UNIVERSITAT DE BARCELONA

Vocal, behavioral, and genetic correlates of pairliving and serial monogamy in owl monkeys (*Aotus azarae*) of northeast Argentina

Correlatos vocales, comportamentales y genéticos de la vida en pareja y la monogamia serial en los monos nocturnos (*Aotus azarae*) del noreste de Argentina

Alba Tamara García de la Chica

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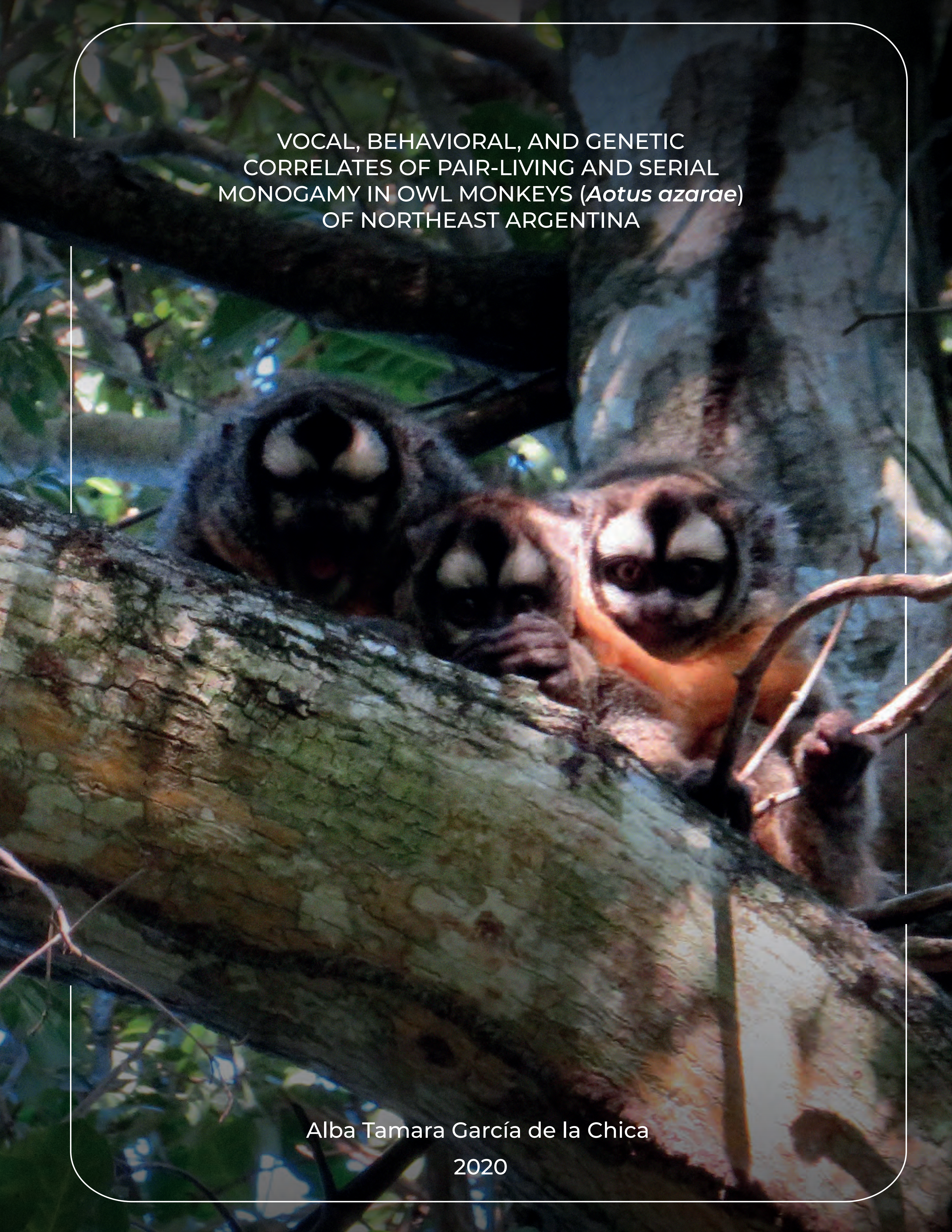

VOCAL, BEHAVIORAL, AND GENETIC CORRELATES OF PAIR-LIVING AND SERIAL MONOGAMY IN OWL MONKEYS (*Aotus azarae*) OF NORTHEAST ARGENTINA

Alba Tamara García de la Chica

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Correlatos vocales, comportamentales y genéticos de la vida en pareja y la monogamia serial en los monos nocturnos (*Aotus azarae*) del noreste de Argentina

Memoria presentada por

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para optar al grado de Doctora por la Universidad de Barcelona

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ABSTRACT

VOCAL, BEHAVIORAL, AND GENETIC CORRELATES OF PAIR-LIVING AND SERIAL MONOGAMY IN OWL MONKEYS (*AOTUS AZARAE*) OF NORTHEAST ARGENTINA

Alba Tamara García de la Chica

Understanding how a social organization and mating system can be beneficial, and hence, persist in populations, requires that we investigate the perspective of all individuals involved. However, in pair-living taxa, the role of solitary floaters, individuals that have dispersed from their groups and range unassociated with other reproductively mature individuals while seeking for a reproductive position in a social group, has been largely ignored when developing hypotheses and theoretical models. This has been so even when the existence of solitary floaters influences the Operational and Adult Sex Ratio of a population and increases the intrasexual competition with mated individuals. In pair living sexually monogamous taxa, despite the fact that the variance in reproductive success likely depends on the relative number of floaters-to-established pairs, the intrasexual competition has usually been assumed to be low. This dissertation explores the role that intrasexual competition between floaters and pairs has in the social organization and mating system of wild Azara´s owl monkeys (*Aotus azare*), a cathemeral, pair living and sexually monogamous South American primate. In the past, intrasexual competition has been associated with sexual dimorphism in several taxa. In chapter two, focusing on identified individuals of known sex and age, I evaluated the degree of sexual dimorphism in loud calls while evaluating the hypothesis of sex-biased vocal behavior. The reduced sexual dimorphism present in sexually monogamous species often hampers to properly evaluate morphological or behavioral traits that may have been influenced by sexual selection. However, in such taxa the formation of new pairs requires individuals to be able to identify, at least, the sex of the caller. This chapter presents evidence of sexual dimorphism in call structure, with females and males

only emitting one type of call, each differing in dominant frequency and Shannon entropy. Further, the data support the hypothesis of sex-biased vocal behavior, with females emitting loud calls up to twice as much as males. Hence, I propose that Azara´s owl monkeys´ loud calls are sexually selected vocal traits that play a role in mate attraction. Likewise, my data suggest that this may be more important for females, likely because due to the extensive involvement of males in parental care in the species, females may face greater intrasexual competition in order to choose the best male. Based on this evidence of sexual dimorphism in loud calls, Chapter 3, explores the behavioral responses of mated pairs towards the simulated presence of male and female unfamiliar conspecific. As such, the main question of this chapter asks whether pairs primarily defend their territory or their mates. The data suggest that male and female owl monkeys guard their mates against competitors. Overall, males reacted more strongly than females and both sexes were more reactive to male than female unfamiliar calls, as evidenced by higher rates of sociosexual and vocal responses, movement towards the speaker, and intergroup encounters. Females guarding their partners against other males may be associated with their need to secure paternal investment. Likewise, the next chapter, four, narrow the focus on this hypothesis even further, and evaluates the relationship between the replacement of a biological father and the age of death of young individuals. My results strongly suggest that the presence of a new unrelated male is associated with lower infant survival in Azara´s owl monkeys, and that this association seems to be more important if the replacement occurs during the first year of life of individuals, when infants are still dependent on direct parental care. I propose that in owl monkeys care by the male is required and, in the absence of direct attacks towards infants, those can still die from neglect or insufficient paternal care. Finally, my dissertation ends with a detailed narrative of one male´s life that shows the different forms of intrasexual competition that Azara´s owl monkeys face through their life. Together, my study adds to our knowledge of

intrasexual competition in pair-living sexual monogamous animals by documenting some of the ways in which social pressures influence the mating and parenting strategies of the species. Specifically, my study emphasizes the need of biparental care in the maintenance of the social organization and mating system of *Aotus azarae*.

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RESUMEN

CORRELATOS VOCALES, COMPORTAMENTALES Y GENÉTICOS DE LA VIDA EN PAREJA Y LA MONOGAMIA SERIAL EN LOS MONOS NOCTURNOS (*AOTUS AZARAE*) DEL NORESTE DE ARGENTINA

Alba Tamara García de la Chica

Entender cómo una organizacion social y sistema de apareamiento pueden ser beneficiosos, y por lo tanto, persistir en una población, requiere que se estudien las perspectivas de todos los individuos involucrados. Sin embargo, en taxones que viven en parejas, el rol de los solitarios o flotadores, individuos sexualmente maduros que se han dispersado de sus grupos y que están buscando una oportunidad reproductiva, ha sido clásicamente ignorado a la hora de proponer y desarrollar hipotesis y modelos teóricos que expliquen dicha organizacion social. Esto ha sido así incluso cuando la existencia de estos solitarios influencia la proporción de machos y hembras en la poblacion e incrementa la competicion intrasexual con individuos emparejados. En especies que son sexualmente monógamas, generalmente se ha asumido que dicha competencia es baja, a pesar del hecho de que la variación en el éxito reproductivo de los individuos, probablemente depende del número relativo de flotadores que haya por cada pareja. Esta tesis explora el rol que tiene la competencia intrasexual entre flotadores e individuos emparejados en el mantenimiento de la organización social y el sistema de apareamiento de una poblacion silvestre de monos nocturnos (*Aotus azare*), un primate sudamericano, caracterizado por ser sexualmente monógamo y formar vínculos de pareja relativamente estables en el tiempo. En el pasado, uno de los factores más considerados a la hora de evaluar la competencia intrasexual ha sido el dimorfismo sexual presente en las especies. En el capítulo dos de mi tesis, evalué el grado de dimorfismo sexual en llamadas de larga distancia en *Aotus azarae*, mediante el análisis de datos acústicos provenientes de individuos identificados de sexo y edad conocidos. El dimorfismo

sexual reducido presente en especies sexualmente monógamas, a menudo dificulta la evaluación adecuada de los rasgos morfológicos o de comportamiento que pueden haber sido influenciados por la selección sexual. Sin embargo, en tales taxones, la formación de nuevas parejas requiere que los individuos sean capaces de identificar, al menos, el sexo del individuo que vocaliza. Este capítulo presenta evidencia de dimorfismo sexual en la estructura de la llamada de los monos mirikiná, con machos y hembras emitiendo únicamente un tipo de llamada, cada uno diferente en su frecuencia dominante y entropía de Shannon. Además, los datos apoyan la hipótesis de un comportamiento vocal sexualmente sesgado, con hembras emitiendo el doble de llamadas de larga distancia que los machos. Por lo tanto, en este capítulo, propongo que las llamadas de larga distancia de los monos son rasgos vocales seleccionados sexualmente que juegan un papel importante en la atracción de pareja. Asimismo, mis datos sugieren que esta búsqueda activa de pareja podría ser más importante para las hembras, probablemente ya que debido a la amplia participación de los machos en el cuidado parental, las hembras podrían estar enfrentando una mayor competencia intrasexual a la hora de elegir al mejor macho. Con base en esta evidencia de dimorfismo sexual en las llamadas de larga distancia y con la implementación de un diseño semiexperimental en el campo, en el Capítulo 3 exploro las respuestas conductuales de parejas hacia la presencia simulada de individuos desconocidos de ambos sexos. Como tal, la pregunta principal de este capítulo es si las parejas defienden principalmente su territorio o sus parejas ante la presencia de un potencial competidor. Los datos sugieren que el recurso que machos y hembras más protegen de los competidores serían sus parejas. En general, las mayores reacciones fueron observadas en los machos, y ambos sexos reaccionaron más a las vocalizaciones de machos que de hembras, como lo demuestran las tasas más altas de respuestas sociosexuales y vocales, el movimiento hacia el altavoz y los encuentros intergrupales cuando se presetaron llamadas de machos. El hecho de que las hembras protejan a sus parejas ante la

presencia de otros machos puede estar asociado con su necesidad de asegurar la inversión paternal. De este modo, el cuarto capítulo, estrecha aún más el enfoque de esta hipótesis y evalúa la relación entre el reemplazo de un padre biológico y la edad de muerte de las crías y juveniles. Mis resultados sugieren que la presencia de un nuevo macho, supuestamente no emparentado, se asociaría con una menor supervivencia infantil en los monos *Aotus azarae*, y esta asociación parece ser más importante si el reemplazo ocurre durante el primer año de vida de las crías, cuando éstas aún son dependientes del cuidado parental directo. Por lo tanto, en mi tesis propongo la necesidad de cuidado paterno en la especie, y que, en ausencia de ataques directos hacia las crías, éstas aún pueden morir por negligencia o cuidados insuficientes. Finalmente, mi tesis presenta una narración detallada de la vida de un macho, Fabian, que muestra las diferentes formas de competencia intrasexual que estos monos enfrentan a lo largo de su vida. En conjunto, mi estudio aporta a nuestro conocimiento de la competencia intrasexual en especies sexualmente monógamas que viven en pareja, al documentar algunas de las formas en que las presiones sociales influyen en las estrategias de apareamiento y crianza de la especie. Específicamente, mi estudio enfatiza la necesidad del cuidado biparental en el mantenimiento de la organización social y el sistema de apareamiento de *Aotus azarae*.

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Chapter 4

Figure 4.1. Median age differences at death/disappearance depending on the breeding adults present in group during the first year of life of individuals (Same Both= Putative mother and father present, Msame=Only the identity of the male was known and it was the putative father, Fsame= Only the identity of the female was known and it was the putative mother, Mnew= The putative father was replaced, Fnew= The putative mother was replaced). The boxplot shows medians (solid line), first, and third quartiles with the lower whiskers including values ≥first Q−1.5 × IQR (interquartile range) and upper whiskers including values ≤third Q+1.5 × IQR.). Outliers that are more than 1.5 times larger or smaller than the median are represented by dots.

Figure 4.2. Median age differences at death/disappearance depending on the breeding adults present in group after the first year of life of individuals (Same Both= Putative mother and father present, Msame=Only the identity of the male was known and it was the putative father, Fsame= Only the identity of the female was known and it was the putative mother, Mnew= The putative father was replaced, Fnew= The putative mother was replaced, Both New= Both putative parents were replaced. In all cases the replacements occurred at different moments, Unknown=Neither the adult male nor adult female in the group had been identified). The boxplot shows medians (solid line), first, and third quartiles with the lower whiskers including values ≥first Q−1.5 × IQR (interquartile range) and upper whiskers including values ≤third Q+1.5 × IQR.). Outliers that are more than 1.5 times larger or smaller than the median are represented by dots.

Figure 4.3. Relationship between the age of individuals when the replacement of their fathers occurred and the age of disappearance/death. The red line indicates the mean and slope of parameters estimated in the model and the green lines represent the confidence intervals at 95% level.

Figure 4.4. Relationship between the age of individuals when the replacement of their mothers occurred and the age of disappearance/death. The red line indicates the mean and slope of parameters estimated in the model and the green lines represent the confident intervals at 95% level.

Figure 4.5. Differences in the mean of infant's age at disappearance between all possible pair of configurations of adults present in group during the first year of infants's life (Same Both= Putative mother and father present, Msame=Only the identity of the male was known and it was the putative father, Fsame= Only the identity of the female was known and it was the putative mother, Mnew= The putative father was replaced, Fnew= The putative mother was replaced). For the statistically significant comparisons the confident intervals did not pass the dotted line (zero).

Chapter 5

Figure 5.1. An Azara's owl monkey life cycle, as illustrated with Fabian's life. Forms of intrasexual competition are symbolized by the black lightening. Dashed lines indicate a potential second reproductive life, although it has never been observed in our population.

CHAPTER 1

INTRODUCTION

Chapter 1. Introduction

For decades, “monogamy” has captivated the research of evolutionary biologists, psychologists and anthropologists, probably because despite the great variation in marriage patterns or parental investment, men and women consistently form special relationships based on persistent emotional attachments that are an integral component of human social behavior (Chapais, 2008; Hawkes, 2004; Quinlan, 2008; Quinlan & Quinlan, 2007; Schacht & Kramer, 2019). When and why “monogamy” and pair bonding behavior evolved in the hominin lineage has been a controversial topic (Lovejoy, 2009). The fossil record and the examination of different traits such as sexual dimorphisim, testis size or concealed ovulation, seem to agree in a low reproductive skew in early humans, suggesting a social organization where both sexes would form a long-term pairbond with a single partner (Schacht & Kramer, 2019).

Classical hypotheses have highlighted the role of male mating competition and paternal provisioning as evolutionary adaptations for two-adult bonds in humans (Fletcher, Simpson, Campbell, & Overall, 2015; Quinlan, 2008). These hypotheses considered several factors for explaining the gradual shift into “monogamy” during the evolution of early hominins; such as sexual dimorphism, brain size, sex-specific costs of breeding, variations in mate quality, and adults sex ratio (Borgerhoff Mulder & Rauch, 2009; Chapais, 2013; Fletcher et al., 2015; Isler & van Schaik, 2012; Quinlan, 2008). Further, some authors have empashized the importance of considering the joint evolutionary dynamics of male and female traits, the incorporation of females as active participants in co-evolutionary interactions, and the need for incorporating between-individual variation in theoretical and empirical studies of early human social behaviors (Borgerhoff Mulder & Rauch, 2009; Gavrilets, 2012).

The use of non-human primate models has proven of much value for investigating the evolution and functioning of monogamous mating systems and male-female bonds. Studies of non-human primates have provided a comparative perspective for considering the behavioral correlates and biological underpinnings of human behavior; offering insights into the classical psychological and anthropological research (Ainsworth & Bowlby, 1991; Emlen, 1995; Kinzey, Menzel, & Susman, 1987; Mason & Lott, 1976).

For many decades, non-human primate research was primarily focused on apes and cercopithecines as typical primates for studying social systems and evolutionary traits of human behavior (Schacht & Kramer, 2019; Strier, 1994). Since the 70s and 80s, much primatological research has been conducted among New World primates and strepsirhines as well (Anzenberger, 1992; Mason & Mendoza, 1998; Snowdon, 1990), clades which also offer interesting variation for broadening the comparative studies of human social systems. For my doctoral research I have studied a New World primate species, Azara’s owl monkeys (*Aotus azarae*) from northern Argentina, as a system model for investigating male-female relationships, “monogamy”, and pair-bonding.

When not everything is “Monogamy”: the importance of terminology

From an evolutionary perspective, the possible benefits of “monogamy” and the factors underlaying its evolution and maintenance, have been huge topics of discussion (Díaz-Muñoz & Bales, 2016; French, Cavanaugh, Mustoe, Carp, & Womack, 2018; Kappeler & van Schaik, 2002; Kleiman, 1977; Kokko & Morrell, 2005; Lukas & Clutton-Brock, 2013; Opie, Atkinson, Dunbar, & Shultz, 2013; Reichard, 2003; Tecot, Singletary, & Eadie, 2016).

A combination of unclear definitions, high variation in methodological approaches and ambiguous targets of selection, continues to challenge our understanding of "monogamy" in mammals and has led to highly contradictory results in the literature (Brotherton & Komers, 2003; Dobson, Way, & Baudoinc, 2010; Kappeler, 2019; Komers & Brotherton, 1997; Lambert, Sabol, & Solomon, 2018; Lukas & Clutton-Brock, 2013; Opie et al., 2013).

This contradiction and variation is notorious even in the amount of primates species classified as "monogamous" (Fuentes, 1998; Lukas & Clutton-Brock, 2013; Opie et al., 2013), likely because in the primatological literature, one often finds that under "monogamy" or "monogamous social systems" researchers have very often included studies describing a social organization, a mating system or a social structure indistinctly (Dixson, 2013; Fernandez-Duque, Huck, Van Belle, & Di Fiore, 2020; Huck, Di Fiore, & Fernandez-Duque, 2020; Kappeler, 2019; Klug, 2018). In other words, "monogamy" or "monogamous social systems" have been used - without further specifications- when referring to who lives with whom (social organization), who mates whit whom (mating system) or even to characterize the content, quality and patterning of social relationships between individuals (social structure) (Kappeler & van Schaik, 2002).

The term "monogamy" has also been often associated with a range of concepts and behavioral traits, such as pair-living, pair-bonding, and biparental care. Consequently, individuals have been often considered to be sexually monogamous in pair-living social organizations without properly evaluating who mates with whom. And more, pair-living monkeys have been usually considered to be pair-bonded, or to show biparental care, without evaluating the characteristics of the social interactions between members of the pair, or the degree of care provided by each sex (French et al., 2018; Fuentes, 1998, 2002; Tecot et al., 2016).

In my doctoral research, I follow the recommendation of several authors for a properly distinguished use of terminology (Fernandez-Duque et al., 2020; French et al., 2018; Huck et al., 2020; Reichard, 2017; Tecot et al., 2016). Specifically, I follow the definitions provided by Fernandez-Duque and collegues (2020) which I syntethized based in their Figure 1: I use **pair-living** when referring to a type of social organization where a reproductive male and female (sometimes with their non-reproductive infants) live together within a common home range and associate with each other (either continuously or intermittently). **Biparental care** is defined as a type of care system, where both members of a pair regularly perform behaviors with presumed positive effects on infant development, growth, well-being, or survival. I use **pair bonded** when referring to a male and a female manifesting an emotional attachment to one another, to the exclusion of other adults, as evidenced by their affiliative interactions, maintenance of spatial proximity, physiological distress upon separation from the pair-mate, and reduced anxiety following reunion with the pair-mate.

I use **sexual monogamy**, as a type of social mating system where a female and a male mate exclusively during at least one reproductive season. When I mention **genetic monogamy**, it refers to a type of genetic mating system where a female and a male reproduce exclusively with one another over a set of multiple births, i.e. over more than one consecutive reproductive season. On this, Huck and colleagues (2020) pointed out that what have been considered "exclusively" or "reproductive season" varied substantially among researchers, giving as a result an unclear operationalization of the monogamous mating systems in the literature.

A final consideration is related to the relative recent findings from studies extending many years, which have shown that what appeared to be sexual monogamy is better explained as **serial monogamy** (Fernandez-Duque & Huck, 2013; Garber, Porter, Spross, & Di Fiore, 2016; Huck & Fernandez-Duque, 2012; Porter, Grote, Isbell, Fernandez-Duque, & Di Fiore, 2015; Van

Belle, Fernandez-Duque, & Di Fiore, 2016). The latter term refers to a situation where adults of a breeding pair are often replaced by non-related same-sex individuals. In other words, a female and a male mate exclusively during at least one reproductive season (i.e. sexual monogamy), but the pair mate may change over time.

Theoretical Background

Hypotheses

All these inconsistencies in terminology are also present in the hypotheses usually proposed to explain "monogamy". It follows that many of them more appropriately explain a social organization than a mating system, and that specific proposed evolutionary drivers that might be relevant for the evolution of certain aspects of the social organization, may not be relevant for understanding the evolution of the mating system, or vice versa (Kappeler, 2019; Klug, 2018; Tecot et al., 2016).

Among the several drivers, or factors, that have been usually proposed in the past to likely influence the evolution and/or maintenance of "monogamy', and on which the hypotheses are built, one finds: 1) resource use and availability, 2) offspring need, 3) parental care, 4) mating dynamics (i.e., the costs and benefits associated with acquiring mates and mate availability), 5) spatial and temporal distribution of females, 6) infanticide, 7) mate competition, and 8) mate guarding (Klug, 2018 offers a a more comprehensive overview). Following, I present a brief summary of the hypotheses more relevant for my research, which are considered in more detail on later chapters.

Infant care hypothesis

This hypothesis states that in taxa where infant care has high costs associated, mothers would need the help of other individuals in order to rear their offspring. Males would obtaing benefits from providing care instead of looking for potential matings in circumstances where mating opportunities are rare and/or paternal care is associated with offspring survival (Wittenberger & Tilson, 1980). The relationship between bi-parental care and pair-living/monogamy has been the focus of several studies, however, whether biparental care precedes or follows the evolution of these social organization and mating system remains quite debatable (Brotherton & Komers, 2003; Dobson et al., 2010; Lukas & Clutton-Brock, 2014; Opie et al., 2013).

Further, according to Tecot et al, (2016), the infant care hypothesis may explain the transition from solitary to pair-living in some species, and may also explain pair-bonding (coordinated care may be necessary among pairs), but not necessarily to a sexually monogamous mating system. In fact, as an example of this statement, some primate species with bi-parental care have been shown to also have extra pair copulation (*Cheirogaleus medius*: Schwensow, Fietz, Dausmann, & Sommer, 2008), while species with genetically monogamous mating system lacked any direct form of biparental care (*Indri indri*: Bonadonna et al., 2019).

Infanticide Risk Hypothesis

According to this hypothesis, the presence of a male deters other males from attacking and killing vulnerable infants; which results in fitness benefits for the male, presumed biological father-, mother and young. Hence, infant survival is expected to be higher if a male helps a female to protect offspring from infanticidal intruders (Palombit, 2000; van Schaik & Dunbar, 1990; van Schaik & Kappeler, 1997). Under this framework it is assumed that females would become receptive and fertile again sooner than expected if their infants are killed (Hrdy, 1974).

Thus, infanticide risk would be less likely in species without lactational amenorrhea or in species where ovulation is triggered by other ecological or external cues and it does not depend to the loss of an infant, as it often happens in seasonal breeding species. Some researchers have interpreted the absence of infanticide in pair living sexually monogamous taxa as evidence of having evolved successful counterstrategies and others, as evidence of infanticide not playing a role in the evolution of such social organization and mating systems (Fernandez-Duque et al., 2020).

Mate Guarding Hypothesis

Also called "Mate Defense Hypothesis" (Tecot et al., 2016), the hypothesis suggests that a male increases his reproductive success by guarding a female from male competitors while ensuring mating access to her. Under this hypothesis, it is predicted that males will not seek to mate with other females even when it may be possible for them to range over more than one female's range. In order to guard their mates, males and females will be more aggressive towards same-sex competitors, especially during mating season. It is worth noting that in certain taxa, or under certain conditions, some of the predictions might be sex-reversed. For example, if males are a scarce resource for parental care, females may benefit by guarding a single male from other females.

Resource Defense Hypothesis

This hypothesis proposes that when resources are highly dispersed, low in quality, or rare, pair-living and defense of the same set of resources represents the most stable strategy (Rutberg, 1983). Given an area that cannot support more than two adults (and a reduced number of inmatures), both males and females are predicted to defend the resources, either together or separately. This defense will be of similar form and strength against same-sex intruders than it will be against members of the opposite sex, and it will vary with changes in resource availability and not with regards to the mating season as predicted in the mate-guarding hypothesis.

Even when I have just presented each hypothesis individually, I must highlight that one needs to consider that the factors on which the hypotheses are built are likely to interact, and the relative importance of each one, can vary across systems and between the two sexes (Klug, 2018). For example, the presence of infanticidal males may affect offspring needs, and resource availability may conditionate spatial and temporal mate distribution.

Subsequently, as many authors have suggested before, one should not expect a single hypothesis to fully explain the variation of social or mating systems in primate taxa (Fernandez-Duque et al., 2020; Fuentes, 1998; Kappeler & van Schaick 2002; Kappeler, 2019; Klug, 2018; Reichard, 2003; van Schaik & Dunbar, 1990). In fact, this call for using multiple hypotheses in ecology, evolution and biological sciences is not recent, Chamberlin already proposed it in 1890, when he stated that scientists tended to have a favourite explanation (or hypothesis) for which they try to find evidence and make the data "fit", instead of trying to find alternative explanations for the observed patterns (Betini, Avgar, & Fryxell, 2017).

We may assume that the complexity of biological and behavioral systems would have led to a frequent use of multiple hypotheses in ecology and evolution, but instead, this method has been rarely used in these fields. Already in 1983, Quinn and Dunham pointed out that the presupposition of simple causation hampered the scientific progress in ecology and evolutionary biology. More recently, Betini and collegues (2017) proposed both intellectual and practical barriers that researchers usually find when incorporating multiple hypotheses in their work such as cognitive bias, or more difficulties when trying to publicate their investigations.

Moreover, the natural processes and outcomes normally studied in ecological and evolutionary research, respond to nonlinear and stochastic interactions of multiple factors, usually observed at multiple spatial and temporal scales. Therefore, the aim should not be to conclude if a certain hypothesis, or factor, is or it is not present in our study system, but to understand its contribution to an observed pattern.

It follows that hypotheses should not be stated in a way that they are mutually exclusive nor stated as the only cause of a natural outcome (Betini et al., 2017; Dochtermann & Jenkins, 2011; Hilborn & Stearns, 1982). As Quinn and Dunham (1983) appropriately stated:

> "The objective of investigation in cases of this sort is not to determine the single cause of a pattern, as not such cases exist, but rather to assign relative importances to the contributions of, and interactions between, a number of processes, all known or reasonably suspected of operating to some degree" (p. 604).

Particulalry in ecological and evolutionary research which so often relies on observational data, the evaluation of multiple hypotheses and perspectives will result in more objectivity and deeper understanding of the phenomena under study (Betini, Avgar, & Fryxell, 2017; Dochtermann & Jenkins, 2011; Hilborn & Stearns, 1982; Quinn & Dunham, 1983). In the following section I discuss the benefits of examining the perspectives of all individuals and both sexes when conducting theoretical analyses of pair-living and sexual monogamy. Historically, the primary focus has usually taken the male perspective when considering the possible cost and benefits of sexually monogamous mating. It has been often assumed that it is the male's fitness that can improve by increasing the number of females, while the female's fitness was primarily associated, and conditioned, to the access to food resources needed to sustain pregnancy and early infant development (Clutton-Brock, 2007; Clutton-Brock & Huchard, 2013; Trivers, 1972).

Males, Females, Solitaries and Pairs: an holistic perspective.

Understanding how sexual/genetic/serial monogamy can be beneficial to individuals, and hence, persist in populations, requires that we investigate the perspective of all individuals involved (Huck et al., 2020; Klug, 2018). A complex mating system cannot be fully explained by examining only the potential benefits to the male when females may also benefit from polyandry or polygynandry (Clutton-Brock, 2017; Jennions & Petrie, 2000; Kokko & Jennions, 2008a). Starting in the 90s, numerous studies began to focus on the behavioral correlates of sexual monogamy as a result of the trade-off between male and female reproductive strategies (Hosken, Stockley, Tregenza, & Wedell, 2009; Kokko & Jennions, 2008a).

Once the focus is on the individual, it becomes necessary to consider all individuals, whether they are part of a social group or live solitarily. In the case of pair-living taxa, we can not fully understand male and female reproductive strategies without considering the role of solitary floater individuals in the population (Huck et al., 2020). In pair-living primates, floaters are often individuals that have dispersed from their groups and range unassociated with other reproductively mature individuals while seeking for a reproductive position in a social group. However, floaters have been largely ignored when developing hypotheses and theoretical models for the evolution of mating systems in human and non-human primates (Coxworth, Kim, McQueen, & Hawkes, 2015; Fletcher et al., 2015; Gavrilets, 2012; Plavcan & van Schaik, 1997).

The existence of solitary floaters can strongly influence the Operational and Adult Sex Ratio (OSR and ASR) of a population. This is so because floaters likely increase the intrasexual competition with mated individuals (Huck et al., 2020). It follows that the degree of intrasexual competition in a population is associated with the OSR or ASR in a dynamic feedback (Kappeler, 2017). While this relationship is well known in polygynous species (Clutton-Brock, 2017), it remains less clear, or simply unknown, for pair living sexually monogamous taxa (Huck et al., 2020). As a matter of fact, intrasexual competition has usually been assumed to be relatively low in pair-living sexually monogamous taxa, following from the assumption that the OSR/ASR should be similar given that there is only one reproducing male and female in each group.

Nevertheless, there are good reasons to assume that the variance in reproductive success strongly depends on the relative number of floaters-to-established pairs present in the population (Fernandez-Duque & Huck, 2013; Huck et al., 2020). Mathematical models indicated that, if for example, the ASR is male biased, male's mate-guarding behaviors would increase, while the female's likelihood of seeking extra pair copulations (whether in very low or very high rates) would reduce male's guarding efforts, this way, promoting male mate-guarding behaviors and sexual monogamy (Harts & Kokko, 2013; Kokko & Morrell, 2005). Similarly, a more recent metanalisys on different taxa indicates that a biased OSR led to more males mate guarding behavior, while direct aggresions initially showed an increase but, started to decrease once the number of same-sex rivals became energetically costly to fight with (Weir, Grant, & Hutchings, 2011). Yet, considering the OSR as only indicator of sexual selection and competition, may be over simplistic, since it does not take into consideration individuals variation in mate choice (Kokko & Jennions, 2008b).

Largely studied in avian systems, floaters may include individuals that left their natal groups to seek for their first reproductive position, individuals that "divorced" their partners, or individuals that have been recently expelled from their groups (Penteriani, Ferrer, & Delgado, 2011). In primatology research, it has been relatively recent, when multi-year studies started to find out that, what were assumed to be "family"group structures included, in fact, non-related individuals that had joined such group as an additional adult, or that had replaced a former resident adult and gained its breeding position (Barelli, Heistermann, Boesch, & Reichard, 2008;

Fernandez-Duque & Huck, 2013; Garber et al., 2016; Huck & Fernandez-Duque, 2012; Porter, Grote, Isbell, Fernandez-Duque, & Di Fiore, 2017; Porter et al., 2015; Tecot et al., 2016; Thompson & Norconk, 2011).

It follows that these voluntary, or forced, replacements and dispersal patterns heavily lead and influence the availability of potential mating partners. Indeed, dispersal may function as an Alternative Reproductive Tactic (ART) in some primate species (Setchell, 2008; Taborsky, Oliveira, & Brockmann, 2008). An ART refers to consistent and discrete variations in the reproductive behavior of one sex in a population, that serve the same functional purpose (Taborsky et al., 2008). Consequently, for an ART to be stable, it must involve some kind of reproductive success for those individuals who "choose" it. Withinpair-living social systems in primates, long ago considered "monogamous", there have been numerous reports of much more variation in their mating systems than previously presumed, as genetic analyses revealed nonrelated individuals and extra-pair copulations (Fietz et al., 2000; Garber et al., 2016). These observations suggest the occurrence of "sneaky" copulations which may, in fact, increase the reproductive success of some floater males in detriment of residents ones (Setchell, 2008).

On the other hand, a floater may increase its reproductive success by gaining a breeding position within an already established group. These replacements can take the form of voluntary transfers, or involve aggressive episodes where a resident is expelled by a floater. Under the first scenario, Porter et al. (2015) detailed the immigration of a new male of saki monkey (*Pithecia aequatorialis*) into an group where the resident male-female pair had been associated for seven years and had two daughters together. Three months after the immigration of the new male, both of them, the new male and the former resident male, left the group together (leaving the resident female and offsprings behind) and associated within an unknown female. In gibbons (*Hylobates lar*), Palombit (1994) documented that pairs in the majority of the studied groups terminated because one member left its partner; in some cases to join a neighboring adult from the opposite sex. Under the second scenario, agonistic behaviors and fights during replacements have been registered in owl monkeys (Fernandez-Duque, 2009; Fernandez-Duque & Huck, 2013; Huck & Fernandez-Duque, 2012) and gibbons (Brockelman, Reichard, Treesucon, & Raemaekers, 1998).

The role that competition between floaters and resident adults has in the evolution and maintenance of pair-living sexually monogamous sistems needs urgent consideration (Fernandez-Duque et al., 2020; Huck et al., 2020). Specifically, it requires an integrated investigative approach that incorporates knowledge about the OSR/ASR of the population and a more detailed consideration of ARTs present in both sexes. In fact, evolutionary models indicate the need to also include parental investment, mating costs and life history as predictors of the intensity of sexual competition (Kokko & Johnstone, 2002).

Among primates, ARTs do not usually involve dramatic alternative morphologies and are expected to evolve when reproduction is skewed and there are high levels of intrasexual competition (Setchell, 2008). As detailed before, recent studies on pair-living primate taxa have put in check the previous concepts of “monogamous” systems, and there is growing evidence that what was once considered lack of intrasexual competion, may in fact be reflecting high levels of competition on both sexes (Huck et al., 2020).

Pair-living, sexual monogamy, competition and ARTs in owl monkeys

In my dissertation, I investigate the role that intrasexual competition between solitary floaters and resident reproducing adults has in the social organization and mating system of wild Azara´s owl monkeys (*Aotus azarae*) from Formosa, Argentina. I combine behavioral, demographic, and life-history data to evaluate how this competition influences the interactions both between floaters and pairs and between the adult male and adult female of a pair; I also examine how the competition between floaters and pairs may affect infant survival.

Owl monkeys (*Aotus* spp.) are small, arboreal and the only nocturnal primates of Latinamerica (Fernandez-Duque, 2012). Another fascinating aspect of the genus is the intensive involvement of the male in infant care (Fernandez-Duque, 2009; Fernandez-Duque et al., 2020; Huck et al., 2020; Huck & Fernandez-Duque, 2013), in which the male is the principal carrier of infants after the first week of life (Rotundo, Fernandez-Duque, & Dixson, 2005) and also plays, grooms, and shares food with it more frequently than females do (Wolovich, Feged, Evans, & Green, 2006; Wolovich, Perea-Rodriguez, & Fernandez-Duque, 2008).

Males and females show extremely low levels of dimorphism in body size (males: 1.26+-0.11, females: 1.26+-0.10), coloration, and even the external genitalia, but some sex differences can be found in hindlimb, and the lengths of canine and subcaudal glands, which are lager in males (Fernandez-Duque, 2011; Huck, Rotundo, & Fernandez-Duque, 2011; Spence-Aizenberg, Williams, & Fernandez-Duque, 2018).

Along the extensive geographical range of *Aotus* (from Panama to Argentina), owl monkeys had been always found in small groups generally composed of an adult heterosexual pair, one infant, and one or two inmature individuals (Aquino, Cornejo, & Heymann, 2013; Cornejo, Aquino, & Jiménez, 2008; Fernandez-Duque, 2011, 2012; Fernandez-Duque et al., 2020; Shanee, Algass, & Shanee, 2013; Svensson, Samudio, Bearder, & Nekaris, 2010); thus, the genus has been always described as pair living. However, in the last 20 years there has been unequivocal evidence that, at least in the *A. azarae* population of Formosa, Argentina, the social organization includes pairs, as well as a subpopulation of floater individuals (Fernandez-Duque et al., 2020).

In our population of Azara's owl monkeys in northern Argentina a substantial number of potentially reproductive individuals (25-30%) do not belong to a pair-living group, but instead range solitarily in the periphery of established groups for a variable period (Corley, 2017; Fernandez-Duque & Huck, 2013; Huck & Fernandez-Duque, 2017). These solitary "floater" individuals are either young adults who have recently emigrated from their natal groups or relatively old adults that have been evicted from their groups by incoming adults.

Wild male and female Azara´s owl monkeys disperse from their natal groups when they are between two and five years old, and, in our population, no individuals have been registered to successfully disperse before they are 26 months old (Fernandez-Duque, 2009; Huck & Fernandez-Duque, 2012). Depending on the species, owl monkeys achieve sexual maturity when they are between two and five years old (Corley, Valeggia, & Fernandez-Duque, 2017; Alan F Dixson, 1994; Alan F Dixson, Gardner, & Bonney, 1980; Gozalo & Montoya, 1990; Huck et al., 2011); thus, the dispersal may occur before, after, or around the time of sexual maturation in both sexes (Corley, Valeggia, et al., 2017; Corley, Xia, & Fernandez-Duque, 2017). Nevertheless, in my study population, no mating behaviors occur while individuals are still in their natal groups. It is possible that, instead of being tightly linked to the sexual maturation of individuals, natal dispersal may be associated with changes in group composition, such as the eviction of the resident adult male or female. In fact, after the replacement of resident adults, subadult monkeys have dispersed at younger ages, on average, than those in stable groups (Corley, 2017).

Owl monkey male and female floaters range solitary, from a few days to 15 months, among the home ranges of pair-living adults (Corley, 2017) while trying to gain a breeding position or taking advantage of vacancies in resident positions that arise through natural deaths (Fernandez-Duque & Huck, 2013; Huck & Fernandez-Duque, 2017). These takeovers, where a resident adult is expelled and replaced by a floater, can be extremely aggressive, or even deadly, for both solitary floaters and resident adults; and the replacements result in a 25% decrease in the reproductive success of a pair (Fernandez-Duque & Huck, 2013). Females in new pairs of wild *A. azarae* do not produce offspring for at least one year after pairing, even if the pair is formed during the mating season (Fernandez-Duque, pers. obs.). In a period of 10 years, there were 27 female and 23 male replacements in a total of 149 group-years, and no new pairs have ever formed from the union of two solitaries (Huck & Fernandez-Duque, 2012; Fernandez-Duque & Huck, 2013; Huck & Fernandez-Duque, 2017). More, only twice in 23 years, we have observed a former expelled reproductive adult to rejoin a group as the adult male, although it remains unkwnown if they actually reproduced in both groups (Fernandez-Duque & Huck, 2013; Huck et al., 2020). Indeed, pair members do not voluntarily leave their partners, but instead the end of a pairing relationship is associated with extrinsic factors, mostly because of individuals´ evictions from pairs (Fernandez-Duque & Huck, 2013). Hence, it seems that both sexes are replaced at similar rates and thus, we may expect variance in fitness to be similar for both sexes.

However, we must be extremely cautious with the estimations of breeding position takeovers. The frequency of successful replacements in our population is likely to be an underestimate since failed attempts of replacements are likely to go unnoticed by researchers, as well as opportunities for documenting the behavioral mechanisms associated with these events. Also, I must emphasize that, even when we know that both sexes leave their natal groups, it is still unknown if all aspects of dispersal are similar for males and females. For example, in another primate species that also exhibits bisexual dispersal, genetic data suggest that males are more likely to remain in areas adjacent to their natal groups after dispersal than females are (*Symphalangus syndactylus*: Lappan, 2007; *Hylobates lar:* Matsudaira, Ishida, Malaivijitnond, & Reichard, 2018). It is also possible that given the reproductive restrictions for owl monkey females associated with the seasonal nature of the environment in Formosa (Fernandez-Duque et al., 2020), females are more likely to try to gain a breeding position during a certain socioecological period. A seasonal pattern of replacements, in turn, could lead to, first, sex-biased mortality among floaters if mortality is associated to dispersal distance (Johnson, Fryxell, Thompson, & Baker, 2009) and, second, to temporally bias the OSR/ASR of the population.

A deeper understanding of the impact of floaters on population dynamics is still needed in order to properly evaluate the role that intrasexual competition has in the evolution and maintenance of the social system in owl monkeys. For example, how are floaters and established groups communicating? Which cues do floaters use to gain information about groups? Which are the behavioral mechanisms associated with replacements? Do members of stable pairs help their mates to avoid being evicted by a solitary individuals? How do floaters impact the variance of males and females reproductive success? My doctoral research aims to answer some of these questions through a combination of behavioral, demographic, and life-history data on the interactions both, between floaters and pairs, and between the adult male and adult female of a pair. My research will contribute to our understanding of whether being a floater can be considered as an ART in owl monkeys. So far, the demographic data collected by the Owl Monkey Project suggest that if being a floater were an ART, it would be the type that some authors have referred as not fixed, but plastic, present in both sexes and age dependent (Engqvist & Taborsky, 2016; Setchell, 2008; Taborsky et al., 2008). Understanding the dynamics of this competition, through an examination of the reproductive strategies of both sexes, will lead to valuable insights into our understanding of the evolution of pair-living, sexual monogamy, pair bonding, and biparental care.

Objectives

In **Chapter 2**, already published (Garcia de la Chica et al., 2020), I present the first assessment of sexual dimorphism in traits linked to vocal communication in owl monkeys (*Aotus azarae*). Emlen and Oring (1977) hypothesized that there is a link between mating system and sexual selection and suggested that sexual selection would be relatively slight in monogamous mating systems. Pair-living and sexually monogamous species are often characterized by reduced sexual dimorphism, making difficult to properly evaluate morphological or behavioral traits that may have been influenced by sexual selection. It is worth noting that, in some species, it has been suggested that reduced dimorphism may be due to high levels of intrasexual competition in both sexes, rather than to a lack of competition (Plavcan, van Schaik, & Kappeler, 1995).

Given the lack of sexual dimorphism in body mass and secondary sexual characteristics, the minimal differences in the appearance of the external genitalia, and their nocturnal habits, it has been proposed that owl monkeys heavily rely on vocal and olfactory cues to identify relatives and members of the opposite sex (Macdonald, Fernandez-Duque, Evans, & Hagey, 2008; Spence-Aizenberg, Kimball, Williams, & Fernandez-Duque, 2018). Loud-calls and duetting have been implied as behaviors likely regulating pair-bonding, group cohesion and inter-group communication in other pair-living and sexually monogamous species (Barlett, 2003; Bonadonna et al., 2017; Bonadonna et al., 2020; Geissmann, 2002; Méndez-Cárdenas & Zimmermann, 2009; Müller & Anzenberger, 2002; Robinson, 1981; Thompson, Norconk, & Whitten, 2012; Yi, Fichtel, Kim, & Choe, 2020). An ability to identify the opposite sex should undoubtedly play an important role during the encounters with floaters that regularly take place in the border of free-ranging owl monkeys' home ranges (Huck & Fernandez-Duque, 2017). If owl monkeys are relying on vocal communication to identify individuals of the opposite sex, one possible mechanism would be for males and females to show differences in the acoustical parameters of their calls.

My objective for this chapter was to evaluate sex differences in loud calls in wild owl monkeys. Using only information from identified individuals of known age and sex, I first compared information on the rate of production of graff and tonal hoots. Second, I compared audio recordings of tonal and graff hoots to test the prediction that there would be acoustic differences in the basic structure of both types of calls. The evidence of dimorphism in vocal traits would suggest that there are different selective pressures for males and females and would allow to further explore predictions derived from the hypotheses proposed. Specifically, based on Trivers' (1972) hypothesis that the sex with less investment in infant care would be the more competitive one, Heymann (2003) proposed that, among New World Monkeys, the degree of male care would be related to the influence of sexual selection on the evolution of chemical and vocal communication. He predicted that in taxa where males were the principal providers of infant care, females would vocalize more than males. In this chapter I further explored whether levels of dimorphism in loud calls are consistent with his hypothesis, i.e, if loud calls are sex-biased in our population.

In **Chapter 3,** I evaluated the hypothesis that, due to the lack of available territories, intrasexual competition between breeding pairs and floaters is regulated through vocal communication and mate-guarding behaviors. My research on loud calls (Chapter 2) strongly suggested that they encode information about the sex of the caller in owl monkeys, and therefore listeners are supposed to be able to identify the caller as a male or female intruder. Hence, I carefully designed and conducted a set of field playbacks experiments in our study area with the goal of describing the vocal and behavioral reactions of pair mates to unfamiliar loud calls in order to test predictions derived from the Resource Defense and Mate Guarding Hypotheses.

The behavioral mechanism associated with replacements or the extent to which members of stable pairs would help their mates to avoid being evicted by a solitary individual or not, still remain largely unknown for owl monkeys. These experiments aimed at improving our understanding of the competition between solitary floaters and groups, namely the extent to which members of stable pairs primarily defend their territory or their mates.

In the final empirical chapter (**Chapter 4**), my objective was to assess the hypothesis that the replacement of resident adults is associated with the survival and development of non-reproductive individuals (infants and juveniles). I did so by evaluating the relationship between parental loss and the age at disappearance of 149 identified infants from our population of wild pair-living sexually monogamous owl monkeys (*Aotus azarae*).

When a floater replaces a resident adult, the infant and juveniles experience the change of a biological parent for a stepfather or stepmother; stepparents are obviously less familiar, and presumablyless related, to them. It is possible then that the loss of a biological parent could reduce the survival of these young individuals.

Although infanticide has never been directly observed in pair-living primates (but see previous section of the introduction) the potential risk of it can be examined indirectly via infant survival after parental replacement (Borries, Savini, & Koenig, 2011; Morino & Borries, 2017). Even though in the past, we were able to observe a former floater male that replaced the resident adult socially interacting with an infant, the last disappeared at 6 months of age (Fernandez-Duque, Juárez, & Di Fiore, 2008). Ultimately, the impact that replacements of male and female have in infant survival, will help us to better understand reproductive strategies developed by both sexes.

In **Chapter 5**, already published online (Garcia de la Chica, Fernandez-Duque, & Rotundo, 2020), I present qualitative and detailed data with some of the most representative examples of the intrasexual competition regulating the social system of Azara's owl monkeys during the different stages in the life of individuals. In doing so, I focused the narrative on the life of one monkey, Fabian, a male who was followed from the moment he started searching for a mate until he died, almost ten years later. In **Chapter 6**, I present a general discussion and a summary of the most important findings of my dissertation. Finally, in **Chapter 7**, I present the conlusions, as well as the main limitations of the study while I propose future lines of research.

CHAPTER 2

SEXUAL DIMORPHISM

SEXUAL DIMORPHISM IN THE LOUD CALLS OF AZARA'S OWL MONKEYS (*AOTUS AZARAE*): EVIDENCE OF SEXUAL SELECTION?

Chapter 2. Sexual dimorphism in the loud calls of Azara’s owl monkeys (*Aotus azarae):* evidence of sexual selection?

Abstract:

Primates use different types of vocalizations in a variety of contexts. Some of the most studied types have been the long distance or loud calls. These vocalizations have been associated with mate defense, mate attraction and resource defense, and it is plausible that sexual selection has played an important role in their evolution. Focusing on identified individuals of known sex and age, we evaluated the sexual dimorphism in a type of loud calls (hoots) in a population of wild owl monkeys (*Aotus azarae*) in Argentina. We found evidence of sexual dimorphism in call structure, with females and males only emitting one type of call, each differing in dominant frequency and Shannon entropy. In addition, both age-related and sex-specific differences in call usage were also apparent in response to the removal of one group member. Future acoustic data will allow us to assess if there are individual characteristics and if the structure of hoot calls presents differences in relation to the social condition of owl monkeys or specific sex responses to variants of hoot calls’ traits. This will provide deeper insights into the evolution of vocal mechanisms regulating pair bonding and mate choice strategies in this and other primate species.

Introduction

Vocal communication has been a central topic of interest for primatologists and evolutionary anthropologists for decades (Ghazanfar & Hauser, 1996; Seyfarth et al., 1980; Snowdon, 1989; Zuberbühler et al., 1999). The study of this type of communication can lead to insights about the evolution and maintenance of the social systems in which they occur (Mccomb & Semple, 2005; Heymann, 2003). Among non-human primates, some of the most studied types of vocalizations have been the long distance or loud calls. Loud calls, like chemical signals, are expected to be relatively more important in arboreal species where visibility may limit the value of visual communication (Epple, 1974). In primates, these vocalizations have been associated with resource defense (Cowlishaw, 1996; Mitani, 1990; Sekulic, 1982; Steenbeek et al., 1999; Rasoloharijaona et al., 2006; Whitehead, 1987; Wich & Nunn, 2002), mate attraction (Caselli et al., 2018; Steenbeek et al., 1999; Wich & Nunn, 2002) and infanticide (Wich et al., 2002; Wich et al., 2004). Further, given their important role in maintaining the spatial cohesion of the group, male–female interactions and assisting individuals in the search for potential mates, it is plausible that sexual selection has played an important role in their evolution (Delgado, 2006).

The formation of a mating pair requires the identification of potential mates, and the ability to differentiate mates from other opposite-sex individuals. Some studies documented variation between the sexes and individual recognition in loud calls in several primate taxa (Benz et al., 1990; Porter, 1994; Rukstalis & French, 2005; Smith et al., 2009; Terleph et al., 2015). In pair-living and sexually monogamous titi monkeys (*Callicebus* spp.) loud calling is commonly emitted as coordinated duets by pairs. Even when no sex-specific duet contributions have been detected (*C. ornatus*, Robinson, 1979; *C. cupreus*, Müller & Anzenberger, 2002; *C. nigrifrons*, Caselli et al., 2015), it is possible that sex contributions differ in the acoustic characteristics of syllables that are assembled to compose the song parts of duets' long sequences, allowing individuals to identify the sex of the caller (Caselli et al., 2015).

Another pair-living and sexually monogamous taxon which can serve as a model to examine the possible sex differences of loud vocalizations is *Aotus azarae*, the Azara's owl monkeys of Formosa Province in Argentina. Owl monkeys live in groups composed of a heterosexual pair that mates monogamously (Huck et al., 2014a), one infant, one or two juveniles and sometimes a subadult (Fernandez-Duque, 2016). In the owl monkey population we study in Guaycolec Ranch, all male and female subadults disperse from their natal groups and become floaters, who range solitarily while looking for a reproductive position in another group (Huck & Fernandez-Duque, 2017). Preliminary analyses indicate that, given the relatively low infant and juvenile mortality, there are more floaters than available breeding positions (Huck & Fernandez-Duque, 2017), which leads to an intense and frequent competition over breeding positions for both males and females (Fernandez-Duque & Huck, 2013). Owl monkeys show extremely low levels of dimorphism in body size, coloration, and the external genitalia, and like other pair-living sexually monogamous taxa, they show an extended form of male care (Huck et al., 2011; Huck & Fernandez-Duque, 2013; Spence-Aizenberg et al., 2017; Spence-Aizenberg et al., 2018).

Based on Trivers' (1972) hypothesis that the sex with less investment in infant care would be the more competitive one, Heymann (2003) proposed that, among New World Monkeys, the degree of male care is related to the influence of sexual selection on the evolution of chemical and vocal communication. He predicted that in taxa where males were the principal providers of infant care, females would vocalize more than males. In contrast to other genera, our knowledge of owl monkey vocal communication that would allow evaluation of the hypothesis remains quite limited. Only two studies on captive animals have assessed the vocal repertoire of *Aotus*

(Kantha et al., 2009; Moynihan, 1964); in two other studies of vocal communication in wild owl monkeys the authors were not able to unequivocally identify the sexes or age of the individuals due to the strictly nocturnal habits of the species studied (Helenbrook et al., 2018; Wright, 1985). These studies suggested that one call, the hoot call, conveys information over long distances and that could be differentiated into two sub-types, graff and tonal ones (Wright, 1985).

The goal of our study was to assess sex differences in hoot calls in wild owl monkeys. Using only information from identified individuals of known age and sex we first assessed whether hoots are sexually dimorphic, comparing information on the rate of production of graff and tonal hoots. We predicted that tonal and graff hoots would be sex-specific. Second, we compared audio recordings of tonal and graff hoots to test the prediction that there would be acoustic differences in the basic structure of both types of calls. Finally, to examine whether the levels of dimorphism in hoot calls are consistent with the hypothesis proposed by Heymann (2003) we tested the prediction that females would emit more hoot calls than males given the high degree of paternal care in owl monkeys.

Methods

Study area and population

The study area, located in the gallery forests along the Pilagá River in the Argentinean Gran Chaco, is part of the 1,500 ha Owl Monkey Reserve established in 2006 (58°13' W, 26° 54'S). The area includes a mosaic of grasslands, savannas, xeric thorn forests and semideciduous forests (van der Heide et al., 2012). The climate is subtropical with no marked wet season (1418mm/yr), and extreme low and high temperatures are frequent (daily minimum temperatures <10°C between April and September and maximum daily temperatures >33°C between September and March; Huck et al., 2017). A system of intersecting transects at 100m intervals covers approximately 300ha of forest where all of the data were collected (Fernandez-Duque, 2016).

Unlike the strictly nocturnal tropical species of owl monkeys, *Aotus azarae* is unique among the genus because of its cathemeral habits. The Azara's owl monkeys show activity both during the day and night (Fernandez-Duque et al., 2010), which allows for detailed behavioral data to be collected from identified individuals during daytime. The relatively small home ranges (mean ± SD: 6.2 ha ± 1.8; Wartmann et al., 2014) make it possible to monitor regularly many focal groups (10-15 groups for behavioral data: Fernandez-Duque, 2016).

Data collection

We used data collected through two different procedures (demographic monitoring and captures with physical exams). All data were extracted from the Owl Monkey Project (OMP) relational Access database. For demographic monitoring, every time a group of monkeys, or a solitary individual, is found, observers enter an "Avistaje" (i.e., a sighting) in the OMP database, where basic demographic data, geolocation and behaviors noted upon encounter are recorded.

We analyzed all avistaje records for which data on hoot calls were available and we analyzed all hoot calls registered during 2001-2017. We analyzed all vocal behaviors entered together with sighting data, not when conducting behavioral focal sampling. To ensure the quality of vocal data, we limited the use of data to those collected by experienced observers, defined as those who stayed in the field at least four months and had experience identifying hoot calls. There were 90 sighting records that included information on hoot calls. Fifty four percent of them (N=48) specified the sex of the caller. For all analyses we classified pair-living adults and floaters as potentially reproductive individuals, and subadults and juveniles still living in their natal groups as non-reproductive ones. We followed Huck et al. (2011) for age classifications of subadults (24.1-48 months) and juveniles (6.1-24 months).

Since 2000, we have conducted 277 captures with physical exams of owl monkeys. In the process, we caught 177 different individuals, whom we physically examined, sampled for biological specimens and fitted with a bead or radio collar (Fernandez-Duque & Rotundo, 2003; Fernandez-Duque et al., 2017). Given the remarkable lack of visible sexual dimorphism (Fernandez-Duque, 2011) these procedures have made it possible to reliably identify individuals in the field. Out of 277 captures, we captured potentially reproductive individuals on 191 occasions (69%) and non-reproductive ones on 86 occasions (31%). No hoots were ever registered during captures of non-reproductive individuals. During 29 captures of pair-living adults (15%) there were hoot calls emitted by members of the group left behind.

During six of the captures of pair-living adults we obtained sound recordings of hoot vocalizations produced by the remaining adult in the group while the captured pair mate was being examined. We made the recordings with a Marantz PMD660 Recorder and a Sennheiser ME66 Short Shotgun Capsule Head for K6 Series, at a visually estimated distance of 10-30m. All recordings were made by two experienced observers (C. Depeine and M. Rotundo). All audio files (n = 111) were recorded in. wav format, with a sampling rate of 44.1 kHz and 16-bit sound resolution. All recordings were made between 0730 and 1100 hs. The material available was obtained from three males and three females (M1 = 6 calls; M2 = 32 calls; M3= 37 calls; F1 = 8 calls; F2 = 15 calls; F3 = 13 calls).

Acoustic analyses

We performed analyses of the audio files by analyzing calls and syllables separately. To analyze calls, we generated spectrograms of them with a Fast-Fourier Transform using the Audacity (v. 2.2.1) acoustic software set with a Hanning window and a 2048 points window size (gain = 30 dB, range: 40 dB). With a 44.1 kHz sampling rate, each sound sample was 22.7 µs in duration. For acoustic parameter measurements, spectrograms were displayed in the 0–1000 Hz frequency range. The best quality recordings were retained for call analysis (n = 98; 88%) and we used sound samples as a unit to accurately measure the parameters call duration, syllable duration, inter-syllabic-intervals and call rate.

To assess sex differences in the acoustic structure of the hoots, we analyzed 69 bisyllabic calls, 30 from females (F1= 7 calls; F2= 11 calls; F3= 12 calls) and 39 from males (M1=2 calls; M2= 9 calls; M3= 28 calls). We next analyzed 94 syllables, 42 from females (F1= 14 syllables; F2=6 syllables; F3= 22 syllables) and 52 from males (M1= 4 syllables; M2= 12 syllables; M3= 36 syllables). The syllables extracted from each call were labeled according to their position (1 or 2) in the call. To ensure that the loudest peak in each file was the same, all sound files were rectified for DC-offset and normalized using SoundExchange (SoX, v. 14.4.1). Individual syllables were exported in wav format for subsequent analysis with the seewave Package, v. 2.0.5 (Sueur et al., 2008). Many recordings (22/69=32%) were contaminated by low-frequency (<100 Hz) sounds due to equipment handling and/or high-frequency (> 800 Hz) sounds, mainly from insects and birds, that overlapped with the signal of interest.

Therefore, using the ‘ffilter’ function of the seewave package, syllables were band-filtered between 100 and 800 Hz where most of the syllable sound energy was concentrated. Subsequent visual inspection of the spectrograms ensured that the signal of interest was devoid of any obvious sound contamination.

To quantify the degree of syllable noisiness, we measured the Shannon spectral entropy using the ‘sh’ function of the seewave package. On a scale from 0 to 1, noisy sounds have high entropy compared to purer sounds. To determine the dominant frequency of the signal, we generated a power spectrum of each syllable using the seewave function ‘spec’ and we elected a window length of 4096 points to increase the frequency resolution (10.8 Hz). Using the ‘fpeaks’ function of the seewave package we then searched for the 10 largest peaks of the frequency spectrum. The largest peak of each spectrum was retained as the dominant frequency. In females, the dominant frequency of multisyllabic calls may go up or down and the change is quite noticeable when listening to the audio files. To determine whether there was a consistent pattern in frequency change, we tracked the pitch of 36 tonal hoot syllables using the Praat software (v. 6.0.52). To improve pitch accuracy, such analysis was done after reducing the background noise on the spectrogram using the ‘noise reduction’ function in Audacity. Tracking the pitch of graff hoot syllables, on the other hand, was not possible due to their noisy content with many tightly packed bands of modulated sound energy covering a broader frequency spectrum.

We automatized all measurements of spectral entropy, syllable duration and dominant frequency together with syllable filtering and graphic displays of frequency spectra with a script written in the R environment (v.3.3.3) (R Core Team, 2017).

Statistical Analyses

In considering the data obtained through demographic monitoring, we used a χ^2 test to estimate the probability of obtaining the observed difference in the frequencies of tonal and graff hoots emitted by females and males, or a more extreme one, assuming equal proportions for both sexes as the null model. Additionally, to evaluate the prediction that hoot calls would be female-biased, we used a χ^2 test to estimate the probability of obtaining the observed difference in the frequencies of loud calls given by females and males, or a more extreme one, given the null model.

All statistical analyses were performed in R version 3.6.0. (R Core Team, 2019). We used a linear mixed model using R package lme4 (v. 1.1-21; Bates et al., 2015) to evaluate how well sex predicts the variation of each parameter mentioned above. Due to the extent of non-independence of calls we included the identity of the monkeys as a random factor while sex was fitted as a fixed factor.

For syllable analyses we used a linear mixed model to evaluate how well sex and, in this case, the position of syllables in call sequence (syllable one or two) explain the variation on each parameter. We included the identity of the individuals as a random factor and sex and syllable's position as fixed ones. To determine the statistical significance of the models we only compared nested models, varying only in one factor in each comparison. Since random effects were the same in each model, we used the "anova" function (likelihood ratio test) of 'stats' package version 3.7.0 in all comparisons.

To estimate the probability of obtaining the observed difference, or a more extreme one, in the pitch of female hoot syllable we performed a Wilcoxon test for paired samples. The significant level was set to 5% in all analyses and the data are presented as means ± SD. We also report confidence intervals since they are more informative than p-values alone (Nakagawa & Cuthill, 2007; Wasserstein & Lazar, 2016; Ziliak & McCloskey, 2008). We tested the assumptions of the linear mixed model using visual diagnostic plots for the residuals. None of our parameters violated the assumptions of normality or homogeneity of variance of the residuals.

Ethical note

We have captured individuals regularly since 2000 using an injection rifle and disposable darts loaded with 0.5 ml of ketamine hydrochloride. Since then, we have evaluated the potential effects of capture on animal welfare and on population structure (Fernandez-Duque et al., 2017; Juarez et al., 2011).

We fitted all individuals with a radio or a bead collar (Fernandez Duque & Rotundo, 2003; Fernandez Duque et al., 2017; Juarez et al., 2011), depending on the age of the monkey and our interest in being able to locate it reliably. The radio collar has consisted of a transmitter package mounted on a ball-chain collar with a 15-cm whip antenna.

All procedures conformed to Argentinean laws and were approved at different times by the National Wildlife Directorate in Argentina and by the animal research committees of the Zoological Society of San Diego (2000-2005), the University of Pennsylvania (2006-2011) and Yale University (2012-2018). All animal procedures followed the guidelines for the treatment of animals for teaching and research recommended by the Animal Behaviour Society (2014).

Results

Owl monkeys produced two perceptually distinct types of hoot calls (see Online Resources 1 and 2 for an audio of tonal and graff hoots). Tonal hoot calls exhibit a narrow-band tonal structure with occasional harmonics whereas graff hoot calls are essentially noisy and broadband, with sound energy appearing fuzzier on the spectrogram (Figure 2.1). Each type of vocalization can be emitted as a single syllable or as a sequence of two or three similar ones (multisyllabic calls). Here, a syllable is defined as a continuous trace on the spectrogram (Figure 2.2).

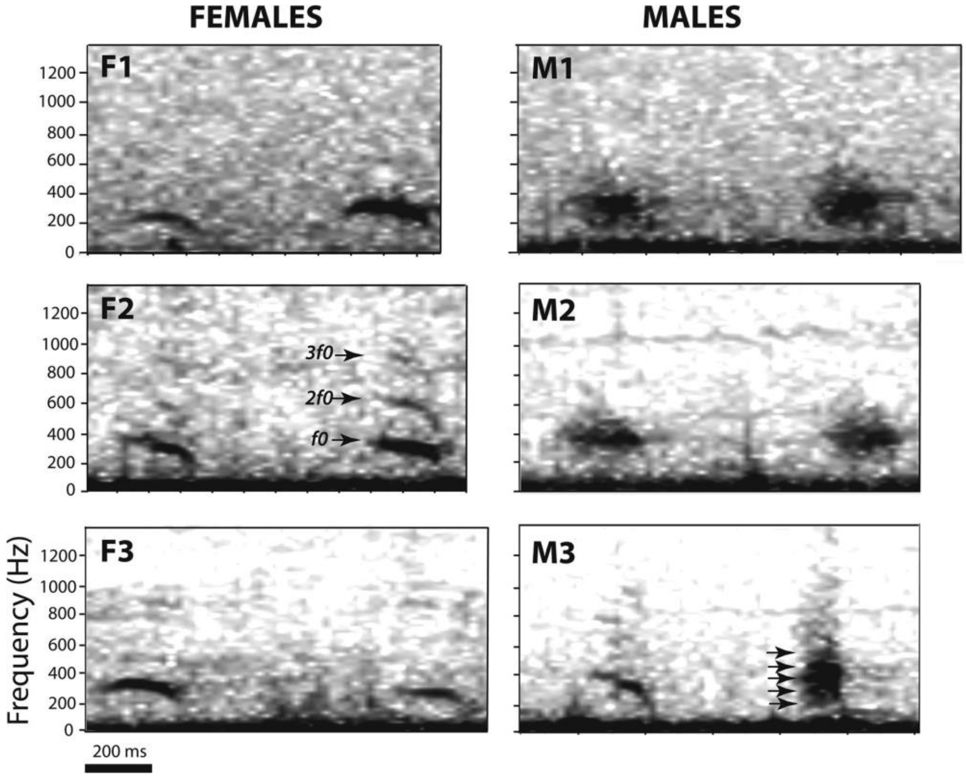

Figure 2.1. Exemplars of *Aotus* hoot calls for three females and three males. Two variants are shown: A tonal hoot from female 2 (F2) showing the presumptive fundamental sound (f0) with two overlaid harmonics (2f0 and 3f0). A graff hoot from male 3 (M3) in which the first syllable is less noisy (lower entropy) compared with the second syllable. The latter displays many bands of sound energy between 200 Hz and 600 Hz (arrows). Note the change in the pitch of the female hoot calls between first and second syllable: the pitch increases (F1), remains stable (F2) or decreases (F3).

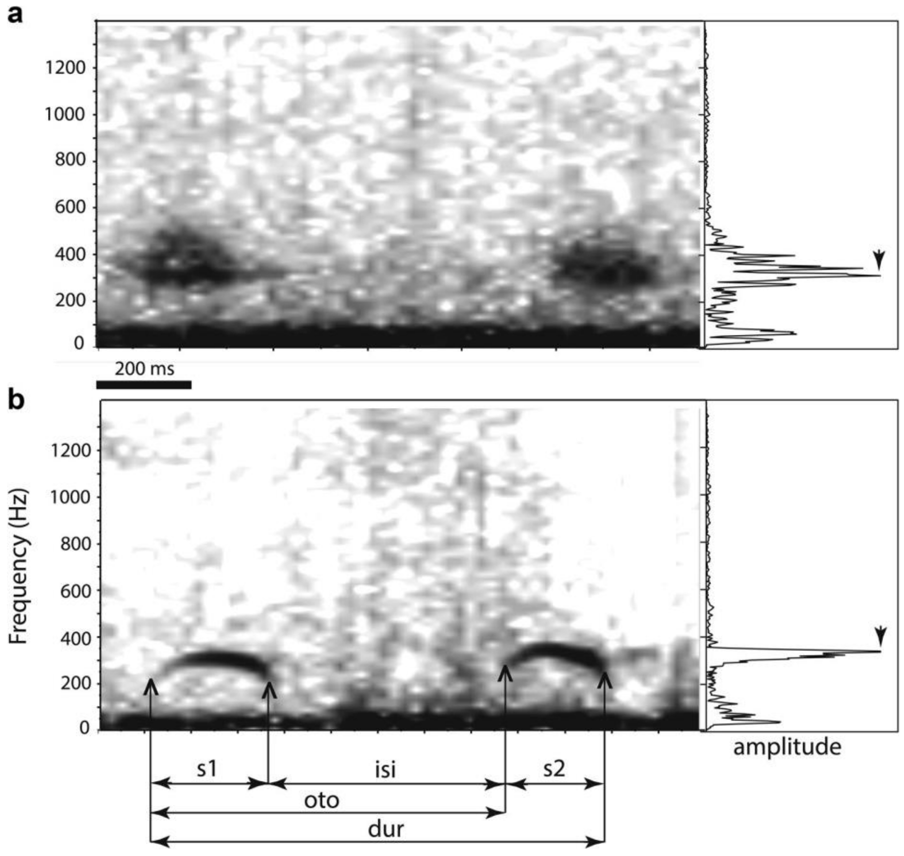

Figure 2.2. Spectrograms of Azara's owl monkeys loud calls: (a) a graff hoot from male 2 and (b) a tonal hoot from female 1. The temporal acoustic parameters measured in this study are shown at bottom. For each type of call, a power spectrum of the second syllable is shown at right. The vertical arrowhead points to the syllable dominant frequency (see text for more details). dur: call duration; s1: duration of syllable 1; s2: duration of syllable 2; isi: intersyllable interval; oto: onset-to-onset time interval.

Further, males and females emitted different types of vocalizations. No graff hoots were registered from females, nor were any tonal hoots registered from males. When examining demographic monitoring data, of all records of vocalizations from identified males (N=16), 88% were graff hoots and 12% were only classified as "hoot" without specifying which type. On the other hand, for all records of vocalizations from identified females (N=32), 85% were tonal hoots and 15% were vocalizations only described as "hoots". Females called more often than males (female, N=32; male, N=16 hoots; Chi-square test for given probabilities, χ^2=5.33, df = 1, p=0.02).

Likewise, the capturing of males or females elicited very different responses from the animals left behind. When we captured the adult female in the group only graff hoots were produced by a remaining member of the group (N=16 captures). On 14 of the 16 captures (N=12 different pairs) it was the adult male who produced graff hoots. On the other hand, when we captured the adult male in the group, only tonal hoots were emitted by a remaining member of the group (N=10 captures). In eight of the 10 captures (N=7 different pairs) it was the adult female who emitted the tonal hoots. As noted, in four captures we could not determine the sex or age of the producer of the calls, however, we never heard a tonal hoot during the capture of an adult female or a graff hoot during the capture of a male. Furthermore, we have never registered any hoot, graff or tonal, emitted by a remaining member of the group during 86 captures of non-reproductive individuals (Chi-square test of independence: χ^2=112.73, df = 1, p<0.001).

Calls of males were, on average, shorter than those of females (879±122 vs 981±149 ms respectively). Further, the intersyllable intervals of males were, on average, shorter than those of females (503±105 vs 527±125 ms respectively). The models assessing how well sex of the caller explains duration and intersyllable intervals did not reach statistical significance (Table 2.1).

Table 2.1 Result of model comparisons among models including single fixed effects (sex) and the null model.

Dependent variable	**Model**	**χ^2**	***df***	**P**
Duration (ms)	Model 1 (Sex), Null	0.25	1	0.62
Intersyllable interval (ms)	Model 1 (Sex), Null	0.02	1	0.88

When analyzing sex differences in the parameters extracted from syllables no model reached statistical significance for explaining statistical variability of duration by the sex of the caller or the position of the syllable. On the other hand, the models did reach statistical significance for explaining variability of entropy and dominant frequency by sex and syllable position (Table 2.2). Specifically, the entropy was higher in male than female calls and was higher on the first syllable of the hoots analyzed (Table 2.3). The percentage of variance explained (R^2) by the fixed effects of the model was 48% while the percentage of variance explained by the random effects (individual) was 8%.

Table 2.2 Result of model comparisons among complete models (including the interaction among predictor variables sex and syllable), models including simple fixed effects (sex and syllable) and models including single fixed effect. When models with only one fixed variable did not account for enough variance to reject the null hypothesis at the specified significance level, we compared the simplest model with the null one.

Dependent variable	**Model**	χ^2	***df***	**P**
Duration (ms)	Complete Model (Sex*Syl), Model 1 (Sex+Syl)	0.84	1	0.34
	Model 1 (Sex+Syl), Model 2 (Sex)	0.16	1	0.7
	Model 2 (Sex), Null	0.09	1	0.8
Entropy (Hz)	Complete Model (Sex*Syl), Model 1 (Sex+Syl)	0.44	1	0.5
	Model 1 (Sex+Syl), Model 2 (Sex)	6.05	1	0.01
	Model 1 (Sex+Syl), Model 3 (Syl)	11.71	1	<0.01
Dominant Freq (Hz)	Complete Model (Sex*Syl), Model 1 (Sex+Syl)	0.21	1	0.6
	Model 1 (Sex+Syl), Model 2 (Sex)	5.3	1	0.02
	Model 1 (Sex+Syl), Model 3 (Syl)	14.1	1	<0.01

Similarly, the dominant frequency was higher in male calls, and the second syllable of hoots showed higher values of the variable (Table 2.3, Figure 2.3). In this case, the random effects did not explain any variance of the response variable, suggesting no inter-individual variability on dominant frequencies. The fixed effect explained the 28% of model's variance.

Table 2.3 Sex differences in the mean, SD and confident intervals (95%) of the statistically significant variables (entropy and dominant frequency) extracted from syllable analyses.

Variable		**Mean**	**SD**	**Confidence interval (95%)**	
				Lower	Upper
Entropy	Females	0.47	0.04	0.46	0.48
	Males	0.52	0.02	0.51	0.52
	Syllable 1	0.50	0.03	0.49	0.51
	Syllable 2	0.49	0.04	0.48	0.50
Dominant Frequency	Females	0.31	0.03	0.30	0.32
	Males	0.34	0.03	0.33	0.35
	Syllable 1	0.32	0.03	0.31	0.33
	Syllable 2	0.33	0.03	0.32	0.34

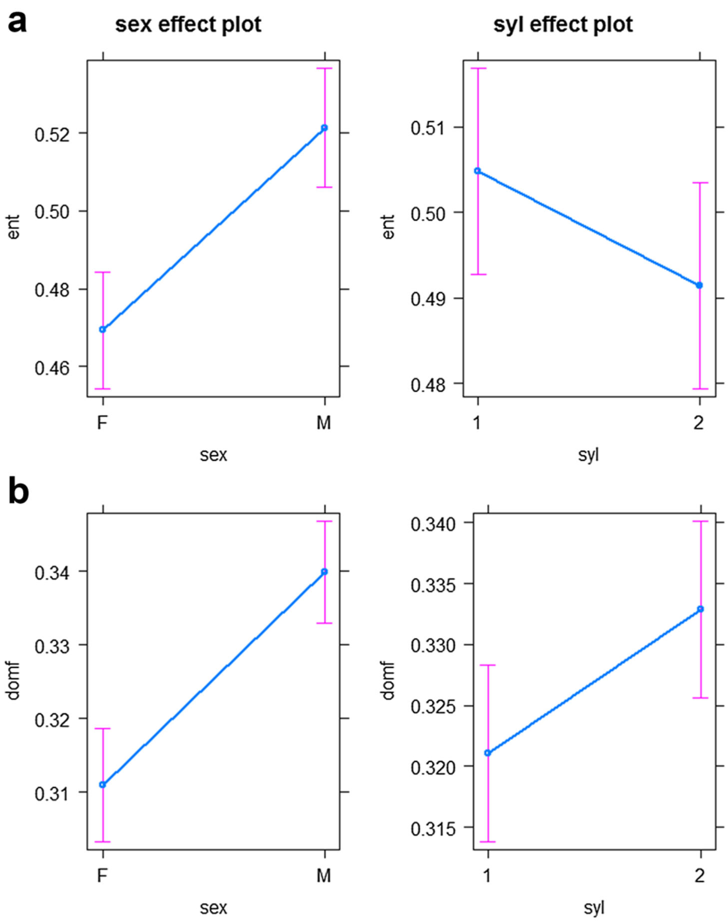

Figure 2.3. Effect plot of entropy (a) and dominant frequency (b). On both graphics, sex differences (F=Females and M=Males) are showed on the left while syllable differences (1=first syllable of the calls and 2=second syllable of the calls) are showed on the right

The pitch of 36 tonal hoot syllables analyzed did not show statistical differences between syllables in any female (Table 2.4, Figure 2.4).

Table 2.4. The pitch value (mean ± SD) of female hoot syllables is shown according to syllable position (S1 vs. S2) within the call. The p-values associated with the paired samples Wilcoxon statistics (V) are reported separately for each female. n = number of calls.

Female	n	S1	S2	V	p-value
F1	6	292.40 ± 14.44 Hz	314.02 ± 31.00 Hz	2	0.0938
F2	6	309.52 ± 31.76 Hz	292.19 ± 9.54 Hz	16	0.3125
F3	6	300.23 ± 9.67 Hz	295.90 ± 22.61 Hz	28	1.0000

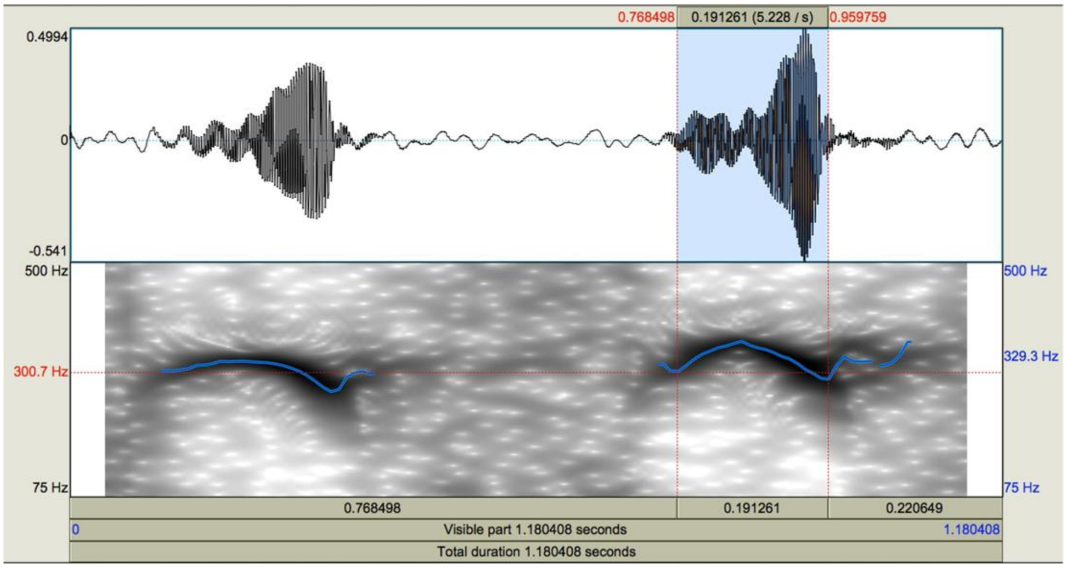

Figure 2.4. Pitch analysis of a hoot call (female 1, call 2). The top panel of the Praat software window shows the amplitude modulation of the call. The bottom panel shows the spectrogram, which displays both frequency values (in red) and pitch values (in blue). After background noise reduction, the blue line falls exactly on the presumptive fundamental of S1 and S2, respectively. The two vertical red lines denote the time interval selected to collect a vector of pitch values, which was saved as a text file.

Discussion

Our study of Azara´s owl monkeys provides evidence of sex differences in vocal communication, specifically in loud calls. Detailed registers from identified individuals indicated that females only emit tonal and males only emit graff hoots. Our data also showed that male calls had higher entropy and dominant frequencies and these parameters also varied depending on the syllable position (one or two). Further, sex and syllable position explained more of the variation of entropy than the variation of dominant frequency.

The quantitative analyses of owl monkey hoots indicate that there are sex-related differences in their calls. Given the fact that owl monkeys from Argentina do not exhibit any striking morphological/anatomical differences between sexes (Fernandez-Duque, 2011), it is likely that such differences arise from allometric traits driven by factors other than body size or body weight (Garcia et al., 2017). In the past, it has been proposed that sexual selection may have played a role on the evolution of sexual dimorphism in loud calls (Delgado, 2006; Snowdon, 2017). The sexual dimorphism we found in *Aotus* calls, has been proposed for other non-sexually dimorphic primate taxa as in indris (*Indri indi*, Gamba et al., 2016), golden lion tamarins (*Leontopithecus rosalia*, Benz et al., 1990), common marmosets (*Callithrix jacchus*, Norcross & Newman, 1993) and Wied's black-tufted-ear marmosets (*Callithrix kuhlii*, Smith et al., 2009). A possible explanation could be that differences in male and female calls allow other individuals to identify the sex of the caller; however, a more definite evaluation of this hypothesis requires an approach that includes certain manipulation of conditions, like playback experiments. From early on in the Owl Monkey Project, we have relied on playing back hoot calls to assess presence/absence of owl monkeys in remote areas and to find groups and floaters for capturing them. In the beginning, we did not have an adequate understanding of their vocal communication. So, it was only retrospectively that we realized that the playing back of graff hoots was more effective in attracting individuals and usually led to the capture of females.

Further, preliminary results from systematic ongoing playback experiments led by one of us (AGC), have shown that male and female pairs reacted differently to graff and tonal hoots recordings, with both sexes showing an increase of socio-sexual behaviors toward their partners when a simulated same sex competitor was played back (see chapter 3). Although beyond the scope of this study, these preliminary findings suggest that some acoustic parameters in owl monkey hoot calls allow individuals for identification of the sex of the caller.

It follows that our data seem to support the hypothesis proposed by Heymann (2003) that in taxa where males are the principal providers of infant care, loud calls would be female-biased. Given that in monogamous species, sexual selection may apply equally to both sexes, and that in owl monkeys, males are heavily involved in energetically costly parental care activities (Huck & Fernandez Duque, 2012; Rotundo et al., 2005) it may be that females face greater intrasexual competition to choose the best male. Our data suggested a female-biased pattern in loud calls with females vocalizing up to twice as much as males. This female-biased pattern in the production of loud calls show contradictory results in the literature. While in captive common marmosets (*Callithrix jacchus*) and golden lion tamarins (*Leontopithecus rosalia*) males and females showed similar rates of loud calls (McLanahan & Green, 1977; Norcross & Newman, 1993), results from captive *Saguinus oedipus* showed adult females emitting almost three times more loud calls than males (McConnell & Snowdon, 1986).

Unlike the cooperative breeding social systems usually observed in callitrichid primates, *Aotus* groups do not contain “helpers” and infant care is provided exclusively by the adults in the group (Huck & Fernandez-Duque, 2013; Rotundo et al., 2005;). Infants are transported by the adult male 84% of the time after the infant’s first week of life (Rotundo et al., 2002); even during the exceptional cases of twin births, which could entail a double effort of transporting the infants, the mothers did not carry them more frequently than mothers of singletons (Huck et al., 2014b). These observations, even from relatively infrequent events, may be indicating that there are selective pressures against *Aotus* females to increase the amount of infant care.

Our findings notwithstanding, like for most of field primatology data ever collected, one must be cautious and consider other factors that may be influencing observational data. First, with only six individuals included in our acoustical analyses the sample size is small, and the contribution of each individual on the analyses is not the same, with a big variability especially for males. Thus, even when this variability should be partially controlled by the design of our statistical models, our results must be interpreted with caution and data from more identified individuals are undoubtedly needed for further comparisons. Further, we cannot rule out the influence of potential observer bias in noting and recognizing tonal hoots more frequently than graff ones or the fact that it is impossible to have a true systematic random sampling design. To address the latter issue, we are currently implementing the use of passive terrestrial acoustic recorders, which allow true systematic recording across the 24 hours. Unfortunately, we still do not know if loud calls encode signals about pair membership, which could inform other individuals about the social condition of callers without the necessity of direct, costly fighting. More acoustic data on identified pairs and solitary individuals will show if the structure of hoot calls present differences in relation to the social condition of owl monkeys, which will provide us deeper insights into the evolution of vocal mechanism regulating pair bonding and mate choice strategies in this species.

CHAPTER 3

MATE GUARDING

RESPONSES OF PAIR-LIVING, SEXUALLY MONOGAMOUS OWL MONKEYS (*AOTUS AZARAE)* TO THE SIMULATED PRESENCE OF SOLITARY INDIVIDUALS: A FIELD PLAYBACK EXPERIMENT

Chapter 3. Responses of pair-living, sexually monogamous owl monkeys (*Aotus azarae)* to the simulated presence of solitary individuals: a field playback experiment.

Abstract

Loud calls, which communicate characteristics of the caller, play an important function in regulating the use of space and structuring social groups and mating systems in a wide range of taxa. In pair-living territorial animals, where encounters with neighbors and solitary unfamiliar conspecifics are relatively common, these calls are mainly associated with resource defense or mate guarding behaviors. Owl monkeys (*Aotus azarae*) live in groups of one pair of reproducing adults and 1-4 younger, non-reproducing individuals. Both sexes disperse from natal groups around 3 years; they become solitary floaters who compete to replace same-sex resident adults from other groups. Our study is aimed at improving our understanding of the behavioral mechanisms regulating the competition between solitary floaters and groups, namely the extent to which members of stable owl monkey pairs primarily defend their territory or their mates. We collected data on sociosexual behaviors from three groups, before, during, and after the playing back of unfamiliar male and female loud calls and of a control stimulus at the center and border of their home ranges. Our results showed that the sex of the caller elicited larger differences than the speaker location in owl monkeys' responses. In agreement with classical conceptions of the Mate Guarding Hypothesis, males reacted more strongly than females to the simulated presence of an unfamiliar conspecific. However, overall, both sexes were more reactive to male than female unfamiliar calls, as evidenced by higher rates of sociosexual and vocal responses, movement towards the speaker, and intergroup encounters. The fact that females guard their mates more often during the simulated presence of other males instead of same-sex individuals suggests that in sexually monogamous species with an extended form of biparental care, females

may guard their mates as well in order to secure paternal investment. This study suggests that paternal care may be an important factor for female's fitness in owl monkeys, and emphasizes, as other authors before, the need to explore the coevolution of reproductive competition, mating strategies and parental care, in the two sexes.

Introduction

Loud calls have been historically associated with territoriality in a wide range of taxa (Baker, 1983; Bates, 1970; Mitani & Stuht, 1998; Mumm & Knörnschild, 2017; Owen-Smith, 1977). It is suggest that they can provide information on the identity, breeding status and genetic quality of the caller (Cinková & Policht, 2016; Clutton-Brock & Albon, 1979; Erb, Hodges, & Hammerschmidt, 2013; Kitchen, Seyfarth, Fischer, & Cheney, 2003; Theis, Greene, Benson-Amram, & Holekamp, 2007; Welch, Semlitsch, & Gerhardt, 1998; Wyman, Mooring, McCowan, Penedo, & Hart, 2008). By communicating varied information on the characteristics of the caller, loud calls play important functions in regulating the use of space, structuring social groups, and mating systems (Hall, 2004; Rogers & Kaplan, 2002) .

The function of loud calls is likely important for pair-living territorial animals whose home ranges overlap, and where individuals need to be able to discriminate between mated neighbors and single strangers (Darden & Dabelsteen, 2008; Goldingay, 1994; Hall, 2004) . Lower levels of aggression towards neighbors than strangers (i.e. "dear enemy effect") is frequent, this is hypothesized to be because unfamiliar signals are perceived as greater threats than familiar ones, since the former may be indicative of nonterritorial floaters prospecting occupied territories (amphibians: Chuang, Kam, & Bee, 2017; crustaceans: Booksmythe, Jennions, & Backwell, 2010; fish: Bruintjes, Lynton-Jenkins, Jones, & Radford, 2016; mammals: Rosell & Bjørkøyli, 2002; Monclús, Saavedra, & de Miguel, 2014).

For some pair-living mammals, encounters with neighbors and solitary unfamiliar conspecifics are relatively common and can be affiliative or aggressive (Brotherton & Rhodes, 1996; Sun, 2003). Among primates, interactions with neighbors and solitary individuals are often accompanied by loud calls in the form of duets (Adret et al., 2018; Barlett, 2003; Bonadonna et al., 2017; Geissmann, 2002; Robinson, 1981; Méndez-Cárdenas & Zimmermann, 2009; Müller & Anzenberger, 2002; Petter & Charles-Dominique, 1979; Thompson, Norconk, & Whitten, 2012; Yi, Fichtel, Kim, & Choe, 2020). Duets are coordinated and stereotyped vocalizations produced jointly, usually by two individuals and sometimes echoed by similar calls from neighboring groups (Adret et al., 2018). The functional significance of primate duetting has been hypothesized to signal the mated status of one or both pair-mates, and some playback experiments have shown differential responses to duets and solo songs (*Hylobates muelleri*: Mitani, 1984; *Hylobates agilis*: Mitani, 1987; *Hylobates lar*: Raemaekers & Raemaekers, 1985; but see Caselli, Mennill, Gestich, Setz, & Bicca-Marques, 2015: *Callicebus nigrifrons*). For example, Javan gibbons (*Hylobates moloch*) initiated movement toward the speaker more quickly in response to songs of strangers and unpaired individuals than to songs of neighbor's songs and paired individuals (Ham, Hedwig, Lappan, & Choe, 2016).

One exception to the production of duets in pair-living primates is the owl monkey (*Aotus* spp.), whose loud calls appear to be performed in form of solos (Garcia de la Chica, et al., 2020). Azara's owl monkeys from northern Argentina are pair-living, sexually monogamous primates that occupy 4-10 ha relatively stable home ranges (Wartmann, Juárez, & Fernandez-Duque, 2014). Intergroup encounters, which are relatively frequent, rarely involve serious fights or injuries; monkeys usually only chase each other while jumping and showing piloerection displays. During these intergroup encounters, individuals emit a distinctive loud call previously referred to as a "resonant grunt" (Moynihan, 1964), or a "resonant gruff-grunt" (Wright, 1978), which to the human ear resembles the sound of a turbine. In contrast to relatively peaceful intergroup encounters, owl monkey pairs have highly aggressive, sometimes even deadly, interactions with solitary floaters (Huck & Fernandez-Duque, 2012; Fernandez-Duque & Huck, 2013). Solitary floaters are both male and female individuals who have dispersed from their natal groups (usually when they are ~3 years old) and range solitarily while trying to gain a breeding position by forcibly replacing a resident adult, or taking advantage of vacancies in resident positions that arise through natural deaths (Fernandez-Duque & Huck, 2013). Floaters mainly range in the borders of multiple groups home ranges while avoiding the core areas. Through this prospecting, floaters may be able to monitor the composition of groups and the physical condition and reproductive status of same-sex adults (Huck & Fernandez-Duque, 2017). Additionally, by wandering at the borders of the groups' home ranges, floaters can more easily and quickly leave the area and avoid serious fights if detected by residents. Indeed, encounters with floaters are more frequent at the periphery of a groups home range than in the core area (Huck & Fernandez-Duque, 2017), and are often preceded by "hoots", a distinctive loud vocalization (Garcia de la Chica, et al., 2020).

The "hoots", in addition to being produced by floaters, are also commonly emitted by male and female non-reproductive subadults during their pre-dispersal prospecting (Fernandez-Duque, 2009; Corley, Valeggia, & Fernandez-Duque, 2017). Although hoots may sometimes elicit responses from other individuals, they are always performed as solos. Thus, it seems likely that hoot calls produced by owl monkey floaters and pre-dispersal individuals are playing a role in mate attraction or intergroup communication associated with home range defense (Moynihan, 1964; Wright, 1989). Hoot calls may allow pre-dispersal individuals to assess the composition of neighboring social groups and to evaluate potential opportunities for reproductive openings. Our earlier work playing back hoot calls allowed us to assess the presence of owl monkeys in remote areas, and to attract floaters that we wanted to capture (Fernandez-Duque, Di Fiore, & Rotundo, *in prep*.; Depeine, Rotundo, Juárez, & Fernandez-Duque, 2008; Juárez, Rotundo, Berg, & Fernandez-Duque, 2011).

Notwithstanding our progress in understanding the behavioral ecology of floaters, it is still the case that opportunities for witnessing interactions between groups and between groups and floaters are relatively scarce. Furthermore, even when we can observe those interactions, they present remarkable challenges for collecting high quality individualized data (Sabol, Solomon, & Dantzer, 2018). Therefore, semi-experimental field studies, such as playback experiments, offer opportunities for researchers to effectively simulate the presence of unfamiliar conspecifics and to trigger reactions from groups (Fischer, Noser, & Hammerschmidt, 2013). For example, playback experiments in pair-living birds showed shorter response latencies (*Laniarius aethiopicus,* Grafe & Bitz, 2004), and more aggressive responses and threat vocalizations to strangers than to neighbors (*Vireo olivaceus,* Moser-Purdy & Mennill, 2016).

We present the results of a field playback experiment that simulated the presence of an unfamiliar, unpaired conspecific to pair-living groups of owl monkeys. The goal was to describe in detail the behavioral reactions of pair mates to unfamiliar loud calls and to test predictions derived from the Resource Defense and Mate Guarding hypotheses for the maintenance of a pair-living social organization (Table 3.1). The Resource Defense hypothesis states that due to highly dispersed resources, living as pairs offers individuals the highest pay-off in terms of access to feeding resources (Rutberg, 1983). We predict that, when facing an intruder, both sexes, either together or separately, will defend the resources, with no regards to the intruder´s sex. On the other hand, the Mate Guarding hypothesis states that, by staying in pairs, males increase their reproductive success by guarding females from competitors while ensuring mating access to them (Brotherton & Komers, 2003; van Schaik & Kappeler, 1997, 2003). We tested the prediction that individuals will be more aggressive towards same-sex intruders than opposite-sex ones (Fernandez-Duque, Huck, Van Belle, & Di Fiore, 2020). In our population, pair members do not voluntarily leave their partners. Instead, the breaking up of pairs is usually associated with extrinsic factors, such as being evicted by floaters. The takeovers appear to occur at similar rates for males and females (27 female and 23 male replacements, in a total of 149 group-years: Fernandez-Duque & Huck, 2013). Only twice, an evicted adult joined a new group as a breeding member of the pair, suggesting that being replaced implies a great cost for individuals who may see their reproductive life terminated (Huck & Fernandez-Duque, 2012; Fernandez-Duque & Huck, 2013). These observations strongly indicate that individuals of both sexes face high levels of intrasexual competition from floaters; thus, we expect both males and females to fiercely defend their breeding positions within a group. Our study is aimed at improving our understanding of the behavioral mechanisms regulating the competition between solitary floaters and groups, namely the extent to which members of stable pairs primarily defend their territory or their mates.

Table 3.1. Hypotheses to explain pair-living and sexual monogamy in non-human primates (Fernandez-Duque, Huck, Van Belle, & Di Fiore, 2020) and predictions derived from them that mainly focus on the reactions of reproductive individuals, but also consider reactions of non-reproductive ones.

Hypothesis	Predictions
1. Resource Defense	1.1 Both adults will respond similarly to hoot calls, regardless of the caller's sex. 1.2 Both adults will show stronger behavioral responses to playbacks from the core area of their home ranges than from the periphery. 1.3 All group members will react to calls of unfamiliar individuals.
2. Mate Guarding	2.1 Each adult will react more strongly to same-sex unfamiliar calls. 2.2 Adults will show similar behavioral responses to playbacks from the core area or from the border of their home ranges. 2.3 Adults will show stronger behavioral responses than non-reproductive individuals to unfamiliar calls.

Methods

Study site

The study area, located in the gallery forests along the Pilagá River in the Argentinean Gran Chaco, is part of the 1,500 ha Reserva Privada Mirikiná established in 2006 (58°13’ W, 26° 54’S) (Figure 3.1). The area is a mosaic of grasslands, savannas, xeric thorn forests and semideciduous forests (van der Heide, Fernandez-Duque, Iriart, & Juarez, 2012). The climate is subtropical with no marked wet season (1418mm/yr), and extreme low and high temperatures are frequent (daily minimum temperatures <10°C between April and September and maximum daily temperatures >33°C between September and March; Fernandez-Duque, 2016). A system of intersecting transects, at 100 m intervals, covers approximately 300 ha of forest.

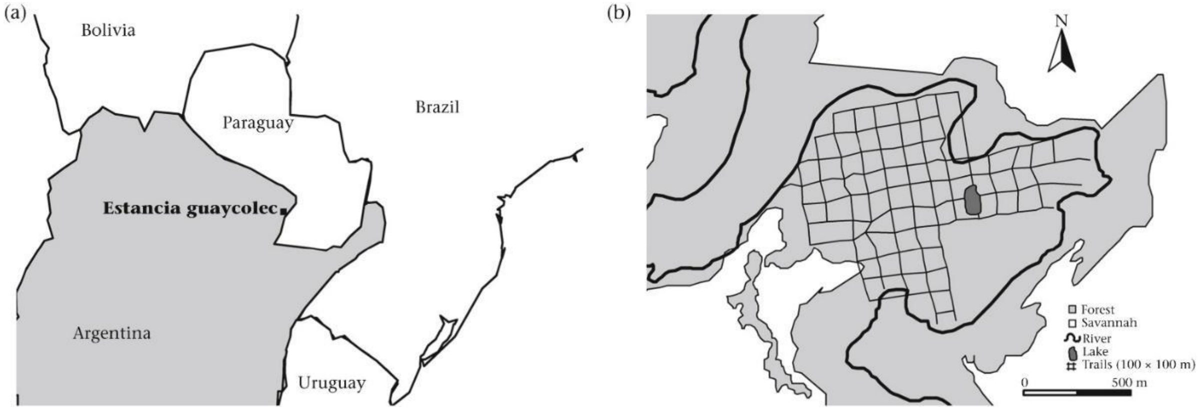

Figure 3.1. (a) Location of the “Estancia Guaycolec” ranch within Argentina (black rectangle). (b) Main study area of the Owl Monkey Reserve within the ranch.

Study population and ranging patterns

Owl monkey groups are usually composed of a heterosexual reproductive pair and 1-4 immature individuals (Fernandez-Duque, 2016). However, studies of our Azara's owl monkey population have shown that the social organization also includes a substantial number of potentially reproductive individuals (25-30%) who do not belong to a pair, but instead range solitarily in the periphery of established groups for a quite variable amount of time (from a few days to 15 months) (Corley, 2017; Fernandez-Duque & Huck, 2013; Huck & Fernandez-Duque, 2017).

In this population, pairs defend home ranges (mean ± SD: 6.2 ha ± 1.8) that remain highly stable between consecutive years. The border parts of the ranges of neighboring groups overlap substantially (48% ± 15); the overlap of core areas, where groups spend as much as 50% of their time, is smaller (11% ± 15) (Wartmann, Juárez, & Fernandez-Duque, 2014). Given all these contiguous and overlapping group's home ranges, it follows that there are no "free" areas available for solitary floaters. Likewise, based on the size of group home ranges and areas of overlap between floaters, Huck and Fernandez-Duque (2017) estimated the number of floaters in the area to be 0.2-0.5/pair. Since the home ranges of floaters are larger than those of groups, at any given time several floaters may be overlapping their ranges within the range of a single group.

Playback Experiment

Stimulus Recordings

Azara´s owl monkeys emit two different forms of hoot vocalizations: graffs and tonals. Since these calls encode information about the sex of the caller (Garcia de la Chica et al., 2020), both human and owl monkey listeners should be able to identify the caller as a male or female. In fact, it was retrospectively that we realized that playing back only male graff hoots to attract individuals usually led to us only capturing females. Furthermore, the spontaneous production of tonal hoots in our area often leads to graff responses, and vice versa.

In order to avoid the potential habituation to the recordings that members of the Owl Monkey Project had used in the area, new recordings of graff and tonal hoots were downloaded from the Macaulay Library of Cornell Lab of Ornithology (http://macaulaylibrary.org) (Table 3.2). These calls had been recorded from one group of Azara's owl monkeys in Paraguay (285 km from our field site) in 1982. It is, therefore, impossible that the individuals in our population had prior experience with these callers.

To evaluate whether the subjects' responses were due to their potential identification of the calls as coming from conspecifics, we also tested each group's response to recordings of a Cream-backed Woodpecker (*Campephilus leucopogon*), as a control stimulus. This species is common in the area (BirdLife International, 2019) and its vocalizations do not seem to disturb the owl monkeys or elicit any observable responses from them (Rotundo, M., personal observation). Hence, three stimuli were presented to owl monkeys: graff hoots, tonal hoots and Cream-backed Woodpecker calls.

Table 3.2. Provenance of the recordings used in the study.

Stimulus	Macaulay Library serial number	Provenance
Graff (male) Hoot	ML90201	3 July 1982, P. Wright La Golondrina Ranch, Paraguay
Tonal (female) Hoot	ML90204	3 July 1982, P. Wright La Golondrina Ranch, Paraguay
Cream-backed Woodpecker (*Campephilus leucopogon)*	ML177746	26 September 2012 I. Holzmann Private property adjacent to Chaco National Park, Chaco Argentina

Preliminary Playback Tests

Prior to the experiment, during early May of 2019, we conducted preliminary trials (N=6) playing back the Macaulay's Library recordings to peripheral groups (at least 1 km away from the study focal groups). During the playing back of graff hoots (N=3), monkeys approached the speaker location twice. When tonal hoots were played back (N=3), monkeys approached the speaker only once. In four occasions, observers had a group in sight, so we could also observe the monkey´s first reactions in addition to approaches. Individuals looked up at the speaker direction in all preliminary trials, regardless of the type of vocalization. We did not observe any floaters moving towards the speaker during the preliminary tests; however, given the cryptic nature of a solitary floater it could be that floaters did approach but went unnoticed by observers. Moreover, we tested our control stimulus twice in the same peripheral groups when the individuals were in sight. Individuals did not show any observable reactions in response to the Cream-backed Woodpecker´s vocalizations.

We also tried different volumes in order to match the level of natural vocalizations produced by owl monkeys based on our field experience with their natural vocalizations. The maximum volume produced by the speaker and MP3 equipment was effective in triggering a response by the monkeys; thus, we used the same volume in the experiment. Finally, we tested our data collection sheets to try their effectiveness in registering all behaviors of interest.

Groups and Subjects

The composition of groups at the time of the experiments is summarized in Table 3.3. In all groups, one reproductive adult was fitted with a radio collar (Fernandez-Duque & Rotundo, 2003; Fernandez-Duque et al., 2017). Considering the remarkable lack of visible sexual dimorphism in the species (Fernandez-Duque 2011), fitting collars allows us to reliably identify individuals. For identifying and classifying non-reproductive individuals, we followed Huck et al. (2011) for age classifications of subadults (24.1-48 months), juveniles (6.1-24 months) and infants (0-6 months). We do not usually capture young juveniles and infants, but these individuals can be recognized within the group based on relative body size. We conducted the playback experiments within the ranges of six different groups during June and July of 2019 and 2020 (Figure 3.2). Following Taborsky's (2010) recommendation of prudent sampling in order to reduce the variance in the data, and to maximize the accuracy in parameters estimation, we also replicated the experiments in groups C0 and D500 on the two consecutive years. Even when we did not include these data in our analyses, we performed parallel exploratory data analysis (EDA) using this subset of data to evaluate the consistency of the behavioral patterns observed during both years. This allowed us to maximize our insight into the data set used for final analyses. The descriptive statistics of these data are presented in the Results section below.

Between the study of 2019 and the one of 2020 (i.e. in December 2019), the adult female of C0 group was replaced and the new female was captured for identification. No other changes in breeding pairs' conformation were observed. Finally, given the density of floaters, and their use of space in the area (detailed previously), the study was designed under the assumption that the playback recordings were also listened to by a minimum of 1-2 floaters per pair.

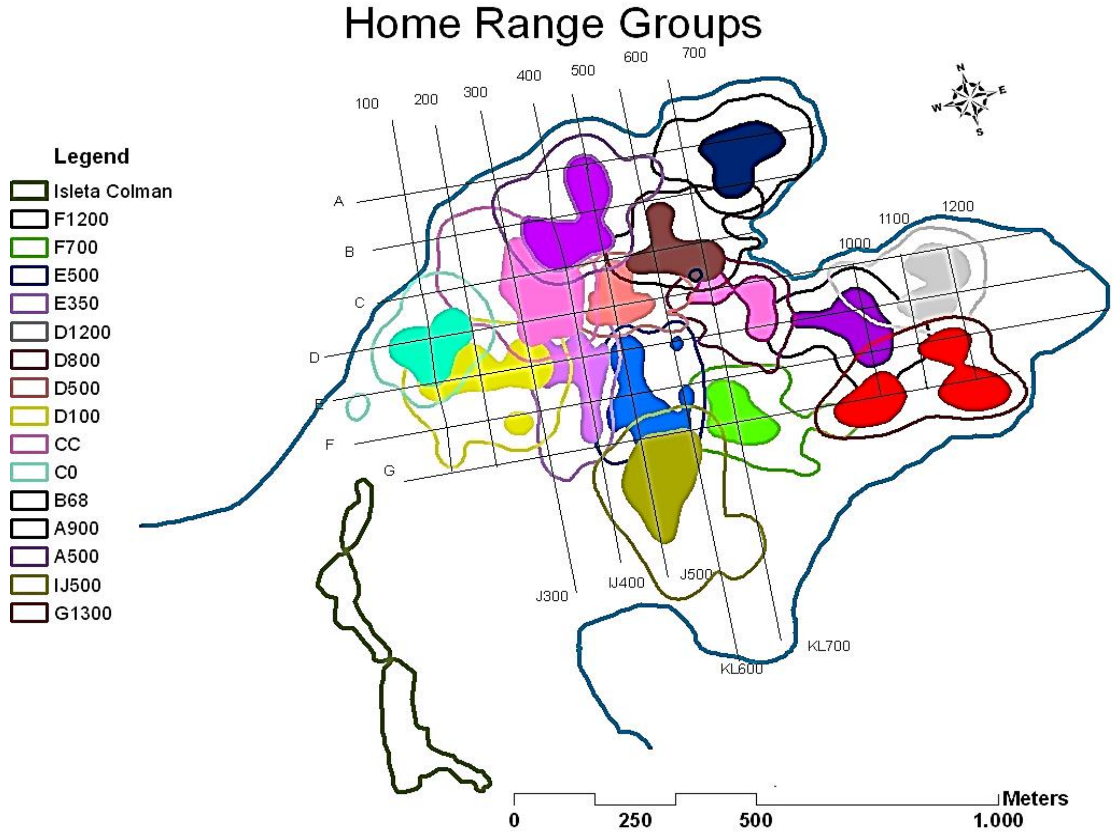

Figure 3.2. Map showing the home ranges of the different groups within the study area of the Owl Monkey Project. The core area for each group appears solid-colored. The groups included in this study: C0=light blue, Cola Corta=pink, D500=coral, E500=blue, D1200=gray, G1300=red.

Table 3.3. Name and composition (age class and sex) of owl monkey groups included in the study (AM=adult male, AF=adult female, SA_16= subadult born in 2016 of unknown sex, Juv_17=juvenile born in 2017 of unknown sex, Juv_18=juvenile born in 2018 of unknown sex, Juv_19=juvenile born in 2019 of unknown sex). (*) denotes individuals fitted with a radio collar. (**) denotes groups not included in the analyses.

Year	Group	Composition
2019	C0	AM
		AF*
		SA_16
		Juv_17
	Cola Corta	AM
		AF*
		Juv_17
		Juv_18
	D500	AM*
		AF
		Juv_17
		Juv_18
2020	C0**	AM
		AF*
		Juv_17
	D500**	AM*
		AF
		Juv_17
		Juv_18
		Juv_19
	D1200	AM*
		AF
		Juv_18
	E500	AM*
		AF
		Juv_17
	G1300	AM
		AF*

Experiment Schedule

We conducted the experiment during the new moon weeks of June and July of 2019 and 2020 (Table 3.4). We worked in the morning, between 07.00-11.30 hrs, centered around the nights of the new moon because this is when Azara's owl monkeys show the most diurnal activity (Fernandez-Duque, de la Iglesia, & Erkert, 2010). The radio collar of the adult female in the group Cola Corta stopped working during the study, this made locating the group early enough in the morning more difficult. Thus, the trials were spread out, with one trial occurring every one or two days.

Experimental Design

In order to simulate the presence of an unknown conspecific, we presented the aural stimuli (i.e. hoots and control recording described above) using an Anchor MiniVox loudspeaker (Anchor, Carlsbad, CA, U.S.A.; frequency response range 100e15 000 Hz, output power: 30W, and maximum SPL: 109 dB) connected to an MP3 where recordings had been saved. The loudspeaker was positioned at a height of approximately 2 meters from the forest floor for two reasons. First, to cut down on interferences from the shrub layer of the gallery forest; and second, to facilitate an easy and accessible height if we needed to change the location of the speaker quickly before the start of trials. The volume was held constant across all trials.

We reproduced all three stimuli (graff hoot, tonal hoot, and the control), from two different locations within each group's home range. Once from the core area, defined as the area within a 2-dimensional 50% kernel density estimation of land utilization, and once from the border, within the area within a 95% kernel, but outside the core areas (Table 3.4) (Wartmann, Juárez, & Fernandez-Duque, 2014).

To simulate the presence of an unknown conspecific, we played back the stimuli from inside each group's range within the group's current location (mean= 118 mts; range= 45-217 mts). We performed EDA that revealed that that there was not apparent association between how far the speaker was (in relation to the monkeys´ position) and response measurements.

Thus, each study group was presented with all three playback stimuli (graff hoot, tonal hoot, and control stimulus) at both locations (center and border) for a total of six individual playback trials for each study group (n= 36 trials, six groups). Each trial consisted of a 20-min pre-playback session to document baseline behavior, a 20-min playback, and a 40-min post playback session.

We only conducted trials if: 1- both the male and female pair-mates were visible while foraging, moving, or resting, and 2- no intergroup encounters had occurred during the 20-min pre-playback session, and 3- the target group had not responded to loud calls of other individuals during the 20-min pre-playback session. During each trial, two observers were hidden behind vegetation near the speaker, while two experienced observers monitored the subject’s reactions for the pre-playback session and for one hour (20-min playback + 40-min post playback) following the start of the trial.

Table 3.4. Schedule of playback trials and number of days before or after the New Moon.

Year	Date	Days from the New Moon	Group	Stimulus	Location
2019	May 30, 2019	-4 days	D500	Control	Border
	May 31, 2019	-3 days	C0	Tonal	Center
	June 2, 2019	-1 day	Cola Corta	Graff	Center
	June 4, 2019	+1 day	Cola Corta	Tonal	Border
	June 5, 2019	+2 days	Cola Corta	Tonal	Center
	June 6, 2019	+3 days	C0	Graff	Border
	June 7, 2019	+4 days	D500	Tonal	Center
	June 8, 2019	+5 days	D500	Graff	Center
	June 27, 2019	-6 days	C0	Tonal	Border
	June 28, 2019	-5 days	D500	Graff	Border
	June 30, 2019	-3 days	D500	Tonal	Border
	July 1, 2019	-2 days	D500	Control	Center
	July 3, 2019	New Moon	C0	Graff	Center
	July 4, 2019	+1 day	C0	Control	Center
	July 6, 2019	+3 days	Cola Corta	Graff	Border
	July 9, 2019	+6 days	C0	Control	Border
	July 10, 2019	+7 days	Cola Corta	Control	Center
	July 11, 2019	+8 days	Cola Corta	Control	Border
2020	June 16, 2020	-5 days	G1300	Tonal	Central
	June 17, 2020	-4 days	G1300	Graff	Border
	June 18, 2020	-3 days	G1300	Control	Central
	July 14, 2020	-6 days	E500	Tonal	Border
	July 14, 2020	-6 days	G1300	Graff	Central
	July 15, 2020	-5 days	E500	Graff	Border
	July 15, 2020	-5 days	G1300	Tonal	Border
	July 16, 2020	-4 days	D1200	Control	Border
	July 16, 2020	-4 days	G1300	Control	Border
	July 17, 2020	-3 days	E500	Control	Central
	July 18, 2020	-2 days	D1200	Tonal	Central
	July 19, 2020	-1 day	E500	Tonal	Central
	July 20, 2020	New Moon	D1200	Graff	Central
	July 21, 2020	+1 day	D1200	Graff	Border
	July 22, 2020	+2 days	E500	Control	Border
	July 23, 2020	+3 days	D1200	Control	Central
	July 25, 2020	+5 days	E500	Graff	Central
	July 26, 2020	+6 days	D1200	Tonal	Border

Data Collection Response Measurements

To evaluate the responses of owl monkeys to each stimulus, during each trial, we collected data on five categorical variables: 1- type of reaction to the stimuli presented: look towards the speaker (an individual points its face towards the speaker), move towards the speaker (an individual displaces itself in the direction that the speaker is located), approach partner (an individual moves to within 0.5 mts of its partner and stays for at least 3 sec in this proximity); 2- identity of the first individual to exhibit a response (look, move or approach); 3- types of vocal responses; 4- identity of individual/s vocalizing; 5- encounter/s with other groups; 6- encounter/s with solitary floaters.

We also registered the start time of the playback and the time of individuals reaction to it. When no reaction was noticed, we recorded the latency to first reaction as 20 minutes for the 20-min playback session.

Additionally, we recorded data on five quantitative variables. We recorded the latency to first response (look towards the speaker, move towards the speaker, approach partner) after initiation of the playback. We recorded the start and end time of each playback session and the time when individuals started any type of behavior. Using these data, we calculated the latency to first response, in minutes, for males and females. If there was no response, we recorded latency as 1 hour to first reaction (20-min playback + 40-min post playback). We also recorded the number of times individuals displayed three types of socio-sexual behaviors (Wolovich & Evans, 2007): scent marking of branches (the anogenital and/or subcaudal region is in contact with a substrate and the body is slid forward or laterally moving the rear part of the body); scent marking over partner (the genital and/or subcaudal area is rubbed over another individual) and urine washing (an individual wets its hands with its own urine and then rubs its hands on a substrate, or on some parts of its body).

Finally, we recorded the distance in meters between the focal group and the speaker location at the onset of each experiment session (20-min pre, 20-min playback, and 40-min post). Since the monkeys do not usually move in a straight line and their proximity to the speaker could go unnoticed by observers, we measured the distances according to our transect system recording geolocation points, meters and degrees on each occasion.

The behavioral data of focal groups were collected by the same observer across all trials (A. Garcia de la Chica), except during four control trials when another experienced observer stayed with the monkeys. Two experienced assistants collaborated with the data collection by standing at the speaker's location during 2019 and 2020. All observations that did not fall into the categories mentioned above, were recorded *ad-libitum*.

Statistical Analyses

All data collected during the experiments were stored and cleaned in Microsoft Excel. All exploratory data analyses, descriptive statistics and statistical analyses were performed in RStudio (version 3.6.1). Generalized linear mixed effects models (GLMMs) were used to analyze two of the three sociosexual behaviors collected: scent marking substrate and scent marking their partner. Due to the small amount of urine washing behaviors observed (N=36), we did not model this sociosexual response in order to avoid inaccuracy in the parameter estimates (Garamzsegui, 2016).

Since we predicted different patterns of responses in males and females depending on the type of stimulus presented, we built our full model to include the fixed effects of speaker location within the pair's home range (border vs. center) and the interaction of sex (male vs. female) with the type of stimulus presented (control vs. graff vs. tonal). The remaining models were subsets of the full model. We accounted for dependence among observations from the same group and subject by including a random effect for individual identity nested within group identity (Table 3.5). Since we only observed a monkey scent mark their partner once during the control trials, the models would fail to estimate any parameter including this level. Therefore, we dropped the control level from the categorical variable 'Type of call' when modeling this sociosexual behavior leaving only graff and tonal call trials. Scent marking substrate behaviors were modelled considering all levels of the stimulus presented (control, graff, and tonal), since these behaviors are usually more frequently observed in natural conditions (Corley, Spence-Aizenberg, & Fernandez-Duque, 2020).

Given the nature of the response variables (counts) and the high amount of zero values present in the dataset, we used GLMMs with negative binomial error distributions accounting for the non-normal distribution and overdispersion of the data. We first performed visual and AIC diagnostics of this theoretical distribution and we built our models using the function glmer.nb (MASS Package) instead of glmer (Bates et al., 2015; ver Hoef & Boveng, 2007).

Table 3.5. Candidate model set proposed for scent marking behaviors (substrate and partner).

Candidate Model	**Fixed and random effects**
Model 1	Type call * Sex + Place + (1|Group/Individual ID)
Model 2	Type call + Sex + Place + (1|Group/Individual ID)
Model 3	Type call * Sex + (1|Group/Individual ID)
Model 4	Type call + Sex + (1|Group/Individual ID)
Model 5	Type call + Place + (1|Group/Individual ID)
Model 6	Place + Sex + (1|Group/Individual ID)
Model 7	Type call + (1|Group/Individual ID)
Model 8	Place + (1|Group/Individual ID)
Model 9 (Null)	(1|Group/Sujeto)

For model selection we calculated corrected Akaike information criterion (AICc) and utilized delta AICc and cumulative Akaike weights (AICc weights) to assess the plausibility of each of our nine candidate models (Burnham & Anderson, 2004). Here we report results of the models within ≤ 2 Delta AICc, as suggested by Burnham & Anderson (2002). Model fits were evaluated using residual plots.

Ethical note

We have captured individuals regularly since 2000 using an $C0_2$ powered rifle and disposable darts loaded with 0.5 ml of ketamine hydrochloride. Since then, we have evaluated the potential effects of capture on animal welfare and on population structure (Fernandez-Duque et al., 2017; Juárez et al., 2011). We fit all individuals with a radio, or bead, collar (Fernandez-Duque & Rotundo, 2003; Fernandez Duque et al., 2017; Juárez et al., 2011), depending on the age of the individual and our interest in being able to locate it reliably. The radio collar consists of a transmitter package mounted on a ball-chain collar with a 15-cm whip antenna.

All procedures conformed to Argentinean laws and were approved at different times by the National Wildlife Directorate in Argentina and by the animal research committees of the Zoological Society of San Diego (2000-2005), the University of Pennsylvania (2006-2011) and Yale University (2012-2020). All animal procedures followed the guidelines for the treatment of animals for teaching and research recommended by the Animal Behaviour Society (2014).

Results

First reaction to stimulus

All adults, but no immatures, reacted during the experiment and only when presented with conspecific vocalizations. During the control stimulus trials (N=12, 6 groups) an adult male looked in the direction of the speaker when the playback stimulus started once, then he immediately continued foraging and no other reaction was observed.

Individuals reacted in all but one of the graff hoot trials (11/12). Of these, the adult male was the first individual to react in most cases (8/11), although on two occasions both pair members reacted at the same time, and once, the adult female reacted first. Twice, adult males looked in the direction of the speaker; one of those times the adult male looked at the speaker and then immediately started urinating. Three times the adult male approached his partner; and twice the adult male approached, and scent marked its partner. On the two occasions when both adults reacted to the graff hoot stimulus, the pair was resting in contact at the start of the trial and both looked in the direction of the speaker. The one time the adult female reacted first she approached her partner and scent marked him.

Individuals reacted in all but two of the tonal hoot trials (10/12). The groups that did not respond to the tonal hoots were different from the ones that did not respond to the graff hoot. In the cases where we observed reactions, it was always the adult female of the pair that reacted first. Twice the adult female looked in the direction of the speaker, on four occasions they approached their partner, and on three occasions the adult female approached, and scent marked their partner. Finally, on one occasion an adult female emitted contact calls after being presented with the tonal hoot stimulus and then her partner approached her and remained in contact. Individuals responded twice as fast to graff hoots than they did to tonal ones (mean± SD: graff= 2.1±5.5min vs tonal= 4.5±8.2min).

Sociosexual behaviors to stimulus

Both sexes scent marked substrate and scent marked their partners more often in response to the graff than to the tonal hoots. Even though urine washing was less frequently observed, both sexes urine washed more in response to the male calls. Although both sexes responded more to the graff hoots than tonals, they did so differently: males scent marked the substrate and their partners more often than females did. Furthermore, males urine washed, scent marked their partners, and scent marked the substrate more often when the speaker was located in the border of their home range than in the center regardless of the experimental stimuli presented. Females appear to show the opposite pattern with higher rates of sociosexual behaviors when the speaker was located in the center, although only when same-sex calls were played back (Table 3.6).

Table 3.6. Number of sociosexual behaviors (Scent Marking Substrate, Scent Marking over Partner, and Urine Wash) performed by males and females according to the type of stimulus presented (Control, Graff and Tonal) and the location of the speaker within their groups´ home range (Center and Border).

	Scent Marking Substrate					
Type of call	Control		Graff		Tonal	
Location	Center	Border	Center	Border	Center	Border
Males	0	5	26	39	5	4
Females	1	5	21	13	22	15
	Scent Marking Partner					
Type of call	Control		Graff		Tonal	
Location	Center	Border	Center	Border	Center	Border
Males	0	1	15	18	2	0
Females	0	0	5	6	8	2
	Urine Wash					
Type of call	Control		Graff		Tonal	
Location	Center	Border	Center	Border	Center	Border
Males	0	1	4	11	0	0
Females	0	0	8	4	6	2

During the replications we performed on groups C0 and D500 in the two consecutive years of this experiment (2019-2020), we observed a similar pattern of responses. Generally, males and females performed more sociosexual behaviors when male vocalizations were played back compared to female vocalizations or the control stimulus; and males scent marked substrate and their partners and urine washed more than females did. Nonetheless, during the second year (2020) the two pairs scent marked the substrate more frequently when the speaker was located in the center of their home ranges (Table 3.7).

Table 3.7. Number of sociosexual behaviors (Scent Marking Substrate, Scent Marking Partner, and Urine Wash) performed by two pairs on which replicates of the experiments were conducted. Behaviors are shown according to the type of stimulus presented (Control, Graff and Tonal) and the location of the speaker within their groups´ home range (Center and Border).

			Scent Marking Substrate			
Type of call	Control		Graff		Tonal	
Location	Center	Border	Center	Border	Center	Border
Males	0	0	21	8	0	1
Females	0	0	19	8	1	7
			Scent Marking Partner			
Type of call	Control		Graff		Tonal	
Location	Center	Border	Center	Border	Center	Border
Males	0	0	11	6	0	0
Females	0	0	3	4	6	6
			Urine Wash			
Type of call	Control		Graff		Tonal	
Location	Center	Border	Center	Border	Center	Border
Males	0	0	3	3	0	3
Females	0	0	2	1	1	1

Model selection indicated that for scent marking substrate, the top models (based on the arbitrary criteria of ≤ 2 Delta AICc from Burnham and Anderson, 2002) were models 3 and 1. Both models included the interaction between 'Type of call' and 'Sex', thus, it seemed that this was an important term. Moreover, the cumulative weight was quite high in the first model (model 3=0.68 cumulative weight, model 1=0.94).

In the case of scent marking partner, two of the three best models also included the interaction between 'Type of call' and 'Sex', although for this variable, model selection included also model 7 with only 'Type of call' as an explanatory variable. Thus, model selection points in the same direction for both variables: that two important terms in explaining the variation of these behaviors are the type of vocalization played back and the sex of the response (center vs. border) (Table 3.8-3.9).

Table 3.8. Models of Scent Marking Substrate, ranked according to their AICc values.

	K	**AICc**	**Delta AICc**	**AICc Wt**	**Cum.Wt**	**LL**
Model 3	9	456.98	0.00	0.68	0.68	-219.05
Model 1	10	458.91	1.94	0.26	0.94	-218.92
Model 7	6	463.28	6.30	0.03	0.97	-225.44
Model 4	7	464.98	8.00	0.01	0.98	-225.22
Model 5	7	465.02	8.05	0.01	0.99	-225.24
Model 2	8	466.66	9.68	0.01	1.00	-224.98
Model 9	4	493.11	36.14	0.00	1.00	-242.46
Model 8	5	495.14	38.16	0.00	1.00	-242.43
Model 6	6	497.25	40.27	0.00	1.00	-242.42

AICc rather than AIC was utilized to select the best approximating models due to our small sample size (Bumham & Anderson, 2002). K=number of estimated parameters; AICc Wt= AICc weigh; Cum. Wt= cumulative weight; LL=log-likelihood. AICc weights, also termed model probabilities (Anderson, 2008; Burnham and Anderson, 2002), indicate the level of support (i.e., weight of evidence) in favor of any given model within the candidate model set (Mazerolle, 2016). Models with delta AICc ≤ 2, which accounted for high of the cumulative Akaike weight, are shaded in gray.

Table 3.9. Models of Scent Marking Partner, ranked according to their AICc values.

	K	AICc	Delta AICc	AICc Wt	Cum.Wt	LL
Model 3	7	200.70	0.00	0.34	0.34	-92.94
Model 7	5	201.55	0.85	0.22	0.56	-95.56
Model 1	8	202.31	1.61	0.15	0.71	-92.62
Model 5	6	203.08	2.38	0.10	0.81	-95.23
Model 4	6	203.72	3.02	0.07	0.88	-95.55
Model 9	4	204.36	3.66	0.05	0.94	-98.04
Model 2	7	205.27	4.57	0.03	0.97	-95.22
Model 8	5	206.44	5.74	0.02	0.99	-98.00
Model 6	6	207.77	7.07	0.01	1.00	-97.58

AICc rather than AIC was utilized to select the best approximating models due to our small sample size (Burnham & Anderson, 2002). K=number of estimated parameters; AICc Wt= AICc weigh; Cum. Wt= cumulative weight; LL=log-likelihood. AICc weights, also termed model probabilities (Anderson, 2008; Burnham and Anderson, 2002), indicate the level of support (i.e., weight of evidence) in favor of any given model within the candidate model set (Mazerolle, 2016). Models with delta AICc ≤ 2, which accounted for relatively high of the cumulative Akaike weight, are shaded in gray.

Since model selection of both types of scent marking included the full model as one of the best candidate models, we provide the interpretation of this model in order to show the estimate values of all parameters of interest (Table 3.10-3.11; Figures 3.2-3.3). However, it should be noted that the full model was not the best model in either case; the best model in both cases only included the interaction of ‘Type of call’ and ‘Sex’ and the reported effect of ‘Place’ is small relative to the effect of the other important variables.

Regardless of the type of stimulus presented (control, graff, or tonal), males would scent mark substrate 1.3 times more if the speaker was located in the border of their home range than if it was in the center. Males would mark the substrate 1.9 times more than females when graff hoots were played back, while females would scent mark the substrate 4.2 times more than males when tonal calls were presented (Figure 3.3). In the case of scent marking partners, during graff and tonal trials both sexes would scent mark their partners 1.6 times more if the speaker was in the center, compared to if it was in the border of their home ranges. When tonals were played back, females would mark their partners 5 times more than males; and when graffs were played back, males would mark their partners 3 times more than females (Figure 3.4)

Table 3.10. Summary of Model 1 for scent marking substrate (Sex* Type call+ Place+ (1|group/individual id)) full results. Reference levels: 'Type of call' = Control, 'Sex' = Female, 'Place' = Border.

Random Effects	**Variance**	**Standard deviation**		
ID:Group (Intercept)	0	0		
Group (Intercept)	0	0		
Fixed Effects	**Estimate**	**Std. Error**	**z-value**	**Pr(>|z|)**
Intercept	-1.74	0.47	-3.72	0
Type call Graff	1.75	0.53	3.3	0
Type call Tonal	1.83	0.53	3.5	0
Sex Male	-0.18	0.67	-0.28	0.8
Place Central	-0.13	0.25	-0.51	0.6
Graff: Male	0.81	0.76	1.1	0.3
Tonal: Male	-1.24	0.81	-1.52	0.1

Std. Error= standard error for the estimate of the fixed effect; z-value= the test statistic; Pr(>|z|)= The probability that a particular z test statistic is as extreme as, or more so, than what has been observed under the null hypothesis. The null hypothesis states that an individual predictor's regression coefficient (Sex, Type of call and Place) is zero, given that the rest of the predictors are in the model.

Table 3.11. Summary of Model 1 for scent marking partner (Sex* Type call+ Place+ (1|group/individual id)) full results. Reference levels: 'Type of call' = Graff, 'Sex' = Female, 'Place' = Border.

Random Effects	**Variance**	**Standard deviation**		
ID:Group (Intercept)	0	0		
Group (Intercept)	0	0		
Fixed Effects	**Estimate**	**Std. Error**	**z-value**	**Pr(>|z|)**
Intercept	-1.39	0.6	-2.42	0.01
Type call Tonal	-0.2	0.7	-0.27	0.8
Sex Male	1.1	0.7	1.61	0.1
Place Central	0.44	0.6	0.79	0.4
Tonal: Male	-2.7	1.2	-2.26	0.03

Std. Error= standard error for the estimate of the fixed effect; z-value= the test statistic; Pr(>|z|)= The probability that a particular z test statistic is as extreme as, or more so, than what has been observed under the null hypothesis. The null hypothesis states that an individual predictor's regression coefficient (Sex, Type of call and Place) is zero, given that the rest of the predictors are in the model.

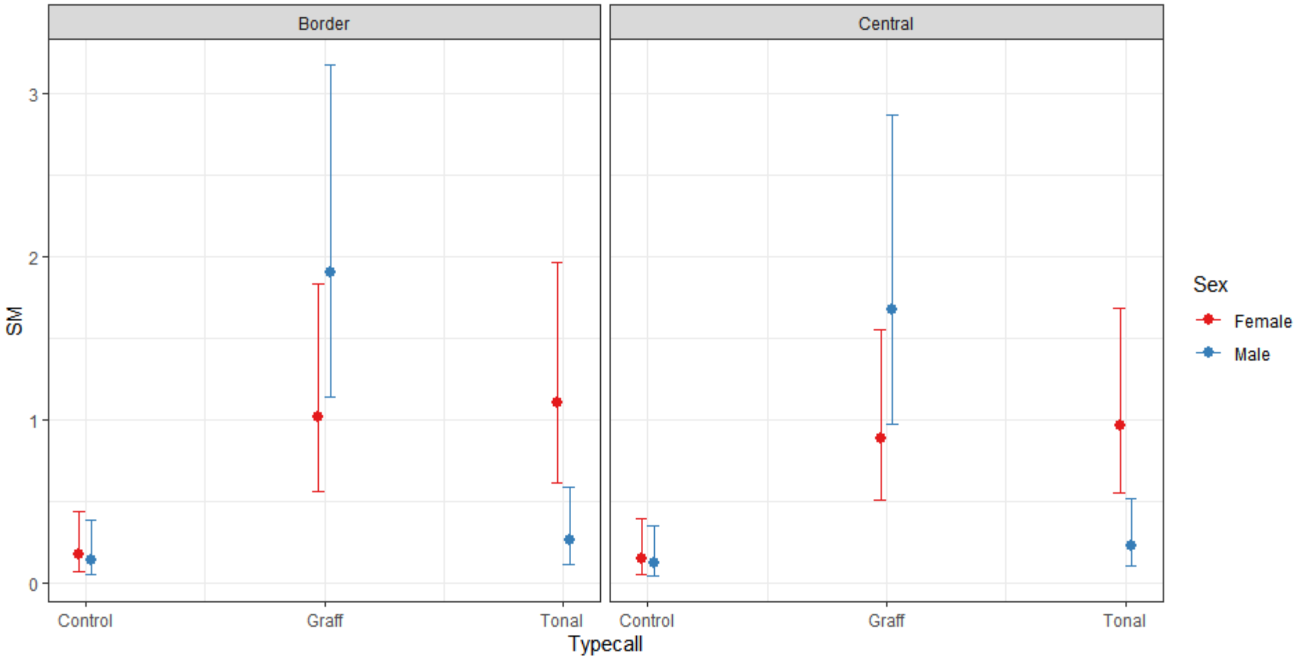

Figure 3.3. Predicted counts for Scent Marking Substrate (SM) behaviors for males and females depending on the type of estimulus presented (Control, Graff and Tonal) and the location of the speaker (Center and Border).

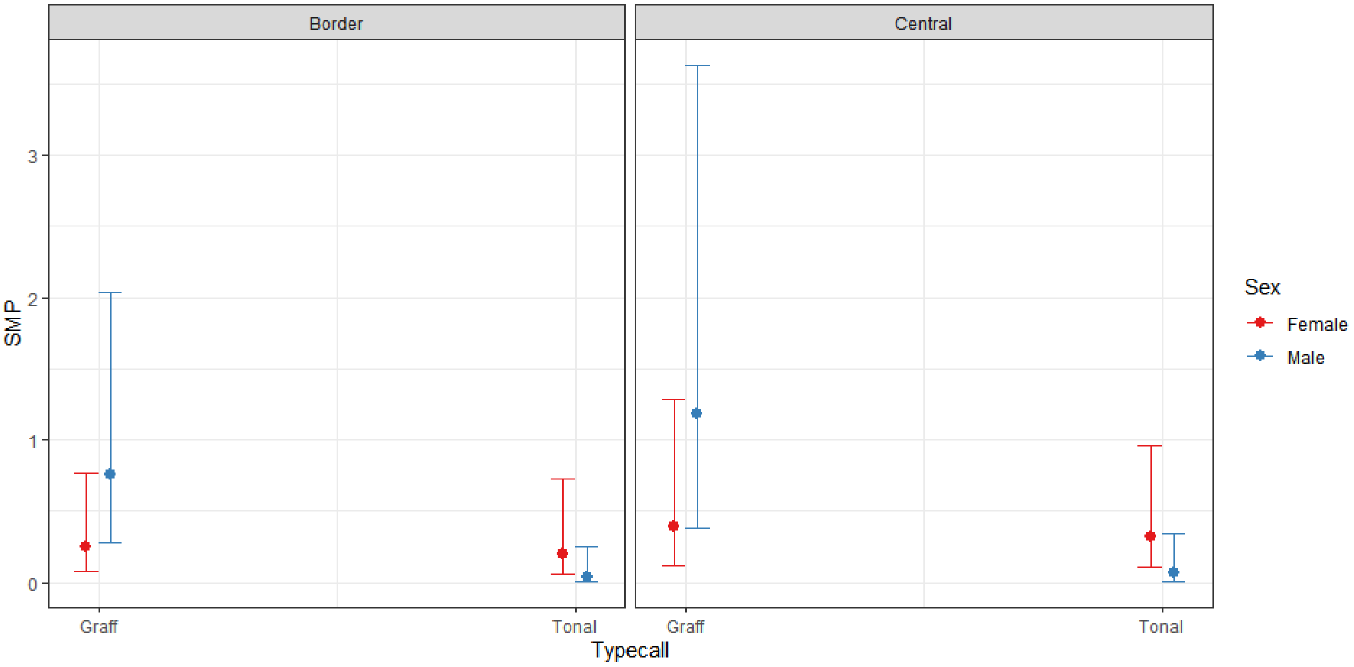

Figure 3.4. Predicted counts for Scent Marking Partner (SMP) behaviors for males and females depending on the type of estimulus presented (Control, Graff and Tonal) and the location of the speaker (Center and Border).

Movement towards the speaker

The monkeys moved closer to the speaker after graff hoots than after tonal hoots or the control stimuli (Table 3.12, Figure 3.5). Yet, only in six trials were these movements towards the location of the speakers clearly perceived by the observers: three occasions when the speaker was at the center (D500, D1200 and Cola Corta), and three occasions when it was at the border of the home ranges (D500, D1200 and C0). All six times this happened following the playback of graff hoots and the adult male led the movement. Movement towards the speaker observed during the presentation of the control stimulus may be due to foraging events, since in 67% of those trials, the monkeys were eating at the beginning of the session.

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Table 3.12. Mean and SD of Distance (meters) between focal groups and the speaker location before (pre) and after (post) the reproduction of the call stimulus (Graff, Tonal, and Control).

Distance	**Type of call**					
	Control		Graff		Tonal	
	Pre	Post	Pre	Post	Pre	Post
Mean	88	84	126	79	139	137
SD	37	36	48	57	34	28

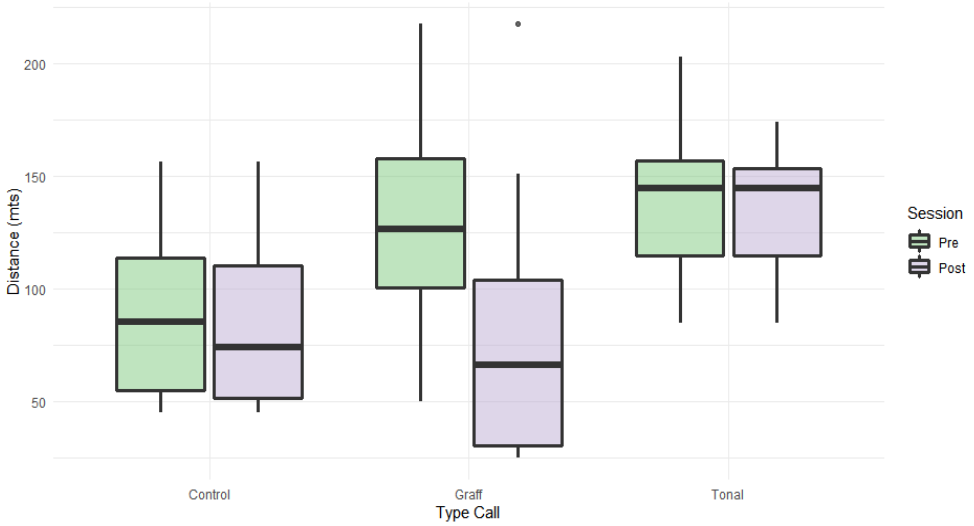


Figure 3.5. Distance (meters) of monkey groups to the speaker location per type call stimulus (Control, Graff and Tonal) and playback session (Pre and Post). The box plots represent the median, first, and third quartiles with the lower whiskers including values ≥first Q−1.5 × IQR (interquartile range) and upper whiskers including values ≤third Q+1.5 × IQR.).

Ad-lib data

Aside from our playback stimuli, no graff hoots were heard during the experiment. However, tonal calls were heard five times (on three different trials: 2 graff trials and 1 tonal trial), all emitted by solitary unidentified individuals. Adults of focal groups emitted "resonant grunts" (Moynihan, 1964) twice during encounters with extra-group individuals. The first of these involved a solitary floater that appeared soon after the start of the "during" session of a graff hoot stimulus trial, emitting tonal hoots approximately 25 m away from the group. At the beginning, the breeding pair did not show any conspicuous response towards the solitary floater, aside from the adult female approaching the male and scent marking him. After five minutes, the adult female started chasing the solitary floater while vocalizing resonant grunts. The adult male and juveniles remained quiet and still, looking in the direction of the chase. After the solitary floater moved away, the adult female returned, approached the male, and stayed in contact with him. Nevertheless, the adult female kept looking in the direction the solitary floater had moved, which also was the direction of the speaker, for approximately 10 more minutes. Then, both pair mates quickly moved together in the same direction the solitary floater had disappeared. During this same trial, the observer handling the speaker noticed another solitary less than 10 meters from it soon after the start of the "during" session of the trial. The solitary urinated on several occasions, but we did not witness any type of interaction between this solitary floater and the pair since the first one arrived at the speaker and left the area before the pair arrived.

An inter-group encounter occurred between the focal group and one of its neighboring groups when the speaker was located at the border of both group home ranges. The encounter took place near the speaker's location at the onset of the "post" session when the playback of the graff hoot stimulus was completed. When both groups saw each other, the adult male of the focal group jumped towards the adult male of the other group and they started chasing each other around the area while emitting resonant grunts. Both adult females remained distant while looking in the direction of their partners. The juveniles from the focal group ran away from the chase towards their home range center. We did not observe the adult males touching or grabbing each other during the fight. After four minutes of chasing and vocal displays, each group went in the direction of their home ranges centers. Before the groups went their separate ways, we observed the adult male from the neighboring group scent mark his partner several times.

Discussion

Through a field playback experiment, we evaluated the role of reproductive competition between resident adults and floaters in wild pair-living, sexually monogamous Azara's owl monkeys. The hypotheses of Resource Defense and Mate Guarding have been systematically proposed when explaining pair-living and sexual monogamy in a wide range of taxa, including primates (Fernandez-Duque, Huck, Van Belle, & Di Fiore, 2020); however, the extent to which members of wild owl monkeys' pairs primarily defend their territory or their mates, remained unknown.

This being the first semi-experimental study of any owl monkey species, it was important to observe that owl monkeys reacted differently to unfamiliar conspecific than control calls. Specifically, all pairs first reacted by looking in the direction of the speaker, approaching or scent-marking their partner during graffs and tonals, but they never did so during the control stimulus trials. The finding is reassuring of our attempts at developing a methodology that will surely offer additional opportunities to further explore the behavioral mechanisms regulating pair-living taking advantage of our research system. Further, monkeys' first reactions appear to be sex-specific, which evidences prior results in our population, that hoot calls encode information about the caller, and that listeners are able to recognize it (Garcia de la Chica, et al.,2020).

It was unexpected that both sexes showed higher rates of all types of sociosexual behaviors in response to graff than tonal hoots. This was especially pronounced for scent marking behaviors (both substrate and partner) which strongly differed for the two types of played back calls. This result does not support the first prediction derived from the Resource Defense Hypothesis since in our experiment the sex of the caller clearly elicited different responses from our study subject. On the other hand, the differences found only partial support the first prediction derived from the Mate Guarding Hypothesis. Even when owl monkey males almost only reacted to same-sex individuals, females also reacted more strongly to unfamiliar male calls than to unfamiliar female calls. Further, groups moved closer to the speaker in response to graff than tonal calls, and in most of these trials, the adult male lead the movement. Our results show that contrary to the prediction from the Resource Defense Hypothesis owl monkeys did not scent mark on substrate and urine washed more often when the speaker was located in the center of their home range. Instead, these sociosexual behaviors were more often conducted when the speaker was in the border. Less clear was the difference found in the case of scent marking partner which was performed more often when the speaker was located in the center of their home ranges, particularly by females.

Our results showed that overall, the sex of the caller elicited higher differences than the speaker location in owl monkey responses. Pairs reacted stronger to graff than tonal hoots, as evidenced by their higher rates of sociosexual and vocal responses, movement towards the speaker, and intergroup encounters. Additionally, males reacted more than females, which follows the classical conception of pair-living sexually monogamous taxa where males guard their partners more often than females do (Brotherton & Komers, 2003; Roberts & Dunbar, 2000). It is worth noting, that the data collected during replications in two groups on the two consecutive years showed consistency in the behavioral patterns that owl monkeys displayed during the experiments. The only apparent difference was a higher number of scent marking behaviors (especially over substrate) observed in the center of the two home ranges during the second year (2020) compared to the first (2019).

The fact that scent markings were the sociosexual behaviors that increased the most is not surprising since scent marking have been shown to function as a form of mate-guarding (Heymann, 2006). Scent marking can be an active form of mate guarding particularly if individuals overmark their partners' scents (Ferkin & Pierce, 2007) as observed in klipspringers (*Oreotragus oreotragus:* Roberts & Dunbar, 2000), round-eared sengis (*Macroscelides proboscideus:* Schubert, Schradin, Rödel, Pillay, & Ribble, 2009) and saddleback tamarins (*Saguinus fuscicollis*: Lledo-Ferrer, Peláez, & Heymann, 2010). Overmarking, sniffing or licking, and other olfactory behaviors are extremely difficult to observe in relatively small arboreal mammals such as primates (Heymann, 2006). Our understanding of olfactory behavior in owl monkeys, as well as our consideration of the findings presented here, benefit from consideration of research done in captive owl monkeys. In our study, owl monkeys scent marked the substrate but also their partners, as previously observed in captive *Aotus nancymaae* when an unfamiliar male conspecific was present (Wolovich, Evans, & Green, 2010). Given that the chemical composition of owl monkeys' scent glands convey information about sex and age (Macdonald, Fernandez-Duque, Evans, & Hagey, 2008; Spence-Aizenberg, Kimball, Williams, & Fernandez-Duque, 2018), individuals likely mark their mates and deposit their scents on them as a mate-guarding strategy (Wolovich & Evans, 2007).

It is worth noting that owl monkey females also showed an increase in the frequency of behaviors associated with mate guarding of their mates. This occurred when we simulated the presence of an unfamiliar same-sex individual, but also during the simulated presence of other males. Given that owl monkey females may as well face high levels of intrasexual competition in our population (Fernandez-Duque & Huck, 2013; Huck & Fernandez-Duque, 2012) , it is not unexpected that they may be also guarding their mates; but why females should guard their partners from other males, may be rather associated with their need of parental care in order to successfully rear their offspring. In other taxa that exhibit paternal care it has been suggested that females may also benefit from guarding their mates, especially if by doing so, paternal duties are facilitated (European starling, *Sturnus vulgaris:* Eens & Pinxten, 1995; Green dart-poison frog, *Dendrobates auratus*: Summers, 1990). Indeed, this is likely to be important in taxa where males' replacements are associated with a reduction in pairs' reproductive success (owl monkeys: Fernandez-Duque & Huck, 2013) or a reduction of offspring survival, as has been suggested for gibbons (*Hylobates lar*: Morino & Borries, 2017) and for owl monkeys based on preliminary analyses (Garcia de la Chica, Borries, & Fernandez-Duque, 2020).

It follows that this reproductive competition and variance in reproductive success may be influenced by the Operational and Adult Sex Ratio of the population (OSR and ASR), or the relative number of floaters-to-established pairs present in the population (Huck, Di Fiore, & Fernandez-Duque, 2020). In fact, several studies have shown the association between male biased OSR-ASR and male mate guarding behaviors on different taxa (Harts & Kokko, 2013; Kokko & Morrell, 2005; Weir, Grant, & Hutchings, 2011).

Nevertheless, a large proportion of theoretical studies have primarily focused on the male perspective when evaluating reproductive competition and its association with the evolution and maintenance of pair-living sexually monogamous social systems (Huck, Di Fiore & Fernandez-Duque, 2020). While male's fitness has been often linked with the number of females or matings, female's fitness has been primarily associated to the food resources needed to sustain pregnancy and early infant development (Clutton-Brock, 2007; Clutton-Brock & Huchard, 2013; Trivers, 1972). Here we suggest paternal care as an important factor for female's fitness in owl monkeys, and emphasize, as other authors before (Clutton-Brock, 2017; Fromhage & Jennions, 2016), the need to explore the coevolution of reproductive competition, mating strategies and parental care, in the two sexes.

CHAPTER 4

PATERNAL CARE

LOSS OF THE FATHER, BUT NOT THE MOTHER, LOWERS INFANT SURVIVAL IN PAIR-LIVING SEXUALLY MONOGAMOUS OWL MONKEYS (*AOTUS AZARAE*)

Chapter 4. Loss of the father, but not the mother, lowers infant survival in pair-living sexually monogamous owl monkeys (*Aotus azarae*)

Abstract

Infanticide has never been observed in pair-living primates. Still, the potential risk of it can be examined indirectly via infant survival after parental replacement. Here we evaluated the relationship between the replacement of a biological parent and the age of death/disappearance of young individuals. The main question of our analysis asks whether the presence of a new male increases the probability for young owl monkeys of dying at younger ages. We evaluated the relationship between parental loss and the age at disappearance of 149 identified infants in wild pair-living sexually monogamous owl monkeys (*Aotus azarae*) from Formosa, Argentina between 1999-2018. Our results strongly suggest that the presence of a new unrelated male is associated with lower infant survival in wild owl monkeys. And this association seems to be more important if the replacement occurs during the first year of life of individuals, when those are still dependent on direct parental care. The replacement of mothers did not lead to a substantially younger age at disappearance, perhaps because all female replacements occurred after weaning. In the absence of observed aggression towards infants by incoming adults, our findings suggest that higher mortality risk after loss of the father in owl monkeys may be associated with a reduction in the quantity and/or quality of care provided by the new male.

Introduction

Among the main hypotheses classically proposed for explaining the evolution of pair-living and sexually monogamous systems, infanticide is the one that has generated more debate in the literature (Dixson, 2013; Lukas & Clutton-Brock, 2014; Lukas & Huchard, 2014; Opie, Atkinson, Dunbar, & Shultz, 2013; van Schaik & Janson, 2000). Likely, but by no means solely, because following the fallacy of affirming the consequent, some researchers have interpreted the absence of infanticide in pair-living sexually monogamous taxa as evidence of having evolved successful counterstrategies and, alternatively, as evidence that infanticide did not play a role in such social organization and mating system (Fernandez-Duque, Huck, Van Belle, & Di Fiore, 2020). In other words, because of conclusions based on a logical fallacy among other reasons, it is still unclear if infanticide has been a particularly effective male strategy in the past, or if it is just not directly associated with the evolution/maintenance of pair-living and sexual monogamy.

Also highly debated has been the idea that infanticide might be adaptive and act as a male reproductive strategy in primates (Bartlett, Sussman, & Cheverud, 1993; Dixson, 2012; Sussman, Cheverud, & Bartlett, 1995). With regards to pair-living taxa, it was later hypothesized that the presence of a male would deter other males from attacking and killing vulnerable infants. Hence, infant survival would be higher if a male helps a female to protect offspring from infanticidal intruders (Palombit, 2000; van Schaik & Dunbar, 1990; van Schaik & Kappeler, 1997; Wolff & Macdonald, 2004). The hypothesis is based on the assumption that the protective male most likely is the father of the infants, such that both, the mother, and the father, have an increased net fitness because of his presence. It follows that infant defense can act as a form of paternal care. In fact, the female´s need of male care in order to successfully rear their offspring has been also previously considered as a driver in the evolution of pair-living social organizations and sexual monogamy mating systems (Fernandez-Duque et al., 2020); nonetheless both sexually selected strategies follow different lines of arguments, and of course, have profound different adaptative consequences. According to the sexual selection hypotheses proposed by Hrdy (1979) for infanticide to be adaptative the infant killed should not be related to the infanticidal male, the male should have a high probability of siring the mother's subsequent offspring, and the killing of an infant should shorten the subsequent interbirth interval of the mother.

It should be noticed that in most primate species the killing of an infant is extremely infrequent to witness. Hence, the consideration of only direct observations likely underestimates the rate of infanticide, especially in small, arboreal, nocturnal or conspicuous species. On these cases, the threat of infanticide by males can be inferred if, for example, infants disappear at a substantially higher rate following male immigration than in its absence, or if predicted countertactics by females or infants can be documented. The killing of infants has been frequently reported to be committed by new males that relatively recently had immigrated into a group (Borries, Savini, & Koenig, 2011; Dixson, 2012; Zhao, Borries, & Pan, 2011). Because of these males joined the group after the infants were conceived or born, it seems reasonable that they were not targeting their own offspring. In further support, males of Hanuman langurs (*Presbytis entellus*) only attacked or killed not related infants after joining a new group and infanticidal males were most likely the fathers of the subsequent infants (Borries, Launhardt, Epplen, Epplen, & Winkler, 1999). Lastly, some studies have also shown that after losing an infant by an infanticidal male, females resumed their cycling sooner (Hanuman langurs: Borries, 1997; Sommer, 1994; Siamangs: Chivers & Raemaekers, 1980; Blue monkeys: Cords & Fuller, 2010; Lar gibbons: Reichard, Ganpanakngan, & Barelli, 2012; Snub-nosed monkeys: Yao et al., 2016; Zhao, Li, Groves, & Watanabe, 2008). Even when there is evidence suggesting that in some cases females may shorten the interbirth interval, using a shorter interbirth interval as a measure of the risk of infanticide is problematic (Dixson, 2013; Fernandez-Duque et al., 2020).

Furthermore, males of annual breeding species who have an infant per year, where the interbirth interval cannot be shortened, have been previously suggested to not benefit from infanticide, although cases of larger litters or improved infant survival after infanticide have been recorded in some seasonal breeding taxa (Borries, 1997; Enstam, Isbell, & Maar, 2002; Hood, 1994; Pereira & Weiss, 1991). This suggest that by killing an infant, males could still improve their reproductive output, even if there is no strong association with the interbirth interval as is the case in annual breeding taxa.

Killing a competitor's offspring is one of the most extreme forms of intrasexual competition. Infanticide has been documented in taxa with completely different social organizations and mating systems (*Ursus arctos*: Bellemain et al., 2006; *Hirundo rustica*: Crook & Shields, 1985; Dunn, Barco, Pabst, & McLellan, 2002; *Tursiops truncatus*: Patterson et al., 1998; *Equus burchelli*: Pluháček, Bartoš, & Víchová, 2006; *Nicrophorus orbicollis*: Trumbo, 2006). In primates, infanticide has been reported only for ~6% of all species, yet the focus has been primarily in colobines such as the Hanuman langur, red howlers, and gibbons (Dixson, 2012; Ma, Brockelman, Light, Bartlett, & Fan, 2019).

Infanticide by males has not been observed in any primate genus with biparental care. Still, what is important to consider is that in taxa where care by the male is required, infants could still die from neglect or insufficient care (Digby, 1995). In species with frequent breeding position takeovers and in the absence of aggression towards infants by incoming adults, a higher mortality risk after the loss of a biological parent could be associated with a reduction in care provided by the new individual. We propose that on these species there would be no need for a strategy of violent attacks to evolve, since the simple fact of not providing the usual paternal care may be enough for the infant to die. The association of paternal care with infant survival has been largely studied in pair living sexually monogamous birds and mammals (*Cheirogaleus* *medius*: Fietz & Dausmann, 2003; *Peromyscus californicus*: Gubernick & Teferi, 2000; *Phodopus campbelli*: Wynne-edwards, 1998).

The pair-living and sexually monogamous Azara´s owl monkeys from northern Argentina present an adequate model to assess the possible association of male replacement and infant loss in a species with extensive biparental care and seasonal breeding. Genetic, behavioral, and demographic data collected in our population has shown that the social organization of Azara's owl monkeys does indeed include pair-living individuals and a few non-adults. But, there are in the population also a substantial number of potentially reproductive individuals (25-30%) that do not belong to a group, but instead range solitarily in the periphery of established groups for a variable amount of time (Fernandez-Duque & Huck, 2013; Huck & Fernandez-Duque, 2017). These solitary "floater" individuals are either young adults that have recently emigrated (dispersed) from their natal groups or relatively old adults that have been evicted from their groups by incoming precisely the floaters (Fernandez-Duque & Huck, 2013). Floaters range solitary for a variable amount of time among the home ranges of pair-living adults while trying to gain a breeding position, or taking advantage of vacancies in resident positions that arise through natural deaths (Fernandez-Duque & Huck, 2013; Huck & Fernandez-Duque, 2017).

These reproductive position takeovers have profound consequences for reproductive individuals. In Azara's owl monkeys the replacements of resident adults by incoming floaters occur at similar rates for males and females (27 female and 23 male replacements, in 149 group-years). These replacements led to a 25% decrease in the reproductive success of the pair mates, and for expelled individuals it may represent the end of their reproductive life since only twice have we seen expelled adults join a new group (2/50: Fernandez-Duque & Huck, 2013). Hence, in our population, it is sometimes the case that the young in the group are not always the biological offspring of both adults.

It must be noted that despite the replacement of breeding adults, in our wild population we have never observed the killing, not even a direct attack, of an infant by a new male or female. However, data suggest that there are also direct consequences for young individuals when a biological parent is replaced. First, the dispersal of subadults owl monkeys appears to be associated with changes in group composition, such as the eviction of the resident adult male or adult female; thus, after the replacement of resident adults, owl monkeys disperse at younger ages, on average, than those in stable groups (Corley, Xia, & Fernandez-Duque, 2017). However, the consequences for younger offspring (infants and juveniles) are less clear. Owl monkeys show an extensive form of biparental care where males are the main caretaker once the infant does not longer depend on lactation (Dixson & Fleming, 1981; Huck & Fernandez-Duque, 2013; Rotundo, Fernandez-Duque, & Dixson, 2005). In only one case, a former floater male that had replaced the resident adult, socially interacted with an infant, although the last disappeared at 6 months of age (Fernandez-Duque, Juárez, & Di Fiore, 2008). Of course, given its young age, and the fact that the youngest successful dispersal ever recorded in our population was at 26 months old (Fernandez-Duque, 2009; Huck & Fernandez-Duque, 2012), the survival of this infant is extremely unlikely.

Here we evaluated the relationship between the replacement of a biological parent and the age of death/disappearance of young individuals. In doing so, we further described if new breeding adults increased their probability of siring offspring during the next season after the loss of the infants present in group. As such, the main question of our analysis asks whether the presence of a new male increases the probability for young owl monkeys of dying at younger ages.

Methods

Study area and population

The study area, located in the gallery forests along the Pilagá River in the Argentinean Gran Chaco, is part of the 1,500 ha Reserva Mirikiná established in 2006 (58°13' W, 26° 54'S). The area includes a mosaic of grasslands, savannas, xeric thorn forests and semideciduous forests (van der Heide, Fernandez-Duque, Iriart, & Juárez, 2012). The climate is subtropical with no marked wet season (mean annual precipitation 1,418 mm), and extreme low and high temperatures are frequent (daily minimum temperatures <10°C between April and September and maximum daily temperatures >33°C between September and March; Fernandez-Duque, 2016). Unlike the strictly nocturnal tropical species of owl monkeys, *Aotus azarae* is unique among the genus because of its cathemeral habits. The Azara's owl monkeys show activity both during the day and night (Fernandez-Duque, de la Iglesia, & Erkert, 2010), which allows for detailed demographic and behavioral data to be collected from identified individuals during daytime. A system of intersecting transects at 100m intervals covers approximately 300ha of forest where the data were collected (Fernandez-Duque, 2016) and the relatively small home ranges (mean ± SD: 6.2 ha ± 1.8; Wartmann, Juárez, & Fernandez-Duque, 2014) make it possible to monitor regularly many groups (Fernandez-Duque, 2016). Here we present demographic data from 22 different groups collected between 1995-2018.

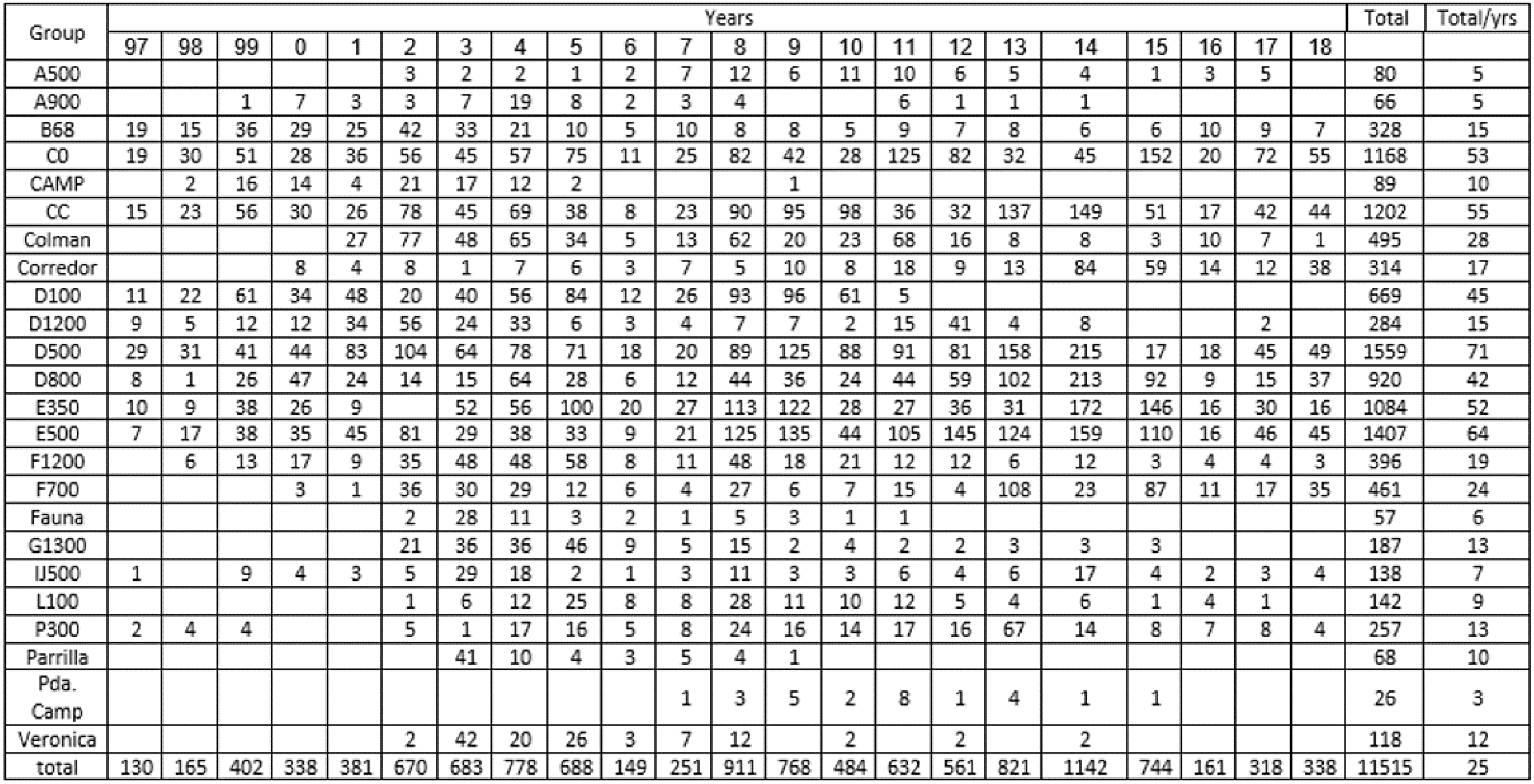
Data collection

Since 2000, we have conducted 285 captures with physical exams of owl monkeys. In the process, we caught 179 different individuals, whom we physically examined, sampled for biological specimens and fitted with a bead or radio collar (Fernandez-Duque & Rotundo, 2003; Fernandez-Duque, Chapman, Glander, & Fernandez-Duque, 2017). Given the lack of visible sexual dimorphism (Fernandez-Duque, 2011) these procedures have made it possible to reliably identify adult individuals in the field. For non-reproductive individuals we followed Huck, Rotundo, and Fernandez-Duque (2011) for age classifications of subadults (24.1-48 months), juveniles (6.1-24 months) and infants (0-6 months). Young juveniles and infants are not usually captured, but they can be recognized within the group based on their body size.

For demographic monitoring, every time a group of monkeys, or a solitary individual, is found, observers enter an “Avistaje” (i.e., a sighting) in the Owl Monkey Project (OMP) database, where basic demographic data, geolocation and behaviors noted upon encounter are recorded. The demographic data allowed us to record changes in group composition as we noted the presence/absence of expected group members and registered observations of new infants. On average, we contacted and collected data 25 times per year/group (Table 4.1).

Of the 290 births recorded during the years in the area monitored by the OMP, 24 individuals were still present in their natal group at the moment of the analyses presented here. For 14 additional births we did not have enough information about the fate of individuals due to big gaps between the dates when the groups were monitored; for 65 subjects the age of death/disappearance/dispersal was calculated within a range of more than 100 days; and finally for 38 individuals the identity of both parents was unknown. Thus, we excluded these births from our analyses resulting in a data set of 149 births for which we had information about at least the identity of one of the parents and a calculated age of death/disappearance within less than 100 days accuracy.

Table 4.1. Number of times that each of the 24 owl monkey groups being studied by the Owl Monkey Project of Argentina was contacted on each of the 22 years since the beginning of the project until 2018.



Group	Years																						Total	Total/yrs
	97	98	99	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18		
A500						3	2	2	1	2	7	12	6	11	10	6	5	4	1	3	5		80	5
A900			1	7	3	3	7	19	8	2	3	4			6	1	1	1					66	5
B68	19	15	36	29	25	42	33	21	10	5	10	8	8	5	9	7	8	6	6	10	9	7	328	15
C0	19	30	51	28	36	56	45	57	75	11	25	82	42	28	125	82	32	45	152	20	72	55	1168	53
CAMP		2	16	14	4	21	17	12	2				1										89	10
CC	15	23	56	30	26	78	45	69	38	8	23	90	95	98	36	32	137	149	51	17	42	44	1202	55
Colman					27	77	48	65	34	5	13	62	20	23	68	16	8	8	3	10	7	1	495	28
Corredor				8	4	8	1	7	6	3	7	5	10	8	18	9	13	84	59	14	12	38	314	17
D100	11	22	61	34	48	20	40	56	84	12	26	93	96	61	5								669	45
D1200	9	5	12	12	34	56	24	33	6	3	4	7	7	2	15	41	4	8			2		284	15
D500	29	31	41	44	83	104	64	78	71	18	20	89	125	88	91	81	158	215	17	18	45	49	1559	71
D800	8	1	26	47	24	14	15	64	28	6	12	44	36	24	44	59	102	213	92	9	15	37	920	42
E350	10	9	38	26	9		52	56	100	20	27	113	122	28	27	36	31	172	146	16	30	16	1084	52
E500	7	17	38	35	45	81	29	38	33	9	21	125	135	44	105	145	124	159	110	16	46	45	1407	64
F1200		6	13	17	9	35	48	48	58	8	11	48	18	21	12	12	6	12	3	4	4	3	396	19
F700				3	1	36	30	29	12	6	4	27	6	7	15	4	108	23	87	11	17	35	461	24
Fauna						2	28	11	3	2	1	5	3	1	1								57	6
G1300						21	36	36	46	9	5	15	2	4	2	2	3	3	3				187	13
IJ500	1		9	4	3	5	29	18	2	1	3	11	3	3	6	4	6	17	4	2	3	4	138	7
L100						1	6	12	25	8	8	28	11	10	12	5	4	6	1	4	1		142	9
P300	2	4	4			5	1	17	16	5	8	24	16	14	17	16	67	14	8	7	8	4	257	13
Parrilla							41	10	4	3	5	4	1										68	10
Pda. Camp											1	3	5	2	8	1	4	1	1				26	3
Veronica						2	42	20	26	3	7	12		2		2		2					118	12
total	130	165	402	338	381	670	683	778	688	149	251	911	768	484	632	561	821	1142	744	161	318	338	11515	25

The estimated dates of birth for new infants were calculated through four different processes based on the information available. First, for 8% (12/149) of births the infant was present at the onset of the study, or the group was not seen for more than one year. Given the fact that reproduction in Azara's owl monkeys is highly seasonal with 80% of births occurring during October-November (Fernandez-Duque et al., 2020), for these individuals we arbitrarily standardized the date of birth as October 1st. Second, for 71 births (48%), the date of birth was calculated based on precise qualitative data about the development of infants as described by an experienced observer (M. Rotundo) (mean=51 days, range: 3-261). On 10 occasions (7%), the group was seen on consecutive days without and with an infant respectively, thus the date of birth was precisely estimated to have occurred within a 24-hour period. When no precise qualitative information was available (37%), the date of birth was calculated as the midpoint between the last day the group was seen without an infant and the first day a newborn was observed. The dates of birth in this case were estimated within an average of 12 days (range=2–83, N=56 births).

During contact with the group, we also recorded the identity of all missing group members. For non-reproductive individuals these were classified, post hoc, as either "dispersed" when the individual was relocated outside of the original group's home range either via telemetry or by direct observation, "dead" when the individual's corpse or a still-closed radiocollar transmitting a mortality signal was recovered, or "disappeared" when the individual was never observed again after it went missing from its group. The dates of dispersal, disappearance, or death were estimated as the midpoint between the last time an animal was observed in a group and the first time it was recorded as absent (mean=25 days, range=0–100, N=149 births). Accordingly, we registered every time a reproductive member of a pair was missing and reported it as a replacement. From 149 individuals included in our sample, 31 experienced the replacement of their putative fathers and 26 experienced the replacement of their putative mothers. Again, the dates of replacements were estimated as the midpoint between the last time an identified reproductive adult was observed in a group and the first time it was recorded as absent (Males: mean=35 days, range=1-181; Females: mean= 41 days, range=1-287). We also calculated the age of individuals when a replacement occurred (Individuals that experienced fathers' replacement: mean= 15 months, range= -6-52; Individuals that experienced mothers' replacement: mean= 24 months, range=7-64).

Data management and analyses

All data analyzed were extracted from the Owl Monkey Project (OMP) relational Access database and organized and cleaned in Microsoft Excel. All statistical analyses were performed in R version 3.6.0. (R Core Team, 2019).

We used a linear model to evaluate how well the presence of putative parents or intruders in groups predicted the variation of age at disappeared of infants. In order to do so, we evaluated two explicative variables 1) adults present in group during the first year of life of the infants, 2) adults present in the group after the first year of life of individuals. The reason to consider these variables separated was due to our a priori consideration of the biology of infant and juvenile development in owl monkeys. Since males and females provide direct care to their offspring at least until they are 8 months old, and, as detailed before, we have never observed a monkey disperse before 2.2 years (Corley, 2017; Fernandez-Duque, 2009; Rotundo et al., 2005), we consider the first year of life of individuals as a critical threshold that needs to be separately evaluated.

We labeled the different configurations of adults present in groups in six different ways. When both putative parents were identified, and no replacement occurred during the life of individuals we coded it as "both parents same". When an identified putative father, or an identified putative mother, was replaced, we codified as “male new” and “female new”, respectively. Additionally, for those groups where only one member of the reproductive pair was identified and no replacement occurred, we codified as “same male” and “same female”. For the period after the first year of life some individuals (N=5) experienced the replacement of both putative parents and it was codified as “both new”. In five additional cases we did not have enough information about the fate of adults after the first year, it was codified as “unknown”. On those cases when either of the putative parents had been replaced, we further used a linear regression to evaluate the relationship between the age at disappearance/death and the age of individuals when the replacement of putative parents occurred.

The inclusion of the variable “Natal Group” as a random effect in the statistical models failed to calculate the variance derived from the group of origin due to a variance estimated as/or very close to zero. Thus, we did not include random effects in our models. To estimate the statistical significance of the models, we only compared each model with a null one using the “anova” function (likelihood ratio test) of ‘stats’ package version 3.7.0 in all comparisons.

The statistical significance level was set to 5% in all analyses, and the data are presented as means ± SD. Following decades of recommendations by researchers, some of whom were prominent psychologists, we also report confidence intervals and effect sizes since they are more informative than p-values alone (Cohen, 1988; Nakagawa & Cuthill, 2007; Wasserstein & Lazar, 2016; Ziliak & McCloskey, 2008). We tested the assumptions of normality and homoscedasticity of all the linear models using visual diagnostic plots for the residuals. None of our parameters violated the assumptions of normality or homogeneity of variance of the residuals.

Results

Most infants (79%, N=118/149) survived the first year and 21% died (N=31/149). For those who died before reaching one year of age, 64% (N=20) had not experience any replacement of putative parents; in 16% of cases (N=5) the father had been replaced; and in 6% (N=2) the mother was replaced. For the rest of the dead infants (N=4), only the fathers had been identified while the identity of the mother was unknown. On these cases, fathers had not been replaced and information about any potential replacement of the mother was not available. For infants who survived the first year of life, 58.5% (N=69) had both putative parents in the group, for 22% (N=26) their fathers were present, and for 8.5% (n=10) their mothers were present. In 7% of cases (N=8) infants had experienced the replacement of their fathers, and in 4% (N=5) the replacement of their mothers.

Infants died at a younger age following the replacement of the putative father, especially if the replacement occurred during the first year of life of individuals (Table 4.2, Figures 4.1-4.2). The difference in age at death/disappearance in function of the adults present in group reached statistical significance for the first year or life of individuals (d.f= 4, F-test= 4.41, p=0.002) but not after (>1st year of life: d.f= 6, F-test=1.34, p=0.25). Overall, the age of death/disappearance was similar for male and female young individuals (sexed infants=63/149, 31 females and 32 males: age of death/ disappearance females= 3.2 ± 0.8 years, age of death/ disappearance males=2.9 ± 0.9 years).

Table 4. 2. Mean and standard deviations (SD) of age of individuals at the time of their death/disappearance for each of the conditions regarding the breeding adults present in the group and number of cases. For example, the first cells show that 88 individuals died/disappeared at a mean age of 2.3 years when both parents stayed in the group during the first year of life of infants. Adults present in group are describes as: Same Both= Putative mother and father present, Male Same=Only the identity of the male was known and it was the putative father, Female Same= Only the identity of the female was known and it was the putative mother, Male New= The putative father was replaced, Female New= The putative mother was replaced, Both New= Both putative parents were replaced. In all cases the replacements occurred at different moments, Unknown=Neither the adult male nor adult female in the group had been identified.

Infants' age at death/disappearance			
Adults present	**1st year of life of infants**		
	mean	SD	N
Same Both	2.3	1.2	88
Male Same	2.3	1.1	30
Female Same	3.1	0.8	10
Male New	1.1	0.8	14
Female New	2.6	1.5	7

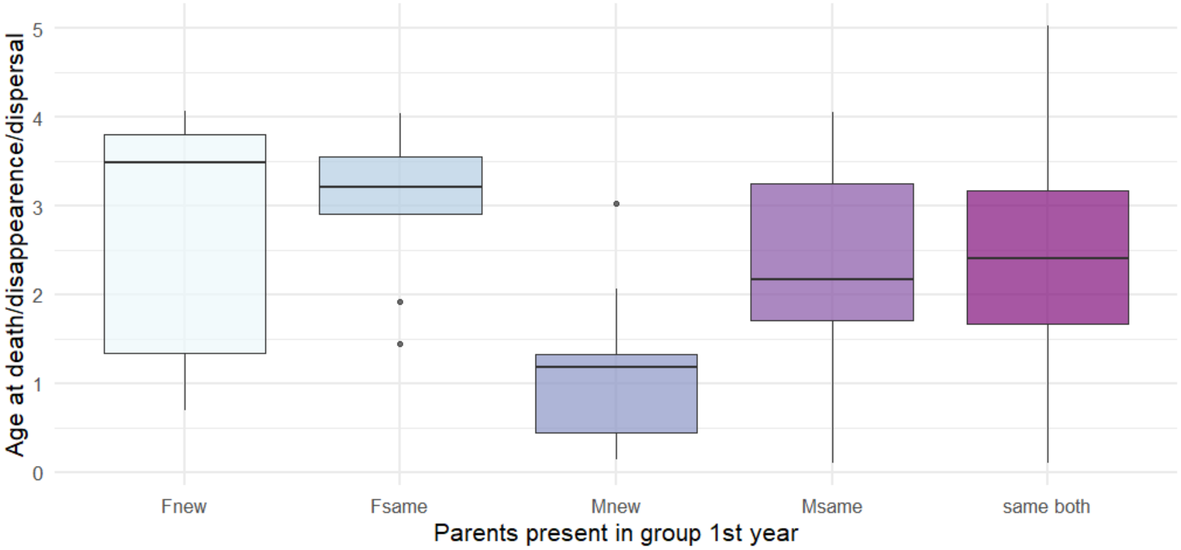


Figure 4.1. Median age differences at death/disappearance depending on the breeding adults present in group during the first year of life of individuals (Same Both= Putative mother and father present, Msame=Only the identity of the male was known and it was the putative father, Fsame= Only the identity of the female was known and it was the putative mother, Mnew= The putative father was replaced, Fnew= The putative mother was replaced). The boxplot shows medians (solid line), first, and third quartiles with the lower whiskers including values ≥first Q−1.5 × IQR (interquartile range) and upper whiskers including values ≤third Q+1.5 × IQR.). Outliers that are more than 1.5 times larger or smaller than the median are represented by dots.

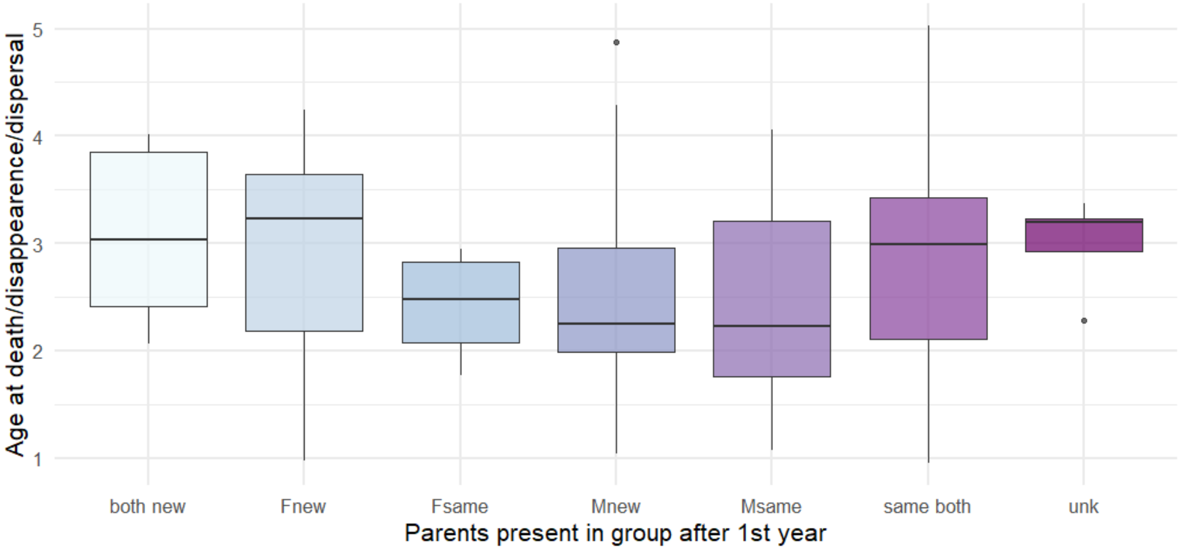


Figure 4.2. Median age differences at death/disappearance depending on the breeding adults present in group after the first year of life of individuals (Same Both= Putative mother and father present, Msame=Only the identity of the male was known and it was the putative father, Fsame= Only the identity of the female was known and it was the putative mother, Mnew= The putative father was replaced, Fnew= The putative mother was replaced, Both New= Both putative parents were replaced. In all cases the replacements occurred at different moments, Unknown=Neither the adult male nor adult female in the group had been identified). The boxplot shows medians (solid line), first, and third quartiles with the lower whiskers including values ≥first Q−1.5 × IQR (interquartile range) and upper whiskers including values ≤third Q+1.5 × IQR.). Outliers that are more than 1.5 times larger or smaller than the median are represented by dots.

For those cases when the putative father was replaced, on average, infants were 1.2 (SD ± 1.5) years old, while infants were a little bit older (1.8 ± 1.2) for those cases when their mothers were replaced. There was high variability on how long young individuals remained in their groups after the replacement of one of their parents; the time was shorter when the father had been replaced than when the mother was (0.9±0.8 years vs 1.1±1.1 years). Infants lived longer if the replacement occurred when they were older, particularly if the parent replaced was the father (Figure 4.3-4.4).

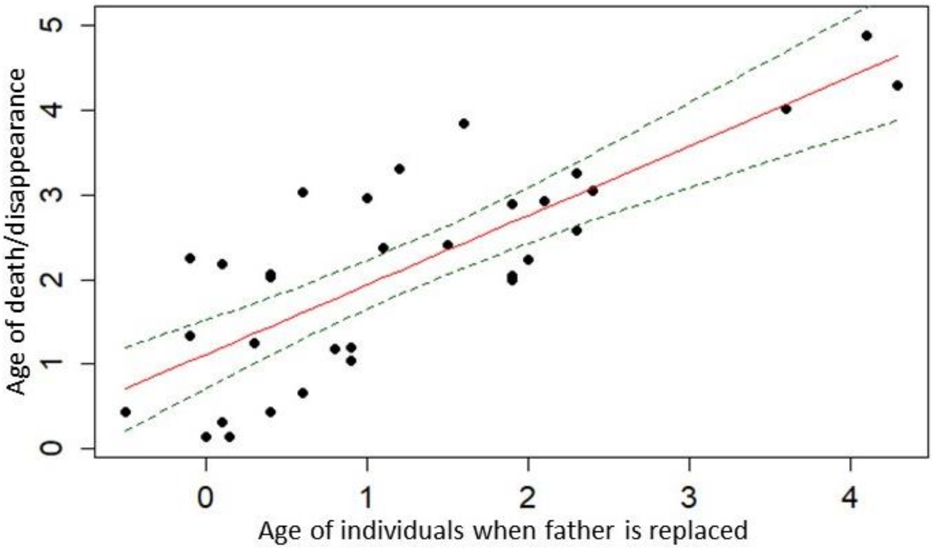


Figure 4.3. Relationship between the age of individuals when the replacement of their fathers occurred and the age of disappearance/death. The red line indicates the mean and slope of parameters estimated in the model and the green lines represent the confidence intervals at 95% level.

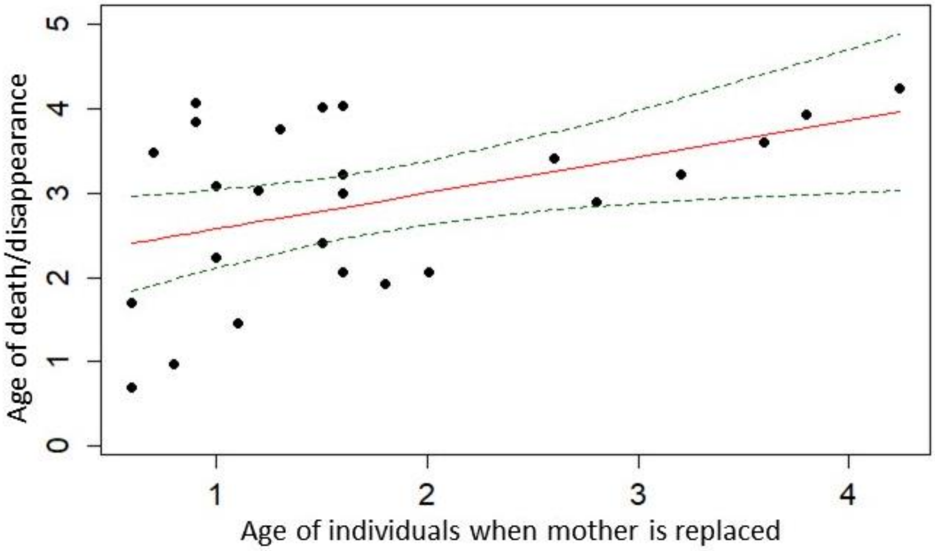


Figure 4.4. Relationship between the age of individuals when the replacement of their mothers occurred and the age of disappearance/death. The red line indicates the mean and slope of parameters estimated in the model and the green lines represent the confident intervals at 95% level.

Post-hoc analyses (Tukey's test with Bonferroni correction) showed that when comparing among all the possible configurations of adults present in group, the differences in age at death/disappearance during the first year of life of individuals, were statistically significant only when new males were included (Figure 4.5). Of those, the effect size was medium (thresholds according to Cohen, 1988) for the comparison of new and same male and for new male and same female. A large effect size was found when comparing the presence of a new male and both putative parents. Finally, the lowest effect size was found when comparing the differences in age at death/disappearance for those individuals whose father was replaced with those whose mother was replaced (Table 4.3).

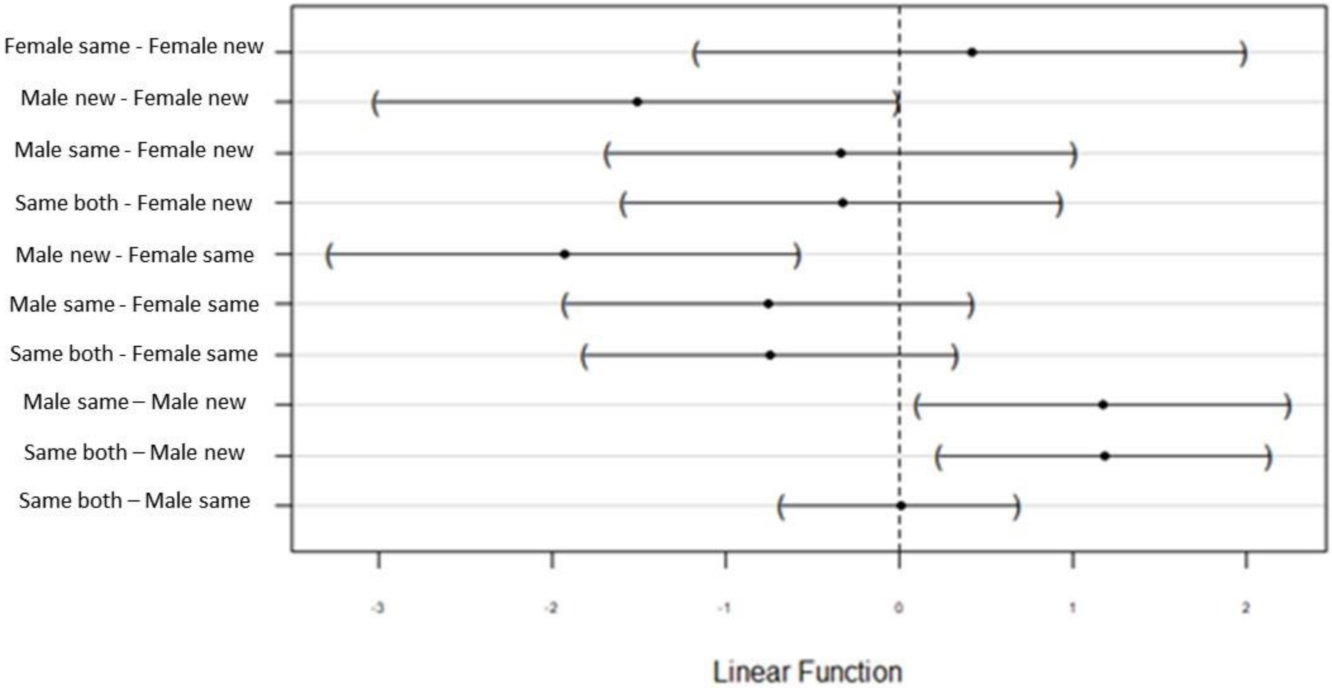


Figure 4.5. Differences in the mean of infant's age at disappearance between all possible pair of configurations of adults present in group during the first year of infants's life (Same Both= Putative mother and father present, Male same=Only the identity of the male was known and it was the putative father, Female same= Only the identity of the female was known and it was the putative mother, Male new= The putative father was replaced, Female new= The putative mother was replaced). For the statistically significant comparisons the confident intervals did not pass the dotted line (zero).

Table 4.3. Effect sizes (d), standard deviations and confidence intervals for the statistically significant comparisons. The sign of effect sizes indicates the direction of means differences. All effect sizes are negative, which in this case indicates the reduction of means in the age of infants at disappearance when a new adult male joined the group.

Comparison	**Effect Size (d)**	**SD (d)**	**Confidence Interval**	
			Lower	Supper
Male New-Female Same	-0.67	0.44	-3.36	0.25
Male New- Female New	-0.49	0.47	-2.78	-0.07
Male New- Male Same	-0.57	0.31	-2.20	-0.18
Male New- Same both	-0.91	0.21	-2.12	-0.54

On 61% (19/31) of male replacements, the intruder had been previously identified with a collar, and thus, we were able to monitor if it remained in the group and reproduced the following season. Of those, seven males entered in a group where infants present were less than one year old, and only three sired an infant in the next breeding season (Table 4.4). For those cases when the mothers were replaced, 58% (15/26) of female intruders were collared, and four joined a new group during the first year of life of the infants.

Table 4.4. Identified male and female intruders and their reproductive success during the following breeding season in the group they entered.

Intruder' Sex	New individual	Tenure new individual in group	Age infant when replacement	Time until infant disappeared	Sired Infant Next year	Time replacement
Male	CC_AM	7 months[a]	0.8	0.4	No	August-Mating
	Sotreta	5 months	0.6	0.05	No	June-Mating
	ElGordo	5 ½ years	0.65[b]	1.4	Yes	June-Mating
	Dardo	14 years	-0.1[c]	2.3	No	October-Gestation
	Inocencio	6 months[d]	0.9	0.3	No	September-Gestation
	Pepe	1-year[e]	0.4	1.7	Yes	April-Mating
	Potro	2 years	0.9	0.14	Yes	September-Gestation
Female	Mony[f]	9 years	0.8	0.9	Yes	July-Mating
	Divertida	4 years	0.7	2.8	Yes	September-Gestation
	Diosa	9 months	0.9	2.9	No	September-Gestation
	Gaviota	14 months	0.9	3.2	No	August-Mating

[a] The tenure of this adult male is unclear. He remained in the group a minimum of seven months, although he may have been the same adult captured and identified a couple of months later who after identification stayed in the group for almost three years.
[b] This infant was part of a set of twins. The other twin died before the replacement occurred.
[c] Replacement before birth.
[d] Inocencio was found dead six months after he entered the group. The identity of the monkey who replaced him is unknown.
[e] The tenure of Pepe was at least one year, although most likely he was in the group for three years
[f] Mony was the third female to replace a former breeding female in that group during a three-month period.

Discussion

The results strongly suggest that the presence of a new unrelated male is associated with lower infant survival in wild owl monkeys. And this association seems to be more important if the replacement occurs during the first year of life of individuals; in other words, when they are still dependent on direct parental care. In fact, given the mean age at disappearance after male replacements (1.1 years), it is extremely unlikely that any of these infants would have survived on their own. By its part, the replacement of mothers did not lead to a substantially younger age at disappearance, although we should be cautious, since all female replacements occurred after the critical period of weaning. In our population, while females usually limit their participation in infant care to nursing, males carry, share food, groom and maintain proximity with infants as soon as after the first week of life of those (Rotundo et al., 2005). Indeed, the close relationship of the male with the infant continues as the infant matures and becomes a juvenile (Dixson, 1983; Huck & Fernandez-Duque, 2013).

It follows that our results also show that infant lived longer if the replacement of parents occurred when they were older, particularly when the father is replaced. Similar results have been reported for wild blue monkeys (*Cercopithecus mitis stuhlmanni*) where older infants were less likely to die or disappear than young infants following a male replacement (Cords & Fuller, 2010; but see Ma, Brockelman, Light, Bartlett, & Fan, 2019 for different results in their review of gibbon species).

Given that no direct aggression by males towards infants has ever been observed in wild owl monkeys, the lower survival of infants after male replacement are better explained as the consequence of a change in the quality and quantity of care received. The importance of male care for infant survival in owl monkeys can be further inferred from some anecdotal observations in our population. The only instance of complete absence of male (or any allomaternal care) comes from the case of a female who was evicted from her group with her one-month dependent infant, soon after her former mate had been also replaced. This female ranged alone with her infant for a month, until the latter died. A few months later, her radiocollar was found on the ground, suggesting she had also died (Huck & Fernandez-Duque, 2013). Furthermore, the infrequent birth of twins offers another opportunity to evaluate the hypothesis that females need the care provided by males in order to successfully rear their offspring. In the population of Formosa, we have only registered three instances of twins, and never did both twins survived to the age of subadult. Despite the additional energetic cost of carrying two young instead of one, the mothers of twins did not carry the infants more often than mothers of singletons did. Instead, in one group, one of the twins was once carried by the juvenile, although from the fourth week after birth, these twins were carried solely by the adult male. When the infants were about two months old, the adult male carried one infant at a time while the other was left behind and moved independently earlier than usual for infants (Huck, Van Lunenburg, et al., 2014). These anecdotal, but relevant observations, raise the question of whether owl monkey females could face the reproductive cost of rearing their offspring without the help of the male and why males would invest so heavily in parental care.

Related to this, our data show that, contrary to what is expected from the sexual selection hypothesis (Hrdy, 1979), the loss of an infant after the replacement of a male does not seem associated with a higher probability of siring an infant the next season. Nonetheless, interestingly, for two of the three males that after joining the group had infants the next breeding season, their infants also lived longer. Multi-year behavioral data on the type and quality of male care and the interactions between pair mates are currently being analyzed to evaluate the possibility of male care as a mating strategy in owl monkeys and of females showing countertactics that secure paternal investment. Recently, results from a similar pair-living and sexually monogamous primate, the titi monkey (*Plecturocebus cupreus*), showed that females contributed more than males in maintaining proximity and grooming their partners, especially during periods of infant dependency. The authors suggested that their data supports the "male-services" hypothesis, where the female would remain with a male in exchange of services such as territorial defense, protection against infanticidal males, or infant care (Dolotovskaya, Walker, & Heymann, 2020).

Accordingly, results obtained through playback experiments in our population revealed that females showed mate guarding behaviors towards their partners when male vocalizations were played back (Garcia de la Chica, Wood, & Fernandez-Duque, 2020). The female's need of parental care may explain why females may want to guard their partners from being expelled by other males, as has been suggested for other taxa with paternal care *(European starling, Sturnus vulgaris*: Eens & Pinxten, 1995; Green dart-poison frog, *Dendrobates auratus*: Summers, 1990).

Indeed, the killing of an unrelated infant has been proposed as the result of high levels of male reproductive competition for those species where there is also a high reproductive skew between floaters and resident adults (Kappeler & van Schaik, 2004). This, in fact, seems to be the case in our population where a study revealed that 35 infants from 17 different pairs were most likely the biological offspring of the adult male in the group at the time the infants were conceived, suggesting no presence of extra pair paternity (Huck, Fernandez-Duque, Babb, & Schurr, 2014). However, although extremely infrequent, at least one extra-pair copulation has been recorded in our population (Garcia de la Chica, Fernandez-Duque, & Rotundo, 2020). This emphasizes the question whether extra-pair copulations may, or may not, led to extra-pair paternity and highlights the need of more genetic data in order to truly evaluate the variation in reproductive tactics in the species (Setchell, 2008) and, how these are linked to the mating and social system in *Aotus spp*. While discussing the evolution of pair-living and sexual monogamy in owl monkeys is beyond the scope of this study, and, despite the fact that there is consensus that paternal care may be rather a consequence than a cause of such social organization and mating system (Kappeler, 2019; Lukas & Clutton-Brock, 2013; Opie et al., 2013), our data suggest that male care is an important factor for the maintenance of the social system in Azara's owl monkeys.

CHAPTER 5

THE LIFE OF FABIAN

THE LIFE OF FABIAN, AN AZARA´S OWL MONKEY (*AOTUS AZARAE*) OF THE ARGENTINEAN CHACO

Chapter 5. The life of Fabian, an Azara's owl monkey (*Aotus azarae*) of the Argentinean Chaco

Abstract

Species-life history patterns provide insights into the adaptative strategies and importance of social behaviors. The cathemeral activity pattern of *Aotus azarae* allowed researchers from the Owl Monkey Project of Formosa, Argentina, to witness remarkable life changing events over the complete lifespan of several individuals. Here we summarize the life of Fabian, a male owl monkey we followed from the moment he started searching for a mate until he died. Although still not consistently considered in models of social evolution of mammals, our discovery of a subpopulation of solitary owl monkey floaters forced us to rethink some aspects of their characteristic social organization and mating system. Through the life of Fabian we present some representative examples of the intrasexual competition regulating the social system of the members of this genus during the different stages in the life of individuals, while reporting the first case of extra-pair copulation in wild owl monkeys.

Why study species-specific life history patterns?

Data on species-specific life history patterns, and their variation, provide insights into adaptative strategies (Cords, 2012) and the evolutionary integration of social, ecological, and demographic variables (Stearns, 2000). However, species-specific life history patterns are the emerging aggregated outcome of individual behavioral phenotypes or life-history milestones. Despite the numerous advantages of an integrated zoo-laboratory-field approach in primatology (Garcia de la Chica, Fernandez-Duque, & Williams, *in press*), the adaptive importance of social behavior and life history of individuals cannot be fully appreciated without information from wild populations. Properly describing those phenotypes and life-history milestones, which are sometimes brief or infrequent, requires multiyear/multi-generation data on identified individuals.

Among primates, characterized by relatively long life-spans, the adequate study of social behavior and life-history requires projects spanning at least many years, sometimes decades (Kappeler & Watts, 2013). Such projects, that allow monitoring of individuals continuously, sometimes through their entire lives, present researchers with endless challenges, including among others the reliable identification of individuals, maintaining levels of habituation to observers and tracking them through difficult terrain (Clutton-Brock & Sheldon, 2010; Setchell & Curtis, 2011).

The Owl Monkey Project of Formosa, Argentina, has been continuously monitoring a population of Azara's owl monkeys (*Aotus azarae*) since 1996 (Fernandez-Duque, 2016). The field site is located barely outside the tropics (58°11' W, 25°58' S). The climate is subtropical, with the lowest monthly mean temperatures from May through August (16 to 18 °C) and highest from October through March (23 to 27 °C). Mean annual precipitation is 1,436 ± SD 333 mm (1977 to 2017) with a drier period in June through August. The forests where we conduct our research grow along the banks of the Pilagá River, which provides ecological continuity with forests in the larger Paraná and Paraguay River systems originating in Brasil and Paraguay. Our main research area is located within the Reserva Privada Mirikiná (named after the local term for owl monkeys), an 1,100 ha private reserve, which is part of 5,000 ha of pristine gallery forest within the ranch.

In contrast to the rest of owl monkey species which are strictly nocturnal, *A. azarae* of the South American Gran Chaco shows activity both during the day and night, allowing for behavioral data collection under adequate light conditions. The cathemeral activity pattern of reliably identified individuals has allowed us to witness remarkable life changing events over the complete lifespan of several individuals. Their diurnal activity notwithstanding, the Azara's owl monkeys of Argentina display substantial nocturnal activity throughout the year (Fernandez-Duque, de la Iglesia, & Erkert, 2010), providing strong evidence that this is a primarily nocturnal taxon which shows temporal niche flexibility (Fernandez-Duque & de la Iglesia, 2021). This, combined with the fact that some of the most general aspects of the genus (e.g. territoriality, biparental care, pair-living) are similar across all species and geographic distribution (Fernandez-Duque, Huck, Van Belle, & Di Fiore, 2020), make our description of the behavior and life-history milestones of one male owl monkey in Argentina of potential value for further inter-specific considerations.

We summarize here the life of Fabian, a wild male owl monkey from the Reserva Mirikiná within the Guaycolec Ranch of Formosa, Argentina. Fabian was a dispersing young adult when we first identified him; we followed him from the moment he started searching for a mate until he died. His life also gives us a glimpse of some representative examples of the intrasexual competition that regulates the social organization and mating system of owl monkeys during the different stages in the life of individuals. Although still not consistently considered in models of social evolution of mammals (Silk & Kappeler, 2017; Smith, Lacey, & Hayes, 2017), our discovery of a subpopulation of solitary owl monkey floaters forced us to rethink some aspects of their characteristic social organization and mating system (Fernandez-Duque et al., 2020; Huck, Di Fiore, & Fernandez-Duque, 2020). We describe Fabian's life with a series of anecdotes, rich in detailed observations that had never been described before, to illustrate milestone events in the species-specific life history of one *Aotus azarae*.

Leaving home: the life as a solitary male

On September 6th 2001, we captured a solitary male owl monkey. Fabian, as we named him, was around 3-4 years old, and appeared to be in good health, even when he had a healed scar on his neck. He had, most likely, recently dispersed from his natal group in search of a partner, initiating, this way, his life as a solitary floater (Fernandez-Duque, 2009; Huck & Fernandez-Duque, 2017).

The life of Fabian as a solitary floater lasted 8.5 months; we followed and monitored him regularly during this period (mean: 6 sightings/month). While he ranged through the home ranges of seven neighboring groups, we watched him being chased away by Cesar, the adult male of Group C0. The aggressive interaction of a resident adult (Cesar) chasing away a solitary floater (Fabian) is the most commonly observed form of competition in our area. It is likely that there is also competition between floaters themselves, but we have no direct evidence of it. Indeed, given that the home ranges of groups are contiguous, leaving no “free” areas available between the groups, at any given time several floaters overlap their solitary ranges within the range of a single group (Huck & Fernandez-Duque, 2017).

Whether Fabian also competed with other solitaries remains unknown. However, while he was a floater, we found him with another monkey on three occasions. Once, Fabian and the unidentified individual slept in contact, groomed each other, and foraged together from the same tree. On a second occasion, the unknown individual who was with Fabian vocalized tonal hoots, a loud call produced by females (Garcia de la Chica et al., 2020). Fabian’s temporary association, possibly with a female, illustrates something that we may have seen only 10-20 times over the years. For example, in 2015, two identified radiocollared young adults, Dixi (Date of birth: 23 Oct 2010) and Discoteca (Date of Birth: 4 Nov 2011), brother and sister who had dispersed from their natal group, D500, within several months apart, were spotted together for at least 24 hours, also sleeping in contact and grooming each other. Late in the day when we found them, they ran away from the group in whose territory they had been ranging in. Why solitary floaters engage in temporary pairs is not clear; we have never seen a temporary couple takeover a territory. In all these years, the only path for both sexes to gain a breeding position appears to be by replacing a resident adult in a group; and Fabian would be no exception.

Finding and establishing a new home

In the morning of May 20th 2002, we found Fabian foraging together with another three monkeys, within the home range of the group E500. Later, when they woke up from their usual mid-day nap, Fabian chased away one of the unidentified individuals. We do not know the fate of that monkey, but from that moment on, we observed only three individuals in the group: Fabian and two adult-size individuals. At the time, we were unclear on whether Fabian had replaced the former adult male in the group or if he had expelled a predispersing subadult. It may be that Fabian cohabited with another adult male for a maximum of six days and a minimum of a few hours before he became the only resident adult male in the group E500.

During the following two months after Fabian joined the group, we captured the remaining group members in order to identify and fit them with radio collars (Fernandez-Duque, Chapman, Glander, & Fernandez-Duque, 2017; Juárez, Rotundo, Berg, & Fernandez-Duque, 2011). First, we captured the smaller monkey, sexed as a 4-5 years old female, named Elina and thus assumed to be the adult female in the group, Fabian’s partner, or so we thought. Four months later, we captured the third individual in the group, another female whom we named Estrella, and we estimated her to be approximately 4 years old (Table 5.1).

Table 5.1. Glossary of names (in order of appearance) of identified Azara´s owl monkeys mentioned in text and their relationship with Fabian.

Name of Individuals	Description
Cesar	Resident adult male from C0 group. He chased away Fabian when the last was a solitary floater ranging in C0's home range.
Elina/Elino	Fabian's step-son. Elino was a subadult male in group E500 when Fabian joined the group as the resident male.
Estrella	Fabian's first partner. Resident adult female of E500 group.
Enrique	Fabian and Estrella's son born in 2005.
Albin	Fabian and Estrella's son born in 2008.
Eloysa	Fabian's second partner. She replaced Estrella and became the resident adult female in E500 group
Dionisio	Resident adult male from D800 group, who may had been involved in an extra-pair copulation with Eloysa.
ElGordo	Male solitary floater who entered in E500 group as the resident adult when Fabian died

During those years, the biological samples obtained from captured individuals were exported to the Zoological Society of San Diego for genetic studies, including sex determination. Several months after we captured Elina, we received a report from the zoo indicating that Elina was, in fact, a male, Elino. We have completed 285 captures of owl monkeys since 1999; only twice we incorrectly sexed individuals and, in both cases, we sexed as females monkeys who turned out to be males. Male and female owl monkeys show extremely low levels of sexual dimorphism lacking any remarkable visible differences even in their genitalia (Spence-Aizenberg, Kimball, Williams, & Fernandez-Duque, 2018). Further, it may be that the lowering of body temperature associated with the anesthesia used during capture procedures may have led to the retraction of the testes, making the sexing of individuals in the field quite a challenging task for researchers.

At the time, we did not have the understanding of *Aotus* social system, pairs social interactions and dispersal patterns that we have today (Fernandez-Duque et al., 2020). Hence, we must admit that it is reassuring that, even when we all thought that Elino was Fabian's pair mate, the missexing did not seem to have clouded our descriptions of their interactions. The behavioral data collected back then, included detailed, somewhat surprising comments on how Elino was consistently separated from Fabian, and how Fabian, instead of interacting with "his pair mate", frequently rested in contact, followed and inspected the other individual, who was identified a bit later as Estrella, the adult female. As a matter of fact, not only Fabian interacted more with his real partner, Estrella, but within a month of his entering the group, we recorded the first instances of direct aggressive intrasexual competition; we observed Fabian chasing away Elino and biting his tail. This aggression from Fabian towards Elino continued for several weeks, and likely triggered Elino´s early socially independent behaviors associated with prospecting; he would remain apart from the group for a few hours or days, before he definitely dispersed (Corley, Rotundo, Dávalos, & Fernandez-Duque, 2018) .

The behavioral mechanisms associated with mate choice and early stages of pair formation in wild owl monkeys have never been described. The interactions of Fabian with Elino and Estrella gives us a glimpse of them. Already, during his first day in the group, he interacted affiliatively with the other members of the group, particularly with Estrella who would become his pair mate; they rested in contact, foraged together, and followed each other closely while moving. The capturing of Estrella generated a situation that (little did we know) would also shed light on the process of mate choice and pair formation.

Back then, when we did not know about floaters and their competition with resident adults, we used to keep captured individuals under health surveillance for 24 hours before releasing them back to the group. The day when Estrella was about to be released back in her group, and only 24 hours after her capture, we found Fabian and Elino already interacting with an unidentified and unsexed solitary individual. Unfortunately, the notes of this encounter did not provide many details on the interaction between the group and the solitary; however, the solitary was reported to be expelled by Fabian and Elino when Estrella was released back.

Life as a resident adult male: pair-living and serial monogamy

The paired life of Fabian and Estrella as the reproductive pair of group E500 went on for seven and a half years, during which they had five infants. Three days after Fabian entered the group, he copulated with Estrella. The mating happened during the season when females in the population usually get pregnant; still, as it is usual for new pairs in our population and in captivity (Garcia de la Chica, Fernandez-Duque, & Williams, *in press*), they did not have an infant that year, suggesting that mating may be part of the process of pair formation and consolidation. During their tenure, Fabian and Estrella had five infants together, four of which survived, at least, until three years of age.

Contrary to long held beliefs, and in the absence of any data to support them, most "monogamous" primates do not pair for life. Fabian and Estrella were no exception, and after eight years together, Estrella was replaced by a female solitary floater. Likewise, Estrella was not present on the day we captured Enrique, Fabian and Estrella's four-and half-year-old son. We captured him while he was ranging solitarily, within his natal group home range, while vocalizing hoot calls. He had a healed scar on his face, probably a sign of his entering the dangerous life stage of competing with resident adults. Only Fabian and Albin (Fabian's son and

Enrique's brother, easily recognizable because he was of a lighter color than usually observed in Azara's owl monkeys) were seen that day; Estrella was missing.

The next time we contacted the group, a month later, there were only three monkeys moving together. Fabian, his son Albin, and a new unidentified monkey, who vocalized alarm calls several times, suggesting that it was not fully habituated to our presence. We could not find either Estrella nor Enrique. The composition of the group remained the same for a few weeks, Estrella had been replaced by a new, and younger, adult female, whom we named Eloysa. Enrique, like his father had done 10 years earlier, dispersed from his natal group seeking reproductive opportunities somewhere else (Figure 5.1). Like we did with Fabian, we monitored the life of Enrique as a solitary, during which, he ranged alone around the territory of a neighboring group (E350) for three months.

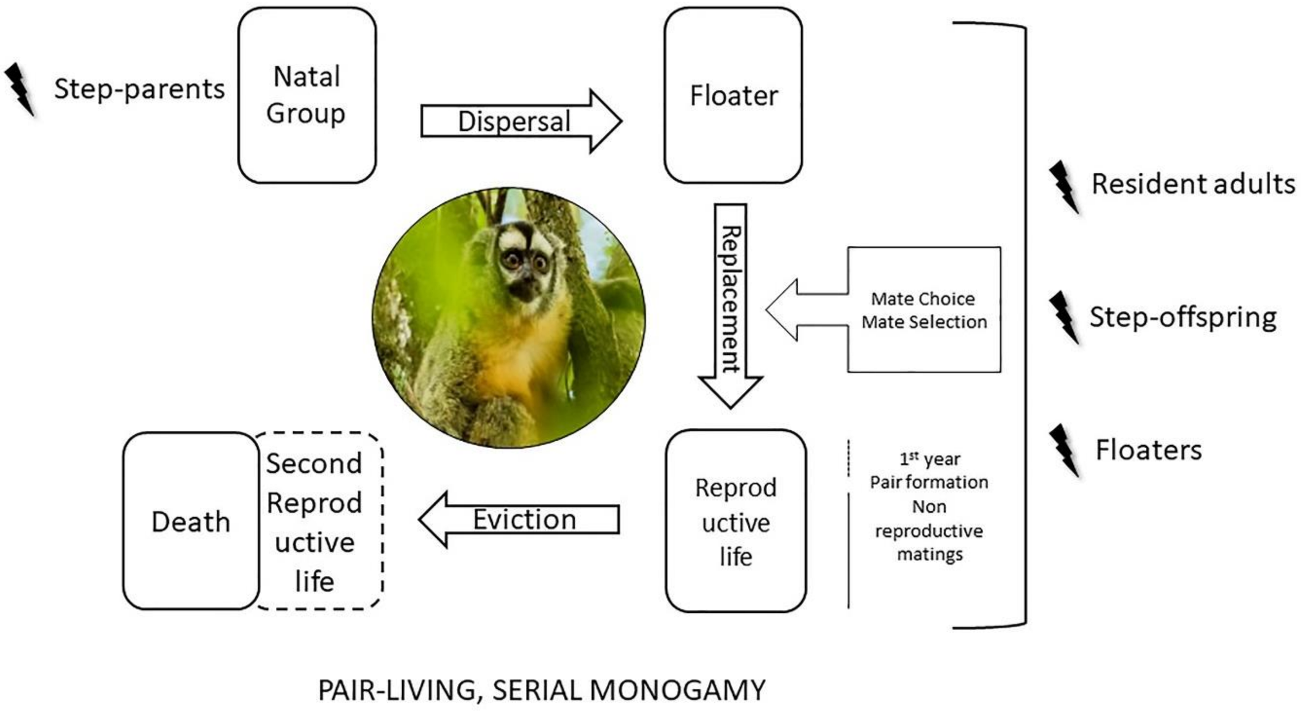


Figure 5.1. An Azara's owl monkey life cycle, as illustrated with Fabian's life. Forms of intrasexual competition are symbolized by the black lightening. Dashed lines indicate a potential second reproductive life, although it has never been observed in our population.

Fabian, Albin (Fabian's youngest son), and Eloysa got along well as a new family. Nonetheless, to our great surprise, two months later, Enrique (Fabian's oldest son) returned home and stayed for three months with his father, brother, and a (supposedly) unrelated female. Even when he was frequently a bit apart from them, he moved and foraged within reasonable proximity. Despite a few displacements of Enrique, we did not observe fights or any intense agonistic interactions among them all.

Until that day when, while Fabian and Albin were sleeping, Enrique followed Eloysa as she moved away from the sleeping tree and copulated with her. Fabian was still resting in contact with Albin when he saw them copulating; immediately, he jumped towards them and bit Enrique in the tail. Enrique ran down the tree, Fabian chased him and they both fell to the ground. Enrique vocalized, but did not defend himself when Fabian bit him again. Enrique hid in a low tree, about 1 meter above the ground, and Fabian returned to the sleeping tree where he stayed in contact with Eloysa and Albin while staring at Enrique's direction (who remained near the ground). Only a few minutes later Fabian attacked Enrique again and bit him, Enrique went back to the ground trying to hide. An hour passed during which Fabian rested in contact with the group and Enrique remained alone, hidden in a lower tree. Then, suddenly, Fabian started another burst of aggression, descending to where his oldest son was, attacked him, urinated, and defecated over him. For 40 minutes, Fabian went up and down between the sleeping tree and Enrique, each time attacking and urinating over him. On several occasions Enrique fell to the ground; eventually Fabian, Eloysa and Albin moved to another tree leaving Enrique behind, where he slept. That was the last time we saw Enrique in the home range of his natal group. We followed him as a solitary floater for almost seven months, until we found him dead.

Enrique had returned to his natal group after his mother had been replaced. His mating with his stepmother was the first, and only, time that we saw an individual copulating with a stepparent; we think it suggests the existence of behavioral mechanisms regulating both inbreeding avoidance and intrasexual competition in owl monkey society. Indeed, subadult females in our population are sexually mature prior to their dispersal; still, we have never recorded them mating while in their natal groups, even when non-related individuals are present (Corley, Valeggia, & Fernandez-Duque, 2017). If Enrique was trying to gain a permanent reproductive position by courting his father's mate, or if this was a "sneaky" copulation is unknown. Some primates may show Alternative Reproductive Tactics (ART) (Setchell, 2008); thus, theoretically, owl monkey floaters may increase their reproductive success 1) gaining a breeding position within an already established group as Fabian did, or, 2) sneaking copulations, as Enrique may have tried, at the cost of residents adults. A previous study of parentage in our population revealed that 35 young individuals from 17 different pairs, including Fabian's offspring, were most likely the biological offspring of the adult male in group, suggesting no extra pair paternity (Huck, Fernandez-Duque, Babb, & Schurr, 2014).

It is worth noting that, as suggested above, recently formed pairs do not produce offspring in their first year together, even when they copulate during a receptive period. The mating between Enrique and Eloysa happened only four months after she became Fabian´s partner, which could explain why Eloysa allowed the mounting. And, related to this, and specially intriguing, was a later encounter with D800 group, where, again, some type of sneaky copulation may have occurred between Eloysa and the resident male from D800. This occurred almost a year after the formation of the pair, and it is unclear if the copulation actually involved Eloysa since, at that time, the adult females of both groups were uncollared. One morning, during a regular monitoring, we saw D800 group accompanied by another adult-size individual, who turned out to be Eloysa. At one point, the adult male from D800, named Dionisio, mounted a female while the other one was less than three meters away from them, but surprisingly no aggressive behaviors or vocalizations were observed. Until Fabian appeared.

When Fabian approached the scene, quickly one of the adult females left, but unfortunately, we do not know if this was the female Dionisio was copulating with, or the other one. Anyway, when Fabian arrived, he chased the other male away, and a fight between the individuals took place. It lasted only a couple of minutes, and after those, both pairs seemed to be peacefully resting, up until Dionisio tried to approach Eloysa, who was in close proximity to Fabian, and Fabian, again, chased him away. These approaches occurred at least three more times, and in all of them Fabian chased the other male away, sometimes by grabbing him. On the last occasion, though, it was Eloysa who approached Dionisio at the same time as Fabian followed her and chased him away. Soon after all the chasings between both males, Eloysa started moving in the direction of E500 home range, and this time both of them followed her, although Fabian inspected her anogenital area and copulated with her. By this time, Fabian and Eloysa were approached by Albin, Fabian´s son, whereas Dionisio retired in the direction where the other female was; who had remained most of the time resting alone 50 meters away from all of them. It is unclear if Eloysa copulated with the other male, although, retrospectively, we know that, at that time, Eloysa was already pregnant with Fabian´s offspring. It follows that these events emphasize the need for more paternity (genetic) data in order to truly evaluate the variation in reproductive tactics in owl monkeys and, and how these, are linked to reproductive success and competition between pairs and between pairs and male and female floaters.

Our window into the life of Fabian has contributed much to our understanding of pair-living, sexual monogamy and intrasexual competition in owl monkeys. Fabian succeeded several challenges from competitors, including his own son, intergroup encounters, and floaters. Indeed, Fabian was the adult male from E500 in, at least, 12 observed intergroup encounters, and in a couple of those, we observed physical aggression between him and the adult male of the other groups. Regarding floaters, surprisingly only once was Fabian seen attacking a solitary floater, but, incredibly, after that episode, the latter remained within the group for eight days! This, although in some way unanticipated given that interactions involving solitaries and resident adults are usually aggressive, it is not totally unexpected since Fabian did exactly the same before, when he gained his position in E500. And again, as it had happened almost 10 years before, the aggressions observed between both males were from the new adult male towards the resident. Only this time, the resident was Fabian, and this time he succeeded in maintaining his position in the group.

As it is often the case in science, each new answer generates twice as many questions. But then again, Fabian is also one of a few individuals we have had the chance to follow during his whole reproductive life, which ended after 10 years holding a breeding position in a group. Very sadly, after so many years of knowing him, we were in good part responsible for his demise. We regularly recapture individuals to remove non-functioning collars, Fabian's leg was broken during such a procedure, the first time this had happened. Upon returning him to the group, even when he frequently fed, he did not use his leg when moving within and between the trees. Three days later, Fabian started to remain a few meters away from his family, Eloysa and their one-year old juvenile offspring. Although they seemed to be around, not further than 30 meters from where Fabian was, he was found alone several hours per day. We found Fabian dead in the canopy a week later; that day we also saw Eloysa and the juvenile ranging together within their home range, but we did not notice any other individual. However, only 24 hours later, we noticed a new adult, with a distinctively short tail, together with Eloysa and the juvenile. We had noticed this floater a few weeks before, ranging within the E500 group's home range. El Gordo, as we named him, became the adult male in E500; like Fabian before him, he faced frequent intrasexual competition which he fended off successfully during six years, when he was finally replaced. That, however, it is a different life (hi)story.

CHAPTER 6 & 7

GENERAL DISCUSSION

CONCLUSIONS AND FUTURE DIRECTIONS

Chapter 6. General Discussion

My thesis aimed to investigate the role that intrasexual competition between floaters and resident adults has in the social organization and mating system of wild Azara´s owl monkeys (*Aotus azare*), a cathemeral South American primate. Through the different chapters, and with a combination of behavioral, demographic, and life-history data, I explored some of the hypotheses classically proposed to explain the evolution and maintenance of pair-living and sexual monogamy in mammals (Fernandez-Duque, Huck, Van Belle, & Di Fiore, 2020). In Chapter 1, I provided an introduction to the theoretical background of my dissertation and my study species. In this chapter I summarized the relevant concepts and the theoretical frameworks classically proposed to study and understand pair living and sexual monogamy (Garcia de la Chica, Fernandez-Duque, & Williams, *in press*; Garcia de la Chica, Spence-Aizenberg, Wolovich, Evans, & Fernandez Duque, 2021). In Chapter 2, I evaluated the degree of sexual dimorphism present in the loud calls of owl monkeys and explored the hypothesis of sex-biased vocal communication (García de la Chica et al., 2020). In Chapter 3, through a set of playback experiments, I assessed the behavioral responses of pair mates towards the simulated presence of a floater, and evaluated the extent to which pairs primarily defend their territory or their mates (Garcia de la Chica, Wood, & Fernandez-Duque, 2020). In Chapter 4, I analyzed the relationship between parental loss and the age at death of infants (Garcia de la Chica, Borries, & Fernandez-Duque, 2020), and finally, in Chapter 5, I detailed the Life of Fabian, a male owl monkey whose life offers important milestones events that adequately illustrates the species-specific life history of *Aotus azarae* (Garcia de la Chica, Fernandez-Duque, & Rotundo, 2020).

Sexual dimorphism in loud calls

The study of vocal communication in primates can lead to insights about the evolution and maintenance of the social systems in which they occur (Heymann, 2003; Mccomb & Semple, 2005). For example, in sexually monogamous mating systems, the formation of a new pair requires the identification of potential mates, and the ability to differentiate mates from other opposite-sex individuals.

I showed that loud calls of Azara's owl monkeys (*Aotus azarae*) are sexually dimorphic, with females only emitting tonal hoots and males only emitting graff hoots; and that the latter ones had higher entropy and dominant frequencies. Across primate taxa, there are sex-specific morphological adaptations unequivocally related to vocal communication, such as the expanded hyoid bone of howler monkeys (*Alouatta spp*: Kitchen, Grassetto, Da Cunha, Holzmann, & Gonçalves De Oliveira, 2015), and the throat sac of male orangutans (*Pongo spp*: Utami, Goossens, Bruford, de Ruiter, & van Hooff, 2002). However, even when more research into the morphological features of the vocal or gular sac of owl monkeys is needed (Hill, 1960), it seems unlike that the results found would be associated with anatomical sex-differences. It has been suggested that sexual selection may have a role in the evolution of acoustic variables such as duration, fundamental frequency and peak frequency in other primates (Ey, Pfefferle, & Fischer, 2006). Thus, my hypothesis has been that the sexual dimorphism in owl monkey hoots is associated with these calls being sexually selected vocal traits.

Sex differences in morphological and behavioral traits have been usually considered as the result of evolution through sexual selection, which among mammals has been generally considered to act via inter-male competition, and to be characteristic of polygynous species. However, in taxa that appear to have little sexual dimorphism, as usually occurs in sexually monogamous taxa, vocal communication may still be subject to intra, or intersexual selection

(Delgado, 2006; Snowdon, 2017). For example, female Lar gibbons (*Hylobates lar*) showed sufficient variation in loud calls for individual identification (Terleph, Malaivijitnond, & Reichard, 2015), and among titi monkeys (*Callicebus* spp.), even when no sex-specific duet contributions have been detected (Caselli, Mennill, Gestich, Setz, & Bicca-Marques, 2015; Müller & Anzenberger, 2002; Robinson, 1979), sex contributions differ in the acoustic characteristics syllables (assembled to compose the song parts of duets' long sequences), which allows individuals to identify the sex of the caller (Caselli et al., 2015).

Nonetheless, it should be noted that sex differences in any given trait can also be the product of different selective pressures acting on males and females, rather than differences driven by sexual selection alone (Badyaev & Hill, 2003). For example, in some birds, sexual dimorphism in plumage colors and calls has been associated not only with the mating system, but with some life-history traits, such as breeding latitude, seasonal migration, nesting behavior, and territoriality (Price, 2015). Under this scenario, Snowdon (2004) proposed a framework for identifying sexually selected traits. He proposed that for a trait to be considered as sexually selected it should meet the following criteria: 1) it is sexually dimorphic, 2) it varies between same-sex individuals, 3) individuals discriminate between variants of the trait and these elicit differential responses, 4) individuals show preference (or avoidance) for a particular trait in context of reproduction or mating, and 5) variations in the trait are related to an individual's fitness, showing differential reproductive success.

Regarding the sexually dimorphic hoot calls of owl monkeys, through this thesis I assessed two of those criteria. First, in Chapter 2, I presented quantitative evidence that hoots are sexually dimorphic. The other criteria was further evaluated in Chapter 3 where, through playback experiments, I showed that resident breeding adults discriminated and elicited differential responses to tonal and graff hoot calls during the mating season. This is further discussed below.

Mate Guarding

In Chapter 3 I semi-experimentally evaluated predictions derived from the hypotheses of Mate and Resource Defense (Dunbar, 1988; Wrangham, 1980), two of the hypotheses classically proposed to explain the evolution and maintenance of pair-living and sexual monogamy. Of these two hypotheses, mate defense has received considerable attention and empirical support (van Schaik & Dunbar, 1990; van Schaik & Kappeler, 1997, 2003), although some studies have also pointed out the importance of resource defense in primates (Caselli et al., 2015; Overdorff & Tecot, 2006).

My study showed that, in response to unfamiliar male and female hoot calls, Azara's owl monkeys from six different pairs increased their frequencies of scent and partner markings and urine washing behaviors. My choice of recording such behaviors was informed by the literature on other pair-living sexually monogamous taxa (Heymann, 2006; Lledo-Ferrer, Peláez, & Heymann, 2010; Roberts & Dunbar, 2000), as well as from my reviewing of all existing literature on owl monkeys' behavior (García de la Chica & Fernandez-Duque, 2018; Garcia de la Chica, Fernandez-Duque, & Williams, *in press*; Garcia de la Chica et al., 2021). In *Aotus azarae* these behaviors are mainly performed by adults (adults 89%, subadults 6%, juveniles 5% and infants <0.1%), which indicates that they are associated with sexual maturity (Corley, Spence-Aizenberg, & Fernandez-Duque, 2020). Consequently, scent marks and urine wash have an important role in mediating the pair mate's sociosexual interactions, as well as the interactions between pairs and floaters, and both, captive and wild individuals, regularly perform them (Corley et al., 2020; Spence-Aizenberg, Williams, & Fernandez-Duque, 2018; Wolovich & Evans, 2007). During behavioral observations, urine washing is the most frequent olfactory behavior in my study population, followed by scent-marking, and partner-marking (Corley et al., 2020). However, during the playback experiments, scent marking behaviors, to the substrate and to partners, were the most frequent behaviors, while only mild differences in urine washing were observed. One possibility is that scent-markings and urine washing behaviors in owl monkeys actually differ in their function, and while scent-marking may be playing a role in mate guarding (Heymann, 2006), urine wash may be rather associated with territory defense.

Furthermore, owl monkey males and females do not differ in the frequency of their scent marking substrate and urine washing behaviors, although partner-marking behaviors between pair mates appear to be male biased in both wild and captive individuals (Corley et al., 2020; Spence-Aizenberg et al., 2018; Wolovich & Evans, 2007). In my study, resident males scent marked the substrate and their partners more frequently than resident females did. Further, when several instances of male and female partner-marking were recorded during the playing back of the stimulus, none of those was ever observed during the previous behavioral data collection neither during the playback of control sounds, strongly suggesting that the unfamiliar calls elicited such behaviors in owl monkey pair mates. A similar study conducted with captive *A. nancymae* pairs did not find remarkable changes in the frequency of scent-marking or urine-washing by males or females, although males showed higher rates of behaviors indicative of arousal (e.g. chirping, arching, piloerecting), and were more responsible for the maintenance of close proximity to their partners when a same-sex unfamiliar conspecific was presented. Given these results, the authors suggested that the olfactory, or acoustic cues, from unfamiliar conspecifics may have, in fact, not been “unfamiliar” for the pairs sampled, due to some of them residing in the same colony before the experiments. Thus, the authors said, this may have muted more responses (Wolovich, Evans, & Green, 2010).

My study also showed that stronger responses were always recorded following unfamiliar male calls. Not only pairs increased their sociosexual behaviors, but they also moved closer to the speaker in response to graff than tonal or control calls. Likewise, even when owl monkey males only reacted to same-sex individuals, females also reacted more strongly to unfamiliar male calls than to those from same-sex individuals. Accordingly, previous studies addressing other pair-living primates´ responses to same-sex individuals or same-sex calls, have also found stronger reactions in males (Anzenberger, 1988; Fernandez Duque, Valeggia, & Mason, 2000; Wolovich et al., 2010; but see: Caselli et al., 2015). Still, the females´ responses I found generate additional questions. In the past, it had been assumed that the distribution of resources needed to support female survival and reproduction would be related to female´s intolerance to same-sex conspecific (Lukas & Clutton-Brock, 2013). However, in pair living taxa, limited resources other than food, such as paternal care, may also constrain females' reproductive output (Huck, Di Fiore, & Fernandez-Duque, 2020). Likewise, in species where biparental care is associated with infant survival, females may choose to guard their mates, and to remain in close proximity to them, in order to increase male´s paternity certainty and thus, male care. Given that multiple mating by females selects against male care (Kokko & Jennions, 2008a), mate guarding behaviors by females may be particularly important during specific socioecological periods, such as the mating season in seasonal breeders, or during simulated, or real encounters with conspecifics.

In my dissertation, the importance of mate guarding behaviors is also implied by the fact that during the experiments, the speaker location, whether in the center or border of the home range, did not elicit any remarkable differences in the reactions of pairs; and by the fact that young individuals did not show any apparent responses to the calls. Furthermore, most likely, if the presence of an unfamiliar conspecific would have simulated a potential food competitor, no sex differences would have been observed. It follows that males and females may guard their mates via the defense of:

(i) their own positions within the pair (Hall, 2004).

(ii) their partners' positions (Appleby, Yamaguchi, Johnson, & Macdonald, 1999).

(iii) commitment signaling, in which an individual prevents its partner from deserting (Hall, 2004).

(iv) paternity guarding, by which males prevent their fertile females from having extra-pair copulations (Brotherton & Komers, 2003).

My results provide some support for all of them. Firstly, by only reacting to same-sex calls, males may be trying to maintain their own breeding positions against simulated floaters. Second, females may be guarding their mates in order to secure their partners position, and/or to prevent males from deserting. If females need the help of their partners to successfully rear their offspring, it seems likely that both forms of mate defense are playing a role in owl monkeys. Finally, because in seasonal breeders paternity guarding can only account for the mate defense function when females are fertile, I cannot reject this fourth form of mate defense in owl monkeys, since my experiments took place during the period when females are most likely to be fertile (Fernandez-Duque et al., 2020).

Parental care…and serial genetic monogamy?

One of the most fascinating aspects of the genus *Aotus* is their extensive form of biparental care (Dixson & Fleming, 1981; Huck & Fernandez-Duque, 2013; Rotundo, Fernandez-Duque, & Dixson, 2005). In my study population, males not only carry the infants most of the time, but also play, groom, and share food with them more frequently than females do (Rotundo et al., 2005; Wolovich, Perea-Rodriguez, & Fernandez-Duque, 2008). Owl monkey males are also more responsible than females of maintaining proximity with infants and with juveniles, and this closer relationship of the male with the infant continues as the infant matures and becomes a juvenile (Dixson, 1983; Dixson & Fleming, 1981; Huck & Fernandez-Duque, 2013). Instead, females usually limit their interactions with infants to those related to nursing, and they reject them more frequently than males (Dixson & Fleming, 1981; Rotundo et al., 2005). Nonetheless, nursing is usually extended until the 5th month of life of infants and no rejection has been observed before the 11th week in wild Azara's owl monkeys (Rotundo et al., 2005).

Furthermore, contrary to observed in Cooperative Breeding species, there is rarely any involvement of the siblings in the care of infants (Huck & Fernandez-Duque, 2013). Sibling care has been recorded infrequently in captive groups of *A. lemurinus* and *A. a. boliviensis* (Dixson & Fleming, 1981; Jantschke, Welker, & Klaiber-Schuh, 1998), and only once in free-ranging *A. a. azarae*, following the eviction from the group of the putative father of the infant (Fernandez-Duque, Juárez, & Di Fiore, 2008).

It follows that the role of paternal care in the species I studied is essential for infant survival and development. In one of the studies I conducted I showed that male replacement is associated with a lower survival of infants, and that this association is more relevant during the offspring´s first year of life, period when they are more dependent on direct parental care. Interestingly, the replacement of mothers did not lead to a substantially younger age at disappearance of infants, although this result should be interpreted with caution since in this data set most female replacements occurred after weaning.

Together, results from Chapters 3 and 4 suggest that male care is required in owl monkeys and that males may discriminate against extra-pair offspring and provide care only to their own infants. Nevertheless, it is still unknown if the lower survival of infants in Azara´s owl monkeys would be associated within a specific type of male care. It may be that the nature of the relationship between young and parents, or stepparents, differs quantitatively and/or qualitatively in owl monkeys. For example, in birds, the presence of extra-pair paternity (EPP) was negatively correlated with some types of male care, but not others. Likewise, in species where EPP was high, male feeding of offspring decreased, although this was not the case for shared incubation, courtship feeding or male nest building (Møller & Cuervo, 2000). In the population I studied, in one case, a floater who replaced a resident male while an infant was still in the group provided some care, in the form of carrying, after a few weeks of the replacement. Still, the infant did not survive passed the six months of life and, even when we could assume that this male was not the biological father of the infant, it is unclear the degree of relatedness, if any, between them (Fernandez-Duque et al., 2008).

Related to this, comparative analyses of birds have suggested that in species where female reproductive success was reduced when her partner was removed, extra-pair paternity was infrequent (Møller, 2003). In the population of Azara´s owl monkeys this seems to be the case. Genetic analyses of 17 infants revealed that the adult male present in the group was the most likely biological father of them (Huck, Fernandez-Duque, Babb, & Schurr, 2014). However, at least one extra-pair copulation was observed in the population. This event, which was described in detailed in Chapter 5, emphasizes the need for more paternity (genetic) data in order to truly evaluate the existence of Alternative Reproductive Tactics (ART) (Setchell, 2008) in owl monkeys and how these, are linked to reproductive success and competition between pairs and between pairs and male and female floaters. With this goal, ongoing analyses are focused on exploring if the only possibility of a floater to reproduce is by gaining a breeding position within an already established group, or, if “sneaking copulations” at the cost of residents adults may also result in reproductive success. In another pair living primate, the indri (*Indris indris*), even when extra-pair copulations occur (Bonadonna et al., 2014), in 92% of cases (11/12), the genetic profile of the offspring matched the paired male of the group for all the loci considered. Thus, the authors conclude that, even when not the rule, genetic monogamy seem to be the norm in the species (Bonadonna et al., 2019).

Information on the reproductive strategies of male and female owl monkeys is still limited, and as it is usual in science, any finding brings as twice as many questions. As shown in my dissertation, there is accumulating evidence indicating that intrasexual competition is an inescapable part of an owl monkey life. My research offers a valuable perspective for understanding how such competition is regulating the social system in Azara’s owl monkeys (*Aotus azarae*).

Chapter 7. Conclusions and future directions

Each of the preceding chapters took a different approach to studying the rol that intrasexual competition has in the lives of Azara´s owl monkeys. While each approach informs our understanding of this phenomenon in its own way, this dissertation strongly suggests that combining multiple types of data, such as acoustic, behavioral, and life history data, is necessary for developing a deeper understanding of owl monkeys´ social system.

Since the early 1980s the concept of monogamy has undergone several re-evaluations, yet much is still to be done to better understand and classify the potential effects of intrasexual competition in the social lives of pair-living species. Throughout this dissertation, I suggest that such competition is a key factor in regulating pairs´ dynamics in Azara´s owl monkeys. Specifically, my dissertation research has shown that:

- Male and female Azara's owl monkeys emit sexually dimorphic loud calls associated with mate attraction that are different in entropy and dominant frequencies. Moreover, according with the hypothesis that the sex with less investment in parental care would be the more competitive one, my data indicated that the emission of loud calls is female-biased in the study population. Likewise, owl monkey females may be competing for males in order to successfully rear their offspring.
- Males and female Azara's owl monkeys face high intrasexual competition, and both sexes display mate guarding behaviors when unfamiliar calls of a conspecific are played back. Overall, males react more strongly than females, and both sexes are more reactive to male than female calls. The reactions of owl monkey males agree with classical conceptions of the Mate Guarding Hypothesis that states that males would defend their own positions within the pair and prevent other males from copulating with their mates. On the other hand, females seem to guard their partners' position within the pair or prevent them from

deserting. The interest of females in maintaining their partners may be related to the care system of owl monkeys. This includes an extended form of biparental care that may be necessary for infant survival.

- When their fathers are replaced, Azara's owl monkey infants die at a younger age than infants in groups where the father, or both parents, are present. In the absence of any observed aggression towards infants by incoming adults, the higher mortality risk after the loss of the father is likely to be associated with a reduction in the quantity, or quality, of care provided by the new male.

Nonetheless, developing a complete understanding of the role that floaters have in the evolution and maintenance of owl monkeys´ social organization and mating system still requires additional research. First, all data and conclusions presented in this dissertation were collected in the Gran Chaco region of Formosa, Argentina, at a permanent field site that the Owl Monkey Project (OMP) has held since 1996, which partially constrains the possibility to generalize the conclusions to other populations of owl monkeys with possibly different social and ecological environments.

When considering a socioecological framework across species of owl monkeys, it is important to keep in mind the wide geographical distribution of *Aotus spp*., from Panama to Argentina, where they inhabit a variety of different forests of both primary and secondary growth, at sea level or up to 3,200 m above sea level. Owl monkeys are found in lowland forest that is flooded seasonally, or terra firma forest that does not flood. In these forests, they can be found in every strata of the trees from 7m to 35 m above the ground; they are found in tropical forests with constant temperature across the year and forests where the daily temperature variation is as much as 20ºC.

Still, regardless of the type of habitat, owl monkeys of all species have been always found in small groups, generally composed, or assumed to be composed, by an adult heterosexual pair, one infant, and one or two immature individuals. Across their distribution, all species, tropical or subtropical, in continuous or fragmented landscapes, apparently have relatively small home ranges that vary between 4 and 10 ha (Fernandez-Duque, 2012). And similar arguments can be made for the presence of paternal care; even when there have been no field studies of sexed individuals besides the ones from the OMP, data from captive individuals indicates that paternal care is present across all species (Dixson & Fleming, 1981; Wolovich, et al., 2006).

All together, these consistencies across the genus range suggest influences in the social organization and mating system of owl monkeys that may exceed the merely local ecological ones. Even then one must be cautious when interpreting my results, since it may be that some social interactions important for mate choice and pair formation are constrained to only some species of the genus *Aotus* (e.g. possibility of encounters with conspecifics in fragmented areas).

Second, while only through field research we can learn about the adaptive value of communication signals and behaviors, we need more than field research alone to fully understand the mechanisms by which male and female owl monkeys regulate their interactions. For example, in agreement with my results, in the presence of unfamiliar conspecifics, male and female captive *A. nancymaae* pairs changed their behavior, with males reacting more strongly to the presence of same-sex individuals than did females (Wolovich, Evans, & Green, 2010). When unfamiliar male conspecifics were present, resident males had higher rates of behaviors indicative of arousal (e.g. chirping, arching, piloerecting), and were more responsible for the maintenance of close proximity to their partners than during control trials. However, the authors did not find remarkable differences in the frequency of scent-marking by males or females. Certain behaviors, such as piloerection and arching which are visual signals often associated with arousal, excitement, or aggression (Wolovich et al. 2007) may be important for the dynamics between pairs and floaters, still in the field are extremely difficult to observe and go easily unnoticed by observers. Furthermore, olfactory communication is undoubtedly important for regulating social interactions and potentially mate choice in owl monkeys (Wolovich et al., 2007; Macdonald et al., 2008; Spence-Aizenberg et al., 2018). The rich chemical signatures of glandular secretions in owl monkeys seem to convey individual identity (MacDonald et al., 2008; Spence-Aizenberg et al., 2018), which could potentially allow for olfactory recognition. Still, the challenges of studying this form of communication in the field make this area of research fertile for a captivity–field approach.

My dissertation sets a strong foundation to pursue several avenues of future research. The analysis of detailed behavioral data collected from identified owl monkeys will provide insights into the potential differences in parental care by biological and step fathers, as well as into the contribution of males and females to their pair bond; and how these differences may change over time in response to varying ecological conditions and different reproductive stages (e.g. gestation or lactation). Future studies will need to further evaluate mate-guarding strategies, especially from the female's perspective, which are still not well understood for many wild populations of pair-living species. Because interactions with extra-group animals are often not observed, future studies will benefit from incorporating experimental methods to simulate encounters and examine how the sexes respond to different social stimuli. Ongoing plans for the collaborative replications of such methods in another wild pair-living sexually monogamous primate such as the titi monkeys of Perú (*Plecturocebus cupreus*: Dolotovskaya, Walker, & Heymann, 2020) may reveal hidden mate-guarding strategies in their behaviors or vocalizations.

This dissertation also opens the question for exploring sexual dimorphism in other aspects of owl monkeys´ behavioral or life-history traits. For other species where both males and females disperse, differences in average dispersal distances have been reported (Huck et al., 2007; Lappan, 2007; Roy et al., 2014). Based on preliminary analyses, it seems that owl monkey parents would invest less in daughters than sons; thus if female subadults disperse earlier (because daughters have less to lose than sons from leaving the natal group), they may have on average a longer time to "float around" and gradually disperse further than male floaters. This, in turn, would affect the context-specific operational sex ratios (OSRs) and more generally the population genetic structure. Understanding these differences might lead to valuable insights into the evolution of pair-bonding and paternal care in both human and non-human primate societies (Brown et al., 2009; Gavrilets, 2012; Hurtado and Hill, 1992; Marlowe, 2000; Rooker and Gavrilets, 2016).

Our understanding of the evolutionary forces favoring pair-living, sexual monogamy, biparental behavior, and nocturnality in owl monkeys will benefit from a comparative approach that considers some of the other more tropical, strictly nocturnal owl monkeys or strepsirhine species, as well as some of the other socially monogamous primates. Combining approaches would provide the opportunity to contrast similar types of data collected in different environments, and this should include research in both captive and field settings. This project further provides us with the basis for drawing comparisons in behavioral, and life history traits across pair-living mammal species and mating systems, and may serve as an interesting model to refine hypotheses for comparisons to the social organization of early humans.

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