanities, and Social Sciences, and the HSU Department of Anthropology for support. The Grenada research was funded by Humboldt State University, Windward Island Research and Education Foundation, National Geographic Society, Yerkes National Primate Research Center, and The Rockefeller University. Research in Benin was funded by NSF (SBR-9528348), Wenner-Gren Foundation for Anthropological Research (Gr. 9562), Leopold Schepp Foundation, and Primate Conservation, Inc.

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Werling K, Ramsier M, Matsuda Goodwin R, Patiño M, Bensen KJ, and Glenn ME. (2015) Loud call variation in *Cercopithecus mona*: a proxy for genetic relatedness? *American Journal of Physical Anthropology* 156 (Suppl. 60): 322.

Werling K, Worsham K, Patiño M, Ramsier M, and Glenn ME. (2013). Copulations calls of *Cercopithecus mona* in the wild. *American Journal of Physical Anthropology* 150(Suppl. 56):288.

Patiño M, Werling K, Worsham K, Matsuda Goodwin R, Glenn ME, and Ramsier M. (2012) A new analysis of boom call variation among populations of mona monkeys (*Cercopithecus mona*) in Grenada, Benin, and Cameroon. *American Journal of Primatology* 74 (Suppl. 1): 38.

Fields of Study

Major Field: Anthropology

Specialization: Primatology

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#### **INTRODUCTION**

*Cercopithecus mona* (mona monkey) is a species of arboreal monkey endemic to West Africa. The original range of *Cercopithecus mona* spanned forested areas from eastern Ghana to central Cameroon (Booth 1955, 1956; Struhsaker 1970; Oates 1988). Mona monkeys are generalists in diet and habitat, thriving in most forest types including seasonally dry forests and mangrove swamps (Glenn 1996; Matsuda Goodwin 2007).

Approximately 300 years ago, during the transatlantic slave trade, mona monkeys were introduced to the island nations of São Tomé and Príncipe in the Gulf of Guinea and Grenada in the West Indies (Glenn et al., 1999 unpub. report). Sailors often brought back exotic animals from their travels to sell to colonists or to keep as pets (Eaden 1931; Sade and Hildreth 1965; McGuire 1974; Denham 1982, 1987). São Tomé and Príncipe were trans-shipping points during the Atlantic slave trade. It is hypothesized that *Cercopithecus mona* was first introduced to São Tome and from there, a single, possibly pregnant female *Cercopithecus mona* was taken to Grenada where she escaped and founded the present island population (Horsburgh et al., 2002).



Figure 1. Geographic map of endemic and introduced populations of C. mona

The ability of *Cercopithecus mona* to be a generalist has allowed them to successfully survive these island introductions, despite experiencing extreme genetic bottlenecks (Glenn and Bensen 2013). The most recent extreme bottleneck occurred in 2004. Hurricane Ivan destroyed Grenada, leveling nearly all of the Grand Etang National Park and Forest Reserve along with most of the forested and urban sections of the island. A census to determine how many monkeys remain on the island has not been conducted post-Ivan.

In order to understand the effect of the genetic bottlenecks on variation in the Grenada mona monkey genome, Horsburgh et al., (2002) examined the mitochondrial DNA control region. This was used as a measure of intraspecific variability. Tissue samples were collected during field seasons on Grenada between 1992 and 1994, and on São Tomé and Príncipe in 1998 (Glenn, 1996; Glenn et al., unpub. report). No fresh tissue samples were available for mainland populations. Skins collected by naturalists during the 1900s were used (samples made available by the Powell-Cotton Museum, Kent, and the Museum of Natural History, London) (Table 1).

Table 1. Sample size and source location of genetic material.

Grenada21São Tomé12Príncipe4Cameroon9Benin1Total47	Country	n
São Tomé12Príncipe4Cameroon9Benin1Total47	Grenada	21
Príncipe4Cameroon9Benin1Total47	São Tomé	12
Cameroon9Benin1Total47	Príncipe	4
Benin 1 Total 47	Cameroon	9
Total 47	Benin	1
	Total	47

Mitochondrial DNA was extracted from samples, amplified using the Polymerase Chain Reaction (PCR), and then sequenced (Horsburgh et al., 2002). To estimate genetic variation of the three island populations and mainland Africa populations, Horsburgh and associates calculated a diversity index using Nei's number. Only shorter chains of DNA could be extracted from the African *Cercopithecus mona* samples. Therefore, longer and shorter sequences of DNA were indexed separately (Horsburgh et al., 2002). Due to degradation of the mainland African genetic samples, the colonizing source of the São Tomé population cannot be determined. The results of Horsburgh et al.,'s analysis (2002) suggest that mona monkeys on Grenada were brought there from São Tomé. We do not know, however, from which mainland Africa population the Grenada lineage stemmed before their arrival to São Tomé.

As viable genetic samples from mainland Africa are unavailable, a proxy to

determine relatedness is needed. Vocalization recordings, however, are available from most mainland African countries were *Cercopithecus mona* resides. Across primates, variation in vocal ability and behavior is traditionally argued to be primarily genetic, with minimal plasticity due to learned variations (Byrne 1982; Jürgens 1995; Hammerschmidt and Fischer 2008; Zuberbühler 2012). If true, then similarities in vocal behaviors among populations can provide estimates of genetic relatedness.

Guenons are behaviorally diverse, thriving in a wide range of forest types and ecological niches across sub-Saharan Africa (Butynski 2002; Grubb et al., 2003). Within this speciose group (subfamily *Cercopithecinae*), guenons show genetic variability and phenotypic plasticity, due to a recent adaptive radiation 7.5-8.5 mya (Disotell and Raaum 2002; Moranto 1986; Jolly 2001). Guenons commonly live in polyspecific groups, and hybridization occurs in several species (Cords 1986; Gautier and Gautier 1988; Jolly 2001; Detwiler 2002). Separate species are unable to mate and produce viable offspring, but guenons regularly do (Jolly 2001; Detwiler 2002). Separate species within the same niche should not be able to be conspecifics, but some guenons are (Cords 1986). Their recent radiation, polyspecific groupings, and hybridization make guenon taxonomy difficult because traditional species definitions are hard to apply.

Studies of genetic relatedness using vocalizations have been conducted in the past. Thomas Struhsaker (1970) completed an analysis of loud calls in guenons. Loud or long calls are used to communicate long distances both within and between groups (Mitani and Stuht 1998). As they are among the most distinctive sounds in primates' vocal repertoire, long calls have been the focus of many wild and captive research studies (e.g. Gautier and Gautier 1977; Robinson 1979a; Hodun et al., 1981; Waser 1982;

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Snowdon and Hodun 1985; Whitehead 1989; Mitani et al., 1992; Hohmann and Fruth 1995; Zimmerman 1995). Struhsaker (1970) used loud calls to establish a comprehensive phylogenetic tree of guenon monkeys. While recent phylogenies do not match those argued by Struhsaker, the vocal approach to phylogeny reconstruction still has merit due to the conservative nature of the intergroup calls (Gautier 1989; LeMasson et al., 2011; Wang et al., 2012).

Recently, the paradigm that primate vocalizations are fixed from birth has begun to shift (LeMasson et al., 2003, 2005, 2011). Variability in call production has been observed that is related to dialects (Green 1975), vocal adjustment (Mitani and Brandt 1994; Sugiura 1998), and differential learning abilities (Masataka et al., 1992; Elowson and Snowdon 1994; Snowdon, Elowson, and Roush 1997; Snowdon and Elowson 1999). LeMasson et al., (2003) found that social elements, such as friendship are thought to influence intragroup calls. While plasticity is possible, it will only occur within group vocalizations (e.g. contact calls), as intergroup calls (e.g. loud calls) are observed as being extremely stable (Snowdon, Elowson, and Roush 1997; LeMasson et al., 2011).

Environment also shapes vocalization structure. Call frequencies (Hz) are a result of the speed and amplitude at which sound waves move. Therefore, the distance vocalizations travel in a specific forest type is also an aspect of frequency. Loud calls are generally low frequency. Generally, these vocalizations are meant to be heard between groups as opposed to within groups. Loud calls scatter less when sound waves bounce off forest structures. Infant calls, on the other hand, are an example of a high frequency call. These travel better over shorter distances. Infant calls need only to be heard within the group. It is not clear how the environment affects the same call in different forest types and densities. Nor is it clear how long it takes for call variation to arise when a species enters a new environment. If the call differences prove not to be primarily genetically determined, then effects of environmental and learning variation are a possible explanation for boom call variability in *Cercopithecus mona*.

Another possible explanation for call variation is genetic drift due to the extreme founder effects and bottlenecks that *Cercopithecus mona* has undergone on Grenada. Since the entire population is tremendously inbred, and vocalizations have a large genetic component (e.g., Byrne 1982, Jürgens 1995; Hammerschmidt and Fischer 2008; Zuberbühler 2012), any idiosyncratic vocal ability that the first mona had on Grenada could be manifest throughout the entire population now.

Determining genetic relatedness through vocalization similarities will significantly improve research on speciation. Vocal variation and similarity may allow for non-invasive estimates of genetic relatedness of populations and species. Call analysis will strengthen our understandings of guenon genetic relationships. Call analysis performed prior to collecting genetic data (e.g., feces, blood, hair) may aid in designing improved approaches to obtaining genetic material. Having to obtain genetic material for all populations in the sample can be expensive and time consuming. Therefore, understanding relatedness through vocalizations will allow for strategic selection of populations for gathering genetic material.

Among 28 species of guenons (Grubb et al., 2003), only nine are known to emit loud call vocalizations referred to as 'boom' calls: *Cercopithecus mona, C. campbelli, C. pogonias, C. neglectus, C. mitis, C. nictitans, C. hamlyni, C. preussi, and C. lomamiensis* (Struhsaker 1970; Marler 1973; Glenn 1997; Hart et al., 2012). In mona monkeys, these

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vocalizations are short, tonal, double-phased calls that occur at low frequencies (Hz). Booms, generally emitted only by lead males in mixed-sex groups, typically are produced as responses to perceived threats, for territorial defense, or to initiate group movement (Struhsaker 1970, Glenn 1996). Calls can occur throughout the day, but the majority of calls occur around sunrise and sunset (pers. comm. Glenn). Individuals from all-male groups do not emit boom calls. One hypothesis is that males in such groups lack their own discrete territory and are constantly encroaching on others' territory (Glenn et al., 1998).



Figure 2. Spectrogram of Cercopithecus mona double boom on Grenada

Because boom calls are unique guenon vocalizations, variation within call structure is ideal for species identification. Struhsaker's (1970) research did not examine variable vocalizations within a single species, but rather across one family. Some loud calls of guenons prove to be extremely stable and are among the best indicators of phylogenetic affinity within the genus *Cercopithecus*. Struhsaker compared calls of different guenon species to determine phylogenetic relatedness. Species with less vocal variation between them are more closely related. I will apply his model to one species. If vocal variation occurs within a single species, populations with more similar vocalization parameters likely are genetically the most closely related.

Although it is clear that mona monkeys were brought to Grenada by slave ships 350 years ago, the source population in Africa has yet been determined. To explore the origin of this population, I examine whether acoustic similarities in boom calls help ascertain from which mainland African country the Grenada population originated. I analyze acoustic parameters of 18 calls from two *Cercopithecus mona* populations in Nigeria and compare them with previously analyzed calls recorded in Cameroon, Benin, and on Grenada.

## MATERIALS AND METHODS

To determine our ability to use vocalizations as a proxy for genetic relatedness within *Cercopithecus mona*, field recordings of boom calls from various sites were analyzed. Recordings were analyzed to discern amount of auditory variation between distinct populations, and to establish which populations were most similar.

## Boom call recording methods

*Cercopithecus mona* calls were recorded by Thomas Struhsaker in Southern Bakundu Forest Reserve, Cameroon using a Sennheiser MCH unidirectional microphone and a Nagra III recorder. Reiko Matsuda Goodwin recorded calls at Lama Forest Reserve, Benin with a Sennheiser directional microphone and a Sony TCM Mono tape recorder. Carrie Vath recorded calls produced at CERCOPAN (a primate sanctuary) in Calabar, Nigeria using a Sennheiser shotgun microphone and a Sony TCM5000 DAT recorder. Grenada recording made by Mary Glenn and Keith Bensen also used a Sennheiser shotgun microphone and a Sony TCM5000 DAT recorder. New vocalization recordings from Nigeria were recorded by Fatsuma Olaleru using hand-held recorders (H1 Hand Recorder). I was not present and did not make any recordings in any African country.

Forest type and densities may influence mona calls, thus requiring that the locations of all recordings be known. Southern Bakundu Forest Reserve (4° 29' N, 9° 22' E) is a lowland forest in Cameroon. Lama Forest Reserve (*la foret classee de la Lama*) (6° 55'-7° 00' N, 2° 04'-2° 12' E) is a seasonal dry forest located in the center of the Lama Depression in southern Benin. The average yearly rainfall at Lama is 1,100 mm, with two wet seasons: April through June (larger wet season) and August through October (smaller wet season) (Matsuda Goodwin 2007). Grand Etang National Park and Forest Reserve (12° 6' N, 61° 42' W) is an evergreen rainforest situated along the central volcanic mountain range on the island nation of Grenada. Trade winds blow across the field site year-round, and the average monthly rainfall is 252.8 mm (SD=143) (Glenn 1996; Glenn and Bensen 2008). CERCOPAN is located in Calabar, Nigeria and is a primate sanctuary. Recordings were obtained near an enclosure containing two rehabilitated adult males rescued from the wild. Only one of the males "boomed" and was recorded. The recordings made by Olaleru were recorded behind the University of Lagos (6° 31' 14.4604" N, 3° 23' 28.0593" E) where a large primary forest fragment containing a large troupe of *Cercopithecus mona* is located. Maps indicating the locations of each field site are available in Appendix A-D.

## Vocal Analysis

Taped recordings were digitized. All recordings were then converted to .WAV files using a downloadable program. Lab assistants including myself reviewed all tapes for instances of boom calls. Each boom call event is considered a 'unit.' Although some calls are only single-phased, most *Cercopithecus mona* boom calls are two-phased (containing two auditory units).

Country	n	
Cameroon - Southern Bakundu Forest Reserve	19	
Nigeria		
CERCOPAN	9	
University of Lagos	9	
Benin - Lama Forest Reserve	17	
Grenada - Grand Etang National Park and Forest Reserve	16	
Total	70	

Table 2. Sample size and location of boom vocalizations

Auditory units were analyzed using Raven Pro v1.4 and Raven Lite. This software was originally developed by Cornell University to analyze bird song. Struhsaker (1970) used bandwidth and unit duration to identify species through vocalizations. Both parameters also vary between populations of *C. mona* (Patiño et. al., 2012). First, unit duration was measured in milliseconds. Duration is the length of time where the call is first distinct from the background noise until the point when it is no longer distinct. Then, I measured the highest and lowest frequency (Hz) at which the call unit was visually distinct from background noise (Figure 3). From there, I determined bandwidth by subtracting the highest frequency from the lowest frequency. All raw measurements are stored by recording date and location in Excel.



Figure 4. Analysis chart of Boom call unit (Patiño et al., 2012).

A total of 50 boom calls were recorded at CERCOPAN. One individual made all 50 boom calls. To prevent Nigeria from being over-represented by one individual, nine calls were randomly selected from the CERCOPAN calls. This is equal in number to the calls available from the other Nigeria population at the University of Lagos. In previous boom call research data (Patiño et al., 2012), three lab assistants analyzed each Grenadian call. To overcome possible interobserver error, their analyses were averaged to create the Grenada data set.

Analysis of call differences was then compared to current genetic understanding of the Grenada *Cercopithecus mona* lineage. If these two analyses map groups similarly, vocalizations are useful proxies for genetic relatedness in *Cercopithecus mona*. ANOVA and LSD post-hoc test were used to determine which, if any, populations are most similar to each other.

## RESULTS

Call durations for all localities are considered normally distributed (Tables 3), allowing further analysis using parametric ANOVA tests. While unit bandwidth in all countries passed the Kolmogorov-Smirnov test for normality, two countries (Nigeria and Cameroon) failed the Shapiro-Wilk test for normality (Tables 3). Therefore, I performed an additional analysis of bandwidth using non-parametric Kruskal-Wallis tests. Calls from Nigerian *Cercopithecus mona* had an average bandwidth of 358 Hz (range ~ 118-774 Hz), and duration of 121 ms (range ~ 60-200 ms). Nigeria calls are most similar to booms recorded from Cameroon that had an average bandwidth of 292 Hz (range ~ 72-424 Hz), and a duration of 144 ms (range ~ 48-214 ms). *Cercopithecus mona* boom calls in Grenada had an average bandwidth of 69 Hz (range ~ 121-233 Hz), and duration of 90 ms (range ~ 39-140 ms). Grenada calls are most similar to *C. mona* calls from Benin that had an average bandwidth of 123 Hz (range ~ 86-281), and a duration of 99 ms (range ~ 43-203 ms).

		Kolm	ogorov-Sı	nirnov <sup>a</sup>		Shapiro-V	Vilk
		Statistic	df	Sig.	Statistic	df	Sig.
Benin	Unit Duration	.173	17	.190	.907	17	.199
	Unit Bandwidth	.119	17	.200*	.974	17	.033
Cameroon	Unit Duration	.172	19	.143	.939	19	.881
	Unit Bandwidth	.190	19	.070	.829	19	.575
Grenada	Unit Duration	.105	16	.200*	.973	16	.090
	Unit Bandwidth	.167	16	$.200^{*}$	.955	16	.888
Nigeria	Unit Duration	.165	17	$.200^{*}$	.928	17	.254
	Unit Bandwidth	.196	17	.082	.881	17	.003

Table 3. Tests of Normality, Call duration and bandwidth

Bolded are found to be not normally distributed.

\*. This is a lower bound of the true significance.

a. Lilliefors Significance Correction

## Unit Duration

Using ANOVA analyses, I determined that there are population differences in boom call unit duration (Table 4). With further analysis using LSD post-hoc test, I determined that duration of *Cercopithecus mona* boom calls in Benin was most similar in the those of Grenada and Nigeria. Call durations in Cameroon were most similar to those from Nigeria. Call durations from Grenada were most similar to those from Benin (Table 5).

### Table 4. ANOVA, Boom call duration

	Sum of Squares	df	Mean Square	F	Sig.	
Between Groups	.031	3	.010	6.699	.001	
Within Groups	.102	66	.002			
Total	.134	69				

(I) Country	(J) Country	Mean Difference (I-J)	Std. Error	Sig.
Benin	Cameroon	045*	.013	.001
	Grenada	.009	.014	.528
	Nigeria	023	.013	.094
Cameroon	Benin	.045*	.013	.001
	Grenada	$.054^{*}$	.013	.000
	Nigeria	.023	.013	.085
Grenada	Benin	009	.014	.528
	Cameroon	054*	.013	.000
	Nigeria	031*	.014	.024
Nigeria	Benin	.023	.013	.094
	Cameroon	023	.013	.085
	Grenada	.031*	.014	.024

## Table 5. Post-hoc LSD multiple comparison, boom call duration

Bolded sites are found to be significant..

\*. The mean difference is significant at the 0.05 level.

## Unit Bandwidth

Using Kruskal-Wallis analyses, I determined that there are population differences in boom call bandwidth (Table 6). With further analysis using pairwise comparisons, I determined that bandwidths from Grenada were most similar to bandwidths determined from Benin. Unit bandwidths of calls from Nigeria were most similar to those from Cameroon (Table 7).

Total N	69	
Test Statistic	56.740	
Degrees of Freedom	3	
Asymptotic Sig. (2-sided test)	p<.001	

Table 6. Independent-Samples Kruskal-Wallis test, unit bandwidth

Table 7. Post-Hoc Pairwise Comparison, boom call bandwidth on Grenada (GD) and in Benin (BJ), Cameroon (CM), and Nigeria (NG).

Country 1-2	Test Statistic	Std Error	Std Test Statistic	Sig.	Adjusted Sig.
GD-BJ	16.500	6.987	2.361	0.018	0.109
GD-CM	41.447	6.807	6.089	p<0.001	p<0.001
GD-NG	-44.735	6.987	-6.402	p<0.001	p<0.001
BJ-CM	-24.947	6.697	-3.725	p<0.001	p<0.001
BJ-NG	-28.235	6.881	-4.104	p<0.001	p<0.001
CM-NG	-3.288	6.697	-0.491	0.623	1.000

Bolded are found to be significant.

Unit durations and bandwidths of boom calls produced in Grenada were statistically similar to those produced in Benin. Grenada boom calls were not statistically similar to calls from any other African country. Unit durations and bandwidths of calls from Cameroon were statically similar to those from Nigeria. Call durations from Benin and Nigeria were statistically similar, but their bandwidths were not.

## Discussion and Conclusion

Unit durations and bandwidth of boom calls were most similar between the mona monkeys from Grenada and Benin. Cameroon and Nigeria populations were also statistically similar in both unit duration and bandwidth. *Cercopithecus mona* populations in Nigeria and Cameroon are the closest geographically. Genetic analyses performed by Horsburgh et al., (2002) determined Grenada *Cercopithecus mona* was brought from São Tomé an estimated 300-350 years ago. Through vocal analysis I have been able to pair populations with one another. The clustering of all mainland African populations and the statistical pairing of Grenada with Benin only further support the hypothesis that mona monkeys on Grenada are descendants of a population from Benin.

My sample was limited due to both new technology and unforeseen postal error. Recordings made in recent years were obtained using a small hand-held recorder instead of the larger, bulky recorders used by most primatologists. Using this technology for the first time, several instances occurred where individuals recorded booms, but when analyzed, booms were neither heard nor observed in spectrograms. A call was heard and a recording made, but due to an equipment issue, calls were not replayable. Microphone sensitivity or improper settings may have contributed, but none were discovered. Another limitation is sample size for vocalizations and fecal collections. About 20% of samples sent by postal service from Grenada to the United States were lost. While this is problematic, sufficient recordings were available to complete this project. Another possible limitation to the research is the lack of vocalizations available from Ghana and Togo. Both countries were exploited during the trans-Atlantic slave trade, and would have used São Tomé and Príncipe as trans-shipping points. The Grenada and Benin boom calls could be statistically most similar because of geographic closeness to Ghana and Togo. Until I am able to find populations and obtain boom recordings from both countries, I cannot make a definitive statement on the relatedness of the Grenada mona monkey to either Ghana or Togo.

Prior research of relatedness by vocalizations was conducted at the family level rather than on a single species (Struhsaker 1970). As such, research results are not available for comparisons with my data. My results correspond with those of Struhsaker (1970), who found call duration to be the primary parameter in species identification. Call frequencies (Hz) are generally reported as more indicative of environmental structure and density (Struhsaker 1970). As discussed previously, calls such as booms that must traverse longer distances have lower frequencies (Hz). Primate vocalizations have a sound window (Waser and Brown 1984), a frequency bandwidth wherein most primate vocalizations lie despite forest types. Location of each call was recorded along with forest type in Grenada and Benin, but I have not undertaken a universal study between the two sites because sufficient data are not available from each *Cercopithecus mona* habitat to compare environmental influences on mona boom calls.

Numerous studies have focused on environmental effects on vocalizations (Blumstein and Turner 2005; Brown and Waser 1988; Brown and Hanford 1996, 2000; Ey and Fisher 2009; Morton 1975; Pattern, Rotenberry, and Zuk 2004; and Waser and Brown 1986). Acoustical physics predict that in denser forests 20 dB of vocal power is lost every 100 meters (Berg and Stork 1982; Rossig 1990). The structure of guenon 'boom' calls is ideal for projecting in dense forest settings. It is sufficiently loud to rattle the ribs of anyone standing under a male when he emits a boom.

Both call parameters tested (unit duration and bandwidth) overlapped with estimates of *Cercopithecus mona* genetic relatedness. Determining genetic relatedness using vocalization similarities may significantly improve our understanding of speciation in the wild. Vocal variation and similarity allow one to non-invasively estimate genetic relatedness among populations and species. Call analysis such as that presented here improves our understandings of guenon genetic relationships. To continue this research on environmental influences on calls, forest types will be quantified using GIS mapping, and botanical analysis. Access to additional genetic samples of current *Cercopithecus mona* populations will also improve species identification analysis.

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APPENDIX A: Map of field location in Benin



APPENDIX B: Map of field locations in Nigeria



APPENDIX C: Map of field location in Cameroon



APPENDIX D: Map of field location in Grenada

