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A theoretical consideration: Understanding primate polyspecific associations through current literature of primate predation and communication

by

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A thesis submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

MASTERS OF ANTHROPOLOGY

Major: Biological Anthropology

Program of Study Committee:
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The student author, whose presentation of the scholarship herein was approved by the program of study committee, is solely responsible for the content of this thesis. The Graduate College will ensure this thesis is globally accessible and will not permit alterations after a degree is conferred.

Iowa State University

Ames, Iowa

2018

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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ABSTRACT

Primates are a unique taxon of organisms found to have complex communication, behavior, sociality and in turn, life histories. One of the areas of primate study with relatively little current knowledge is regarding natural polyspecific interactions in which two different species interact in a mutualistic or commensalistic relation suggested to be due to predation threats or foraging benefits. While polyspecific associations have been identified in a wide array of organisms including primate species, the causes are not always clear. Causes are suggested to include reducing predation threats and the ability to communicate information, particularly about predators. This paper will review the current knowledge on primate predation, vocal communication, and naturally occurring polyspecific associations before highlighting the current gaps in the literature. It will attempt to show what is presently understood about the influence of predation on behaviors, knowledge of communication systems, and known polyspecific interactions across the Order Primates. The current openings in the subject materials will be discussed and steps forward will be suggested. A new method of understanding polyspecific interactions and the primate life features related with the associations through different scopes will be presented as a new direction for the field.

CHAPTER 1. INTRODUCTION

There are many different characteristics key to primate social systems, life histories, and individual lives. One feature of primate life that is unique compared to other characteristics is the presence of polyspecific associations. Polyspecific interactions are relationships between two different species that have a suggested foraging and anti-predation benefit. There are related features of primate life including predation and communication, both suggested to be key components of instigating and using polyspecific interactions.

After an introduction to the primates, this paper will review a portion of the current literature knowledge of each feature will be followed by a review of the current methods of the field and the implications for understanding polyspecific associations. The review percentage of current knowledge is approximately ten percent of the published works, though a wide range of information is covered in this text. After a complete review of both literature and methods, this paper will offer reflections and recommendations for the future of the field in each of these areas by identifying current gaps in the knowledge. The recommendations are to serve as guides to future primate studies by suggesting methods and modes of thinking for the field. The paper will conclude with suggested new viewpoints for understanding polyspecific interactions and the associated primate life features.

In regard to the human species' relationship with each of these reviewed characteristics, this paper will lightly touch on the current understanding of humans use and interaction with predation, communication, and polyspecific interactions. This paper will focus primarily on non-human primates as to not digress to extensive detail on human behaviors or current understanding of ethnoprimatology.

Primates

The Order Primates includes some of the most complex species on Earth in regard to their cognition, behavior, and extended life history. Primate species range across three continents and fill a wide variety of ecosystem niches. Primate species are found around the world, are each unique, and have a diverse array of life history characteristics.

The Order Primates is composed of approximately 350 known extant species of primates on the planet. There are two parvorders within the broader taxonomic category: Strepsirrhini (lemurs, lorises, aye-ayes, pottos, and galagos) and Haplorhini (tarsiers, New World monkeys, Old World monkeys, and apes). Strepsirrhini has one extant infraorder of Lemuriformes composed of two superfamilies: Lemuroidea (lemurs and aye-ayes) and Lorisidea (lorises, pottos, and galagos). Haplorhini has two infraorders: Tarsiiformes (tarsiers within the family Tarsiidae) and Simiiformes composed of parvorders Platyrrhini (New World monkeys) and Catarrhini (anthropoids divided into Old World monkeys within superfamily Cercopithecoidea and apes in superfamily Hominoidea). The primate taxonomy is complex with many levels of classification to organize the many primate species as seen in Figure 1.

There are certain characteristics that can be found throughout the entire order of Primates. Some traits shared between primates are considered primitive including a generalized body plan of being pentadactyl and having retained a clavicle (Szalay & Delson, 2013). Derived characteristics of primates include: orthograde posture, bipedal ability, grasping prehensile digits, dermatoglyphics, and opposability (Szalay & Delson, 2013). Orthograde posture refers to the ability to walk upright with the face tilted upward (Szalay & Delson, 2013). Some species are able to maintain a bipedal locomotion for some periods of time. Bipedal ability is the vertical stance a primate's body can take when moving forward

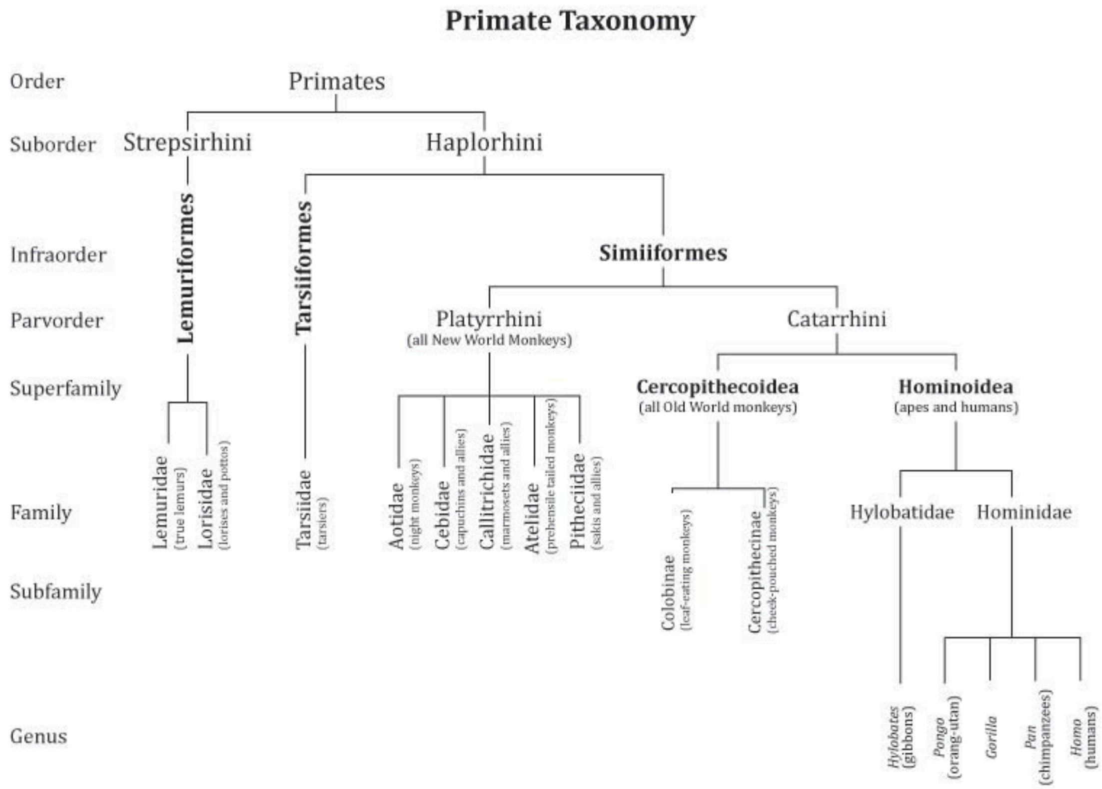

Figure 1. Used with permission. Primate Taxonomy (Dean, 2017)

(Szalay & Delson, 2013). Grasping prehensile digits refers to the ability of primates to hold and grasp objects with their hands and/or feet (Szalay & Delson, 2013). Dermatoglyphics are the fingerprints on the digits (and prehensile tail in some species) of primates. Opposability is the ability to move the hands and feet in manner that digits can touch each other to allow grasping (Szalay & Delson, 2013). Each of these primitive and derived traits are characteristic of the Order Primates that are used for their taxonomic classification.

Other shared, derived characteristics of primates are related to an increase in visual ability in many species. The visual features of primates considered to be derived traits are binocular stereoscopic (frontally oriented) eyes via an optic nerve that allows three-dimensional vision, and color vison through the use of cones in Old World monkeys and apes. There is a thin layer of reflective tissue found in Strepsirrhines which create a tapetum lucidum for night vision by enabling rods to detect more light (Martin & Ross, 2005).

Reduced reliance on olfaction is a derived trait that varies somewhat within the Order Primates. Olfaction is reduced in many species, allowing a reduction in snout length. Strepsirrhines, however, retain a prognathic snout (protruding lower face), have a wet rhinarium (wet nose pads) and communicate intensely through scent (Scordoto & Drea, 2007). For example, lemurs and New world monkeys aid olfactory communication through the use of vomeronasal organs and various scent glands (Hunter et. al. 1984).

Intelligence is found across the animal kingdom, including within the Primates order. The brain of the primate taxon is one of the most important features of the group and is characterized by numerous derived traits. A significantly larger brain relative to body size than other animals is a derived trait that allows increased complexity in the cerebrum and cerebral cortex, language capabilities, and speech (Rauschecker & Scott, 2009).

As in all social species, reproduction and socialization are two key aspects of primate life. Primates are social animals with only few species such as some lemurs and orangutans functioning as solitary foraging individuals. Groups of primates typically interact in tight-knit social systems where group members know of each other and surrounding groups. As in many social organisms, the social behavior within these groups allows for learning tool use, maternal instincts, and other important properties of primate life. These complex social behaviors are in part allowed by an extended life history in which individuals have a comparatively longer childhood than other social organisms, are raised by parents, participate in adolescence (having a period of time between maturity and reproduction), have a breeding age range, and then are able to survive for years after reproduction (Swedell, 2012).

There are characteristics specific to the different primate groups that determine the categorization of species into the different taxa (Table 1). Extant Strepsirrhines provide the best living representatives of the ancestral primate condition. They have traits related to their predominantly nocturnal niche, such as dichromatic vision, a tapetum lucidum, a post orbital bar, and large eyes compared to other groups (Charles-Dominique & Martin, 1970). The Lemuroidea superfamily within the infraorder Lemuriformes contains the lemurs of Madagascar. Lemurs are small, mainly arboreal primates that life in small social groups and forage primarily on flowers, herbs, barks, and sap (Charles-Dominique & Martin, 1970). Lemuroid species have a shorter life history than other primates and often have more than one offspring at a time which is uncommon in the order. The superfamily Lorisoidea includes the lorises and pottos of Africa and Asia. These primates are arboreal, nocturnal, and only weigh between 200 and 400 grams (Nekaris & Starr, 2015). They forage on insects and gums (thick tree nectar) while moving by vertical clinging and leaping or slow quadrupedal motion.

The Haplorhine classification contains the tarsiers, New World monkeys, Old World monkeys, and apes. These primates are found around the world in tropical and subtropical habitats. They range in size from a few grams to hundreds of pounds. Haplorhines have a wide variety of life histories in relationship to foraging, social structure, behavior, habitat, and life stages.

Tarsiers are a small bodied primate in the Tarsiidae family found on the Southeast Asian islands (MacKinnon & MacKinnon, 1980). They are nocturnal insectivores also known to forage on lizards and snakes. Tarsiers move through the jungle via vertical clinging and leaping. These small primates have very primitive large eyes that allow astonishing night vision (Niemitz, 1984). They have a head capable of moving 180 degrees that is useful because they cannot swivel their large eyes. Tarsiers live in breeding pairs with offspring.

The most characteristic feature of this primate is a long tarsal bone not found in any other primates that is used for leaping capabilities (Niemitz, 1984).

The New World monkeys are organized into five families within the superfamily Ateloidea: Callitrichidae (tamarins and marmosets), Cebidae (capuchins and squirrel monkeys), Aotidae (night monkeys), Pithecidae (titi, saki, and uakari monkeys), and Atelidae (woolly, howler, and spider monkeys). The natural range of New World monkeys extends from Mexico and Central America through the Amazon River Basin, living in forest, jungle, and woodland habitats (Schwarzkopf & Rylands, 1989). They are characterized by having a flat face and outward facing nostrils. New World monkeys are small to medium sized primates ranging from twenty grams (the pygmy marmoset (*Cebuella pygmea*)) to twenty pounds (the muriqui (*Brachyteles*)) (Hershkovitz, 1977). These primates are primarily arboreal but do have the capability of coming to the ground. There is relatively little sexual dimorphism in New World monkeys (Hershkovitz, 1977).

Old World monkeys are found primarily in Africa and Asia, both on the continental main lands and on islands. There are two different subfamilies within the Old World monkeys, Colobinae and Cercopithecinae. The Colobinae are characterized by having a specialized sacculated stomach that is divided into sections where various food items can be digested by bacteria (Watermann & Choo, 1981). This specialized stomach is used to aid in the digestion and processing of the often-toxic leaves, fruit, flowers, and twigs they eat (Watermann & Choo, 1981). The Cercopithicines include baboons (*Papio* sp.), patas monkeys (*Erythrocebus* sp.), macaques (*Macaca* sp.), and guenons (*Cercopithecus* sp.). Most of these primates live in large social groups performing either as one unit or as a series of units combined into one super troop. These monkeys' social groups are highly dominance-based and function with a strict hierarchical structure, especially among females. The majority of Old World monkeys are frugivores or folivores, eating fruit or leaves (Strier, 2017). They are found through Africa and Asia, both in arboreal and terrestrial variations. Cercopithicines have cheek pouches in which they store seeds and unripe fruit (Cords, 2012). These cheek pouches are helpful for maximizing food gathered and aid in digestive breakdown of food products through salivary enzymes (Cords, 2012).

The apes within the superfamily Hominoidea are categorized into two families: Hylobatidae (siamangs and gibbons) and Hominid (gorillas, chimpanzees, bonobos, and humans). Each family has specialized characteristics that define the species within them.

The siamang (*Symphalangus syndactylus*) and gibbon (Hylobatidae) are considered "lesser apes" and are found on the islands of Asia. These species are considered "lesser apes" primarily due to their smaller stature compared to the large ape species. These primates are smaller than the other apes but include the most critically endangered of the superfamily. Siamangs and gibbons are strictly arboreal and move via brachiation through the trees with their long arms and short legs (Gittins & Raemaekers, 1980). They are frugivorous and folivorous, feeding on fruits and leaves.

The orangutan species within the family Pongidae are found today only on the islands of Sumatra and Borneo (Knott, 1999). Only three species of orangutan are currently identified in the world. They are arboreal with quadrumanous movement also considered suspensory locomotion (Delgado & Van Schaik, 2000). They are the most sexually dimorphic living primate with the males being two times larger than the females and having large cheek pads not seen in females (Knott, 1999). Orangutans are frugivorous and will sway trees to move from foraging bout to foraging bout.

The family Hominidae contains the gorillas, chimpanzees, bonobos, and humans. The genus *Gorilla* contains one of the largest primates in the world with males reaching up to 400 pounds (Schaller, 1963). Gorillas are folivorous, knuckle-walking primates that form large social groups and can be found in Africa forests. *Pan* is the genus of human's sister taxa containing the bonobos and chimpanzees (Cawthon, 2006). These primates live in fusion-fission social systems in which smaller groups of known community members split apart and come back together over various temporal periods based on resource distribution (Boesch & Boesch-Achermann, 2000). Chimpanzees are relatively the same size as bonobos but are considered more high energy and more easily upset, giving them a reputation for being aggressive (Boesch & Boesch-Achermann, 2000). Chimpanzees are not truly more aggressive than bonobos but have more visible displays of frustration and take emotion out in a less passive manner such as extravagant displays of dominance.

Within the Hominidae family, humans are often categorized into their own group. Humans one of the most proliferate species on the planet through extreme intelligence and tool development. They have managed to inhabit the entire planet, adapting via culture to all climates and habitats. The characteristics of humans are similar to those of chimpanzees and bonobos, but we have lost the majority of our body hair and are obligatorily bipedal (Groves, 1989). Social organization in human beings is highly complex, with a variety of social connections and relationships, expanding beyond those recorded in other primate groups (Boyd, 2006). People have certain sets of beliefs, ideas, and concepts that are shared through social learning called culture. Though other organisms and primates have some aspects of culture, human beings are the considered the only species that have true culture (Ramsey, 2013).

The various taxa of primates found around the planet have specialized characteristics that help classify them to their specific group (Table 1). The different life histories of primates can alter their interaction with and reliance on communication, predation, and polyspecific associations.

Table 1. Primate group specialized characteristics

Streprrhines	**Haplorhines**			
	Tarsiiformes	**Platyrrhines**	**Colobines**	**Cercopithicines**
Dichromatic vision, tapetum lucidum, post-orbital bar, grooming claw, dental comb, Madagascar	Largest eyes, only obligate carnivore primate, long tarsal bone, Asia	Flat face, forward facing nostrils, primarily arboreal, Central and South America	Specialized sacculated stomach, Africa and Asia	Super troops, cheek pouches, Africa and Asia
Hominoidea				
Hylobatidae	Pongidae	Hominidae		
"Lesser apes", true brachiation, throat sac, Asia	Quadrumanous movement, Asian islands	Complex social structures, complex culture capabilities, Africa, Worldwide (man)		

Primate Evolutionary Theory

While primates are closely related to the Lagomorpha (hares, pika, rabbits), Scandentia (treeshrews), Dermoptera (colugos) and Rodentia (rodents), there are certain characteristics that have been derived within the primates separating the order from other mammalian taxa (Springer et. al. 2004). The characteristics of primates that set them physically apart from other taxa are related to vision, body plan, olfaction, and digit use

(Hofstetter, 1977). There are multiple hypotheses that aim to explain why such characteristics developed in the Order Primates (Crompton, 1995). Each hypothesis has both strengths and weaknesses related to the occurrence and level of importance. The hypotheses are considered not mutually exclusive and could have been occurring simultaneously to drive primate evolution.

There are currently four accepted hypotheses in the literature. The arboreal living hypothesis focuses on the required features of a primate to live only in an arboreal habitat pressuring for grasping hands, forward facing eyes, and keen sense of smell (Conroy, 1990). The visual predation hypothesis created by Cartmill proposes that these characteristics are for successful predation of small prey items (Cartmill, 1972). The angiosperm radiation hypothesis developed by Sussman is used to understand why primates may have forward facing eyes with color vision due to the similar timing of the expanse of flowering plants and the evolution of primate species (Berendse & Scheffer, 2009; Sussman, 1991). The snake hypothesis focuses on the effects of snake predation pressure causing the need for stereoscopic vision, mobility through the environment, and dexterous digits (Isbell, 1994).

While it is not obvious which hypothesis or hypotheses may be the best explanatory power, each of these ideas has aided in developing the understanding of the primate origin. Each theory currently stands as a potential explanation for the evolution of primate characteristics. In relationship to understanding primate polyspecific associations, these primate evolution hypotheses have features related to foraging, predation of prey, and the pressure of predation. Each of these characteristics are considered features of polyspecific interactions. These characteristics of primate life are derived early in the evolution of primates, suggesting they are important for extant species.

Predation and Communication

Although there are a wide variety of characteristics found in the primates of the world, there are certain features similar across species. The similar features across primate species, though not unique to the order, include a drive for maximizing reproduction, fitness increase, foraging success, social structure, relationships, predation, and communication. Two of the major characteristics of primate life that greatly alter behavior and thus life histories are predation and communication. These features have been suggested by the field to be two of the most important factors in determining primate life, including perhaps the cause of polyspecific associations.

Predation can be an impactful feature of a primate's sociality, communication, behavior, and other features of life history due to the dire consequences if there is successful predation (Isbell, 1994). Predation can lead to severe injury or death if the predator is successful in capture and kill. This greatly reduces the chance for maximum fitness of an individual. Predation is a continuous threat to most primate species, causing behaviors and interactions that attempt to minimize the success of predators. Even without a visible threat, the possibility of predation can have enough effect on the individual primate to alter or set behaviors (Isbell, 1994). The threat of a predator can cause species to be active in certain layers of the environment, certain times of the day, and behave in particular manners. One way of connecting primates is through communication about predation threats.

Communication in primates is one of the most important characteristics in behavior, sociality, and life history. The ability to transmit and share information between individuals is important for the interconnectivity of kin, social groups, and perhaps even polyspecific species (Snowdon et. al. 1982). Communication can occur in a multitude of manners including physical, vocal, and silent. Physical communication is most commonly seen through gesturing, movement, or contact (Snowdon et. al. 1982). This form of interaction requires individuals to be in close enough proximity to receive touch or have visual contact to see movements. Vocal communication occurs through audible sounds emitted from one individual to others (Todt et. al. 2012). The information transmitted through sound is related to the frequency, pitch, length, volume and context of the call. Vocal interactions are less reliant on spatial features of the scenario and can often be given successfully across larger areas. Silent communication is similar to physical in that the sender and receiver must be close enough to have visual contact with one another (Hewes et. al. 1973). Silent information can be sent through body language, facial expressions, eye movement, and other quiet forms of communication. Communication is considered one of the key features of polyspecific associations.

Polyspecific Associations

Natural polyspecific associations occur when one or more different species not only live sympatrically but appear to interact with one another in either a mutually beneficial or commensalistic relationship. These associations are found throughout the natural world and are suggested to be a key component of ecosystem structures through the interconnectivity of species in mutually or commensalistically reliable relationships.

In the primate taxon, naturally occurring associations have been seen between two or more different species of primate and between a primate species and another taxon species. These interactions are suggested to be important to wild primates for the protection against predation threats and by benefitting each other in foraging bouts (Goodale et. al. 2010). The interacting species benefit one another in feeding by foraging on slightly different resources in close proximity in order to increase success while having minimal increased foraging competition.

The collaborations have certain characteristics that identify them as polyspecific instead of simply sympatric including spatial features, communication, and the interaction itself (Magrath et. al. 2015). The species interacting have to be within close proximity to each other, either within a canopy level or as close as possible due to vertical constraints for an association to be considered (Goodale et. al. 2010). This proximity requirement is typically within meters of each other to ensure the observed interaction is not just sympatric. One of the main characteristics of these interactions is multi-species communication.

Communication between the interacting species is often key to the identification of the association. The organisms can share information about the surrounding environment or situations. The communication is considered effective if there is a behavioral reaction related to the shared knowledge. For example, alarm vocalizations from one species resulting in anti-predation behaviors in another (Oda & Masataka, 1996). The behavioral interaction, often instigated by communication, is the mark of the polyspecific interactions due to the reliance, trust, and response placed into the other species' behavior (Goodale et. al. 2010). Though not all of the associations require each of these characteristics, many have at least two. Most of these interactions have been understood as being either mutualistic or commensalistic in which the association is either beneficial for both parties or does not affect one while benefitting the other (Heymann & Hsia, 2015). While these interactions have been identified across the Order Primates, the instigation and causes are not always well known.

There is much still needed to be known about the polyspecific associations found in primate species. The field of primatology can expand its reach to extend further into these interactions by changing the methods and thinking about the relationships.

CHAPTER 2. REVIEW OF CURRENT LITERATURE

Predation

Predation of Primates and Anti-Predation Responses

Predation acts as a strong selective pressure on the actions of prey species due to the possibility of injury and even death. Though we know predation is a powerful factor in primate species, there has been some difficulty in capturing predation events in previous data collection due to the rarity of such scenarios (Stanford, 2002). It is significant that predation events are seen at all in primate observational studies in spite of the generally limited amount of time study animals are observed (Eilam et. al. 2011). Though the significance of predation is only understood through estimated rates of threat via theory models and observed predation events, the behaviors exhibited by prey species are consistent with predation serving as a powerful selective pressure.

Primate species can serve as both predator and prey in systems. Most primates are non-carnivorous and instead often function as a prey species across the planet. The primate taxon has a wide array of possible predators found across the globe, ranging from snakes to mammalian carnivores. The large variety of threats to primates has created behavioral and physical anti-predation responses across the taxa including a series of behaviors to reduce the chance of predator success. These behaviors include an increase in vigilance, movement away from or toward the predator location, freezing, and alarm vocalizations that are also seen in other animal species (Eilam et. al. 2011).

Vigilance in an individual primate is defined as awareness of surrounding environment including other organisms (Treves, 2000). It is often detected in behavioral observations as a halt in forward motion and an increase in scanning behavior where the individual looks around the area intently (Treves, 2000). An amplified level of scanning behavior by primates is suggested to be an attempt to locate a predator (Isbell, 1994). Once a predator has been spotted, the primate can respond accordingly to the threat. Increased vigilance can be instigated by different means including unidentified foliage movement, predator scent, predator vocalizations, and alarm calls from fellow group members (Isbell, 1994).

Physical motion away or toward the assumed location of a predator or freezing in place can aid in the avoidance of predation. The direction in which the primate moves from the predator location is dependent on the presumed predator species as well as the primate species or individual involved (Barros et. al. 2002; Ouattara & Zuberbühler, 2009). Movement toward the predation threat is often seen when the predator can be deterred when the element of surprise is gone. Moving at the predator can also be considered mobbing if aggression from the group is shown to the predation threat. Movement away from the supposed position of the predator is an attempt to place more distance between the primate and the predation threat (Anderson, 1986). Running away from a predator is important for reducing the chance of predation by creating more distance between the threat and prey. Movement away can be referential in that primates will move downward in response to an aerial threat and upward due to a terrestrial threat (Cäsar & Zuberbühler, 2012). The primates often move inward as well to increase canopy cover or hide from the terrestrial threat in the brambles above. In some instances, the best way to reduce the chance of predation is to not move at all. Freezing in place enables primates to reduce the chance of being detected by the predator by minimizing noticeable movement (Searcy & Caine, 2003). Reducing all movement gives the primate a chance to blend in with the environment and not draw unwanted attention. These lack-of-movement responses are dependent on the type and location of the predator as freezing can also be harmful if it increases chances of predation. If freezing behavior is not possible or optimal, movement away from the predator is used to place as much space between the individual and the predation threat (Friant & Campbell, 2008). This can occur on both a vertical and horizontal plane and the direction of movement is often directly related to the type of predator. Each of these movement types is most beneficial in different circumstances related to the type of the predator and the environment.

Alarm call vocalizations are an important benefit of group living and found broadly across the order. Once an individual detects a threat, they give a vocalization specific to that predator warning the other group members (Bergstrom & Lachmann, 2001). The alarm calls in many species are referential, stating what type of threat is eminent as either terrestrial or aerial (Cäsar & Zuberbühler, 2012). Predator type information in the call enables group members to respond in a beneficial way to the specific predator (Cäsar & Zuberbühler, 2012). Alarm vocalizations are key to the accomplishment of a group avoiding a predation threat and rely on individuals giving the calls (Bergstrom & Lachmann, 2001).

Primates use alarm calls to warn others about the presence of a predator (Hauser, 1996). The vocalization allows members of the social group to use anti-predator behaviors (Charnov & Krebs, 1975), and young primates learn predator knowledge (Curio et. al. 1976). Individuals within a group will give an alarm vocalization in response to spotting a predator to warn group members of the type and location of the predator. This is increased when kinship is high in social groups, relating to inclusive fitness (fitness including that of offspring, siblings, and parents) and altruistic behavior (behavior benefitting others often at self-cost). One of the main supporting ideas for alarm calling is kin selection. Primates are more likely to call when they are in a social group of closely related kin, suggesting inclusive fitness benefits by protecting relatives (Charnov & Krebs, 1975). This provides the opportunity for closely related kin to escape predation (Maynard-Smith, 1965). Such benefits suggest why it is adaptive for an individual to send an alarm call to the social group; the signal is beneficial to the survival of its kin (Zuberbühler et. al. 1999).

Primates have a series of behaviors that can aid in the reduction of predation risk including vigilance, movement away or toward the predator, mobbing, alarm calls, and freezing. All of these reactions may be necessary to reduce predation or only a certain reaction combination. Primate species each also have their own specialized reactions to predators.

Primate Predators and Behavioral Responses

Each primate group has its own set of predation threats dependent on the location of the primate, size, behaviors and defensive mechanisms. The different primate parvorders, infraorders, superfamilies, and families have a more specific and often more similar guild of predators due to similar life history characteristics and physical locations of each classification level (Hart, 2007). Specific predation and response information about each primate group is key to understanding the effects of predation as well as perhaps giving support to the suggested cause of polyspecific associations. This section will dive into the specifics of the predators of species within both parvorders to show the current understanding of the affecting predators and the behavioral responses seen in primate species.

Strepsirrhini

The predators of lemurs, aye-ayes, lorises, pottos, and galagos including twenty different known predator species of lemurs, of birds, snakes, and carnivorous mammals found sympatrically on the island of Madagascar (lemurs and aye-ayes), on the continent of

Asia (lorises), and throughout Africa (pottos and galagos) (Scheumann et. al. 2007). These lemur primate species have a body size range from a few grams up to ten pounds and have highly specialized life histories, allowing a broad guild of predation threats (Table 2). Each species has particular predator species they are most concerned about due to the coevolution of predators to the characteristics of the primate (Hart, 2007).

Predators of the smaller Strepsirrhines include the Henst's goshawk (*Accipiter henstii*) and the Barn Owl (*Tyto alba*) that are primarily nocturnal threats (Barre et. al. 1988; Goodman et. al. 1993). Threats in the trees include the Madagascar boa constrictor (*Boa manditra*) that can constrict lemurs of all sizes to death (Sauther, 1989). Mammalian predators are found on all vertical scales and include the fossa (*Cryptoprocta ferox* and *Euplores goudoti*) and mongoose (*Mungoticitis decemlineata*, *Galidia elegans*, and *Galididictus fasciata*). They pose a threat to lemur species across all sizes throughout Madagascar (Russell, 1977; Wright, et. al. 1997; Petter et. al. 1977; Wright & Martin, 1995). This wide variety causes lemurs to have both diurnal and nocturnal predators, maximizing predation threats and initiating diverse anti-predation responses. Many lemur species are functional during either the daylight or night time hours to reduce the maximum number of active predators at one time (Charles-Dominque, 1975). The majority of predators are active during the day, though some have adapted to be nocturnal in response to the behavioral patterns of the primates. One effective method of hiding from threats found in groups and solo lemurs is nocturnality in order to reduce predation due to the limited active predator guild at night (Wright, 1989; Wright, 1994). Some lemur species will form large groups to increase their vigilance and maximize dilution of predation risk for each individual organism (Hamilton, 1971; Pulliam & Caraco, 1984). This social living is not driven only by predation, but the benefits related to minimizing the threat are a key feature of group living. Individuals are also pushed to increase their crypsis and hiding behavior in order to minimize the chance of successful predation (Cowlishaw, 1994; Terborgh & Wright, 1998). The more difficult is it to be spotted by a predator, the less likely predation is a threat to an individual. Each of these anti-predation responses aids lemur species in reducing the chance of death.

Aye-ayes are primarily nocturnal primates that use avoidance behaviors as their main form of reducing predation threats. The only natural predator of the aye-aye is the fossa (*Cryptoprocta ferox* & *Euplores goudoti*) (Petter, 1977). Aye-ayes share predator information through alarm vocalizations to warn group members but have little defensive mechanisms beyond avoidance. One way of increasing avoidance is to be a nocturnal dwelling primate by reducing the number of predators they can possibly encounter.

Lorises in Asia have a similar predator guild as the Madagascar lemurs including the reticulated python (*Python reticulatus*) and hawk eagle (*Stephanoaetus mahery*) (Wiens & Zitzmann, 1999; Wiens & Zitzmann, 1985). However, due to their smaller size, there are more possible predators in the environment. The loris is threatened by the orangutan and python species of Indonesia (Pliosungoen et. al. 2010; Wiens & Zitzmann, 1999). It is also suggested that civets and bears could be potential predators of the loris species (Nekaris et. al. 2007). These small primates have an interesting anti-predator response found only in their taxa: poison. When frightened, the loris will freeze in the hope that the predator will leave it alone. If the predation threat does not dissipate, the loris will secrete a toxic liquid from the prachial gland found on the wrist and raise its arms over the head to expose the predator to the toxin (Hagey & Fitch-Snyder, 2007). The loris can also lick the secretion, creating a toxic bite (Nekaris et. al. 2013). Lorises are suggested to do all of this to mimic cobras (Hagey &

Fitch-Snyder, 2007). This is the only case of a poisonous primate found in the Order Primates. While the loris is poisonous, the main type of anti-predation behavior found in the loris species is being nocturnal to avoid potential predators.

Pottos and galagos are small primates found in the scrub forests of Africa that have a large variety of predators. These predation threats include the blue monkey (*Cercopithecus mitis*), cats of all sizes, snakes, owls, mongooses, and even chimpanzees (*Pan trogolotes*) (Butynski, 1982). Galagos have minimal avoidance responses by hiding, fleeing, mobbing, and signaling alarm calls. Pottos primarily use crypsis to hide from predation threats by reducing communications within their small social groups and remaining still for hours at a time (Nekaris et. al. 2007). They also have elongated spines at the cranial cervical bite location to harm predators by having the sharp defense features be at a key site for a kill bite (Cowgill, 1969). When threatened, pottos are known to roll up in a protective ball (Caro, 2007). As the smallest Strepsirrhines, these galago and potto species are greatly impacted by predation threats. Reducing the chances of engaging with a predator and then having mechanisms for minimizing predation are the two main methods of predator avoidance found in pottos and galagos.

The Strepsirrhines have a wide variety of predation threats due to the broad range of body size and habitats found among the species. Although there can be a broad array of predation threats, the lemurs, lorises, aye-ayes, and galagos have developed their own mechanisms to minimize the impact of these predators. Each strategy related to the particular environment and predation threats uses a series of avoidance and defense to reduce the chances of successful predation.

Table 2. Strepsirrhini Predation and Response

Species Grouping	Location	Predators	Responses
Lemur	Madagascar	Boa, Fossa, Mongoose	Avoidance, Crypsis
Aye-Aye	Madagascar	Fossa	Avoidance
Loris	Madagascar	Boa, Fossa, Mongoose	Poison
Potto	Africa	Snake, Cats, Owl, Mongoose	Crypsis
Galago	Africa	Blue monkey, Chimpanzee, Snake, Cats, Owl, Mongoose	Avoidance

Haplorhini

Haplorhini is the suborder containing all primates other than the lemurs, lorises, aye-ayes, pottos, and galagos. The species within this classification are typically found on the African, Asian or South American continents, allowing there to be a broad range of predator threats across the suborder (Table 3). The behavioral responses of Haplorhines to a predator serve to reduce the chance of successful predation. Each grouping of the suborder is discussed below in regard to their known predators and anti-predation behaviors.

Tarsiers (Tarsiidae) are primarily nocturnal primates with a variety of predators including the reticulated python (*Pyton reticultus*), civet (*Fossa fossana*), lizards, and raptor species (Gursky, 1997 & 2002; Jachowski & Pizzaras, 2005). Avoidance is the main mechanism of predation response in the tarsier by being a nocturnal primate. Nocturnality in the tarsier is the primitive (ancestral) activity pattern maintained from ancestors and serves to aid in reducing the number of active predator threats. If avoidance has not been successful, tarsier groups have been known to mob threatening snakes (Gursky, 2003). Social living aids tarsiers in mobbing of snakes and reduces the chance of predation. Tarsiers use their social relationships to reduce predation threats through avoidance by social movement and mobbing if necessary.

New World primates (*Platyrhinni*) are composed of five families and found in the jungles of Central and South America. These primates have a large variety of predation threats including felids such as jaguars (*Panthera* onca), ocelots (*Leopardus pardalis*), jaguarondis (*Puma yagouraroundi*), tayras (*Eira barbara*), many snakes (*Lachesis*, *Micrurus, Bothriopsis, Boa, Eunectes, etc.*), and large birds of prey, such as the Harpy eagle *(Haroisa haroyja*), the Gray-lined hawk *(Buteo nitidus*), Great Black hawk *(Buteigallus urubitinga*), and the Roadside hawk *(Buteo magnirostris*) (Emmons et. al. 1993; Salvador et. al. 2011).

New World primates respond to predators through increasing group size, mobbing, alarm calls, freezing, and movement away (Anderson, 1986). An increase in group size is beneficial to New World primates by raising the possible level of vigilance, enabling the group to spot a predator more easily and quickly (Bicca-Marques & Garber, 2003). Mobbing is also more effective when more individuals are present due to the aggressive nature of a mob attack on a predator. The more individuals present, the more likely the group is to successfully fend off a predation threat. Alarm calls seen across the order, high frequency warning calls given in the identification of a predator, are a key feature of social living (Charov & Krebs, 1975). The wide variety of anti-predation responses found in New World primates, frequently done in a sequence of reactions, allows them to reduce the chance of predation.

Old World primates (*Catarrhini*) are found both in Africa and Asia but have similar predator guilds. Predators of African Old World primates include pythons, crocodiles, eagles, leopards, and lions. This predator guild guarantees that any habitat type and vertical level always has the possibility for a predator. Primates found in Asia have the same predators as those in Africa of raptor, snake, reptile, and felid species but have tigers as the largest felid predator. Both continent varieties of Old World primates will respond to a predation threat with a canine barre, large group sizes, mobbing, alarm calls, and throwing objects (Srivastava, 1999; Chetry et. al. 2002). A canine barre occurs when an individual faces a predator, opens its mouth, and exposes sharp canines in an attempt to frighten the predator off. Multiple individuals at once can do this to maximize the chances of predation avoidance (Tello et. al. 2002). Large group sizes are instrumental in fending off or attacking a predator. The larger the group, the more chance they have of minimizing predation events. Mobbing requires multiple individuals all attacking a threat at one time to harm or frighten away the predator. Throwing objects at a predator can be done by one or more individuals to threaten a predator away from the social group. Alarm vocalizations similar to other primate groups can be also found in this parvorder. The calls are similar in purpose and function to those found in Platyrrhini but can occur at lower audio frequencies.

The lesser apes (Hylobatidae) are the gibbon and the siamang native to Asia (Tuttle, 1990). These primates are similar to the great apes but are smaller in size, have less sexual dimorphism, and do not make sleeping nests. Lesser apes can be threatened by leopards, snakes, and raptors (Choudhury, 1991). They respond in similar behaviors to the Old World primates by mobbing and threatening the predator or by moving away. The lesser apes are also known to harass predators for entertainment or showing off strength. Siamangs and gibbons are often able to avoid predation through their intelligence and agility.

The great apes (Hominidae) include the orangutans of Malaysia and Indonesia, the gorillas, chimpanzees, and bonobos of Africa, and human beings. Great apes are not predated on by many species due to their large stature and dangerous defenses of body slamming and attacks. Orangutans (*Pongo*) are threatened only by tigers on the islands of the Pacific

(Delagado & Van Schaik, 2000). Chimpanzees and gorillas can be predated on by leopards and lions, though predation is considered low (Boesch, 1991; Tsukahara, 1993). Bonobos are attacked by crocodiles along the rivers of the Congo on the African continent (D'Amour et. al. 2006). Large eagles can be a threat to young individuals of each ape species by lifting them from the ground, dropping them, or using sharp talons to kill. While snakes are not a major threat, their venom could be dangerous to the great apes and the snakes entice a panic response in groups (McGrew, 2015). Even if a snake is not venomous, it is common to see apes respond warily to the presence of a snake.

Great apes respond to predators with tool use, fighting, mobbing, screaming, and running. Orangutans also attempt to remain arboreal in order to avoid tiger threats (Knott, 1999). Tool use to deter predators includes throwing rocks and other objects. Fighting and mobbing are dependent on the number of individuals willing to physically take on a predator. Great apes are strong and able to inflict major physical damage to an attacked predator. Screaming is used primarily as a scare tactic in an attempt to avoid physical confrontation (Slocombe & Zuberbühler, 2007). If great apes do not wish to fight, they have been known to run from predation threats in order to minimize the danger from the predator. Each great ape species has its own mechanisms for reducing predation threats but have similar limited predation event occurrences.

Humans are a separate circumstance all of their own when compared to the other extant primate species. While there are species around the world that can predate on humans, the possibility of predation is dependent on a human individual's accessibility and knowledge of tools. Most any large predatory species is able to kill a human if the person is not armed against it. The ancestors of modern human beings were greatly affected behaviorally, genetically via reproduction of survivors, and through evolution by the threat of predation (Treves & Naughton-Treves, 1999).

Modern man is still threatened by predators but can use technology to mitigate the danger. The rate of modern day predation is dependent upon the area that people live in related to the level of civilization. Different regions of the world have various levels of natural predator threats. These differences are based on the abundance of predators, the availability of natural environment, the structure of the civilization, and the relationship between man and nature. The human in a heavily modernized society with large amounts of human landscapes does not typically worry about predation threats by wild animals. There are few encounters throughout the civilized world compared to previous rates. This is partly related to the massive die-off of the natural predators due to human disturbance. The almost complete destruction of the natural environment and overhunting has left carnivore populations dwindled and thus reduced the chance for human-predator interaction. There is a great dichotomy between the predation of humans before and after technology.

Table 3. Predators and responses of Haplorrhines

Species Grouping	Location	Predators	Response
Tarsier	Africa	Snakes, civets, lizards, raptors	Avoidance, mobbing
New World monkeys	Central & South America	Raptors, cats, snakes	Avoidance, mobbing, alarm calls
Old World monkeys	Africa & Asia	Cats, snakes	Canine barre, mobbing, object throwing
Lesser apes	Asia	Cats	Aggression, avoidance
Great apes	Africa & Malaysia	Cats	Arboreality, aggression, screaming
Humans	Globe	Snakes, cats, bears, canines	Tool use, avoidance

Primates as Predators

While most primates serve as a prey species in the ecosystem, there are a few examples in which they have become the predator (Table 4). These species are not common in the order but show great implications of the importance of predation. The reasons for primates consuming other organisms are broad, from increasing body condition (including weight and nutrition) to creating social status. The primates have gained the ability to consume other warm-blooded and reptilian organisms, shifting the ancestral behavior to a predator position in the order.

The primate species that are able to be a predator have a certain set of characteristics that allow them to reverse the scenario. They typically have keen eyesight, high hearing capabilities, sharp teeth, and the ability to kill other organisms. It is also common for hunting primates to live in large, cooperative social groups or oppositely live as solitary hunters.

There are two types of predatory primate groups for the sake of this paper: insectivores and hunters. The insectivores are often smaller-bodied species while the hunters are typically larger primates. Insect-eating primates eat a large mass of insects at a time to gather enough protein for sustenance, eating insects as frequently as possible. Hunters are primates that eat animal protein from other mammalian, fish, amphibian, and reptilian species. Hunters do not necessarily engage in hunting behavior frequently but are known to participate in hunting opportunistically.

Within the insectivorous primate species, there are obligate and opportunistic species that differ in the rate and reliance of insect protein in their diet. Obligate insectivorous primates eat insects as a large component of their diet. There is only one primate that forages only on insects and is considered the only truly carnivorous primate: the tarsier (Fogden, 1974). Tarsiers are also known to eat other organisms such as frogs, birds, and snakes but are primarily insectivorous (Jablonski & Crompton, 1994). Not all known tarsier species eat other animal protein beyond insects and the family is considered the most insectivorous primate group, eating a wide range of insect types (Gursky, 2000b). Tarsiers are the only primate solely reliant on animal protein, mostly insects, for their dietary needs. Other species are more opportunistic in their insectivorous diet components.

Insects are often an additional source of protein for the majority of other primate species, but primarily opportunistically. These include lemurs, Old World monkeys, and apes (Isbell, 1998). Many New World monkeys have an insect component to their diet but are not dependent on this forage type. Some species of these monkeys have a certain portion of insects in their diet that needs to be met for optimal fitness but do have other optimizing resources. Apes are known to forage for insects such as termites using fishing tools (Lonsdorf, 2006). These termites provide the apes with an additional source of protein, supplementing their diet (Uehara, 1982). The species that eat insects only when it is easily accessible, or the opportunity requires little energy are considered opportunistic insectivores.

Hunting primate species include a similar variety of reliance levels. Some species will hunt intentionally and throughout their life consistently while others only hunt mammals opportunistically. Primates that eat meat consistently over their life include the chimpanzee (*Pan*) that is known to hunt colobus monkeys, bush babies, civets, and other species. Chimpanzees are known to work together in social groups to herd, drive, and kill monkey species (Mitani & Watts, 2001). These hunts often include many individuals working together to capture and kill an organism, highlighting the importance of social status. Meat consumption order in chimpanzees is directly related to the social status of participating individuals (Boesch, 994). They are also capable of creating and using tools to kill organisms, highlighting similarities to humans (Gibbons, 2007). Other primate species only kill and eat other species opportunistically and not on a regular basis. There are some adaptable hunters such baboons who will kill young impala when given the chance and orangutans that will eat bird eggs and small animals (Harding, 1975: Russon et. al. 2009). These instances of predation are more so showcasing the adaptability and resourcefulness of primate species in opportunistic scenarios.

Humans are the most effective predator primate on the planet through the use of intelligence and tools. The human species (*Homo sapiens sapiens*) is the only organism on the planet able to consciously alter its position in the food web and be a predator of all other species. Naturally, humans have many predators that can harm or kill an individual including bears, large cats, canids, and other carnivores (Hart & Sussman, 2008). Modernized man is able to circumvent this predation threat through the use of weaponry and tools, actually jumping into the predator position for their natural predators (Frayer, 1981). Humans are able to kill and/or predate on any living species at this time due to the invent of guns and other damaging weapons. While prehistoric man may have once had many predators, modern man equipped with a weapon has few true threats. Without the tools and weapons of modernity, *Homo sapiens* reverts back to having a natural balance of predators and species that they can predate on.

Table 4. Primates as predators

Species	Predation Habit	Predates On
Tarsier	Obligate	Insects, invertebrates, birds
Lemur	Opportunistic	Insects
New World Monkey	Opportunistic/Partial Obligate	Insects, invertebrates, small mammals
Old World Monkey	Opportunistic	Invertebrates, mammals
Apes	Opportunistic	Insects, invertebrates, primates, mammals
Human	Opportunistic	Insects, invertebrates, fish, primates, mammals

Primate Vocal Communication

Communication is key to information exchange in primates and comes in many forms. Information is sent from one individual to signal a receiver through sound, body language, movement, and silent cues. One animal's behavior serves to change another's behavior, whether on purpose or involuntarily. Complex communication is one of the derived hallmarks of the Order Primates, as the species within this classification are often heavily reliant on shared information to maximize individual and group fitness.

Communication is reliant on two components of the interaction: the motivation and the meaning. The mental state in which the individual is signaling another is important to understanding why the information was sent (Strier, 2017). Mental states include aggression, fear, alarm, excitement, and other conditions that elicit an individual to give a signal. Mental states do not necessarily have to be consciously made and can be instinctually shared with others.

The meaning is at the receiving end of the communication interaction. Meaning is the message received by the recipient that translates into information about the surrounding environment, sympatric individuals, a threat, or other features of a scenario (Strier, 2017). It is difficult to determine how primates determine the meaning of communication, but it is known that they do in some way identify a signal's meaning. The understood meanings found in primatology are determined through context clues and reaction of surrounding individuals occurring multiple times in repeated studies.

While there are several different forms of communication, often occurring together, found in the primate taxon, vocalization is one of the most characteristic forms of communication for primates. The pitch, boldness, loudness, and duration of vocalization combine to give meaning to the sender (Mitani & Stuht, 1998). There are several different types of communications that primates use including alarm calls, territorial vocalizations, food calls, personal identification information, and dominance vocalizations with some being specialized into a language. Communication in primates can be generalized or referential (meaning focusing on certain information to share) (Cäsar & Zuberbühler, 2012). All the varieties of vocalizations make them important for conveying the information properly from sender to receiver.

Vocalization communication is one of the most specialized forms of communication found in the Order Primates. It is key for primate social groups and order, allowing it to be a significant feature of polyspecific associations. Since the primate social groups rely so heavily on vocal interactions and polyspecific associations often have a vocal component, the vocalizations may indicate the strength and importance of such polyspecific interactions. This section will describe the specific vocalizations and their purpose for each of the large primate groups.

Primate Parvorder Vocal Communication

Strepsirrhini

The Strepsirrhine suborder contains species that are primarily dependent on olfaction communication to share information with other individuals. They have wet rhinariums that enable them to use scent as a prime form of information transfer (Scordoto & Drea, 2007). Although vocal interactions are not the main form of communication seen in this classification, each primate group within the Strepsirrhines does have some form of vocal communication.

Lemurs have twenty-eight distinct calls found in their vocal repertoire with twenty-two adult vocalizations and six distinct in young (Jolly, 1966). There are nine vocalization categories used for social cohesion and interactions including: contacting affiliative moans, group cohesion increasing “meows”, “wails” of separation, male howls for dominance, grooming “purrs”, movement “chirps” (Jolly, 1966), male fighting “yips”, and subordinate “yips” answered by dominant “chutters” (Macedonia, 1993). Each of these vocalizations serves to share information within the group about the individuals present or the interactions between group members. Another set of calls is used to warn group mates of the dangers of things exterior to the social group. These are called alarm calls and can instigate a reaction in others to aid in preventing predation. Lemurs use “gulps” for low-flying birds, “clicks” for fearful curiosity, and “yaps” in mobbing events (Sauther, 1989; Macedonia, 1993). The vocalizations of lemurs are beneficial for social dynamics and sharing information across scenarios.

Aye-ayes have a small repertoire of vocalizations that are used primarily as affiliative interaction (Stanger & Macedonia, 1994). There are four categories aye-aye calls fall into: affiliative, distress, agnostic, and mating. Over fifty percent of calls are used for affiliative purposes (Sterling, 1995). Interactions between two adult aye-ayes may include a “ggnoff” vocalization that suggests social cohesion, often leading to social grooming or collaborative foraging (Andriamasimanana, 1994). Short and long “eeps” are used for affiliative calls in the wild while “creees” aid in mother-infant relationship cohesion (Sterling, 1995; Petter & Charles-Dominique, 1979). This same “creee” call is found in captive individuals when young are separated from their mothers for any substantial amount of time, suggested to signal pain and distress (Winn, 1994). Alarm vocalizations can be found in the aye-aye family in the form of a “ron-tsit” call that warns of threats to the social group (Petter, 1977). Aggressive calls include “aacks” used to maintain distance between two unknown individuals or groups. Whimpers can be found in less territorial disputes related to copulation, food, and male-female social interaction (Sterling, 1995). Other calls found in the aye-aye vocal range include “scream”, “plea”, “sneeze”, “snort”, “hai-hai”, “groan”, and “whirr” (Sterling, 1995). The minimal range of vocalizations found in the aye-aye provides enough vocal signaling when accompanied by scent marking to properly convey social information.

Lorises and pottos have a smaller vocal range than the closely related lemurs with only about six call types. Social communications include whistles of excitement or aggression, “chitters” as a defensive threat, “sic” calls of infants, and” krik” calls to appease chittering females (Nekaris, 2003; Nekaris et. al. 2007). There are no alarm vocalizations in loris or potto social groups, but defensive calls are used in attempt to warn off predators. Growls are used in a vocal threat to a predator and can develop into a “scream” if the threat is prolonged (Schulze & Meier, 1995b). The scream is often met with the initiation of toxin secretion in lorises (Nekaris, 2003). The six call types found in lorises and pottos are beneficial in conveying information in social groups related to individual or environmental factors.

The galago species of the planet are often only distinguishable by their vocalization type and range (Ambrose, 2003). Different species of galago share only certain calls with others, while some calls are distinct. Loud advertisement calls are one of the call types used to identify the species (Butnski et. al. 1998, Zimmerman, 1995). There are also agnostic, attention, and alarm calls in galago vocal communication (Zimerman, 1990). Young galagos will “soft click” for social interactions while adults do so loudly. Cries can be used to gain attention while “barks” are used in more aggressive scenarios. Alarm calls are given to warn others of environmental or predatorial danger (Zimmerman, 1990). Galago species rely on vocalizations to share information across social groups, often related to predation events.

Haplorhini

The Haplorhines are known for their reliance on vocal communication in the sharing of information even to the extreme of man's speech. These primate groups are often large and spread over broad areas of terrain, making vocal communication a helpful tool for quick information transfers. The groups within the Haplorhine classification have their own specialized vocalizations used for certain scenarios, situations, and contexts.

The tarsier is known for the vocal duets conducted by bonded pairs in the morning that aid in mate bonding and territoriality (Niemitz et al. 1991; Tremble et al. 1993; Shekelle 2003; Merker & Groves 2006). These duets are instigated by the female and can last for several minutes (Gursky, 2000). While the duet is known in the group, only three of the five species participate in these bonding calls. Tarsiers have fifteen different possible calls, primarily for territoriality and spacing and include alarm "whistles", alarm calls, distress calls, female screams, mid-intensity calls, contact trills, contact whistles, play whistles, food calls, infant squeaks and other whistle types (Nietsch, 2003). Their calls occur at an ultrasound frequency up to 70kHz for the creation of both distress and mate vocalizations. Certain species of tarsier will produce particular vocalizations with some species almost always refraining from vocalizing. Tarsier calls are used for social connectivity, sociality, and sharing environmental information, making them key for survival.

New World monkeys have a wide variety of calls across species used for a range of purposes. Howler monkeys have a large, loud territorial call due to a specialized hyoid bone that deepens the pitch, resonates the calls, and amplifies the sound (Thornington et. al. 1979; Crockett & Eisenberg, 1988). Titi monkeys have specialized duet calls for bonding purposes in which a male and female call in unison (Müller & Anzenerger, 2002). Callitrichids including tamarins and marmosets have ultrasonic calls of “trills” and “twitters” to aid in communication within and between species (Snowdon, 2001). These calls can share information about identity, status, predation threats, and interactions. New World primates vocalize in a variety of ways to share information about individual, group, social, and environmental dynamics, making this form of communication important for primate life.

Old World monkeys have little communication about the surrounding habitat and only have specialized calls related to particular stimuli. Old World monkeys have stress, alarm, and affiliative calls. There are excitement calls used to deal with stressful scenarios (Andrew, 1962). Alarm cries include snake “chutters”, bird “chutters”, and terrestrial predator “chirps” (Hall & DeVove, 1965). Macaques have also been known to “bark”, “coo”, “gecker”, and “scream” (Hauser et. al. 1993). While there are minimal vocalizations in Old World primates, those that are used can serve important roles in sociality and group reliance.

The apes have a wide range of vocalizations ranging from small social interactions to large territorial calls. The lesser apes, the gibbons and siamangs, have a very loud call often found in a duet used for territoriality and social bonding. The great apes have a variety of calls. Gorillas will “whimper”, “cry” and “scream” when they are young to gain attention and keep with the group (Fossey, 1972). Adults grunt up to eight times per hour to determine the whereabouts of others and engage in social interactions (Harcourt et. al. 1993). Threating displays include “barks” to predators (Harcourt et. al. 1993). Chimpanzees have similar calls used for social interactions. The closest human relative has only twelve noise varieties including contact “grunts”, excitement “hoots”, fear “screeches”, distress “whimpers”, and a playful “panting laugh”. Bonobos have a high “hoot”, low “hoot”, contest “hoot”, greet “grunt”, and “wieew-bark” all used for social interaction and information exchange (de Waal, 1988). Orangutans have thirty-two varieties of vocalizations specific to age classes (Ross & Geissmann, 2007). Play grunts can be used in playful interactions as well as raspberries (Ross & Geissmann, 2007). Long calls and “barks” are more complex for information sharing while “chomps” and fear squeaks indicate stressful scenarios. The vocalizations in the lesser and greater apes are used in a wide variety of situations, making the communication a very important aspect.

Human beings have the most complex vocal communication found in the Order Primates. The species is considered to be the only extant primate to have a true spoken language. While there are noises that can convey basic information to social groups, humans have developed a language with a set of vocabulary that can be altered to interpret any scenario. There are currently 6909 living languages in the human species. These languages are equipped with alphabets of letters or symbols and a method of placing them together to create words or phrases. The words are then strung together in a continuous thought to form a meaning and convey a message. While some languages are able to be written, the majority are orally transmitted from one generation to the next. Whether written or not, spoken language serving as human vocal communication is one of the key components of human sociality and complexity.

Understanding the importance of the communication in typical primate groups can help primatologists realize the relationship within the polyspecific association when communication is a key feature. The communication common to primate social interaction seen in multi-species interactions can highlight the importance of the association.

Polyspecific Associations

Polyspecific associations are relationships that form between two different species and are identified as intentional close proximity or coordinated activities (Rehg, 2017). These interactions, whether intentional via both species' or asymmetrical to one species, are a key component to natural ecosystem structure and systems (Thompson et. al. 2012; Walsh, 2013). The interactions of these species can be beneficial mutually (mutualistic), beneficial to one and neutral to the other (commensalism), beneficial to one and harmful to the other (parasitism), neutral to one and negative to the other (amensalism), or negative to both species (competition) (Deshmukh, 1986; Kricher, 2011). The possibility of mutualistic or commenalistic associations may stimulate species to interact with another species and are the most common of these relationship types. These forms of interactions can be seen in mixed-species groups of fish (Ehrich & Erlich, 1973), birds (Morse, 1970), ungulates (Sinclair 1985), and primates (Waser, 1987). Polyspecific associations are seen across the animal kingdom in a wide variety of species, suggesting they are an important feature of ecosystem dynamics (Goodale et.al. 2010).

Polyspecific associations are suggested to benefit participating species in many ways including through increased anti-predation and foraging benefits balanced by the cost of competition and opportunity costs (Rehg, 2017). Anti-predator benefits are primarily related to eavesdropping of alarm vocalizations and vigilance of the other species (Altmann & Altmann, 1970; Esenberg & Lockhart, 1972; Magrath et. al. 2015). Suggested less direct benefits of anti-predation include dilution of risk in a larger group and reduced vigilance costs (Magrath et. al. 2015). Foraging benefits are typically asymmetrical to the non-primate species in which the species will gain more out of the interaction than the primate (Heymann & Hsia, 2015). The non-primate species follows the primate to forage on the dropped fruit or leaves while the primate receives no increased benefit from the interaction. Only few cases support both species.

The amount of benefit is also habitat related in which Neotropic associations are suggested to only have foraging benefits while African and Asian interactions are hypothesized to have both anti-predation and foraging benefits due to the species size and other characteristics (Heymann & Hsia, 2015). The habitat possibilities are important for the number of suggested interactions as the associations are related to the habitat features of canopy cover, species density, and foraging material allocation (Figure 2). Associations in which both the non-primate and primate species can benefit are only in anti-predation situations, though the honesty of calls may still be asymmetrical to the primate (Stensland et. al. 2003). Though the benefits are not typically even between the interacting species, these associations do not normally harm the primate species, allowing the interaction to continue occurring.

Naturally occurring polyspecific associations found in the Order Primates can be between two primate species or between a primate and a non-primate (Stensland et. al. 2003). There are certain characteristics of primates that make them more or less likely to engage in a polyspecific interaction including body size, group size, diet, habitat, and activity patterns (Heymann & Hsia, 2015). Larger primates are suggested to have more interactions due to the chances of them flushing out more prey and using more food that another species could benefit from. Due to this, a large majority of polyspecific associations occur in Africa and Asia where the primate species are larger (Heymann & Hsia, 2015). Larger groups of primates may also be more likely to be in an interaction because of more food droppings possible. Species that live in larger social groups may be much more likely to have an association than small groups or individuals.

Primates are known as wasteful foragers by which frugivores will often not eat a whole fruit before dropping it, folivores may disturb more leaves than they eat, and insectivores will flush out more than they can capture. This wasteful behavior makes primates optimal species to associate with for foraging benefits (Heymann & Hsia, 2015). Primates with more wasteful behaviors are more likely to be in a polyspecific association due to the increased benefit of the other species from this behavior. These associations are more common in jungle or forest habitat versus woodland or savannah due to availability of species and opportunity of association. Even though the number of associations may be larger in forested areas, the anti-predation benefit may be more likely the cause in open habitats (Heymann & Hsia, 2015). Primates that are diurnal are the most likely to have interactions with other species due to the larger number of species active during the day. These characteristics of primates make them more likely to be in polyspecific associations with another primate species or a species of another taxon.

There are four different variations of primate polyspecific associations including primate-bird, primate-mammal, primate-reptile, and primate-fish. Each of these polyspecific types has at least one primate species in association with a species from another order. The majority of the interactions are commensalistic in which the primate is not affected by the association while the other species benefits from foraging on dropped material.

There are several different examples of primate-bird interactions in most habitats around the world, making it the most common type of interaction. These associations can be either commensalistic or have an aggressive component in which the primate will drive the bird away. One of the most common is the Neotropical kite with small New World monkeys that can last between five minutes and five hours (Heymann & Hsia, 2015). The kite will forage on flushed prey that the primates frighten as they move through the canopy. Other primate-bird interactions are based upon the bird eating dropped fruit from the foraging monkeys.

Primate-reptile interactions are not commonly seen in the polyspecific literature. There is only one association known in which a lizard follows primates in order to gather dropped fruit. (Glander, 1979). The basilisk lizard (*Basiliscus basiliscus*) forages on fruits dropped by mantled howler monkeys (*Alouatta palliata*) (Glander, 1979). The rarity of this interaction may be due to the different vertical levels the species live in, a difference in foraging needs, and the difficulty of identification.

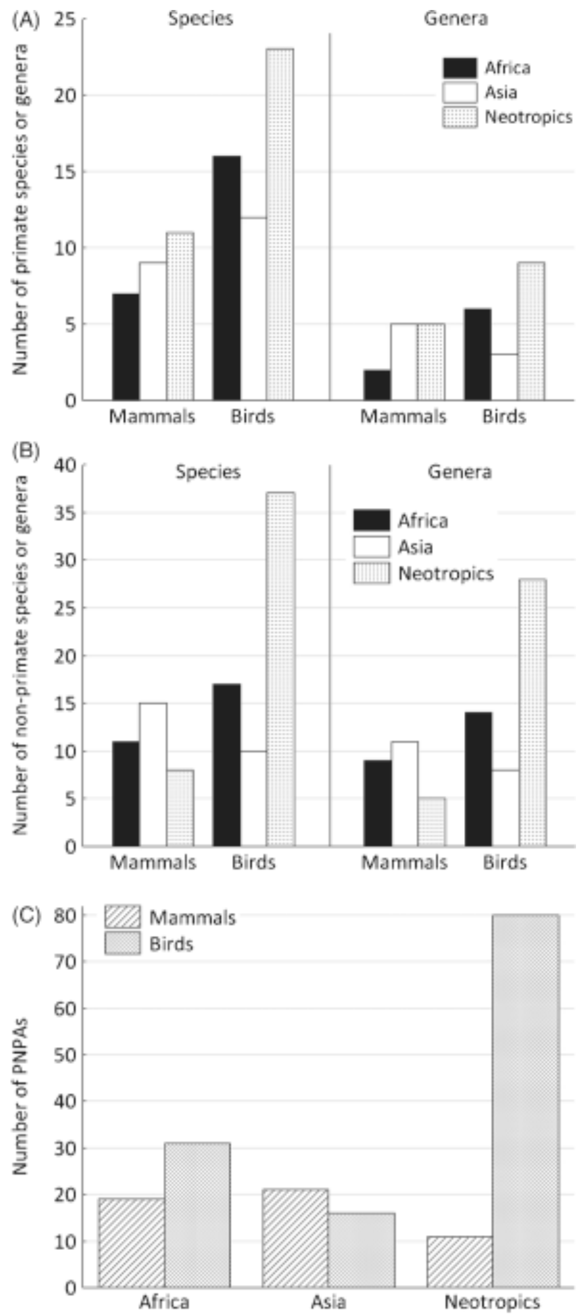

Figure 2. Used with permission from Heymann & Hsia (2015). Primate-non-primate associations distributions across continent and non-primate taxa.

In comparison, primate-mammal interactions are fairly common. The most known and studied system is the langur (*Semnopithecus entellus*) and the chital deer (*Axis axis*) (Heymann & Hsia, 2015). The deer will follow the langurs, eating dropped vegetation for up to three hours a day. Primate-mammal associations are seen across the order and are the most commonly identified in studies.

Out of all the interaction types, the primate-fish association is the most curious. There is only one example of this form in which the fish will follow the primate for up to 100 meters as it forages on leaves and fruits (Sabino & Sazima, 1999). The fish are limited to following the water source edge, giving great restriction to the interaction. There are few known associations of this manner due to the environmental features required for an interaction.

The different variations of polyspecific associations show the broad range and wide diversity of these interactions as seen in Figure 2 above where (A) is the number of primate species associated with mammals or birds and (B) is the number of non-primate species genera associated with primates (Heymann & Hsia, 2015).

Each of these association variations has a seasonal component. The time spent in the interaction may be related to the time of the year, the weather, and the time of day. The true cause of polyspecific associations cannot always be determined through current scientific data collection. The ability to identify such an interaction has become more common in the field, but the underlying causes of the associations are not known in all cases.

Primate-non-primate polyspecific associations are found across the Order Primates, primarily in commensalistic or mutualistic interactions. The primates in these interactions are often not harmed and are instead followed by opportunistic species. Anti-predator benefits through cross-species alarm vocalizations can be seen in some scenarios, giving a benefit to the primates. While these are the associations known to primatology at this time, there are interactions between species that may need further study to determine if they also qualify as a polyspecific association.

While these interactions are found in many species across the primate taxa, the current questions of polyspecific associations are wide and cover broad information topics about the interactions. There is currently a set of characteristics scientists look for to identify an interaction, but no definitive definition used across the field. It is not known what the instigation is in most interactions, let alone the true benefits or costs. Acknowledging what is currently known and unknown in the field of polyspecific associations is the first step into developing a more distinct set of features that define the interactions.

Primate-Primate Associations

Primate-primate interactions are suggested to be important to wild primates for the protection against predation threats and benefitting each other in foraging bouts by feeding on slightly different foods in the same habitat. Mixed group species have been suggested to forage together in large groups to aid in forage discovery and predator detection (Terborgh, 1986; Windfelder, 2001). The period of time spent with the heterospecific group is considered to be of great value for the foraging groups. The number of individuals in the larger group increases the probability of food discovery and sharing, reducing the amount of effort required for each individual to exert in order to locate food (Terborgh, 1986). Group living expanded into multi-species group associations in primates is suggested to have many beneficial features.

Beyond further success in foraging due to more individuals, an increased group number is suggested to reduce the possibility of predation (Petracca & Caine, 2013). This occurs due to the increase in the number of eyes able to detect a predator and the use of predator deterrents. Studies have seen relations between local primate species groups lead to greater reduction of predation threats through the use of alarm calls (Zuberbühler et. al. 1997; Seyfarth & Cheney, 1990; Searcy & Caine, 2003). Dependence between species groups for the reduction in predation is a key aspect of polyspecific association occurrences.

There are few associations found in Strepsirrhini, perhaps due to the specific and separated niche partitioning within the Madagascar ecosystems. While many of the species are threatened by the same predator species, there are few known interactions between the lemurs. The Mahafaly sifaka (*Propithecus verreauxi*) and ring-tailed lemur (*Lemur catta*) join in larger groups during reproductive seasons to minimize predation events (Freed, 2006). The increase in risk due to the distraction of the reproductive season is suggested to be the instigator of the association. The ring-tailed lemur is also able to recognize the sifaka's alarm vocalization as an example of communication of alarm call communication across species (Loudon, 2013; Oda & Masataka, 1996; Sauther, 1989). The Verreaux's sifaka (*Propihecus verreauxi verreauxi*) and the redfronted lemur (*Eulemur fulvus rufus*) have a similar interaction in which the species can understand one another's alarm vocalizations and respond according due to the predation threat (Fitchel, 2004). Current studies are investigating if there are more lemur polyspecific interactions among Strepsirrhines currently unknown to science.

There is a large number of polyspecific associations found in the Old World primates. Many of the interactions found in the Old World primate-primate polyspecific associations are related to reducing the possibility of predation. One of the most well-known examples is the red colobus (*Procolobus badius*) and the Diana monkey (*Cercopithecus Diana*) who form polyspecific associations to minimize the possibility of chimpanzee predation (Bshary & Noe, 1997). The two species hold slightly different canopy levels, amplifying the possibility of spotting the chimps before an attack can begin. Diana monkeys (*Cercopithecus Diana*) also associate with Campbell's mona monkey (*Cercopithecus campbelli*), the lesser spot-nosed monkey (*Cercopithecus petaurista*), the Western red colobus (*Piliocolobus badius*), king colobus (*Colobus polykomos*), and sooty mangabey (*Cercocebus atys*) by each responding to alarm calls in reaction to a chimpanzee threat (Oates & Whitesides, 1990). Chimpanzee threats also increase connectivity through communication in red tailed monkeys (*Cercopithecus adiate*), red colobus, blue monkey (*Cercopithecus m*itis), Wolf's mona monkey (*Cercopithecus w*olfi), mantled guereza (*Colobus guereza*), black crested mangabey (*Lophocebus aterrimus*), and Allen's swamp monkey (*Allenopithecus nigroviridis*) (Chapmann & Chapmann, 2000). Primate-primate interactions are common in Old World monkeys due to the shared predation threats of the savannah. Working together to identify and alert others to the predators appears to be an established strategy for Old World monkeys. While these associations are primarily due to the pressure of predation, it is suggested that the primates also forage together in these interactions to increase foraging output. It is also considered that the threat of predation in this system may outweigh any cost of multi-species foraging groups.

New World primates also have a plethora of polyspecific interactions partially due to the large amount of species found within ecosystems and the overlapping of predator threats. There are many primate-primate associations found in the New World primates primarily related to reducing predation threat pressures. Emperor (*Saguinus imperator subgrisiscens)* and saddleback (*Leontocebus weddelli)* tamarins have been found to coexist in multi-species groups to minimize predation (Bicca-Marques & Garber, 2003; Windfelder, 2001). Saddleback tamarins have also formed groups with mustached tamarins (*Saguinus mystax*) and Goeldi's monkeys (*Callimico goeldii*) (Peres, 1993; Porter, 2001). Golden headed lion tamarins (*Leontopithecus chrysomelas*) form similar relationships with the Wied's marmoset (*Callithrix kuhlii*) (Oliveria, 2011). Squirrel monkeys (*Saimiri*) are often associated with capuchin (*Cebus*) groups, although their purpose is unclear (Haugaasen & Peres 2009).

Several of the interactions between New World species are suggested to be predominately related to increased foraging success. The buffy saki (*Pithecia albicans*) is known to form relationships with tamarin and capuchin species. Spider monkeys (*Ateles*) and brown bearded sakis (*Chiropotes israelita*) associate in foraging bouts (Lehamn & Fleagle, 2006). New World monkeys are suggested to interact with other species in order to maximize foraging and minimize predation threats in the dense jungles of Central and South America.

There are many associations between different primate species, with the majority of them being suggested to minimize predation pressure and/or increase foraging output by forming multi-species groups. These interactions within the primate order may be able to provide some background on how human social interactions with other species developed and evolved into the associations we engage in today.

Primate-Non-Primate Associations

Polyspecific interactions occurring between a primate and a non-primate are more common than previously thought. There are 95 non-primate species that associate with 64 primate species to form 174 interactions (Figure 2) (Heymann & Hsia, 2015). The relationship is biased to the non-primate species and can be viewed as a mutualism, commensalism, or commonly as a parasitism. Most of these polyspecific interactions are seen only when the primate is functioning in a natural manner and the non-primate species is using that action to benefit itself.

Old World primates have several examples of primate-non-primate associations ranging from highly dependent on foraging benefits to multi-species predator avoidance via shared alarm vocalizations. There appears to be an equal percentage of interactions related to both of these benefits in the Old World primates.

Foraging benefits of the non-primate species are commonly seen in interactions in which the organism follows a foraging primate and interacts in a commensalistic manner. Rock kestrels (Falconidae) have been found foraging with desert baboons (*Papio hamadryas*), suggested to increase foraging output for the kestrel (King & Cowlishaw, 2009). Golden jackals (*Canis aureus*) have been found to follow hanuman langurs (*Semnopithecus*) to forage on dropped fruit (Newton, 1985).

Alarm vocalization communication is seen in the Old World primates, both where the primates are responding to an alarm and are giving the original vocalization. African hoof stock such as impala (*Aepyceros melampus*), wildebeest (*Connochaetes*), zebra (*Equus quagga*), and tsessebe (*Damaliscus lunatus*) can recognize olive baboon (*Papio adiat*) alarm calls, helping with anti-predation (Kitchen et. al. 2010). Diana's monkey alarm calls can be understood by hornbills (*Bucerotidae*) (Rainey, Zuberbühler & Slater, 2004).

In the reversed scenario, vervets (*Chlorocebus pygerythrus*) can respond to starling (*Sturnus vulgaris*) alarm vocalizations (Rainey et. al. 2004b; Seyfarth, 1986). Bonnet macaques (*Macaca adiate*) also respond to Sambar deer (*Rusa unicolor*) calls in a similar way (Ramakrishan, 2000). These examples are scenarios in which the primates are responding to the predator-specific alarm communication of another species.

Chital deer (*Axis axis*) and hanuman langurs (*Presbytis entellus*) are also an example of a deer-primate interaction found in the wild in which the species share food, alarm call responses, and group movement (Newton, 1989). These interactions occur similarly in the Japanese snow macaque (*Macaca fusculata*) and the Sika deer (*Cervus nippon*) (Tsuji et. al. 2007) though this interaction has been also recently studied for bizarre sexual encounters between the two species that is instigated by the primate (Pelé et. al. 2017). Old World primates have many different interactions with non-primate species, primarily related to other species foraging on dropped food.

New World primates also form polyspecific associations with non-primate organisms. These include the collared peccaries (*Pecari tajacu*) and black howlers (*Alouatta caraya*) in which the peccaries will forage on dropped fruit and react to howler alarm calls (Desbiez et. al. 2010). Capuchins are followed by Characidae fish that eat forage droppings (Sabino & Sazima, 1999). The majority of interactions found between Neotropical primates and non-primates occur with bird species with upwards of 80 interactions currently known in the literature. One well known example is the double toothed kites (*Harpagus bidentatus*) that will associate with capuchins for foraging benefits (Boinski & Scott, 1988). New World monkeys have more interactions with other non-primate species than the Haplorhines and these associations appear to be primarily commensalistic with few mutualistic relations.

There are only two associations related to predation threat reduction and foraging benefit in which the primates are suggested to be the key instigator of the interaction. The squirrel monkey (*Saimiri ustus*) is known to follow coatis (*Nasua nasua*) for foraging benefits (Haugaseen & Peres, 2008). Tantalus monkeys (*Chlorocebus tantalus*) are also known to instigate following African bushbuck (*Tragelaphus scriptus*) (Henshaw, 1972). These two interactions are interesting as the primate is actively initiating the association versus being followed passively by the non-primate organism.

The different interactions between primates and non-primates highlight the cross-taxa associations seen throughout the animal and plant kingdoms. The interactions are important for ecosystem connectivity, function, and livelihood. These associations can teach man about the true relationships between various organisms and the connections that run through the planet.

Humans

The species of *Homo sapiens* has its own unique set of associations with a wide range of species also known as ethnoprimatology. Briefly, without stepping too far into ethnoprimatology, there are three kinds of human-other species interactions: domestication interactions, sympatric species, and the shared relationships.

Each of these association types is highly complex due to the nature of human beings and their relations with other species. Domestication interactions occur when humans keep animals as pets or livestock for either companionship, work, or food (Serpell, 1996; Walsh, 2009). Sympatric species are those organisms that live alongside humans in human landscapes (Adams, 1994). Shared relationships are interactions between man and animals that appear more mutualistic in which both parties benefit from working together in a certain scenario such as in dolphins that fish with local fishermen (Busnel, 1973).

Every culture, group of people, family, and even individual has their own relationships with animals based on their own beliefs and lives, making this a more complex topic (Morris, 2000). It is up for debate if these interactions are truly polyspecific associations as the relationships are often forced by human activity and are not always reciprocally beneficial. While the interactions today may be considered as domestication, sympatric, and shared, each of the polyspecific associations are suggested to have started as mutual associations and developed into specialized relationships.

Identifying the interactions that man engage in and discussing the origins of them can expand our understanding of man's place within nature. The relationships that man has developed closely may tell us more about our past than we currently believe. The many associations that man has and will be a part of are important to understand our history, both evolutionary and culturally.

CHAPTER 3. REVIEW OF CURRENT METHODS

The basic methodologies of primatology are based in the scientific method, as the field does use scientific data collection to understand the ecology, behavior, and lives of primate species. The path of the scientific method is to develop questions based on the gaps in current knowledge, create hypotheses, generate methods and conduct data collection through experimentation and/or observation, transform the data into quantitative material, analyze data to develop new understandings of the topic, and then start again with the updated gaps in the knowledge (Gauch, 2003). If the data findings support the original hypotheses, a new line of questions, either similar to the original or not, can be started. This circular series of questioning, experimentation, and analyzing to start again can be found throughout the scientific field. It is applicable to the world of primatology just the same.

One of the most important parts of primatology is understanding the currently known literature. The first step in any scientific study is to acknowledge what is known and more importantly unknown about the subject. This lets the gaps in the current knowledge come to light, showing what could be expanded upon through further study. The main ways of doing this are to read extensively, discuss with colleagues, and think outside the box as to what could be known about a primate species. Once the gaps are identified, the testable questions can be developed, and the data collection methodology created.

There are several different formats of experiments and observations used to understand primate communication, predation, and associations. These attempts to further the knowledge about primates can be divided into two categories: experimental and observational. Each study has a particular protocol of methods that are developed specifically for that study question, making each data collection unique in methodology.

Experimental studies can gather behavioral responses in both wild and captive organisms to understand how primates react to either natural or artificial scenarios. The experiments allow scientists to have some control over the input primates can respond to, specifying certain circumstances that can give detailed context to the reaction of the primates. Experiments are important for understanding the different variables and components of scenarios. Most experimental methodologies attempt to test only one feature of a situation to fully understand the effects of it individually on the whole system.

Communication studies can use playback experiments in which the studied call is recorded or digitally mastered and then broadcasted to the primates to elicit a response (Petracca & Caine, 2013; Seyfath & Cheney, 1990). Playback recordings have to be high quality in order to properly replay the full call throughout the frequency spectrums of primates.

There are protocols set by previous studies that are established to minimize primate habituation to study calls, reduce group stress, and maximize data collection strength. According to the current literature, the experiment must occur after at least half an hour up to two hours without a natural vocalization of the wanted playback to ensure the reactions are not due to after effects of the natural call (Zuberbühler et. al. 1999). Playbacks can only be conducted after 10 minutes of no vocalizations within or exterior to the group as to limit the possibility of the primates responding to a naturally instigated vocalization (Zuberbühler et. al. 1999). Limited trials per group per day and week are required in order to reduce habituation to the recorded vocalization (Charnov & Krebs, 1975; Tincoff et. al. 2005). Groups can only be exposed the call a maximum of once a day as to not over habituated the individual to the call in which the primates will not respond to the call. Each group is typically only exposed to a playback of a call a maximum of six times a week with at least 24 hours between each trial (Macedonia & Yount, 1991; Petracca & Caine, 2013; Wich et. al. 2002). These protocols are put into effect for communication studies to ensure the primates do not become habituated or stressed to the calls.

Predator models can be used either to instigate an alarm call or to observe the natural behavioral response to the threat (Jones et. al. 2007). There are different levels of predator models ranging from not similar at all in detail to highly detailed in order to see the characteristics that enable primates to identify a threat. Calls are often instigated using a model of a local species placed on the ground or in the trees in the direct path of the group at a distance of several meters (Ouattara et. al. 2009). Control objects of are used in order to determine if the primates are only reacting to a new object or if they are responding to the model (Joslin et. al. 2003; Meno, 2013). The use of models in experiments must be carefully monitored as to reduce habituation and fear responses from the primates to be able to use the them to understand primate predation responses, predator identification, and communication.

One of the problems that experimental designs must account for is to ensure that the study primates do not associate humans with either a call or model. The researchers must move far enough away from the playback to not allow the individuals to assume the vocalization is coming from the human. It is also dangerous to have primates associate scientists with calls for habituation issues and behavioral follows. Protocols must be in place and followed for every trial in order to minimize the threat of these problems.

Observational studies use scientist observation in attempt to understand particular phenomena seen in the primate species (Altmann, 1974; Mench, 1998). There are a few common methods of observational data collection including focal and scan. Focal data follows a protocol in which a single individual is focused upon for a set period of time (typically ten minutes) and all behavior is continuously recorded (Altmann, 1974). These focals are rotated on each group member as to not bias the data to certain individuals. Focal data aids in understanding detailed behavioral patterns. Scan data is when observers will record what every group member is doing at ten-minute intervals with a two-minute timer of finding all members (Da Cunha et. al. 2006). The behavior recorded is that which the individual is doing the moment the group member is spotted in the scan. Scan behavior data is beneficial in understanding group and species behavior. Though other forms are known, these are the two major methods of behavior data collection commonly found in the studies.

The behaviors studied in primate observational and experimental designs come from the previously understood knowledge of the species and system of interest. All of the behaviors that a species is known to participate in is called an ethogram (Bekoff, 1972). These large lists of defined behaviors are specific to each primate species and can be pulled from to create a behavioral catalog for the experimental study. A behavior catalog is the subset of behaviors from the ethogram that is used in a study (Bekoff, 1972).

Data collections often use a behavioral catalog that are created through the merging of previous studies and tailored to the study. There are main categories of behavior that are typically recorded with detailed behavior types related to the study. Each behavior can occur simultaneously with another but can be considered mutually exclusive dependent on the study parameters (MacNulty et. al. 2007). Each of the behaviors is described in a studied chart to ensure there is a certain definition to identify the behavior similarly across trials. Scientists participating in data collection are often pushed to memorize the catalog to timely identify primate behavior. Below is an example behavioral catalog that could be found in a research design (Table 5).

Table 5. Behavioral catalog example

Behavior	Definition
Vocalization	
Long Vocalization	High frequency, longer call
Alarm Vocalization	High frequency, short call, repeated notes
Unknown Vocalization	Mixture of call or unknown
Movement	
Downward Movement	Move downward $\geq$ 1 meters from supposed predator location
Upward Movement	Move upward $\geq$ 1 meters up from supposed predator location
Freeze	Not move for < 3 seconds
Scanning	
Upward Scanning	Scan up immediately after playback
Downward Scanning	Scan down immediately after playback
Circular Scanning	Mixture of scanning upward & downward immediately after playback
Aggression/Mobbing	Aggressive actions toward another or the environment including mobbing
Resting	Relaxed motion for more than 10sec
Foraging/Feeding	Moving through forage material/Placing forage into mouth
Groom/AutoGroom	Grooming another individual/Grooming oneself
Out of Sight	Not visible at the time of scan

The different varieties of study used in data collection are selected based on the questions being asked and the environment in which they are being tested in. Whether organisms are in captivity or in the wild can alter the study protocols. Captive studies are typically able to use more experimental designs due to the containment of individuals and over-habituation to humans (Mench, 1998). The primates in captivity have become so used to humans and captivity has changed their behaviors enough that the experiments or observations are no longer affected by the presence of humans. Wild studies use less experimental protocols due to lack of habituation, stricter regulation on wild-primate experimentation, and logistical constraints. Both wild and captive scenarios can more easily support observational studies. The protocols of studies are highly environmentally-dependent on the species, groups, and individuals of the primates of interest as well as the physical environment and scientists on the study team.

There can be some error is using either experimental or observational data in which the observer is main source of mistake. Human error is a difficult thing to overcome in studies but can be attempted through strictly taught protocols, field observer tests, and awareness of possible error. Ensuring that team members are all learned in the same protocols is key for having unbiased, un-skewed data collection. Field observer tests are in-field "exams" used to measure the correct behavioral identification during focals and scans based on the used behavioral catalog (Shoukri, 2010). Being aware of error is important to realizing and coping with it. Human bias in studies can also pose a threat to data collection. Reducing the power and presence of bias and error is key to producing the most qualitatively sound data.

Studying Polyspecific Interactions

Polyspecific associations in primate species can be difficult to identify, understand, and study due to the limited occurrence and undetermined causes. The definition of polyspecific associations is not a constant in the primatology field at this time but is instead the series of characteristics seen in unison during the interaction. There is difficulty in defining the interactions because the associations are different based on each scenario, making it more complex to study such interactions.

These forms of associations are often found through the ad libitum observations of field scientists. Once an affiliation has been recorded, transects are often conducted to continue the study of the interaction. The number of times a certain association is seen can indicate the rate of occurrence. Behavioral sampling can be conducted on troops in order to quantify the frequency of the polyspecific association. The frequency of these interactions is important for determining the importance of the association to the involved primate species.

Though the presence of a polyspecific association can be seen through observational data collection, it is more difficult to quantitatively analyze the benefits of such interactions. There are several polyspecific associations studied across the primate taxa both between two primate species and between a primate and a non-primate species, though the latter has fewer studies (Tables 6 & 7). These tables have select interactions that have been studied across the order highlighting the variety of species associating in these interactions. This shows a slim variety of the currently published studies on primate-primate interactions though a majority of the studies focus on the Ceropithicines and Callitrichids. It is easier to identify many of the written work on primate-non-primate associations as there are few.

In regard to increased foraging success, only few studies have actively measured the calorie intake levels of associating species. The nutritional value of forage material dropped by Japanese macaques (*Macaca fuscata*) is higher than foraging material not altered by the primate for the sika deer (*Cervus nippon*) (Tsuji et. al. 2007). It is more difficult to place statistical data onto the anti-predation benefits of shared and reduced vigilance in interacting groups. These benefits are the only association characteristics that are suggested to be shared equally by both participating parties. Since these benefits are only behavioral, it is more difficult than measuring forage material. Few observational studies are able to quantify the benefit of interacting in polyspecific associations. While polyspecific associations are not

Table 6. Commonly studied primate-primate associations

Species Involved	Suggested Interaction	Studies
Strepsirrhines Mahalfay sifaka (*Propithecus* verreauxi) & Ringtailed lemur (*Lemur catta*); Sifaka (*Propithecus verreauxi verreauxi*) & Redfronted lemur (*Eulemur fulvus rufus*)	Predator avoidance	Fichtel (2004); Freed (2006); Loudon (2013); Oda & Masataka (1996); Sauther (1989)
Playtrrhines Emperor tamarin (*Saguinus imperator subgrisiscens*) & Saddleback tamarin (*Leontocebus weddelli*); Squirrel monkey (*Saimiri*) & Capucin (*Cebus*); Spider monkey (*Atles*) & Brown bearded saki (*Chiropotes israelita*); Goeldi's monkey (*Callimico goeldii*), Moustached tamarin (*Saguinus mystax*) & Saddleback tamarin (*Saguinus fusicollis*); Golden headed lion tamarins (*Leontopithecus chrysomelas*) & Wied's marmoset (*Callithrix kuhlii*)	Predator avoidance & foraging benefit	Bicca-Marques & Garber (2003); Buchann-Smith (1999); Haugaasen & Peres (2009); Heymann (1992); Lehamn & Fleagle (2006); Oliveria (2011); Peres (1993), Porter (2001); Windfelder (2001)
Catarrhines Red tailed monkeys (*Cercopithecus adiate*), Blue monkey (*Cercopithecus m*itis), Wolf's mona monkey (*Cercopithecus w*olfi), Mantled guereza (*Colobus guereza*), Black crested mangabey (*Lophocebus aterrimus*), and Allen's swamp monkey (*Allenopithecus nigroviridis*); Diana's monkey (*Cercopithecus Diana),* Lesser spot-nosed monkey (*Cercopithecus petaurista*), Red colobus (*Colobus badius*); Campbell's monkey (*Cercopithecus campbelli*), King colobus (*Colobus polykomos*) & (*Cercocebus atys*)	Predator avoidance & foraging benefit	Bshary & Noe (1997). Chapmann & Chapmann (2003); Noë, R., & Bshary, R. (1997); Oates & Whitesides (1990); Walters & Zuberbühler (2003)

Table 7. Commonly studied primate-non-primate associations

Species Involved	Suggested Interaction	Studies
Platyrrhines Collared peccaries (*Pecari tajacu*) & black howlers (*Alouatta caraya*); Characidae, Double toothed kites (*Harpagus bidentatus*) & capuchins (*Cebus*); Squirrel monkey (*Saimiri ustus*) & coati (*Nasua nasua*)	Commensal foraging benefit	Boinski & Scott (1988); Desbiez et. al. (2010); Haugaseen & Peres (2008); Sabino & Sazima (1999)
Catarrhines Rock kestrels (Falconidae) & Hamadryas baboon (*Papio hamadryas*); Impala (*Aepyceros melampus*), wildebeest (*Connochaetes*), zebra (*Equus quagga*), tsessebe (*Damaliscus lunatus*) & olive baboon (*Papio* adiat); Tantalus monkeys (*Chlorocebus tantalus*) & African bushbuck (*Tragelaphus scriptus*); Golden jackals (*Canis aureus*) & hanuman langurs (*Semnopithecus*); Chital deer (*Axis axis*) & hanuman langurs (*Presbytis entellus*); Vervet (*Chlorocebus pygerythrus*) & starling (*Sturnus vulgaris*); Hornbill (*Bucerotidae*) & Diana's monkey (*Cercopithecus Diana*); Bonnet macaque (*Macaca adiate*) & Sambar deer (*Rusa unicolor*)	Commensal foraging benefits, mutual predator avoidance, foraging benefit, movement	King & Cowlishaw (2009), Kitchen et. al. (2010); (Henshaw, 1972); Newton (1989); Rainey et. al. 2004b; Rainey, Zuberbühler & Slater (2004); Ramakrishan (2000) Seyfarth (1986)

commonly studied qualitatively, the world of science should continue to push for greater statistic understanding and measurable factors of these interactions.

Sharing Findings

Once the data collection is completed, the raw data must be transformed, analyzed, and then conveyed as findings. Raw observational and experimental data is often subjective materials taken from primate behavioral responses to the scenario. These data must be altered into a qualitative measure to be run through statistical tests. Once the data has been changed into an objective form, they can be placed into statistical models and tests to determine the correlations, relationships, and interactions between variables and the behaviors. The statistical tests allow the qualitative data to become significant or not related to a particular hypothesis. The significance or insignificance values of a statistical test indicates the lack of or presence of a relationship between the studied variables within the scenario. These values can be interpreted as the importance or nonimportance of a relationship within the behavioral situation. Once these test values are determined, the researchers can transform the numeric significance into words discussing the found relationships and interactions within the scenario. The collection, transformation, testing, and conveying of data is important for sharing the findings of primatological work.

CHAPTER 4. REFLECTION AND RECOMMENDATIONS

Primatology strives to expand our understanding of primate species. Identifying the characteristics of the Order Primates species is not only important for the field, but for broadening the knowledge about human beings. Many of the major characteristics and features of primates are well known to science, while others have only the surface identified.

The data collection of the primatological field strives to expand our understanding of primate species, but also furthers the gathering of more knowledge. As we find new information or revise older information, the opportunity for even more understanding is possible. This section will reflect on the current knowledge, the gaps in the information, and recommendations for the field, moving forward in regard to methodology errors, predation, vocal communication, and polyspecific associations.

Methodology Errors

Observational and experimental studies of primatology have the opportunity for error to occur within the data collection period and analysis (Table 8). There is a typical set of errors common for data collection in part because of a mode of thinking related to methodology often caught in older methods with a fear of stepping forward in regard to data collection, researcher roles, and possible used technology. This established mindset is in part due to the nature of primate behavioral studies, a reliance on technology, and the possibility of human error. Experimentation and observation in the primatological studies in field or captive scenarios have many features that can cause problems, errors, or difficulties in the data collection period.

Primate behavioral studies have difficulties due to the nature of the primate subjects themselves. Primates are not always easily followed through their natural habitat, making observational data often difficult to collect. These intelligent organisms have their own autonomy both in the wild and in captivity, enabling them to choose whether or not to allow the experiment and/or observation to be conducted.

Beyond following difficulty, there is room for error during behavioral scans if an individual is out-of-sight at the time of the scan. These blanks in the data sheet may bias the suggested behavior due to the removal of individuals from the data set. Attempting to reduce the number of missed data observations through extensive practice following the primates can minimize the effect.

It can also be difficult to cope with the subjectivity of observational studies due to human nature and experience. One of the best ways to combat these features of primate research is strict protocols learned by all members of the research team. Training and practice both in the field and lab are important for team cohesion on methodologies. Having common methodologies is key to reducing the difficulty of behavioral studies. It is also wise to conduct observer reliance tests to ensure the protocols have been understood and used by all scientists participating in the study.

Technology, while adding to the possible information gathered in data collection, can be difficult to use. The various types of technology used in the primatology world includes speakers for vocalization broadcasts and playbacks, recorders such as Zoom© and handhelds for vocalization recording, computers for data entry, GPS for track recording and point data, and video recorders for reviewable film collection. Reliance on technology, particularly in rugged terrain, can have its disadvantages. The technology is often required to work for extended periods of time in often rough terrains, severe weather, high humidity, and possibly damage caused by transport or human error. Technological problems may occur but can be avoided due to extra preparations.

Beyond withstanding the habitats, the technology must be used correctly. Scientists have to properly use the current technology in the studies' contexts. User error can be a common issue for technology and can be avoided through training. The primatology world needs to continue to use the new technologies but ensure that they are being used correctly. Proper training on the use of equipment can expand the possibilities of the field.

Even with the invent of new technology pieces such as state of the art GPS systems, field camera traps, and behavioral data systems, there is a common distaste for using new technology among scientists. This is not only due to resistance to change, but the fear of losing data with the use of new technology methods. Lost data due to technology errors is one of the most common responses as to why primatologists are wary to use new technology pieces.

While there may not be a way to remove all possible experimental or observational error, there are methods that can be implemented to minimize the compounding factors of error. One way to do this is to acknowledge that there are some areas of primatological research such as intelligent organisms' cooperation, minimizing human error, and technology functionality that need to be attended to in regard to dealing with inaccuracies and then stepping forward in solving these issues. These gaps in the primatology studies should be addressed and can be reduced in future experiments.

Taking steps forward in regard to methodology is not only reliant on reducing the error through understanding primate intelligence, reducing human mistakes, and embracing new technologies (Table 8). It is also important for researchers to embrace and develop new methods related to each component of data collection. The flexibility of researchers is important to the expansion of the field in regard to methodology.

Table 8. Methodology Error Gaps

Known	Question	Possible Solution
Primates can be difficult study subjects	What is the best way to reduce over-habituation while still having full data sets?	Train scientists, understand primate behavior
Human observation has error	What are other ways to combat human observation errors besides observer reliance tests?	Training, tests
Technology is key to the broadening capabilities of primatology	How does the field ensure it properly uses technology and has materials able to withstand the field?	Expand acceptance of new technology, use new technology

Predation

The body of knowledge currently available on primate predation is limited to the few instances of observed predation and our comprehension of anti-predation behaviors in the wild and via captive settings. Even though observational studies are not able to capture all predation situations, the information about the reactions to predators, social group interactions regarding predation, and predation events have given a great deal of knowledge to the primatology world regarding predation. Predation is now seen as an important feature of a primate's life history and has great pressure on the characteristics of primates. The known information about primates and their relationship to predation does have several areas that could be expanded upon (Table 9).

The lack of detailed information about primate predation in part due to the mode of thinking related to the topic. Researchers are often interested in the subject but sometimes assume there is no plausible way to truly understand the predation pressure in primates. This can reduce the number of studies focused on predation, the instances captured by researchers, minimal time dedicated to this topic, a bias in study species and habitat, and technology.

Steps forward in the method of thinking about predation can include expansions and changes to these subtopics of predation studies.

Predation of primates has been studied in a wide variety of species around the world. Predation has been physically observed in several scenarios, from tamarins being eaten by raptors and snakes (Heymann, 1987) to red colobus being attacked by chimpanzees (Boesch, 1994). The instances that have been recorded by scientists are most certainly an underestimate of actual predation. Due to the number of instances captured compared to the limited amount of time the scientists have in the field, the rate and pressure of predation is much larger than what is visible to researchers. This is also true for the cases in which the primate is the predator. Predation behavior in primates may be more common and regular than known to scientists due to research time constraints.

The true rate of predation in primates is a difficult thing to determine due to the rarity of predation sightings and the limited amount of time researchers have to capture such events. An expanse of research time could aid in minimizing the rarity of sightings. This could be difficult due to the necessary funds for extended research field seasons. However, if scientists are able to take more data on primates and spend more time with them in the field, the chance of gaining more information about the frequency of predation and predation threats would increase greatly.

Beyond additional time of researchers in the field, predation studies may benefit from an increase in studies focusing on them. There have been several studies working to understand the effects, the social structures pressured, and individual behaviors associated with predation. Even with an increase in these studies, further detail could be given to the subjects. It is also often an issue due to a bias in study species. Species in which the predators are more well known to science and those who can be more easily studied due to habitat or habituation are more likely to be studied. Information about certain species can be beneficial, but not always applicable across the entire order. An increase in predation studies across a broader range of species could greatly benefit the field.

The bias reduction could also lead to an increase in the number of habitats these studies are conducted in. Many studies up to date are experimented or observed in either captive scenarios or wide-open habitats, such as the savannah. This is due to the logistics required to have data on predation reactions. The captive situations have contained organisms that can be exposed to models or live predators safely while gathering large amounts of data, making them optimal scenarios for understanding primate behavioral responses to predation threats. Open areas, such as savannah habitats, allow researchers to more easily observe predation events and primate responses due to easy visibility. While these studies are able to give insight into natural reactions of primates in predation situations, there is a need to expand the habitats these observations are taken in. Dense habitats are often secluded from these observational or experimental studies, leaving a gap in the predation effect knowledge. Future studies should attempt to include these more difficult environments, as the species within them may have altered or different responses to predation threats due to the habitat type. An expanse of this kind in the primatological field study of predation may greatly add to the current body of knowledge.

Primate predation studies could gain from the expanse of technology use in the field. Though challenging, the primatological field is attempting to use as much of the available technological advances in the wild. Using radio telemetry for tracking individuals and groups, video cameras for recording behaviors, voice recorders for recording vocalizations or behaviors, camera traps for capturing images of passing organisms, global positioning systems for understanding movement and location of primates, and other technologies allows scientists new capabilities in documenting primate lives (Bailey & Burch, 2017). Primatological studies can try to figure out new ways to use these tools, diversifying what can be captured in the field. While the new abilities have greatly expanded the possibilities of science, it is wise to continue attempting to bring new technology forward.

One viewpoint of predation studies that is not often considered and could lead to an expanse in the known information of predator-prey interactions and responses is the predator viewpoint. While some designs have used predator models or calls to instigate reaction from the prey item, not many have reversed the scenario to the predator's side. The predator should have its own set of reactions and behaviors when realizing there is a potential prey organism near. Primatology can expand to studying the behaviors, reactions, and ecology of the predators to further understand the scenario. Some studies have used radio tracking to identify habitat use patterns in predators, while others have conducted behavioral studies on the carnivore. These studies are few and could be expanded in number. An even more beneficial study could look at both the primate reaction to predation and the predator's behavior in a predation attempt. Understanding multiple points of view on the same scenario could greatly further the knowledge of predation in primates.

The gaps within the predation events of primate lives are broad due to the lack of sightings, understanding of the predation rate, study biases, and technology lags (Table 9). These errors are not intentionally allowed by the primatology field but come with the rarity of seen predation events. Predation is often considered one of the key factors altering a primate's life history and behavior, though there needs to be more data supporting this. An increase in the number of studies focused on wild primates in a wide variety of habitats can reduce the bias of the field currently seen. Experimentation using the latest technology may aid in furthering the field's understanding of primate predation. Attempting to remove the unknown from predation of primates can expand the knowledge of its impact on primate lives.

These different components of predation studies that could be altered are rooted in changing the mode of thinking around primate predation. Researchers need to remove any mental biases or blocks to the progressive development of primate predation knowledge. This change in thinking can enable the previously discussed gaps to be acknowledged and addressed.

Table 9. Primate Predation Knowledge Gaps

Known	Question	Possible Solutions
There are a minimal number of predation sightings	How does the field maximize the number of predation events seen by scientists and recorded?	Increase time in the field, broaden knowledge of predation sightings
Predation is a key factor for a primate	How does primatology properly understand how much influence and how often predation occurs in a primate's life?	Expand studies
There are few studies focusing on predation with a species bias	How does the field expand the number of studies and species of predation observation?	Increase number of studies
Habitat bias occurs in predation studies	How does primatology make wild primate predation studies more plausible?	Expand predation studies into more habitats
Technology may be able to expand knowledge of predation	What are the best ways to use technology in studying predation in primates?	Use new technologies in studies
Experiments in primate predation are few	How does primatology use experimentation to understand primate predation?	Study predation beyond observation

Vocal Communication

Communication in primates covers a wide range of interactions including vocal information exchange, physical, movement, and silence. Vocal communication has been a prominent area of study in primatological studies. There has been an expansive array of communication studies conducted on many different species across the world. Studies are often used to expand our knowledge of primate communication and broaden the information about early human vocalizations. Several species have had their entire vocal repertoire studied by researchers, while others have had little communication studies at all. While the varieties of communication have been thoroughly studied, vocal interaction is one type that could be expanded upon by the field (Table 10).

The understanding of vocal communication in the primatology field is often biased due to how researchers perceive the current knowledge of the topic and the importance of the vocalizations. Understanding primate communication is more important than often perceived in the field. Expanding the understood vocalizations, reducing species and habitat bias, limiting excluded calls, and conducting both wild and captive studies can each be used to change the current method of thinking about primate communication.

One aspect of vocal communication that could be expanded upon is simply documenting the vocal repertoire within the Order Primates vocal repertoire. While most species have a majority of their vocalizations described and some studied extensively, not all primate groups have been observed in this manner. Ensuring that the entire vocal spectrum found in extant primates is known can provide us with a new understanding of the development of vocalizations and the steps taken to reach human speech. Expanding the catalog of vocalizations to as many species as possible can also reduce any species-bias currently seen in the literature.

Beyond capturing the variety of calls found in primates, vocal communication has a great issue with understanding and categorizing recorded calls. There is difficulty in placing meaning to calls or call types that have not been placed into one of the predefined categories of calls. The largest issue is that many researchers will disregard or omit these calls from any findings. While some will acknowledge that there were unidentified calls in the data few attempt to analyze them. The vocal communication knowledge could greatly benefit from individuals taking time to determine the category these unknown calls fit into, realizing the function of these calls through context of field notes, or creating new divisions within the categories to place these vocalizations. The most important thing this gap in the vocal communication understanding needs is time and dedication. With focused time, new types and functions of calls may be found.

Vocal communication studies in primates often appear to be quite simplistic in that they are commonly only used to identify calls or call types. A majority of work focuses on accumulating the calls of primates. As discussed before, this is key to our understanding of the vocal communication in primates but should not be the only focus of these studies.

Vocalizations are used by primate species in a wide variety of situations and circumstances (Snowdon et. al. 1982). Some studies have determined reactions to kin versus non-kin, group versus non-group, and other comparative reactions to calls. However, these could be expanded to new heights. Further experimental designs may aid the primatological field in understanding these scenarios in which vocal communication is relied upon. These experiments could use vocalizations to determine more social interactions within and between groups, age effects, cross-species communication, cross-taxa interaction, and other broader vocal interactions (Snowdon et. al. 1982). The benefits of widening the experimental aspect of communication studies include expanding our understandings of ecosystem interactions and polyspecific communication beyond the group or species.

There is a particular bias seen in the vocal communication experimental literature of captive studies. Captive studies provide a secure location to test a primate multiple times with easy observation, repeated data recordings, multiple trials ensured, and extensive knowledge of tested individuals (Rees, 2015). This setting allows detailed data with large amounts of trials to be carried out. The experiments in vocal interaction trials are understandably more commonly conducted in a captive scenario than the wild. While these data provide great insight to the field, the need for extensive wild trials is present. More studies need to be conducted in wild populations to minimize the effects of human habituation, captivity pressures, and changed behaviors due to captive settings. There is great reason for such a limited number of wild experiments as the primates are not contained, individual information may not be known, repeated trials may be limited, and the constraints of wild experiment logistics (Swart, 2004). Even though there is great difficulty in conducting wild-primate studies, there is a need to conduct them. Wild experiments can be used to determine the status of captive populations in regard to social skills, interactions, and health (Swart, 2004). Wild populations also provide a scenario in which human effects are minimized, showing more natural behaviors and responses to experiments (Swart, 2004). An increase in the number of wild experiments can reduce this bias and add to the current knowledge of primate vocal communication.

The gaps seen within primate communication knowledge are often related to a bias in experimentation, a misunderstanding of vocalizations, and difficulty organizing calls (Table 10). The bias of communication studies stems from most experiments and collections being of captive organisms of certain species (Snowdon et. al. 1982). A reduction in this bias could expand the known repertoire of the Order Primates and minimize human factors of captivity on calls. Minimizing the number of vocalizations placed into an unknown bin can expand the known capabilities of primate communication. This can also broaden the field's understanding of what information can be shared between individuals. Reducing the bias and simple assortment of calls can widen primatology's understanding of primate vocal communication. These different methods of expanding the understanding of primate vocalization can be used as components of changing researchers' perception of the current knowledge.

Table 10. Primate Vocal Communication Knowledge Gaps

Known	Question	Possible Solutions
The primate vocal repertoire can be expanded	What is the best way to broaden the known primate vocal repertoire?	Study new/unknown species calls
There is difficulty in organizing primate calls	Should there be a universal library of call types with definitions and characterizing features?	Make distinctive characteristics for each call types
There is greater meaning in primate calls than previously thought	What is the best way to determine the true meanings of calls?	Broadly use contexts and previous studies to understand calls
There is a captive setting bias in communication studies	What is the best way to minimize the bias in the communication field away from captive settings?	Study wild populations

Polyspecific Associations

The knowledge basis in regard to polyspecific associations is more limited than many other areas of focus in primatology. While the occurrence of these interactions has been identified in many species across the world, the instigation cause of the polyspecific association is not always clear. The widespread findings of these multi-species interactions across many taxa and throughout the Order Primates indicate they may be key in maintaining ecosystem connectivity and function (Heymann & Hsia, 2015). Either mutual or commenalistic reliance between species across taxa illustrates the importance of these interactions. More damaging associations may be more harmful to one species than the other but are still key for system interactions. Polyspecific associations may be more important than previously believed in the Order Primates. There are great gaps in the scientific data collection capabilities for the study of polyspecific associations (Table 11). At this time, there is no consistent method of studying these interactions. Some changes and new methods may be able to increase the understanding of these associations.

The currently low level of detailed understanding of polyspecific associations in partly due to the idea that they may not be as important to primate species as recently determined. Researchers have often dismissed these interactions as spontaneous and random events that do not serve as regular beneficial associations. Specifically, the relationships between primates and non-primates have not been considered as important as seen primate-primate interactions. These associations have not been studied extensively, even just in comparison to the studies on primate-primate interactions.

One of the great gaps in the knowledge of polyspecific associations is a detailed list of interaction characteristics that can be applied across species. There are currently very basic features that are accepted as characteristics of the association, but they are not broadly applicable. Future studies should push to gather detailed information on the features of polyspecific associations in order for others to be identified in systems more easily. Knowing the existence of a phenomena without features to look for makes them more difficult to acknowledge as occurring. Current knowledge agrees that the organisms have to be in relatively close proximity, an obvious interaction often dealing with food resources, a persistence time of several minutes, and indicators of the association being maintained purposely (Waser, 1982). There is no universal definition of a polyspecific interaction and the field could benefit greatly from the creation of one.

The presence of polyspecific associations can be difficult to identify, causing great problems in their study. Many associations are identified by happenstance during other research of species. Oftentimes, the interaction is not acknowledged as a true association until several different observations have been noted. This can be a problem for properly identifying the interactions as they may be written off as a one-time sighting in field notes. New experimental or observational designs should have methods such as a set of characteristics used for identification and required criteria that can more easily identify polyspecific interactions. Awareness of the occurrence of these associations and placing them into data collection protocols may enable more interactions to be recognized in future studies.

Even once an association is properly identified as a repeated interaction, there is great trouble in studying these scenarios. Polyspecific associations are not normally continuous and can occur spontaneously. The interaction may be short in duration, not always allowing enough recognition time for researchers. Additionally, associations may not fit all of the suggested criteria every time they occur, minimizing chances of documentation. Beyond the identification of the associations, it is challenging to collect data due to the sporadic nature of the multi-species interactions. There is often a large amount of activity at one time, causing difficulty in data collection. One of the goals the primatological field should attempt to meet is the ability to identify polyspecific interactions faster while also enabling better data collection. This could be a challenging advance in the field but will be required for furthering the understanding of polyspecific associations.

The primatological field could benefit from experiments and observational studies that focus solely on polyspecific associations. The majority of studies do not have these interactions as their primary field of interest, making it difficult to gain any true headway in the topic. An increase in the number of field studies using polyspecific associations as the core questions may give the opportunity to broaden the understanding of these important ecosystem interactions. Experimentation surrounding polyspecific associations appears to be a difficult feat, but future studies should attempt to develop methods of testing species' reliance, communication success, interaction frequency, and association characteristics through trials. The development of methods to test these questions is key to the understanding of polyspecific interactions.

The current gap in understanding primate polyspecific associations begins with the definition. There is not a broadly accepted definition at this time with a standard of characteristics that an interaction must have to be considered a polyspecific association. There are some suggestions for the features of a scenario for the interaction to be considered polyspecific, but there is no universally accepted set. This is due to the lack of extensive study of these interactions, related to the rarity and sporadic nature of these associations. A definition can be the first step to broadening the understanding of these multi-species associations. Once a definition is established, more studies can focus on the field and widen the knowledge of such interactions. Until then, the currently running studies can attempt to understand the associations through the known information. More extensive study of polyspecific associations in most features of the interactions can aid the field.

Each of these changes and developments to the understanding of polyspecific associations, particularly in relationship to more studies on both types of interactions can be beneficial for the field moving forward. The different expansions through previously mentioned methods can broaden the knowledge of polyspecific associations and alter the field's understanding of the interactions' importance (Table 11). Beyond new studies with a new way of studying polyspecific associations, a mode of thought can be added to the field in regard to how to use the multi-species interactions to benefit the subjects of primate communication, predation, and polyspecific relationships. This new mode can use the suggested methods of filling knowledge gaps related to polyspecific interactions and will be discussed in greater detail in a later section.

Table 11. Primate Polyspecific Assocation Knowledge Gaps

Known	Question	Possible Solutions
There is no set definition of a polyspecific association	What would be the best way to define a polyspecific association? Would it be possible to carry across all interactions?	Determine universal features of polyspecific interactions
It is difficult to identify polyspecific associations	What are the criteria a situation must have to be a polyspecific interaction?	Identify required contexts, spread broadly
There is great difficulty in studying polyspecific associations	Could protocols be developed from a definition to successfully collect data on the interactions?	Develop study protocols and methods
There are few studies focusing on polyspecific associations	Would scientists be willing to focus on polyspecific associations? Could the study be added to other studies successfully?	Increase the number of studies and/or add to existing studies

CHAPTER 5. FUTURE DIRECTIONS

Merging the Features

While it is important to understand and narrow the gaps in each of the characteristic features of primate behavior, it is important to acknowledge the connectivity between them. Primates' complexities lead to greater relationships between various parts of their lives. Studies in one area may be able to shed light on another, even those considered unconnected. An advancement in one area of primate behavior such as communication may be able to broaden the understanding of another such as predation. Acknowledging the interconnectivity of primate behaviors and features, particularly when studying specific interactions, is key to true expansion of knowledge about primate lives. Studies disconnected from the rest of the field are not fully extending their new understandings into the field.

Polyspecific associations are a relatively unknown aspect of primate behavioral ecology. While the field is aware and notes these interactions, the underlying mechanisms are not always clear. It is also difficult for scientists to identify these associations due to a simplistic definition that does not allow for easy identification of such associations in nature. An expanse on the definition may be benefitted by further studies determining the key characteristics of the interactions and ease the difficulty of identifying them. Once the relationships can be identified, more information can be gathered about these polyspecific interactions regarding their cause, frequency, and benefits.

In relationship to primate vocal communication, predation, and polyspecific associations, there can be several different relationships between them. Polyspecific associations give an opportunity for various features of primate life to be studied due to the nature of the interactions. Polyspecific interactions occur either between two primate species or a non-primate species and a primate for the hypothesized benefits of predation threat minimization and increased foraging output. The interaction between multiple species highlights the key pressures of primate environment and life. There are two ways that further studies on these interactions may expand our understandings of primates: understanding the association and understanding the features of the association.

The study of primate communication (often associated with predation) and predation threats to understand polyspecific interactions is one way to broaden the field's knowledge of primates. This method of studying the associations is heavily reliant on the measure of predation risk, predator abundances, communication signals, vocalization meaning, and other related features of both communication and predation. The studies focus on the specifics of the interaction instead of the association as a whole. Detailed information about responses to predation threats and communication related to predators are the core of this use type. Methods could include playbacks, predator models, images, and other mechanisms for studying communication and predation. Filling in the gaps in predation and communication areas of primate life could bring the field one step closer in understanding polyspecific associations. Determining the extent of importance these features have in a primate's life can highlight the mechanisms for the creation of polyspecific associations and their true power. Using predation and communication studies is one way to understand the importance and strength the associations can hold.

The opposite manner of using polyspecific associations is to use them to aid in the knowledge of predation and communication. Using only the multi-species interaction as a way to broaden knowledge about predation and communication allows the study to highlight the significance of the features. Substantial work on the specifics of polyspecific associations may be able to answer questions of primate communication and predation. Methods can be similar to the opposite version but have an alternative goal in mind. The polyspecific associations can have characteristics that display the true relationships between primates and their environment, sympatric species, and life features. The interaction is created due to the importance of these things and must have some benefit in order for the primate to allow it as to maximize fitness. This version of study uses the interaction to understand the power of predation and communication via the presence of the interaction.

While these two thoughts of mind may have different bases, they both end up with similar questions. Do polyspecific associations form due to the importance of predation and communication in primates? Are predation and communication strong enough factors to push for multi-species interactions? Either way the methods are derived from, the answerable questions could be answered differ lightly. Successful studies may be able to take a multi-angled approach at the topic and come at polyspecific associations both ways.

The two types of polyspecific associations, primate-primate and primate-non-primate, are both beneficial to study for the knowledge of the interactions. However, within the polyspecific association literature, there are fewer studied and known primate-non-primate relationships. This may be due to the rarity of the interactions or due to the obscurity of the associations. These interactions are seen across the continents, though few are scholarly studied including the vervet monkey reaction to starling alarm calls (Seyfarth & Cheney, 1990). They are primarily seen in anecdotal forms such as field notes and thusly often overlooked. Even though they are a rarer event, these primate-non-primate interactions may have more to tell about the association and components than those between primate species.

It may be beneficial to focus more so on the primate-non-primate associations in order to determine the characteristics of the polyspecific interactions, in part due to the minimal previous study of these interactions. These interactions may be eye-opening in truly understanding the causes and features of multi-species exchanges. Associations among primates and other taxa may be more easily identified in the field due to the stark contrast of the species interactions. There may be more drastic interaction characteristics visible between primates and non-primates than in primate-primate associations. The associations may be able to show the characteristic qualities of polyspecific interactions and identify the key features of primate life, including those related to communication and predation. The polyspecific interactions between primates and non-primates may give a different viewpoint on the interactions primates engage in, communication importance, and the significance of predation pressures. Primatologists may find new knowledge within expanded studies on primate-non-primate associations.

Polyspecific associations provide an opportunity to expand the knowledge of primate life characteristics and features in interesting new ways. Though some of the systems have begun to be studied, there is a great gap in the literature about the qualities, abundances, and mechanisms of many other known associations. Primatology has a unique chance to use a complex interaction to broaden the understanding of many features of primate life through the study of polyspecific associations, particularly primate-non-primate interactions.

Beyond Literature

While the primatological field has expanded its knowledge of primate communication, predation, and social interactions including polyspecific associations, there is still much to be learned. An expansion of knowledge related to these characteristics of primate life can add to the understanding of non-human primate life histories and behavior in broader contexts. New experiments, observations, and modes of thinking about primate interactions, communication, and predation could be the next step to gaining more information about humans' closest living relatives. Data on these subjects can expand to other features of primate life and even to human behavior.

The most important aspect of this collected knowledge is that primatology does not simply acknowledge the literature. Primatological work should be willing to alter methods, recognize biases, and seek new outcomes through changes in both methodologies and ways of thinking. Collected literature with recommendations for the field moving forward serves as a catalyst for future endeavors, plans, and experiments. Understanding the current knowledge and the errors occurring presently in the field is the first step in making changes to better the scientific field of studying extant non-human primates.

The many gaps discussed in this paper on the topics of polyspecific associations, predation, and communication do not serve as a collection of what primatology will never gain, but rather what could bet next on the horizon.

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