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Do Actions Speak Louder than Words? Communicative Frequencies and Multimodality in Ring-Tailed Lemurs (Lemur catta)

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Abstract

The study of multimodal communication in primatology has increased only recently. At present, there are no on-going investigations of multimodal communication in ring-tailed lemurs (*Lemur catta*), despite the body of research on this species. I investigated how different modes of *L. catta* inter-individual multimodal communication are socially coordinated and integrated by examining frequencies of occurrence within four potential biological and social factors: age, troop affiliation, sex, and dominance rank. Research was conducted over four months at the Duke Lemur Center, Durham, NC, on 14 individuals from three separate troops of captive, free-ranging *L. catta*. Results demonstrate communicative variation in unimodal, but not multimodal, signals correlating to sex and rank in this species. Dominant females appear to utilise visual signal components more frequently than males, while males rely more on auditory means of communicating, consistent with troop spatial organization. This research provides a baseline for future investigations into primate multimodal communication.

Keywords

Ring-tailed Lemur, *Lemur catta*, Primate Communication, Multimodal Signals, Behavioural Ecology, Duke Lemur Center, Auditory, Visual, Tactile, Olfactory.

Summary for Lay Audience

Ring-tailed lemurs (*Lemur catta*), like other primates including humans, have a diverse range of communicative modes. These are the ways in which individuals send information to each other and include four common sensory channels: auditory (hearing), visual (sight), tactile (physical touch), and olfactory (smell). My research focused on ring-tailed lemur social communication, but what sets my work apart from previous studies is that I collected and analyzed data from both unimodal and multimodal signals. While multimodal communication is by no means a new concept, it has only recently begun to appear in the primatology literature. The majority of studies on primate communication have been unimodal, which focuses on one type of signal from one sensory channel, but this approach simplifies the complexity of primate communication. My approach acknowledges that a single signal can use combinations of the senses, like auditory and visual together, and for this reason preserves signal complexity. I am interested to learn if ring-tailed lemurs show a preference for how they communicate and determine which factors potentially influence this by studying both unimodal and multimodal signals together. To do this, I followed one individual at a time (focal animal sampling) over the course of four months and tallied each time they used a communicative mode, which for ring-tailed lemurs includes auditory, visual, tactile, and olfactory modes, and importantly combinations of those. When I combined this frequency data with each individual's personal information (their age, sex, dominance rank, and troop affiliation) I was able to determine whether the lemurs have unique preferences for certain modes over others, and whether one or more of the above personal factors influences this preference. I found that dominant females use the visual mode of communication more frequently than males do, while males rely more on the auditory mode. Furthermore, this difference was reflected only in unimodal signals. Multimodal signals appeared much more consistent between individuals despite differences in age, sex, dominance rank, and troop affiliation. Since at present there are no investigations of multimodal communication in lemurs, this study is intended to provide a baseline for future research into primate multimodal communication.

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Table of Contents

List of Tables

List of Figures

List of Appendices

Chapter 1

1 Introduction

The ring-tailed lemur (*Lemur catta*) is the best studied lemur species in the world, with field data on *L. catta* stretching back to the early 1960s (*see* Jolly, 1996a), and it is also the primate species that the zoo-going public will most often encounter (LaFleur et al. 2017). Despite being the most common primate species in captivity, the rapidly dwindling wild populations of *L. catta* are highly threatened by anthropogenic changes to their landscape, such as habitat loss, agricultural intensification, and mining enterprises (Andriaholinirina et al., 2014; Estrada et al., 2018; Gould & Sauther, 2016). Researching this species to better understand their behavioural ecology can contribute to current knowledge of the evolution of primate behaviour broadly, in addition to better conservation action to protect this endangered species from extinction in the wild (*see* LaFleur & Gould, 2020).

Primates as social animals often utilize a number of different subtle and explicit signals to communicate with members of the same species (conspecifics). This means the full context of an individual's behaviour and signal usage, and how these change between contexts, species, and especially over time are important factors to consider when studying their behaviour through an evolutionary lens. All communicative signals engage at least one sensory channel (auditory, visual, tactile, olfactory) in the receiver of that message, but it is erroneous to assume every signal makes use of only one sensory mode of communication. Lemurs, like other primates including humans, create complex multimodal signals to communicate with one another. I investigated how the different modes of *L. catta* inter-individual communication are socially coordinated and integrated by examining frequencies of occurrence against four biological and social factors: age, troop affiliation, sex, and dominance rank.

1.1 Aims & Research Proposal

While multimodal communication is by no means a novel concept, its incorporation into primatology has only recently begun to appear in the literature. At present, there are no investigations of multimodal communication in ring-tailed lemurs, despite the large body of research on this lemur species in particular. Multimodal research provides a more accurate representation of the complexities of animal communication, including that of humans, and offers a novel approach to the study of social complexity in primates (Peckre, Kappeler & Fichtel, 2019). Studying communication otherwise (i.e. exclusively using a unimodal approach; *see* Baker, Taylor, & Montrose, 2018; Gamba et al., 2017) limits the evolutionary understanding of how different ways of communicating have developed and changed over time on an ultimate level (*see* Fröhlich & van Schaik, 2018). This study takes a multimodal approach to data collection and analysis to determine whether individual *L. catta* show a preference for different communicative mode components (auditory, visual, tactile, olfactory), including combinations, and whether factors like individual age, troop affiliation, sex and dominance rank correlate with communicative mode frequencies. I accomplished this by gathering observational data on all four communicative modes simultaneously upon occurrence, as well as examining and comparing the frequencies and compositions of *L. catta* unimodal and multimodal signals. These observational data were collected on 14 individuals (10 females and 4 males) from three separate troops of captive, free-ranging *L. catta* at the Duke Lemur Center (DLC) over the course of four months. Using a multimodal communication approach sets my work apart from previous investigations of social communication in this species and fills a gap within the literature (*see* Peckre, Kappeler & Fichtel, 2019). My thesis research examines how multimodal communication is utilized in ring-tailed lemurs. I report on the extent to which inter-individual variation in multimodal communication is present in ring-tailed lemurs, and how that variation is expressed across different age groups, troops, sexes, and dominance ranks. Furthermore, this thesis will establish a baseline for future investigations into the multimodal communication of lemurs in the wild. My research hypotheses are:

1. H_O: Individual ring-tailed lemurs will not differ in their communication modes. H_1: Individual ring-tailed lemurs will differ in their multimodal communication based on variables such as sex, age, troop affiliation, and dominance rank.
2. H_O: Ring-tailed lemurs will exhibit little to no variation in the proportional use of unimodal signals and multimodal signals. H_1: Ring-tailed lemur use of unimodal

signals and multimodal signals will exhibit considerable inter-individual variation.

3. H_O: Modal components within each signal type will not differ between individuals. H_1: Individual ring-tailed lemurs will exhibit preferred communication modalities.

Each of the above questions is investigated based on social factors (troop affiliation and dominance rank) and biological factors (age and sex). Analysis of communication patterns relative to these social and biological factors was accomplished by first establishing the frequencies of communicative modes for each individual under study, then identifying whether preferences for certain communicative modes or combinations exist on an individual level or between each distinct troop, and finally to analyze the composition and frequencies of occurrence of both unimodal and multimodal signals. By employing a comprehensive and multimodal approach to study communicative mode frequencies in *L. catta*, my innovative research will contribute to the greater understanding of this species' communication, the growing body of multimodal communication studies in primatology, and studies of animal behaviour more broadly.

This chapter has presented an overview of the focal species and primate communication, as well as outlined the questions to be addressed in this thesis. Chapter 2 provides more thorough background information relating to the research site, the focal species *Lemur catta*, previous research on communicative modes in ring-tailed lemurs and other primates, and finally an overview of theoretical frameworks and previous research on multimodal communication more broadly. Chapter 3 explains the methodology used in this study, including observation method, ethogram, and statistical analyses. Chapter 4 presents the results, examining how these data correlate with the biological and social factors examined and outlined above. Chapter 5 contextualizes those results into a discussion that ties back to the main questions of this thesis, summarizes the key findings, and brings together suggestions for future research.

Chapter 2

2 Background

The aims of this chapter are to: 1) introduce the reader to the field site, the Duke Lemur Center, 2) to briefly introduce the lemur species of focus in this thesis, 3) provide an overview of previous research into multimodal communication in non-human animals, 4) present the four communicative modes to be examined, including primate examples of different applications in signalling behaviour, 5) familiarize the reader with the theoretical background of, and current hypotheses within, multimodal communication research at present, and finally 6) a restatement of my thesis aims.

2.1 The Duke Lemur Center

The Duke Lemur Center is a unique, lemur research facility located outside the city of Durham, North Carolina. The Center was founded in 1966 (previously called the Duke University Primate Center) with the collaboration of Dr. John Buettner-Janusch, a lemur geneticist at Yale University, and Dr. Peter Klopfer, who was a researcher at Duke studying maternal behaviour in mammals (The Duke Lemur Center, n.d.). The two saw the merits of conducting their research on lemurs in a more open and natural setting that laboratories did not have the space for and set their eyes on Duke Forest (The Duke Lemur Center, n.d.). Once the two were able to acquire land, Dr. Buettner-Janusch moved his lemurs to Durham where the two researchers had access to 80 acres of wooded land for the primates to explore and be studied (The Duke Lemur Center, n.d.).

Today, the Center continues to house the largest population of lemurs outside Madagascar. It supports research on 14 different species of lemur ranging from behavioural observation and genetics to the paleontology and evolutionary origins of lemurs (The Duke Lemur Center, n.d.). A unique feature of the Center is that it provides a total of nine Natural Habitat Enclosures (NHEs) for many of the lemurs to explore, ranging from 0.6 to 14.3 acres of Carolinian Forest (*see* Appendix A). These enclosures are fenced-in areas that are often shared between two or three different species and which allow the lemurs space to forage in and trees to climb or leap between. As a facility dedicated to researching one of the most threatened family of primates in the world, the DLC is dedicated to the conservation of habitats and lemur species in Madagascar, as well as promoting education through guided tours and public outreach events in both Madagascar and at home in North Carolina. The Center offers the opportunity for research to be conducted on these endangered species in a controlled and monitored space, enabling investigations into behaviour, growth and development, or other topics that would be more challenging to conduct in the wild.

Free-ranging lemurs at the DLC have open access to their NHE from about late spring into early fall, weather and temperatures permitting. They have year-round access to the building connected to their NHE, which includes an outdoor transition-like section and indoor enclosures, and often share their enclosure with one to two other lemur species depending on building size, overall temperament, and general ecological niche. For example, all three of the ring-tailed lemur troops examined in this thesis free-ranged with a sifaka troop because the two species generally get along well with each other and tend to occupy different areas of their enclosure: the sifaka are usually up in the tree canopy while the ring-tailed lemurs are below on the ground. Since lemurs are not native to North America, they are not able to fully free-range year-round and are restricted to their building when temperatures drop below 45°F/7.2°C or when serious weather threats are predicted (i.e. hurricanes or tornadoes). Once temperatures remain above 45°F/7.2°C for a few consecutive days the lemurs are granted outdoor access to their NHEs. Free-ranging lemurs are checked by caretakers at least once each day during the scheduled provisioned meal, in addition to morning "opening" and evening "closing" routines at the Center, which include cleaning the building and adjacent transition-like section as well as checking the electric fence that runs along the top of the enclosure fence lines. The DLC also maintains regular veterinarian check-ups and weight checks for all individuals, scheduled based on the species and age of the individual.

The lemurs at the DLC, as endangered species, are under strict breeding programs, Species Survival Plans (SSPs), which work to maintain the genetic diversity of captive species all over the world. As a result, almost all sexually mature females at the DLC are on a hormone contraceptive to prevent unplanned pregnancies and incest, since many lemurs are housed in “family” units with siblings and their parents. The only exceptions are females who have received mating recommendations and if accepted are then housed with the approved male. All females and all males in this study were non-breeding at the time of observation from May until September 2019.

2.2 Meet the Lemur: *Lemur catta*

The ring-tail lemur (*Lemur catta*) is the best studied lemur species in the world, and is recognizable as a prominent species used to promote lemur conservation (LaFleur et al., 2017). Despite being the most common primate species in captivity, the rapidly dwindling wild populations of *L. catta* are highly threatened by anthropogenic changes to their landscape, such as habitat loss, agricultural intensification, and mining enterprises in addition to the illegal wildlife pet trade (Andriaholinirina et al., 2014; Estrada et al., 2018; Gould & Sauther, 2016; LaFleur et al., 2019). Researching this species to better understand their behavioural ecology can contribute to current knowledge of the evolution of primate behaviour broadly, in addition to better conservation action to protect this endangered species from extinction in the wild (*see* LaFleur & Gould, 2020).

L. catta has a diverse range of communicative modes, the sensory channels they employ to communicate with conspecifics, which makes research on this species valuable to studies of primate behaviour and evolution. While this species’ vocalizations have been studied extensively, other communicative modes include tactile signals, visual cues, and scent-marking to monitor group members, attain mating opportunities, warn group members of threats, defend territory, and maintain their matriarchal social organization (Baker, Taylor & Montrose, 2018; Bolt, 2013a; Bolt, 2013b; Bolt & Tennenhouse, 2017; Gamba et al., 2017; Jolly, 1966b; Kappeler, 1998; Mertl-Millhollen, 2000; Macedonia, 1986; Macedonia, 1993; Nakamichi & Koyama, 1997; Palagi, Telara & Tarli, 2004; Palagi & Norscia, 2015; Palagi, Norscia & Spada, 2014; Rushmore, Leonhardt & Drea, 2012; Walker-Bolton & Parga, 2017).

Despite the clear complexity in how they communicate, the majority of studies on *L. catta*, and on many other primate species, have been unimodal: focusing on only one communicative mode and excluding all others (*see* Bolt & Tennenhouse, 2017; Drea &

Scordato, 2008; Kappeler, 1998; Macedonia, 1986; Palagi, Norscia, and Spada, 2014; Shepherd & Platt, 2008). While understanding the meaning behind individual signals is undeniably important, focusing research exclusively on a unimodal methodology limits the intelligibility of cross-study comparisons (Liebal & Oña, 2018; Slocombe, Waller & Liebal, 2011). Furthermore, unimodal research simplifies the potential complexity of primate communication, which is often a signal composed of two or more modes at once, like a visual cue with a vocalization (Figure 1; Liebal & Oña, 2018; Partan & Marler, 1999). Multimodal research addresses these limitations by recognizing the complex whole of primate social communication (Waller et al., 2013; Peckre, Kappeler & Fichtel, 2019).

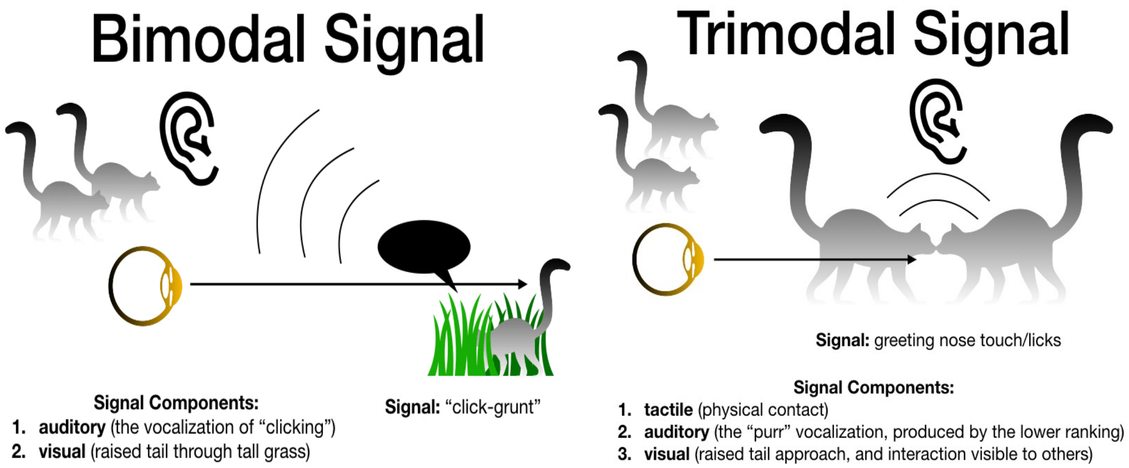

Figure 1: Example of multimodal signals in *Lemur catta*. Note that the trimodal signal example may also include olfactory, taste, and vomeronasal organ (VNO)/accessory olfactory system (AOS) involvement, but these likely constitute more "background" components in the signal relative to the three listed above (*see* Colquhoun, 2011; Smith et al., 2015 for more on VNO).

2.3 Existing Literature

Earlier work to describe multimodal signals identified two main elements: the redundant and non-redundant components (Partan & Marler, 1999). When these individual communicative components that make up a signal are received independently, they can either elicit the same responses in a receiver (be redundant) or elicit completely different responses (Figure 2; Partan & Marler, 1999). As Partan and Marler (1999, p. 1272) explain, “redundancy is common and ensures that the message will get through in the face of environmental noise (backup signals). Nonredundant [*sic*] components have the advantage of providing more information per unit time (multiple messages)”. The main difference between the two can either be in the type of response elicited or, if the responses are the same (i.e. the signals are redundant), differences can be seen in the level or extent of the receiver’s reaction (Partan & Marler, 1999). When combined into a multimodal signal, the responses can elicit: 1) the exact same response, 2) the same response but to varying degrees of strength, 3) a combination of responses, or 4) an entirely new response (Figure 2; Partan & Marler, 1999).

Previous studies on social communication broadly have examined the role that either social or ecological contexts might play in communicative signalling. With regard to the social context, studies can be generally split between testing hypotheses for 1) social complexity and communicative complexity (Bray, Krupenye, & Hare, 2014; Freeberg, 2006; Peckre, Kappeler & Fichtel, 2019) or 2) the affiliative or agonistic attention of conspecifics in the same troop. The latter encompasses both courtship and territorial displays as well as the potential mitigation of agonistic or aggressive encounters with group-members (Bolt, 2013a; de Luna, Hödl, & Amézquita, 2010; Kappeler, 1998; Nakamichi & Koyama, 1997; Palagi, Telara, & Tarli, 2004; Smith, Taylor, & Evans, 2011). As increasing environmental change continues to be of concern to endangered species, more research recently has been addressing this with regard to ecological contexts. What is of particular interest in these studies are the impacts of environmental “noise” on communication in various species. This branch of research examines how individuals communicate through or around different obstructions or interference, but also ways in which the habitat is taken advantage of to maximize displays and signal reception, which often includes the use of multimodal signals (de Jong et al., 2018; Gomes et al., 2017; Gordon & Uetz, 2011; Grafe et al., 2012; Secondi et al., 2015; Sicsú et al., 2013; Uy & Safran, 2013). For example, in audibly nosier environments female painted gobies (*Pomatoschistus pictus*) were found to pay more attention to the visual component of multimodal courtship signals from males, but when in quieter environments they tended to rely on the acoustic component (de Jong et al., 2018).

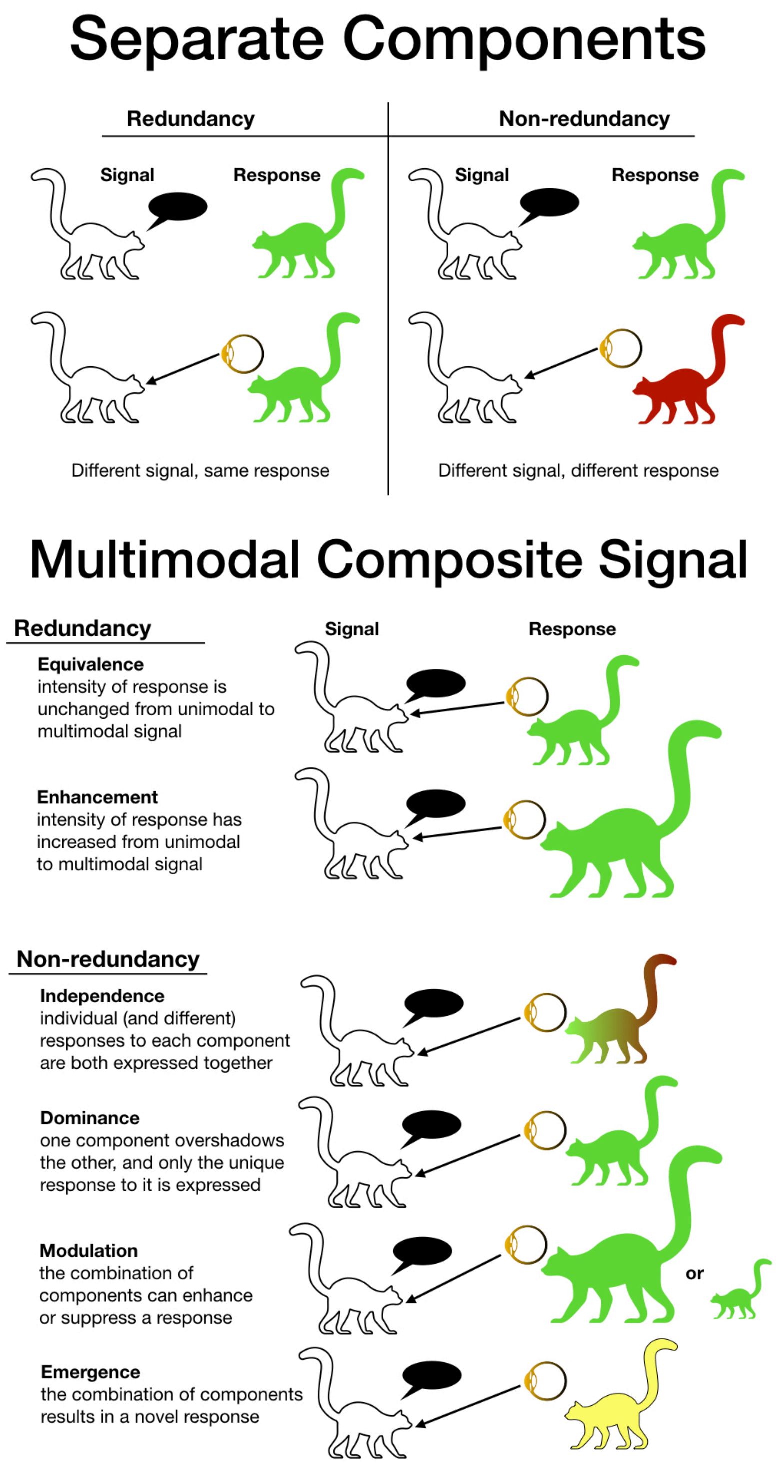

Figure 2: Visual representation of unimodal (separate components) and multimodal signals, depicting signal structure and observer response to either redundancy or non-redundancy of components. Adapted from Partan & Marler, 1999.

This change in selective trait also had an impact on the spawning success of males, demonstrating a shift in sexual selection as a result of environmental noise (de Jong et al., 2018). A more concerning example can be drawn from research on the hybridization of two species of newt, the Palmate newt (*Lissotriton helveticus*) and the Smooth newt (*L. vulgaris*). Both modes of communication used by these two species in multimodal mate signals, olfactory and especially visual, were found to be obscured in water stained by decaying vegetation (Secondi et al., 2015). This obscuration negatively impacted females' ability to discriminate between species and increased the likelihood of disadvantageous hybridization occurring, demonstrating that not all multimodal signals are effective at overcoming environmental noise (Secondi et al., 2015).

Multimodal communication is more complex to study because it often involves different recording and measuring techniques per sensory mode and signal component, let alone per species or context, but will likely reflect the actuality of primate communication more accurately. As Peckre and colleagues (2019) argued, conducting more studies of multimodal communication will help future research to develop better tests of social complexity, following the social complexity hypothesis for communicative complexity. Nevertheless, the vast majority of studies examining multimodal communication have been conducted on non-primate species (Hebets & Papaj, 2005; Partan & Marler ,1999). These include many species of birds (Freeberg, 2006; Gomes et al., 2017; Ota, Gahr, & Soma, 2015; Ręk & Magrath, 2016; Rubi & Stephens, 2016; Sicsú et al., 2013; Smith, Taylor, & Evans, 2011; Uy & Safran, 2013), amphibians, (de Luna, Hödl, & Amézquita, 2010; Grafe et al., 2012; Secondi et al., 2015), insects and arachnids (Gordon & Uetz, 2011; Rowe & Halpin, 2013; Stoffer & Walker, 2012; Uetz, Roberts, & Taylor, 2009), and aquatic life (de Jong et al., 2018; Mowles, Jennions, & Backwell, 2017). Even within these, a consistent trend is the analysis of only two sensory modes in a single signal, usually visual and auditory, with a few examining the subcomponents of either a multimodal signal or complex unimodal signal (de Luna, Hödl, & Amézquita, 2010; Freeberg, 2006; Ota, Gahr, & Soma, 2015; Rubi & Stephens, 2016; Uetz, Roberts, & Taylor, 2009). In addition, the majority of previous work focuses on the use of multimodal communication in one particular signal type, that being mate choice displays.

Multimodal communication research in primatology is still in its infancy and is only just beginning to gain more ground (Fröhlich & van Schaik, 2018; Waller et al., 2013; Peckre, Kappeler & Fichtel, 2019). As Peckre, Kappeler, and Fichtel (2019) described, part of the challenge is overcoming "sensory biases" as they relate to how and which communication data are collected in addition to the equipment that has been developed to collect that same "biased" data. For example, the few studies that have examined multimodality in primates have focused mainly on the readily visible gestural communication of Great Apes, chimpanzees for the most part (Fröhlich & van Schaik, 2018; Fröhlich et al., 2019; Leavens, Russell, & Hopkins, 2010; Pollick & de Waal, 2007; Taglialatela et al., 2015), or the connections between vocal-visual displays and rank in macaques (Ghazanfar, 2013; Higham et al., 2013). It is only more recently that we begin to see research shifting to include the more distant relatives of humans, like lemurs, tarsiers, and non-*Macaca* species of monkey (Singletary & Tecot, 2020). My project follows a growing trend in behavioural primatology to examine more complex social communicative constructions of meaning through the utilization of a multimodal approach in both data collection and analysis.

2.4 Repertoire: The Sensory Signals

2.4.1 Auditory

Primate vocalizations are a popular behavioural communication to study for many primatologists, but this often-characteristic behaviour of many species can be challenging to study. Some of the challenges a researcher may face are habitat and environmental or background "noise", especially when relying on recording tracks (Maciej, Fischer, & Hammerschmidt, 2011). Factors like the makeup of the habitat itself, for example density of the forest or the position of the receiver (the researcher or a conspecific) in a habitat relative to the signal sender, can alter the quality and level of degradation of a vocal signal (Maciej, Fischer, & Hammerschmidt, 2011). These factors influence the vocalization's range and durability when attempting to communicate at longer physical distances, but vocalizations can also be used for communicating with conspecifics in close contact. For some primate species, it has even been argued that the visual perception of a vocalization, or the resulting mouth and facial movements, can be just as important as the meaning or function of the vocalization itself (Ghazanfar, 2013). Rather than being a “fixed” element of an auditory signal, or even a redundancy measure, Ghazanfar (2013) argues that visual speech perception in macaques (*Macaca sp.*) functions to enhance the auditory signal.

Even the social environment of a primate can influence how they vocalize and communicate with conspecifics. A recent study on the variation seen in the vocalizations of captive common marmosets (*Callithrix jacchus*) demonstrates that changes to the social environment, but not the physical environment, influenced the properties of some of the calls used by this species (Zürcher, Willems, & Burkart, 2019). When translocated to the near proximity of a novel colony, the translocated group adopted the dialect of their new neighbour for two of the three examined call-types after a few months together (Zürcher, Willems, & Burkart, 2019). The third vocalization type they examined, food calls, remained distinct between the two groups and actually became more different over the same period of time (Zürcher, Willems, & Burkart, 2019). Another example of where the social environment influences vocal communication has been described in captive chimpanzees (*Pan troglodytes*). Taglialatela and colleagues (2015) found that half of the vocalizations observed co-occurred with signals from another sensory modality, and the majority of those multimodal signals were found to be directed signals. In other words, multimodal signals that include an auditory component are common in chimpanzees, and these signals are largely intended for communication with a specific individual in the troop rather than used as a generalized signal. Clearly there is more to be investigated across different primate species with regard to their vocalizations, especially when examining this communicative mode from a multimodal perspective.

Ring-tailed lemurs are often lauded on their broad range of vocalizations relative to other lemurid vocal repertoires, utilizing over 20 different calls (Macedonia, 1993; McComb & Semple, 2005). In their investigation of the coevolution of sociality and communication in primates, McComb and Semple (2005) found that of the lemur species there were repertoire data for, ring-tailed lemurs had the largest at 22 structurally distinct calls. This large repertoire size is closest to the mantled howler monkey (*Alouatta palliata*), which scored 22 as well, and the bonnet macaque (*Macaca radiata*) with 21, and exceeds many other Old and New World primates, including orangutans (*Pongo pygmaeus*), by the authors' examination (McComb & Semple, 2005). As a result, there is a fairly substantial body of research on *L. catta* vocalizations from different contexts to better understand the significance, meaning, and function of these, some of which being unique to certain age groups or sexes (Bolt, 2013a; Bolt, 2013b; Bolt & Tennenhouse, 2017; Macedonia, 1993). For example, Bolt (2013a), found that the rate of "squealing", a vocalization unique to males, was positively correlated with rank, and in another study that "howling", another vocalization unique to males, was likely used to broadcast an individual's position and audibly mark the troop's territory as a way of discouraging non-natal males from migrating into their troop (Bolt, 2013b). Work has even been done, and repeated more recently, to establish whether individual identification was possible based on vocal signatures alone (Gamba et al., 2017; Kulahci, Rubenstein, & Ghazanfar, 2015; Macedonia, 1986; Oda, 1996). Kulahci, Rubenstein, and Ghazanfar (2015) in particular have demonstrated that not only is individual identification possible through vocalizations alone, but it also shows a degree of social discrimination that is even higher than that seen in grooming partner preferences.

Figure 3: Griselda (female, troop 3) performing a "moan" vocalization. Photo taken by author at the DLC, 2019.

The distance an individual travels away from the "core" or the rest of the troop is very closely related to their rank. As a result of males being of lowest social rank in ring-tailed lemur troops, they are most likely to be found relatively dispersed or along the fringes of a troop, whereas the core is largely made of up females and their younger offspring, all of which are subordinate to the matriarch (Bolt & Tennenhouse, 2017; Gabriel, Gould, & Kelley, 2014; Jolly, 2012; Oda, 1996). It is most important for those ranging at the fringes to remain in contact with the core of the troop, as a means of protection against predation and maintaining social relationships (Gabriel, Gould, & Kelley, 2014), though it can be disadvantageous for an individual to signal their location while foraging, since competition for food is common (Oda, 1996). Nevertheless, contact calls like the "moan" (Figure 3), or even affiliative vocalizations like the "*hmm*", are frequently, though not exclusively, heard from males (Bolt & Tennenhouse, 2017; Macedonia, 1993). These findings together emphasize the important role vocalizations play in ring-tailed lemur social groups in not only keeping track of troop mates, but also their ability to recognize individual voices and remain physically close to those they are *socially* closer to.

2.4.2 Visual

The next most studied communicative signals in primates can broadly be grouped together as visual components, which from a behavioural ecology standpoint combine gestures and facial expressions with display movements and colouration. It is also one of the more common research topics examined in multimodal primatology in the form of Great Ape gestural communication (Fröhlich et al., 2019; Hobaiter & Byrne, 2011; Pollick & de Waal, 2007; Taglialatela et al., 2015). Visual signals can be identified in bouts or sequences that furthermore can be silent, audible, or include tactile contact (Hobaiter & Byrne, 2011). Manual gestures are a common visual signal used by Great Apes, and at least in chimpanzees (*Pan troglodytes*) are likely to be learned behaviours that improve in efficiency and efficacy over time (Hobaiter & Byrne, 2011). Researchers Hobaiter and Byrne (2011) observed bouts of gestures, largely used by juveniles in trial-and-error type sequences, which contained pauses for the receiver to respond within and then developed over time into more efficient use of contextually correct gestures in adulthood. Interestingly enough, it has been argued that bonobos (*Pan paniscus*), when compared to chimpanzees, actually show greater flexibility and variability in the use of multimodal combinations of gestures with facial or vocal signals (Pollick & Waal, 2007).

In a more recent study, Roberts and Roberts (2016) argued that wild chimpanzees will change their mode of communication based on the social bonds they have. Simple visual gestures were more likely to be used when an individual was communicating with a relatively small number of familiar individuals who regularly interact, whereas gestures containing tactile or auditory components were used more when communicating with a larger number of individuals who had relatively weaker social bonds with the focal individual (Roberts & Roberts, 2016). Roberts and Roberts (2016) argued that compared to tactile and auditory gestures, simple visual gestures may require more nuanced interpretation and therefore are more likely to be interpreted correctly by individuals who are more familiar with the sender of that signal because they possess a stronger social bond with one another. On the other hand, when tactile and auditory components are added to a visual gesture the signal likely becomes not only more emotionally charged, but, in the case of auditory components, is also able to travel a further distance and attract the attention of other conspecifics not in the immediate vicinity of the sender (Roberts & Roberts, 2016).

A spectacular visual component common in communication studies is the use of colouration, and although avian plumage may come to mind first, primates are not excluded from this subcategory. Male mandrills (*Mandrillus sphinx*) in particular undergo remarkable changes in colouration when the highest dominance rank is achieved (Renoult et al., 2011). This change represents a complex unimodal visual signal, involving both red and blue hues, which can also be combined with signal components from other modalities to create multimodal displays and signals. Research on this colouration has revealed that the blue pigmentation actually aids in emphasizing the red colouration against background foliage to make the signal all the more noticeable (Renoult et al., 2011). Renoult et al. (2011) argued that perhaps when the red hue came up against evolutionary constraints the blue hue evolved to emphasize what could be accomplished and therefore acts as an amplifier for the rest of the facial colouring in this primate. Of course, visual signals are not unique to any one primate genus, though they can manifest in very different ways. Research into rhesus macaques (*Macaca mulatta*) for example has suggested that males use multiple modalities, in the form of various bodily colouration and “luminosity” as well as vocalizations, to transmit different types of information to females and inform mate choice (Higham et al., 2013).

Visual components are also key in the signalling repertoire of ring-tailed lemurs. A few examples of how *L. catta* use visual signalling in their daily lives can be found in their agonistic behaviours. This broad category of signalling includes body posturing and the threat stare, a common signal in lemurs, as well as tail waving, which is a signature component of a male ring-tailed lemur's "stink fight" (*see* Jolly, 1966a: 103; Greene et al., 2016; Kappeler, 1998; Jolly, 1993; Jolly, 2012; Walker-Bolton & Parga, 2017); however, these signals are not necessarily exclusive to agonistic contexts. Like many other primate species, and other animals in general, components commonly used to signal a fight, territoriality, or an otherwise real conflict are also often used in play.

Figure 4: Griselda (female, troop 3) performing a "play face" while rolling into an older, female troop mate. Photo taken by author at the DLC, 2019.

Ring-tailed lemurs share in common with many other primates a visual signal that is incredibly important during play: the relaxed open-mouth play face (Figure 4; *see* Darwin, 1872; Fagen, 1981). In fact, play bouts in ring-tailed lemurs involve a mix of visual and tactile signals, including both tail movements and facial expression as well as vulnerable posturing and biting (Palagi, 2009; Palagi, Norscia, & Spada, 2014). It is interesting to note that as opposed to other primates like chimpanzees, ring-tailed lemurs do not adjust play signalling or behaviour based on surrounding troop members, a phenomenon referred to as "audience effect" (Palagi, Norscia, & Spada, 2014). They will nevertheless increase the complexity and visibility of signals when play bouts become riskier, for instance when more than two individuals are involved, which is a behavioural response commonly found in other primates (Palagi, 2009). Play has also been demonstrated as a less-risky means of testing one's strength with other troop mates (Palagi, 2009).

Even outside the contexts of conflict and play, ring-tailed lemurs have been shown to be fairly visually oriented. While they clearly do use the other sensory modes examined here to communicate with conspecifics, visual signalling and tracking individuals by sightline are nevertheless important. *L. catta* rely in part on visual signals for group cohesion when moving through forested environments. Perhaps the more obvious component used in their visual signalling is their striped tail, which camouflages well in the canopy, but acts as a "guiding flag" while moving terrestrially (*personal observation*). Shepherd and Platt (2008) produced similar findings of visual preference in their own investigation on *L. catta* mobile orientation. Using a gaze-tracking system, it was shown that male ring-tailed lemurs are acutely aware of not only body, but also and preferentially the head-orientation of troop mates (Shepherd & Platt, 2008). By following the postural orientation of conspecifics, individuals are able to follow and track the same general line of sight and subsequently the directional movement of a troopmate (Shepherd & Platt, 2008). This visual preference has also been demonstrated in foraging behaviours, though *L. catta* can use it both in combination with and isolated from their sense of smell (Rushmore, Leonhardt, & Drea, 2012). The above examples demonstrate the importance of visual components in ring-tailed lemur social communication.

2.4.3 Tactile

Tactile communication is largely recognized as an important element of all primate sociality, including humans. It plays an important role as a communicative component in both aggressive confrontations as well as, if not more critically, affiliative ones. Affiliative behaviours, which largely consist of close contact, are important for individual and troop health, thermoregulation during cold nights or months, and the resulting close proximity of groupmates increases protection from predation (Gabriel, Gould, & Kelley, 2014). Touch can be used in assertions of rank or as a response to stress more broadly, it has been demonstrated as an important means of reconciliation after conflict for many species, and especially so to initiate or increase the likelihood of copulation in the form of courting behaviours (Hertenstein et al., 2006). One area of tactile research in primates that had received a great deal of interest in the past is the attachment bond between mother and infant, and the consequences of breaking that contact for long periods of time or indefinitely, especially within the contexts of animal and human psychoanalyses (Hertenstein et al., 2006). More recent work has demonstrated a shift in the focus of primate tactile research to almost exclusively examining grooming behaviours, which varies not only between age groups and sex, but also between species.

A large body of research has been devoted, for example, to the grooming behaviours of baboons (*Papio spp*.) as a result of their incredibly complex social organization. This complexity is unique among other monkeys, and even varies between species within the genus (Chalyan et al., 2012). In particular, hamadryas baboons (*Papio hamadryas*) have four structural levels to their social organization: one-male multi-female unit harems, “bachelor” clans, bands, and finally the much larger herd as a whole (Chalyan et al., 2012). Grooming in this species is argued to function as a means of not only facilitating and strengthening this existing social structure and the subsequent hierarchies within, but it also plays a part in establishing future groupings (Chalyan et al., 2012). For instance, Chalyan and colleagues (2012) found that a young bachelor was able to form his own harem before older counterparts as a result of being a more active groomer of lower ranking females from large harems. These females in particular have more “freedom” than those of higher rank to interact with non-harem individuals, both male and female, and were themselves observed as largely responsible for maintaining relationships both within their haram as well as the group as a whole via grooming (Chalyan et al., 2012).

As a result of sex differences in the social organization of a primate troop, the learning process of grooming behaviour, and importantly its allocation among troop members, can also be sex dependent. In an investigation of stumptailed macaques (*Macaca arctoides*) infant males and females were found to learn who to groom and how much to do so based on different factors (Mondragón-Ceballos et al., 2010). In their investigation, Mondragón-Ceballos and colleagues (2010) found that female offspring would expand their social circle beyond their mothers sooner than their male counterparts and began interacting independently with other, older females at a younger age to develop their own connections. Stumptailed macaques have a female-bonded matrifocal social organization, where females remain in their natal group and males disperse upon sexual maturity, so the kinship bonds between female individuals are very important (Mondragón-Ceballos et al., 2010). In this respect, female infants learn to allocate their grooming based on kin relations, but males require more strategic bonds based on rank that could be useful for future alliances once evicted from the natal group (Mondragón-Ceballos et al., 2010).

The amount of grooming an individual receives can depend largely on their rank, but it can also be influenced by other factors or “services” at play in the biological marketplace (Port, Clough & Kappeler, 2009). For example, reciprocal grooming in lemurs is common, but redfronted lemurs (*Eulemur rufus*) have been observed to perform reciprocal grooming of even duration only with another individual from the same ranking (Port, Clough & Kappeler, 2009). When there were differences in the social position of the individuals, in male-male, male-female, and female-female dyads, unequal reciprocal grooming took place (Port, Clough & Kappeler, 2009). Port, Clough, and Kappeler (2009) described that low-ranking females, who are most threatened by eviction in this species when the troop size becomes too large, provided significantly more grooming to those of higher rank than they received. The authors argued that, since this pattern resembles that in other non-lemurid primates and mammals, perhaps this differential occurs for similar tolerance-winning purposes as a means to avoid or delay eviction (Port, Clough & Kappeler, 2009). They also suggested that the observed inequality of reciprocal grooming in male-female dyads, where males received more grooming regardless of rank, might be a means for females to trade grooming services for access to other resources, though further research to investigate this suggestion is needed (Port, Clough & Kappeler, 2009).

The strategic allocation of grooming is a common thread in research on primate tactile communication since it, along with other affiliative behaviours, provides a number of benefits for individuals. Grooming in particular not only reduces infection rates in the troop by removing insects and other ectoparasites, but it also strengthens relationships between individuals (Gabriel, Gould, & Kelley, 2014). Jolly (2012) argued that, while aggressive territoriality does play an important part in *L. catta* daily life in the wild, they also spend a considerable amount of time performing more affiliative behaviours like grooming and cuddling (Figure 5). Understandably, the level of familiarity between individuals is another suggested factor influencing the frequency of grooming in ring-tailed lemurs. In their investigation and comparison of the social behaviour of two wild troops of ring-tailed lemurs, Nakamichi and Koyama (1997) found that closely related females were much more likely to be observed grooming one another as opposed to a grooming dyad formed with an unfamiliar female. Affiliative behaviours in *L. catta* have even been demonstrated as variable with climactic changes, habitat composition, dispersal patterns or lack thereof, and the seasonality of their restrictive mating cycle (Gabriel, Gould, & Kelley, 2014). In addition, and in agreement with much of the above, both the age of an individual as well as their dominance rank have been argued as significant factors to the frequencies of grooming bouts and contact (Hosey & Thompson, 1985; Nakamichi & Koyama, 1997). In an earlier study on tactile communication in a troop of captive *L. catta*, higher ranked individuals were found to receive the most physical contact from troop-members broadly, and although older individuals more frequently initiated grooming bouts, younger individuals and those of lower ranking initiated simpler "touching" contact more often (Hosey & Thompson, 1985).

Figure 5: Ring-tailed lemur pair performing a greeting nose-lick and face groom. Left is Randy (male, troop 2) and right is Sophia (dominant female, troop 2). Photo taken by author at the DLC, 2019.

2.4.4 Olfactory

While the sense of smell is an important tool used for foraging in many other mammal species, and *L. catta* appear no different (Rushmore, Leonhardt, & Drea, 2012), olfactory signals are also important in social contexts as a form of communicating via secretions, scent marking, and often subtle chemical signals. Scent marking and other more visible olfactory signalling encompass various gland secretions, saliva marking, urine marking and washing, and other latrine behaviours used for individual identification, mate choice, and marking territory (Colquhoun, 2011; delBarco-Trillo et al., 2012; Drea & Scordato, 2008; Eppley, Ganzhorn & Donati, 2016; Palagi & Norscia, 2009; Tinsman, Hagelin, & Jolly, 2017). For example, Eppley and colleagues (2016) found that the southern bamboo lemur (*Hapalemur meridionalis*) uses specific and conspicuous locations within their territory as regular latrine sites to mark territory without incurring risky agonistic encounters with other troops. While clearly an important mode of communication, olfactory signals also represent a particular area of primate behavioural ecology that is in need of further work across species. One of the main challenges to studying olfactory and other chemical signals is the limitation humans have in personally accessing them using our own sense of smell or receptive organs, which are greatly reduced compared to that of many other primates, and can be contrasted with the relative ease at which the majority of visual and auditory signals are detected by human eyes and ears respectively (Colquhoun, 2011; Peckre, Kappeler & Fichtel, 2019). Another is the analysis of the complex chemical components of those olfactory signals, which often involves multiple approaches and different instruments to complete (Drea et al., 2013). Nevertheless, recent research examining a combination of behavioural observations with chemical analyses allows researchers to more fully address questions pertaining to olfactory signalling (Crawford, Boulet, & Drea, 2011; Drea et al., 2013; Greene et al., 2016; Grogan et al., 2019), and represents a growing area for potential behavioural work to continue. The importance of olfactory signals has traditionally been emphasized in strepsirrhine primates, like *L. catta*, owing to their retention of a rhinarium along with the level of development of other scent-receptor organs, like the vomeronasal organ and complex (*see* Smith et al., 2015, for *L. catta* microanatomical analysis), but the use of this sensory mode of communication is not exclusive to this suborder of primates (Colquhoun, 2011).

In their review of the literature on scent marking behaviour in New World Monkeys (NWM), Heymann (2006) outlined three key hypotheses that are used to describe the functional purposes of scent marking: 1) territoriality, 2) the regulation of social and reproductive dominance, and 3) mating competition and attraction. At the time of their publication only about nine species of NWM were represented, with data from either captive investigations or anecdotal observations, and the majority of those were callitrichid species (marmosets and tamarins; Heymann, 2006). The lack of similar investigations on wild populations and the small sample sizes of the studies made some of the comparisons more challenging to make, but they were able to identify a few interesting patterns relating to the above hypotheses (Heymann, 2006). Heymann (2006) found very little support for scent marking behaviours as a form of territorial boundary setting, based on location of the marking, rate of deposition, and context of occurrence. More support was found for scent marking as a response to and means of intrasexual mating competition (male-male or female-female) as well as intersexual mate choice and attraction (Heymann, 2006). There was, however, too little previous research to fully examine whether social and reproductive dominance might also be influencing rates of occurrence or location (Heymann, 2006). The studies that have been done, when compared across species and sometimes between different groups of the same species, show contradictory results (Heymann, 2006). Clearly, more research is needed on the olfactory communication of NWM as well, and in particular how this sensory mode is utilized in respect to social organization in the wild.

Differences in social organization, even within a single genus, can result in very different uses of olfactory signals. For example, in his comparison of the olfactory behaviours of nocturnal and cathemeral strepsirrhines, Colquhoun (2011) found that, while for the most part the behaviours and their uses were similar between the two groups, differing social organization within the species *Eulemur* seemed to influence differences in scent marking behaviour. Mongoose lemurs (*E. mongoz*) and red-bellied lemurs (*E. rubriventer*) are both pair-bonded species, and when compared to *Eulemur* species that have multi-male, multi-female social organizations they appeared to rely more on scent marking and counter marking during agonistic territorial displays (Colquhoun, 2011). The species of *Eulemur* in multi-male, multi-female groups will instead utilize visual and vocal displays during intergroup encounters more heavily than olfactory signals (Colquhoun, 2011). It is also interesting to note that in mongoose and red-bellied lemurs, both males and females will scent mark the other anogenitally, while only males will scent mark females this way in multi-male, multi-female *Eulemur* species (Colquhoun, 2011). In a subsequent study on this same genus of lemurs, delBarco-Trillo and colleagues (2012) found that the complexity of their olfactory signalling was likely selected for with increasing social complexity. Further observational investigations with wild populations of these species and others may reveal further information on how social organization influences olfactory signal use, and even communicative repertoire, between taxa.

In *L. catta*, scent marking (Figure 6) represents a fairly information-heavy, but “honest” mode of communication (Crawford, Boulet, & Drea, 2011; Greene et al., 2016; Grogan et al., 2019). This means the information a marking communicates is genuine or truthful of the state of the dispositor. These olfactory signals can be grouped into two main types, that each provide different information to the receiver: glandular secretions and urine marking. Glandular secretions are the most commonly studied, and encompass the deposits left by anogenital scent glands present on both males and females, as well as the brachial and antebrachial glands present in male individuals only (Drea & Scordato, 2008). Urine marking is a more common form of olfactory communication in nocturnal strepsirrhines (Colquhoun, 2011; Drea, Goodwin, & delBarco-Trillo, 2019), but is still used by their diurnal relatives, like ring-tailed lemurs, to convey important information (Drea, Goodwin, & delBarco-Trillo, 2019; Palagi & Norscia, 2009; Smith et al., 2015). This latter example of olfactory communication was not scored in the current study, but does represent an area of research that is in need of further investigation at both the observation and chemical assay levels.

In females, glandular scent marking appears to function seasonally as a way to attract males by advertising their reproductive state, as a means of competing with intragroup females for future copulation with males, and to demarcate territory (Drea & Scordato, 2008; Kappeler, 1998; Palagi, Telara, & Tarli, 2004; Tinsman, Hagelin, & Jolly, 2017). It nevertheless also contains identity and relational information, which is likely used by conspecifics for kin recognition (Crawford, Boulet, & Drea, 2011).

Figure 6: Two dominant females performing an anogenital scent mark within their respective NHEs. Left is Sophia (troop 2) and right is Liesl (troop 3). Photo taken by author at the DLC, 2019.

In their analysis of secretion compositions from captive *L. catta* at the DLC, Crawford and colleagues (2011) demonstrated that a commonly used hormone contraceptive actually changed the composition of the secretions, which masked not only the usually honest indicators of health and sexual receptivity of that female, but also her unique chemical signature and genetic diversity. Hormone contraceptives are commonly used in captivity as a means of controlling the breeding periods and occurrence for many endangered species. This is largely done to prevent inbreeding in that captive population and to maintain a global, genetically diverse captive gene pool. As a result, hormone contraceptives are effective by reducing the incidence of unmonitored copulations and even the interest of males in females on contraceptives (Crawford, Boulet, & Drea, 2011). It is worth noting that the researchers suggested the additional masking of individual chemical signatures may interfere with normal kin recognition that occurs via scent marking in ring-tailed lemurs (Crawford, Boulet, & Drea, 2011). As a result, hormone contraceptives may alter certain kin-specific or mate choice behaviours in captive species (Crawford, Boulet, & Drea, 2011), although further observational work is needed to assess these potential behavioural changes and clarify this suggestion.

Similar to females, the glandular signalling of *L. catta* males is an honest signal which identifies not only individual rank to compete for matings, but also their individual genetic diversity relative to the receiver (Grogan et al., 2019; Kappeler, 1998; Walker-Bolton & Parga, 2017). In males specifically, the secretions they produce from different olfactory glands (anogenital and ante-brachial) can be deposited either independently or mixed together to provide the receiver with different information about the depositor (Greene et al., 2016).

The short interval between deposition and investigation by another individual suggests that *L. catta* are aware of the actions of their troop-mates to some extent, but a scent mark is likely more of a general signal rather than a directed one (Kappeler, 1998; Drea et al., 2013). Scent marking is not subject to an "audience effect" nor is it directed towards a particular individual, but rank, especially in females, has been argued to influence the number of "visitors" a scent mark is investigated by (Kappeler, 1998). As an aside, in their investigation of the complexity of olfactory communication in ring-tailed lemurs, Drea and Scordato (2008) found that individuals were only able to determine dominance rank from the scent mark of a familiar individual, suggesting a level of associated learning occurring to accomplish this discernment. In contrast to scent marking, a male's stink fighting/flirting behaviour is more of a directed signal than a general one (*see* Jolly, 1966a: 103; Greene et al., 2016; Kappeler, 1998; Jolly, 1993; Walker-Bolton & Parga, 2017). This behaviour is unique to male ring-tailed lemurs and is usually directed at either a rival male or used to attract the attention of females (Greene et al., 2016; Kappeler, 1998; Jolly, 1993; Walker-Bolton & Parga, 2017). The male will curl his tail up against his chest and into his arms where it can be anointed by secretions from the glands on his wrists and underarms, then the tail is whipped back around and up over the top of his head where he begins to flick it to waft the scent from his secretions towards the targeted male or female. This signal is also usually accompanied by a high-pitched squeal and the flattening of the signalling male's ears, forming a fairly complex olfactory-visual-auditory signal.

2.5 Evolution & Multimodal Theory

To examine communicative modes within different social groups, while considering how social and demographic variables may influence and produce communicative preferences, I am working within the theoretical frameworks of evolutionary theory and behavioural ecology. Brought together, this theoretical orientation defines communicative signals as functional for interacting with conspecifics while navigating an often dangerous and rapidly changing environment.

The theory of evolution describes changes in the traits of an organism over time, with all species sharing a common ancestor from which they diverged at various points in the past. Evolutionary theory provides a link connecting humans to our primate relatives by attempting to locate when common primate behaviours and traits may have evolved, in which contexts, and how those are adaptive and variable (Hinde 1987; Loy & Peters, 1991).

Multimodal research is often initiated with the goal of piecing together an evolutionary trajectory for the origins of human language, especially when studying the Great Apes (Fröhlich & van Schaik, 2018; Fröhlich et al., 2019; Waller et al., 2013). Previous research in human psychology has revealed that the main cognitive components of human communication, believed to be major milestones in its evolution, are, "intentionality, reference, iconicity, combinatoriality, turn-taking, neural control and ontogenetic plasticity" (Fröhlich et al., 2019, p. 1813). At present, there is support for most of these elements in gestural/visual and auditory communication of many of the other Great Apes, suggesting that the origins of human language are very likely to be multimodal (Fröhlich et al., 2019). Intentionality, reference, turn-taking, and ontogenetic plasticity, to greater and lesser degrees, have been described in research on Great Apes (Fröhlich et al., 2019). Intentionality in particular has been described in both chimpanzees and Thomas langurs (*Presbytes thomasi*), though so far only in both the vocalizations and gestures of chimpanzees (Fröhlich et al., 2019). The evidence for reference in signalling has been demonstrated largely in vocalizations of non-human animals more broadly, but Fröhlich and colleagues (2019) described the lack of standards in how to conduct these investigations on the gestures of apes as a particular hurdle for future research, for example whether to focus on manual signals exclusively or to include body posturing and even eye movements. Turn-taking has been demonstrated in both chimpanzees and bonobos within the contexts of coordinated mother-offspring travel, but the research remains exclusive to Great Apes and is in need of further investigation to examine the potential role multimodal communication plays in these turn-taking bouts (Fröhlich et al., 2019). Finally, ontogenetic plasticity has also received particular attention in chimpanzee research and has been demonstrated in both vocalizations and gestures (Fröhlich et al., 2019; Hobaiter & Byrne, 2011).

On the other hand, combinatorial signal sequences, iconicity, and neural control require further research in non-human primates (Fröhlich et al., 2019). Part of the challenge with these three "milestones" is missing data for one of the modes in question, so both auditory and visual signalling research is needed (Fröhlich et al., 2019). In addition, more consistency across studies in how cognitive concepts are defined and how they are used in practice is required (Fröhlich et al., 2019).

Another means of examining the evolution of multimodal signals is to address its adaptive function. In this branch of the investigation, many researchers, both within primatology and in other fields, have turned their focus to multimodal communication used specifically in courtship behaviours (de Jong et al., 2018; Ghazanfar, 2013; Gomes et al., 2017; Gordon & Uetz, 2011; Higham et al., 2013; Mowles, Jennions, & Backwell, 2017; Ota, Gahr, & Soma, 2015; Ręk & Magrath, 2016; Singletary & Tecot, 2020; Secondi et al., 2015; Sicsú et al., 2013; Smith, Taylor, & Evans, 2011; Stoffer & Walker, 2012; Uetz, Roberts, & Taylor, 2009; Uy & Safran, 2013). The reason for this focus is likely because of the substantial selective pressures involved in successful mate attraction for an organism as it relates to fitness. As a result of these selective pressures, multimodal signals in this behavioural suite are understood as having evolved as a functional and adaptive mode of communication. As is evident in my own data, not every signal is a multimodal one. The reason for this is that signals can be costly, including physiological or energetic costs as well as increased risks of aggressive encounters from competitors or even predation (de Luna, Hödl, & Amézquita, 2010; Rubi & Stephens, 2016; Singletary & Tecot, 2020; Sicsú et al., 2013; Smith, Taylor, & Evans, 2011). From an evolutionary standpoint, the flexibility of an organism in the ways in which it communicates, and its ability to utilize multiple modalities to do so, may be indicative of greater social complexity, behavioural plasticity, and an ability to adaptively respond to current and growing anthropogenic pressures (Peckre, Kappeler & Fichtel, 2019; Singletary & Tecot, 2020). For example, the shift in which signal component, visual or auditory, is focused upon for mate selection in painted gobies (*Pomatoschistus pictus*) based on presence or absence of audible environmental noise (de Jong et al., 2018), or the use of multiple modalities in the courtship signals of wolf spiders (*Schizocosa ocreata*) depending on substrate quality with respect to the efficacy of signal transmission (Gordon & Uetz, 2011).

Part of the challenge in studying multimodal communication is the various ways in which “multimodal”, “mode”, and even “complexity” are defined across studies and fields (Fröhlich & van Schaik, 2018; Fröhlich et al., 2019; Peckre, Kappeler & Fichtel, 2019). The main fields of research concerned with multimodal communication are behavioural ecology, where I find myself situated, and comparative psychology (Fröhlich & van Schaik, 2018; Fröhlich et al., 2019). Each of these two fields understandably approaches the investigation of multimodal communication in non-human animals from different understandings of what “multimodal” is. Behavioural ecology examines the influence and pressures an organism’s living surroundings have on that organism as they relate to the evolution of certain behaviours (Hinde, 1987; Loy & Peters, 1991; Waller et al., 2013). This includes both the physical environment or habitat an organism lives in, as well as their social environment, which is composed of the many interactions and associations they experience with other organisms and especially conspecifics (Hinde, 1987; Loy & Peters, 1991; Waller et al., 2013). In behavioural ecology, a “modality” (mode) refers to the sensory channel (visual, auditory, tactile, or olfactory) a signal or component of a complex signal is perceived by (Fröhlich et al., 2019). This is how the current study will be defining “modality” and “mode”.

This is contrasted with comparative psychology, which has research dominated in large part by that done on Great Apes, where a “modality” is defined as a vocalization, gesture, or facial expression, and a multimodal signal can be either the simultaneous or sequential combination of those three components (Fröhlich et al., 2019). As Fröhlich et al. (2019) explained, these different definitions and ways of thinking about multimodal communication make it challenging to draw comparisons or conclusions from across different species and studies. They provided the example that a single gesture like "slap object" would be multimodal for the behavioural ecologist since it represents an auditory-visual signal, but is unimodal for the comparative psychologist since for this latter group it contains only a single "mode": a manual gesture (Fröhlich et al., 2019). The reverse can also be the case, where a silent visual gesture like an arm wave combined with a facial expression would be considered multimodal for the psychologist, involving both facial and manual "modes", but a unimodal visual signal by the ecologist (Fröhlich et al., 2019).

Multimodal research can again be further divided into two functional approaches. The first is content-based research, which is concerned mainly with identifying whether and which components of a complex signal are redundant, complimentary, used to enhance or emphasize the message or response, or even a combination therein (Hebets & Papaj, 2005; Fröhlich & van Schaik, 2018; Partan & Marler, 1999). The research that has been done so far on multimodal communication largely indicates its use in clarifying a message, especially when components can be used flexibly in different contexts and in varied combinations (Fröhlich et al., 2019; Singletary & Tecot, 2020). For example, a ring-tailed lemur may tackle or grab at a conspecific in an aggressive context, but this same tactile signal component could be combined with a visual component like a relaxed open-mouth to indicate play and non-aggression. The second approach is efficacy-based research, an area that is in need of further investigation in primates, which is concerned with how and how well a signal overcomes environmental "noise" and limitations (Hebets & Papaj, 2005; Fröhlich & van Schaik, 2018).

As opposed to the previous approach, the efficacy-based approach is less concerned with what the signal is communicating and why, and more with how the signal is produced and transmitted, as well as the signal's perception and how it is biologically processed by the receiver (Hebets & Papaj, 2005; Fröhlich & van Schaik, 2018). As Hebets and Papaj (2005) explained, there are two key hypotheses within this approach: the efficacy backup hypothesis and the efficacy trade-off hypothesis. The former involves similar adaptations to environmental “noise” as discussed above, where an individual uses multiple modalities together to increase the likelihood of obtaining a desired response from the receiver of the signal by producing “backup” components (Hebets & Papaj, 2005). The components themselves mean the same thing, they are “redundant” components (Partan & Marler, 1999), but are better emphasized under different environmental conditions, so when they are used together one component can compensate for the other and vice versa. The efficacy trade-off hypothesis describes cases where multiple modalities are used to increase the ability of the signal being received, but each component addresses a different environmental obstacle (Hebets & Papaj, 2005). For example, male Bornean rock frogs (*Staurois parvus*) adjust their vocalizations to overcome audible environmental noise for long-range attention-grabbing, then follow up with a bodily visual display, like foot flagging or flashing, to provide conspecifics with their specific location and further individual information (Grafe et al., 2012).

Both of the above approaches assume that the components in a multimodal signal are independent of one another, which as Hebets and Papaj (2005) described, is not always the case. Inter-signal interaction can occur and forms its own category of hypotheses within efficacy-based research. This includes the multitasking hypothesis, increased detection and discrimination by way of amplification or altering, context/increased understanding, emergence/novelty, increased learning and memory, and finally increased deception (Hebets & Papaj, 2005). Each of these examines instances wherein at least one component of a signal, or one particular signal in a complex display, interacts in some way with the other in either a positive or constraining way (Hebets & Papaj, 2005).

The current investigation will not be investigating the above hypotheses directly. Instead, this study will involve a more straightforward examination, as best as can be done with this inherently complex topic, to examine the potential social and biological influences on multimodal communication and signal composition in ring-tailed lemurs.

2.6 Statement of Thesis

The aim of this thesis is to investigate the use-frequencies of four different sensory modes (auditory, visual, tactile, and olfactory), and multimodal combinations of those, in the social communication of a population of captive ring-tailed lemurs (*Lemur catta*). Both biological (age and sex) and social (troop affiliation and rank) factors will be considered in the analysis of these use-frequencies to better understand the common patterns or diverging trends observed. By approaching this investigation using a stable captive population, a number of variables are controlled for, which improves the consistency of the troops examined: troop composition and make-up, location, and food availability. This investigation represents a novel examination of primate social communication in a single species using a multimodal approach, and is intended to provide a general baseline from which further research on this topic can be conducted.

Chapter 3

3 Methods

In this chapter I will present the methods used in data collection and analysis, including a review of the ethogram used and definitions for terminology.

3.1 Data Collection

Data were collected over four consecutive months from May first to the end of August 2019, in Durham, North Carolina, at the Duke Lemur Center (DLC) for a total of 85 research days. No ethics protocol approval was required from the DLC for this observational research as it was non-invasive. Data collection was focused on the three larger troops of outdoor free-ranging *L. catta* at the DLC, two of the troops numbering four and the other numbering six individuals. From these three troops, four males and ten females were observed, ranging in age from three to 28 years old and totalling 14 individuals (Table 1). Troop compositions remained stable throughout the course of the four-month observation period. Continuous focal-animal sampling was used to collect frequency of occurrence data. This method of data collection is commonly used in primatology, and entails following a specific individual within the focal troop during each observation session and recording all occurrences of the behaviour of interest that occur within the sampling period (Altmann, 1974). Observations of focal individuals were conducted on a shifting schedule to spread sampling across individuals and study groups as equally as possible. For this study, the behaviours of interest are all the social signals a focal individual makes using one or more components from the four main sensory channels: auditory, visual, tactile, and olfactory.

	Troop 1: Sprite’s Troop Natural Habitat Enclosure 9		Troop 2: Sophia’s Troop Natural Habitat Enclosure 2		Troop 3: Liesl’s Troop Natural Habitat Enclosure 4	
	Individuals	Ages	Individuals	Ages	Individuals	Ages
Total	4		4		6	
Females	2	18 & 5	3	14, 3 & 3	5	27, 11, 7, 3, & 3
Males	2	7 & 7	1	13	1	28

Table 1: Subject demographic data, organized by troop. Adapted from “DLC Animal List BY SPECIES, January 2019” (N = 25, n = 14). See Appendix B for family trees.

To collect frequency data on mode use, simple tallies of each communicative event performed by the focal individual during a sampling period were recorded (Table 2). Research days were divided into “morning” and “afternoon” sampling periods of three hours each, for a total of six hours of observations per day (Table 3). This allowed me to alternate between focal individuals every day to collect data from both “morning” and “afternoon” contexts for each individual, and to control for behaviour and activity levels that may vary between these two time periods. An approximate total of six research “days”, defined by one morning and one afternoon observation period, was achieved for all 14 individuals (Table 3). Of the total 14 individuals used in this study, six were missing one observation period, either “morning” or “afternoon”, due to changes in the recording medium used after the first three days of observational work. These first three days in the field represent a refinement phase of my data collection, since I was unfamiliar with ring-tailed lemur behaviour prior to the start of this project.

<table>
<tr><th colspan="9">Sprite (Dominant Female NHE9, age 18, mother to Jones and LuLu in troop)</th></tr>
<tr><th>Date</th><th>Weather</th><th>Time</th><th>Auditory</th><th>Visual</th><th>Tactile</th><th>Olfactory</th><th>Comments</th><th>Modal Code</th></tr>
<tr><td rowspan="10">May 20</td><td rowspan="10">mostly cloud, some broken w sunlight, high of 31°C; afternoon = partly cloudy, mostly just a few white puffy clouds</td><td>13:07</td><td></td><td>2</td><td>1</td><td></td><td>walks over to LuLu tail up, grooms</td><td>VT</td></tr>
<tr><td>13:09</td><td>1</td><td>1</td><td></td><td></td><td>clicking walks to LuLu tail up and takes her spot</td><td>AV</td></tr>
<tr><td>13:11</td><td></td><td>1</td><td>1</td><td></td><td>nose licks with LuLu who approaches</td><td>VT</td></tr>
<tr><td>13:12</td><td></td><td>1</td><td>1</td><td></td><td>leans back into LuLu for grooming (is groomed)</td><td>VT</td></tr>
<tr><td>13:13</td><td></td><td>1</td><td>1</td><td></td><td>leans back and away for nap, but feet touching LuLu still</td><td>VT</td></tr>
<tr><td>13:17</td><td></td><td>1</td><td></td><td></td><td>Sits up when LuLu moves</td><td>V</td></tr>
<tr><td>14:02</td><td></td><td>1</td><td>1</td><td></td><td>let's LuLu close again, LuLu grooms her</td><td>VT</td></tr>
<tr><td>14:08</td><td></td><td>1</td><td>1</td><td></td><td>let's LuLu close again, LuLu grooms her</td><td>VT</td></tr>
<tr><td>14:20</td><td></td><td></td><td>1</td><td></td><td>grooms LuLu, others napping including LuLu</td><td>T</td></tr>
<tr><td>…</td><td>…</td><td>…</td><td>…</td><td>…</td><td>…</td><td>…</td></tr>
<tr><td colspan="3" rowspan="2">Occurrence Totals</td><td>321</td><td>807</td><td>250</td><td>34</td><td colspan="2" rowspan="2"></td></tr>
<tr><td colspan="4">1412</td></tr>
</table>

Table 2: Sample of table used for data collection and tracking. Information specific to the individual was recorded at the top, then the date of observation, and the weather conditions for both morning and afternoon observation periods. Communicative events were time stamped and anecdotal comments were left to keep track of and explain what was observed. Tallies for each mode were converted to numerical values in post, as were the modal codes for each signal.

LuLu	Afternoon	Morning	Afternoon	Morning	Afternoon	Morning	Afternoon	Morning	Afternoon	Morning	Afternoon	Morning	
Stewart	Morning	Afternoon	Afternoon	Afternoon	Morning	Morning	Morning	Afternoon	Afternoon	Afternoon	Morning	Morning	
Jones	Afternoon	Morning	Morning	Morning	Afternoon	Afternoon	Afternoon	Morning	Morning	Morning	Afternoon	Afternoon	
Sprite	Morning	Afternoon	Morning	Afternoon	Morning	Afternoon	Morning	Afternoon	Morning	Afternoon	Morning	Afternoon	
Narcissa	Afternoon	Morning	Morning	Afternoon	Morning	Afternoon	Afternoon	Morning	Afternoon	Morning	Morning	Afternoon	
Nemesis	Afternoon	Morning	Afternoon		Morning	Morning	Afternoon	Morning	Morning	Afternoon	Morning	Afternoon	Afternoon
Randy	Morning	Afternoon	Morning	Morning	Afternoon	Afternoon	Morning	Afternoon	Morning	Afternoon	Afternoon	Morning	
Sophia	Morning	Afternoon	Afternoon		Afternoon	Morning	Morning	Afternoon	Afternoon	Morning	Afternoon	Morning	Morning
Griselda	Afternoon	Morning	Afternoon	Afternoon	Morning	Afternoon	Afternoon	Morning	Afternoon	Morning	Morning	Morning	
Hedwig	Afternoon	Morning	Afternoon	Afternoon	Morning	Afternoon	Morning	Afternoon x2	Morning	Morning	N/A	Morning	
Gretl	Morning	Afternoon	Morning	Morning	Afternoon	Morning	Afternoon	Morning	Afternoon	Afternoon	Afternoon	Morning	
Liesl	Afternoon	Morning	Afternoon	Morning	Afternoon	Morning	Morning	Afternoon	Morning	Afternoon	Morning	Afternoon	
Shroeder	Morning	Afternoon	Morning	Morning	Afternoon	Morning	Afternoon	Morning	Afternoon	Afternoon	Afternoon	Afternoon	
Aracus	Morning	Afternoon	Morning	Afternoon	Morning	Afternoon	Morning	N/A	Morn. & Aft.	Morning	Afternoon	Afternoon	
	Wed. May 1 — Thurs. May 9 **CYCLE 1**	Fri. May 10 — Mon. May 20 **CYCLE 2**	Tues. May 21 — Thurs. May 30 **CYCLE 3**	Fri. May 31 — Mon. June 10 **CYCLE 4**	Tues. June 11 — Wed. June 19 **CYCLE 5**	Thurs. June 20 — Fri. June 28 **CYCLE 6**	Mon. July 1 — Wed. July 10 **CYCLE 7**	Thurs. July 11 — Fri. July 19 **CYCLE 8**	Mon. July 22 — Tues. July 30 **CYCLE 9**	Wed. July 31 — Thurs. Aug. 8 **CYCLE 10**	Fri. Aug. 9 — Mon. Aug. 19 **CYCLE 11**	Tues. Aug. 20 — Wed. Aug. 28 **CYCLE 12**	**Buffer (Aug. 29 & 30)**

Table 3: The track record for "morning" and "afternoon" sampling periods. Diagonal shading indicates the individuals who are missing one observation period, due to a change in recording medium that occurred after the first few days of observations. Dark grey boxes in the centre identify two individuals whose original observation time was rescheduled to later in the summer. Light grey boxes in the centre indicate where individuals were recorded for twice within the 7-day cycle of observations.

The DLC holds regular research hours from 8:30 AM - 4:30 PM Monday through Friday, excluding holidays, of which there were two during the summer. To allow for some flexibility in data collection duration, I collected data roughly from 9:00 AM until 12:00 PM and then again in the afternoon from 1:00 until 4:00 PM, for an approximate total of six hours of observations and data collection per day. Tallied field data were recorded and combined with individual life history information, including rank, sex, age, and familial relation relative to the other individuals within the same enclosure and to the captive population sampled (n=14). With this information, I was able to determine whether individual *L. catta* display unique preferences for certain modes over others, and whether their social position is an influencing factor in this preference, or if there is a general use of all modes and combinations equally across individuals and groups.

3.2 Ethogram & Definitions

For the purposes of this project, a communicative signal is delineated broadly by a change in the state of an individual either within or outside the visual field of another individual of the same species while using at least one sensory mode of communication. This encompasses changing from a stationary position to an active state or from being active to stationary, including pauses that last longer than three seconds. This time element is based on the first few days of observation, where it was observed that pauses lasting longer than three seconds more often resulted in a change to the individual's state (i.e. a new signal), but a pause three seconds or shorter more often resulted in a continuation of the activity which preceded the pause. All behaviours were recorded as one compound signal until a change of state occurred, or a pause lasting longer than three seconds, which then delineated a new signal. This then includes both simultaneous and sequential mode uses within a single communicative signal, which was important to include for an individual signalling while in motion. All signals were only recorded if performed, initiated, or permitted by the focal individual, the latter in the case where another individual was acting toward the focal individual. While the lemurs at the DLC do free-range with other species of lemur, observations were restricted to *L. catta* behaviours and intra-species interactions.

Multimodality as operationalized in this project follows that used in behavioural ecology (*see* Fröhlich et al., 2019), where “mode” (modality) is defined as the sensory channel used to perceive a signal (auditory, visual, tactile, or olfactory), and multimodal describes the use of more than one component, each from different sensory modes, performed simultaneously or sequentially as a single communicative signal. A component is defined as the individual action performed to send a signal or one which is produced as a result of another communicative action. For example, an individual vocalization is one component of a signal while any visual element linked to that vocalization, like a head tilt, or another action occurring simultaneously or immediately after that vocalization, like walking or tail waving, would be another component of the same signal. Since both of these components occupy different sensory modalities (auditory and visual respectively), this would be classified as a multimodal signal. Rapid and repeated use of a particular signal or signal component was recorded as a single continuous event. Examples of repeated components includes grooming bouts, for which durations were estimated, rapid vocalizations that were repeated like “clicking/click”s or “wakwak”s, and walking or otherwise moving through the enclosure.

Fröhlich et al. (2019) make the distinction between multimodal signals and multimodal signal combinations. The former consists of two or more components from different sensory channels that are “fixed” or obligatorily coupled (Fröhlich et al., 2019; Partan & Marler, 2005), like head tilting or facial changes while vocalizing. Multimodal signal combinations, then, have two or more components from different sensory channels that are more flexibly coupled or “free”, and can be performed independent of the others (Fröhlich et al., 2019; Partan & Marler, 2005). This distinction, as well as that between multimodal and “complex” signals, was not made in the current study to reduce analytical complexity while observing this particular species of primate.

L. catta behaviours were classified based on the sensory channel (mode) with which they are associated, which was then used to collect data and to code for modal frequencies. Only social actions, defined here as either those occurring in proximity of or directly involving another individual, as best as could be determined during the observation period, were counted toward scoring for this project. For example, individual grooming (i.e. autogrooming) was not recorded, but grooming of another individual (i.e. allogrooming) was recorded since it represents a form of tactile communication.

Auditory signals were coded when I heard any vocalization, oral or nasal, within the *L. catta* repertoire. These included moans (quiet or squeaky), squeals, howls, hmms, and click grunts (Bolt, 2013a; Bolt, 2013b; Bolt & Tennenhouse, 2017; Gamba et al., 2017) as well as grooming "purr"s and two alarm calls: "wakwak"s and the aerial warning call.

Visual signals were coded more broadly as any action occurring within the visual field of a conspecific as estimated by my own line of sight. This included general physical proximity of the focal individual to conspecifics (moving closer to or further away from), and more distinctive actions like tail waving/flicking ("stink fights" – *see* Jolly, 1966a: 103), raised tail during locomotion, agonistic signals (lunging, chasing, swiping, pushing, pulling, threat stares), and facial expression (such as the relaxed, open-mouth "play-face" – *see* Darwin, 1872; Fagen, 1981; Kappeler, 1998; Nakamichi & Koyama, 1997; Palagi et al., 2014; Walker-Bolton & Parga, 2017). Visual signals that overlapped with other categories were also tracked, such as those involving physical contact (agnostic or affiliative), scent/olfactory signals, and vocalizations that required head or facial movement to form the sound (i.e. moans and alarm calls).

Tactile signals were predominantly observed in play, fighting or otherwise aggressive acts (cuffing, grabbing, biting), allogrooming, or greeting conspecifics (licking and touching another's muzzle) (Collins et al., 2017; Nakamichi & Koyama, 1997). Also tracked as tactile signals were individuals sitting against another or brushing past others while navigating through their enclosure.

Olfactory signals were described as the action of an individual male or female pressing their anogenital region to a substrate, or of a male rubbing his antebrachial wrist spurs or brachial scent glands (upper arm) on his own tail or a substrate (Kappeler, 1998; Palagi, Telara & Tarli, 2004; Walker-Bolton & Parga, 2017). As such, this signal type included the glandular scent marking behaviours of both males and females, as well as "stink fighting" and "stink flirting" (*see* Jolly, 1966a: 103; Walker-Bolton & Parga, 2017) which are uniquely used by male *L. catta* to either compete with rival males or attract females, respectively. More subtle olfactory signals and urine marking were not included (Drea et al., 2013; Drea, Goodwin, & delBarco-Trillo, 2019; Palagi & Norscia, 2009).

3.3 Data Analysis

The data collected through focal-animal sampling are of a longitudinal nature, defined as data collected separately from the same individual at different points in time (Muth et al., 2016). This also means that, contrary to the assumptions of many common parametric statistical methods of analysis, the data points produced through focal-animal sampling will not be independent because they will be repeated samples from the same individuals. Pseudoreplication and data aggregation are two of the major errors that can occur in longitudinal data analyses (Pollet et al., 2015). The former is the artificial inflation of a sample by assuming independence in the data, and the latter occurs when the averages from individuals are used to inform population patterns (Pollet et al., 2015). In addition, there is unevenness in the total amount of data collected for each individual. While regulated sampling periods were employed, the focal individuals have different activity levels and patterns throughout the day, across the four-month period of this study, and especially when compared to other conspecifics. In order to address and account for these challenges in the structure of the data, raw tallies were divided by the total tallies recorded (all occurrences together) to establish a proportion of the total that was represented by components from each mode. This was done to ensure each mode-proportion could be compared between individuals, regardless of variation in individual activity pattern or limitations to observer recording due to weather conditions.

Initial data analysis was conducted in Numbers© (version 6.1) to produce the proportion of each mode used by an individual. This proportion was calculated by taking the total occurrence of a particular mode and dividing it by the total occurrence of all modes, thereby producing a mode-proportion of their total mode-use for each mode. Proportional data were normalized to total 100% per individual when represented in pie charts for ease of visualization. The data were then collated into different groupings, described below, to assess the potential impacts troop affiliation, age, rank, and sex had on mode-use proportions. Further analysis was conducted in RStudio© (version 1.2.1335) to investigate the statistical significance of results using MANOVAs (multivariate analysis of variance), two-way ANOVAs (analysis of variance), and one-factor ANOVAs (where each mode proportion was a "factor") where applicable. As the first study of multimodal communication in *L. catta* and that describing signal components in both their unimodal and multimodal signals, this analysis represents a novel approach to this type of investigation.

The modal proportion data for all 14 individuals were then examined together in a cluster analysis and visualized in a dendrogram using base graphics in RStudio$^{©}$. This final processing of the data examined the strength of the groupings broadly used throughout this project, as will be described below, by visualizing which individuals had the most similar component proportions. Average linkage clusters were used, which bases clusters and their distance from others on the mean of the dissimilarity between it and the other clusters.

3.3.1 Variables

To analyze the effect of troop affiliation on communicative mode, each individual was grouped together with the members of their troop for a total of three groups, and their data were then compared to the other two troops in RStudio$^{©}$. The analysis of age as a factor in mode use was conducted first in Numbers$^{©}$ then in RStudio$^{©}$. Individuals were clustered into age cohorts of approximately the same sample size, resulting in four groups: age 3 (n=4), age 5 to 7 (n=4), age 11 to 14 (n=3), and age 18 or over (n=3). Signal component proportions for each individual were then combined to produce the average mode use per age cohort, which was then compared in Numbers$^{©}$. Additional analysis in RStudio$^{©}$ used each individual's component proportions to better examine the distribution of data points within each cohort. This allowed me to test for statistically significant differences between age cohorts and corroborate the findings from the Numbers$^{©}$ analysis.

To determine whether dominance rank was a factor in mode-use proportions, individuals were designated a number based on intra-troop rank as determined by personal observation and conversations with keepers at the DLC: "1" being dominant female (n=3), “2” the second ranked female (n=3), “3” the remaining subordinate female(s) (n=4), and finally “4” for all males (n=4). Four rank groupings were chosen to distinguish the dominant female and the next highest rank female from others because these two positions hold the highest social influence in the troop. The remaining females were grouped together, since the observable differences between their ranking positions were more subtle. Finally, males were clustered together since a total of only four males were observed in this study and only one troop had two males. While this latter case did result in a male hierarchy at some level, it was not enough so to justify making a fifth grouping for one individual. To analyze sex as a potential factor, individuals were grouped into two categories: male or female. Results for both of the above factors were visualized and analyzed independently in Numbers$^{©}$ and RStudio$^{©}$.

Further analysis was conducted using both Numbers$^{©}$ and RStudio$^{©}$ to examine the potential correlation between rank and sex together for each individual and their respective signal component proportions. This analysis was conducted as a result of the close relationship between sex and dominance rank in *L. catta*. Three groupings were used in this analysis: dominant females (n=3), subordinate females (n=7), and males (n=4). Only the dominant females’ high-ranking position was recognized, all other females were pooled together, and males remained pooled together.

3.3.2 MANOVAs

MANOVA was conducted using the program RStudio$^{©}$ to establish the variance in the distribution of communicative mode proportions across all three troops based on troop affiliation, age, rank, sex, and rank and sex together. MANOVA allows for more complex analyses of variance where there is more than one dependent, and even for more than one independent, factor by creating a matrix of the data provided. For this study, each factor (troop affiliation, age, rank, sex, and rank and sex together) was compared in separate analyses with individuals’ mode proportions. A simple one-factor ANOVA can be used as a *post-hoc* analysis of the factors in a MANOVA to determine which of those were contributing to a statistically significant finding and which were not.

For troop affiliation, all three troops were analyzed together to examine inter-troop differences in mode-use proportions. For age, all three troops were again analyzed together to examining differences between age cohorts. For rank, all three troops were first analyzed together, then comparatively in groups of two to assess contrasts within and between each troop (Table 1). For both sex, and rank and sex together, each grouping (male-female, or male-female-dominant female) was analyzed relative to each of the four communicative modes (auditory, visual, tactile, olfactory). Follow-up or *post hoc* analysis was conducted using one-factor ANOVA to establish significance for each individual variable (i.e. the four sensory modes) analyzed per MANOVA test. Additional two-way ANOVAs were run to examine the relation between rank and mode-use within each troop individually. When MANOVAs were attempted for this particular factor (within troop ranking) results were inconclusive as a result of the small sample size. The results for the above analyses were then visualized using either bar-graphs or boxplots created through the package *ggplot2* in RStudio©.

3.3.3 Multimodal Analysis

Multimodal analysis was first conducted in Numbers© for six of the total 14 focal individuals, the three dominant females and three lowest ranked males, totalling two individuals from each troop. Each observed signal for these six individuals was converted to a letter code, where the occurrence of each mode within that signal corresponded to a letter and any combination of the modes under investigation would be represented by subsequent combinations of letters: A for auditory, V for visual, T for tactile, and O for olfactory signal involvement (Table 2). The order of the letters in a combination was not weighted for the purposes of this investigation. Complex signals, which are those composed of more than one component occupying the same sensory channel, were not explored in this analysis. The total number of letter codes, whether multimodal or unimodal, was taken as the total number of communicative signals made by an individual over the course of the observation period. The total number of multimodal signals was calculated as the sum of the number of bimodal (consisting of two sensory modes), trimodal (consisting of three modes), and tetramodal (consisting of all four modes) letter codes for an individual. The total number of multimodal signals was then subtracted from the total number of signals to obtain the total number of unimodal signals (consisting of one mode alone) for that individual. The values for unimodal and multimodal signals were then expressed as a proportion of an individual's total signals for each of the six focal individuals. Proportional data were normalized to total 100% when represented in pie charts. This comparison of the proportion of signal types, unimodal or multimodal, for each of the focal individuals was then further examined in RStudio© using MANOVA. The data for this analysis were grouped by dominant females (n=3) and males (n=3), and visualized in boxplots using the package *ggplot2*.

The sensory component compositions of an individual's unimodal and multimodal signals were then examined using Numbers© and RStudio©. This was done to address how much of each signal type was represented by signals containing a particular sensory component (auditory, visual, tactile, or olfactory) for the examined males (n=3) and dominant females (n=3). When analyzed in RStudio©, the data were again grouped into two sets, dominant females (n=3) and males (n=3), and visualized in boxplots using the package *ggplot2*.

The proportion of multimodal signals that was composed of bimodal, trimodal, and tetramodal signals was also examined for each individual in Numbers©. As a result of the majority of multimodal signals being bimodal for each individual, this signal type was singled out for further analysis in RStudio©. Attempts to run the bimodal composition data through a MANOVA returned results that were inconclusive, so a cluster analysis was run to produce a visualization of any potential relationships between individuals, again using average linkage clusters.

Chapter 4

4 Results

The goals of this chapter are to present the results for the various stages of analysis on these data. I begin with an overview of the results for the initial analysis of the dataset, then present results on each social and biological factor examined: troop affiliation, age, dominance rank, sex of the individual, and finally dominance rank and sex together. The analysis of multimodal signals follows and presents the results for composition and comparative analyses.

4.1 Initial Data

To establish modal proportions for each individual, and accommodate natural variation in activity patterns, the total occurrence of a particular mode (auditory, visual, tactile, or olfactory) was divided by the total number of mode occurrences as represented by the total tallies for an individual. As mentioned previously, this produced the percentage of the total mode occurrence for an individual that was represented by a particular mode. These proportional data were then normalized to total 100% per individual when represented in pie charts for ease of visualization. This unimodal processing of these data allowed for further comparison between individuals within the same troop and across the three different troops observed, despite variation in the total number of signals and total occurrence of modes. For example, due to changes in the recording medium used after the first three days of observational work six of the total 14 individuals used in this study are missing one observation period, either “morning” or “afternoon”.

4.1.1 Signal Analysis: Baseline

Troop 1 (Sprite’s troop, n=4; Appendix B figure B1) consisting of two females and two males was the first troop analyzed. Results were visualized using pie charts to better express any trends between individuals, since proportions were being used (Figure 7). The dominant female, Sprite, showed a predominance for the use of visual modes of communication (57%), followed by auditory (23%) and tactile (18%), with olfactory only representative of 2% of the modes she employed. A similar pattern is seen in the next highest ranked individual, LuLu, with visual modes accounting for 50% of her modes used, auditory at 33%, and tactile and olfactory modes falling behind at 16% and 1% respectively. The trend then shifts when examined in the two lowest ranked individuals, males Jones and Stewart. Jones shows almost an even proportion in the use of visual (46%) and auditory (42%) modes, with tactile (9%) and olfactory (4%) again taking up smaller proportions. Finally, Stewart shows a slight shift towards increased occurrence and use of auditory (46%) modes, rather than visual (41%), though tactile and olfactory again show relatively less frequent use (11% and 2% respectively).

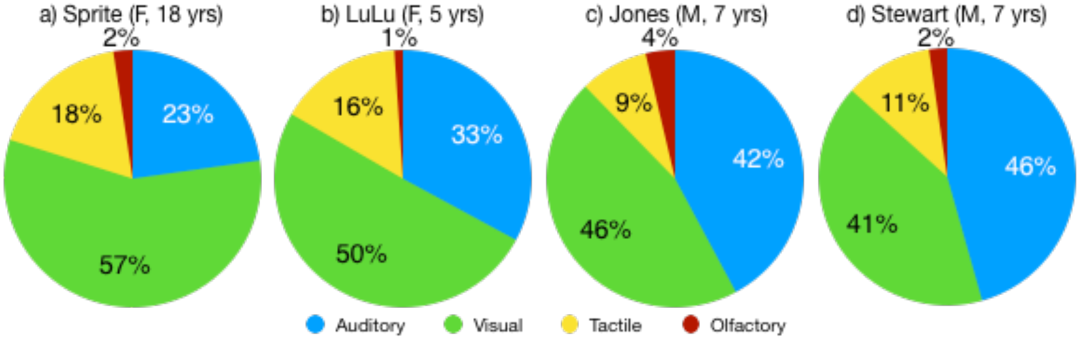

Figure 7: Mode-use proportions for individuals in troop 1 (n=4), where F = female, M = male, and age of the individual is given as the number in each parenthesis. Individuals are presented in ranking order from left to right, starting with the dominant female (a) to the two lowest ranking individuals (c) and (d), which are both males. See Appendix C table 1 for further numerical detail.

Troop 2 (Sophia's troop, n=4; Appendix B figure B2) consisted of three females and one male, and free-ranged in the enclosure directly adjacent to troop 3. Analysis for troop 2 followed the same progression as for troop 1 (Figure 8). However, the results differed substantially, with the only exception being the consistently lower relative proportions of tactile and olfactory mode use. In contrast to troop 1, all four individuals in troop 2 show approximately the same proportional use of each of the four modes examined despite differences in age, sex, and rank. For dominant female Sophia, visual (47%) occurrences were still slightly higher than auditory (40%), which were almost the same in both of the next highest ranked individuals, twins Nemesis (48% and 40% respectively) and Narcissa (50% and 38% respectively). The lowest ranked individual in this troop, male Randy, shows similar proportions still for visual (42%) and auditory (43%) modes. It is interesting to note all four individuals also show about the same proportion of tactile (either 10% or 11%) and olfactory mode use (2%), with the exception of Randy for the latter (4%).

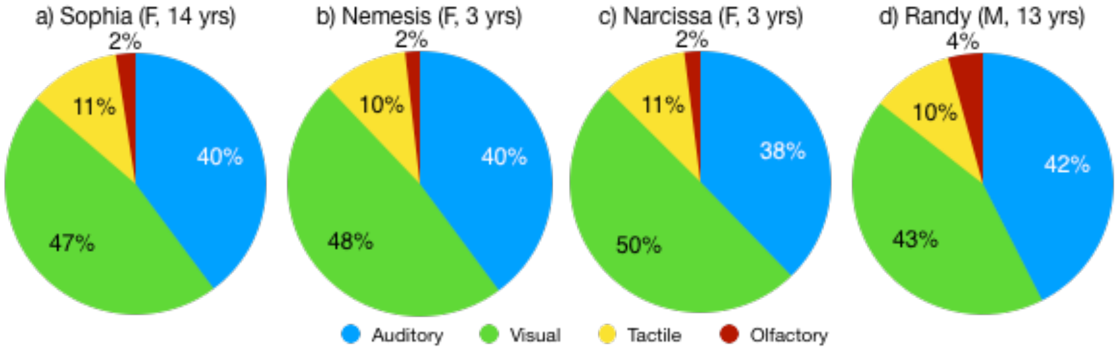

Figure 8: Mode-use proportions for individuals in troop 2 (n=4), where F = female, M = male, and age of the individual is given as the number in each parenthesis. Individuals are presented in ranking order from left to right, starting with the dominant female (a) to the lowest ranking individual (d), which is male. See Appendix C table 2 for further numerical detail.

Troop 3 (Liesl's troop, n=6; Appendix B figure 3) consisted of five females and one male, and free-ranged in the enclosure directly adjacent to troop 2. Analysis for troop 3 again followed the same progression as for troops 1 and 2, and showed a pattern more similar to that seen in troop 1 (Figure 9). The dominant female, Liesl, showed a higher proportional use of visual modes (59%) than auditory (25%), with tactile (10%) and olfactory (6%) again showing lower percentages. The next highest rank, Griselda, showed a uniquely high percentage of auditory mode use (47%) relative to the other individuals studied. Visual modes (44%) represented the next highest mode used, with tactile (8%) and olfactory (1%) lowest. The next three individuals in rank, Hedwig and Gretl, and Liesl's dam, Shroeder, showed very similar mode proportions to each other despite differences in their ages and ranks. For these three, auditory mode use remained fairly high at 53%, 60%, and 52% respectively. Auditory modes represented the next most frequent mode used at 33%, 29%, and 34% respectively. Consistent with the previous individuals examined, tactile (12%, 9%, and 13% respectively) and olfactory

(2%, 2%, and 0.3% respectively) modes represented the lowest proportions. Finally, the lowest ranked individual, male Aracus, demonstrated a higher visual mode (46%) proportion than auditory (39%), but also had the highest proportion of olfactory mode use (12%) and lowest tactile mode use (4%) of all examined individuals.

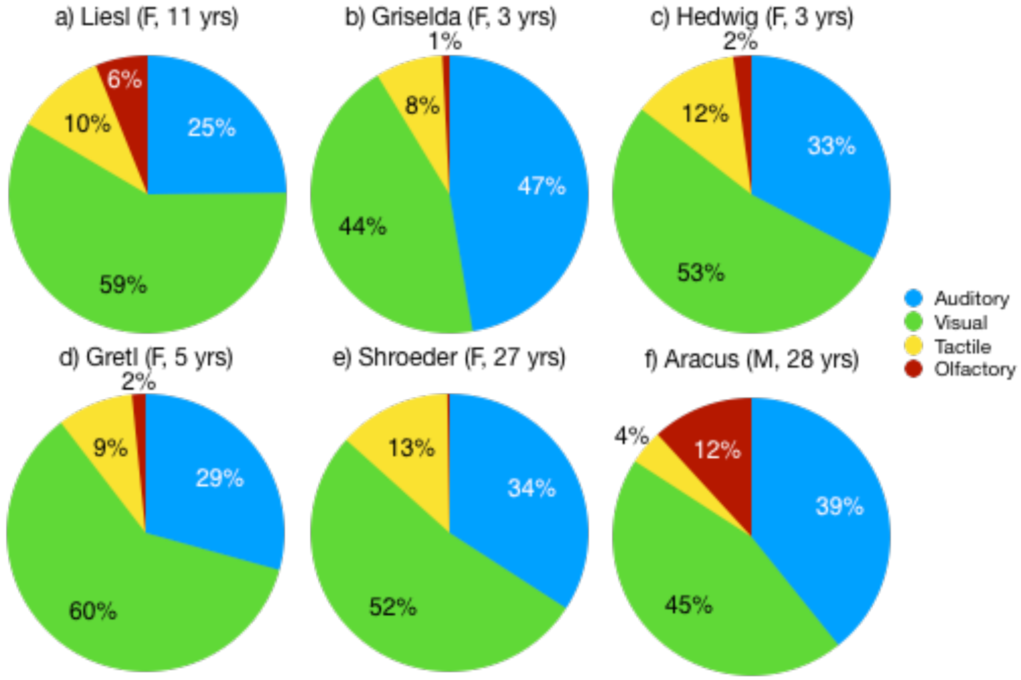

Figure 9: Mode-use proportions for individuals in troop 3 (n=6), where F = female, M = male, and age of the individual is given as the number in each parenthesis. Individuals are presented in ranking order from left to right, starting with the dominant female (a) to the lowest ranking individual (f), which is male. See Appendix C table 3 for further numerical detail.

4.2 Troop Affiliation

To address whether troop affiliation influenced mode component proportions, a MANOVA (multivariate analysis of variance) was conducted to analyze whether statistically significant differences were present in the distribution of mode proportions across and between all three troops. The result of that analysis returned no statistically significant differences in the proportions of modes used between the three troops, though the range of proportions within each troop did vary (Figure 10).

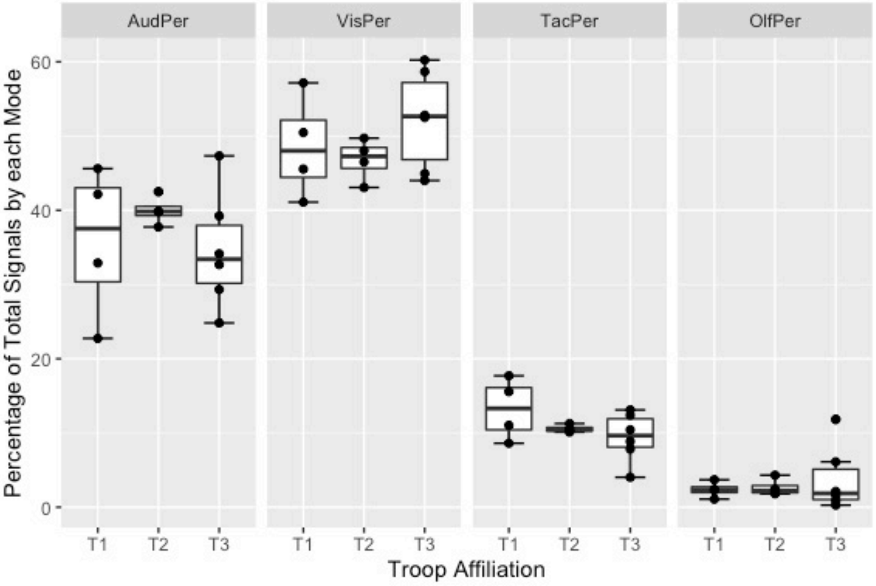

Figure 10: Boxplot depicting the variation in distribution of mode component proportions between each troop. Where T1 is troop 1 (n=4), T2 is troop 2 (n=4), and T3 is troop 3 (n=6). "AudPer", "VisPer", TacPer", and "OlfPer" designate the communicative mode proportion being compared, corresponding to "auditory", visual", "tactile", and "olfactory" respectively. The line between either hinge represents the median, the upper hinge the upper quartile, and the lower hinge the lower quartile. Whiskers depict the highest and lowest value, and dots outside the boxes representing outliers. Data points have been displayed to show the distribution of values within each box. See Appendix D for additional numerical detail.

4.3 Age of Individual

To examine whether age was a factor influencing mode component use frequencies, each individual was clustered into age cohorts of approximately the same sample size, resulting in four groups: age 3 (n=4), age 5 to 7 (n=4), age 11 to 14 (n=3), and age 18 or over (n=3). The bar graphs depicting each mode (Figure 11) suggest no significant correlative trends between the age of an individual and the average proportion of modes used for an age cohort, with auditory components as a possible exception, for this population. Additional analysis testing for potential significant differences provided a visualization of the distribution of data points within each age cohort and corroborated the above finding of no supporting data for age influencing communicative mode use across all four sensory modes examined (Figure 12).

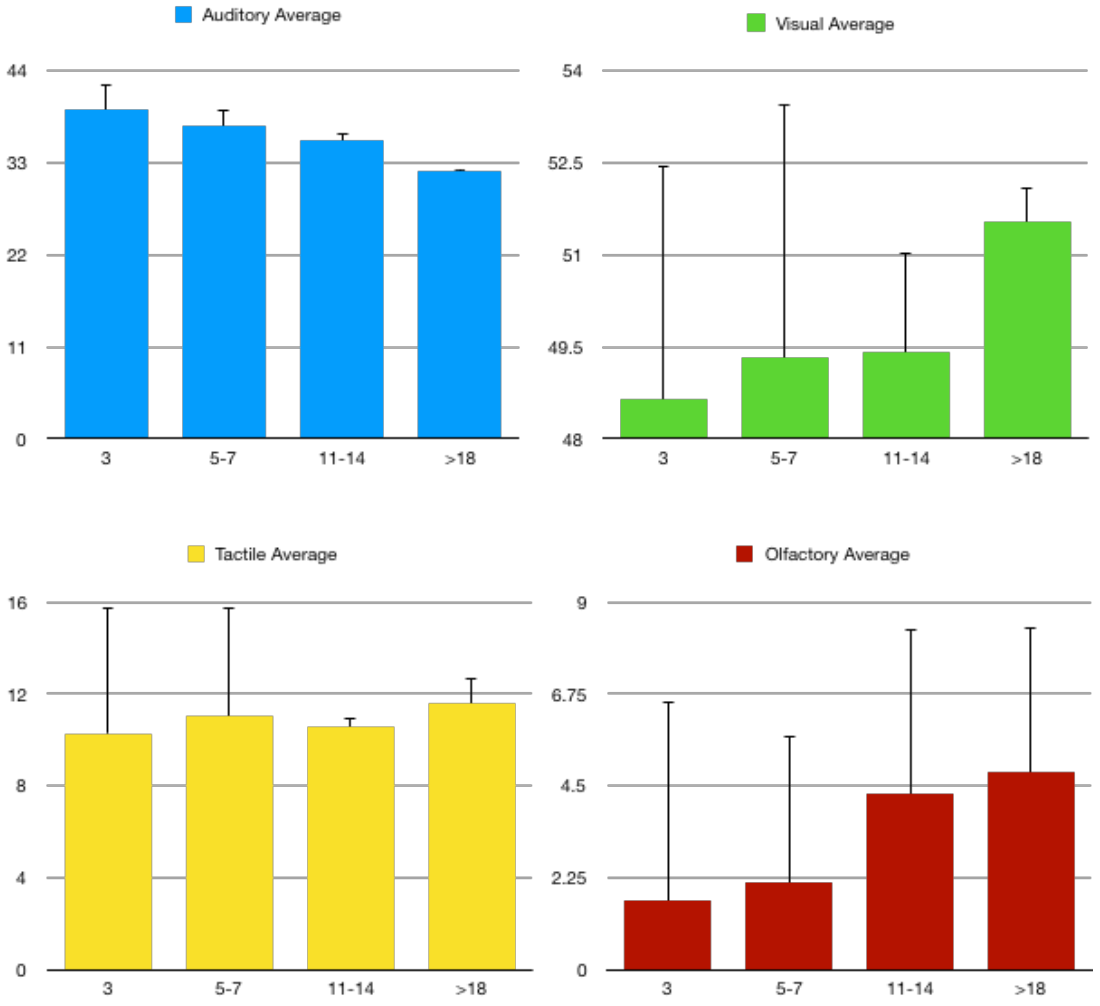

Figure 11: Bar graphs depicting the relationship between age of all focal individual (n=14) and the average relative mode component proportions for their age cohort. See Appendix E tables E1-E4 for additional numerical detail.

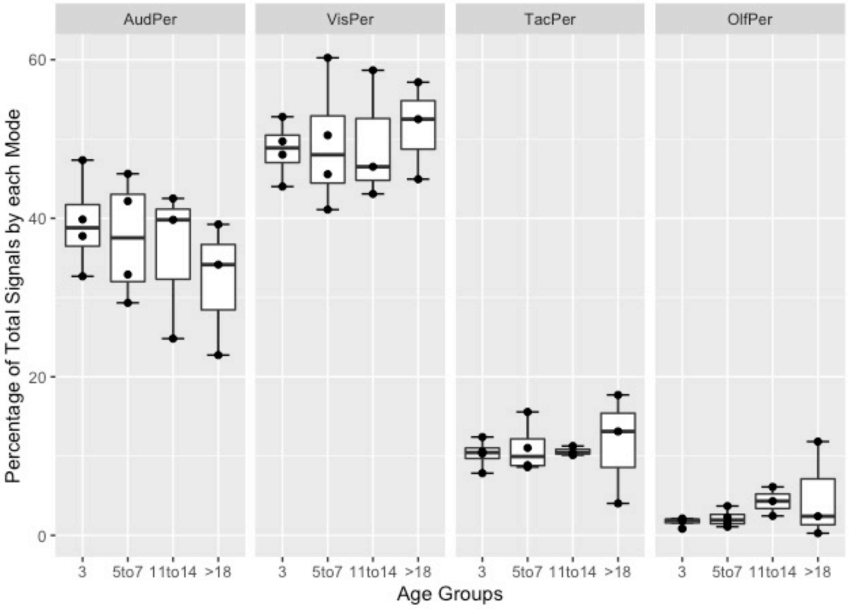

Figure 12: Boxplot depicting variation in distribution of mode component proportions between each age cohort: age 3 (n=4), age 5to7 (n=4), age 11to14 (n=3), and >18 (n=3). Where "AudPer", "VisPer", TacPer", and "OlfPer" designate the communicative mode proportion being compared, corresponding to "auditory", visual", "tactile", and "olfactory" respectively. The line between either hinge represents the median, the upper hinge the upper quartile, and the lower hinge the lower quartile. Whiskers depict the highest and lowest value. Data points have been displayed to show the distribution of values within each box. See Appendix E tables E5-E6.

4.4 Dominance Rank

Dominance rank was examined in three different ways for this dataset: across all three troops together, between paired troops, and within each individual troop to determine where any patterns may lie.

4.4.1 Across Three Troops

First, a MANOVA was used to examine the variance in distribution of mode component proportions by rank (1 being highest rank, 4 being lowest) across all three troops combined (Figure 13). The MANOVA returned results that were not statistically significant for this dataset as a whole (12 and 27 degrees of freedom, Pr(>F) = 0.1597). A *post hoc* one-factor ANOVA (analysis of variance) was used to compare each individual mode proportion, and showed significant differences for auditory (3 and 10 degrees of freedom, Pr(>F) = 0.04892) and visual percentages (3 and 10 degrees of freedom, Pr(>F) = 0.01983), but not for tactile (3 and 10 degrees of freedom, Pr(>F) = 0.3306) or olfactory (3 and 10 degrees of freedom, Pr(>F) = 0.1446) percentages.

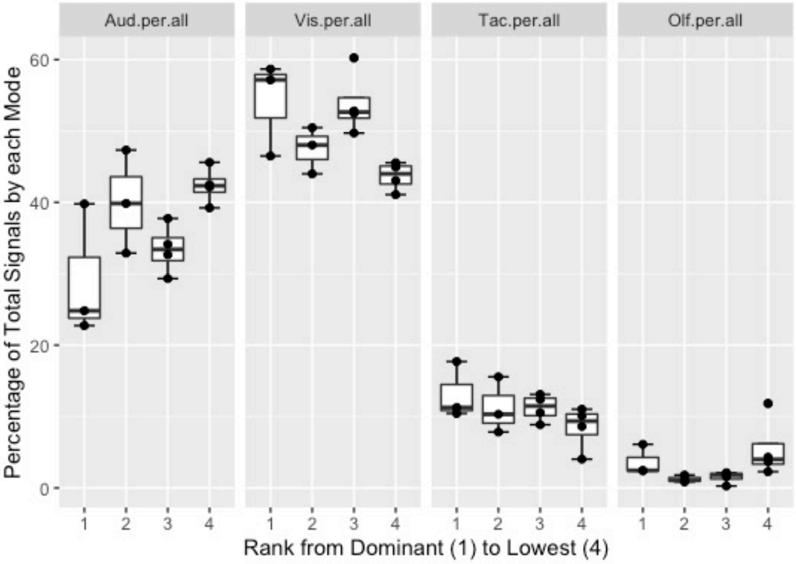

Figure 13: Boxplot depicting variance in the distribution of mode component proportions by rank across all three troops together. Where 1(n=3) denotes the highest rank and dominant female, 2 (n=3) the next highest, 3 (n=4) the remaining subordinate females, and 4 (n=4) the males as the lowest ranking individuals. "Aud.per.all", "Vis.per.all", Tac.per.all", and "Olf.per.all" designate the communicative mode proportion being compared, corresponding to "auditory", visual", "tactile", and "olfactory" respectively. The line between either hinge represents the median, the upper hinge the upper quartile and the lower hinge the lower quartile. Whiskers depict the highest and lowest value, and dots outside the boxes representing outliers. Data points have been displayed to show the distribution of values within each box. See Appendix F tables F1 and F2 for additional numerical detail.

4.4.2 Between Troop Pairs

Three additional MANOVAs were conducted to further analyze the distribution of mode component proportions between troops by combining them into three groupings: troops 1 and 2 (Figure 14), troops 2 and 3 (Figure 15), and finally troops 1 and 3 (Figure 16). The MANOVA that combined troops 1 and 2 showed the distribution of mode proportions between rank across these two troops was not statistically significant (12 and 9 degrees of freedom, Pr(>F) = 0.66; Figure 14). This same finding was the case for the other troop-combinations mentioned above. The MANOVA combining troops 2 and 3 (12 and 15 degrees of freedom, Pr(>F) = 0.32; Figure 15), and that for troops 1 and 3 (12 and 15, Pr(>F) = 0.29; Figure 16), both returned with non-statistically significant results; however, *post hoc* analysis was completed to break-down the analysis for each of the four mode components examined.

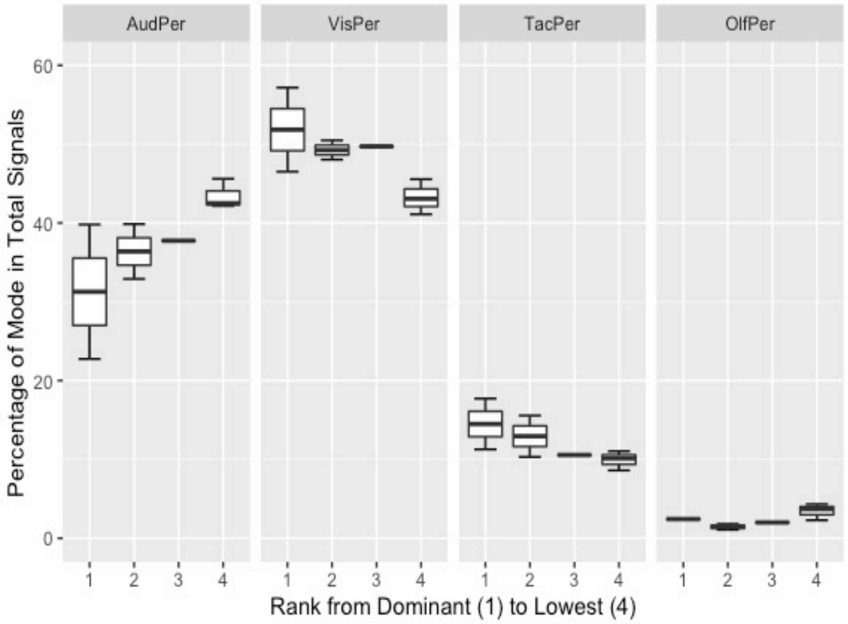

Figure 14: Boxplots depicting variance in the distribution of mode component proportions by rank between troops 1 and 2. Where "AudPer", "VisPer", TacPer", and "OlfPer" designate the communicative mode proportion being compared, corresponding to "auditory", visual", "tactile", and "olfactory" respectively. The line between either hinge represents the median, the upper hinge the upper quartile and the lower hinge the lower quartile. Whiskers depict the highest and lowest value. See Appendix F tables F3 & F4 for additional numerical detail.

The *post hoc* one-factor ANOVAs for the MANOVA of troops 1 and 2, and that for 2 and 3, again returned results for each mode proportion which were not statistically significant. For troops 1 and 2 there were 3 and 4 degrees of freedom, where Pr(>F) = 0.37 for auditory, Pr(>F) = 0.26 for visual, Pr(>F) = 0.47 for tactile, and Pr(>F) = 0.17 for olfactory. For troops 2 and 3, results were 3 and 6 degrees of freedom, Pr(>F) = 0.18 for auditory, Pr(>F) = 0.16 for visual, Pr(>F) =0.29 for tactile, and Pr(>F) = 0.083 for olfactory. The one-factor ANOVA conducted on the MANOVA of troops 1 and 3 did return statistically significant differences for two of the four modes examined: auditory (3 and 6 degrees of freedom, Pr(>F) = 0.021) and visual (3 and 6 degrees of freedom, Pr(>F) = 0.012). Proportions of tactile (3 and 6 degrees of freedom, Pr(>F) = 0.43) and olfactory modes (3 and 6 degrees of freedom, Pr(>F) = 0.32) did not show significant differences in their distribution across rank within these combined troops.

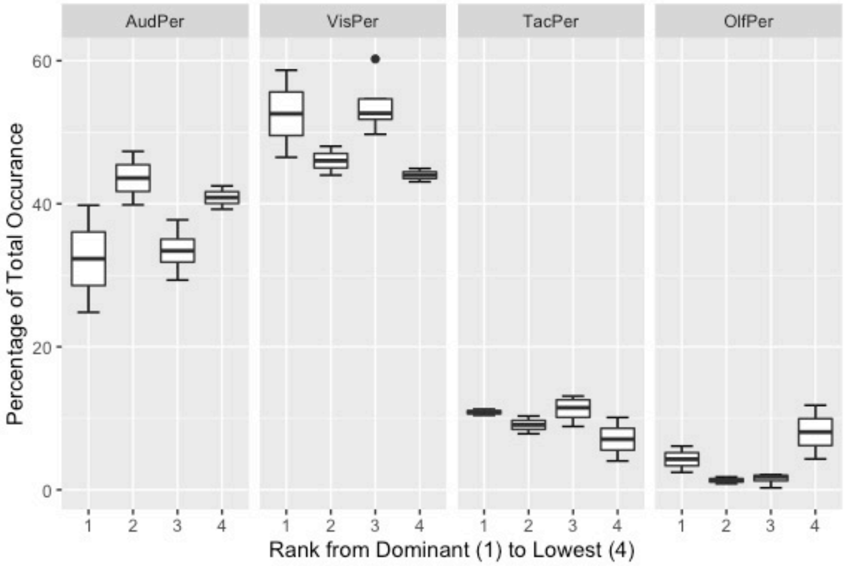

Figure 15: Boxplots depicting variance in the distribution of mode component proportions by rank between troops 1 and 2. Where “AudPer”, “VisPer”, TacPer”, and “OlfPer” designate the communicative mode proportion being compared, corresponding to “auditory”, visual”, “tactile”, and “olfactory” respectively. The line between either hinge represents the median, the upper hinge the upper quartile and the lower hinge the lower quartile. Whiskers depict the highest and lowest value, and dots outside the boxes representing outliers. See Appendix F tables F5 & F6 for additional numerical detail.

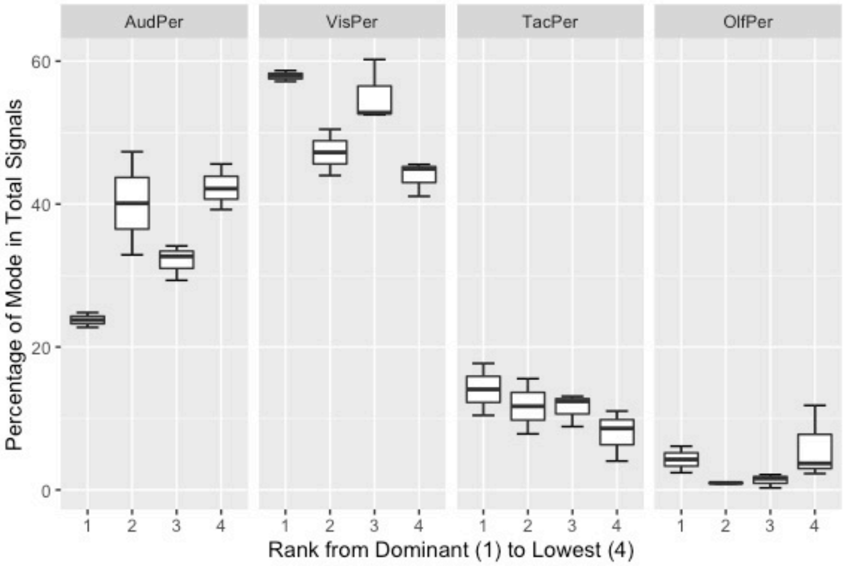

Figure 16: Boxplots depicting variance in the distribution of mode component proportions by rank between troops 1 and 2. Where “AudPer”, “VisPer”, TacPer”, and “OlfPer” designate the communicative mode proportion being compared, corresponding to “auditory”, visual”, “tactile”, and “olfactory” respectively. The line between either hinge represents the median, the upper hinge the upper quartile and the lower hinge the lower quartile. Whiskers depict the highest and lowest value. See Appendix F tables F7 & F8 for additional numerical detail.

4.4.3 Within Each Troop

Finally, to examine the differences observed within troops, simple two-way ANOVAs were used to assess the variation in distribution of mode component proportions across rank within each examined troop (Figure 17). Analysis for troop 1 returned statistically significant results for differences between mode proportions (3 degrees of freedom, Pr(>F) = 2.61e-05) and for mode by rank (6 degrees of freedom, Pr(>F) = 0.0085; Figure 17a). Likewise, analysis for troop 3 showed significant results for mode proportions (3 degrees of freedom, Pr(>F) = 5.35e-09) and for that as it relates to rank (9 degrees of freedom, Pr(>F) = 0.0026; Figure 17c). Analysis for troop 2 did not return statistically significant results (Figure 17b).

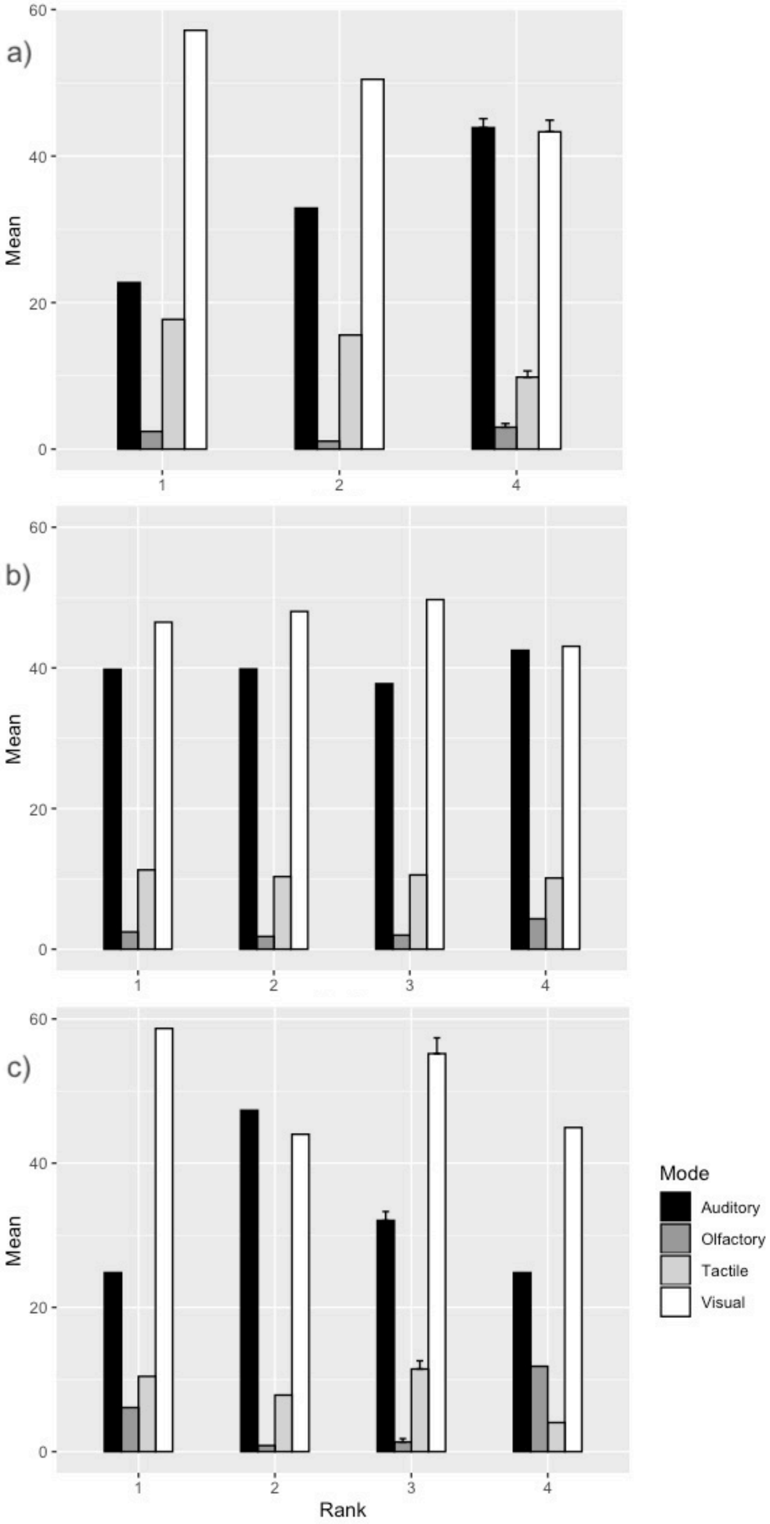

Figure 17: Bar graphs depicting the mode component data within each troop, organized by rank. Where 1 is the highest rank and 4 is the lowest. Where, (a) represents Troop 1 (n=4), (b) Troop 2 (n=4), and (c) Troop 3 (n=6). Note in (a) there is no individual for rank 3, since this troop consists only of the dominant female (rank 1), one of her daughters (rank 2), and two males (both rank 4). Standard error bars are present where more than one individual in that troop hold the same rank. See Appendix F tables F9-F11 for additional numerical detail.

4.5 Comparing Sex

Analysis of how the sex of an individual, regardless of rank, might relate with their mode component frequencies demonstrated a pattern of significance across modes between females and males (Figure 18). The results show females used auditory mode components less often than visual, as well as using them less often than their male counterparts. Males on the other hand used auditory components more frequently and visual components less frequently than females (Figure 18), but used both modes to about the same extent when compared to other males (Figure 19). The differences between males and females for tactile components is relatively smaller, but that for olfactory modes appears significant, with males showing a higher use frequency. Additional analysis was conducted to determine the statistical significance of this observed trend (Figure 19). For all four modalities, there is a significant difference between proportional occurrence in males relative to females. The differences were strongest for olfactory and visual signals (p=<0.05), and less so for auditory and tactile signals (p=<0.1).

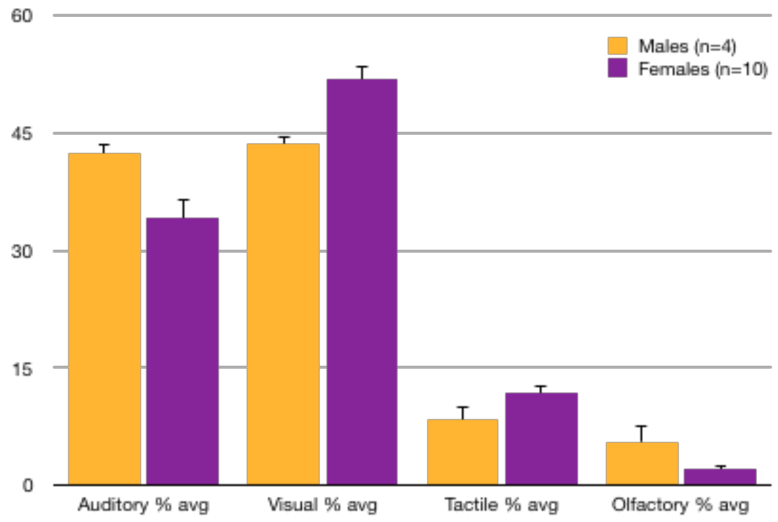

Figure 18: Bar graph depicting average mode component use by sex. See Appendix G tables G1 and G2 for additional numerical detail.

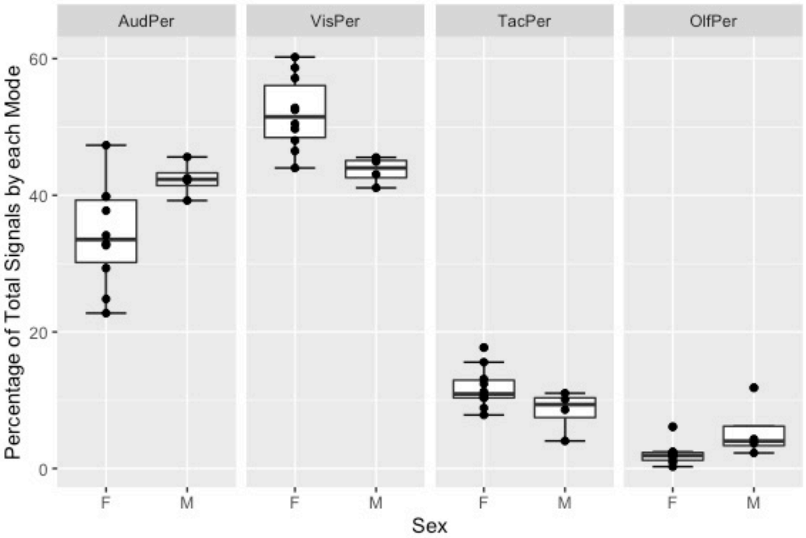

Figure 19: Boxplot depicting mode component use by sex. Where for females n=10 and for males n=4. "AudPer", "VisPer", TacPer", and "OlfPer" designate the communicative mode proportion being compared, corresponding to "auditory", visual", "tactile", and "olfactory" respectively. The line between either hinge represents the median, the upper hinge the upper quartile and the lower hinge the lower quartile. Whiskers depict the highest and lowest value, and dots outside the boxes representing outliers. Data points have been displayed to show the distribution of values within each box. See Appendix G tables G3 and G4 for additional numerical detail.

4.6 Comparing Rank & Sex Together

Recognizing the overlap between dominance ranking and sex in ring-tailed lemurs, where all females are dominant to all males, one last analysis was conducted combining rank and sex as a single factor (Figure 20). Only three variables were recognized to do this: dominant female, non-dominant female, and male. The MANOVA returned a statistically significant result (Pr(>F) = 0.048), so *post hoc* analysis was conducted to more carefully examine the relation between each mode and sex-rank grouping and determine which components were contributing to this significance (Figure 21). Statistically significant differences were found for auditory (Pr(>F) = 0.047), visual (Pr(>F) = 0.032), and olfactory (Pr(>F) = 0.058) mode component proportions.

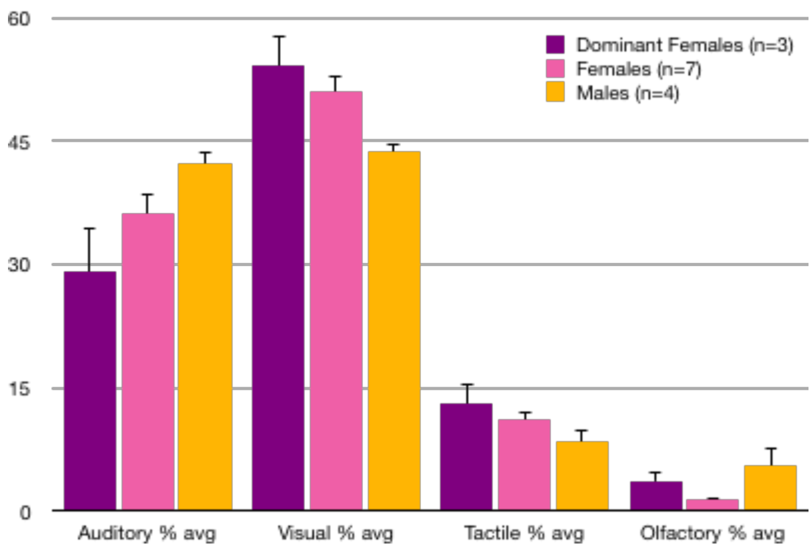

Figure 20: Bar graph depicting average mode component use by sex and rank together. See Appendix H tables H1-H3 for additional numerical detail.

4.7 Cluster Analysis

The modal proportion data for all 14 individuals were then examined together in a cluster analysis and visualized in a dendrogram using base graphics in RStudio (Figure 22). This final processing of these data was based on each individual's component use proportions to examine the strength of the groupings broadly used throughout this project and illustrate which individuals had the most similar component proportions. Two of the three dominant females, Sprite (troop 1) and Liesl (troop 3), clustered more closely together, but the third dominant female, Sophia (troop 2), clustered more closely with her daughters, Nemesis and Narcissa, with whom she free-ranges (Figure 22). Most males clustered together, with one of the four males, Aracus, forming his own branch on the far left (Figure 22). Liesl's daughter and the second ranked female of troop 3, Griselda, clusters more closely to the males and to the females of troop 2. The remaining cluster groups the females LuLu (troop 1), Hedwig (troop 3), and Shroeder (troop 3) together.

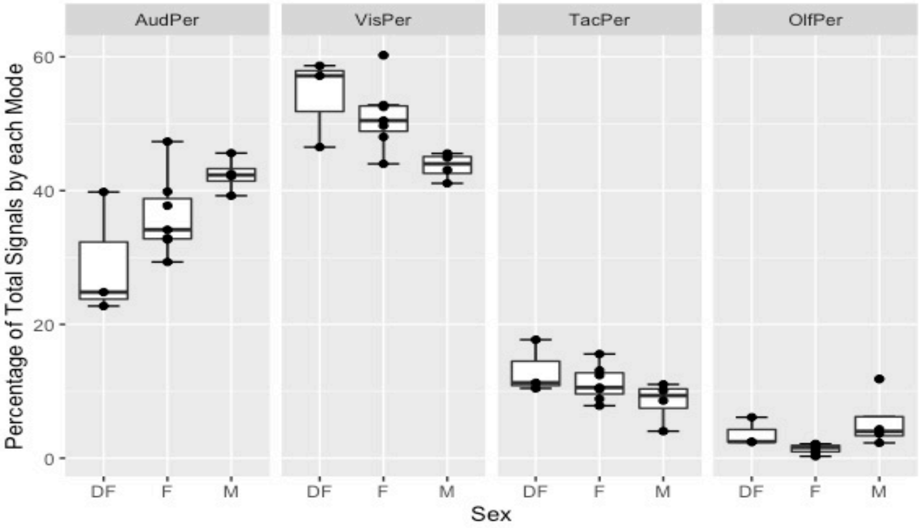

Figure 22: Boxplot depicting mode component use by sex and rank. Where for dominant females (DF) n=3, for subordinate females (F) n=7, and for males (M) n=4. "AudPer", "VisPer", TacPer", and "OlfPer" designate the communicative mode proportion being compared, corresponding to "auditory", visual", "tactile", and "olfactory" respectively. The line between either hinge represents the median, the upper hinge the upper quartile and the lower hinge the lower quartile. Whiskers depict the highest and lowest value, and dots outside the boxes representing outliers. Data points have been displayed to show the distribution of values within each box. See Appendix H tables H4 and H5 for additional numerical detail.

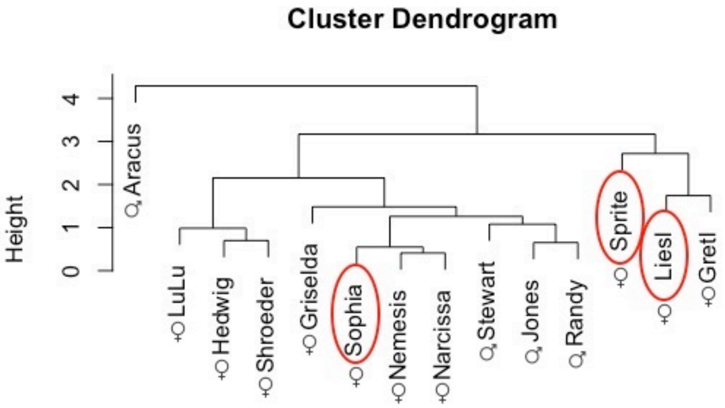

Figure 21: Dendrogram of all 14 individuals showing similarities between component proportions by using average linkage clusters and individual mode proportions. Males and females have been marked using symbols. Dominant females (n=3) are circled in red.

4.8 Multimodal Analysis

For multimodal analysis, focus was placed upon the highest ranked individual (i.e. the dominant female) and the lowest ranked individual (i.e. the lowest ranking male) in each troop (n=6). The values for unimodal and multimodal signals were then expressed as a proportion of an individual's total signals for each of the six focal individuals (Figure 23). These proportional data were normalized to total 100% to be visualized in pie charts. In five of the six focal individuals for this analysis, the frequency of unimodal versus multimodal signalling approximated 50:50. One male individual, Aracus (Figure 23f), shows a relatively higher proportion of unimodal (61%), and lower multimodal (39%), signals. For all individuals, bimodal signals were the most common multimodal signal type observed (Figure 23). Further analysis in RStudio demonstrated no statistically significant differences in proportions of unimodal and multimodal signal use between individuals when examined relative to sex, although males do appear to show greater intrasexual variation (Figure 24).

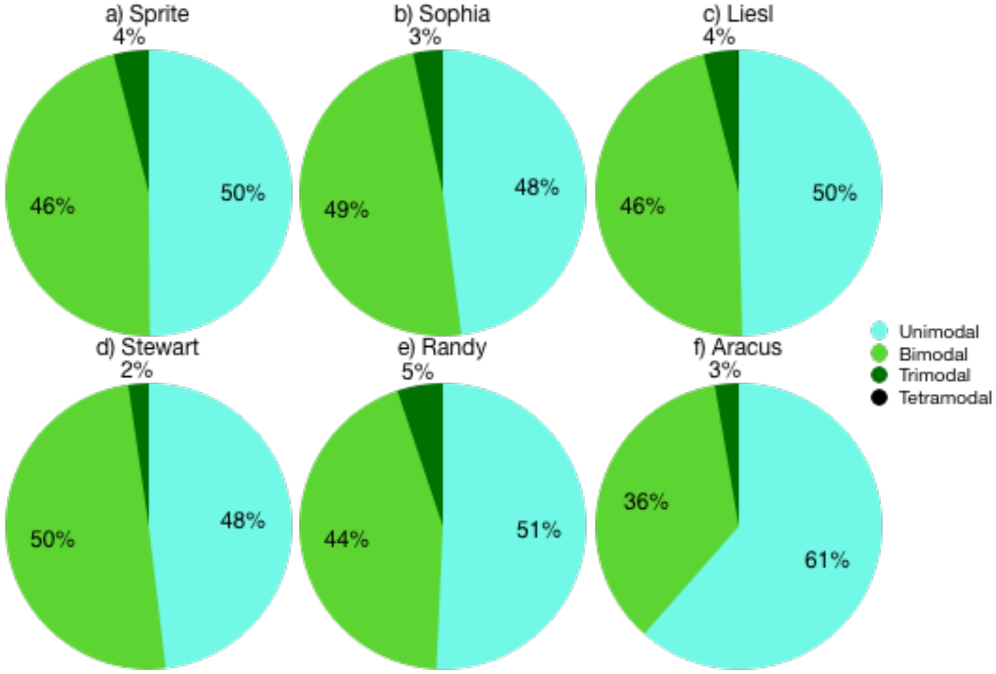

Figure 23: Pie charts depicting proportion of total signal type per individual (n=6). Top row contains all 3 dominant females, and bottom row contains all 3 lowest ranking males. Left to right: Troop 1 (a & d), Troop 2 (b & e), and Troop 3 (c & f). Tetramodal signals only occurred once in this sample, for Liesl (c), and represented a minute percentage of her total signals (1/1911). See Appendix I table I1 for additional numerical detail.

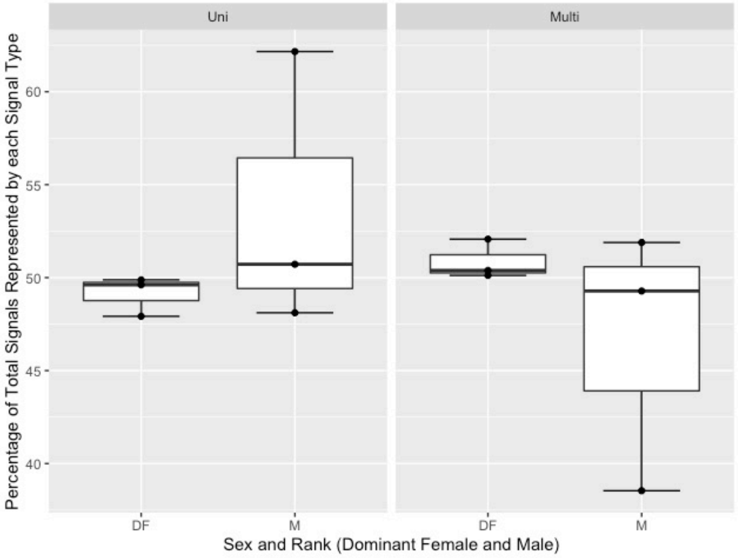

Figure 24: Boxplot depicting signal type (unimodal or multimodal) use by sex and rank. Where "DF" is dominant females (n=3) and "M" is males (n=3). The line between either hinge represents the median, the upper hinge the upper quartile and the lower hinge the lower quartile. Whiskers depict the highest and lowest value. Data points have been displayed to show the distribution of values within each box. See Appendix I tables I2 and I3 for additional numerical detail.

4.8.1 Composition Analysis

The proportional composition of sensory components in each signal type, unimodal and multimodal, was also examined. The results show how much of each signal type in total, for the examined males (n=3) and dominant females (n=3) separately, are represented by signals containing a particular sensory mode (auditory, visual, tactile, or olfactory).

The composition of unimodal signals per individual shows a fairly consistent high occurrence of visual components, though there is some variability between individuals (Figure 25). As with previous analyses, tactile and olfactory components remain a relatively small proportion of the total here in unimodal signals, with the exception again of Aracus who shows a higher relative frequency of olfactory signals (Figure 25f). Dominant females Sprite (Figure 25a) and Liesl (Figure 25c) are relatively similar in their component proportions, but dominant female Sophia (Figure 25b) appears more similar to male Stewart (Figure 25d). Randy shows the highest frequency of occurrence of auditory components in this sample (Figure 25e). A MANOVA revealed that the proportions of visual components were significantly different between individuals (p=<0.05), while auditory components were less so (p=<0.1), and both tactile and olfactory components showed no statistically significant differences (Figure 26).

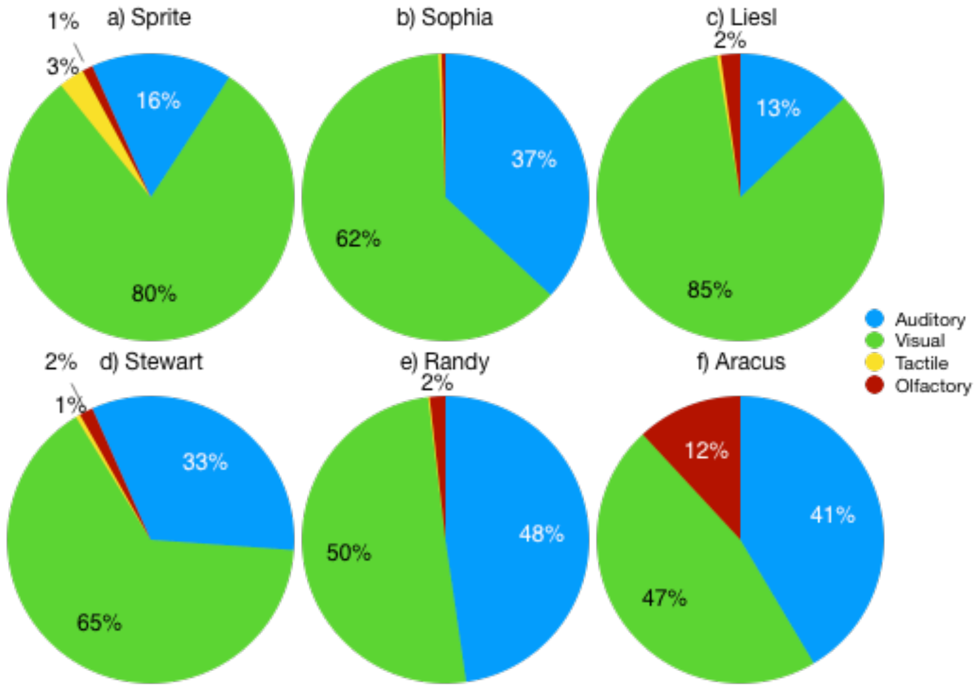

Figure 25: Pie charts depicting unimodal signal composition for 6 individuals. Top row contains all 3 dominant females, and bottom row contains all 3 lowest ranking males. Left to right: Troop 1 (a & d), Troop 2 (b & e), and Troop 3 (c & f). See Appendix I table I1 for additional numerical detail.

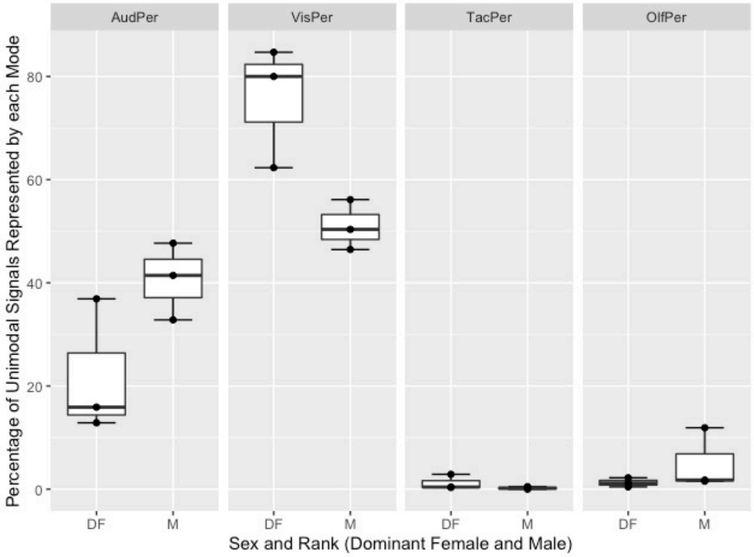

Figure 26: Boxplot depicting unimodal component compositions by sex and rank. Where "DF" is dominant females (n=3) and "M" is males (n=3). "AudPer", "VisPer", TacPer", and "OlfPer" designate the communicative mode proportion being compared, corresponding to "auditory", visual", "tactile", and "olfactory" respectively. The line between either hinge represents the median, the upper hinge the upper quartile and the lower hinge the lower quartile. Whiskers depict the highest and lowest value. Data points have been displayed to show the distribution of values within each box. See Appendix I tables I4 and I5 for additional numerical detail.

For the composition of multimodal signals, initial analysis of each individual's signal proportions revealed fairly consistent values across all four modes with only some variation between individuals (Figure 27). Further analysis in RStudio was conducted using the proportional values for each individual to examine for statistically significant differences (Figure 28). Visual components represent the majority of frequency occurrences in multimodal signals with no significant differences between males and females (Figures 27 & 28). Auditory and tactile components were the next most common signal components for both males and females, with Aracus as the only exception (Figure 27f). While there is slight variation between males and females in both tactile and olfactory component proportions, differences are not statistically significant (Figure 28).

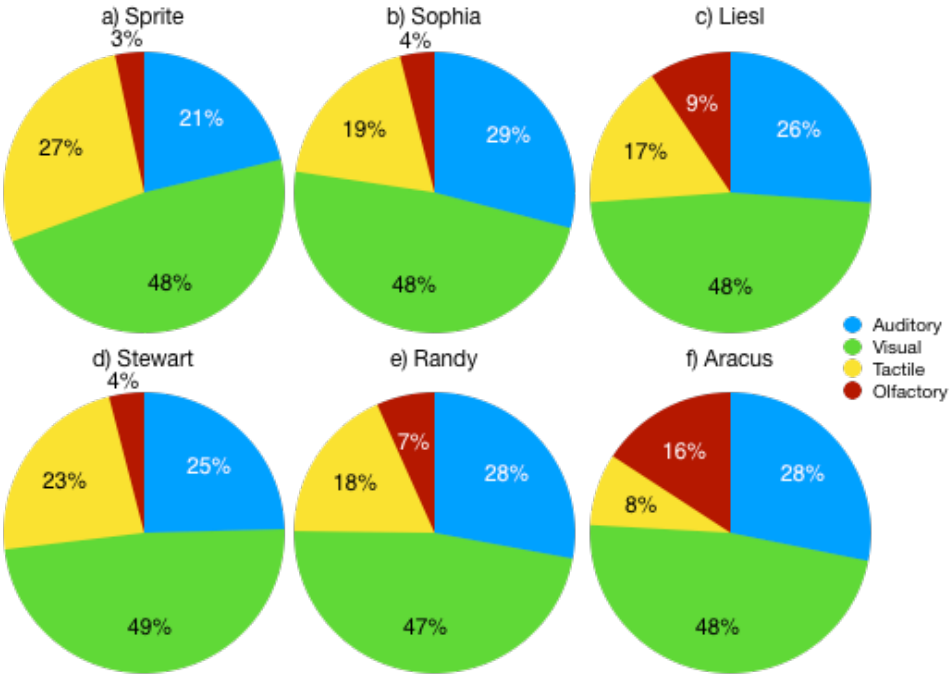

Figure 27: Pie charts depicting multimodal signal composition for 6 individuals. Top row contains all 3 dominant females, and bottom row contains all 3 lowest ranking males. Left to right: Troop 1 (a & d), Troop 2 (b & e), and Troop 3 (c & f). See Appendix I table I1 for additional numerical detail.

As a result of bimodal signals being the most frequently occurring multimodal signal (Figure 23), they were singled out for further analysis. These encompass multimodal signals containing components from only two sensory modes. A cluster analysis was used to examine the strength of the groupings, dominant female and male, for this subset with regard to their relative bimodal signal combination compositions. Results show no significant differences between individuals based on sex or rank (Figure 29).

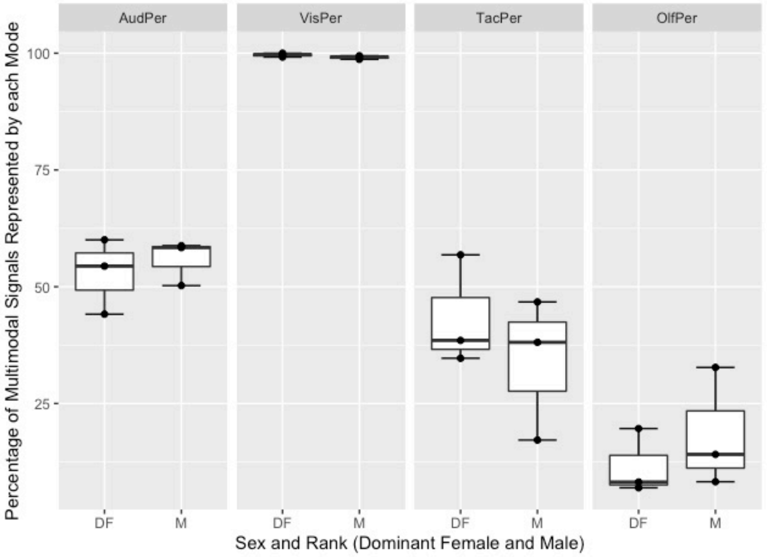

Figure 29: Boxplot depicting multimodal component compositions by sex and rank. Where "DF" is dominant females (n=3) and "M" is males (n=3). "AudPer", "VisPer", TacPer", and "OlfPer" designate the communicative mode proportion being compared, corresponding to "auditory", visual", "tactile", and "olfactory" respectively. The line between either hinge represents the median, the upper hinge the upper quartile and the lower hinge the lower quartile. Whiskers depict the highest and lowest value. Data points have been displayed to show the distribution of values within each box. See Appendix I table I6 and I7 for additional numerical detail.

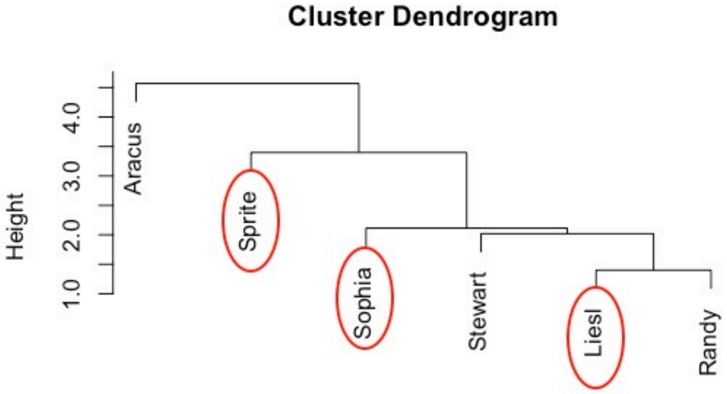

Figure 28: Dendrogram of dominant females (n=3) and one male from each troop (n=3) showing similarities in component combinations, based on bimodal signal compositions, using average linkage clusters. Dominant females (n=3) are circled in red. No significant differences.

Chapter 5

5 Discussion & Conclusion

This final chapter connects the results from data analysis to broader contexts. I begin with a summary of the results before focusing the discussion on the two key questions of my thesis: 1) is there a difference in the sensory modes *L. catta* use to communicate, and 2) is there a difference in the proportional use of unimodal signals and multimodal signals between individuals? The chapter then presents my suggestions for future work in primate multimodal communication, and addresses areas where specifically more research is needed. Finally, the chapter ends with a conclusion for these findings.

5.1 Summary of Results

Through this investigation I found support to reject my first null hypothesis, that individual ring-tailed lemurs will not differ in their communication modes, for two of the four examined factors: sex and dominance rank. The ways in which ring-tailed lemurs in this study communicate with troop mates seems to correlate with these two factors to an extent, which is reasonable considering how these two factors overlap for this species. I found that females tend to utilize visual components in their signals more frequently and auditory signals less, although as will be discussed this is as reflective of their troop organization. Males on the other hand tend to use auditory components more than, or at about the same frequency as, visual ones. Both tactile and olfactory components were the least frequent to be observed across all individuals. Tactile signals did not appear to correlate with any of the factors examined, producing proportions that were roughly even across all 14 examined individuals. Olfactory components on the other hand did appear to vary significantly when compared between males and females, and between dominant and subordinate females and males. Troop affiliation and an individual's age did not produce statistically significant differences for modal component proportions.

The proportions of unimodal and multimodal signal use, when compared across a subset of six individuals, did not show significant differences with respect to any of the examined factors and all individuals, except one, presented an occurrence ratio of approximately 50:50. This result for the majority is as predicted in the second null hypothesis, ring-tailed lemurs will exhibit little to no variation in the proportional use of unimodal signals and multimodal signals, which I fail to reject. The composition of unimodal signals resembled the previous analysis for all 14 individuals, showing statistically significant differences with respect to rank and sex, but the composition of multimodal signals did not. This final result demonstrates mixed support for my third and final null hypothesis, modal components within each signal type will not differ between individuals, and therefore I fail to fully reject the null. Below I will examine each of these points more specifically.

5.2 Do Ring-Tailed Lemurs Differ in the Sensory Modes they use to Communicate?

As a reminder, a communicative signal broadly is delineated in this investigation by a change in the state of an individual either within or outside the visual field of another individual of the same species while using at least one sensory mode of communication. A "mode" is defined by the sensory channel used to perceive a signal (i.e. auditory mode, visual mode, tactile mode, or olfactory mode). These modes are expressed as components of a signal; the individual action performed to send information or one which is produced as a result of another communicative action. For example, an individual vocalization is one component of a signal while any visual element linked to that vocalization, like a head tilt, or another action occurring simultaneously or immediately after that vocalization, like walking or tail waving, would be another component of the same signal. Since both of these components occupy different sensory modalities (auditory and visual respectively), this would be classified as a multimodal signal. Only social actions, those occurring in proximity of or directly involving another individual, as best as could be determined during the observation period, were counted toward modal codes and scoring for this investigation.

This project has demonstrated that overall there is a difference between individuals in which sensory modes of communication they use. In the examination of component proportions per individual, the most significant differences in mode use between individuals was the proportional use of auditory and visual signals. Tactile signals and olfactory signals surprisingly occurred at much lower proportions and frequencies for all individuals, though did show inter-individual variation to some extent. I examined two biological factors, age and sex, and two social factors, troop affiliation and rank, as well as rank and sex together as potential elements which could account for this variation.

5.2.1 Troop Affiliation

The analysis of troop affiliation was conducted to investigate whether each of the three troops represented a unique communicative environment, perhaps relating to who the dominant female was or even the location and size of their NHE (Natural Habitat Enclosure). However, there were no statistically significant differences found between troops for this factor. This suggests that each individual troop, as a separate unit, is using largely similar proportions of auditory, visual, tactile, and olfactory signal components as the other two troops. As figure 10 shows, while the troop proportions fall within the range of each other, the distribution of points within two troops in particular, troop 1 (n=4) and troop 3 (n=6), demonstrate that while there may be no troop-specific patterns that are unique, there is variation occurring at another level. One exception appears to be troop 2 (n=4) that shows very little variation between individuals. It is of interest to note that troops 2 and 3 are free-ranging in neighbouring NHEs and frequently interacted (indirectly) with each other. The two troops are neighbours, but are blocked off from physical contact by two rows of chain-link fence and approximately two-meters of "no-man's-land" between those fence lines. Despite this proximity, or perhaps as a result of it, the two troops do not resemble each other with respect to their component proportions. Previous work comparing different troops of ring-tailed lemurs in the wild demonstrate that habitat rather than troop affiliation *per se* resulted in behavioural differences (Gabriel, Gould, & Kelley, 2014); however, all three troops examined here are housed at the same facility, exposed to the same or similar vegetation, and are subject to the same climactic variation. Further observational work could be done with this troop, and others in captivity, to investigate this finding further and better establish whether the lack in variation between individuals in troop 2 is an unusual case for ring-tailed lemur communication or simply an alternative "norm" in this species.

5.2.2 Age

Between the three troops examined, ages ranged from 3 years to 28 years of age with the majority of individuals under the age of 18 (n=12). Individuals were grouped into age cohorts of approximately even sample sizes, and initially compared by calculating the average component proportions for each cohort. As is shown in figure 11, preliminary analysis appears to show auditory signal use following a slight negative trend with increasing age and olfactory a slight positive trend with increasing age, but further analysis in RStudio determined that these trends are not statistically significant (Figure 12). The proportions appear to be quite variable within each age cohort, especially for auditory and visual components (Figure 12). Perhaps further data collection on other individuals to increase the sample sizes might clarify any potential trends otherwise obscured here (*see* Bolt, 2020, for similar findings for auditory signals in males). The results here demonstrate no supporting data for age being a determining factor in component preferences or the proportional use of different sensory modalities to communicate in this population. It has been argued elsewhere that age may be a factor of particular types and frequencies of tactile communication in captive ring-tailed lemurs, where older individuals were more likely to initiate grooming bouts and younger individuals simple touching contact (Hosey & Thompson, 1985). The lack of support for this finding in the current study could be a result of how tactile components were tracked during data collection, where both the initiation and receiving of any physical contact was grouped together. Should further analysis of the contextual occurrence of an individual's tactile components be done, perhaps these more particular trends would be revealed. Nevertheless, the results at present demonstrate broadly that age is not a significant factor to be considered in communicative mode preferences, including the frequency of tactile components broadly, in ring-tailed lemurs.

5.2.3 Rank

Rank is an important element of ring-tailed lemur life and cannot be ignored in any investigation of their behavioural ecology. Based on the initial analysis of each individual it appears that, at least for two of the three troops examined, there is a gradual difference between individuals of higher rank and lower rank within each troop (Figures 7 & 9).

There was one troop, troop 2, for which the differences in component proportions were not significantly different between individuals, as discussed above (Figure 8). When more in-depth analysis was conducted on these data, discussed below, support was found for the observed differences in proportional use of both auditory and visual signal components between rankings ($p<0.05$; Figure 13).

5.2.3.1 Analysis of Paired Troops

Each troop was paired together to examine whether the observed differences in proportions would be present in smaller sample sizes, rather than all three troops pooled together, and to better examine trends within each of the three troops since it was anticipated that troop 2 was obscuring some of the significance of these data. Interestingly, significance was in fact lost across all modalities when troop 2 was paired with either troop 1 or troop 3 (Figures 14 & 15). This result was expected since troop 2 shows the least amount of difference between individuals. The only exception to this occurred for the comparison of troop 2 with troop 3 (Figure 15), where there was slight significance for the difference in olfactory signal components across ranks ($p<0.1$). This is likely owed to the oldest male, Aracus (troop 3), who had the highest occurrence of olfactory signalling of all 14 individuals examined (Figure 9f). In the initial analysis of troops 1 and 3, they appeared to show very similar trends and did in fact produce the highest significance scores for auditory and visual modalities when analyzed together ($p<0.05$; Figure 16). It should be noted that visual mode proportions scored the closest to high significance ($p<0.01$) for the analysis of troops 1 and 3 together ($Pr(>F)=0.01187$; Figure 16) as well as that for all three troops together ($Pr(>F)=0.01976$; Figure 13). This indicates that of the communicative modes examined, visual components demonstrate the most variation in use by dominance rank for this captive population.

5.2.3.2 Analysis of Individual Troops

To examine this correlation more closely, two-way ANOVAs were used to assess the variation in distribution of component proportions across rank within each examined troop. Analysis for troop 1 returned statistically significant results for differences between both mode proportions (3 degrees of freedom, $Pr(>F) = 2.61e-05$) and for mode by rank (6 degrees of freedom, Pr(>F) = 0.0085). Likewise, analysis for troop 3 showed significant results for mode proportions (3 degrees of freedom, Pr(>F) = 5.35e-09) and that as it relates to rank (9 degrees of freedom, Pr(>F) = 0.0026). This indicates that both of these two troops not only demonstrate significant variation between individuals, but also that it seems to correlate with differences in rank as well. As anticipated from the analyses conducted previously, analysis for troop 2 did not return statistically significant results, showing that these individuals are quite consistent in their component use despite differences in rank.

This analysis demonstrates that there is a significant difference between the proportional use of auditory and visual signals between dominance ranks for two of the three examined troops. Higher ranked individuals tend to use visual components proportionally more frequently than the other individuals below them in rank. With decreasing rank, the use of modes shows an increasingly higher proportional use of auditory modes until either it becomes about even with that for visual component use or rises above the others. This suggests that the dominant females are more likely to communicate using visual components within their signals, or at the very least that they remain largely within the visual field of troop mates, while the lower ranking individuals, predominantly males, are more likely to show either a more even distribution of visual and auditory components or more auditory components in their signalling over all. However, due to the troop compositions and small sample size, a male dominance ranking could not be properly explored and represents an area were future research could expand into in a wild population to compare these current findings.

These results show some logical consistency with previous work examining the relationships between sociality, special organization, and communication (Peckre, Kappeler & Fichtel, 2019) and research describing ring-tailed lemur troop spatial organization more specifically. Males, as the lowest ranked individuals in the troop, are often found on the periphery of the “core”, which consists of the dominant female and the rest of the female cohort (Bolt & Tennenhouse, 2017; Gabriel, Gould, & Kelley, 2014; Jolly, 2012; Nakamichi & Koyama, 1997; Oda, 1996). As a result, they are likely to utilize contact call vocalizations more frequently to maintain proximity to the troop and females, as well as vocalizations used to denote submissiveness or non-aggression when approaching either higher ranked males or females in the core (Bolt & Tennenhouse, 2017; Gabriel, Gould, & Kelley, 2014; Macedonia, 1993). My findings support this, as well as suggest that the dominant female, and perhaps all those in the "core", can rely more heavily on visual components to communicate with troop mates, at least during periods of relative peace as is the case at the DLC, where all troops have their own territory maintained by fence-lines and human monitoring.

The lack of correlations within troop 2 is more challenging to understand taking the above into consideration. While the analysis which examined troop affiliation returned results suggesting the three troops were more similar than different, and age does not appear to be a factor influencing component proportions of individuals, troop 2 stands out against troops 1 and 3 when examining differences between dominance rank. As mentioned above, one possible added element to this finding could be the proximity of troop 2 with troop 3. Since these troops are free-ranging in neighbouring NHEs, perhaps their hierarchies are somehow more overlapping than observed, although it is difficult to suggest anything beyond speculation with the data collected at present. Based on my own observation of the territorial behaviours performed by either troop against the other, and no clear evidence showing submissive behaviour in the dominant female of troop 2 to the dominant of troop 3, I find that suggestion difficult to believe. Further work is needed either with this same population or others in captivity to clarify these results and provide a more concrete assessment of the apparently divergent behavioural patterns of troop 2.

5.2.4 Sex

In ring-tailed lemurs the sex of an individual is very closely related to their dominance rank, so this factor was examined as well. As was expected because of the close connection between sex and rank, when the data were examined to compare component proportions between sexes the trends appear approximately the same as those for rank with a few added elements. Initial results again show statistically significant differences between auditory and visual occurrences, with the addition of more clear variation in tactile and olfactory proportions (Figure 18). When analyzed further, significant differences were found across all modes to greater or lesser degrees. Of particular interest, visual and olfactory mode proportions scored the highest significance ($p<0.05$), whereas auditory and tactile mode proportions were less so ($p<0.1$; Figure 19). Again, visual signal components showed the most significant difference (Pr(>F)=0.01155) with females utilizing auditory components more frequently than males.

As a cautionary note, the stronger statistical significance for comparisons between sexes might be due to the reduced number of groupings and subsequent pooling of data, which drops from 4 groups in the rank analysis to 2 groups (male and female). The significant difference found in olfactory component proportions, where males are utilizing this mode more frequently, is again likely owed to one individual in particular, Aracus, although there is some evidence to support males utilizing this mode of communication more than females depending on the season (Drea & Scordato, 2008; Kappeler, 1998; Tinsman, Hagelin, & Jolly, 2017). Likewise, the reduced significance found in auditory signals relative to that found in the analysis for rank is likely owed to another individual from troop 3, Griselda, who is second rank as one of Liesl's youngest daughters and had the highest auditory percentage of all 14 individuals (Figure 9b). The distribution in proportions per group is best seen in figure 19, where each point represents an individual and it becomes clear that a single individual can influence these averages.

5.2.5 Rank & Sex

In order to better address the overlap of sex with rank in ring-tailed lemurs, another round of analysis was conducted that partitioned dominant females out from non-dominant females. Individuals in this analysis were split into three groups: Dominant Female, Female, and Male (Figure 20). The MANOVA results of this additional step showed slightly reduced statistical significance compared to that for sex alone; however, and in accordance with the previous analyses, auditory and visual component proportions returned significant differences between the three groupings ($p<0.05$; Figure 21). Olfactory again scored minor significance ($p<0.1$), although that is likely owing to Aracus. Nevertheless, this iteration of the dataset suggests that males and dominant females use olfactory signals more frequently than non-dominant females, and is partially corroborated by previous research on olfactory behaviours in ring-tailed lemurs.

While females are the predominant territory protectors, males have been noted to present higher frequencies of scent marking than females (Kappeler, 1998) and their rate of scent marking has been shown to be correlated to dominance rank (Walker-Bolton & Parga, 2017). These rates are also highly seasonal for both males and females, increasing with more agonistic behaviours during the mating period when females are briefly receptive and competition is highest (Drea & Scordato, 2008). The work directly addressing rates of scent marking in females is a little more abstract, but in general has been shown to be less frequent than males (Kappeler, 1998; Drea & Scordato, 2008) and their rates of counter marking in particular have been correlated to dominance rank (Palagi, Telara & Tarli, 2004). What became apparent in this investigation is that for *L. catta*, more work has been done to compare sex and rank differences in the rates of investigation of scent marks from conspecifics, as well as the composition of secretions, rather than differential frequencies of deposition as is discussed here. Perhaps additional work on this aspect of scent marking will further elucidate the olfactory behaviours of ring-tailed lemurs, in both captive and wild settings. Nevertheless, the results of the current investigation suggest that both rank and sex, as closely intertwined elements of ring-tailed lemur social life, impact the frequency of components used to communicate with conspecifics.

5.2.6 Cluster Analysis

The cluster analysis conducted to examine the similarities between all 14 individuals in this study, with regard to their baseline component proportions, showed interesting results that make the interpretation of many of the above findings more complicated. Two of the three dominant females, Sprite (troop 1) and Liesl (troop 3), cluster together on their own branch with one of Liesl's eldest daughters whom she currently free-ranges with, Gretl (Figure 22). Gretl was not identified as a dominant female nor a second-rank in the above analyses, as this clustering may suggest, though it should be noted that she did displace one of her younger sisters partway through the observation period of this study, which did result in the two females switching dominance rank positions. This shift in ranking position was noticeable at the feed-site and during dominance displays at the fence line, but occurred late in the summer and was not taken into consideration for this study since both females were identified as "third-ranking" regardless. Griselda, who was the second-rank in Liesl’s troop, maintained her position throughout the summer, but clustered more closely with the cluster of males and the majority of Sophia’s troop (Figure 22). Not surprisingly, Sophia, the dominant female of troop 2, forms her own cluster with her two daughters who she free-ranges with (Figure 22). Aside from Aracus, who forms his own branch apart from all other individuals, the males form their own cluster as well. The remaining females in Liesl’s troop form their own cluster with the second-ranking female in Sprite’s troop (Figure 22). This analysis demonstrates well the challenges of working with biological data since not every individual appears to fit well in the categories and clusters I had put them into for comparison.

5.2.7 Variation in Communicative Mode: Summary

As demonstrated above, there appear to be patterns relating rank and sex. In addition, there are also patterns in the proportional use of both visual and auditory signal components in particular, and olfactory components to a lesser degree.

Overall, visual signal components appeared to be the most frequently used by the majority of individuals studied. Females, and dominant females especially, seem to use visual components more frequently than males do, whereas males either use them at about the same frequency as, or less than, auditory components, at least in this captive population. This finding is also reflective of the spatial organization common in ring-tailed lemurs as a result of how visual components were delineated and data on them collected. In this investigation, all signals containing a visual component, whether it was “fixed” or “flexible” (*see* Higham & Hebets, 2013; Partan & Marler, 2005), were recorded and grouped together if performed within the visual field of conspecifics. This broad definition represents a limitation in the analysis of these data by biasing the results in the favour of females, which as the dominant sex generally remain within the troop’s “core” and thus within the visual field of others more frequently than males. Should this investigation be repeated or expanded upon, I recommend all visual components be recorded whether they occur within the visual field of a conspecific or not, to better account for male performances of this particular sensory mode and present a more accurate comparison between individuals.

The auditory component proportions collected in this study likely reflect a more realistic analysis and comparison between individuals, in large part owing to the ease with which these particular signal components are observed. Males appeared to use significantly more auditory components in their communication than most other females with a few exceptions, mainly the three females from troop 2 and one individual from troop 3, Griselda. This individual, as mentioned above, had the highest number of auditory component occurrences of the 14 individuals in the study, despite being the second ranked female in her troop. One possible explanation for her especially vocal tendencies, which can be extended to a few other individuals examined, is simply individuality.

In their comparison of two wild troops of ring-tailed lemurs, Nakamichi and Koyama (1997) found that some female individuals seemed to be more aggressive toward non-troop members than others in their respective troops. This variation in frequencies and willingness to engage in aggressive behaviours was not, interestingly enough, found to be correlated to dominance rank (Nakamichi & Koyama, 1997). Another more recent study on ring-tailed lemurs at the DLC and on St. Catherines Island, Georgia, uncovered that some individuals were especially social, while others were again more likely to initiate aggressive encounters (Kulahci, Ghazanfar, & Rubenstein, 2018). Still yet, there were particular individuals who seemed to respond to contact calls and scent marks more often than others, and that some were more frequent groomers (Kulahci, Ghazanfar, & Rubenstein, 2018). In essence, both of these studies describe individual behavioural variation in ring-tailed lemurs. Kulahci, Ghazanfar, and Rubenstein (2018) clarifed that their results were very likely influenced by sex, age, and overall composition of the particular troop, but this is nevertheless an interesting potential factor and an added layer of complexity to consider in studies of behaviour in a social primate species like *L. catta*. Further research testing the viability of these findings in other populations would help to clarify these results and potentially broaden our understanding of ring-tailed lemur social behaviours.

There are nevertheless other important aspects that should be addressed within the current analysis and taken into consideration for future work. In particular for ring-tailed lemurs, their auditory repertoire is quite large and numbers a little over 20 different vocalizations that are context, age, and sex dependent (*see* Macedonia, 1993). In the current investigation, it represented the sensory mode with the highest number of observable and easily scored behaviours, and as a result it comes as no surprise that this component had such high proportions relative to tactile and olfactory signal components; each encompassing less than 10 behaviours.

Tactile signals and components in this study largely continued to show no significant differences between individuals despite differences in age, rank, and sex, contrary to some earlier work (*see* Hosey & Thompson, 1985; Nakamichi & Koyama, 1997), but like olfactory components, these represented a much smaller proportion of the total signals for each individual. These results suggest that affiliative behaviours broadly in ring-tailed lemurs are evenly performed by both males and females. However, constraints on the observation period used in this study mean that only a four-month "snapshot" of behavioural trends was possible. This study was conducted outside the normal breeding period of ring-tailed lemurs and all female individuals in this study were non-breeding, meaning they were on hormone contraceptives. These factors, along with the relatively limited mobility and regular provisioning that life in captivity provides, likely effect their behaviour and subsequentially contribute to these consistent findings.

In their study of four populations of wild ring-tailed lemurs, Gabriel, Gould, and Kelley (2014) found that factors such as habitat composition and resource availability, in addition to the timing of mating and migration seasons, likely influencing the differences observed in rates and occurrences of male ring-tailed lemur affiliative behaviours between three different forest types. As expected, the occurrences of male-male affiliative behaviours dropped considerably during the mating period, which is defined by high competition between males (Gabriel, Gould, & Kelley, 2014). The rates then increased during female gestation and lactation periods, which the authors noted coincides with the dry season and when males often attempt to migrate into new troops (Gabriel, Gould, & Kelley, 2014). Increased affiliative behaviours during this period likely strengthen social relationships between in-troop males when outsiders are attempting to migrate in and maintains the benefits gained from close proximity with others during a period of time when females are largely inaccessible or busy with infants

(Gabriel, Gould, & Kelley, 2014). It is interesting to note that the authors further suggested individual female temperament, habitat composition, and proximity to other troops are additional factors influencing the differences observed between troops (for instance, one of the troops had very few occurrences of male dispersion relative to the others), although they also argue that more research is needed to confirm these findings (Gabriel, Gould, & Kelley, 2014).

It should be noted that the majority of tactile behaviour in primates has been focused on grooming, whereas the delineations made in this investigation to track tactile signal components encompassed both the initiation and receiving of any physical contact, not just grooming. Further investigation into the tactile behaviours of ring-tailed lemurs is needed to better elucidate its use and more importantly the contextual occurrence in *L. catta*. Perhaps this would then clarify any patterns or differences otherwise obscured in the current study.

In interpreting the olfactory data for this population, initial analyses revealed a general lack of trend for this mode of communication when comparing individual dominance ranking, although there did appear to be a slight trend when individual sex was taken into consideration. Males appear to use this modal component more frequently than most females, with one individual exception in the dominant female of troop 3, Liesl (Figure 9a). When both sex and rank were compared together, dominant females had the next most frequent use of olfactory components after males, with subordinate females showing relatively few occurrences at all. It is worth acknowledging how few occurrences of this particular sensory mode there are for each individual relative to the other three modes examined. This aspect of the dataset makes it challenging to comment definitively about this particular group of signal components and any potential trends observed. The low occurrence could be a result of olfactory signals for this thesis being limited to those most readily observed and with which I was most familiar with: scent marking and stink-fighting/-flirting. As a consequence, potential trends involving more subtle olfactory signalling (*see* Bailey, 1978, flehmen behaviour in *L. catta*; Smith et al., 2015) and latrine or urine marking behaviour (Drea, Goodwin, & delBarco-Trillo, 2019; Colquhoun, 2011; Palagi & Norscia, 2009) remains unexplored. In addition, olfactory communication in lemur species broadly represents an area in need of further investigation (Drea, Goodwin, & delBarco-Trillo, 2019; Colquhoun, 2011).

Despite the emphasis that seems to be placed on the role of olfactory signalling in strepsirrhine primates more broadly, the occurrence of olfactory signal components was very small in this study. The causes behind this could be a combination of seasonality and the use of birth control on females at the DLC, which together perhaps results in a "scent-scape" that is limited when compared to what might be encountered in the wild or during the mating period. As the first investigation into ring-tailed lemur multimodal communication, a comparison between a captive "scent scape" and that in the wild was beyond the scope of this research. Nevertheless, it does represent an area for future research into olfactory communication. Ring-tailed lemurs, like many other species in Madagascar have a very restrictive and seasonal mating period with females only receptive for a few days out of the entire year (Jolly, 2012). As a result, this period of time, and even the following birthing period, marks a particularly active and exciting time for ring-tailed lemurs with increased displays, scent-marking, including stink fights and stink flirting, and aggression (*see* Drea & Scordato, 2008; Jolly, 1966a: 103; Jolly, 1993; Palagi, Telara & Tarli, 2004; Walker-Bolton & Paraga, 2017). Not only was my data collection timed outside of this period, but the female lemurs at the DLC are on hormone contraceptives to control which males they end up mating with as part of their Species Survival Plan. With this period of receptivity controlled by hormone contraceptives and closely monitored at the DLC, it is possible that ring-tailed lemurs in captivity do not display the same frequencies of olfactory component and signal use as is seen in wild populations. Additional research comparing the rates of olfactory signal use in captivity and the wild could be conducted to better determine whether there is in fact a difference between these two populations in this regard.

5.3 Is there Variation in the Proportional use of Unimodal signals and Multimodal Signals?

The results describing the proportion of signals that were multimodal, as opposed to unimodal, show that for the individuals examined, the distribution is approximately 50:50. Since the results from the initial analysis for this dataset show that sex and rank had the most influence on modal proportions, or at the very least demonstrated results with statistical significance, only the dominant females (n=3) and lowest ranking males (n=3) were examined for this aspect of my investigation. Despite differences in sex and rank, all individuals, save one, showed similarly even proportions of unimodal and multimodal signal use. Aracus showed a much higher proportion of unimodal signal use over multimodal (Figure 23f). Multimodal signals were further broken down into bi-, tri-, and tetra-modal signals to account for those containing two modes, three modes, and four modes respectively. This breakdown allowed for the finding that bimodal signals were the most frequently used multimodal signal, with tetra modal signals rarely occurring. Complex multimodal signals, those containing more than one component per sensory mode, were not investigated, but do represent an area for future work into the weighting of the different multimodal signals used.

These results suggest that despite the variation described above, almost each individual was using about equal proportions of unimodal and multimodal signals regardless of sex or rank. When the composition of those signals, unimodal and multimodal, were examined, the results varied between the two signal types. The composition of unimodal signals resembled the composition of all signals together, as was examined first in this thesis, where there were significant differences in proportions between the dominant females and males (Figure 25 & 26). On the other hand, the composition of multimodal signal proportions were found to be even across individuals, showing very little variation relative to that seen in the previous analyses (Figure 27 & 28). These results suggest that there is more variation between individuals in their unimodal signalling, which appears to correlate more-or-less with rank and sex, whereas multimodal signals hold about the same relative compositions regardless of rank or sex.

5.3.1 Do modal components within each signal type differ between individuals?

The proportional composition of unimodal signals for dominant females reveals that nearly all signals recorded were visual, with a significantly smaller proportion of the total signals being composed of auditory components. The one slight outlier to this finding is Sophia, who is the dominant female of troop 2 (Figure 25b), which was the troop that showed almost no variation between all four members despite differing rank and sex. Males also used unimodal visual signals more frequently than other modes, though not to the same extent as was the case for dominant females. Furthermore, the auditory component proportions for males was much higher than two of the three females, with Sophia's as the only exception. It should be noted that this analysis did not extend to include that for complex unimodal signals in order to simplify this analysis. These findings are fairly consistent with those from the analysis above, where generally the dominant females utilize visual signal components more frequently than males do, and males utilize auditory signal components more frequently than females.

In contrast, the multimodal signals for each of the six individuals of the sub-sample show about the same proportions for all four of the examined modal components. As a result of this consistency, individuals were grouped together to compare the averages of all males (n=3) and all females (n=3; Figure 27). Nearly all of the multimodal signals for each individual contained a visual component, resulting in its significantly higher representation (Figure 27). The next most frequent component for both males and females is auditory, where a little over half of the multimodal signals from each individual contained an auditory component. Dominant females tended to use slightly more tactile components compared to males, whereas males appear to utilize olfactory components slightly more often, though the differences are not significant (Figure 28). These results suggest that visual and auditory components are common elements of multimodal communication in ring-tailed lemurs and do not correlate with the rank and sex of an individual. On the other hand, the use of tactile and olfactory components in multimodal communication does appear to, though not significantly, and more research could be done to explore this potential correlation further by examining contextual occurrences as well as using a larger sample size. Perhaps limiting the multimodal analysis to the two available extremes in the sample population has limited some of the intelligibility of the trends, and so extending the analysis to include a few of the subordinate females if not all other remaining individuals would act to clarify any potential correlations between dominance rank and/or sex and multimodal signal composition.

Since the majority of the multimodal signals of the examined subset (n=6) were bimodal, this signal type was singled out for further analysis to address whether combinations of modes differed between individuals. A cluster analysis was used to assess this based on the strength of similarities between component proportions (Figure 29). In parallel to the above analysis, the results show no significant differences between individuals based on rank nor sex in their mode component combinations of bimodal signals. In general, all of the examined individuals used auditory-visual combinations most frequently, though two individuals, one male and one dominant female, show an exception and have higher occurrences of visual-tactile signals. Males appear to use visual-olfactory signals more frequently than females, though this combination was not exclusive to males nor was it the case when compared to all three females. Auditory-tactile and auditory-olfactory signals were rare across all individuals, with some not showing this combination of signals at all. No individuals were observed performing a tactile-olfactory signal.

5.3.2 Variation in Unimodal & Multimodal Signals: Summary

In summary, the frequency of use of unimodal and multimodal signals in ring-tailed lemurs does not vary significantly between individuals. In contrast, the composition of unimodal signals does vary between sexes and across dominance ranking in ring-tailed lemurs, but that for multimodal signals remains consistent. What this may suggest is that multimodal signals in this species are more limited or restricted in their use, whereas unimodal signals are more flexible in their usage and as a result are subject to individual variation. This variation is based on biological and social factors (i.e. rank and sex), but, to complicate things further and as suggested above, it may also reflect the idiosyncratic tendencies of an individual.

As discussed previously, Nakamichi and Koyama (1997) found that some ring-tailed lemur females seemed to be more aggressive than others regardless of that individual's dominance rank, and a more recent investigation conducted on captive ring-tailed lemurs found similar results (Kulahci, Rubenstein, & Ghazanfar, 2015). While factors like individual sex, age, and the overall composition of the troop are likely still present, idiosyncratic behaviour presents an interesting factor to consider in studies of behavioural ecology in a social primate. With this in mind, I suggest that unimodal signals in *L. catta* might be more "free" to occur in different contexts and used in different ways by individuals, resulting in the statistically significant variation described in the discussion above, but that this same "freedom" or "mobility" is not available for multimodal signals. Perhaps unimodal signals are more reflective of the proximate level of ring-tailed lemur communication, relating to the adaptive advantage it provides for a single individual, but multimodal communication is more reflective of the ultimate level of *L. catta* communication, relating to the adaptive advantage it provides to multiple generations.

The consistency of multimodal signal use in ring-tailed lemurs, as well as the combinations of modal components within those, suggests something more restrictive for this signal type. As discussed previously, signals can come with physiological or energetic costs as well as increased risks of aggressive encounters from competitors or even predation (de Luna, Hödl, & Amézquita, 2010; Rubi & Stephens, 2016; Singletary & Tecot, 2020; Sicsú et al., 2013; Smith, Taylor, & Evans, 2011). Multimodal signals by definition are more conspicuous and are therefore more costly for an individual to make, but might be the most efficient way available for an individual to send more information to a receiver or to clarify a message. What I suggest is unlike unimodal signals, the multimodal signals *L. catta* use may be limited to specific contexts and have a specific adaptive purpose that does not or cannot vary, at least not significantly, between individuals at the risk of that signal failing to be received or failing to produce the desired response in the receiver. Further research to examine and test these hypotheses more thoroughly should be conducted on larger populations in the wild to capture more natural stimulants, the possibly of year-round variation, as well as an overall larger sample size.

An alternative view of these findings could be that these results merely reflect the ways in which data on multimodal signals should be collected differently from that for unimodal signals. Perhaps multimodal variation cannot be addressed by examining signal compositions and frequencies of occurrence alone, but requires context and the signal's meaning to be taken into consideration as well. In other words, the study would consider variation in what messages are being sent (i.e. alarm call, contact call, submission, asserting dominance, etc.), or the specific components used to do so (i.e. grab, "howl", “moan”, nose lick, charge at, etc.), rather than analyzing the fact that one or more “auditory-visual” signals were observed for example.

5.4 Future Directions

As mentioned above there are a number of areas where future research can expand upon and clarify the findings presented, as well as areas where additional work is needed. I begin with a comment on my own methodological approach to multimodal communication research before delving into specific areas of the project. With respect to how data for each individual sensory mode were collected, three of the four modes showed clear areas where more research could improve upon the methods used here. The results from one of the three troops examined also prompted questions that could be answered with additional work in both captive and wild populations. Furthermore, one consequence of doing research with a small captive population was establishing only a partial rank analysis and missed the potential influence of male ranking on modes of communication. As a still relatively novel research path in behavioural primatology, multimodal communication studies should continue to explore behavioural differences and similarities in other populations. Complex signals are not limited to one component per mode, and additional research that compares unimodal signals to multimodal ones may better explain why each is used when they are and what factors are influencing those occurrences. As always in behavioural work, more long-term studies of multimodal communication would greatly expand our understanding of how habitat and a changing environment potentially influence communication, especially considering the unprecedented global changes humans continue to cause. Finally, multimodal communication research in primates would benefit from better and more even integration of ultimate and proximate levels of analysis, which would not only improve our understanding of this behavioural trait as a whole, but would also contribute to the debate on the evolutionary origins of human language.

5.4.1 Methodology

The first three days of data collection for this thesis represented a short period of time where I was adjusting to behavioural data collection on an unfamiliar scale and to a primate species I had not worked with previously. The result was a shift from using paper and pen to track mode use and behaviours to using a digital spreadsheet, and the loss of three days of data collection on six individuals. Nevertheless, this “loss” helped to maintain the consistency of the data being collected and analyzed in my study, and I highly recommend any future work being conducted on multimodal communication budget for about the same amount of time.

The fact that this topic is so new to primatology means that there is room to experiment with different methods and intensities of data collection. The current study utilized and intensive approach to collection and analysis on a small sample size, but future work could also investigate a broader approach on a larger population. While a captive population allows for this type of intensive data collection, a wild population may not. This alternative approach may help us to discover how best to study multimodal communication in primates by providing a different approach for comparison.

In addition, my thesis examined the components of communicative signals, but this topic should be expanded into a comprehensive report of specific multimodal and unimodal behaviours, rather than concluding simply with the signal parts, as suggested by Peckre and colleagues (2019). By combining these data together with their social and biological contexts, we can better address questions relating to the evolution of these complex forms of communication in primates.

5.4.2 Visual Components

In the present investigation, visual signals were only recorded if they occurred within the visual field of conspecifics, as estimated by my own line-of-sight. While this specificity delineated a visual signal that was more likely to be received by troop mates, it unintentionally may have biased results to favour female individuals, who are more likely to be around troop mates than males as a result of the typical spatial organization of this species (Bolt & Tennenhouse, 2017; Gabriel, Gould, & Kelley, 2014; Jolly, 2012; Nakamichi & Koyama, 1997; Oda, 1996). A more accurate comparison of visual signals and signal components between members of a troop is likely to be accomplished by tallying all occurrences of a visual component, whether or not it is performed within the visual field of conspecifics. This should produce a less biased assessment of visual components for ring-tailed lemurs and better account for male performances of this mode regardless of the troop's spatial organization.

5.4.3 Tactile Components

For this sensory mode component, further investigation more broadly is needed. The majority of tactile behaviour in primates has been focused on grooming, and while in this analysis more behaviours were coded as "tactile" than simply grooming alone, no significant differences were observed in the present study. Perhaps since resources were largely provisioned and there are no immediate threats to territory in captivity, tactile communication was less critical for individuals in this population to maintain strong social bonds and guard the resources they currently control within their enclosure. Alternatively, it is possible more variation is seen per specific tactile behaviour, for example grooming a specific individual or the occurrence of nose-touch greetings, rather than across the category as a whole. Both the initiation of as well as the willing reception of any physical contact was tracked in my thesis, which includes grooming, but also sitting against or otherwise in contact with an individual, hitting, biting, or pulling, the greeting nose-touch or lick, and play behaviours like rolling into an individual or tackling. Additional research examining this suite of behaviours more closely may better elucidate why no significant trends were found in the current study.

5.4.4 Olfactory Components

The obvious area where future work can contribute to that conducted in the present study is the consideration of hormone contraceptives and the mating period in ring-tailed lemurs. As a result of conducting this research with a captive population, a number of factors otherwise uncontrollable in the wild, can be relatively controlled for; however, it comes with a potential limitation as a result of controlled breeding. Comparative research examining the olfactory behaviours on ring-tailed lemurs in captivity, under birth control, and those in the wild is needed (*see* Crawford, Boulet, & Drea, 2011). Moreover, a comparison of the "scent-scape"s in captivity and in the wild, over the course of different seasons (mating and non-mating), could be conducted by combining observation with chemical analyses to improve our understanding of olfactory communication in lemur species. In addition, there have been more studies in *L. catta* examining the differential rates of a scent mark being investigated by another individual as opposed to differential frequencies of deposition, which was examined here. Further work examining olfactory communication from this angle may better clarify the scent marking behaviours of ring-tailed lemurs described here as well as their role in social lemurs, ideally with larger sample sizes than what could be accomplished with the present study. As mentioned above, olfactory signalling in lemurs is in need of further investigation, and research into the more subtle chemical signals used by this species may reveal trends that were not observed in the current study.

5.4.5 Troop 2

When the proportional data for each mode component were compared across the three troops, troop 2 stood out from the others in showing no significant differences between individuals despite differences in rank, age, and sex. The reasons behind this consistency, when variation was clearly visible in the other two troops, remain unclear, so further work is needed. Additional observations should be made with other *L. catta* troops in captivity and in the wild to investigate whether this within-troop consistency across mode proportions is present in other troops or if it is a unique characteristic of this specific one. Studies examining these trends in other *L. catta* populations can aid in determining whether this is an alternative “norm” for the species or at the very least what might be contributing to the findings presented here.

5.4.6 Rank

Due to the troop compositions, their separation from each other, and overall small sample size (n=4), a male dominance ranking could not be properly explored in this project. As a result, the current rank analysis results may only be reflective of a female-based dominance hierarchy. While this does reflect the reality of female dominance in ring-tailed lemurs broadly, it obscures entirely any variation that may be occurring between the dominance rankings for males, who in larger captive troops and in the wild do establish their own hierarchy (*see* Bolt, 2020). So, while the males in this study were more likely to show either a more even distribution of visual and auditory components or more auditory components in their signalling overall, it remains unexplored whether a dominant male differs in communicative mode use from the lowest ranking male. Future research could address this by focusing on tracking multimodal communication in males from a captive or wild population, though male dispersal and immigration in a wild troop may present a challenge.

5.4.7 Unimodal Signals

What is presented here only represents one side of unimodal communication and does not address complex unimodal signals in the analysis. Complex unimodal signals are those that contain more than one component from the same sensory mode, so it could be a signal made up of two or more different visual components, two or more different auditory components, two or more tactile components, or two or more olfactory components. Additional research could examine these signals to paint a more context or meaning-based understanding of the patterns described here. For example, does the variation we see between rank and sex in unimodal signals occur as a result of specific differences in signal combinations within a sensory mode?

5.4.8 Multimodal Signals

As is the case with unimodal signals above, the analysis here did not include complex multimodal signals. These signals are multimodal, but contain more than one component within at least one of the sensory modes. For example, it could be a complex bimodal signal like visual-visual-auditory, or a complex trimodal signal like auditory-auditory-visual-visual-tactile. Again, further research that incorporates these signals into the analysis may produce more contextually or meaning-based correlations in the dataset.

In addition, the analysis of multimodal signal compositions returned results for olfactory and tactile components that were not statistically significant, but they do appear to vary slightly and at the very least more than that for visual and auditory components. Should more research be conducted on additional *L. catta* populations, both in captivity and the wild, investigating these components of multimodal signals may produce more significant differences. Ideally a larger population size would be used, as well as a full analysis of the ranges in rank as opposed to the two extremes (dominant female, and lowest ranked male) as was used here. Perhaps limiting the multimodal analysis to these two available extremes in the sample population has limited some of the intelligibility of the variation in these two components, and so extending the analysis to include a few of the subordinate females if not all other remaining individuals would act to clarify any potential correlations between dominance rank and/or sex and multimodal signal composition.

5.4.9 Unimodal versus Multimodal

As a result of the finding that unimodal signals in ring-tailed lemurs appear to show more variation in composition based on rank and sex than multimodal signals do, more questions arise that can be addressed through future research. The two explanations for these results I propose are: 1) unimodal signals are more “flexible” in this species and can be influenced by idiosyncratic behaviour or by the individual’s dominance rank and sex, while multimodal signals are more “restricted” and must remain consistent across individuals to maintain signal meaning or intelligibility, or 2) that these results are merely reflective of the differences between unimodal and multimodal signals in the data they produce. The current analysis examining composition and frequencies is well suited for a unimodal analysis and can detect variation therein, but is perhaps not as well suited for an investigation of multimodal signals which may rely more on the variation of a signal’s meaning or context. I do not believe these two hypotheses to be entirely mutually exclusive, and together may in fact complement each other. However, additional research on the multimodal communication of ring-tailed lemurs in both captive and wild settings is needed to better clarify and examine these suggestions. Ideally this would either confirm the findings here, that unimodal signal compositions vary while multimodal signals remains relatively consistent, or provide the ground work for how to better detect variation in multimodal signals in this species and perhaps others.

5.4.10 The Environmental Significance

The environmental significance of these findings is beyond the scope of an investigation conducted with a captive population, let alone one located outside the natural habitat of this species. Nevertheless, I am confident this work will serve as a baseline for future investigation into this topic and at the very least is a glimpse into the influence of the social environment on communication in ring-tailed lemurs. With global climatic change becoming of more concern as time goes on, how habitat changes are impacting communicative strategies in different species broadly should be examined. This future investigation may uncover the level of adaptability possible in primate communication, which could reflect our own communicative origins, and act as an indicator for how well a species is adapting to anthropogenic changes to their landscape in different sensory channels (i.e. their "sound-scape", "scent-scape", and visibility or camouflage).

5.4.11 Multimodal Primatology Moving Forward: Proximate Suggestions

There are, in the most basic sense, two key ways to further examine multimodal communication: investigating it from both the proximate and the ultimate levels. As MacDougall-Shackleton (2011) argues, studying and integrating both of these levels of analysis is the only way to produce comprehensive understandings of animal behaviour and ecology. The proximate level of analysis addresses questions of "how" a behaviour occurs by examining the biological processes or mechanisms (i.e. genetic, neural, hormonal, cognitive/psychological) which cause that behaviour at the level of the individual or their generation (Fröhlich & van Schaik, 2018; MacDougall-Shackleton, 2011; Waller et al., 2013). The ultimate level on the other hand addresses questions of "why" a behaviour is performed by analysing that behaviour at the broader adaptive and evolutionary scales and aims to uncover the function of that behaviour (Fröhlich & van Schaik, 2018; MacDougall-Shackleton, 2011; Waller et al., 2013). It does not take long, however, to realize that both of these levels are inseparable when studying animal behaviour as a whole, which is an argument made by an increasing number of researchers (*see* Fröhlich and van Schaik, 2018; MacDougall-Shackleton, 2011; Waller et al., 2013). Multimodal communication investigations represent a particularly promising area of behavioural research for combining these two levels of analyses (Waller et al., 2013).

While investigation into the functional aspects (ultimate level) of multimodal communication have by far received the most attention (i.e. why does multimodal behaviour occur, what is the adaptive function), there is still a need for more comparative research across different species to establish definitively why this complex communicative method is adaptive (Fröhlich & van Schaik, 2018; Fröhlich et al., 2019). As mentioned previously, the majority of multimodal communication investigations in primates to date have been focused heavily on the Great Apes as the closest living relatives to humans, but this bias in current research limits our understanding of signals in different contexts and used by different species. As a result, variation in how multimodal signals are used across different social groupings and demographics, habitats, environments, and other contextual factors need to be addressed (Fröhlich & van Schaik, 2018). Following the recommendations made by MacDougall-Shackleton (2011), in order to better understand a particular behaviour, research should begin at the proximate level to establish the conditions and constraints needed to continue that research at the ultimate level, like the first stepping-stone in a study's trajectory. I strongly believe the next step in multimodal research needs to be an expansion further into hypotheses at the proximate level before examining those at and in combination with the ultimate level. A potential avenue to be explored would be my suggestion that unimodal signals are more reflective of the proximate level of ring-tailed lemur communication while multimodal communication is more reflective of the ultimate level of *L. catta* communication.

Some additional examples of areas where future research can be applied at the proximate level are outlined by Fröhlich and colleagues (2019) in their presentation of the main cognitive components of human communication: intentionality, reference, iconicity, combinatoriality, turn-taking, neural control and ontogenetic plasticity. In short, further work investigating the occurrence and presence of these cognitive components in non-Great Ape species is needed. Crucial to this is the establishment of better standards for data collection (i.e. which behaviours or displays to include or exclude) and clarifying the operational definitions used, particularly when transferring concepts from human cognitive science to primatology observations (Fröhlich et al., 2019).

5.5 Conclusion

In conclusion, I have been able to describe some of the behavioural patterns observed in a captive population of ring-tailed lemurs (*Lemur catta*), and analyzed the potential correlative factors that may be acting upon those same behaviours. The combination of small sample size (n=14) and idiosyncratic variation present in this study makes it challenging to draw many concrete or conclusive statements about ring-tailed lemur social communication as a whole. However, it is possible to address my questions within the context of this captive population at the very least. In this species, individual sex and rank appear to influence unimodal signalling more than age and troop affiliation do, but multimodal signals remain fairly consistent between individuals regardless of those same factors. Overall this investigation has contributed to the body of research on *L. catta* as well as that on multimodal communication in primates. Having conducted this research in a controlled setting, I am confident that these findings form a baseline from which further research into the contextual nuances of these results can be explored, in both captive settings and in the wild, to strengthen our understanding of lemur communication.

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Appendices

Appendix A: Partial maps of the DLC (not to scale)

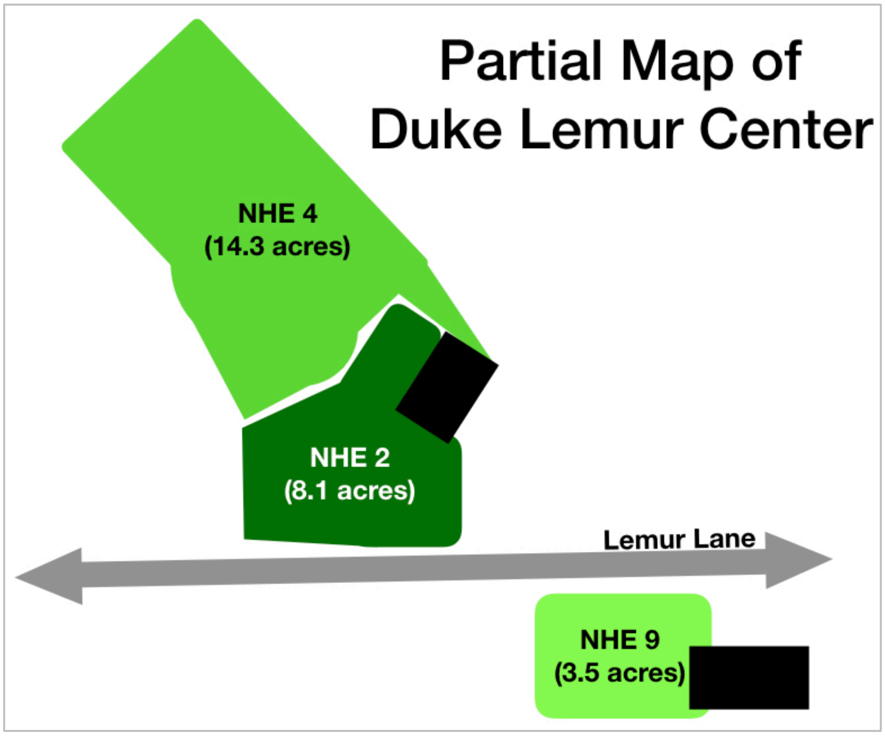


Figure A1: **Partial map of the Duke Lemur Center showing the Natural Habitat Enclosures (NHEs) for each of the three focal troops as well as the acreage. Troop 1 is from NHE 9, troop 2 from NHE 2, and Troop 3 from NHE 4.**

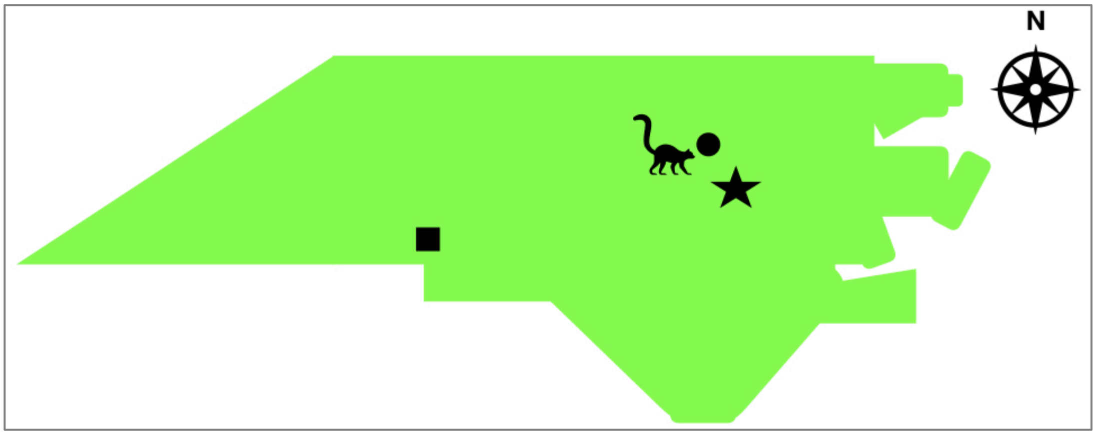


Figure A2: **Simplified map of North Carolina showing the relative location of the DLC (ring-tailed lemur shape) to the cities Durham (circle), Charlotte (square), and the state capitol Raleigh (star). The left of the state crosses into the Appalachian Mountains and the right side meets the Atlantic Ocean.**

Appendix B: Troop family trees

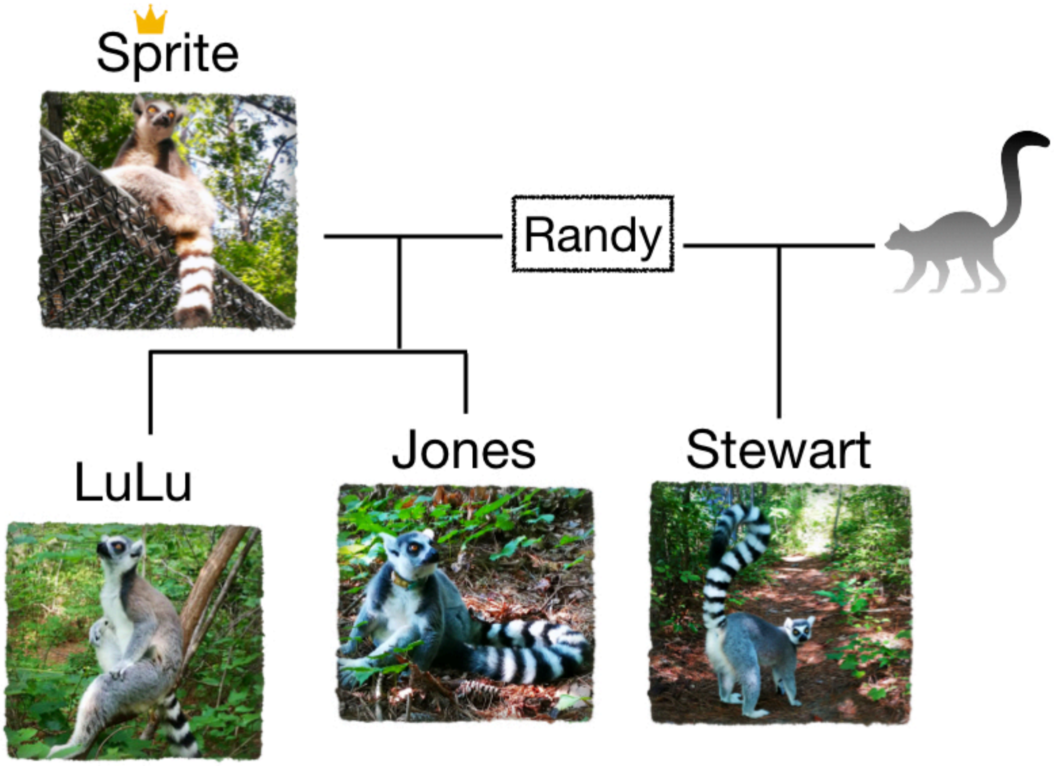


Figure B1: **Visual representation of troop 1. Photographs indicate individuals who were free-ranging together as a troop during the observation period. Dominant female Sprite, marked with a crown, is dam to LuLu (female) and Jones (male). Stewart (male) shares a sire (Randy) with Jones and Lulu. Photos taken by author at the DLC, 2019.**

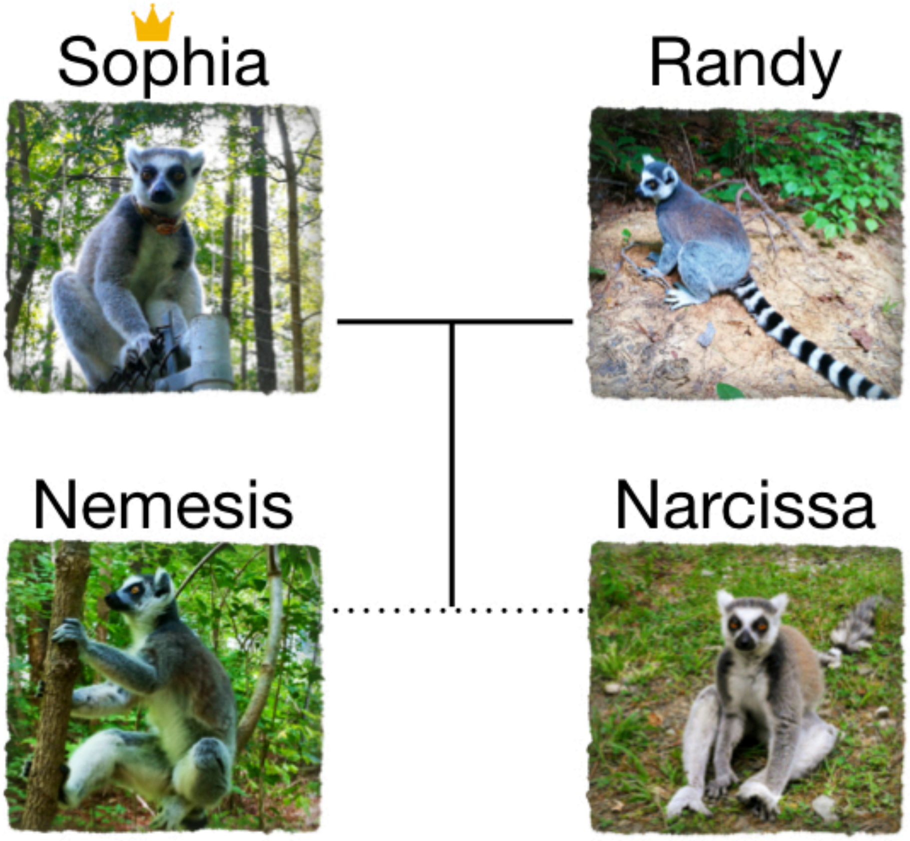


Figure B2: **Visual representation of troop 2. Photographs indicate individuals who were free-ranging together as a troop during the observation period. Dominant female Sophia, marked with a crown, is dam to twins Nemesis (female) and Narcissa (female). Randy (male) is the sire. Photos taken by author at the DLC, 2019.**

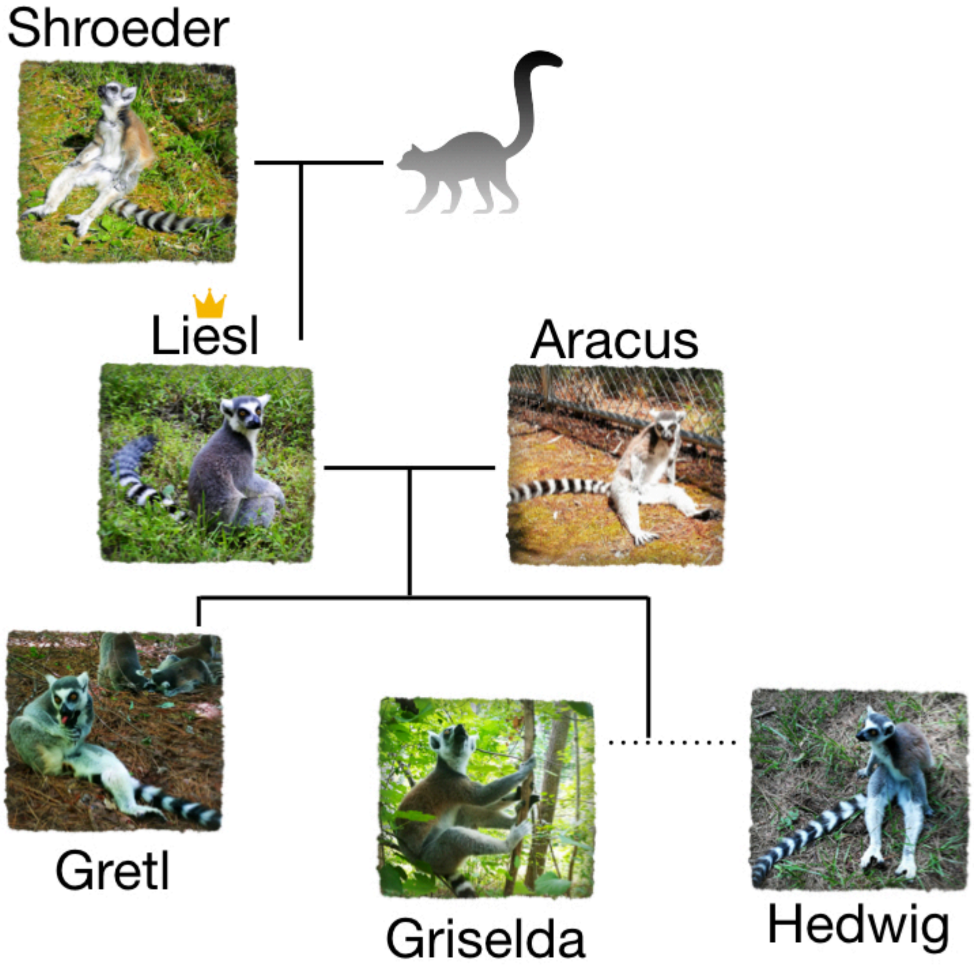
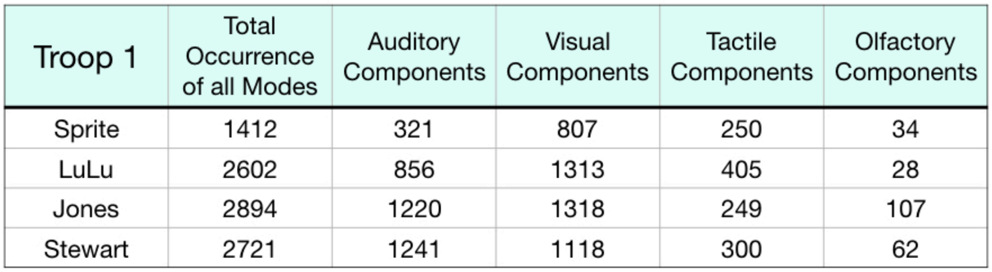


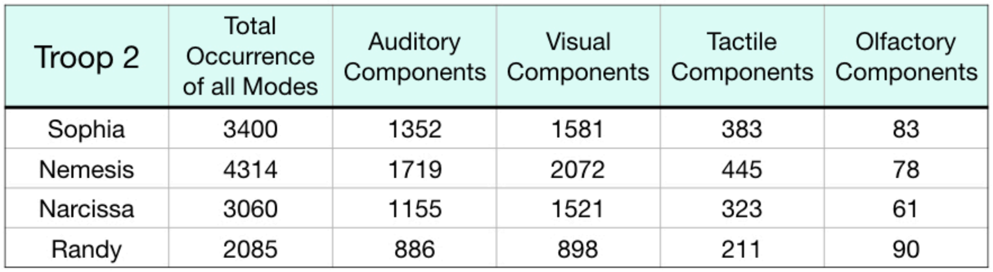
Figure B3: **Visual representation of troop 3. Photographs indicate individuals who were free-ranging together as a troop during the observation period. Dominant female Liesl, marked with a crown, is dam to Gretl (female), and twins Griselda (female) and Hedwig (female). Aracus (male) is the sire. Shroeder (female) is the dam of Liesl. Photos taken by author at the DLC, 2019.**

Appendix C: Data values for mode occurrence per troop



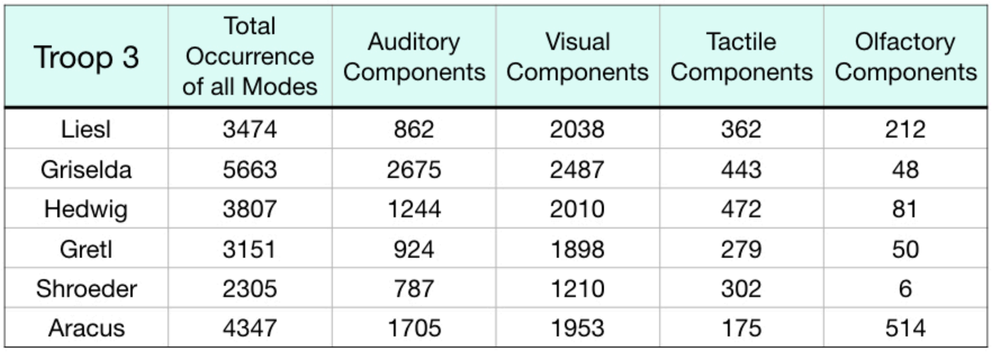
Troop 1	Total Occurrence of all Modes	Auditory Components	Visual Components	Tactile Components	Olfactory Components
Sprite	1412	321	807	250	34
LuLu	2602	856	1313	405	28
Jones	2894	1220	1318	249	107
Stewart	2721	1241	1118	300	62

Table C1: **Raw data for troop 1. Individuals listed in ranking order.**



Troop 2	Total Occurrence of all Modes	Auditory Components	Visual Components	Tactile Components	Olfactory Components
Sophia	3400	1352	1581	383	83
Nemesis	4314	1719	2072	445	78
Narcissa	3060	1155	1521	323	61
Randy	2085	886	898	211	90

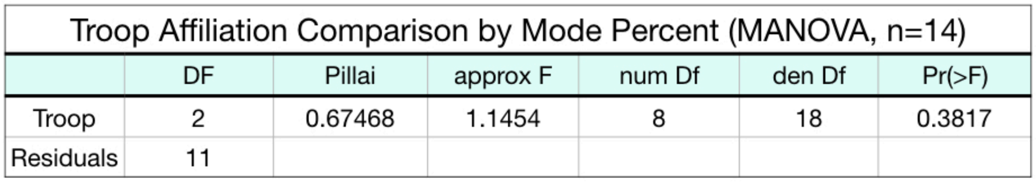
Table C2: **Raw data for troop 2. Individuals listed in ranking order.**



Troop 3	Total Occurrence of all Modes	Auditory Components	Visual Components	Tactile Components	Olfactory Components
Liesl	3474	862	2038	362	212
Griselda	5663	2675	2487	443	48
Hedwig	3807	1244	2010	472	81
Gretl	3151	924	1898	279	50
Shroeder	2305	787	1210	302	6
Aracus	4347	1705	1953	175	514

Table C3: **Raw data for troop 3. Individuals listed in ranking order.**

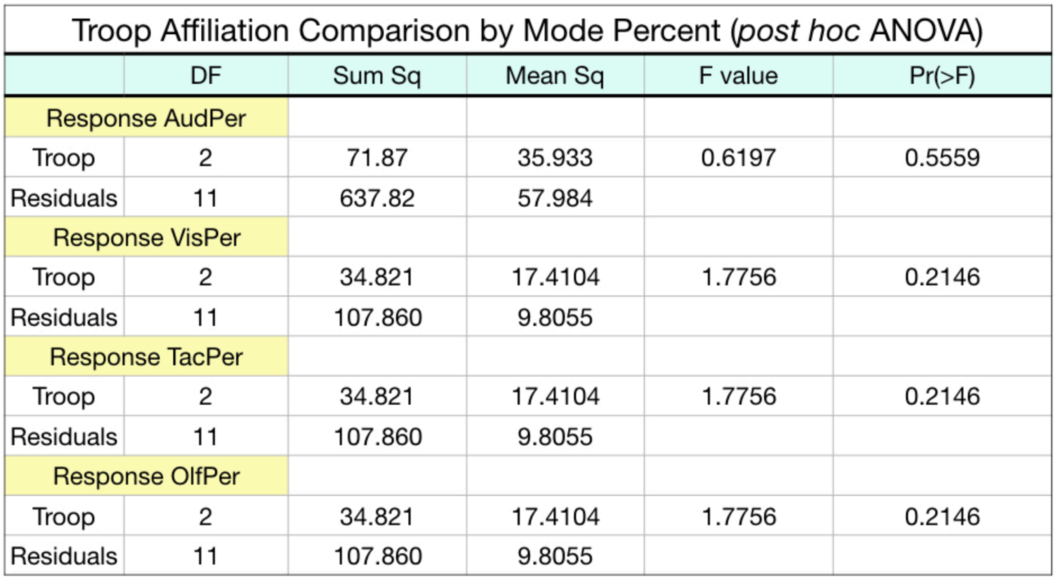
Appendix D: Numerical results for troop affiliation analysis



Troop Affiliation Comparison by Mode Percent (MANOVA, n=14)

	DF	Pillai	approx F	num Df	den Df	Pr(>F)
Troop	2	0.67468	1.1454	8	18	0.3817
Residuals	11					

Table D1: **Numerical results of the troop affiliation MANOVA. The Pillai test statistic is the default used to calculate the F-ratio. Reproduced from RStudio©.**

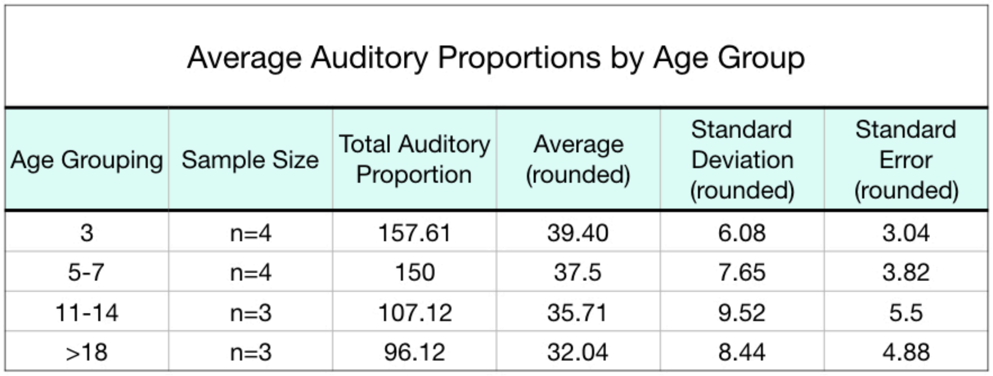


Troop Affiliation Comparison by Mode Percent (*post hoc* ANOVA)

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Response AudPer					
Troop	2	71.87	35.933	0.6197	0.5559
Residuals	11	637.82	57.984		
Response VisPer					
Troop	2	34.821	17.4104	1.7756	0.2146
Residuals	11	107.860	9.8055		
Response TacPer					
Troop	2	34.821	17.4104	1.7756	0.2146
Residuals	11	107.860	9.8055		
Response OlfPer					
Troop	2	34.821	17.4104	1.7756	0.2146
Residuals	11	107.860	9.8055		

Table D2: **Numerical results of the *post hoc* one-factor ANOVAs of the troop affiliation MANOVA. Where "AudPer", "VisPer", "TacPer", and "OlfPer" represent mode percent (proportions). Reproduced from RStudio©.**

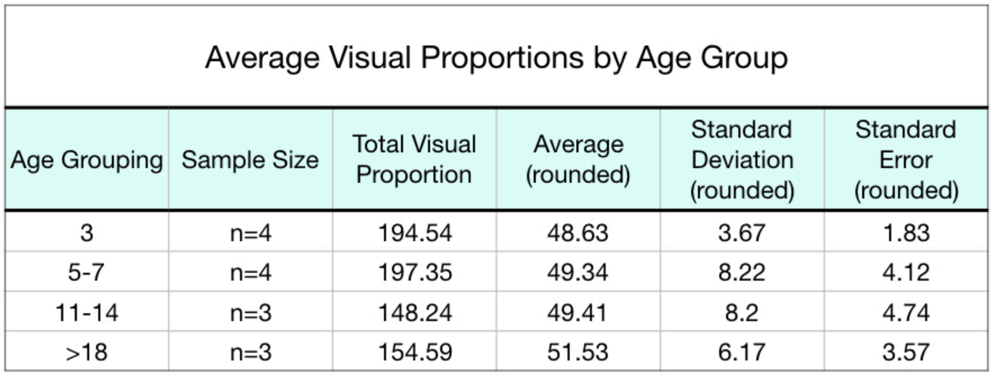
Appendix E: Data values for age group comparison



Average Auditory Proportions by Age Group

Age Grouping	Sample Size	Total Auditory Proportion	Average (rounded)	Standard Deviation (rounded)	Standard Error (rounded)
3	n=4	157.61	39.40	6.08	3.04
5-7	n=4	150	37.5	7.65	3.82
11-14	n=3	107.12	35.71	9.52	5.5
>18	n=3	96.12	32.04	8.44	4.88

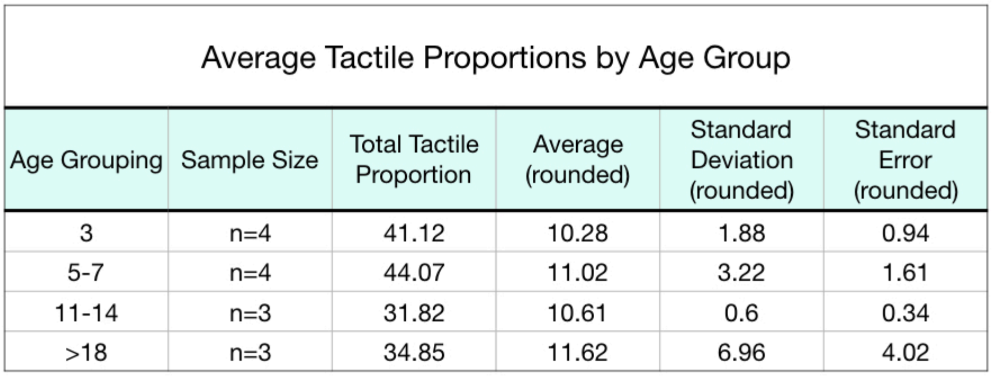
Table E1: **Data values for the age group analysis, examining the average auditory signal component proportions per age grouping.**



Average Visual Proportions by Age Group

Age Grouping	Sample Size	Total Visual Proportion	Average (rounded)	Standard Deviation (rounded)	Standard Error (rounded)
3	n=4	194.54	48.63	3.67	1.83
5-7	n=4	197.35	49.34	8.22	4.12
11-14	n=3	148.24	49.41	8.2	4.74
>18	n=3	154.59	51.53	6.17	3.57

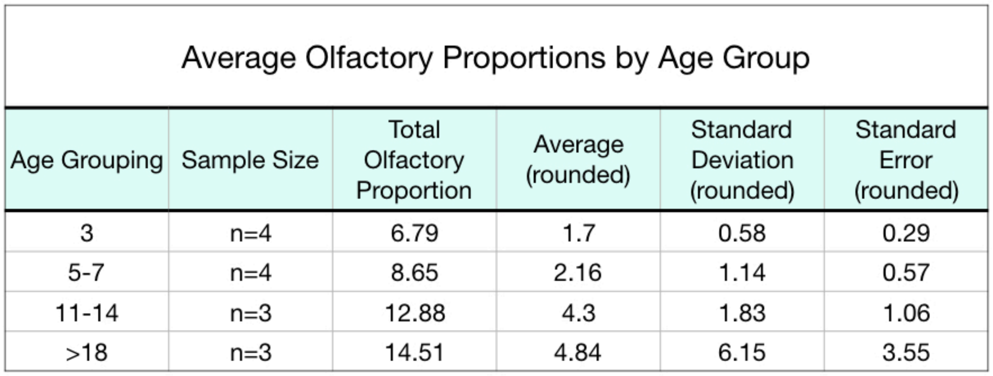
Table E2: **Data values for the age group analysis, examining the average visual signal component proportions per age grouping.**



Average Tactile Proportions by Age Group

Age Grouping	Sample Size	Total Tactile Proportion	Average (rounded)	Standard Deviation (rounded)	Standard Error (rounded)
3	n=4	41.12	10.28	1.88	0.94
5-7	n=4	44.07	11.02	3.22	1.61
11-14	n=3	31.82	10.61	0.6	0.34
>18	n=3	34.85	11.62	6.96	4.02

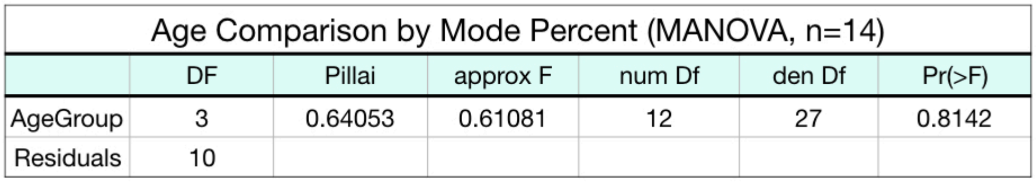
Table E3: **Data values for the age group analysis, examining the average tactile signal component proportions per age grouping.**



Average Olfactory Proportions by Age Group

Age Grouping	Sample Size	Total Olfactory Proportion	Average (rounded)	Standard Deviation (rounded)	Standard Error (rounded)
3	n=4	6.79	1.7	0.58	0.29
5-7	n=4	8.65	2.16	1.14	0.57
11-14	n=3	12.88	4.3	1.83	1.06
>18	n=3	14.51	4.84	6.15	3.55

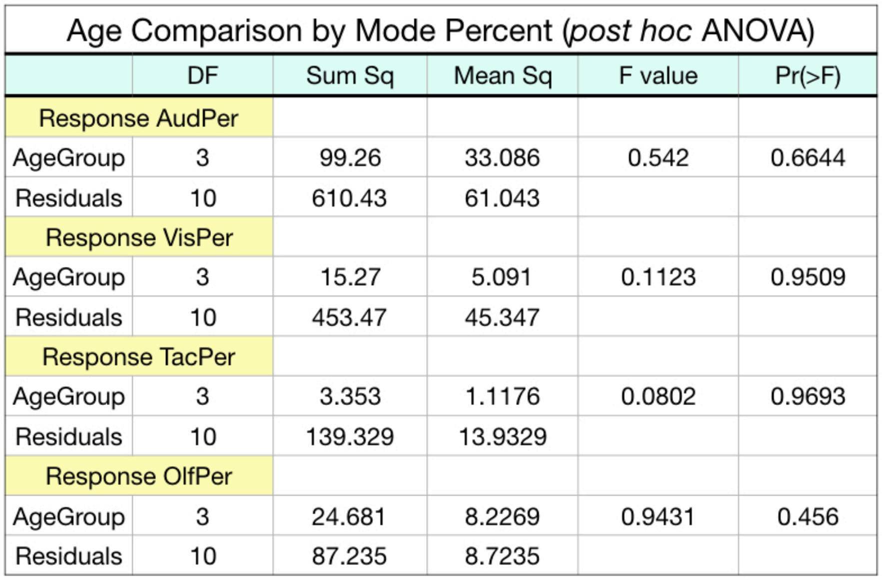
***Table E4:* Data values for the age group analysis, examining the average olfactory signal component proportions per age grouping.**



Age Comparison by Mode Percent (MANOVA, n=14)

	DF	Pillai	approx F	num Df	den Df	Pr(>F)
AgeGroup	3	0.64053	0.61081	12	27	0.8142
Residuals	10					

***Table E5:* Numerical results of the age comparison MANOVA. The Pillai test statistic is the default used to calculate the F-ratio. Reproduced from RStudio$^{©}$ (version 1.2.1335).**

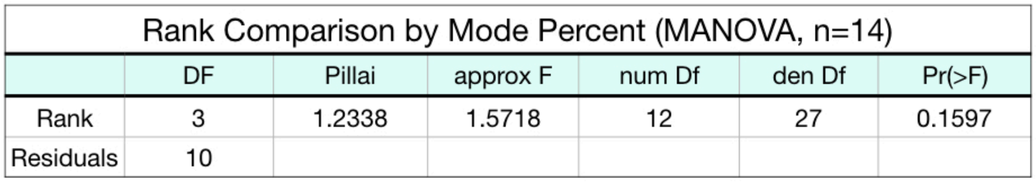


Age Comparison by Mode Percent (*post hoc* ANOVA)

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Response AudPer					
AgeGroup	3	99.26	33.086	0.542	0.6644
Residuals	10	610.43	61.043		
Response VisPer					
AgeGroup	3	15.27	5.091	0.1123	0.9509
Residuals	10	453.47	45.347		
Response TacPer					
AgeGroup	3	3.353	1.1176	0.0802	0.9693
Residuals	10	139.329	13.9329		
Response OlfPer					
AgeGroup	3	24.681	8.2269	0.9431	0.456
Residuals	10	87.235	8.7235		

***Table E6:* Numerical results of the *post hoc* analysis of the age comparison MANOVA. Reproduced from RStudio$^{©}$.**

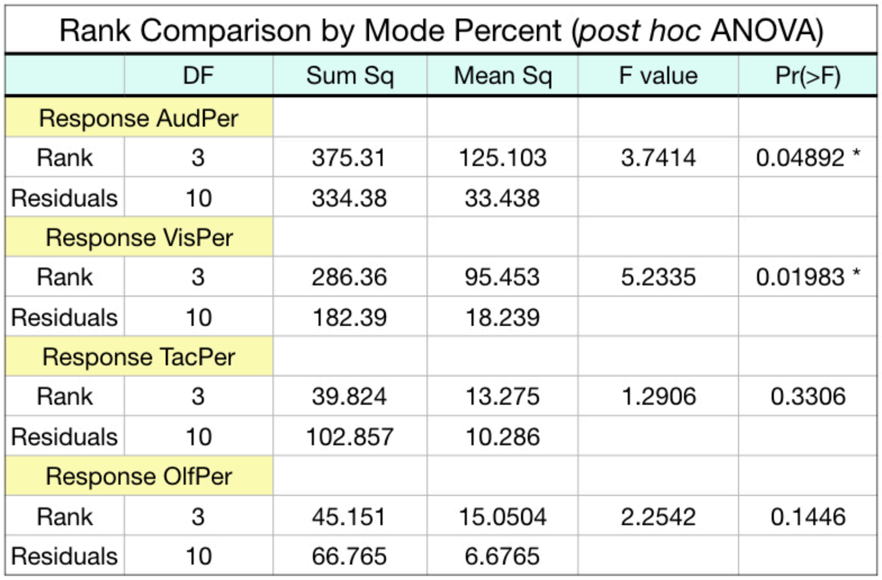
Appendix F: Numerical results for dominance rank analyses



Rank Comparison by Mode Percent (MANOVA, n=14)

	DF	Pillai	approx F	num Df	den Df	Pr(>F)
Rank	3	1.2338	1.5718	12	27	0.1597
Residuals	10					

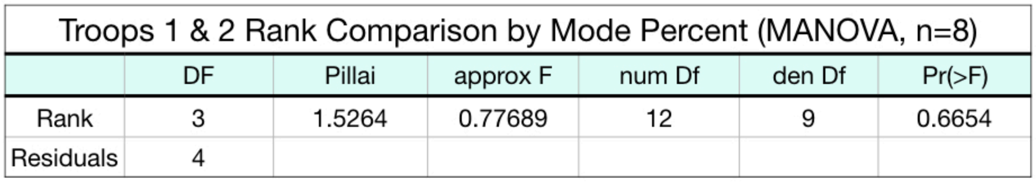
Table F1: **Numerical results of the dominance rank MANOVA. The Pillai test statistic is the default used to calculate the F-ratio. Reproduced from RStudio©.**



Rank Comparison by Mode Percent (*post hoc* ANOVA)

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Response AudPer					
Rank	3	375.31	125.103	3.7414	0.04892 *
Residuals	10	334.38	33.438		
Response VisPer					
Rank	3	286.36	95.453	5.2335	0.01983 *
Residuals	10	182.39	18.239		
Response TacPer					
Rank	3	39.824	13.275	1.2906	0.3306
Residuals	10	102.857	10.286		
Response OlfPer					
Rank	3	45.151	15.0504	2.2542	0.1446
Residuals	10	66.765	6.6765		

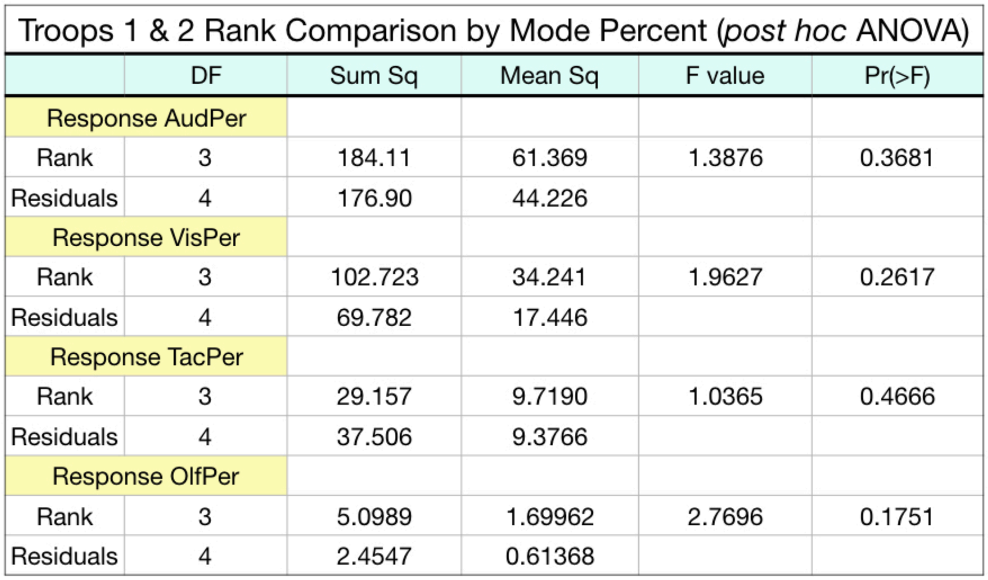
Table F2: **Numerical results of the** ***post hoc*** **analysis of the dominance rank MANOVA. Reproduced from RStudio©. Statistical significance at 0.05 marked by "*".**



Troops 1 & 2 Rank Comparison by Mode Percent (MANOVA, n=8)

	DF	Pillai	approx F	num Df	den Df	Pr(>F)
Rank	3	1.5264	0.77689	12	9	0.6654
Residuals	4					

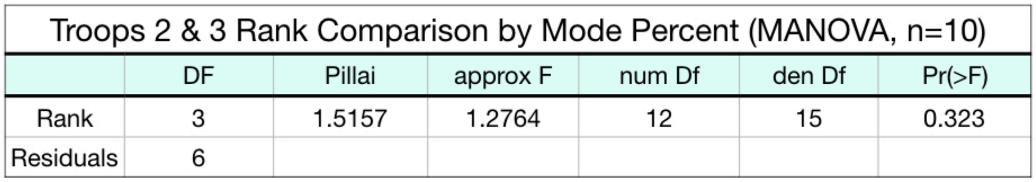
Table F3: **Numerical results of the dominance rank MANOVA for paired troops 1 and 2. The Pillai test statistic is the default used to calculate the F-ratio. Reproduced from RStudio©.**



Troops 1 & 2 Rank Comparison by Mode Percent (*post hoc* ANOVA)

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Response AudPer					
Rank	3	184.11	61.369	1.3876	0.3681
Residuals	4	176.90	44.226		
Response VisPer					
Rank	3	102.723	34.241	1.9627	0.2617
Residuals	4	69.782	17.446		
Response TacPer					
Rank	3	29.157	9.7190	1.0365	0.4666
Residuals	4	37.506	9.3766		
Response OlfPer					
Rank	3	5.0989	1.69962	2.7696	0.1751
Residuals	4	2.4547	0.61368		

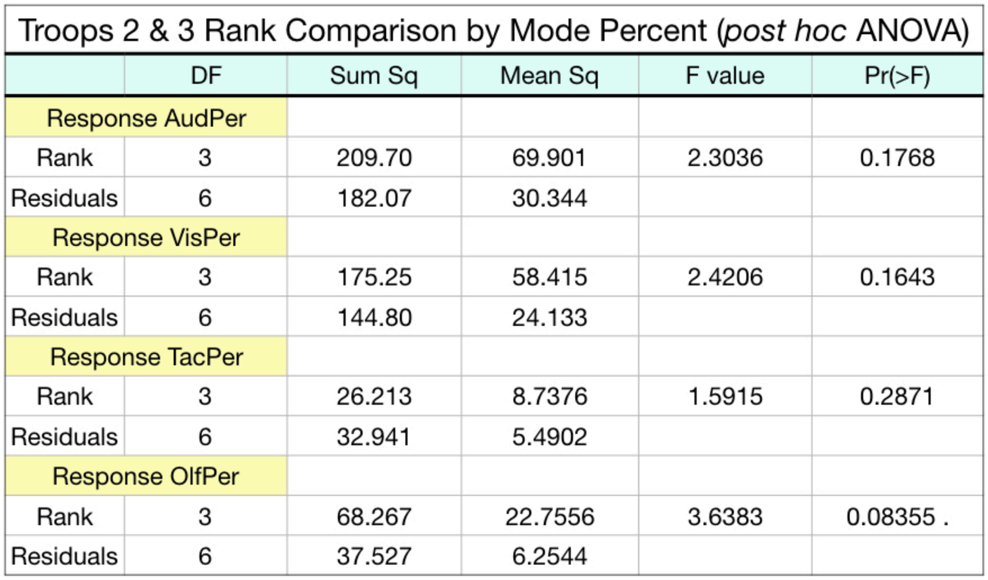
Table F4: **Numerical results of the *post hoc* analysis of the dominance rank MANOVA for paired troops 1 and 2. Reproduced from RStudio©.**



Troops 2 & 3 Rank Comparison by Mode Percent (MANOVA, n=10)

	DF	Pillai	approx F	num Df	den Df	Pr(>F)
Rank	3	1.5157	1.2764	12	15	0.323
Residuals	6					

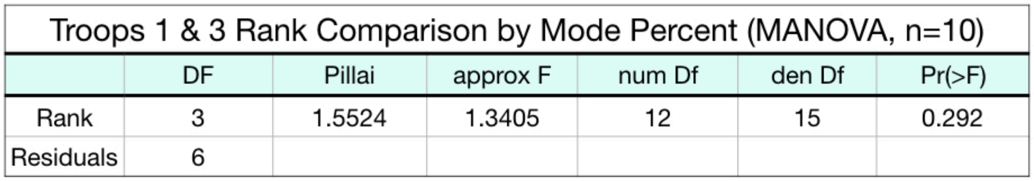
Table F5: **Numerical results of the dominance rank MANOVA for paired troops 2 and 3. The Pillai test statistic is the default used to calculate the F-ratio. Reproduced from RStudio©.**



Troops 2 & 3 Rank Comparison by Mode Percent (*post hoc* ANOVA)

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Response AudPer					
Rank	3	209.70	69.901	2.3036	0.1768
Residuals	6	182.07	30.344		
Response VisPer					
Rank	3	175.25	58.415	2.4206	0.1643
Residuals	6	144.80	24.133		
Response TacPer					
Rank	3	26.213	8.7376	1.5915	0.2871
Residuals	6	32.941	5.4902		
Response OlfPer					
Rank	3	68.267	22.7556	3.6383	0.08355 .
Residuals	6	37.527	6.2544		

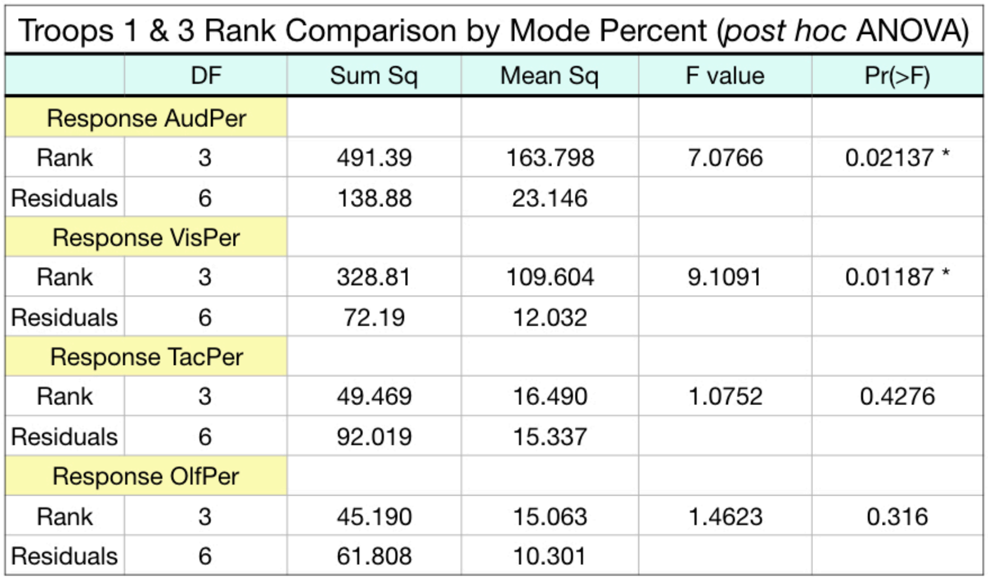
Table F6: **Numerical results of the *post hoc* analysis of the dominance rank MANOVA for paired troops 2 and 3. Reproduced from RStudio©. Statistical significance at 0.1 marked by ".".**



Troops 1 & 3 Rank Comparison by Mode Percent (MANOVA, n=10)

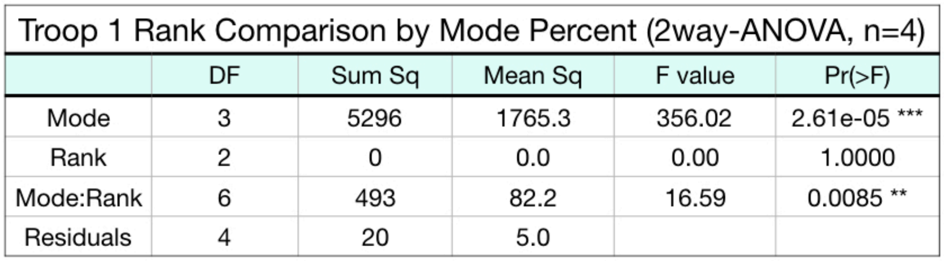
	DF	Pillai	approx F	num Df	den Df	Pr(>F)
Rank	3	1.5524	1.3405	12	15	0.292
Residuals	6					

Table F7: **Numerical results of the dominance rank MANOVA for paired troops 1 and 3. The Pillai test statistic is the default used to calculate the F-ratio. Reproduced from RStudio©.**



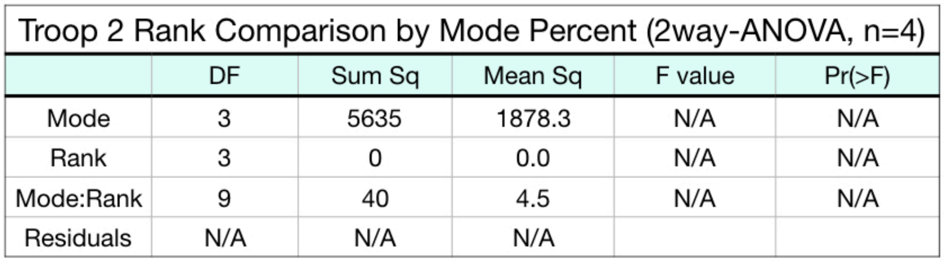
Troops 1 & 3 Rank Comparison by Mode Percent (*post hoc* ANOVA)					
	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Response AudPer					
Rank	3	491.39	163.798	7.0766	0.02137 *
Residuals	6	138.88	23.146		
Response VisPer					
Rank	3	328.81	109.604	9.1091	0.01187 *
Residuals	6	72.19	12.032		
Response TacPer					
Rank	3	49.469	16.490	1.0752	0.4276
Residuals	6	92.019	15.337		
Response OlfPer					
Rank	3	45.190	15.063	1.4623	0.316
Residuals	6	61.808	10.301		

Table F8: **Numerical results of the *post hoc* analysis of the dominance rank MANOVA for paired troops 1 and 3. Reproduced from RStudio©. Statistical significance at 0.05 marked by "*".**



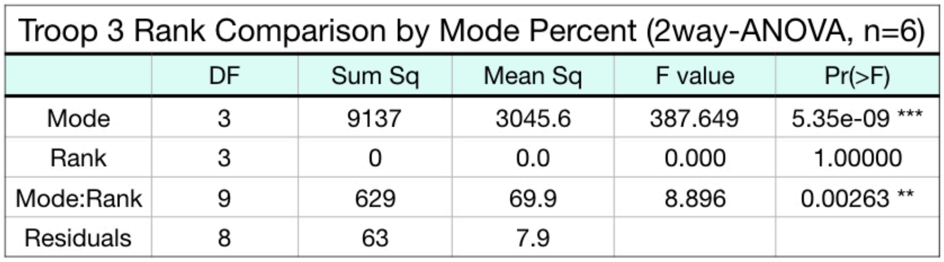
Troop 1 Rank Comparison by Mode Percent (2way-ANOVA, n=4)					
	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Mode	3	5296	1765.3	356.02	2.61e-05 ***
Rank	2	0	0.0	0.00	1.0000
Mode:Rank	6	493	82.2	16.59	0.0085 **
Residuals	4	20	5.0		

Table F9: **Numerical results of the dominance rank 2-way ANOVA for troop 1. Reproduced from RStudio©. Statistical significance at 0.01 marked by "**", at 0.001 by "***".**



Troop 2 Rank Comparison by Mode Percent (2way-ANOVA, n=4)					
	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Mode	3	5635	1878.3	N/A	N/A
Rank	3	0	0.0	N/A	N/A
Mode:Rank	9	40	4.5	N/A	N/A
Residuals	N/A	N/A	N/A		

Table F10: **Numerical results of the dominance rank 2-way ANOVA for troop 2. Reproduced from RStudio©.**

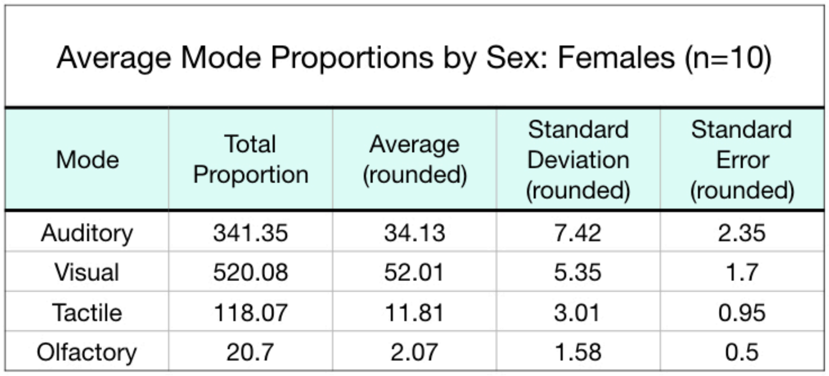


Troop 3 Rank Comparison by Mode Percent (2way-ANOVA, n=6)

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Mode	3	9137	3045.6	387.649	5.35e-09 ***
Rank	3	0	0.0	0.000	1.00000
Mode:Rank	9	629	69.9	8.896	0.00263 **
Residuals	8	63	7.9		

Table F11: **Numerical results of the dominance rank 2-way ANOVA for troop 3. Reproduced from RStudio$^{©}$. Statistical significance at 0.01 marked by "**", at 0.001 by "***".**

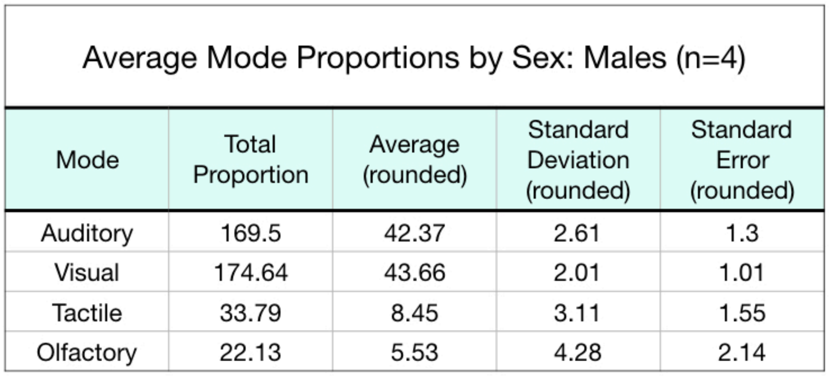
Appendix G: Data values for sex comparison



Average Mode Proportions by Sex: Females (n=10)

Mode	Total Proportion	Average (rounded)	Standard Deviation (rounded)	Standard Error (rounded)
Auditory	341.35	34.13	7.42	2.35
Visual	520.08	52.01	5.35	1.7
Tactile	118.07	11.81	3.01	0.95
Olfactory	20.7	2.07	1.58	0.5

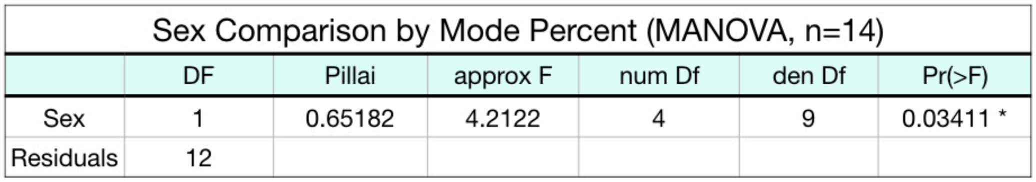
Table G2: **Female data values for the sex analysis, examining the average signal component proportions by mode, per sex.**



Average Mode Proportions by Sex: Males (n=4)

Mode	Total Proportion	Average (rounded)	Standard Deviation (rounded)	Standard Error (rounded)
Auditory	169.5	42.37	2.61	1.3
Visual	174.64	43.66	2.01	1.01
Tactile	33.79	8.45	3.11	1.55
Olfactory	22.13	5.53	4.28	2.14

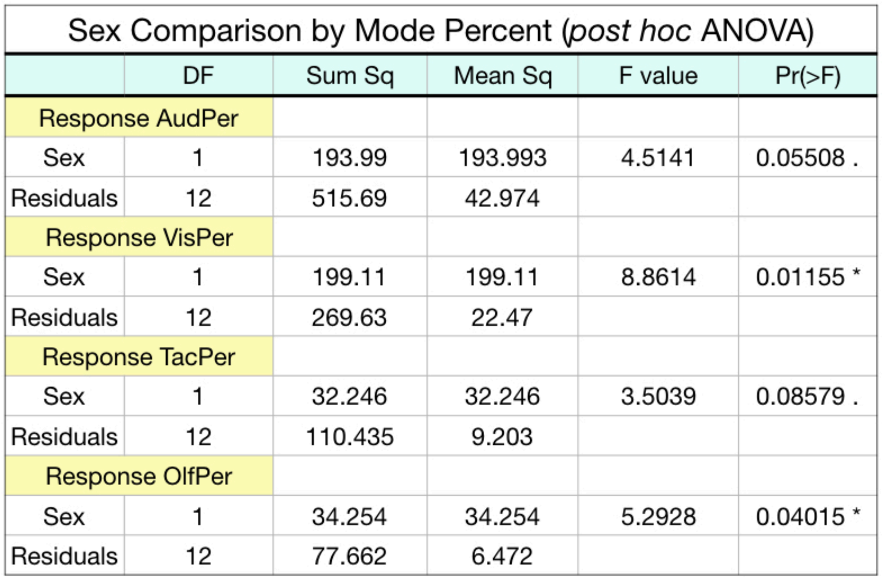
Table G2: **Male data values for the sex analysis, examining the average signal component proportions by mode, per sex.**



Sex Comparison by Mode Percent (MANOVA, n=14)

	DF	Pillai	approx F	num Df	den Df	Pr(>F)
Sex	1	0.65182	4.2122	4	9	0.03411 *
Residuals	12					

Table G3: **Numerical results of the sex comparison MANOVA. The Pillai test statistic is the default used to calculate the F-ratio. Reproduced from RStudio©. Statistical significance at 0.05 marked by "*".**

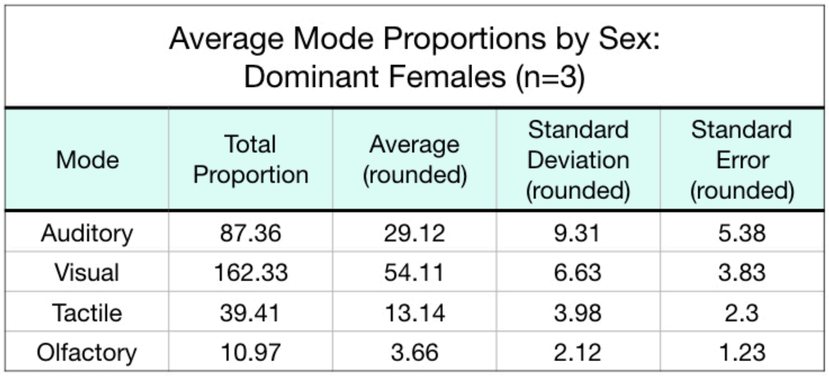


Sex Comparison by Mode Percent (*post hoc* ANOVA)

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Response AudPer					
Sex	1	193.99	193.993	4.5141	0.05508 .
Residuals	12	515.69	42.974		
Response VisPer					
Sex	1	199.11	199.11	8.8614	0.01155 *
Residuals	12	269.63	22.47		
Response TacPer					
Sex	1	32.246	32.246	3.5039	0.08579 .
Residuals	12	110.435	9.203		
Response OlfPer					
Sex	1	34.254	34.254	5.2928	0.04015 *
Residuals	12	77.662	6.472		

Table G4: **Numerical results of the *post hoc* analysis of the sex comparison MANOVA. Reproduced from RStudio©. Statistical significance at 0.1 marked by ".", at 0.05 by "*".**

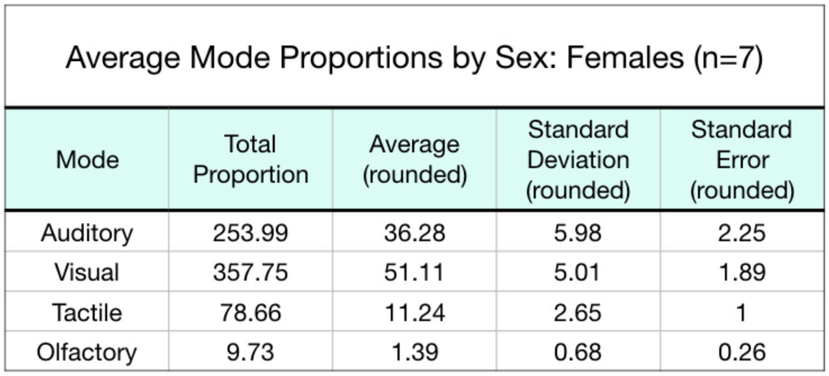
Appendix H: Data values for rank & sex comparison



Average Mode Proportions by Sex:
Dominant Females (n=3)

Mode	Total Proportion	Average (rounded)	Standard Deviation (rounded)	Standard Error (rounded)
Auditory	87.36	29.12	9.31	5.38
Visual	162.33	54.11	6.63	3.83
Tactile	39.41	13.14	3.98	2.3
Olfactory	10.97	3.66	2.12	1.23

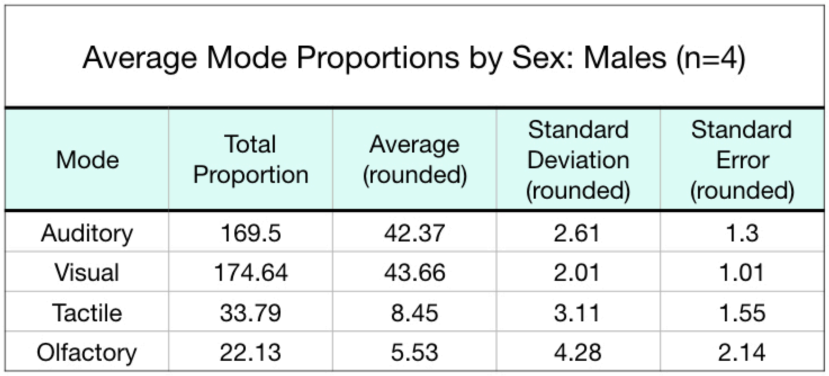
Table H1: **Average dominant female data values for the rank and sex analysis, examining the average signal component proportions by mode, per sex including dominant female rank.**



Average Mode Proportions by Sex: Females (n=7)

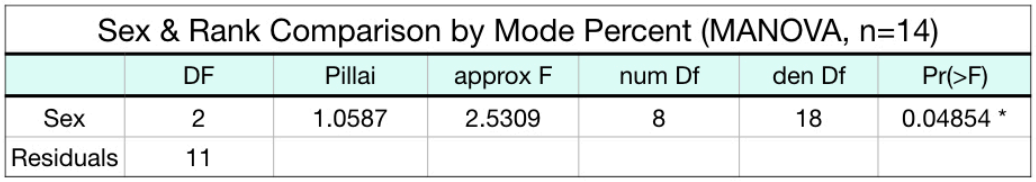
Mode	Total Proportion	Average (rounded)	Standard Deviation (rounded)	Standard Error (rounded)
Auditory	253.99	36.28	5.98	2.25
Visual	357.75	51.11	5.01	1.89
Tactile	78.66	11.24	2.65	1
Olfactory	9.73	1.39	0.68	0.26

Table H2: **Average female data values for the rank and sex analysis, examining the average signal component proportions by mode, per sex including dominant female rank.**



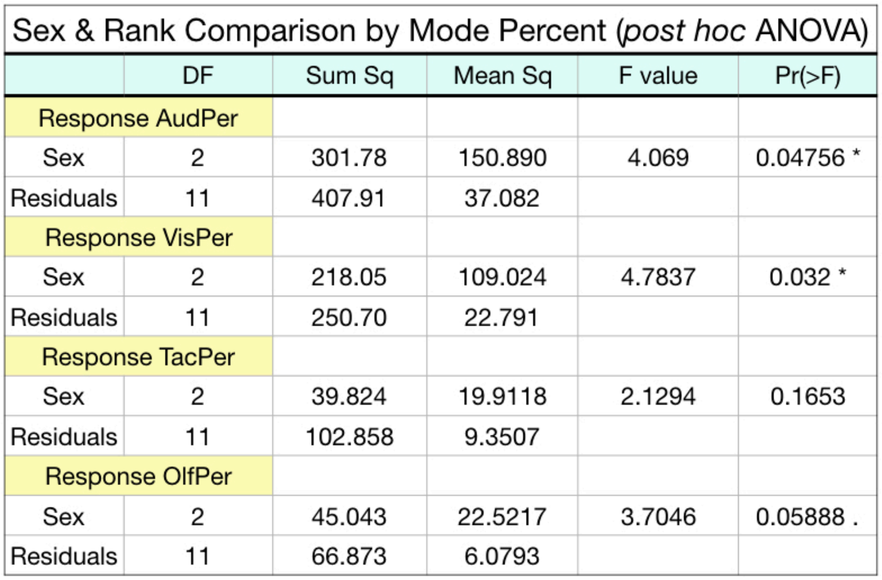
Average Mode Proportions by Sex: Males (n=4)				
Mode	Total Proportion	Average (rounded)	Standard Deviation (rounded)	Standard Error (rounded)
Auditory	169.5	42.37	2.61	1.3
Visual	174.64	43.66	2.01	1.01
Tactile	33.79	8.45	3.11	1.55
Olfactory	22.13	5.53	4.28	2.14

Table H3: **Average male data values for the rank and sex analysis, examining the average signal component proportions by mode, per sex including dominant female rank.**



Sex & Rank Comparison by Mode Percent (MANOVA, n=14)						
	DF	Pillai	approx F	num Df	den Df	Pr(>F)
Sex	2	1.0587	2.5309	8	18	0.04854 *
Residuals	11					

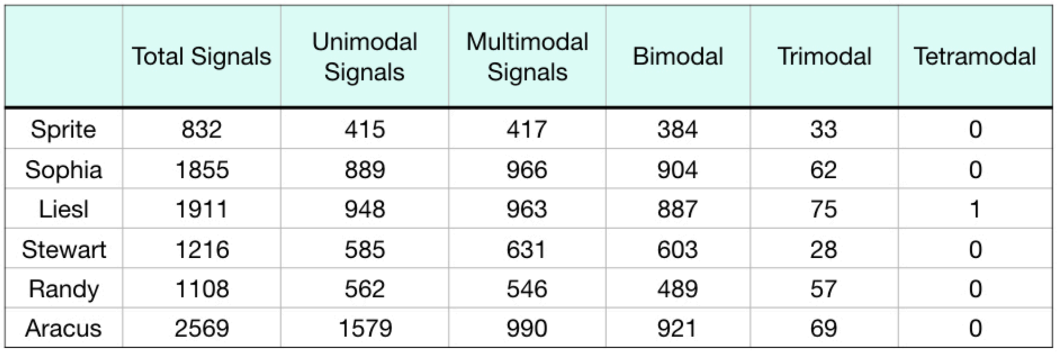
Table H4: **Numerical results of the rank and sex MANOVA. The Pillai test statistic is the default used to calculate the F-ratio. Reproduced from RStudio©. Statistical significance at 0.05 marked by "*".**



Sex & Rank Comparison by Mode Percent (*post hoc* ANOVA)					
	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Response AudPer					
Sex	2	301.78	150.890	4.069	0.04756 *
Residuals	11	407.91	37.082		
Response VisPer					
Sex	2	218.05	109.024	4.7837	0.032 *
Residuals	11	250.70	22.791		
Response TacPer					
Sex	2	39.824	19.9118	2.1294	0.1653
Residuals	11	102.858	9.3507		
Response OlfPer					
Sex	2	45.043	22.5217	3.7046	0.05888 .
Residuals	11	66.873	6.0793		

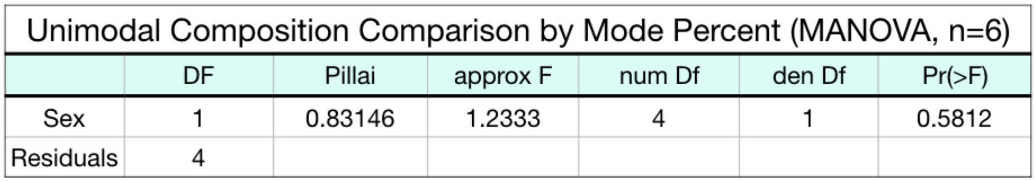
Table H5: **Numerical results of the *post hoc* analysis of the rank and sex MANOVA. Reproduced from RStudio©. Statistical significance at 0.1 marked by ".", at 0.05 by "*".**

Appendix I: Numerical results for signal-type & composition analyses



	Total Signals	Unimodal Signals	Multimodal Signals	Bimodal	Trimodal	Tetramodal
Sprite	832	415	417	384	33	0
Sophia	1855	889	966	904	62	0
Liesl	1911	948	963	887	75	1
Stewart	1216	585	631	603	28	0
Randy	1108	562	546	489	57	0
Aracus	2569	1579	990	921	69	0

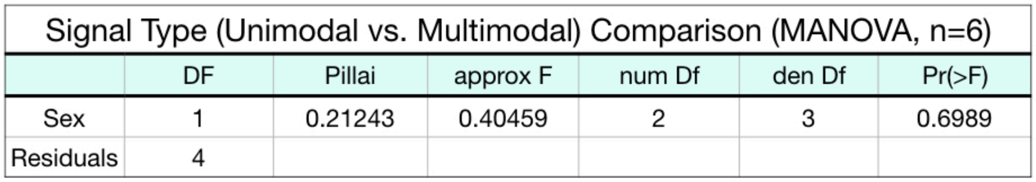
Table I1: **Data values for the signal-type (unimodal versus multimodal) analysis.**



Unimodal Composition Comparison by Mode Percent (MANOVA, n=6)

	DF	Pillai	approx F	num Df	den Df	Pr(>F)
Sex	1	0.83146	1.2333	4	1	0.5812
Residuals	4					

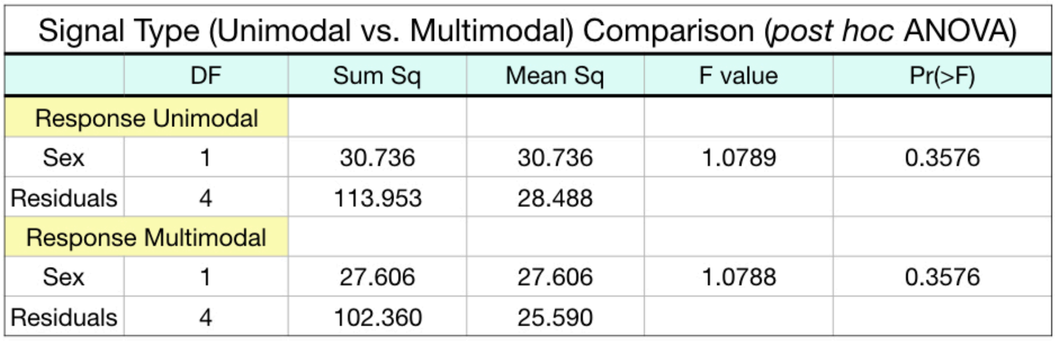
Table I2: **Numerical results of the signal type MANOVA, comparing proportion of unimodal and multimodal signals. The Pillai test statistic is the default used to calculate the F-ratio. Reproduced from RStudio©.**



Signal Type (Unimodal vs. Multimodal) Comparison (MANOVA, n=6)

	DF	Pillai	approx F	num Df	den Df	Pr(>F)
Sex	1	0.21243	0.40459	2	3	0.6989
Residuals	4					

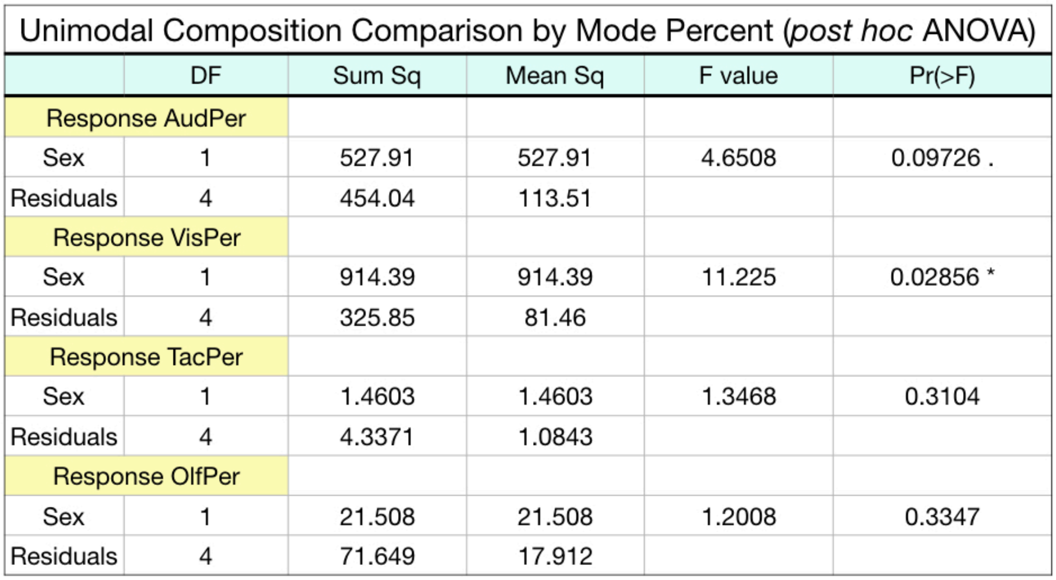
Table I3: **Numerical results of the *post hoc* analysis of the signal type MANOVA, comparing proportion of unimodal and multimodal signals. Reproduced from RStudio©.**



Signal Type (Unimodal vs. Multimodal) Comparison (*post hoc* ANOVA)

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Response Unimodal					
Sex	1	30.736	30.736	1.0789	0.3576
Residuals	4	113.953	28.488		
Response Multimodal					
Sex	1	27.606	27.606	1.0788	0.3576
Residuals	4	102.360	25.590		

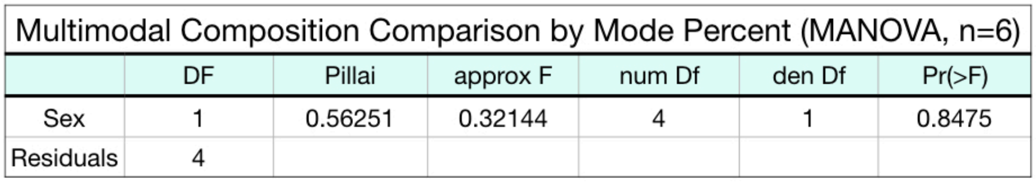
Table I4: **Numerical results of the unimodal signal composition MANOVA, comparing proportion of signal components by mode. The Pillai test statistic is the default used to calculate the F-ratio. Reproduced from RStudio©.**



Unimodal Composition Comparison by Mode Percent (*post hoc* ANOVA)

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Response AudPer					
Sex	1	527.91	527.91	4.6508	0.09726 .
Residuals	4	454.04	113.51		
Response VisPer					
Sex	1	914.39	914.39	11.225	0.02856 *
Residuals	4	325.85	81.46		
Response TacPer					
Sex	1	1.4603	1.4603	1.3468	0.3104
Residuals	4	4.3371	1.0843		
Response OlfPer					
Sex	1	21.508	21.508	1.2008	0.3347
Residuals	4	71.649	17.912		

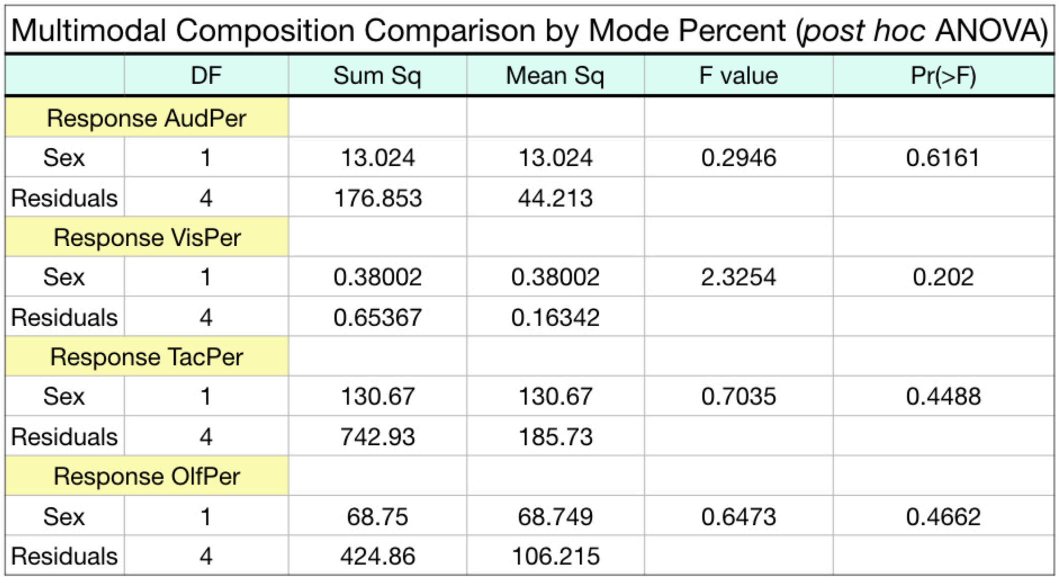
Table I5: **Numerical results of the** ***post hoc*** **analysis of the unimodal signal composition MANOVA. Reproduced from RStudio©. Statistical significance at 0.1 marked by ".", at 0.05 by "*".**



Multimodal Composition Comparison by Mode Percent (MANOVA, n=6)

	DF	Pillai	approx F	num Df	den Df	Pr(>F)
Sex	1	0.56251	0.32144	4	1	0.8475
Residuals	4					

Table I6: **Numerical results of the multimodal signal composition MANOVA, comparing proportion of signal components by mode. The Pillai test statistic is the default used to calculate the F-ratio. Reproduced from RStudio$^{©}$.**



Multimodal Composition Comparison by Mode Percent (*post hoc* ANOVA)

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Response AudPer					
Sex	1	13.024	13.024	0.2946	0.6161
Residuals	4	176.853	44.213		
Response VisPer					
Sex	1	0.38002	0.38002	2.3254	0.202
Residuals	4	0.65367	0.16342		
Response TacPer					
Sex	1	130.67	130.67	0.7035	0.4488
Residuals	4	742.93	185.73		
Response OlfPer					
Sex	1	68.75	68.749	0.6473	0.4662
Residuals	4	424.86	106.215		

Table I7: **Numerical results of the *post hoc* analysis of the multimodal signal composition MANOVA. Reproduced from RStudio$^{©}$.**

Curriculum Vitae

Name: Hilary Hager

Post-secondary Education and Degrees:

University of Toronto, St. George
Toronto, Ontario, Canada
2014-2018 H.B.A. with high distinction

Western University
London, Ontario, Canada
2018-2020 M.A.
Supervisor: Dr. Ian C. Colquhoun

Honours and Awards:

Western Graduate Research Scholarship (WGRS)
Department of Anthropology, Western University
2019-2020

Christine Nelson Graduate Award for Research in Archaeology and Bioarcheology
Department of Anthropology, Western University
Summer 2019

Western Graduate Research Scholarship (WGRS)
Department of Anthropology, Western University
2018-2019

Dean’s List Scholar, Faculty of Arts and Science
University of Toronto, St. George
2018

Innis College Alumni Association Scholarship
University of Toronto, St. George
2017-2018

Dean’s List Scholar, Faculty of Arts and Science
University of Toronto, St. George
2017

Innis College Exceptional Achievement Award
University of Toronto, St. George
2016-2017

Dean’s List Scholar, Faculty of Arts and Science
University of Toronto, St. George
2016

Innis College Exceptional Achievement Award
University of Toronto, St. George
2015-2016

Dean’s List Scholar, Faculty of Arts and Science
University of Toronto, St. George
2015

Entrance Scholarship: Innis College “Kitchen Sink” Award
University of Toronto, St. George
2014-2015

Related Work Experience

Teaching Assistant
Anthropology Department, Western University
2020: ANTHRO 1022B – Introduction to Biological Anthropology and Archaeology
2019: ANTHRO 2265F – Primate Behaviour
2019: ANTHRO 2226B – Biological Anthropology
2018: ANTHRO 1026F – Introduction to Biological Anthropology and Archaeology

Related Volunteer Experience

STEM Outreach Event, Presenter and Activity Runner
Hosted in partnership with the Canadian Association for Girls in Science (CAGIS)
“Evolutionary Anthropology: An Introduction to Behavioural Primatology”
Department of Anthropology, Western University
April 2019

Publications:

Hager, Hilary. (2020). “Investigating Communicative Frequencies and Multimodality in Ring-Tailed Lemurs (*Lemur catta*)”. Thesis results presented at the 8th annual Western Anthropology Graduate Student (WAGS) Conference, Western University, London, Ontario, Canada. ***cancelled due to COVID-19***

Hager, Hilary. (2020). “Frequencies of Communicative Modes in Ring-Tailed Lemurs (*Lemur catta*)”. Preliminary results presented at the annual Environment and Sustainability (E&S) Student Conference, EnviroCon, as a 3 Minute Thesis “Lightning Talk” hosted by the graduate students of the E&S collaborative specialization, Western University, London, Ontario, Canada. ***cancelled due to COVID-19***
Also presented at – the annual 3 Minute Thesis “Gong Show” hosted by the Anthropology Department, Western University, London, Ontario, Canada. (2019)

Hager, Hilary & Ian Colquhoun. (2019). "Investigating Communicative Frequencies and Multimodality in Ring-Tailed Lemurs (*Lemur catta*)". Poster presented at the 47th Annual Meeting for the Canadian Association for Physical Anthropology (CAPA), Banff, Alberta, Canada.

Hager, Hilary. (2019). "Communicative Frequencies in *Lemur catta* (ring-tailed lemurs)". Preliminary results presented at the Anthropology Graduate Research Seminar, Department of Anthropology, Western University, London, Ontario, Canada.

Hager, Hilary. (2019). "Social Hierarchy in *Lemur catta*: How Dominance Influences Communicative Mode Frequencies". Thesis research outline presented at the 7th annual Western Anthropology Graduate Student (WAGS) Conference, Western University, London, Ontario, Canada.

Hager, Hilary. (2018). "Determining the Upper Hand: An Investigation of Laterality on the Individual Level in Captive *Hylobates lar*". Independent research presented at the Arts and Science Students' Union (ASSU) Undergraduate Research Conference, University of Toronto, Toronto, Ontario, Canada.
Also presented at – Divinations: The Cross-Disciplinary Anthropology Undergraduate Colloquium, University of Toronto, Toronto, Ontario, Canada. (2017)

Non-Peer Reviewed Publications:
Hager, Hilary. (2020 *in press*). "*Decolonizing Extinction: The Work of Care in Orangutan Rehabilitation* by Juno Salazar Parreñas." *Contingent Horizons: The York University Student Journal of Anthropology*, York University, Toronto. 6.

Hager, Hilary. (2018). "A Whole New World: The Complex Development of the Human Infant Gut Microbiome." *Anthropology Undergraduate Journal*, University of Toronto, Toronto. 6, 19-31.

Hager, Hilary. (2015). "Culture, Identity, and Language: An Anthropological Perspective on Linguistic Boarders." *Anthropology Undergraduate Journal*, University of Toronto, Toronto. 4, 26-31.