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Isabelle Hanna
SIT Study Abroad

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Behavioral Responses to Ancestral Predators in Vervet Monkeys (*Chlorocebus pygerythrus*) on Misali Island, Tanzania

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Zanzibar: Coastal Ecology and Marine Resource Management

Spring 2019

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Acknowledgments

This study was made possible through the advisement and the efforts of many people in Zanzibar. A special note of gratitude is due to Dr. Richard Walz, Said Omar, and the entire SIT staff in Stone Town for logistical support through the course of our stay on Misali. Thanks are given as well to my dedicated advisor, Salim Khamis, for academic support throughout the study. A special thanks goes to the Misali Island Rangers, Haji and Mohammad, for their endless support and positivity. Lastly, I would like to thank the entire Misali Crew, Natalie, Nelle, and Gabe, for making my time on the island one of best months of my life, filled with love, laughs, and countless once in a lifetime experiences.

ABSTRACT

The success of a species depends largely on their ability to recognize and respond to predatory cues. These responses can be controlled through genetic or social factors. This study aimed to assess the ability of vervet monkeys (*Chlorocebus pygerythrus*) to identify and respond to ancestral predatory cues following long-term isolation on Misali Island, Zanzibar, Tanzania in order to determine if anti-predator behaviors are innate or learned. This was accomplished through exposure of troops to auditory predator cues and the documentation of their behavioral responses. The results of these trials suggest that predator recognition is an innate behavior in *C. pygerythrus*, as seen through increased levels of vigilance and agitation.

DHAHANIA

Hisia hizi zinadhibitiwa na mfumo wa kimaumbile au mahusiano ya kimaumbile katika jamii ya viumbe wa aina moja na mazingira. Utafiti huu una madhumuni ya kuangalia uwezo wa Kima aina ya Tumbili “Vervet monkeys” (*Chlorocebus pygerythrus*) kutambuwa na kuwajua maadui zao na kuwasiliana na jamii yao kufuatia kutenganishwa nao kwa muda mrefu katika kisiwa cha Misali Misali, Zanzibar, Tanzania ili kuweza kujua kama tabia za wasikokuwa maadui kurithi tabia zao au wanajifunza. Haya yanakamilishwa kwa kuweka wazi makundi audio za maadui zao na kurikodi tabia zao. Matokeo ya utafiti huu ni kuwa kutambuwa maadui zao ni tabia ya kuzaliwa kwa kima *C. pygerythrus*, kama inavyoonekana kwa kuongezeka kwa kuangalia kwa karibu hatari na kuongezeka kwa hisia, utayari.

INTRODUCTION

Studying the fundamentals of animal behavior is pivotal in order to further understand the mechanisms of interspecies and intraspecies relationships, as well as organism interactions with the environment. By improving understanding on social behaviors and vocal communication, specifically in primates, there exists the potential to further the study of the biological origins of vocal communication in humans. Previous studies in vervet monkeys (*Chlorocebus pygerythrus*) have shown that individuals have the ability to differentiate between predators and respond appropriately, often through vocal communication (Digweed et. al 2005; Ducheminsky et. al 2014; Khayi and Franklin 2018; Manser 2013; Murphy et. al 2012).

Misali Island, located off the west coast of Pemba Island in the Zanzibar Archipelago, contains two troops of *C. pygerythrus* (Jessin 2017: 15). Although the origin of these troops is unclear, including when, from where, and how they arrived on the island, it is evident that they have not been exposed to ancestral predators that exist on the Tanzanian mainland for several generations. This lack of exposure could lead to the loss of their ability to recognize these predators. This study seeks to analyze anti-predator responses within these two troops and to record whether they are able to recognize and produce the appropriate responses to predatory cues.

BACKGROUND

In order to examine the ability of *C. pygerythrus* to recognize ancestral predators, this study focuses on a troop located on Misali Island, Tanzania. It is unclear as to how long this troop has been isolated from either Pemba Island or mainland eastern Africa, however it is known that individuals have not been exposed to ancestral predators within their lifetimes. In order to properly analyze the exhibited behaviors on Misali by *C. pygerythrus*, research was conducted on both anti-predator behaviors as a whole and common anti-predator behaviors of *C. pygerythrus*.

I. Study Area

Misali Island (S05°15'; E039°36') is a 0.9 km² island off the west coast of Pemba Island within the Zanzibar Archipelago, Tanzania (Poonian 2008). Following a major bleaching event

in 1998, the island was placed under protected status that established extraction and non-extraction zones to protect the reefs and allow for coral reef prosperity (Poonian 2008). This island has no permanent inhabitants; however, a small group of rangers live on the island and rotate in management. Artisanal Pemban fishermen also camp on the island for two weeks out of every month near the non-extraction zone. There are few tourists that frequent the island for snorkeling or diving purposes; however, the overall human presence in the forests on the island is minimal.

Currently, there are few studies that have examined the conservation history of Misali Island, especially the forests and organisms on the island. Its dry, coral rag forests are extremely dense, have few pathways (which reduces the amount of fragmentation) and are under environmental protection. There are few resident mammals, the largest of which is *C. pygerythrus*. By studying their behaviors on Misali, this study serves to increase understanding on the species and to further research about the coastal forests on the island. These goals are pivotal to its terrestrial ecosystem due to recent developments concerning the potential construction of a hotel on Misali. Further research on the terrestrial species of the island is necessary to determine the feasibility of human development on the island and can provide insights about possible effects.

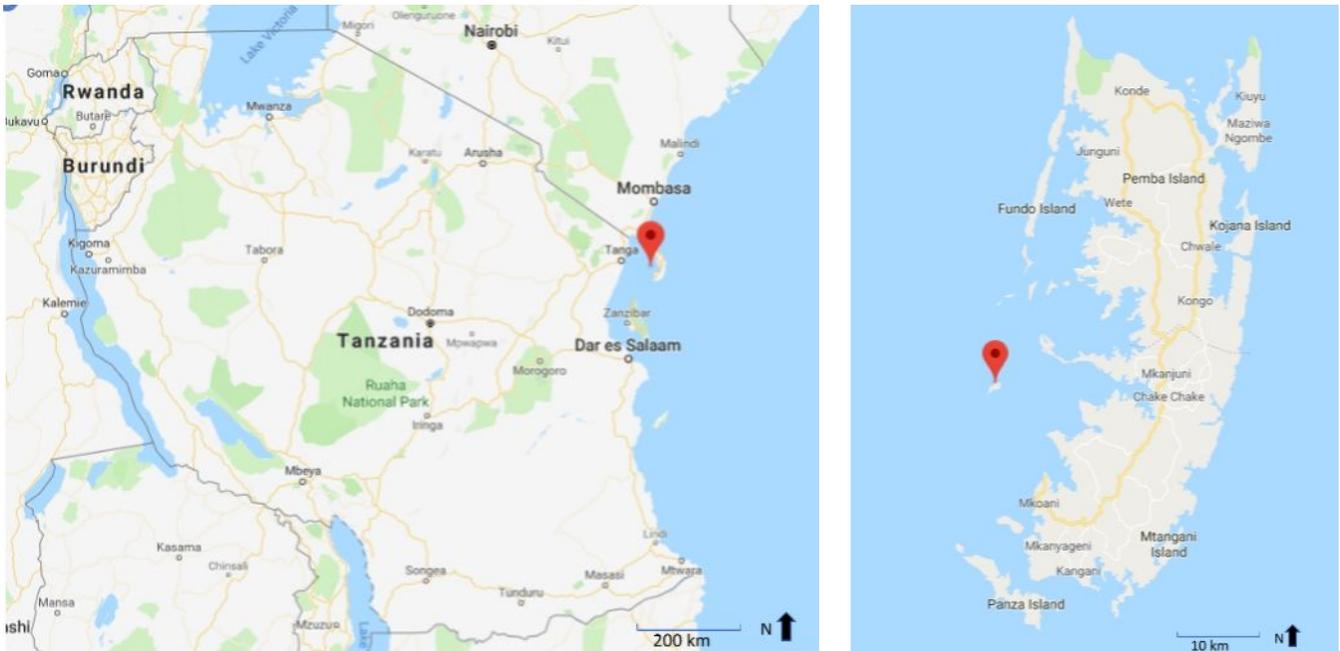


Figure 1. The Zanzibar Archipelago lies east of Tanzania and west of Pemba Island. Red markers indicate the location of Misali Island. (Google Maps, March 31, 2019).



Figure 2. Satellite Image of Misali Island. Image obtained from Google Maps. Accessed March 31, 2019

II. Anti-predator Responses and Social Behavior

The ability of an organism to recognize and respond to predators is essential to the survival of individuals within a species. If an individual is unable to do so, it will result in the necessary employment of defensive behaviors, which are energetically costly and pose a high risk of injury for the preyed upon organism. The resulting evolution of anti-predatory behaviors acts in response to this cost. These behaviors range across an organism's ability to confuse, communicate with, or startle predators in order to avoid predation altogether or to minimize potential injury. Visual cues are often utilized through differing patterns in coloration or anatomy and can include crypsis, aposematic coloration, or false limbs. Crypsis, mimicry, and aposematic coloration serve as signals that are intended to confuse predators and can include camouflage, false-eye coloration, bright coloration indicating toxicity, and non-essential false limbs that are often preyed upon but cause little injury to the organism. Direct communication and signalling between predator and prey, as well as within prey species, allow for more efficient predator evasion and can include physical reactions as well as vocal communication.

Movement-based signalling is essential to reduce individual harm and to send messages to others within or among species. These movements are created based on an individual's perception of risk and the amount of energy to be used in reaction to this risk. In a concept described as "landscape of fear" by behavioral ecologists, species with greater cognitive abilities are able to recognize the spatial variation present in predation risks, as well as spatial variation of other potential hazards to respond with greater efficiency (Gaynor et. al 2019). This mental framework is created through vigilant behaviors that assess risk. Behaviors such as increased vigilance or alarm calls serve as potential precursors to more costly anti-predatory responses, such as flight responses or communications with predators that startle or confuse an

oncoming attacker (Gaynor et. al 2019). In order to maximize energetic efficiency, low cost behaviors are typically employed prior to other options in any type of behavioral response. This being said, vigilance behaviors are employed prior to other behaviors following the detection of potential risk. More extreme responses typically follow, including escape or startling responses. The less costly of these is escape responses, including flight from the site of risk. The greatest cost associated with anti-predatory responses is a physical altercation with the predator itself. Fighting off predators expose individuals to maximum risk and typically is implemented as a last resort.

Communication within species and with predators allows individuals to evade predation risks altogether by attempts to scare or confuse predators, as well as to produce alarm signals to each other to motivate escape responses. This requires that the individual recognize potential predators and differentiate between predator and non-predator species. Previous research has indicated that there are discrepancies in types of communication that suggest some species can produce alarm calls that differentiate between different predators (Digweed et. al 2005). An ongoing debate among behavioral biologists considers whether communication is semantic, or, alternatively, if acoustic calls are determined by the type of predator and contain predictable structures (Ducheminsky et. al 2014). Previous studies have suggested that acoustic signalling is dependent on motivation and can be easily influenced by present stimuli (Ducheminsky et. al 2014), such as general agonistic communication resulting in an entirely different variety of calls than fear responses.

Semantic communication, on the other hand, implies that organisms have the ability to assign vocal signals unrelated to type of stimuli present, forming a type of functional reference

(Manser 2013). This is comparable to human language, where words themselves are not necessarily indications of their assigned values. Studies of semantic communication enable further understanding of how organisms are able to communicate and the possible similarities between communication mechanisms across species of mammals and across the animal kingdom. In order to be functionally referential, vocalizations must correlate with the presence of specific stimuli and produce a specific response without of direct cues (Manser 2013).

Anti-predator behaviors can vary between learned and innate responses. Evidence for the presence of both origins of behavior is apparent in several classes of vertebrates (Burns-Cusato et. al 2016). Many species have presented anti-predator behaviors to predator species that they have not yet encountered, implying that there is a strong innate response to recognize predators and exhibit an appropriate response (Burns-Cusato et. al 2016). Learned behaviors are either learned through exposure to the predator or through social learning. Social learning typically is developed through parent-offspring relationships, usually offspring learning behaviors from their mothers. Learned behaviors, whether through exposure or social learning, are more susceptible to loss if a specific stimulus is removed from a population for several generations. The loss of socially maintained behaviors through loss of stimuli can substantially shift behavior and can spur speciation in isolated populations. Radically different behavioral patterns in isolated groups, such as on Misali, can impact breeding or among populations, leading to gradual genetic isolation.

III. Vervet Monkeys (*Chlorocebus pygerythrus*)

Due to their complex social structure and relation to humans, primates have been the focus of many behavioral studies focused on social group dynamic and communication. Primates employ group behavior in anti-predatory responses, which requires an extensive communication network to respond accordingly to predation risk. Movement based signalling can be utilized to evade predation and often acts in response to vocal communication. Primates have been observed to employ a complex system of communication mechanisms, and vocalizations have been shown to vary depending on type of stimulus (Ducheminsky et. al 2014). Many recorded vocalizations are considered to be through semantic communication that employs high variability between calls regardless of how similar the stimulus may be (Digweed et. al 2005). Acoustic signalling has been observed in specific situations, including the anti-predator responses of many primates (Manser 2013). These vocalizations are likely to indicate urgency of a situation and threats from predators and do not necessarily indicate the presence of specific predators (Digweed et. al 2005). Due to variation in location of primate predators, it is likely that groups would utilize a combination of acoustic and semantic vocalizations to communicate the presence of predators and note the proper anti-predatory response. Acoustic communication is likely utilized in higher frequencies to induce a general escape response, whereas semantic communication is necessary to convey location and method of escape. Studies conducted in Santa Rosa, Costa Rica have shown that primates were able to differentiate between the type of predator present (birds, snakes, or mammals) and were able to produce specific alarm calls that varied based on predator type (Digweed et. al 2005).

Vervet monkeys (*C. pygerythrus*) are a small primate species that is widely distributed throughout Africa and is preyed upon by a variety of aerial and terrestrial species, including crowned eagles (*Stephanoaetus coronatus*), rock pythons (*Python sebae*), and leopards (*Panthera pardus pardus*) (Makin et. al 2012). Typically, they utilize all of the space around them and spend equal amounts of time in trees and foraging on the ground (Makin et. al 2012). *C. pygerythrus* employs the same spatial utilization in anti-predatory and escape responses. Several studies have indicated that *C. pygerythrus* are able to detect different types of predators and use utilize vocal communication and escape responses when presented with predatory cues (Ducheminsky et. al 2014; Makin et. al 2014; Mikula 2017). Studies also have indicated that *C. pygerythrus* utilizes semantic communication in alarm calls to alert other troop members about the type of predator present and to elicit an escape response (Manser 2013). These studies suggest that these primates are not only able to detect and recognize different types of predators, but they also to use alarm calls specific to certain predators.

It is not currently known if anti-predatory alarm calls are innate or learned behaviors in *C. pygerythrus*. Due to their widespread distribution, populations of these primates exist that have not come into contact with ancestral predators for generations, which has lead to the potential loss of certain behaviors. In a study of a closely related primate, the Barbados green monkey (*Chlorocebus sabaesus*), Burns-Cusato (2016) found that individual monkeys were able to recognize and respond to ancestral predators following 350 years of isolation. The results of this study suggest that aspects of anti-predator responses, particularly in vocal communication, are controlled by genetic factors rather than socially learned.

This study on Misali Island seeks to further understand of the nature of anti-predator responses in *C. pygerythrus* through an analysis of their ability to respond to ancestral predators after generations of isolation. Vocal communication in alarm calls, flight behavior, and avoidance were assessed in two troops of vervet monkeys on Misali Island, Zanzibar, Tanzania in response to auditory cues of *P. pardus*, *S. coronatus*, as well as a non-predatory mammal (zebra, *Equus quagga*). *E. quagga* will be tested in order to determine whether the responses exhibited by the *C. pygerythrus* are specific to the presence of a predator or if responses are due to the presence of other large mammals. Through these analyses, this study will provide insights into whether anti-predator responses are innate behaviors or are learned through experience or social example.

METHODS

Data were collected from April 5, 2019 to April 28, 2019 on Misali Island, Zanzibar, Tanzania. In addition to data collection with the predator and non-predator audio cues, a 20-minute behavioral survey will be conducted to determine the average behaviors of the troop when not exposed to any sound. Data were collected through focal data recorded every minute for 20 minutes. A baseline survey of 20 minutes was completed, followed by the projection of the audio recording of a leopard (*P. pardus*), a crowned eagle (*S. coronatus*), or a zebra (*E. quagga*). This projection was as far from the researcher as possible to reduce error and to strategically place the sound to resemble the probable location of the specific predator. Following the recording, focal data were collected for 20 minutes. Only one recording was

projected per day of study. The troop was subjected to audio recordings on a rotating schedule to reduce the potential of habituation to each sound, reducing the potential association with the lack of presence of the predator.

Audio clips were obtained online based on availability, clarity, and length. Audio clips were downloaded onto a laptop. Three zebra sounds and two leopard sounds were downloaded from freesoundeffects.com (Zebra 1, 4, and 6 and Leopard 1 and 3). Crowned eagle calls were downloaded from xeno-canto.org (Crowned Eagle, James Bradley and Crowned Eagle, Frank Lambert). They were projected to the troops using a JBL Flip 4 audio speaker from a distance of approximately 10 meters. The sound level on both the speaker and the laptop was at maximum volume in order to ensure that the predator cue was clearly audible to the troop, even to those located further from the study site.

Behavioral responses were recorded during a baseline study on May 5th, 2019, in order to determine the common behaviors exhibited by vervet monkeys and the expected anti-predatory behaviors obtained through previously published research (Estes 1991) (Appendix A). In order to determine the response to the auditory cues present, the averages of the collected baseline data were subtracted from the experimental data, which consisted of the 20-minute observation following the projection of cues. Data were analyzed using Microsoft Excel and tested for significance using VassarStats One-Way ANOVAs. Data analysis included which responses were recorded according to the predatory cue present, the frequency at which they were recorded, and the frequency of anti-predatory responses and relaxed responses exhibited by the troop as well as latency to return to a relaxed behavior following the projection of the cue. The analysis of this information will serve to improve knowledge on the origins of anti-predator

communications in primates and also provide insights into the effect of human habituation on the ability of non-human primates to recognize and respond to predators. Through the study of an isolated species, this project will offer a unique opportunity to investigate how behaviors are affected following inbreeding connected to low population size, close proximity between troops, and lack of exposure to ancestral predators.

RESULTS

Results were recorded through timed behavioral observation of a troop of *C. pygerythrus* before and after the projection of an auditory predator or non-predator cue during a study period from April 5th, 2019 to April 30th, 2019. There were a total of 26 trials. Further analysis was conducted through a 20-minute behavioral survey in order to determine if observed reactions arose from the presence of any projected sound or if they were more similar to normal behaviors. In order to quantify reactions to the specific audio cues, the baseline focal data of each trial was subtracted from the treatment focal data that were recorded following the projection of an audio cue. Averages of each trial were taken (Appendix B). Behaviors more closely related to an anti-predatory response were compared to one another. Tests of significance were conducted to determine the effect of specific predator or non-predator cues (Table 1). Similarly, behaviors more closely related to a relaxed state were compared. Tests of significance were completed to measure disturbance to the troop when exposed to predator and non-predator cues (Table 2). Lastly, latency to forage was measured to determine the length of time a startled reaction would persist before a return to a relaxed state in which the monkeys felt comfortable enough to forage.

Table 1. Average frequency at which vervet monkeys (*C. pygerythrus*) exhibited anti-predator behaviors when exposed to predator and non-predator cues; results analyzed using VassarStats one-way ANOVA and Tukey’s HSD test. CB = Climbing on Branches, CH = Chutter, CR = Crouching, ES = Escape Response, LA = Alert Looking Around.

Behavior	Leopard	Eagle	Zebra	Survey	Significance	Post-hoc
CB	4.6	6	3	6.33	No	N/A
CH	2	0.2	0.5	0.5	No	N/A
CR	0	0.4	0	0	No	N/A
ES	1	2	0	0	Yes ¹	E ≠ Z, S
LA	7	9.4	3.25	0.083	Yes ²	L ≠ S; E ≠ Z, S

¹One-way ANOVA, $F = 6.66$, $df = 3$, $p < 0.01$; Tukey’s HSD, $p < 0.01$.

²One-way ANOVA, $F = 16.47$, $df = 3$, $p < 0.0001$; Tukey’s HSD, $p < 0.01$.

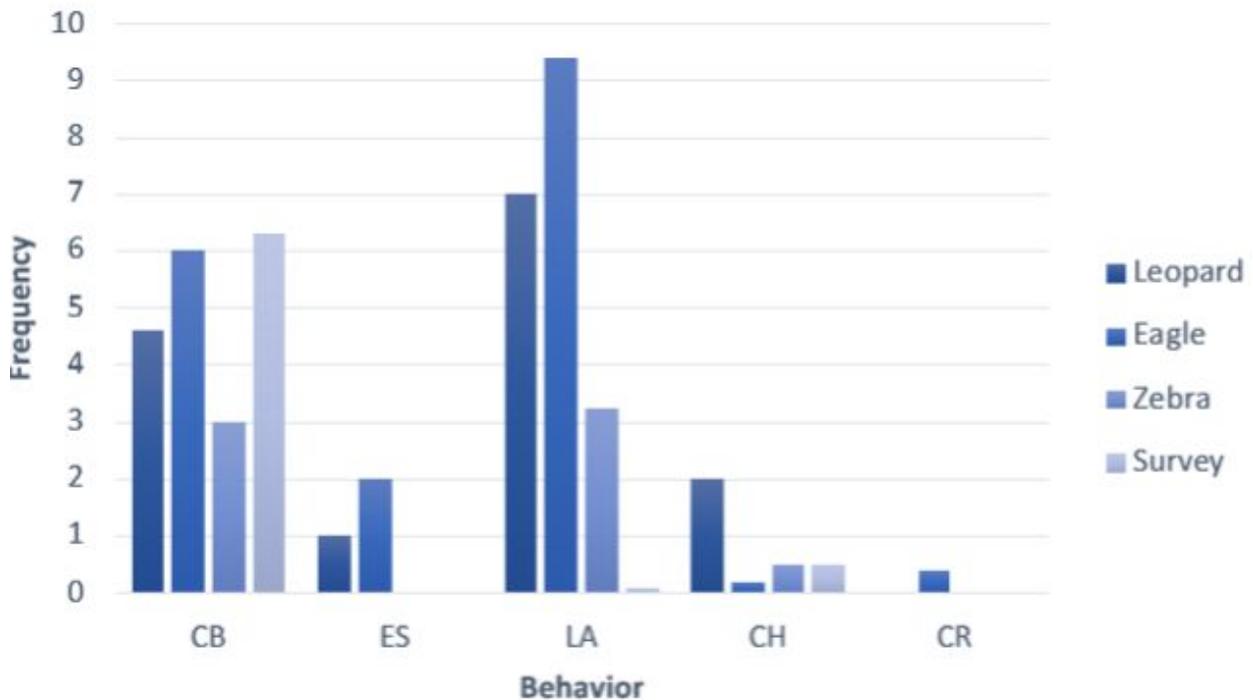


Figure 3. Average frequency at which vervet monkeys (*C. pygerythrus*) exhibited anti-predatory behaviors when exposed to predator and non-predator cues. CB = Climbing on Branches, ES = Escape Response, LA = Alert Looking Around, CH = Chutter, CR = Crouching.

Behaviors more closely related to anti-predatory responses in *C. pygerythrus* were compared to one another to determine whether or not the chosen predator or non-predator cue elicited an anti-predatory response. As different cues could produce very different responses, the results of each type of cue were compared. Table 1 shows the average frequencies of anti-predatory behaviors when exposed to different cues as well as the results of one-way ANOVAs that determine whether behaviors were significantly different depending on the cue present. Figure 3 shows a comparison to the frequency at which the focal troop exhibited behaviors to provide visual aid to the averages reported in Table 1.

Table 2. Average frequency at which vervet monkeys (*C. pygerythrus*) exhibited “relaxed” behaviors when exposed to predator and non-predator cues; results analyzed using VassarStats one-way ANOVA and Tukey’s HSD test. FGC = Foraging, GR = Grooming, PL = Playing, SB = Sitting on Branches, SG = Sitting on Ground.

Behavior	Leopard	Eagle	Zebra	Survey	Significance	Post-hoc
FGC	-1.8	0	6.25	6.59	Yes ¹	L ≠ Z, S; E ≠ S
GR	-0.6	-0.4	1	1.08	No	N/A
PL	0.8	-0.6	1.25	1.92	No	N/A
SB	-3.2	0	1	3.17	Yes ²	L ≠ Z, S
SG	0.2	0	0.25	0.75	No	N/A

¹One-way ANOVA, $F = 7.62$, $df = 3$, $p < 0.01$; Tukey’s HSD, $p < 0.05$, $p < 0.01$; $p < 0.05$.

²One-way ANOVA, $F = 8.04$, $df = 3$, $p < 0.001$; Tukey’s HSD, $p < 0.05$, $p < 0.01$.

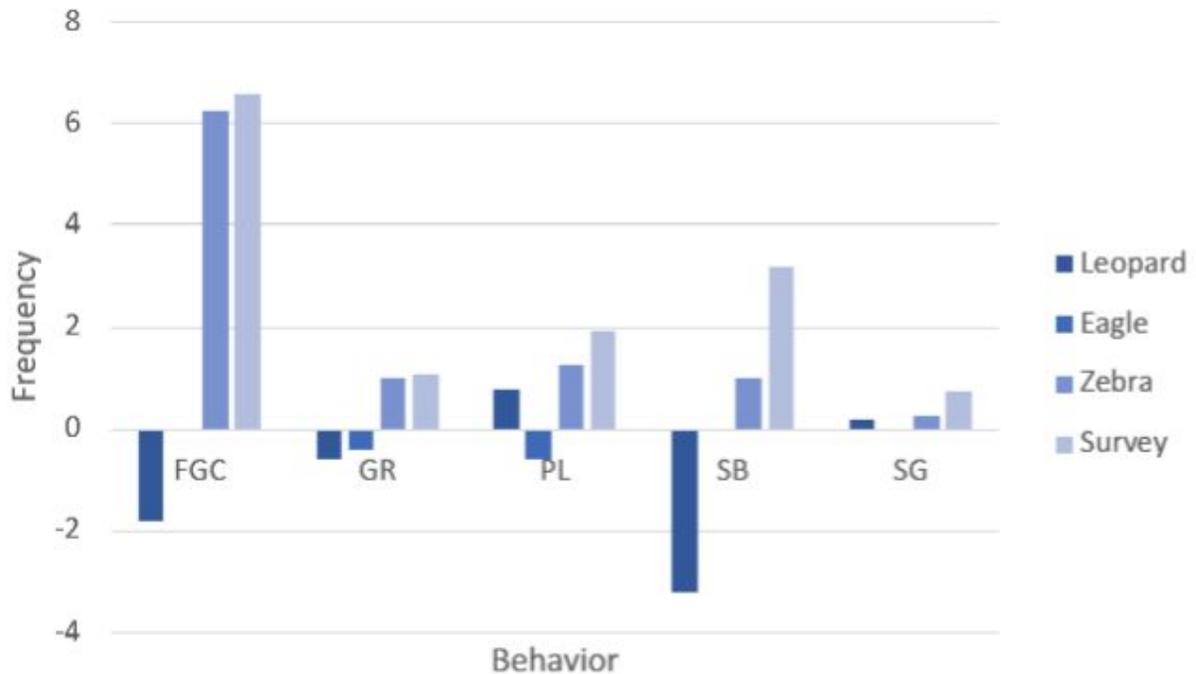


Figure 4. Average frequency at which vervet monkeys (*C. pygerythrus*) exhibited “relaxed behaviors when exposed to predator and non-predator cues. FGC = Foraging, GR = Grooming, PL = Playing, SB = Sitting on Branches, SG = Sitting on Ground.

Average frequencies at which *C. pygerythrus* exhibited behaviors associated with a relaxed state assists with determining the amount of disturbance caused by the projection of auditory cues. These results are important to determine whether or not the focal troop is more likely to exhibit alert behaviors when aware of the presence of other animals within their proximity. Foraging, grooming, playing, and sitting behaviors all are not associated with the alert state of *C. pygerythrus*. Foraging, grooming, and playing behaviors could expose vulnerability when in the presence of a potential predator due to the general lack of focus on the broader environment. Table 2 depicts the average frequency at which vervet monkeys exhibited relaxed behaviors. One-way ANOVAs were conducted to determine significant differences in this data (Figure 4).

Table 3. Average latency to forage in vervet monkeys (*C. pygerythrus*) following exposure to predator and non-predator cues; results analyzed using VassarStats one-way ANOVA and Tukey’s HSD test. LF = Latency to Forage.

Behavior	Leopard	Eagle	Zebra	Significance	Post-hoc
LF	2:18	3:56	1:18	Yes ¹	E ≠ Z

¹One-way ANOVA, F = 4.17, df = 3, p < 0.05; Tukey’s HSD, p < 0.05.

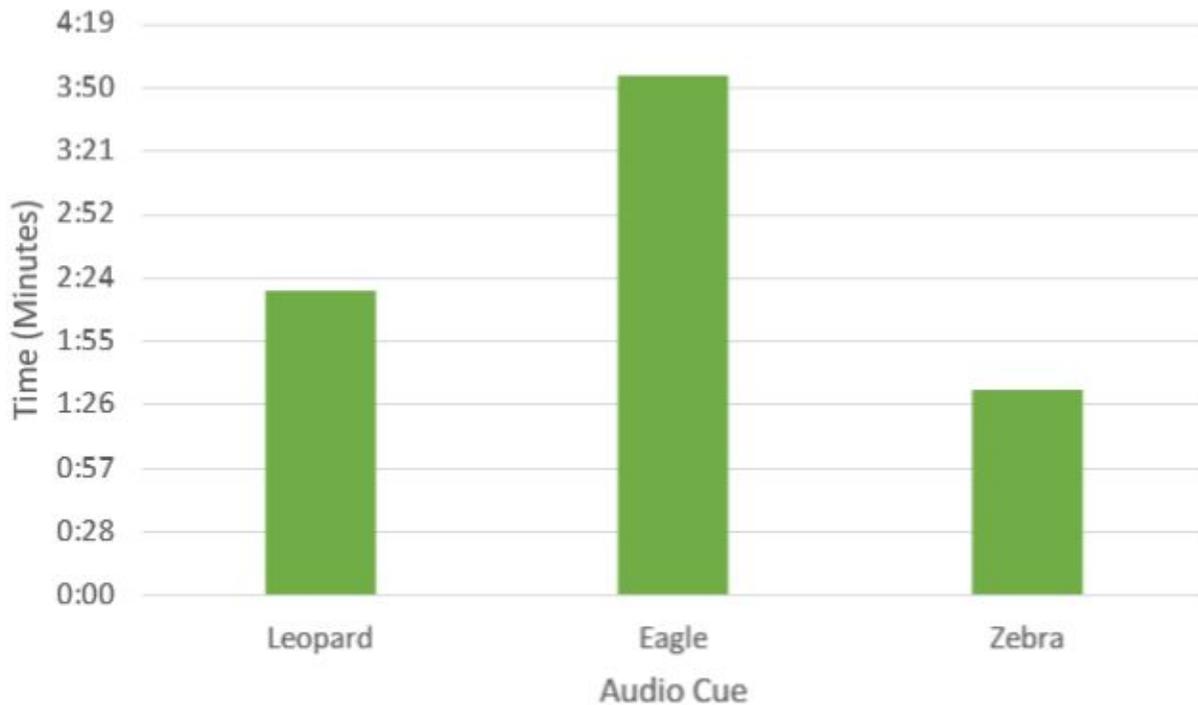


Figure 5. Average latency to forage in vervet monkeys (*C. pygerythrus*) following exposure to predator and non-predator cues.

Measurements of latency to foraging behavior provide insights in to the lasting effects of the projected audio cues. Conclusions can be made about the level of concern over a potential predator located near the troop, as the monkeys will spend a greater amount of time alert to determine the location of the predator. Increased vigilance might suggest that the focal troop exhibits anti-predatory behaviors and recognizes the urgency of the situation. Through

differences in vigilance and recognition of urgency, results suggest if individuals recognized if the projected cue was a predator of *C. pygerythrus*. Table 3 depicts average latency to forage following the projection of leopard, eagle, and zebra auditory cues and one-way ANOVA to determine significant differences among these averages (Figure 5).

Appendix A depicts raw data collected from each trial including of the total frequency at which the focal troop each behavior in each experimental trial. Behavioral survey results also are included. Appendix B depicts VassarStats one-way ANOVA outputs of the five highlighted anti-predatory behaviors and the five highlighted relaxed behaviors. It also shows post-hoc analyses through Tukey's HSD tests for all behaviors that indicated significance following the ANOVA.

DISCUSSION

The results of this study indicate that *C. pygerythrus* has the ability to recognize predators, despite having little or no exposure to them over the course of their lives. Visual observations indicated that the troop appeared to respond to predatory audio cues in an anti-predator response. This can be clearly seen through the significantly higher instances of escape responses and looking around in an alert state in trials where the troop was subjected to *P. pardus* or *S. coronatus* cues when compared to cues from zebras and from behavioral surveys (Table 1). When they did not exhibit behaviors classified as anti-predatory, the troop was notably disturbed by the possibility of a potential predator within the vicinity. This is demonstrated by significantly lower instances of relaxed behaviors, such as foraging and sitting on branches in

leopard and eagle trials when compared to zebra trials and surveys (Table 2). Furthermore, latency to forage was significantly lower in zebra trials when compared to eagle trials. This demonstrates the disturbance to the troop by the amount of time they spent exhibiting vigilance before returning to a common relaxed behavior.

Due to uncertainty about when the troops of *C. pygerythrus* on Misali were relocated to the island, as well as from where, it is not possible to determine how much time has passed since their last exposure to ancestral predators. While the current generation on Misali has not experienced any exposure to *P. pardus* through the course of their lives, it is possible if their ancestors were translocated from mainland eastern Africa. If this is the case, recent generations would have been exposed to this predator. This experience could help monkeys with recognizing this particular predator. There is a higher possibility that the individuals on Misali have had exposure to *S. coronatus*, as eagles have the ability to move from the mainland to Pemba and Misali, although none were observed during the course of this study. Regardless of whether the focal troop has had exposure to this particular eagle, the presence of other large predatory birds could instill an anti-predator response associated with birds of prey. It is likely that the focal troop reacted to the general sound of a predatory bird, rather than exhibiting a reaction specific to *S. coronatus*. Recent exposure to this type of predator might explain the notably higher frequencies of anti-predatory responses when exposed to the audio cue of a large predatory bird.

Long-term human impacts also serve as an explanation for the frequency of recorded behaviors over the course of this study. As noted previously, the resident human population on the island is minimal, consisting of few park rangers, as well as fishermen who live on the island for two weeks every month. Motorized boats are used frequently among both parties, including

powerful motorized boats that ferry tourists to the island as often as once daily. The presence of these factors provide a possible explanation to the lower frequency at which troops exhibit anti-predatory behaviors when exposed to leopards when compared to eagles. The downloaded audio clips of leopard growls sound similar to the revving of boat engines. Reducing their ability to distinguish between predatory cues and human factors potentially impacted the monkeys' level of response.

The results of this study indicate the potential of anti-predatory behaviors in *C. pygerythrus* to be innate rather than learned. This is not only evident in the high frequency of responses to *S. coronatus*, a species not known to be present on Misali Island, but also in the ability of the focal troop to respond to *P. pardus* cues. While other large, predatory birds exist on Misali Island, *S. coronatus* was not observed during the study. Thus, there was little to no exposure to this particular predator, which would lead to the deduction that anti-predatory responses are innate behaviors, rather than learned ones. However, significant monkey responses were exhibited when exposed to leopard cues, in comparison to zebra cues or during general behavioral surveys (Table 1), particularly when the source of the cue was well hidden in dense foliage toward the interior of the island. This provides strong evidence of innate anti-predatory behaviors in *C. pygerythrus*.

The survival of a species is more tenuous when all anti-predator behaviors are learned, due to the ease at which learned behaviors can be lost with lack of exposure. If a predator species were to experience an increase in population or a relocation, prey species would be at considerable risk of drastic population decline, as they would have little established reaction to the presence of potential predators, and therefore the frequency at which they are preyed upon

would increase. Increasing human land development and habitat fragmentation increases wildlife relocation. Without concern for the behavioral roots of species, wildlife relocation of inappropriate scale has the potential to cause disorder in the natural state of an ecosystem. If prey species have had little or no exposure to specific predators, their survival would rely on the ability to call on innate behavioral responses to properly evade the predator. The study of the origins of behavior is essential to predict the interactions that may occur between species that were not previously associated with one another.

While few studies have examined innate anti-predatory behaviors in *C. pygerythrus*, studies of closely related primates indicate the innate roots of behavior. In a study of Barbados green monkeys (*Chlorocebus sabaesus*), Burns-Cusato et. al (2016) found that individuals were able to recognize and respond to ancestral predators despite a separation time of over 350 years. This study exposed individuals to visual predatory leopard cues and found that they exhibited several anti-predatory behaviors, such as increased avoidance, specific alarm calls, and escape responses. Further analysis indicated that anti-predatory responses also were exhibited when monkeys were exposed to predator features, such as the rosettes of a leopard or forward-facing eyes. These results suggest that genetic factors primarily influence the ability to respond to predatory cues.

Movement based responses are common in *C. pygerythrus* when exposed to predator cues. A 2012 study analyzed response type and location when exposed to terrestrial and aerial predator cues (Makin 2012). When exposed to aerial predators, it was common for individuals to move to interior branches of trees or to the ground under the cover of foliage. Terrestrial predators typically motivated moved to higher foliage toward interior branches (Makin 2012).

Several studies also have analyzed the ability of *C. pygerythrus* to respond to predators using vocal communication (Digweed et. al 2005, Ducheminsky et. al 2014, Khayi and Franklin 2018, Manser 2013, Murphy et. al 2012). These studies address the topic of message encoding in *C. pygerythrus*, and have determined that individuals have the ability to differentiate between predators and respond to predation risk.

Due to the nature of behavioral observation, the results of this study could have been influenced by a variety of factors. While the behavioral survey and baseline of the focal data collection serve as controls for the presence of the researcher, it was not possible to control for the presence of other people moving through the island. For example, due to the opportunistic foraging nature of *C. pygerythrus*, the focal troop typically was located near the kitchen of the rangers' station. Data collection located near this building was subject to the movement of rangers that could easily have influenced behaviors. It was also impossible to control for loud noises created by fishermen and tourists. Further human influence was created by an increased amount of fishermen camping near the rangers' station. The treatment of monkeys by these fishermen was somewhat hostile. When fishermen were present, the troop became more cautious of the researcher. Fear responses associated with the researcher were controlled by the baseline survey; however, it became increasingly difficult to locate the troop and to stay within close enough proximity to them to record for 40 minutes.

This study could have been improved through better strategic placement of the audio cue. Due to limited resource availability, it was difficult to place the cue in a similar location to the expected location of a specific predator. Leopard and zebra cues were placed in the expected location of the predator; however, eagle cues were not placed in high enough locations to

resemble the presence of an *S. coronatus*. The cues were, however, strategically placed away from the troop to try to simulate an eagle, but more precise data could have been collected through placement of audio cues in high branches of trees. In order to avoid the potential of reduced behavioral responses to leopard cues due to human impacts, such as boat engines, it would be helpful to test other terrestrial predators in addition to *P. pardus*, such as a lion, a hyena, or a baboon as terrestrial predators or competitors.

CONCLUSION

This study aimed to increase understanding on the origins of behavior in vervet monkeys (*C. pygerythrus*) through exposure to audio cues from ancestral predators. The results of this study show a significant increase in certain anti-predator behaviors when exposed to ancestral predators in comparison to non-predators and behavioral surveys, indicating that anti-predator responses in certain primates are controlled through genetic factors rather than through learned behaviors. Studies of innate and learned responses can provide insight into the behaviors of primates and may be applied to other different.

RECOMMENDATIONS

Misali Island is often overlooked in the field of terrestrial research. This isolated environment provides an extremely unique view into many different biological issues, as the island is scarcely populated by humans, bears protected forests, and has been in isolation from

Pemba and the East African mainland for thousands of years. The mammalian population of the island has been rarely studied despite the opportunity to study the lives of an isolated species. There are at least two species of primate present on the island, including *C. pygerythrus* and at least one species of galago. Through further study, these species can provide extremely useful information on the long term effects of isolation, which can be applied to rising issues such as habitat fragmentation.

Further studies that focus on anti-predator behaviors in *C. pygerythrus* might include the introduction of different types of predator cues. Different types of cues, such as visual cues rather than audio, also might provide insight into the senses relied upon more heavily by *C. pygerythrus*. These studies might also be applied to the other troop present on Misali island and comparisons made concerning the impact of human habituation on the ability of individuals to identify and respond to predators. In addition, this study could be repeated on Pemba Island and on mainland Tanzania. Through comparison of behaviors between troops on Misali and Pemba and mainland troops, a future study has the potential to determine the origins of the troops on Misali.

Similar anti-predatory studies could be repeated on the other primate species on the island, as well as with other small mammals. Such work could provide information for application of the origin of anti-predator behaviors across many different species of primates. Furthermore, outcomes might enhance knowledge of whether predator avoidance strategies differ depending on the time of day or with different nocturnal hunters.

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Appendices

Appendix A. Common anti-predatory and relaxed behaviors of vervet monkeys (*C. pygerythrus*) and behavioral codes; vocal signals from *Behavior Guide to African Mammals* (Estes 1991).

Behavior	Behavioral ID	Description
Foraging on the Ground	FG	Searching for or eating food on the ground
Foraging in Trees	FGT	Searching for or eating food in trees
Sitting on the Ground	SG	Sitting at rest on the ground
Sitting in Branches	SB	Sitting at rest in trees
Climbing on Branches	CB	Moving significantly on a branch or jumping from branch to branch
Moving to Branches	MB	Moving from the ground to branches
Moving to the Ground	MG	Moving from branches to the ground
Grooming	GR	An individual grooming itself or others
Mother Holding Baby	MHB	The infant is clinging to it's mother's torso
Mother Nursing Baby	MNB	A mother is nursing its infant
Startled	ST	Notably startled
Escape Response	ES	Move in a fast motion, clearly moving away from something
Looking Around	LA	Stopping current behavior to look around in an alert manner
Playing	PL	Typically juveniles, chasing or wrestling with one another
Chutter	CH	Typically females and juveniles, low monotonous sound requesting support
Chirp	CP	Mostly juveniles, high pitched noise indicating minor predator
Squeal	SQ	Mostly juveniles, high pitched, elongated noise associated with fear
Purring	PR	Low frequency, quiet noise associated with calm behavior
Crouching	CR	Physically crouches, usually accompanied by ES or LA
Out of View	OV	Troop is out of view from the researcher
Latency to Relaxed Behavior	LR	Following the projection of audio cues, the latency to return to a relaxed behavior

Appendix B. Complete list of the average frequency of exhibited behavioral responses in vervet monkeys (*C. pygerythrus*) when exposed to predator and non-predator cues.

Behavior	Leopard	Eagle	Zebra	Survey
FGT	-2	0.2	3	3.17
FG	0.2	-0.2	3.25	3.42
CB	4.6	6	3	6.33
MG	-0.2	1.4	0.75	0.5
MB	0.2	1	0.5	0
GR	-0.6	-0.4	1	1.08
MHB	-0.4	0.2	-0.5	0.5
MNB	0	0.2	-0.5	0.083
ST	0	0.2	0	0
ES	1	2	0	0
LA	7	9.4	3.25	0.083
PL	0.8	-0.6	1.25	1.92
CH	2	0.2	0.5	0.5
CP	0	-0.2	0	0.167
SQ	0.6	0.8	0	0.167
PR	-0.2	0	0	0
CR	0	0.4	0	0
SB	-3.2	0	1	3.17
SG	0.2	0	0.25	0.75
OV	0.2	0.2	1	0
LF	2:18	3:56	1:33	N/A

