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Anti-Predator Behaviors in Nocturnal Strepsirrhines

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THE FLORIDA STATE UNIVERSITY
COLLEGE OF ARTS & SCIENCES

ANTI-PREDATOR BEHAVIORS IN NOCTURNAL
STREPSIRRHINES

By

CODY J. MOSER

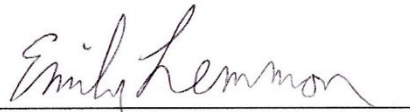
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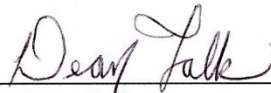
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Introduction

Nocturnal primates compose a large representation of extant primate species, with at least one-third of all primate species discovered exhibiting nocturnal behaviors. Despite this context, few studies tie together behavioral relationships between related and unrelated taxa. In this project, I attempt to elicit antipredator reactions in four separate taxa of nocturnal primate differing in body size, degrees of sociality, and phylogenetic background along with one diurnal control species. I record any reactions that individuals exhibit including behavioral cues, movements, and vocalizations in order to clarify the relationship between nocturnal strepsirrhines and their predators.

Fossil and genetic evidence shows that the earliest primates were nocturnal (Seiffert et al, 2005; Ross & Martin, 2007). Several theories exist to account for the appearance of primates more than 60 million years ago. Among the earliest was the arboreal hypothesis in which F. Wood Jones (1916) argued that primate traits such as binocular vision, grasping hands and feet, and increased cognition arose due to challenges associated with arboreality. The second, developed in 1974 by Matthew Cartmill, was the visual predation hypothesis. Cartmill, observing trends found in other animals in nature, proposed that forward facing eyes, grasping hands and feet, and increases in brain size were associated with the cognitive and mechanical challenges associated with acquiring mobile prey. The third, developed by Robert Sussman (1991), was the angiosperm radiation hypothesis. He proposed that traits such as increased brain size and binocular color vision (a trait unaccounted for in other theories) evolved to exploit the fruits and flowers of flowering angiosperms which emerged at the same time as the earliest primates.

These theories do not come without their own explanatory problems. The arboreal hypothesis fails to account for other arboreal animals lacking similar anatomical adaptations. Current fossil evidence shows that the earliest primates were most likely carnivorous or insectivorous, making the angiosperm theory less likely, as well (Silcox et al., 2007). The most likely route for primate evolution was through visual predation with other radiations of primate evolving later.

Most nocturnal primates are omnivorous, and much of their diet relies on animal protein. Nocturnal primates rely a great deal more on animal protein than their diurnal relatives. The only fully carnivorous primate, the tarsier, is exclusively nocturnal (Gursky et al., 2003). Nocturnality provides several advantages in primates and mammals in general. One is the ability to avoid competition with diurnal taxa who use the same resources by accessing them at a different time. Second is the ability to take advantage of resources only available at night. The ability to hunt is greatly improved provided you have sensory adaptations better than your prey, and sleeping animals may become prey. Third is the ability to evade predators that are active during the day. While predators are also present in the dark, evasion strategies may be very different and more energetically efficient due to the sensory difficulties associated with life at low light.

Many of the adaptations associated with nocturnal living are not as easily explicable. For example, nocturnal primates tend to be much smaller than their diurnal counterparts. Nocturnal primates often communicate in the ultrasonic gradient at a frequency higher than 20 kHz. Few animals communicate in frequencies as high as nocturnal primates with the highest recorded at 70 kHz in the Philippine tarsier (*Tarsius syrichta*) (Ramsier et al., 2012). Several ideas have been presented to account for ultrasonic communication in small nocturnal primates.

The first consideration for ultrasonic vocalizations is size. Size may have an influence on a primate's outward behavior, even in individuals of the same species. Ultrasonic communication, although inaudible to human ears, is simply any communication emitted at a frequency above 20 kHz. Frequencies themselves may be a biomechanical consequence of the size of vocal folds in animals. If body size is not the primary factor contributing to frequency, ultrasonic communication may serve a functional purpose such as predator deterrence, prey deception, or possibly as a strong signal in environments riddled with loud background noise (Ramsier et al., 2012).

Additionally, nocturnal primates possess behavioral adaptations that distinguish them from their diurnal counterparts. One of the most salient adaptations of nocturnal primates is their form of locomotion, predation, and predator evasion that manifests in the form of crypsis. During crypsis, animals attempt to evade detection by moving slowly or not at all. Although not explored across taxa, crypsis has been observed in several species of primates, most frequently in lorises (Nekaris et al., 2007). Slow lorises are masters of crypsis, with previous studies finding that some species move as little as ten meters a night; moving in very small, unobservable increments towards their prey and then rapidly moving with their lanky arms when they are within a limb's reach.

Vertical-clinging-and-leaping (VCL) is another potential anti-predator adaptation found in nocturnal tarsiers, galagos, several species of diurnal lemur, the nocturnal *Avahi laniger* lemur, and nocturnal lemurs of the genus *Lepilemur* (Napier & Walker, 1967). There are several potential origins for vertical-clinging-and-leaping. Galagos and tarsiers, both of which rely heavily on an invertebrate protein diet, use VCL as a rapid form of locomotion to catch flying insects. Yet other VCL primates, such as species of lemur on Madagascar and several species of Lorisidae do not exploit animal protein in their diet. This raises questions on the origins of VCL. Whether or not it evolved due to exploitation of the environment or due to predator evasion is still argued, and while

the relationship is yet unclear it has been theorized that some species of diurnal VCL lemur evolved from a previous nocturnal species (Ankel-Simons & Rasmussen, 2008).

The idea that crypsis has evolved to provide additional defense against predators at night is undermined by the presence of VCL in nocturnal taxa. Nocturnal species that have been observed exhibiting crypsis live in sympatry with nocturnal species that use VCL. Additionally, the presence of cryptic strategies across the primate order has not been catalogued. It is possible that crypsis is not a locomotor strategy for all nocturnal primates, but instead is exclusive to small taxa that are already less apparent to larger predators. For example, the aye-aye (*Daubentonia madagascariensis*) has only one natural predator on the island of Madagascar, but the significantly smaller grey mouse lemur (*Microcebus murinus*) may have more than ten.

Other ways of evading predators have been observed in nocturnal primates. Several species of loris produce poison in their saliva, and many nocturnal primates “park” their infants as opposed to carrying them short distances on their backs when gathering food (Ross, 2001). Although one of the main benefits of group living and sociality in mammals is predator detection and defense, nocturnal primates tend to live solitarily, monogamously, or in small social groups. Alarm calls have been recorded and observed in some species, and the tarsier has a long-distance recruitment vocalization which functions to gather conspecifics to mob predators (Gursky, 2006).

Theoretically, from an evolutionary standpoint, not all nocturnal primates would want to utilize alarm calls. Alarm calls, which are immediate reactions to detected predators, should not be universal. Individuals should only produce alarms calls in the event that their calls dissuade predators. These calls would act as detection signals for predators that rely upon unprepared prey, a theory known as the perception advertisement hypothesis (Bergstrom & Lachmann, 2001). Individuals should also only alarm call if such calls increase the chances of escape for themselves

or closely related conspecifics, a theory known as the conspecific warning hypothesis (Flasskamp, 1994).

Most nocturnal primates exist within limited degrees of sociality. It is unlikely that it would be beneficial for these primates to produce alarm calls, yet we have observational accounts of them doing so. Based on our current understanding of nocturnal primates and their communication, it is possible that radiations of nocturnal primates have found a way to shed themselves of the disadvantages incurred by alarm calling, most noticeably chances of detection, through the use of ultrasonic communication. In such a case, nocturnal primates can keep their system of crypsis while having the ability to alert nearby conspecifics to the presence of predators.

I hypothesize that crypsis is a nocturnal strategy limited to smaller taxa. If this is the case, the aye-aye, which is amongst the largest of the lemurs in Madagascar, should not resort to cryptic strategies when exposed to predators. I predict the species will instead appear aggressive or standoffish with reactions that mirror those when encountering aggressive conspecifics. The smaller nocturnal primates should resort to crypsis and attempt to conceal themselves or hide when exposed to predatory stimuli. If it is the case that all the nocturnal primates resort to crypsis, then it would support the conclusion that crypsis is a nocturnal strategy used by most radiations of nocturnal strepsirrhine.

I also hypothesize that ultrasonic communication is used by nocturnal taxa as a private communication channel for predator evasion. For this, two assumptions must hold during experiments: individuals will use alarm calls in the presence of predatory stimuli and that alarm calls will be at a higher frequency than typical vocalizations in these species. The assumption is not made that these vocalizations must simply be in an ultrasonic frequency because some vocalizations are already in the ultrasonic range and are unrelated to predator contexts.

Both of these hypotheses have implications for our understanding of the evolution of our earliest primate ancestors as well as for the nature of nocturnality. Because of the large diversity of nocturnal primates in the wild and their dispersion across vast geographic spaces, few cross-comparative studies have been undertaken. The information collected in these experiments may yield scientific insights on the underlying processes behind antipredator behaviors in nocturnal primates.

Primate Information

Suborder Strepsirrhini

Each species examined in this study, as well as all primates at the Duke Lemur Center, are members of the Primate Order and the Suborder Strepsirrhini. Strepsirrhines, which are a distinct clade of primates including the lemurs, lorises, and galagos, are distinguishable from members of the Suborder Haplorrhini, including the monkeys, apes, and tarsiers, with the latter of which have anatomical specializations including a toothcomb, a grooming claw, a *tapetum lucidum*, and a wet rhinarium.

Strepsirrhine primates have smaller body sizes, shorter lifespans, and are marked by a number of cognitive distinctions from the Haplorrhine primates including an inability to intentionally fabricate false information (Whiten & Byrne, 1988). The majority of nocturnal primates are strepsirrhines. Nearly all species of Lorisoidea, a clade containing all lorises and galagos, and many species of Lemuroidea, a clade containing all lemurs, are nocturnal or cathemeral. In contrast, only two radiations of Haplorrhine primates are nocturnal: owl monkeys in the genus *Aotus* and the infraorder Tarsiiformes. Figure 1 shows a basic strepsirrhine phylogeny with species examined in this study highlighted for clarification.

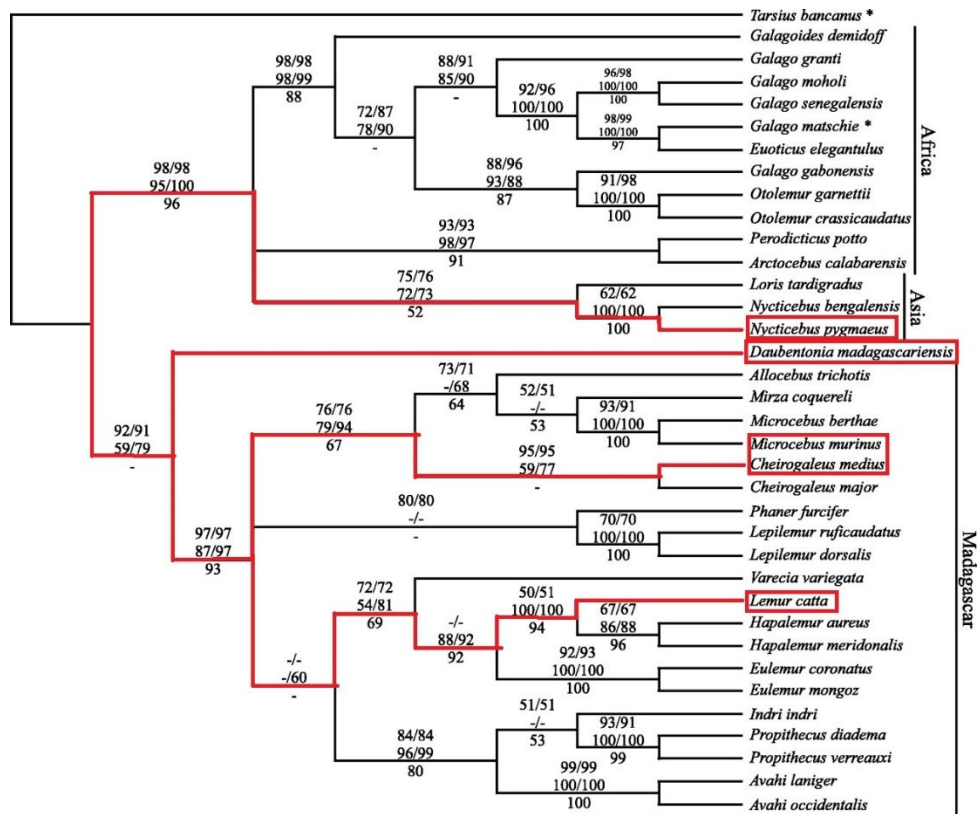


Fig 1. Strepsirrhine phylogeny with taxa utilized in this study highlighted in red. Adapted from Roos (2004)

Lemur catta

The sole diurnal species used in this study, *Lemur catta*, also represents the most social and terrestrial lemur in this study. Like all other lemurs, ring-tailed lemurs are endemic to the island of Madagascar. Ring-tailed lemurs are opportunistic omnivores, eating fruit, leaves, flowers, and small insects (Budnitz & Dainis, 1975). These lemurs are the second largest primates in the study, with similar body dimensions to a large cat.

Life history data collected from the Duke Lemur Center's long-term research database show a mean lifespan of 16.87 years on average, with the maximum age of a DLC lemur being 31 years of age. Mean weights for the species are 2.45 kilograms, with females weighing an

average weight of 2.35 kilograms and males weighing an average of 2.54 kilograms (Zehr et al., 2014).

Research on ring-tailed lemurs in the wild has been very extensive, and several catalogues of vocal repertoires have been published on the species. Ring-tailed communication is highly complex amongst prosimians, and separate distinct predator-warning calls have been recorded for aerial and terrestrial predators (Sauther, 1983). Ring-tails are highly vocal, and their cooing sounds have been found to be an important factor for group dynamics and cohesion in the species (Macedonia, 1993). Ring-tailed lemur vocalizations are within the range of human hearing, lower than the ultrasonic range (>20 kHz).

Cheirogaleidae

The two species represented from the family Cheirogaleidae, *Microcebus murinus*, or the gray mouse lemur, and *Cheirogaleus medius*, or the fat-tailed dwarf lemur, are among some of the smallest of lemurs. Both species, as well as all Cheirogaleidae, are exclusively nocturnal, and members of both *M. murinus* and *C. medius* are omnivorous and store fat in their tails for seasonal hibernation and torpor (Schmid & Kappeler, 1998; Fietz & Ganhorn, 1999).

While both species are similar in their diet and feeding ecology patterns, their social organizations highly differ. *Microcebus murinus* lives in large multi-male, multi-female groups. Individuals leave their nesting sites to forage independently at night, and return to nest in groups of up to 15 individuals (Radespiel, 2000). Males often sleep alone, while females may sleep with the same females. During the mating season, individual males can be found with up to seven females at individual nesting sites.

Cheirogaleus medius lemurs live in smaller groups, with seasonal flexibility arising during periods of torpor (Müller, 1999). Males are intolerant of one another, and social

organization is found to be consistent with small, dispersed, monogamous family groups. During periods of torpor, nesting size may increase from one to five individuals sharing the same tree hole.

Life history data collected from the Duke Lemur Center's long-term database show a mean lifespan of 8.34 years in *M. murinus*, with the maximum age of a DLC lemur being 17.96 years of age. Mean weights for the species are 82.65 grams, with slight sexual dimorphism towards females weighing an average of 85.93 grams and males weighing an average of 79.82 grams; it is unknown if measurements analyzed in the dataset were taken during periods of pregnancy in females or during breeding periods for males when significant drops in weight are expected (Zehr et al., 2014).

Longer lifespans have been recorded in *C. medius*, and their unusual age-body mass ratio is currently being explored as a topic of research for its applications to human longevity. The mean lifespan of a lemur at the DLC is 14 years, with the maximum age measured at 28.98 years old. The mean weight for adults is 241 grams, with females weighing 247 grams and males weighing 236 grams on average (Zehr et al., 2014).

Vocalizations in both of these species reach into the ultrasonic range, with *M. murinus* vocalizing at much higher frequencies than *C. medius*. Ranges for *M. murinus* have been found to exist in a range up to 40 kHz and ranges for *C. medius* have been recorded in the ranges up to 25 kHz (Cherry et al., 1987).

Daubentonia madagascariensis

Daubentonia madagascariensis, a species in a genus of its own and known more commonly as the aye-aye, is perhaps the strangest of all primates. Although still considered a lemur, aye-ayes separated from ancestral lemurs millions of years before their massive adaptive radiation on Madagascar, and are commonly used as a genetic outgroup from which to base the phylogenetic positions of all other lemurs. Consequently, they are regarded as the most genetically basal species in the primate order (Perry et al., 2012).

The aye-aye is highly specialized in its environment, filling a niche commonly found on other continents occupied by woodpeckers or large rodents. The aye-aye has a suite of adaptations including an elongated third digit used to extract grubs from holes bored in trees with its continuously growing incisors and located with its large dish-like ears. Aye-ayes feed on fruit, insects, fungi, and nectar, and are the largest primate represented in this study (Andriamasimanana, 1994).

Life history data collected from the Duke Lemur Center's long-term database show a mean lifespan of 24 years in *D. madagascariensis*, with the maximum age of a DLC lemur being 32.37 years of age. Mean weights for the species are 2.67 kilograms, with females weighing an average of 2.72 kilograms and males weighing an average of 2.6 kilograms. It is unlikely that lifespans of aye-ayes in the wild approach those seen at the Lemur Center, as physical ailments such as loss of incisors and breakage of the elongated third digit are common with age in individuals (Zehr et al., 2014).

Little research has been carried out on the vocal characteristics of aye-aye communication (Sterling & Richard, 1995). Aye-ayes forage using a method called percussive foraging in which the elongated third finger is used to locate grubs and other food sources

underneath wood by tapping as the aye-aye listens with its large ears (Erickson, 1991). This indicates a strong reliance on audible sensory systems in the species. In addition to hearing adaptations, the aye-aye retains visual dichromacy, possibly as a method for predator detection during day times (Perry et al., 2007).

Socially, aye-ayes are solitary with very large overlapping ranges. Male and female interactions tend to be affiliative, while solitary female interactions are aggressive. Male-male interactions may be either affiliative or aggressive (Andriamasimanana, 1994). Aye-aye social communication relies highly on olfactory cues, and while studies have linked the brain-body size quotient within primates to high degrees of sociality, aye-ayes have one of the largest and most developed brains within the prosimians (Dunbar, 1998; Kaufman et al., 2005).

Nycticebus pygmaeus

The sole non-lemur primate used in this study, *Nycticebus pygmaeus*, or the pygmy slow loris, is found in Southeast Asia in China, Cambodia, Laos, and Vietnam. Favored by the pet trade, the taxonomic classification of *Nycticebus* lorises is still under construction (Chen et al., 2006). Although nocturnal like the Cheirogaleidae and the aye-aye, *N. pygmaeus* differs from them in diet, locomotion, and social patterns.

All lorises are nocturnal, and the pygmy slow loris is omnivorous. One-third of their diet is composed of animal prey, while the remaining two-thirds is almost entirely composed of tree gums. In the wild, these lorises have been observed to periodically visit the same trees within their home ranges and leave noticeably large gouges in the tree trunks, making identification of their nesting sites easy (Nekaris, et al., 2010).

Life history data collected from the Duke Lemur Center's long-term database show a mean lifespan of 11.25 years in *N. pygmaeus*, with the maximum age of a DLC loris being 19.26

years of age. Mean weights for the species are 487 grams, with females weighing an average of 480 grams and males weighing an average of 496 grams (Zehr et al., 2014).

Lorises have a number of adaptations separating them from other primates. Lorises have hands with shortened second digits, highly mobile ankles and wrists, and their bodies allow for the exchange of oxygen and waste materials in the absence of bodily movement (Grand, 1967; Davies, 1947). These adaptations allow for prolonged grip on branches with little fatigue. Loris bodies are also elongated, allowing for navigation across gaps in their terrain by stretching (Curtis, 1995). In addition to their body morphology, slow lorises are toxic (Wilde, 1972). The function of their toxicity is still debated in the literature, with suggestions ranging from the use of poison as an anti-predatory or defense mechanism to the possibility that it may be an adaptation for protecting infants left on branches for short periods of time (Grow et al., 2015).

The vocalizations of pygmy slow lorises have not been fully explored, but preliminary research shows that these animals communicate in a range both within the human range of hearing and in the ultrasonic gradient (Daschbach et al., 1981; Zimmermann, 1985). Socially, the pygmy slow loris may be monogamous like *C. medius* and several other nocturnal taxa, sleeping in groups of 1-4 individuals consisting of male/female pairs with additional offspring (Wiens & Zitzmann, 2003).

[Cryptoprocta ferox](#)

The fossa, the main predator model in this study should also be described, as it is the apex predator of the island of Madagascar and has been documented hunting and consuming nearly every species of lemur, from the smallest mouse lemurs to the largest of all lemurs, the indri (*Indri indri*) (Hawkins & Racey, 2008).

The fossa, the sole species of its unique genus, is also endemic to Madagascar. For many decades thought to be a cat, the fossa most resembles felines, but is genetically closer to a group of mammals including the civets (Yoder et al., 2003). Fossas have been severely underexplored by both the scientific and conservation community, but current studies show that they are both nocturnal and solitary except during the mating season.

Fossas are the largest carnivore on Madagascar, with adults weighing between 5.5-8.6 kilograms. Fossas have distinct anatomical adaptations for hunting arboreal prey, including semi-retractable claws, flexible ankles, and a very large tail allowing them to travel vertically up and down trees head-first. Sexual maturity in the fossa occurs at three to four years of age, and the average life expectancy for captive individuals is up to 20 years of age.

Half of a fossa's diet consists of lemurs, and it is the only predator capable of preying upon all 100+ species of lemur on Madagascar. During the non-breeding season fossas are solitary hunters, but during the breeding season animals may be seen in cooperative hunting pairs, performing chasing-and-trapping techniques seen in other arboreal predators in the wild. While fossas generally prey upon medium sized to larger sized lemurs in the wild, they have been observed eating prey as large as indris (6.8kg) to prey as tiny as small birds (Dollar et al., 2007).

Methods

This study was completed at the Duke Lemur Center (DLC) in Durham, North Carolina over the summer of 2015 from June 14th to July 22nd with statistical analyses conducted during subsequent semesters in the fall of 2015 and the spring of 2016 using SAS.

The Duke Lemur Center is a non-profit research and conservation center located across 80 acres of forest located near Duke University in the central area of North Carolina. Hosting over 240 individuals across at least 21 species of strepsirrhine, 18 belonging to the superfamily Lemuroidea, the DLC is the largest prosimian research center of its kind in the world.

I tested five species in this study: *Lemur catta*, *Nycticebus pygmaeus*, *Daubentonia madagascariensis*, *Cheirogaleus medius*, and *Microcebus murinus*. The Cheirogaleidae, composing the grey mouse (*Microcebus murinus*) and fat-tailed dwarf lemurs (*Cheirogaleus medius*) are kept in colony-type indoor enclosures in which individuals are held in large home enclosures within a single room connected to other enclosures that contain multiple lemurs of the same species. Pathways to and from other enclosures in the room are changed periodically depending on a number factors including behavioral enrichment, social behaviors, and mating seasons. Aye-ayes (*Daubentonia madagascariensis*) and pygmy slow lorises (*Nycticebus pygmaeus*) are housed in very large indoor concrete enclosures alone or with one other individual.

Keepers and researchers control diet and temperatures day and night in indoor enclosures. For nocturnal primates, nocturnal periods are adjusted to coincide with human daylight hours, usually beginning at 9:00am and ending at 8:00pm. Diurnal *Lemur catta* live in outdoor free-range enclosures which extend several acres. Feeding, medical examinations, and laboratory work occur at central locations connected to outdoor enclosures accessible by workers and veterinarians.

For the experiments, I used a research design modified from Rahlfs and Fichtel (2010). Rahlfs and Fichtel conducted experiments to elicit reactions from eight captured grey mouse lemurs in the wild using false predator models of a fossa (*Cryptoprocta ferox*), a rubber snake, and a raptor. These experiments failed to elicit any vocalizations from the mouse lemurs, and individuals continued to forage in their makeshift habitat. Playbacks of mouse lemur alarm calls, a synthesized lemur call, and a bat call were played, but also failed to elicit any reactions from individuals.

This experiment draws many elements from the original, including the use of false predator models, but unlike the original experiment (designed to elicit reactions to predators *or* to conspecific alarm calls), this experiment was designed simply to elicit *any* anti-predator reaction. I increased the sample size by adding representatives of four species to the study, and I played vocalizations in conjunction with predator models.

To begin, a worker separated individual primates from their living quarters and placed them in dark isolation for a period of time less than one hour before experiments began, typically after nocturnal conditions were restored to the enclosures and prior to first feedings. The primates were then taken to an experiment room and placed solitarily in a large room designed for in-house experiments at the Lemur Center. During this period and throughout the length of the experiment, I played a continuous track of rainforest background noise in order to ensure a neutral sound field for predator playbacks.

I then monitored individuals for neutral behaviors (foraging, resting, sitting, absence of pacing) before experiments began. If neutral behaviors were not shown by a primate after a period of <5 minutes, we returned the individual to its holding room and replaced it with the other individual in waiting. Upon neutral behaviors, playback experiments began with six vocalizations;

the first three vocalizations played were of the rainforest scops owl (*Otus rutilus*), the Madagascan owl (*Asio madagascariensis*), and the Madagascar harrier-hawk (*Polyboroides radiatus*). The final three vocalizations were variants of calls and growls of the fossa (*Cryptoprocta ferox*), a primary predator of lemurs on the island of Madagascar. Upon the second fossa call, a worker exposed a hidden chamber containing a model fossa, providing a visual representation of the wild predator.

I recorded a variety of reactions: freezing or running, orientation toward the stimuli, presence of audible vocalizations, and the time these behaviors stopped during experiments. Pauses between individual playback stimuli were held for one minute after the return of neutral behaviors in individuals, followed by the next successive vocalization. Before the model fossa and second fossa vocalization sequence, we closed the chamber until the return of neutral behaviors and subsequently kept it open for three minutes after playing the third fossa vocalization. To capture vocalizations, I placed a Pettersson M500 ultrasonic recording microphone out of sight in the experiment room. Animals were then held in the room until the return of neutral behaviors and subsequently returned to the holding room to be taken back to their original enclosures. Experiment times typically lasted no more than 15 minutes.

Each primate species was observed and recorded outside the context of playback experiments in their normal habitats. Basic observation techniques were used, as established by Altmann (1974), to assess neutral behaviors and correlate any vocalizations given by individuals during playback experiments to those made in their daily lives. Table 1 shows a list of all DLC primates used in this study.

Species	Name	Sex
<i>Lemur catta</i>	Teres	Male
<i>Lemur catta</i>	Perisidies	Male
<i>Lemur catta</i>	Nikos	Male
<i>Lemur catta</i>	Onyx	Male
<i>Lemur catta</i>	Persephone	Female
<i>Lemur catta</i>	Sierra Mist	Female
<i>Lemur catta</i>	Brigitta	Female
<i>Lemur catta</i>	Hybernia	Female
<i>Nycticebus Pygmaeus</i>	IO Moth	Male
<i>Nycticebus Pygmaeus</i>	Roach	Male
<i>Nycticebus Pygmaeus</i>	Junebug	Female
<i>Nycticebus Pygmaeus</i>	Sovani	Female
<i>Daubentonia madagascariensis</i>	Norman	Male
<i>Daubentonia madagascariensis</i>	Merlin	Male
<i>Daubentonia madagascariensis</i>	Poe	Male
<i>Daubentonia madagascariensis</i>	Nosferatu	Male
<i>Daubentonia madagascariensis</i>	Lucrecia	Female
<i>Daubentonia madagascariensis</i>	Ozma	Female
<i>Daubentonia madagascariensis</i>	Morticia	Female
<i>Daubentonia madagascariensis</i>	Andora	Female
<i>Cheirogaleus medius</i>	Tanager	Male
<i>Cheirogaleus medius</i>	Auklet	Male
<i>Cheirogaleus medius</i>	Thrasher	Male
<i>Cheirogaleus medius</i>	Francolin	Male
<i>Cheirogaleus medius</i>	Osprey	Male
<i>Cheirogaleus medius</i>	Crow	Male
<i>Cheirogaleus medius</i>	Jaeger	Male
<i>Cheirogaleus medius</i>	Hottenton	Female
<i>Cheirogaleus medius</i>	Quetzal	Female
<i>Cheirogaleus medius</i>	Towhee	Female
<i>Microcebus murinus</i>	Bullrush	Male
<i>Microcebus murinus</i>	Daikon	Female
<i>Microcebus murinus</i>	Shisho	Female

Table 1. List of individuals used in the study, including information on species and sex

A predator model was created using a bobcat (*Lynx rufus*) mold used by taxidermists to mount specimens and hunter's trophies and modelled to look like a fossa. As the fossa and American bobcat have similar body dimensions, construction of the predator was a matter of

applying properly colored fabrics to the body of the mold and constructing a tail out of wire. The ultrasonic microphone was connected to a Microsoft Windows Surface 3 tablet computer with accompanying BatSound recording software used for collecting and recording vocalizations. Parameters for recording vocalizations were set accordingly for each species and can be found in Table 2.

Species	Frequency Ranges
<i>Cheirogaleus medius</i>	0kHz-30kHz
<i>Microcebus murinus</i>	10kHz-60kHz
<i>Daubentonia madagascariensis</i>	0kHz-30kHz
<i>Nycticebus pygmaeus</i>	0kHz-40kHz
<i>Lemur catta</i>	0kHz-20kHz

Table 2. List of species in the study and frequency ranges set on the recorded

For behavioral observations, a simple ethogram of behaviors exhibited by the lemurs was constructed including running/evading, stopping, and orientation towards objects. Any unique behaviors of note taken during response times to the stimuli were recorded *ad libitum* (Altmann, 1974). All behaviors were measured focally, and special note was taken with the use of a stopwatch to record lengths of time spent frozen by each animal. To rank whether behaviors exhibited were cryptic or non-cryptic, a scoring system was set up in alignment with behaviors seen across all taxa. Tables 3 shows scores given for each behavior.

Score	Behavior
+1	30 Second Stop
+1	Stop & Immediate Orientation Towards Stimulus
+1	90 Second Stop
+1	180 Second Stop
-1	Run/Evade
-2	Audible Vocalizations

Table 3. Scores given for each behavior exhibited during exposure to stimuli. Points given were cumulative, e.g. an individual stopping for a period of 100 seconds would receive a score of +2, and a score of +3 if it oriented itself towards the stimuli

Results

Experimental Behaviors

This study was completed at the Duke Lemur Center (DLC) in Durham, North Carolina over the summer of 2015 from June 14th to July 22nd with subsequent statistical analyses conducted during fall 2015 and spring 2016. Out of all thirty-one primates tested, five were non-responsive to stimuli and were dropped from datasets for analysis. The figures shown below are statistical ANOVA models run in the program SAS including post hoc Fisher's LSD tests. Appendices in the back of the book include individual graphs along with the results for Fisher's LSD tests uncorrected for multiple comparisons. Each comparison is held as an individual t-test between species to account for uneven sample sizes.

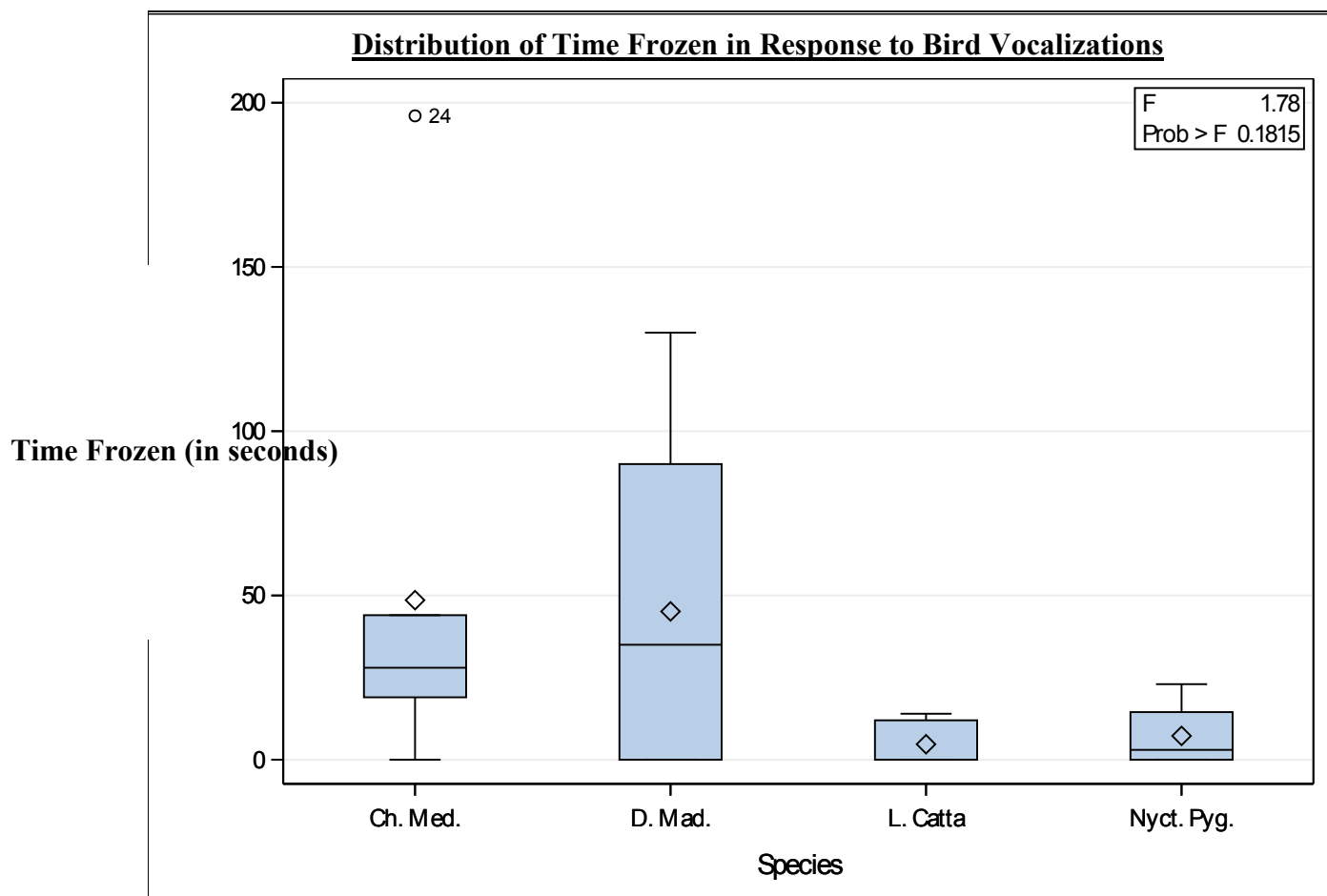


Figure 1. Times Spent Frozen (in Seconds) When Exposed to Bird Vocalizations

In tests using bird vocalizations, individuals were largely either nonresponsive or had little response to vocalizations (Figure 1). One point was awarded to *Lemur catta* for their reactions to birds, none to *Nycticebus pygmaeus*, eight to *Daubentonia madagascariensis*, and eight to *Cheirogaleus medius*. *L. catta* came to a complete stop from bird stimuli for an average of 4.33 seconds, *N. pygmaeus* for an average of 7.25 seconds, *D. madagascariensis* for an average of 45 seconds, and *C. Medius* for an average of 23 seconds. Significant differences at the 0.05 level on t-tests were not found between any species. See Appendix 2 for details.

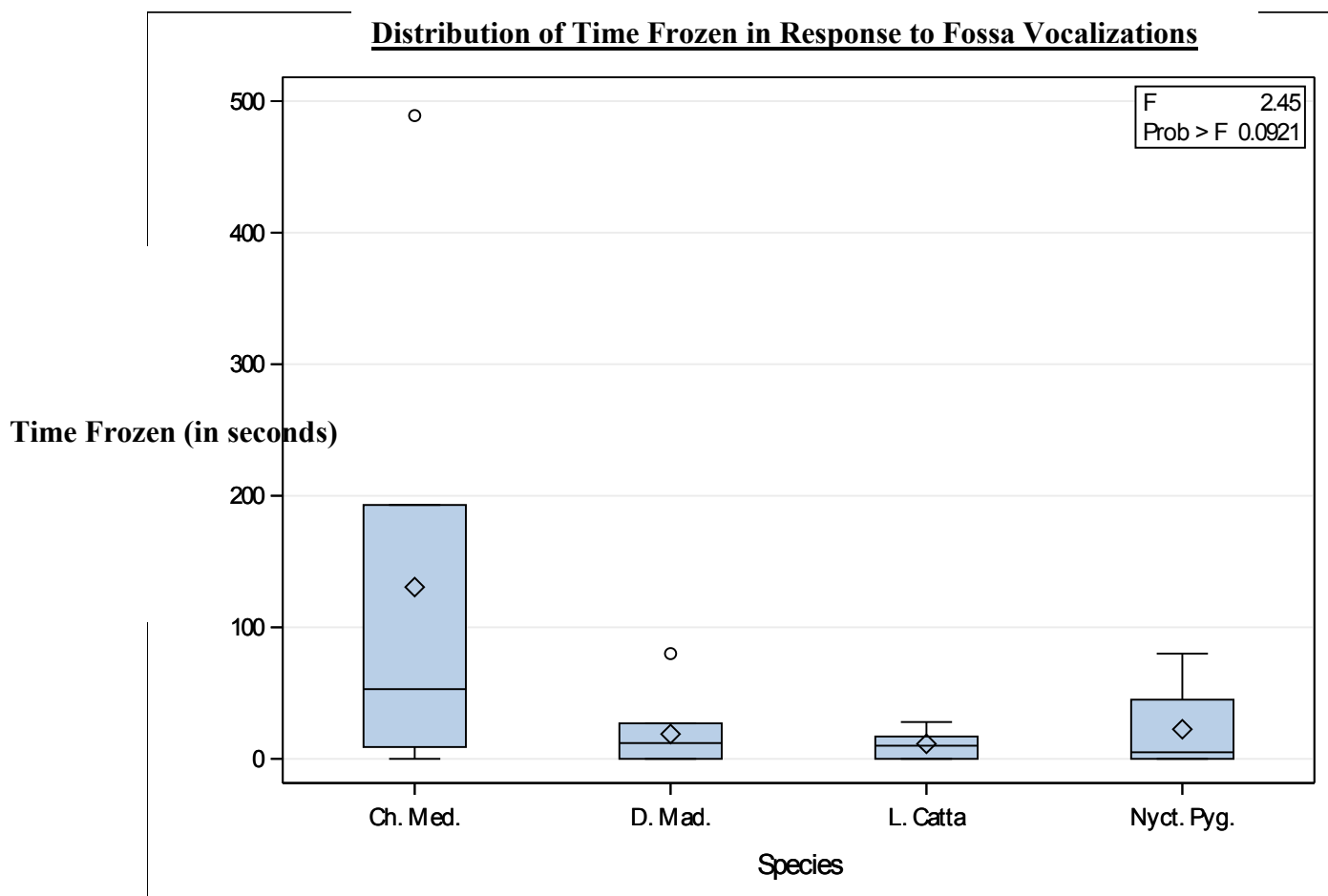


Figure 2. Times Spent Frozen (in Seconds) When Exposed to Fossa Vocalizations

In tests using only fossa vocalizations, primate responses greatly varied (Figure 2). Negative two points were given to *L. catta* for their reactions to fossa vocalizations, four points were given to *N. pygmaeus*, thirteen were given to *D. madagascariensis*, and twenty-two points

were given to *C. medius*. Mean stop times within species were 11.43 seconds in *L. catta*, 22.5 seconds in *N. pygmaeus*, 18.86 seconds in *D. madagascariensis*, and 130.57 seconds in *C. medius*. Significant differences were found between the *C. medius* and *D. madagascariensis*, as well as between the *C. medius* and *L. catta*. See Appendix 3 for details.

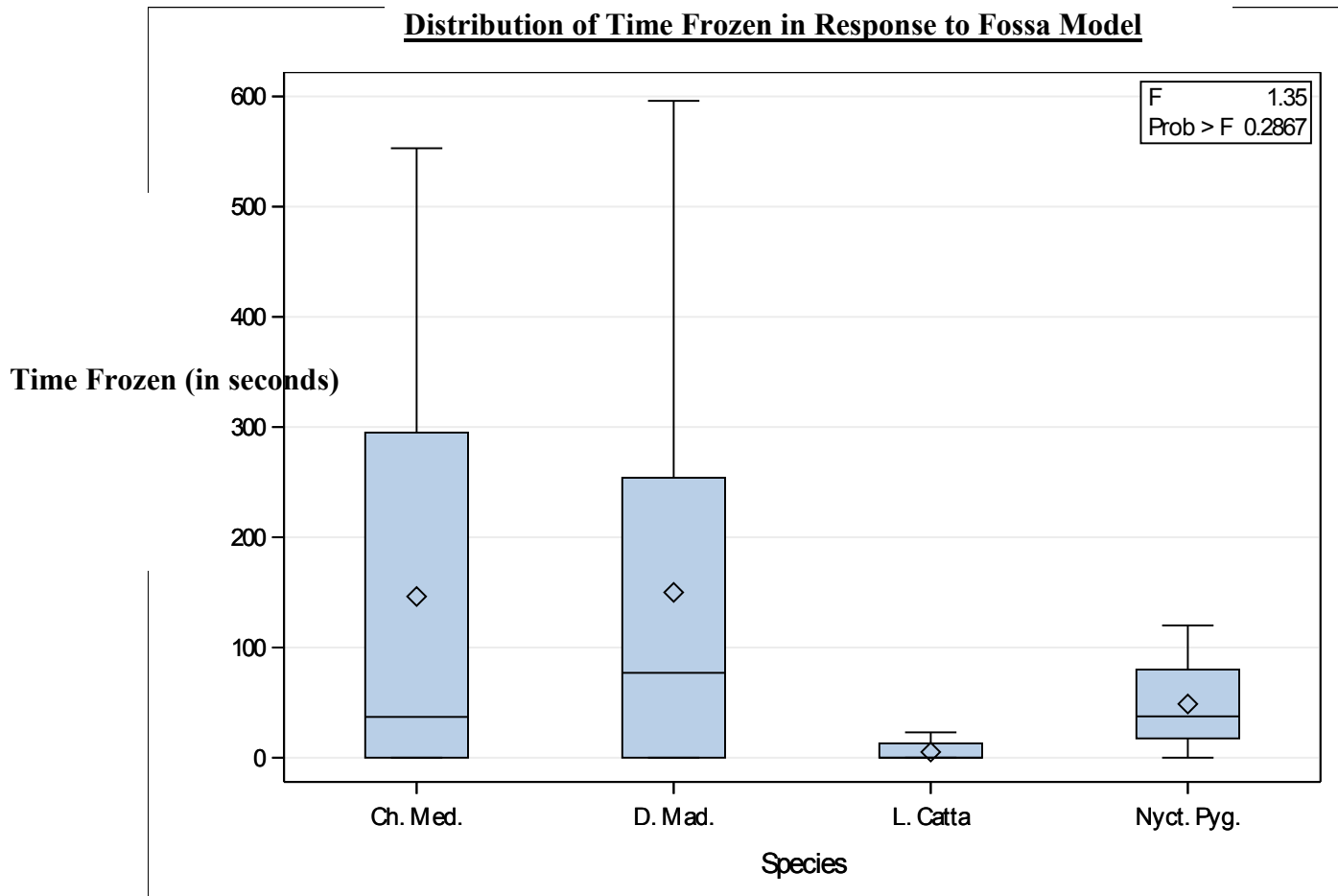


Figure 3. Times Spent Frozen (in Seconds) When Exposed to Fossa Model

In times spent frozen from the model, a non-significant result was recovered from the ANOVA ($P > 0.2867$), although clear differences exist between *L. catta* and the rest of the primate species (Figure 3). Negative one point was given to *L. catta* for their reactions to fossa vocalizations, eight points were given to *N. pygmaeus*, fourteen were given to *D. madagascariensis*, and thirteen points were given to *C. medius*. On average, *L. catta* stopped for

5.14 seconds, *N. pygmaeus* stopped for 48.75 seconds, *D. madagascariensis* stopped for 150 seconds, and *C. medius* stopped for 146.29 seconds. See Appendix 4 for details.

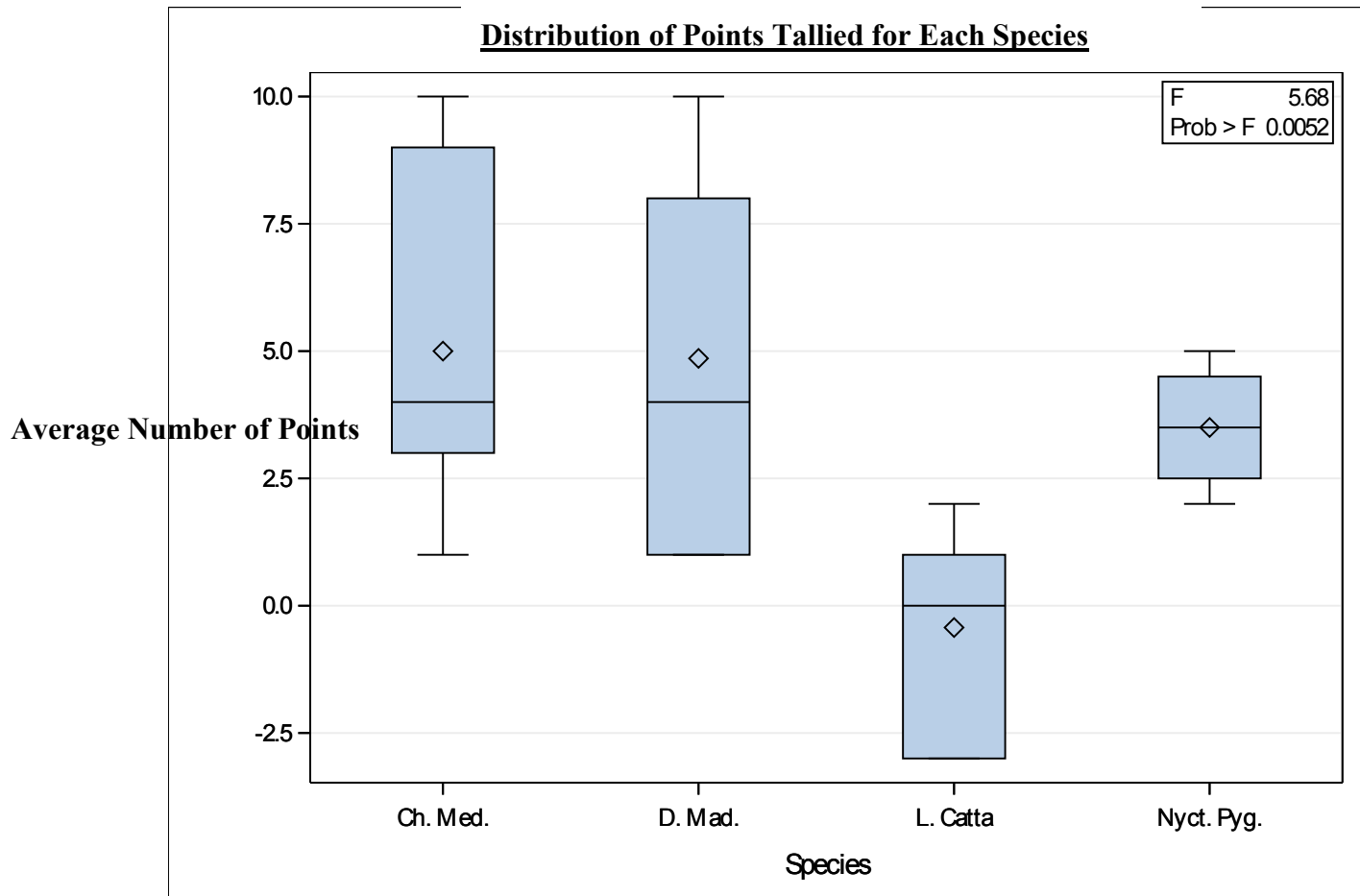


Figure 4. Average Points for Crypsis Awarded to Each Species, refer to Methods table 3

The ANOVA for points awarded to species of primates found strong significance ($P > 0.0052$) indicating that there was a difference between groups (Figure 4). Points given to species showed an average of -0.43 points for *L. catta*, 3.5 points for *N. pygmaeus*, 4.86 for *D. madagascariensis*, and 5 for *C. medius*. These differences were significant between *L. catta* and all nocturnal species, while nocturnal species did not significantly separate from each other. See Appendix 1 for details.

Vocalizations

During observations, a total of 2,067 vocalizations were collected from five species of lemur, including *Microcebus murinus*. Many of the vocalizations had associated contexts, others were general calls collected when primates could not be seen or contexts could not be confirmed. One call in particular was used by *Lemur catta* on two separate occasions during experimentation which was later confirmed to be a terrestrial predator call through observations when a fox entered the *Lemur catta* enclosure, sparking a large interspecific anti-predator cacophony. *Lemur catta* were also confirmed to have separate calls for terrestrial and aerial predators as observed in Macedonia (1993).

During experiments, only *Lemur catta* made any audible sounds. Later sound analysis on recordings taken of nocturnal species showed that all species were completely silent during exposure to stimuli. Vocalizations collected during observations related to antagonism, pain responses, and play were completely absent during individual experimentation and not picked up by ear or by ultrasonic microphone.

Discussion

The results from these experiments show high variation in response to predators within the *Cheirogaelus medius*, as well as a significant separation of *Lemur catta* from the other species in the study. Although the results do not show much evidence for separation of *Nycticebus pygmaeus* from *Lemur catta* or other groups, this is likely due to the small sample size of four rather than a behavioral similarity to *Lemur catta*.

The most striking result from the experiments shows the presence of crypsis in *Daubentonia madagascariensis*. No previous work has been published on the antipredator behaviors of aye-ayes, and current thought regards crypsis as an adaptation of smaller, more basal primates. This is clearly not the case, as *Lemur catta* and *D. madagascariensis* have nearly similar body sizes and weights, but significantly different antipredator strategies. Other potentially important factors possibly contributing to the presence of crypsis in a nocturnal lemur as large as the aye-aye are the presence of nocturnality and their lower degree of sociality shared with the other nocturnal primate species.

My first hypothesis posited that crypsis was a nocturnal strategy limited to smaller taxa, such as the dwarf lemurs and slow lorises, but this was not the case. Whether the primary factor contributing to crypsis in the aye-ayes is their nocturnality or their lesser degree of sociality is unknown. However, testing primates based on differing levels of sociality would be difficult, as low primate sociality is rare outside of nocturnal taxa. Ultimately, low degrees of sociality found in nocturnal species may be specifically due to nocturnality. Group predator detection has been theorized as a primary benefit of social living in animals, and my small-body primate hypothesis relied on the idea that early predator detection had little use for small-bodied terrestrial lemurs at night.

Evidence from the aye-aye in these experiments changes this perspective and raises further questions regarding the evolution of cryptic behaviors, nocturnality, and sociality. The grubs, fruits, and fungi eaten by aye-ayes are just as present during the day-time as they are at night, and no other animal on Madagascar possesses the adaptations necessary for extracting these sources of food. Perhaps as extreme dietary specialists, the benefits of nocturnality take second place to a need for wide spatial separation between individuals and was not the primary driver in their behavioral evolution. The lack of social groups rather than nocturnality may have therefore driven the evolution of crypsis in the aye-aye.

My second hypothesis was that ultrasonic communication was used as a private communication channel by nocturnal taxa. Rather than solely being a by-product of small body size, I analyzed two predictions that individuals would use alarm calls in the presence of predators and that alarm calls would be at higher frequencies than their normal vocalizations. While *Lemur catta*, a social and diurnal species, used alarm calls during the experiments, all nocturnal taxa remained completely quiet. Even after recalibrating the ultrasonic microphone to receive frequencies up to 90 kHz, placing it on high sensitivity, and manually recording the entire duration of the lemur experiments - the primates did not vocalize.

These results do not necessarily mean that ultrasonic communication does not serve a functional purpose. Individuals were isolated from their social groups, and while all of the nocturnal primates tend to forage alone during the night it is possible that they would be more likely to give an alarm call if placed around other individuals. These findings are similar to those found in Rahlfs & Fitchel (2010), which additionally observed that mouse lemurs (*Microcebus murinus*) did not vocalize in response to predator models or vocalizations. The methods in this

experiment were very similar to the methods in the *M. murinus* study, and in both the animals were isolated from conspecifics.

The fact that the animals did not vocalize cannot be ignored, and there are several considerations that future research must take to explain this trend. First is the addition of more individuals to the sample; larger sample sizes leads to a larger statistical probability that this is a repeated trait across the primate order. Second is modification to the isolation protocol in the experiments. In the future, more social animals should either be tested with conspecifics or vocalizations from recordings of conspecifics should be included in the background noise of the experiments to insure the factor of sociality is not a neglected role in the utterance of alarm calls. Further research should also include more *Microcebus* samples. These lemurs were included in the tests, but disruptions beyond my control forced experiments to end early with a small sampling of only three individuals. Additionally, the role that the owl monkey (*Aotus*) plays in the evolution of nocturnal and cryptic behaviors should be explored, as they are the only nocturnal anthropoid and have not been found to vocalize in the ultrasonic spectrum.

Overall, these experiments show that crypsis is widespread across nocturnal strepsirrhines, regardless of factors such as diet, body size, or social group tendencies. These experiments and their results additionally show that, in isolation, nocturnal strepsirrhines will not vocalize in the presence of a perceived predatory threat. As the primates in this study are amongst the most basal of all primates, we can hypothesize that our far distant ancestors were once silent, fearful, nocturnal primates that subsisted on a diet of insects and grubs. As primate conservation becomes more challenging each year, studies on behavior are essential for understanding not only the evolution of the Primate order, but also for understanding the impact that human activity has on their environments and the consequences for their behavior.

Acknowledgements

I would like to acknowledge several people for their contributions to this project and my career at Florida State University. First and foremost are the very helpful and wonderful staff at the Duke Lemur Center, to whom I owe great thanks. Specifically I would like to mention Dr. Erin Ehmke, the director for research at the DLC and David Brewer, their head research technician. Erin was a tremendous help during the planning process, and she was extremely good with accommodating me at the Lemur Center, keeping me up date on all of the current research happening, and was great to talk to. David was my partner during the experiments, and it was his job to physically carry out the experiments, catch the lemurs, and was a great friend during my time at the Lemur Center.

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Statistical Appendices

Appendix 1: Points

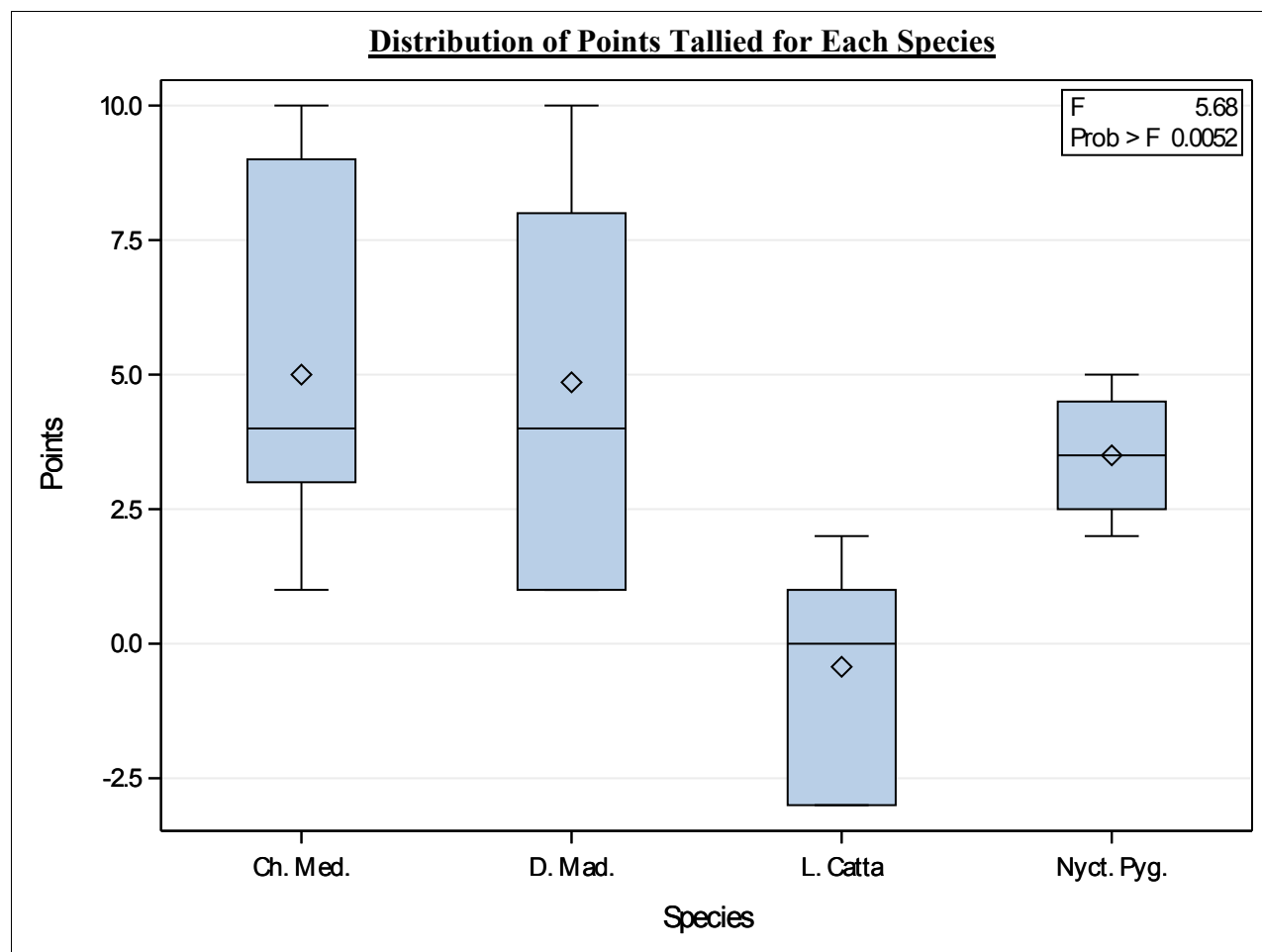
*Results from the ANOVA test on points given to each species yielded significance ($P > 0.0052$). Results from the Fisher's LSD showed significant differences between *L. catta* and the three other species in the study, which did not statistically separate from each other.*

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	134.4285714	44.8095238	5.68	0.0052
Error	21	165.5714286	7.8843537		
Corrected Total	24	300.0000000			

R-Square	Coeff Var	Root MSE	Points Mean
0.448095	87.74716	2.807909	3.200000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Species	3	134.4285714	44.8095238	5.68	0.0052

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Species	3	134.4285714	44.8095238	5.68	0.0052



t Tests for (LSD) for Points

Alpha	0.05
Error Degrees of Freedom	21
Error Mean Square	7.88435
	4
Critical Value of t	2.07961

Comparisons significant at the 0.05 level are indicated by ***.				
Species Comparison	Difference Between Means	95% Confidence Limits		
Ch. Med. - D. Mad.	0.143	-2.978	3.264	
Ch. Med. - Nyct. Pyg.	1.500	-2.160	5.160	
Ch. Med. - L. Catta	5.429	2.307	8.550	***
D. Mad. - Ch. Med.	-0.143	-3.264	2.978	
D. Mad. - Nyct. Pyg.	1.357	-2.303	5.017	
D. Mad. - L. Catta	5.286	2.164	8.407	***
Nyct. Pyg. - Ch. Med.	-1.500	-5.160	2.160	
Nyct. Pyg. - D. Mad.	-1.357	-5.017	2.303	
Nyct. Pyg. - L. Catta	3.929	0.269	7.589	***
L. Catta - Ch. Med.	-5.429	-8.550	-2.307	***
L. Catta - D. Mad.	-5.286	-8.407	-2.164	***
L. Catta - Nyct. Pyg.	-3.929	-7.589	-0.269	***

Appendix 2: Time Frozen in Response to Bird Vocalizations

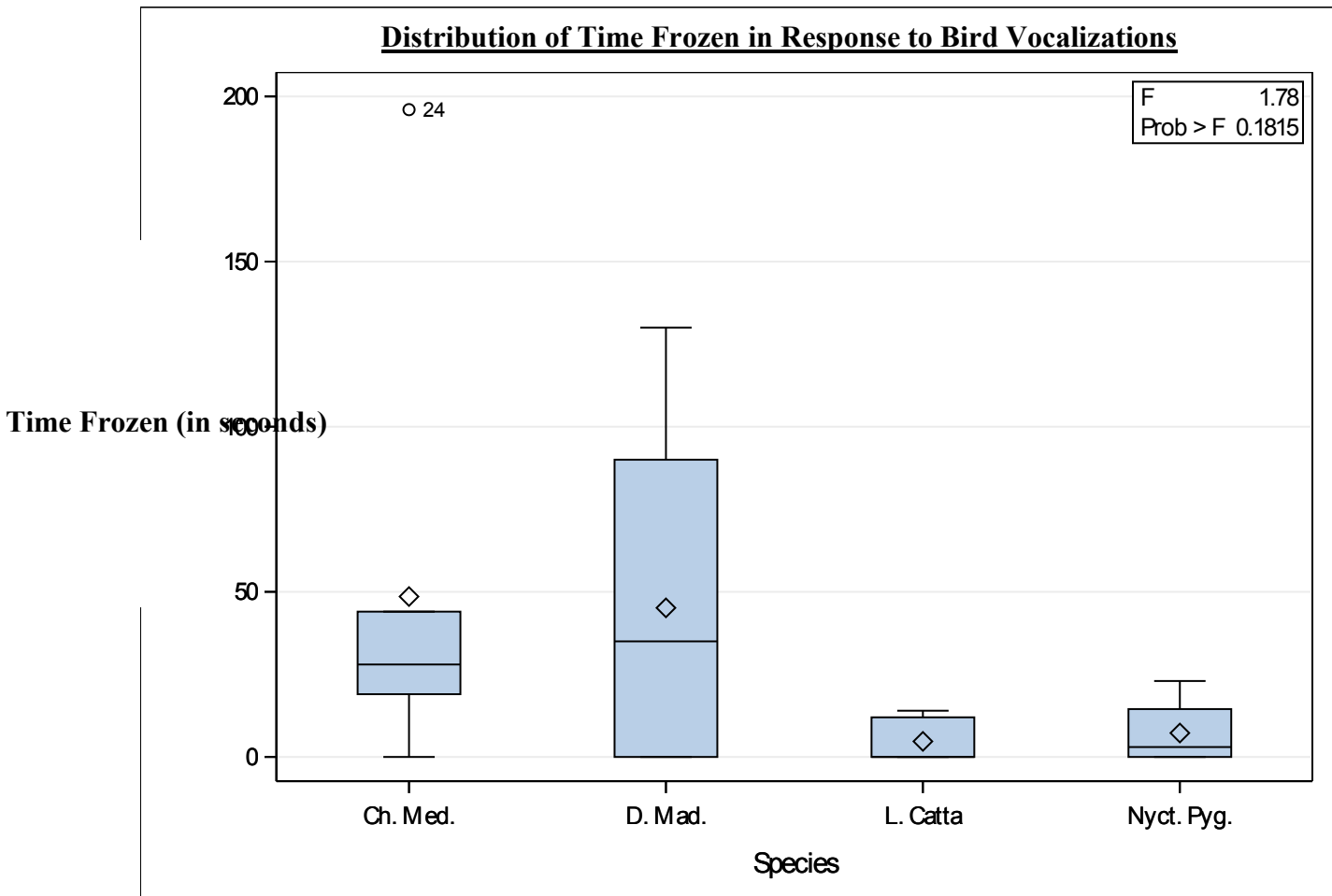
Results from the ANOVA on seconds frozen after bird vocalization playbacks were not significant ($P > 0.1815$), and primates did not differ in ad-hoc Fisher's LSD tests.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	10524.29000	3508.09667	1.78	0.1815
Error	21	41352.75000	1969.17857		
Corrected Total	24	51877.04000			

R-Square	Coeff Var	Root MSE	TimeBirds Mean
0.202870	154.5105	44.37543	28.72000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Species	3	10524.29000	3508.09667	1.78	0.1815

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Species	3	10524.29000	3508.09667	1.78	0.1815



Alpha	0.05
Error Degrees of Freedom	21
Error Mean Square	1969.179
Critical Value of t	2.07961

t Tests for (LSD) for Time Frozen in Response to Bird Vocalizations

Comparisons significant at the 0.05 level are indicated by ***.				
Species Comparison	Difference Between Means	95% Confidence Limits		
Ch. Med. - D. Mad.	3.43	-45.90	52.76	
Ch. Med. - Nyct. Pyg.	41.32	-16.52	99.16	
Ch. Med. - L. Catta	43.86	-5.47	93.18	
D. Mad. - Ch. Med.	-3.43	-52.76	45.90	
D. Mad. - Nyct. Pyg.	37.89	-19.95	95.73	
D. Mad. - L. Catta	40.43	-8.90	89.76	
Nyct. Pyg. - Ch. Med.	-41.32	-99.16	16.52	
Nyct. Pyg. - D. Mad.	-37.89	-95.73	19.95	
Nyct. Pyg. - L. Catta	2.54	-55.31	60.38	
L. Catta - Ch. Med.	-43.86	-93.18	5.47	
L. Catta - D. Mad.	-40.43	-89.76	8.90	
L. Catta - Nyct. Pyg.	-2.54	-60.38	55.31	

Appendix 3: Time Frozen in Response to Fossa Vocalizations

Results from the ANOVA on seconds frozen after fossa vocalization playbacks were not significant ($P > 0.0921$). Ad-hoc Fisher's LSD tests showed significant differences between *C. medius* and *D. madagascariensis*, as well as between *C. medius* and *L. catta*.

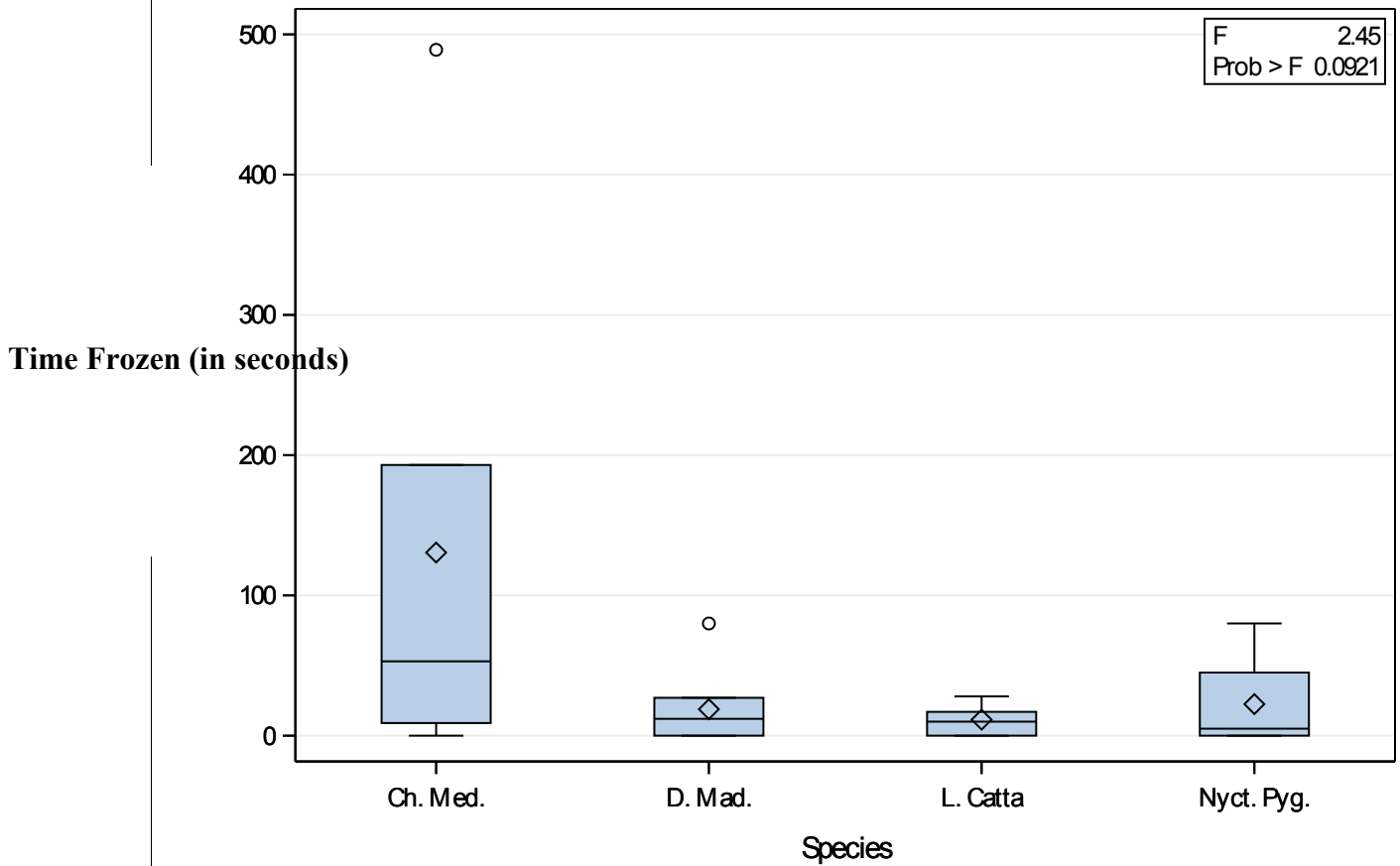
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	65624.4743	21874.8248	2.45	0.0921
Error	21	187741.2857	8940.0612		
Corrected Total	24	253365.7600			

R-Square	Coeff Var	Root MSE	TimeFossa Mean
0.259011	194.3912	94.55190	48.64000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Species	3	65624.47429	21874.82476	2.45	0.0921

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Species	3	65624.47429	21874.82476	2.45	0.0921

Distribution of Time Frozen in Response to Fossa Vocalizations



Alpha	0.05
Error Degrees of Freedom	21
Error Mean Square	8940.061
Critical Value of t	2.07961

t Tests for (LSD) for Time Frozen in Response to Fossa Vocalizations

Comparisons significant at the 0.05 level are indicated by ***.				
Species Comparison	Difference Between Means	95% Confidence Limits		
Ch. Med. - Nyct. Pyg.	108.07	-15.17	231.32	
Ch. Med. - D. Mad.	111.71	6.61	216.82	***
Ch. Med. - L. Catta	119.14	14.04	224.25	***
Nyct. Pyg. - Ch. Med.	-108.07	-231.32	15.17	
Nyct. Pyg. - D. Mad.	3.64	-119.60	126.89	
Nyct. Pyg. - L. Catta	11.07	-112.17	134.32	
D. Mad. - Ch. Med.	-111.71	-216.82	-6.61	***
D. Mad. - Nyct. Pyg.	-3.64	-126.89	119.60	
D. Mad. - L. Catta	7.43	-97.68	112.53	
L. Catta - Ch. Med.	-119.14	-224.25	-14.04	***
L. Catta - Nyct. Pyg.	-11.07	-134.32	112.17	
L. Catta - D. Mad.	-7.43	-112.53	97.68	

Appendix 4: Time Frozen in Response to Fossa Model

Results from the ANOVA on seconds frozen after the fossa model was exposed were not significant ($P > 0.2867$), and primates did not differ in ad-hoc Fisher's LSD tests.

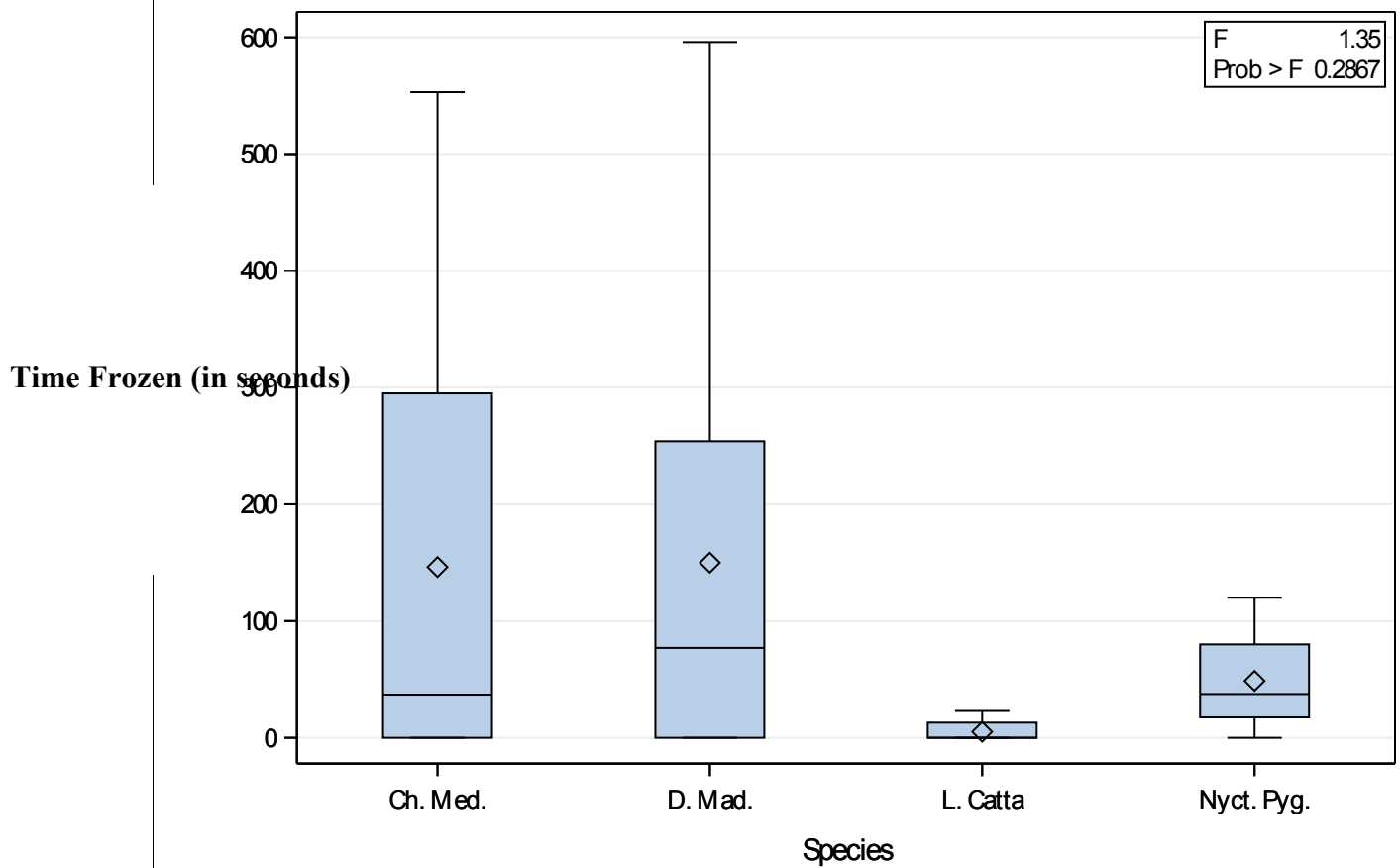
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	104466.9643	34822.3214	1.35	0.2867
Error	21	543677.0357	25889.3827		
Corrected Total	24	648144.0000			

R-Square	Coeff Var	Root MSE	TimeModel Mean
0.161179	174.5139	160.9018	92.20000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Species	3	104466.9643	34822.3214	1.35	0.2867

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Species	3	104466.9643	34822.3214	1.35	0.2867

Distribution of Time Frozen in Response to Fossa Model



Alpha	0.05
Error Degrees of Freedom	21
Error Mean Square	25889.38
Critical Value of t	2.07961

t Tests for (LSD) for Time Spend Frozen in Response to Fossa Model

Comparisons significant at the 0.05 level are indicated by ***.				
Species Comparison	Difference Between Means	95% Confidence Limits		
D. Mad. - Ch. Med.	3.71	-175.14	182.57	
D. Mad. - Nyct. Pyg.	101.25	-108.48	310.98	
D. Mad. - L. Catta	144.86	-34.00	323.72	
Ch. Med. - D. Mad.	-3.71	-182.57	175.14	
Ch. Med. - Nyct. Pyg.	97.54	-112.19	307.27	
Ch. Med. - L. Catta	141.14	-37.72	320.00	
Nyct. Pyg. - D. Mad.	-101.25	-310.98	108.48	
Nyct. Pyg. - Ch. Med.	-97.54	-307.27	112.19	
Nyct. Pyg. - L. Catta	43.61	-166.12	253.34	
L. Catta - D. Mad.	-144.86	-323.72	34.00	
L. Catta - Ch. Med.	-141.14	-320.00	37.72	
L. Catta - Nyct. Pyg.	-43.61	-253.34	166.12	

Picture Appendix

Photos of primates courtesy of David Haring.



Figure 5. Fossa (*Cryptoprocta ferox*)



Figure 6. Fat-tailed Dwarf Lemur (*Cheirogaleus medius*)



Figure 8. Aye-aye (*Daubentonia madagascariensis*)



Figure 7. Pygmy slow loris (*Nycticebus pygmaeus*)



Figure 10. Grey mouse lemur (*Microcebus murinus*)



Figure 9. Ring-tailed lemur (*Lemur catta*)