

LEAVING HOME: DEMOGRAPHIC, ENDOCRINE, AND BEHAVIORAL CORRELATES  
OF DISPERSAL IN MONOGAMOUS OWL MONKEYS (*AOTUS AZARAE*) OF ARGENTINA

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## ABSTRACT

LEAVING HOME: DEMOGRAPHIC, ENDOCRINE, AND BEHAVIORAL  
CORRELATES OF DISPERSAL IN MONOGAMOUS OWL MONKEYS (*AOTUS*  
*AZARAE*) OF ARGENTINA

Margaret K. Corley

Theodore G. Schurr

Natal dispersal, the movement of individuals from their birthplace to new areas in which they may breed, is an important aspect of life history that influences a variety of processes. Understanding dispersal not only increases our theoretical knowledge of the evolution of mating systems and social dynamics, but also provides insights essential for effective population management and for predicting the consequences that environmental changes may have on species' distributions. This dissertation takes a holistic approach to explore natal dispersal at the level of the population, group, and individual in Azara's owl monkey (*Aotus azarae*), a social monogamous primate native to South America. All data presented in this dissertation were collected at a long-term field site of the Owl Monkey Project in the Gran Chaco region of Formosa, Argentina. Chapter two examines dispersal at the level of the community, by exploring how demographic changes and environmental variables are associated with dispersal. The timing of dispersal was highly flexible, suggesting that delaying dispersal may be an adaptive strategy that owl monkeys utilize to minimize dispersal costs and maintain access to benefits provided by the natal group. Chapter three narrows the focus to the level of the group, and finds that behaviors, particularly

agonism among group members, may function to regulate dispersal as well as mediate competition amongst adults and predispersed offspring. The next two chapters narrow the focus even further, to the individual level. Chapter four, which examines hormonal correlates of development and dispersal, finds that females experience the onset of sexual maturity prior to dispersing. Chapter five follows dispersing individuals through the entire process of dispersal to investigate the ultimate fates of dispersers. Dispersal strategies were highly variable, but individuals often prospected prior to permanently dispersing and almost always spent time as solitary “floaters”. Together, these investigations provide insight into both proximate and ultimate causes for dispersal and allow for the development of a multifaceted understanding of dispersal patterns in a socially monogamous primate. The holistic approach to understanding dispersal taken in this dissertation is one that could be useful for increasing our understanding of dispersal in many other taxa.

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## PREFACE

This dissertation explores natal dispersal in Azara's owl monkeys (*Aotus azarae*), a social monogamous primate native to South America.

Chapter one provides an introduction to the study species and the topic of dispersal. It summarizes the theoretical frameworks that researchers have utilized to study and understand dispersal patterns, with a focus on primates and socially monogamous species in particular. Each subsequent chapter then describes an investigation into one or more aspects of natal dispersal in owl monkeys. First, chapter two examines dispersal at the level of the community, by exploring how demographic changes and environmental variables are associated with dispersal patterns and variation in the timing of dispersal. Chapter three narrows the focus to the level of the group, and investigates how behavior, particularly agonism, among group members may function to regulate dispersal. Chapters four and five narrow the focus even further, to the individual level. Chapter four examines hormonal correlates of development and dispersal in juvenile and subadult females and Chapter five follows individuals through the entire dispersal process and describes what we know about the ultimate fates of dispersers.

Together, these investigations provide insight into both proximate and ultimate causes for dispersal patterns in this socially monogamous primate. Evolutionary theory has long recognized that addressing different types of questions, or "levels" of explanation, is essential for developing a comprehensive understanding of a behavioral trait [Mayr, 1961; Tinbergen, 1963]. While drawing a strict distinction between proximate and ultimate explanations is not always useful [Laland et al., 2011], an approach that investigates a behavior by addressing several or all of Tinbergen's questions provides complementary

insights and leads to a more complete understanding [Barrett et al., 2013; Bateson and Laland, 2013; Holekamp and Sherman, 1989; Tinbergen, 1963].

The work presented thus here takes a more holistic approach than many previous studies of dispersal, and aims to provide a template for a more integrative method of examining dispersal patterns. Specifically, this project evaluates mating and resource competition avoidance hypotheses for explaining the evolution and maintenance of dispersal patterns, examines endocrine and behavioral mechanism that may function to regulate dispersal, and explores the ontogeny of these mechanisms to provide a multifaceted understanding owl monkey dispersal. In addition to expanding our understanding of owl monkeys, it is my hope that the results will be utilized to refine hypotheses and stimulate additional empirical research into dispersal and provide a better understanding of dispersal patterns in socially monogamous species of primates and other organisms in general.

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## Chapter 1. Introduction

### What is dispersal and why is it important?

Natal dispersal, the movement of individuals from their birthplace to new areas in which they may breed, is an important aspect of life history that influences a variety of processes at the level of the individual, group and population. From the perspective of an individual, it is a behavioral strategy that has consequences for health, reproductive opportunities, and fitness [Bonte et al., 2012; Clobert et al., 2001; Ekman, 2007; Ekman et al., 1999; Kesler et al., 2007]. Dispersal also influences group dynamics and social interactions among group members, which makes it essential for explaining the evolution of social monogamy and other mating systems [Dobson, 1982; Emlen, 1997; Greenwood, 1980; Lawson Handley and Perrin, 2007]. At a population level, patterns and sex-biases in dispersal impact gene flow and community dynamics [Clobert et al., 2009]. Understanding dispersal therefore not only increases our theoretical knowledge of the evolution of mating systems and social dynamics, but also provides insights essential for effective population management and predicting the consequences that environmental changes may have on species' distributions [Cote et al., 2010; Flesch et al., 2010].

While dispersal is important on many levels, I must first address the question of *why* individuals disperse. Leaving a natal group typically confronts dispersing offspring with a variety of potentially substantial costs, in terms of time, energy, and risk. Potential costs include decreased access to resources or foraging efficiency after leaving the natal territory, increased rates of aggression from unfamiliar conspecifics, social isolation and an increased

risk of predation (particularly if dispersal entails ranging solitary for a period of time), all of which may be associated with increased risk of mortality or delayed reproduction [Berger, 1987; Bonte et al., 2012; Jones, 2003; Nishida et al., 2003]. Yet, in spite of these costs, natal dispersal by at least some individuals is a behavior common to many animals, including all primate taxa [Isbell and Van Vuren, 1996; Pusey and Packer, 1987]. If dispersal has evolved to be so widespread a phenomenon, then it must provide dispersers with benefits that outweigh the costs. Commonly proposed benefits of dispersal include decreasing the risks of inbreeding and avoiding competition for resources and/or mates [Dobson, 1982; Greenwood, 1980; Isbell, 2004; Perrin and Mazalov, 1999; Pusey, 1987]. However, precisely which of these benefits are most important and how they co-vary with aspects of ecology and social systems remains a topic of ongoing research and debate.

### **Explaining patterns of natal dispersal: Socioecological models and variation**

In many vertebrate taxa, only a portion of individuals disperse, while the rest remain in the natal group to breed. One factor that may determine the division of dispersers and non-dispersers is sex. In fact, it has long been recognized that many species of birds and mammals exhibit sex-biases in dispersal, where one sex tends to disperse further or more frequently than the other. A tight link between dispersal patterns, mating systems, and life history traits has been proposed to explain how these sex-biased patterns have evolved [Dobson, 1982; Greenwood, 1983; Greenwood, 1980; Nagy et al., 2007; Trochet et al., 2016; Wolff, 1994].

The framework for our current understanding of how sex-biased dispersal patterns are related to mating systems originates primarily from work by Greenwood [1980, 1983] and Dobson [1982]. Greenwood [1980] predicted that dispersal is male-biased in female-defense

polygynous species (e.g., many mammals) and female-biased in mating systems associated with resource defense (e.g., many birds). These predictions are based on the idea that the sex that invests more in offspring care or the defense of a territory and other resources will be the one to stay, because individuals of that sex benefit the most from philopatry. Dobson [1982] expanded upon this link between mating system and sex-biases in dispersal to consider monogamous mammals. He proposed that, since competition for mates should be approximately equal for males and females in monogamous mating systems, *both sexes* should disperse at similar rates.

Following this seminal work, numerous studies have utilized behavioral and/or molecular data to test the link between dispersal and mating system in a variety of avian and mammalian taxa [Lawson Handley and Perrin, 2007]. While the predicted relationships have been documented in many species [Clarke et al., 1997; Dobson, 1982], many other species do not conform to expected patterns [Clarke et al., 1997; Clutton-Brock, 1989; Moore, 1992]. Primates are an excellent example of a taxon in which variation in dispersal patterns does not fit traditional theoretical formulations. While the expected mammalian pattern of male-biased dispersal occurs in the majority of primates [Pusey and Packer, 1987], a substantial number, including chimpanzees and bonobos [Kano, 1992; Pusey, 1980], spider monkeys [McFarland Symington, 1987], and muriquis [Strier, 1996], typically exhibit *female-biased dispersal* [Furuichi et al., 2015]. In other polygynous primate species, both sexes may disperse (e.g., gorillas [Harcourt et al., 1976; Robbins et al., 2009; Stokes et al., 2003], hamadryas baboons [Hammond et al., 2006], howler monkeys [Clarke and Glander, 2008; Crockett and Pope, 1993; Glander, 1992], woolly monkeys [Di Fiore et al., 2009], langurs [Stanford, 1991];

Sterck, 1998], colobus monkeys [Struhsaker, 2010; Teichroeb et al., 2009], golden snub-nosed monkeys [Yan, 2012]).

Bisexual dispersal appears to be common among socially monogamous species of a variety of mammals (Alabama beach mouse: [Swilling Jr and Wooten, 2002], titi monkey: [Bossuyt, 2002]; gibbon: [Brockelman et al., 1998; Reichard, 2003], Japanese serow: [Ochiai and Susaki, 2007]; owl monkey: [Fernandez-Duque, 2009], foxes and jackals: [Kapota et al., 2016], beavers: [Mayer et al., 2017]). However, even when both sexes leave the natal group, it does not necessarily mean that *all* aspects of dispersal are similar for males and females. For example, while Sumatran siamangs (*Symphalangus syndactylus*) exhibit bisexual dispersal, genetic data suggest that males are more likely than females to disperse to areas adjacent to their natal groups [Lappan, 2007], whereas hamadryas baboon (*Papio hamadryas*) males are less likely than females to disperse out of social bands [Stadele et al., 2015]. In contrast, males generally disperse further than females in mountain gorilla (*Gorilla beringei beringei*) [Roy et al., 2014] and tarsiers (*Tarsius spectrum*) [Gursky, 2010].

It is now evident that the relationship between dispersal patterns and mating systems is not a simple one, and there is no one “typical” primate dispersal pattern [Lawson Handley and Perrin, 2007; Strier, 1994]. It has been suggested that the evolutionary history of the taxon may be more useful than its mating system for predicting which sex disperses [Di Fiore and Rendall, 1994; Perrin and Mazalov, 1999]. While there is some evidence to support this view, sex-biases in dispersal do not strictly follow phylogenetic patterns, either [Mabry et al., 2013], and different patterns can be found in closely related taxa [Blair and Melnick, 2012; Boinski et al., 2005]. Instead, a more detailed knowledge of the social and mating systems and the behavioral ecology of a species is typically important for predicting the sex that

disperses [Clobert et al., 2001]. For example, among polygynous mammals, factors such as the tenure length of adult males and patterns of relatedness within groups can help to explain which individuals will disperse [Clutton-Brock, 1989]. This observation highlights the importance of considering factors that may influence dispersal on an individual basis for each species of interest, rather than assuming that variation in sex-biased dispersal within taxa is necessarily caused by social mating system or phylogeny.

Theoretical work has developed a variety of explanatory models that look beyond mating system to provide ultimate explanations for observed patterns of dispersal [Johnson and Gaines, 1990; Kokko and Lundberg, 2001; Perrin and Mazalov, 2000]. These are generally organized around three hypotheses related to the avoidance of either inbreeding, mate competition, or resource competition. The *inbreeding avoidance hypothesis* proposes that the evolution of dispersal from the natal group is driven by the risk of mating with close kin [Clutton-Brock, 1989; Dobson, 1982; Greenwood, 1980; Perrin and Mazalov, 1999; Pusey and Wolf, 1996; Pusey and Packer, 1987; Wolff, 1994]. *Competition avoidance hypotheses* propose that the evolution of dispersal is driven by a need to minimize the fitness detriments of competing with kin for mating opportunities or for food resources [Dobson, 1982; Greenwood, 1980; Perrin and Mazalov, 2000].

Socioecological models were essential in driving the development of our understanding of patterns of behavioral variation, and continue to inform our understanding of dispersal patterns. Despite this extensive theoretical work, evolutionary explanations for patterns of dispersal are still hotly debated. The relative importance of inbreeding, mate competition, and resource competition as factors driving the evolution of dispersal patterns likely vary from species to species, and consequently there remains a need to bridge the gap

between theory and empirical observations [Duputié and Massol, 2013; Jack and Isbell, 2009; Lawson Handley and Perrin, 2007; Taborsky, 2008].

Researchers are now acknowledging more explicitly the importance of extensive *intraspecific variation* and flexibility in dispersal and other behaviors [Strier, 2017]. Sex biases in dispersal within a species may show geographical and/or temporal variation [Clarke et al., 1997], with primate dispersal strategies often varying from year to year or from site to site, based on local ecological or social conditions [Aureli et al., 2013; Minhos et al., 2013; Miyamoto et al., 2013]. Even within a relatively small geographic area, there may be variation among groups, as has been observed in colobus monkeys [Wikberg et al., 2012]. At an even smaller scale, variation can exist within a single group. For example, some chimpanzee females disperse while others forgo dispersal and breed in their natal community [Walker, 2015]. Individuals in some species may also disperse in parallel with other members of their natal group, potentially influencing patterns of relatedness among groups [Cheney and Seyfarth, 1983; Jack and Fedigan, 2004; Jones, 1983; Mitchell, 1994; Schoof et al., 2009; Teichroeb et al., 2009]. This variation in dispersal strategies among members of a single species suggests that many primate taxa can flexibly respond to signals in their social and physical environments, which in turn may help them minimize risks and optimize fitness [Strier, 2017].

As empirical evidence on widespread intraspecific variation among primates accumulates, much recent theoretical work has taken a more individual-based approach to studying dispersal [Bonte and Dahiriel, 2016; Jack and Isbell, 2009; Murren et al., 2001]. Some of this work views dispersal as a multi-phase life-history process, consisting of departure from the natal area, a transient phase of movement while searching for a new place

to live, and finally settlement in a new area [Bonte et al., 2012; Clobert et al., 2009; Ronce, 2007; Travis et al., 2012]. Each of these stages may be under selection to reduce the overall cost of dispersal [Bonte and Dohirel, 2016; Travis et al., 2012]. Unfortunately, empirical studies often do not distinguish between these three stages, and this omission can confound our understanding of the influences that social or ecological factors have [Cote et al., 2010].

Explicitly incorporating dispersal into life-history theory can be valuable.

Importantly, it allows researchers to understand the connection between dispersal and other life-history traits (i.e., “dispersal syndromes”) [Ronce and Clobert, 2012]. Viewing dispersal as a context-dependent dimension of life history that can be understood in terms of trade-offs can also aid in explaining variation in dispersal strategies among and within species, and help to integrate proximate and ultimate approaches [Stamps, 2001]. Some theoreticians even advocate placing dispersal at the center of a life-history theory approach, as a principle axis of variation influencing fitness, though a unifying theory describing how dispersal and other life-history traits change with local ecological conditions is presently lacking [Bonte and Dohirel, 2016].

### **Dispersal in “monogamous” primates**

Monogamous mammals are predicted to have bisexual dispersal. Both sexes are expected to disperse prior to reproducing because the only available members of the opposite sex present in the natal group are generally assumed to be close kin (parents or siblings) [Dobson, 1982]. However, in reality, both the composition of “monogamous” groups and patterns of dispersal among its members are more varied.



Monogamy, within non-human primates, has traditionally been defined as a prolonged association between one male and one female, characterized by exclusive mating [Wittenberger and Tilson, 1980]. While monogamy is a *mating system*, the terms “monogamous” and “socially monogamous” are often used to describe the *social systems* of a variety of taxa [Díaz-Muñoz and Bales, 2016]. Monogamy has therefore come to be associated with several concepts and behaviors, such as pair-living, pair-bonding, and living in “nuclear family groups” consisting of closely related kin. While pair-living and family groups may sometimes be associated with monogamous mating systems, these are distinct phenomena that do not always come hand-in-hand with strict monogamy [Fuentes, 1998; Garber et al., 2016; Tecot et al., 2016].

Some pair-living species do mate monogamously and can be characterized as genetically monogamous (e.g., birds: [Goncalves da Silva et al., 2010; Morton et al., 1998; Piper et al., 1997; Quinn et al., 1999]; fish: [DeWoody et al., 2000; Taylor et al., 2003]; primates: [Huck et al., 2014a]). However, many other pair-living species live in social groups consisting of pairs in which either the male, the female, or both engage in mating behaviors with other individuals (i.e., extra-pair copulations) (e.g., birds: [Blomqvist et al., 2002; Brooker et al., 1990; Brouwer et al., 2011; Cockburn et al., 2003; Westneat and Sherman, 1997]; primates: [Fuentes, 1998; Palombit, 1994; Reichard, 1995]; other vertebrates: [Bull et al., 1998; Cohan and Allaine, 2009; While et al., 2009]).

Further complicating matters, some species that are generally referred to as socially monogamous may live in social groups with more than one adult male or female. Among primates, for example, social structures of gibbons and saki monkeys are more flexible than traditionally assumed [Norconk, 2011; Sommer and Reichard, 2000], with groups of white-

faced sakis (*Pithecia pithecia*) and white-handed gibbons (*Hylobates lar*) at some sites frequently containing more than one adult male [Barelli et al., 2008; Reichard and Barelli, 2008; Thompson and Norconk, 2011]. Many taxa categorized as “monogamous” would therefore be better described as pair-living [Fuentes, 1998; Palombit, 1994; Sommer and Reichard, 2000; Tecot et al., 2016], since they typically do not contain just one male, one female, and their genetically related offspring.

Serial monogamy, or the replacement of one adult in a breeding pair, can also produce group structures that differ from the nuclear family groups commonly assumed for monogamous species. This is true even for genetically monogamous species in which extra-pair copulations are rare or absent, such as owl monkeys (*A. azarae*) [Fernandez-Duque and Huck, 2013]. In addition to owl monkeys, the replacement of reproductive adults is also frequent in equatorial saki monkeys (*Pithecia aequatorialis*) [Di Fiore et al., 2007; Van Belle et al., 2016] and several species of gibbon [Brockelman et al., 1998; Koda et al., 2012; Palombit, 1994].

The use of monogamy to refer to a range of social systems, behaviors, and a mating system makes it difficult to evaluate the selective pressures for these phenomena [Tecot et al., 2016]. Likewise, explaining patterns of dispersal observed in socially monogamous taxa is complicated by the fact that “monogamous” species really encompass a variety of social and mating systems. The costs and benefits of philopatry and dispersal clearly differ between genetically and socially monogamous systems and between pair-living “family” groups and groups containing unrelated (extra-pair) adults. We thus might expect taxa with genetically monogamous mating systems to show different patterns of dispersal than pair-living taxa in which extrapair paternity is frequent. Under the consideration of strict monogamy, it is

hypothesized that offspring of both sexes must typically disperse prior to reproducing due to a lack of unrelated mates [Greenwood, 1980; Perrin and Mazalov, 1999; Pusey and Wolf, 1996]. However, as discussed above, serial monogamy and extra-pair copulations often result in situations in which offspring in monogamous groups are residing with unrelated adults of the opposite sex. Lower levels of relatedness among group members compared to what is traditionally expected under a strictly monogamous mating system could thus help to explain why evidence for some hypotheses, particularly the inbreeding avoidance hypothesis, has been inconsistent [Brooker et al., 1990; Brouwer et al., 2011].

### **Delayed Dispersal**

Dispersal is generally considered to be “delayed” when offspring remain with their natal group after they become physiologically capable of reproducing [Ekman et al., 2004]. In monogamous taxa, potential mating partners available in an individual’s natal group are often close relatives (e.g., parents or siblings). In such cases, individuals must disperse prior to reproducing if they are to avoid inbreeding. Even in taxa where unrelated mates may be available in the natal group, due to extra-pair copulations or serial monogamy, offspring frequently do not reproduce prior to dispersing [Fernandez-Duque, 2009; Palombit, 1995; Reichard and Barelli, 2008; Van Belle et al., 2016]. Since lifetime reproductive success can be increased by beginning reproduction early [Altmann et al., 1988], delayed dispersal in monogamous taxa seems somewhat counterintuitive. In spite of this seeming contradiction, offspring of many taxa delay dispersal, and thus delay opportunities to reproduce, by remaining in their natal groups even after they reach sexual maturity. The reasons why

individuals delay dispersal and, at least temporarily, forgo their own reproduction requires further explanation.

One explanation is that delaying dispersal may benefit individuals by allowing them to eventually inherit natal territories [Koenig et al., 1992; Kokko and Johnstone, 1999; Wiley and Rabenold, 1984; Zack and Stutchbury, 1992]. This phenomenon, sometimes referred to as queuing, is “delayed” dispersal at its most extreme, as it allows an individual, who would otherwise need to disperse to avoid breeding with relatives, to avoid the costs of dispersing entirely. However, queuing carries its own risks. While queuing order may be relatively strict in some cases [Creel and Rabenold, 1994; East and Hofer, 2001; Field et al., 2006; Russell and Rowley, 1993; Wiley and Rabenold, 1984], the individual who fills a breeding vacancy in a territory is not necessarily the one who has been queuing for it the longest, and individuals may be evicted by natal group members who inherit a breeding position ahead of them [Balshine-Earn et al., 1998; Cant et al., 2006]. Vacancies may also be filled by dispersing individuals from neighboring territories or by solitary “floaters” through scramble competition, rather than by those in the queue [Cant and English, 2006; Lazaro-Perea et al., 2000; Stiver et al., 2006]. Thus, queuing can be a risky strategy that does not guarantee the inheritance of a breeding position.

Another popular explanation is that individuals may receive indirect fitness benefits by remaining in their natal groups to care for younger siblings. In some taxa, individuals who delay dispersal become nonbreeding helpers in their natal group [Baglione et al., 2002; Brown, 1993; Cockburn, 1998; Ekman et al., 2004], even if they do not typically inherit natal territories [Baglione et al., 2003]. However, delayed dispersal and allocare do not always occur together [Kokko et al., 2001]. Even amongst cooperatively breeding taxa, helping

behavior may actually be an epiphenomenon of delayed dispersal, rather than the underlying cause or explanation for it [Cockburn, 1998; Dillard and Westneat, 2016; Ekman et al., 2001; Koenig et al., 1992].

While inheriting the natal territory and/or providing alloparental care may be sufficient for explaining delayed dispersal in some taxa, other taxa in which individuals frequently delay dispersal are not characterized by territorial inheritance or cooperative breeding. For example, in some species of birds, offspring delay dispersal from their natal territory, but do not provide help at the nest [Curry, 1988; Ekman et al., 1994; Gamero et al., 2014; Gayou, 1986; Green and Cockburn, 2001; Strickland, 1991; Veltman, 1989]. Similarly, monogamous owl monkey offspring frequently delay dispersal without either providing *allocare* or inheriting breeding positions within their natal territory. For these taxa, researchers must seek other explanations for delayed dispersal.

Ecological constraints have often been proposed to explain the retention of offspring in natal groups [Emlen, 1982; Emlen, 1995; Koford et al., 1986; Stacey and Koenig, 1990; Walters et al., 1988], and there is evidence from some species of birds and reptiles to support this claim [Halliwell et al., 2017; Komdeur, 1992; Pruett-Jones and Lewis, 1990; Walters et al., 1992; Zeng et al., 2016]. However, there is also evidence from both quantitative modeling and empirical studies in a variety of taxa to suggest that attempts to explain delayed dispersal primarily through ecological constraints outside the natal territory (e.g., habitat saturation) are too simplistic [Ekman et al., 2002; Koenig et al., 2016; Kokko and Ekman, 2002; Stacey and Ligon, 1991].

Rather than ecological constraints, the benefits of philopatry have been posited as a force selecting for the retention of offspring in the natal group [Stacey and Ligon, 1991].

Delaying dispersal can allow individuals to prolong their access to the benefits associated with living in their natal group, while postponing potential costs of dispersal until those costs are lessened or individuals become more equipped to handle them. For example, by extending their time in the natal group, offspring may maintain access to group-held resources or increase skills, such as foraging efficiency [Gamero and Kappeler, 2015].

Prolonged access to natal group members may also provide offspring with benefits of social living, which would be eliminated if they dispersed to become solitary floaters [Ekman et al., 2004; Koenig et al., 2016]. Being part of a group provides a variety of benefits [Silk, 2007]. Group-living may provide important thermoregulatory benefits, particularly in climates that have cold seasons or have large temperature fluctuations [Hayes, 2000; Weidt et al., 2004]. Being in a group can also increase vigilance for predator detection and avoidance, which can benefit individuals in both cooperative and non-cooperative breeding taxa [Caro, 2005; Ebensperger and Wallem, 2002; Groenewoud et al., 2016; Lima, 1995; Tanaka et al., 2016; Treves, 1998; Wrona and Dixon, 1991]. Social bonds within groups may further be important for the health and fitness of individuals [Seyfarth and Cheney, 2012]. Evidence to support this idea comes from baboons, in which social bonds in females have been shown to increase infant survival [Silk et al., 2003]. Among social species, departing from a group to range solitarily, even for relatively brief periods, can negatively impact individuals [Young and Monfort, 2009].

Beyond the general benefits of group living, remaining in a natal group in which close kin are present may also provide offspring with “nepotistic benefits”, ranging from tolerance to pro-social behaviors, like cooperation and grooming [Ekman et al., 2000; Kokko and Ekman, 2002; Strier, 2008]. Both kin selection theory [Hamilton, 1964] and empirical

studies suggest that remaining with close kin in the natal group offers benefits that would likely be unavailable to dispersing individuals, even if they could forgo a solitary life-history stage and directly enter a new group with unrelated conspecifics.

Explanations for delayed dispersal based on nepotistic benefits (i.e., the safe haven hypothesis) [Ekman et al., 2000; Kokko and Ekman, 2002], have received empirical support in a variety of taxa. Maintaining residence in a group that provides opportunities to cooperate with kin is linked to increased offspring survival in a variety of mammals [Arnold, 1990; Silk et al., 2009; Viblanc et al., 2010]. Nepotistic benefits other than increased survival are also possible. Among birds, experimental evidence from Siberian jays (*Perisoreus infaustus*) indicates fathers provide a safe haven in which offspring can take advantage of natal territory resources without serious competitive interference from extra-group individuals [Ekman and Griesser, 2002]. Western bluebird (*Sialia mexicana*) sons also receive access to space and resources by delaying dispersal when parents are present [Dickinson et al., 2014]. Among mammals, prairie dogs are less likely to disperse when their genetic mother and siblings, with whom they often cooperate, remain in the natal group [Hoogland, 2013]. Thus, the presence of parents or other close kin may frequently encourage individuals to delay dispersal and utilize their natal group as a safe haven while waiting for breeding opportunities to arise [Kokko and Ekman, 2002].

Delaying dispersal may also help offspring monitor conditions or reproductive opportunities in nearby territories, while still maintaining access to safe havens provided by their natal group. Separating from the natal group and exploring extra-territorial areas prior to permanently dispersing is commonly known as “prospecting”, and this behavior appears to be common in a variety of birds and mammals [Kingma et al., 2016; Mares, 2012; Raihani et

al., 2010; Reed et al., 1999; Ridley et al., 2008; Solomon, 2003]. The relative costs and benefits of remaining in a natal group *versus* dispersing typically vary over time as climatic conditions, environmental quality, and local reproductive opportunities fluctuate [Jones, 2005]. Consequently, prospecting can benefit individuals by providing them with information about the quality of nearby territories or mates [Dittmann et al., 2005; Selonen and Hanski, 2010]. It may also allow them to time their dispersal to coincide with periods of relatively low costs (e.g., when vacancies are available in neighboring groups), or allow males to engage in extra-group breeding prior to dispersing [Eikenaar et al., 2008; Griffin et al., 2003; Young et al., 2007].

While prospecting can allow individuals to gather information about breeding vacancies or the quality of nearby territories or potential mates, it often entails costs [Kingma et al., 2016; Young and Monfort, 2009]. Individuals may receive aggression from residents in whose territories they are prospecting [Doolan and Macdonald, 1996; Lazaro-Perea, 2001; Raihani et al., 2010], and prolonged prospecting expeditions may result in chronic stress [Young and Monfort, 2009]. Individuals may selectively time prospecting expeditions to minimize these costs, although the cues individuals utilize to make prospecting decisions are still unclear for most taxa [Mares et al., 2014].

In summary, delaying dispersal offers a variety of potential benefits that may outweigh the costs of delaying one's own reproduction. Remaining in familiar natal group territories while monitoring reproductive opportunities via prospecting can allow individuals to minimize dispersal costs. The incentives for delaying dispersal may be particularly high when nepotistic benefits are available due to high relatedness within the natal group [Ekman et al., 2001; Kokko and Ekman, 2002]. To explain variation in age at dispersal and better



understand why individuals eventually stop delaying dispersal and finally leave the relative safety of their natal group requires closer examination of both the solitary stage of the dispersal process and the proximate mechanisms involved in dispersal decisions. These topics are discussed in the next two sections.

### **The solitary stage of dispersal**

After dispersing, individuals of many group-living species spend time as solitaires, also frequently referred to as “floaters”, because they lack permanent association with a group or territory [Penteriani et al., 2011]. The ecological and social challenges faced by individuals during the solitary stage of dispersal can greatly impact a disperser’s ability to attain a breeding position, and thus have important consequences for their fitness and the inclusive fitness of their relatives. However, of the three stages of dispersal (emigrations from the natal group, solitary vagrancy, and immigration to a new group), the solitary stage is typically the least well-studied and least understood [Grabowska-Zhang et al., 2016; Ronce, 2007].

Spending time as a solitary floater is common for individuals in a variety of socially monogamous primates (owl monkeys [Huck and Fernandez-Duque, 2016], siamangs [Palombit, 1995], sakis [Soini, 1986; Thompson, 2015]), as well as some individuals in primate species with polygynous mating systems (e.g., howlers [Cuarón, 1997], macaques [Duboscq et al., 2016], baboons [Alberts and Altmann, 1995a]). Among socially monogamous primates, floating as a solitary may be an unavoidable part of dispersing, as it may be the only way for individuals to find a mate and reproduce.

Being a solitary can entail many costs. Floaters typically face mortality risks from increased predation, physical damage, and other physiological changes [Bélichon et al., 1996; Bonte et al., 2012; Ims and Andreassen, 2000; Yoder et al., 2004]. Empirical studies have demonstrated these costs in a variety of taxa. For example, in pied babblers (*Turdoides bicolor*), juveniles roaming alone spend less time foraging and experience a loss of body mass, which negatively impacts their ability to enter a new group in a breeding position (compared to individuals who do not spend time as solitaires) [Ridley et al., 2008]. In addition, solitary dispersing male baboons (*Papio cynocephalus*) have mortality rates at least twice as high as group-living males [Alberts and Altmann, 1995a].

Solitary floaters often face aggression from conspecifics in established groups. Among socially monogamous primates, resident saki males are aggressive towards floaters [Thompson, 2015], and gibbons exhibit intrasexual aggression towards floaters [Brockelman and Srikosamatara, 1985; Mitani, 1987]. Both male and female Azara's owl monkeys also frequently interact aggressively with solitary floaters [Fernandez-Duque and Huck, 2013]. To deal with this aggression, floaters may develop strategies to minimize risk of agonistic encounters while maintaining access to information about breeding opportunities in nearby groups. For example, ranging patterns of owl monkey solitary floaters suggest that they stay relatively close to groups, but avoid groups' core home ranges. This strategy likely allows them to monitor mating opportunities in groups, while also being able to escape aggression from residents if detected [Huck and Fernandez-Duque, 2016; Huck and Fernandez-Duque, in press].

To better understand the costs of the solitary life-history stage, more data on the behavior of solitary floaters and their attempts to immigrate into established groups are

needed. To shed light on this issue, I discuss data from identified dispersing owl monkeys that spent time as solitary floaters in the final chapter of this dissertation.

### **Proximate mechanisms: Hormones and behavior**

Socioendocrinological research in primates has offered insight into many key aspects of primate behavior and social systems. The relationship between hormones and social behavior is complex. The social environment both influences and is influenced by an individual's sociosexual behavior and neuroendocrine mechanisms, which in turn interact with one another to influence reproductive success. Socioendocrinology thus provides a framework for understanding the factors that regulate differential reproductive success among individuals and provides a means of connecting reproductive endocrinology with evolutionary biology and behavioral ecology [Bercovitch and Ziegler, 1990].

Studying hormonal and behavioral changes that occur during development and maturation is essential for understanding the mechanisms regulating natal dispersal. In addition to interacting with social behavior, hormones are associated with body condition and play a substantial role in determining the timing of sexual maturation, both of which have consequences for the costs and benefits of retaining relationships with natal group members *as opposed to* dispersing [Dufty and Belthoff, 2001; McShea, 1990; Monard et al., 1996].

To evaluate hypotheses proposed to explain dispersal, specifically the inbreeding and mate competition avoidance hypotheses, it is necessary to know when offspring develop interest in mating or become physiologically capable of reproducing. Specifically, the inbreeding avoidance hypothesis predicts that the onset of sexual maturity will not occur until after dispersal, while the mate competition avoidance predicts that sexual maturity will take

place prior to dispersal. Examining reproductive hormones, such as estrogens and androgens, allows researchers to identify when individuals undergo puberty, and evaluate how the timing of sexual maturity relates to dispersal or the onset of pre-dispersal behavior, such as prospecting.

Behavioral interactions with group members, particularly agonism and sexual interactions, can also provide valuable insight into the mechanisms of and hypotheses for natal dispersal. Specifically, sexual interactions between subadults and natal group members provide clear evidence for mate competition within the natal group, while the inbreeding avoidance hypothesis predicts that subadults will not engage in sexual behaviors with natal group members. Higher aggression and the overall deterioration of relationships between adults and pre-dispersed, sexually mature subadults are also predicted by the mate competition avoidance hypothesis, particularly after the replacement of a genetic parent of the opposite sex [Emlen, 1997]. The resource competition avoidance hypothesis, on the other hand, predicts that agonistic behavior between adults and pre-dispersing subadults will occur primarily in contexts of foraging rather than mating or socializing with potential mates.

The remainder of this section will first outline and discuss how sex hormones, particularly estrogens and progesterone in females and testosterone in males, are involved in the onset of sexual maturity and sexual behaviors, and then explore how they relate to the social environment in the natal group and ultimately dispersal. Subsequently, it will discuss how behaviors, particularly aggression and sexual behavior, may function as proximate mechanisms regulating natal dispersal in primates.

### **Hormonal correlates of sexual maturation**

Primates undergo many physiological changes during adolescence. These include pubertal increases in the secretion of certain hormones (typically androgens such as testosterone in males, and estrogens and progesterone in females) and the development of secondary sexual characteristics [Dixson, 1994; Dixson and Nevison, 1997; Mann et al., 1983; Martin et al., 1977; Muehlenbein et al., 2001]. While the timing of these changes is influenced by age, nutritional status, and physical condition [Cameron, 1996; Coe et al., 1981], physical and hormonal changes experienced during reproductive maturation may also be influenced by the social environment.

Among males, puberty may be delayed by exposure to adult male conspecifics [Bercovitch, 1993; Rose et al., 1978]. For example, evidence that the presence of adult males may delay development of secondary sexual characteristics and inhibit elevations of androgens in younger, more subordinate males comes from both mandrills [Wickings and Dixson, 1992] and orangutans. Among orangutans, the presence of adult males may delay the development of secondary sexual characteristics, such as cheek flanges and mature vocal sacs [Maggioncalda et al., 1999]. Some male orangutans remain in an adolescent-like form for a decade or more after the age of sexual maturity, and these arrested males have lower Testosterone levels, which they maintain throughout their lives, even years after developing into flanged males [Emery Thompson et al., 2012]. This observation suggests that early exposure to dominant adult males can have long-term organizational effects on male orangutan physiology. While it had been suggested that arrested development is the result of chronic stress from exposure to aggressive mature males, levels of urinary glucocorticoids and prolactin in arrested male orangutans support the hypothesis that arrested development is

actually an adaptation for stress avoidance during the adolescent period, rather than a result of stress itself [Maggioncalda et al., 2002].

Exposure to adult conspecifics may also either hasten or decelerate the pace of reproductive maturation in females. Many female primates are characterized by a rather unique life history period of adolescent subfecundity [Dixson, 1998]. Socioendocrine factors may help to explain the delayed onset of adult-like reproductive function associated with this period [Bercovitch and Ziegler, 2002]. Exposing adolescent females to adult males stimulates changes in reproductive hormones and/or behavior in several species. For example, exposure to adult males stimulates increased estradiol production in squirrel monkeys [Mendoza and Mason, 1991] and hastens the onset of first estrus in galagos [Izard, 1990]. Female muriquis have been observed to commence cycling of ovarian hormones only after transferring out of their natal groups and into groups with unfamiliar adult males [Strier and Ziegler, 2000]. Similarly, young cotton-top tamarin females removed from their families and paired with an unfamiliar male were also observed to experience accelerated puberty [Widowski et al., 1990; Ziegler et al., 1987].

In light of this evidence, adolescent subfecundity could be a nonadaptive consequence of the need to fine-tune the coordination of various neuroendocrine system components. However, it could also be adaptive, by allowing females to postpone first conception until socioecological conditions are favorable [Bercovitch and Ziegler, 2002]. The proximate and ultimate causes of adolescent subfecundity are an area ripe for future research.

Dispersal is a major event that drastically alters both the physical and social environment that a dispersing individual experiences [Clobert et al., 2001]. It is thus unsurprising that hormonal changes are frequently associated with dispersal. Changes in

androgens and glucocorticoids are among those most commonly proposed to be associated with dispersal, but it is usually unclear whether hormonal changes are causal or a consequence of leaving the natal group [Dufty and Belthoff, 2001]. For most taxa, only correlational data are available (though spotted hyenas seem to increase testosterone as a *result* of dispersing to non-natal groups [Holekamp and Smale, 1998]). While changes in reproductive hormones may occur after dispersing, possibly as the result of exposure to new potential mates [Strier and Ziegler, 2000], in other cases, changes in hormones may occur *prior to* dispersal. These changes may influence predispersal behaviors, such as prospecting, and eventually trigger dispersal [Dufty and Belthoff, 2001]. Sexual maturation of predispersed subadults may also cue adults, or other natal group members, to alter their behavioral interactions with subadult individuals. All of this suggests that changes in endocrine function may be closely linked to behaviors associated with dispersal, such as increased aggression or decreased prosocial interactions among predispersed individuals and natal group members.

In sum, while both endogenous factors and cues from the physical environment may play major roles in determining the timing of sexual maturity [Bronson, 1989; Coe et al., 1981], it is clear that socioendocrine factors also substantially contribute to the regulation of reproductive development in both male and female primates. The ability to flexibly respond to social conditions and adjust endocrine mechanisms and development accordingly is likely adaptive [Bercovitch and Ziegler, 1990]. However, defining exactly how delaying the onset of puberty or mating behavior translates into increased reproductive success requires further investigation.

## **Behaviors associated with dispersal**

Agonistic behavior may be an important mechanism driving dispersal. In particular, aggression seems to be a mechanism important in the peripheralization and eventual dispersal of young males in many species (e.g., baboons [Altmann and Altmann, 1970], howler monkeys [Crockett and Pope, 1988; Cuarón, 1997], langurs [Boggess, 1980; Mohnot, 1978; Rudran, 1973], macaques [Drickamer and Vessey, 1973; Pusey and Packer, 1987], etc.). However, this pattern of aggression is not observed across all environmental conditions [e.g., long-tailed macaques *Macaca fascicularis* in anthropogenic environments [Lute et al., 2014]], and appears to be absent or relatively unimportant in other species [e.g., capuchin monkeys [Jack and Fedigan, 2004], crab-eating macaques [Van Noordwijk and Van Schaik, 1985; Van Noordwijk and Van Schaik, 2001], etc.). Thus, variation in the role that agonism plays in dispersal plainly exists even within related taxa.

One well-described type of agonistic behavior that may be linked to dispersal in some taxa is “episodic targeting aggression”. The phrase episodic targeting aggression is used to describe aggression during which 1-2 individuals receive persistent attacks from other group members, generally until the victim or victims are forced to leave the group [Vick and Pereira, 1989]. Episodic targeting aggression was initially described after being observed in several species of lemur (*Lemur* spp.) in naturalistic captive settings [Digby, 1999; Vick and Pereira, 1989], although this behavior may also occur among lemurs in the wild [Jolly, 1998]. Episodic attacks can be carried out by individuals who are close kin, and targeted individuals are often severely injured and usually expelled from their groups [Vick and Pereira, 1989].

There are similarities between episodic targeting in lemurs and patterns of aggression experienced by dispersing offspring in other taxa. For example, aggression similar to episodic



targeting in lemurs occurs in meerkats (*Suricata suricatta*), in which dispersing individuals are targeted and often injured or forced out of their groups [Doolan and Macdonald, 1996]. However, episodic targeting aggression in lemurs can be directed at almost any type of individual, including adults, which make it distinct from the aggression directed primarily toward adolescent or dispersing offspring in other taxa [Vick and Pereira, 1989]. Currently, the term “episodic targeting aggression” is generally reserved for descriptions of episodic aggression amongst all types of individuals in lemurs [Jolly, 1998]. Therefore, to avoid confusion, severe episodes of aggression targeted at dispersing individuals in other taxa should not be referred to as episodic targeting aggression.

While intense aggression may be linked to dispersal in a variety of primate taxa, the causes and manifestation of this aggression vary. In some cases, a specific act of aggression from a natal group member can be linked directly to the onset of sexual behavior in a predispersed individual (e.g., genital inspections or copulations) [Huck and Fernandez-Duque, 2012]. In most cases, the immediate cause of aggression is less clear, but rates of aggression directed at predispersed individuals may increase as individuals approach sexual maturity [Altmann and Altmann, 1970; De Benedictis, 1979; Drickamer and Vessey, 1973]. Dispersal events resulting from severe aggression are not always culminations of repeated agonism or received aggression that gradually increased over time. Intense aggressive events may occur without precedent, as the first instance of severe aggression observed between an offspring and its attacker(s). For example, in owl monkeys, a single bout of severe aggression, which includes biting and wounding, has been observed to occur on the same day that the recipient of the aggression permanently dispersed from their natal group [Corley, personal observation; Huck and Fernandez-Duque, 2012].

While agonistic behavior, particularly intense aggression, can trigger dispersal events, other times dispersal may not be associated with aggression of any kind [Ekernas and Cords, 2007; Lute et al., 2014]. Even in taxa in which intense aggression frequently drives individuals from their natal groups, some individuals appear to leave voluntarily, particularly when presented with opportunities to join members of the opposite sex [Cant et al., 2001]. Thus, while aggressive behavior is an important factor to consider when examining dispersal patterns, it must be considered in the context of other social and ecological factors.

### **Owl monkeys of the Argentinean Chaco: A model for understanding dispersal in monogamous species**

Owl monkeys (*Aotus* spp.) are small, arboreal New World primates, notable for their nocturnal activity patterns, pair-living social system, and biparental care [Fernandez-Duque, 2011; Wright, 1994]. They are the only nocturnal anthropoids, although at least one species, Azara's owl monkey (*A. azarae*), has evolved cathemeral activity patterns (i.e., is potentially active during the night and day) [Fernandez-Duque and Erkert, 2006; Tattersall, 1987]. *A. azarae* thus offers a unique opportunity for collecting data on owl monkeys during daylight, and most of what is known about wild owl monkey demography and behavior comes from observations of this species at a single location in Argentina.

In the Argentinean Gran Chaco, Azara's owl monkeys display both social and genetic monogamy [Fernandez-Duque and Huck, 2013; Huck et al., 2014a]. Groups consist of just one adult male, one adult female, and generally between one and four offspring who have yet to disperse [Fernandez-Duque et al., 2001; Huck et al., 2011]. Groups occupy home ranges of 4-10 ha (mean =  $6 \pm 2$  ha), which they may defend aggressively from solitary floaters or

other social groups [Fernandez-Duque, 2011; Wartmann et al., 2014]. Social groups are very cohesive: the reproductive pair has a close socio-spatial relationship and all group members typically remain within 5-10 m from one another as they rest, move, and feed together [Huck and Fernandez-Duque, 2012]. Only the reproductive pair breeds, generally producing no more than one infant annually [Huck et al., 2014b]. Births are very seasonal, with 80% occurring in October or November [Fernandez-Duque et al., 2002].

Males provide intensive paternal care to offspring. Starting one week after a birth, males carry the infant 84% of the time [Juárez et al., 2003; Rotundo et al., 2002]. The adult male will also play, groom, and share food with offspring, even after infancy [Fernandez-Duque, 2011; Rotundo et al., 2005; Wolovich et al., 2008]. Adult males will even provide care to offspring to whom they are not related; after an adult male replacement, the new male will take over carrying and interacting socially with the previous male's infant [Fernandez-Duque et al., 2008]. Unlike cooperatively breeding taxa, older offspring in the group do *not* carry infants or assist in providing care to their siblings [Rotundo et al., 2005].

All offspring disperse from their natal groups prior to reproducing, typically sometime between two and five years of age. After dispersing, most individuals spend some time as solitary "floaters", before becoming part of a reproductive pair in a non-natal group [Fernandez-Duque, 2009]. Solitary floaters represent intense intra-sexual competition for resident adults, who are regularly replaced by intruding floaters, leading to a social system that is best described as serial monogamy [Fernandez-Duque and Huck, 2013].

The processes of leaving a natal group, ranging solitarily, and finding a reproductive position are vital to understanding monogamy in owl monkeys, yet they remain poorly understood phases of owl monkey life history. The following chapters in this dissertation

examine aspects of these dispersal processes by utilizing demographic, behavioral, and hormonal data. To place these chapters in context, the remainder of this section provides background information describing what we currently know about development and the onset of reproductive maturity in male and female owl monkeys and our ability to detect it using hormonal data.

## **Owl Monkey Reproductive Endocrinology and Sexual Maturation**

### *Female reproductive endocrinology and sexual maturation*

Unlike some primate species, which have sexual swellings that advertise estrus, there are no visual signals that can be used to identify ovarian cycling in owl monkeys [Bonney et al., 1979; Dixson, 1994; Wolovich and Evans, 2007]. Therefore, changes in hormone levels must be utilized to ascertain the reproductive status of females.

Ovarian cycles are characterized by fluctuations in ovarian hormones, specifically with peaks of estrogen and progesterone in the luteal phase. Peaks of progesterone in particular are typically considered to be evidence of ovulation, as progesterone is secreted by the corpus luteum formed in the ovarian follicle after an oocyte is released [Mayor et al., 2015]. Owl monkeys excrete progesterone mainly as 6 $\beta$ -hydroxy-pregnanolone, with 16 $\alpha$ -hydroxypregnanolone and pregnanediol also being important metabolites [Bonney and Setchell, 1980]. Measuring pregnanediol-3 $\alpha$ -glucuronide (PdG) can therefore provide estimations of progesterone excretion during the ovarian cycle, and PdG levels can be monitored to detect ovarian cycling in owl monkeys [Bonney et al., 1979; Dixson, 1983; Fernandez-Duque et al., 2011].

The age when female owl monkeys become sexually mature is not well-established. While ovarian hormones have been monitored in both captive and wild adults [Bonney et al., 1979; Dixson, 1983; Fernandez-Duque et al., 2011], hormone profiles of younger females have not been systematically examined. Data on age at first birth and ovarian morphology of captive subadults suggest that females may reach sexual maturity between 2-3 years of age. The mean age at first birth for nine females living in a captive population in Iquitos, Peru, was  $40.56 \pm 7.82$  (SD) months, with one female giving birth at the age of only 25 months [Gozalo and Montoya, 1990]. Additionally, ovaries from captive *A. nancymaae* and *A. vociferans* females as young as three years old showed formation of corpus lutea, indicating the presence of ovarian cycles [Mayor et al., 2015].

However, the pace of development and reproductive maturation in captive and provisioned primates can be substantially different than in the wild [Alberts and Altmann, 1995b; Altmann and Alberts, 1987; Altmann et al., 1981; Altmann et al., 1977; Dunbar, 1990; Milton, 1981; Mori, 1979; Rowell and Richards, 1979]. In the wild, females must disperse and pair with an individual in a non-natal group before they can reproduce. Since dispersal does not typically occur until individuals are 2-5 years old, it is unsurprising that reproduction in individuals less than four years of age has not been observed in the wild [Huck et al., 2011]. Studies have not yet investigated hormone cycles in wild subadult owl monkeys, so it is unknown whether females begin to undergo sexual maturity before or after they disperse from their natal groups.

#### *Male reproductive endocrinology and sexual maturation*

Studies examining the reproductive physiology or sexual development of wild male owl monkeys are lacking. Everything we know about this subject comes from studies done in captivity [Dixon et al., 1980; Dixon, 1983; Dixon, 1994; Gozalo and Montoya, 1990], thus we must rely on these studies to generate hypotheses and predictions for wild individuals.

Data on age at first birth suggests that, like captive females, captive males may reach sexual maturity at 2-3 years of age. The mean age at first birth for 12 males living in a captive population in Iquitos, Peru, was  $42.17 \pm 10.73$  (SD) months, and conception occurred in the partner of a male as young as 23.5 months [Gozalo and Montoya, 1990]. A longitudinal study examining increases in testosterone (T), growth, and development of other physiological characteristics to assess the onset of puberty indicates an even younger age of sexual maturity in males [Dixon et al., 1980]. Six captive *Aotus griseimembra* males showed increases in testosterone when males were less than one year old (median = 313 days, range 211-337 days). The onset of puberty, as indicated by increases in testosterone, did not correspond to marked increased in body weight or testicular volume. In contrast, the onset of puberty was correlated with marked growth and development of the subcaudal scent-gland, which occurred when males were between 282 and 370 days old [Dixon et al., 1980; Dixon, 1994]. Administration of testosterone to a prepubertal male also stimulated the growth of the subcaudal gland prematurely, further suggesting a close link between testosterone and the development of this gland [Dixon et al., 1980].

In free-ranging *A. azarae* in the Argentinean Gran Chaco, secretions from the subcaudal gland produce a stain visible to observers. The size of the subcaudal stain is positively associated with age in both wild males and females. Individuals <12 months do not have any subcaudal staining and some continue to have very little staining until they reach

subadulthood (24 months). Staining continues to increase until individuals reach about four years of age [Huck et al., 2011]. The hormonal correlates of subcaudal gland staining have not been investigated in *A. azarae*, nor in females of any owl monkey species. Thus, how observations of subcaudal gland development in the wild relate to sexual maturity, as indicated by increases in T, is unclear.

The captive study of six *A. griseimembra* males also provides important insight into how social environment may influence the timing of male puberty. The timing of the hormonal and physiological changes associated with puberty was the same in three males which remained housed with their natal groups as in males that were removed from their natal group and housed solitarily [Dixson et al., 1980]. Thus, at least for captive individuals, there does not seem to be evidence that remaining in the natal group delays or suppresses the onset of sexual maturity in males. While the pace of growth and reproductive maturation in captive and provisioned primates is known to often differ substantially from individuals in the wild [Alberts and Altmann, 1995b; Altmann and Alberts, 1987; Altmann et al., 1981; Altmann et al., 1977; Dunbar, 1990; Milton, 1981; Mori, 1979; Rowell and Richards, 1979], being housed socially with natal group members did not retard the onset of adult-like androgen production and puberty, suggesting that males may be predicted to reach sexual maturity prior to dispersing in the wild as well.

Unfortunately, there are several aspects of male owl monkey physiology and reproductive biology that make it difficult to assess sexual maturity in wild individuals using only levels of T. Owl monkeys have unusual testicular physiology, indicative of arrested spermatogenesis and/or low numbers of spermatozoa [Dixson, 1983]. However, captive adult males with this testicular physiology are still able to sire offspring. Exactly how testosterone

levels relate to sperm production and what minimum levels are necessary for male owl monkeys to conceive in the wild remain to be determined [Dixson, 1994]. It should also be noted that substantial variation among individuals in levels of circulating testosterone has been observed even with a relatively small sample of six captive males [Dixson et al., 1980]. These findings make utilizing testosterone, by itself, somewhat problematic for assessing reproductive function in owl monkeys. Data from five predispersed juvenile and two predispersed subadult males suggests that wild *A. azarae* males do not increase testosterone to levels similar to those of adult males prior to dispersing from their natal group [Corley et al., 2016]. Therefore, additional data on testosterone levels in wild adult males throughout the mating season is needed to assess whether testosterone levels found in wild subadult males may be sufficient for siring offspring.

#### *Using fecal samples to monitor steroid hormones: benefits and challenges*

Studying primates in the wild often requires the use of non-invasive sampling techniques, such as the collection of urine or feces. This approach provides the tremendous benefit of allowing researchers to regularly collect hormonal data without capturing or extensively disturbing their study subjects. While utilizing feces to obtain endocrine data is now a common practice among field primatologists, it can make analyses of hormones more complicated. The main reason is that mammals typically excrete primarily hormone metabolites rather than native hormone in their feces, and the specific metabolites excreted are variable from species to species and may be unknown for the taxa of interest [Higham, 2016].



Enzyme immunoassays (EIAs) used to assess hormone concentrations in feces should therefore have specificity for a metabolite/form of the hormone that is known to be excreted in the feces of the study species. Previous studies have validated that progesterone metabolites (PdG) and secreted estradiol (E1G) can be detected in owl monkey feces and can be used to detect ovarian cycles and pregnancy [Fernandez-Duque et al., 2011]. Validations also indicate that testosterone is present, at least in small amounts, and detectable in owl monkey feces (C. Vallengia & T. Ziegler, personal communication). Furthermore, the cross-reactivity of antibodies can be determined to assess what hormone or hormone metabolites an assay may be detecting. EIA manufacturers, such as Arbor Assays, typically evaluate and report the cross-reactivity of antibodies used in their commercially available assay kits, and this information has been used to ensure that the assays used to analyze owl monkey fecal samples are appropriate for assessing concentrations of the steroid hormones of interest (e.g., PdG, E1G, and androgens; Chapter 4).

Collection methods and the conditions and duration of storage can also influence hormone concentrations [Khan et al., 2002; Lynch et al., 2003]. It is therefore necessary to be consistent in the methods and storage conditions utilized throughout a study. Fixing feces in alcohol immediately after collection is a common method utilized to preserve fecal hormones. In various studies, hormones in non-extracted feces stored in ethanol have been found to be relatively stable at ambient temperatures: glucocorticoid metabolites up to 28 days [Shutt et al., 2012], cortisol up to 5 months [Cavigelli, 1999; Khan et al., 2002], and corticosterone and testosterone up to 180 days [Santymire and Armstrong, 2010]. Samples in ethanol can be stable for even longer periods of time when stored at -20°C [PdG and E concentrations were still stable after 270 days [Daspre et al., 2009]].

While storage conditions can influence the amount of detectable hormone in a sample, this is not necessarily a problem that needs to be overcome in order to compare concentrations among samples collected and stored in the same manner. In other words, while comparisons of hormone levels obtained from feces stored in different conditions or comparisons among samples that have been stored for substantially different durations before extraction should be treated with caution, samples that are processed and stored in similar conditions (as is the case in the data reported in this dissertation, Chapter 4) should produce results that can, at least, be compared to one another. Furthermore, overall patterns of hormone data may remain detectable even if the absolute values of hormone concentrations vary in different storage conditions. The assay results from feces stored in unfrozen conditions were found to be robust in terms of the general pattern of the data (e.g., estrogen levels could still be used to distinguish pregnant vs. non-pregnant females, GC profiles of age classes were similar to those obtained from samples frozen or processed immediately, etc.) [Lynch et al., 2003]. Thus, if consistency in storing and analyzing is maintained, feces remain a good non-invasive source of information about the endocrine function of primates.

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## **Chapter 2. Patterns of dispersal in monogamous owl monkeys: an evaluation of demographic changes and environmental factors influencing natal dispersal**

### **Abstract**

The timing of natal dispersal may be highly flexible and dependent upon a variety of ecological and social factors. Delaying dispersal may be an adaptive strategy that individuals utilize to minimize dispersal costs and maintain access to benefits provided by the natal group. Understanding proximate factors that influence the timing of dispersal can provide insight into ultimate explanations of dispersal patterns in a species. We investigated social and ecological factors associated with the age and timing of natal dispersal in socially monogamous owl monkeys (*Aotus azarae*) in the Argentinean Gran Chaco. Specifically, we examined how proximate factors, such as adult replacements, births, group size, and rainfall (as a proxy of resource abundance) explained variation in the age and timing of dispersal. Owl monkey dispersal was highly flexible (age at dispersal ranged from 1.7-5.3 years), but all individuals dispersed prior to reproducing. Experiencing an adult replacement, particularly the replacement of a same sex adult as a subadult, was associated with dispersal. Dispersals occurred throughout the year, but were concentrated in the spring and early summer. Individuals were more likely to disperse outside of this preferred season if there had been a recent infant birth in their natal group and if there was less than average rainfall, and thus increased resource scarcity, during the fall/winter season. Our results suggest that inbreeding *and* competition avoidance may explain dispersal in different circumstances. Including individuals that disappeared produced somewhat different results from analyses limited to individuals with confirmed dispersals. Our findings suggest that researchers should be cautious when drawing inferences about dispersal from the disappearances of offspring.

## **Introduction**

Natal dispersal, the movement of individuals from their birthplace to new areas in which they may breed, is an important aspect of life history that influences a variety of processes. Taxa should evolve dispersal patterns that minimize the costs of dispersing and maximize fitness. Interspecific variation in which individuals disperse and when they disperse may be explained by differences in the social and ecological factors that influence the costs of benefits of dispersal for a particular species [Bonte et al., 2012; Jones, 2003]. Understanding proximate factors associated with dispersal decisions can therefore provide insight into ultimate explanations of dispersal patterns. Studies examining the influence that ecological and social factors have on individuals' dispersal decisions are also crucial for developing an understanding of spatial structure and dynamics of populations, which has important implications for population management and conservation [Bowler and Benton, 2005]. However, dispersal dynamics are complex, and there remains a need for empirical work to increase our understanding of dispersal, particularly in long-lived vertebrate species [Bowler and Benton, 2005; Ronce, 2007].

Among primates, dispersal by at least some individuals is universal, and it is often essential for individuals to disperse before they can successfully reproduce [Pusey and Packer, 1987]. Yet, dispersal is also risky and poses many potential costs, such as increased risk of predation, decreased foraging efficiency, social isolation, and aggression from unfamiliar conspecifics [Bonte et al., 2012; Isbell and Van Vuren, 1996; Jones, 2003]. Additionally, postponing dispersal can allow individuals to increase foraging and other skills in the relative safety of a familiar home range and maintain access to nepotistic benefits by

remaining in close contact with kin in the natal group [Ekman and Griesser, 2002; Hamilton, 1964].

Delaying dispersal may therefore be an adaptive strategy that individuals utilize to minimize dispersal costs [Ekman, 2007; Ekman et al., 2001; Ekman et al., 2004; Kokko and Ekman, 2002]. The timing of dispersal in a given taxa is expected to depend upon when an individual develops the body size, physical condition, and skills sufficient for withstanding the costs of ranging solitarily and finding a mate [Bowler and Benton, 2005; Tarwater and Brawn, 2010]. However, in some taxa, individuals may delay dispersal beyond the point when these conditions are met to maintain access to nepotistic benefits or to time dispersal to coincide with improved conditions anticipated to arise (e.g., when resources or mating opportunities are more abundant in the local environment) [Ekman et al., 2004; Kokko and Ekman, 2002].

When individuals delay dispersal, and make dispersal decisions based on local conditions, it can result in a great deal of variation in dispersal *within* a species. While it has long been recognized that dispersal patterns vary among taxa [Trochet et al., 2016], more recently researchers have begun to explicitly acknowledge that there is often substantial heterogeneity in the timing of dispersal among individuals within species and populations, as well [Clobert et al., 2009; Strier, 2017]. Intraspecific variation in the timing of dispersal has been linked to many different factors, including intrinsic variables, like hormones, body condition, and personality and temperament, as well as extrinsic variables, such as ecology and the social environment in the natal group [Cote et al., 2010; Dufty and Belthoff, 2001; Ims and Hjermand, 2001]. When the timing of dispersal is highly variable within a species, as it is in many primate species [Alberts and Altmann, 1995; Cheney, 1983; Fernandez-Duque,

2009; Jack and Fedigan, 2004; Morelli et al., 2009], it is likely that a combination of social, ecological, and physiological variables are responsible for it [Jack et al., 2012].

The timing of dispersal has been linked to a variety of social factors. The size and composition of the social group is one factor that may influence dispersal decisions. As a larger group size entails more competition with kin in the natal group, increases in group size, through births or emigrations, may be predicted to trigger dispersal [Dobson, 1982]. Empirical support for this idea is mixed, as larger group size is associated with higher probability of dispersal in some cases [Clutton-Brock et al., 2008; Pope, 2000; VanderWaal et al., 2009], but not always [Teichroeb et al., 2009].

The disappearance or replacement of a parent can also have enormous impacts on behavior, including dispersal decisions. The death or replacement of a parent removes a close kin member from the natal group, which may reduce the benefits of philopatry, particularly for taxa in which cooperation with close kin is common [Hamilton, 1964; Strier, 2008]. In some taxa, males whose mothers die disperse at younger ages [Alberts and Altmann, 1995]. Empirical evidence also suggests that take-overs or replacements of resident adults in the natal group often influence the timing of dispersal. For example, turn-overs in the adult male or males in the natal group appear to contribute to the dispersal of male offspring in several primate taxa [Ekernas and Cords, 2007; Jack et al., 2012; Morelli et al., 2009; Robinson and Janson, 1987; Rogers and Chism, 2009].

Adult replacements can trigger offspring to disperse at times that are less than optimal for the survival and fitness of the offspring. Individuals that experience an adult replacement may disperse when they are too young or small or when their body condition is otherwise poor [Ims and Hjermmann, 2001; Stamps, 2006]. Replacements may also influence



individuals to disperse during environmental conditions or times of the year when mates or resources are relatively scarce and their chances of survival may be lower. For example, among lions (*Panthera leo*), the arrival of an unfamiliar adult male to the natal group can trigger males with poor body condition and males who are too young to survive on their own to disperse. This leads to the deaths of many of these dispersing individuals and can be viewed as a type of “delayed infanticide” [Elliot et al., 2014]. Adult replacements may thus be associated with unsuccessful dispersals, and complicate attempts to explain the timing of dispersal based on other social and/or ecological factors.

Among “family” living species, in which an adult pair resides with one or more young, the replacement of either adult can have profound effects on social relationships within the group [Emlen, 1995]. Parents may provide benefits to pre-dispersing offspring in the form of tolerance or protection. Removal of a genetic parent reduces nepotistic benefits, decreasing the value of the natal group as a “safe haven”, which can trigger dispersal if either parent is replaced [Ekman and Griesser, 2002]. Furthermore, replacement of the same sex parent may increase the chances of inbreeding (i.e., mating with the remaining opposite sex parent), leading to earlier dispersal. The replacement of an opposite sex parent is also predicted to influence dispersal decisions, as it introduces a potential mate to the natal group and increases mating competition with the same sex parent [Emlen, 1995; Emlen, 1997]. Adult replacements in socially monogamous groups could thus be expected to either delay or expedite dispersal, depending on the sex of the adult that is replaced relative to the sex of the dispersing offspring and the offspring’s age and level of sexual maturity at the time of the replacement. Empirical evidence from several socially monogamous taxa generally support the prediction that adult replacements will impact intragroup social dynamics, but the

influence of replacements on dispersal is not consistent [Eikenaar et al., 2007; Huck and Fernandez-Duque, 2012; Piper and Slater, 1993].

In addition to the social environment, ecological factors and conditions outside of the natal group are predicted to impact dispersal decisions. Dispersing may impose costs on individuals in terms of decreased foraging efficiency in unfamiliar environments or competition for resources from aggressive conspecifics in non-natal territories [Jones, 2003; Pusey and Packer, 1987]. Individuals that disperse during periods of low resource availability may suffer mortality, and resource scarcity may thus act as a constraint on the timing of dispersal [Bonte et al., 2012]. Individuals may therefore be predicted to disperse during times when resources are relatively abundant, to buffer themselves from these costs while ranging solitarily after dispersing. There is empirical evidence from lions (*P. leo*) suggesting that individuals that time dispersals to coincide with favorable conditions may increase their chance of survival [Elliot et al., 2014]. On the other hand, competition with natal group members is typically highest during periods of resource scarcity, and individuals may be evicted or voluntarily disperse when resources are scarce in response to this heightened competition [Jones, 2003]. Therefore, individuals may be predicted to disperse during periods when resources are scarce and delay dispersal when they are abundant. Experimental evidence from carrion crows (*Corvus corone*) supports a link between increased resource abundance and prolonged natal philopatry [Baglione et al., 2006]. Whether individuals disperse during times of relative resource abundance or scarcity can provide insight into whether dispersal is influenced more by resource competition with natal group members or ecological constraints on ranging solitarily.

Abiotic factors, such as rainfall or extreme climatic events, may be useful proxies for determining relative resource abundance. Examining the timing of dispersal during years with very wet or dry periods versus “normal” years can provide insight into the ecological conditions that influence dispersal. Specifically, if individuals disperse in response to increased resource abundance, we would expect to see a greater number of dispersals occur during the season(s) typically marked by scarcity during years when climatic conditions increased resource abundance in these seasons. On the other hand, if resource competition during periods of scarcity primarily influences dispersal decisions, we would expect to see higher rates of dispersal during or following climatic events associated with decreased resource abundance. Natural disasters and extreme climatic events, like droughts or heavy rainfall associated with El Niño Southern Oscillation (ENSO) events, may provide “natural experiments” that provide clues as to how ecological conditions influence dispersal. For example, during a two-year drought, >80% of male ring-tailed lemurs (*Lemur catta*) disappeared or dispersed from their natal groups [Gould et al., 1999]. However, natural disasters and extreme climatic events can also effect mortality rates. Mortality events can be difficult to distinguish from dispersal if individuals that disappear are not followed after they leave the natal group [Fernandez-Duque and van der Heide, 2013]. Therefore, associations between disappearances and these kinds of events should be interpreted with caution.

In many populations, ecological factors influence the times in which mating and births typically occur. Seasonality in dispersal may thus be linked to mating opportunities, rather than directly to the abundance of food resources. If mating opportunities play an important role in influencing dispersers’ decisions, then we expect the timing of dispersal to coincide with mating season. In support of this prediction, the timing of dispersal coincides

with the mating season in a variety of seasonally breeding primates [Borries, 2000; Cheney, 1983; Drickamer and Vessey, 1973; Pusey and Packer, 1987; Sprague, 1992; Sussman, 1992]. In other taxa, the timing of dispersal coincides with the birth season. For example, in Azara's owl monkeys (*Aotus azarae*) both births and dispersal were concentrated in the spring through early summer [Fernandez-Duque, 2009; Fernandez-Duque et al., 2002].

Multiple factors could explain why dispersals coincide with the birth season. It is possible that the addition of infants to the natal group triggers dispersal. Alternatively, rather than being directly influenced by births, dispersal and births may coincide with one another because they are both influenced by resource abundance. If the latter is true, then we expect individuals to disperse more frequently during the peak-resource season regardless of whether a birth recently occurred in their natal group.

Azara's owl monkeys (*A. azarae*) in the Argentinean Gran Chaco are socially and genetically monogamous primates that live in groups containing just one adult male, one adult female, and generally one to four offspring who have yet to disperse [Fernandez-Duque et al., 2001; Huck et al., 2014; Huck et al., 2011]. Almost everything we know about natal dispersal in owl monkeys comes from a population of *A. azarae* in Formosa, Argentina that the Owl Monkey Project has monitored since 1997. Observations from the first decade of this project (June 1997 - March 2008) indicate that all offspring disperse from their natal group prior to reproducing, and typically range solitarily after dispersing before finding a mate. However, the age at dispersal is variable (age range = 2-5 years) [Fernandez-Duque, 2009; Fernandez-Duque and Huntington, 2002]. Thus far, the proximate factors underlying this variation in age at dispersal remain unclear. The role that social factors, such as group size

and demographic changes (e.g., infant births and adult replacements), may contribute to the observed variation in dispersal age requires systematic examination.

The timing of owl monkey dispersal throughout the year is also somewhat flexible and may be influenced by social or ecological conditions. Data on owl monkey dispersals that occurred prior to 2008 suggest that dispersal is seasonal, with a peak of dispersals (31%) occurring in October and 71% of offspring dispersing between September and February. However, dispersals also occurred in other months throughout the year [Fernandez-Duque, 2009]. The peak in dispersals corresponds to several social and ecological factors. First, mid-September through February corresponds to the spring and early summer in Argentina, a time when food resources are increasing or at their peak. This preferred dispersal season also overlaps largely with the birth season. Births at this site are highly seasonal, with almost all occurring between mid-September and mid-January and 80% occurring in October or November [Fernandez-Duque et al., 2002]. The higher rates of dispersal during the dispersal season require further examination to determine which proximate factor, resource abundance or infant births in the natal group, is primarily responsible for the observed seasonality in dispersal.

In this study, we utilize 20 years of demographic data from a population of Azara's owl monkey (*A. azarae*) in Formosa, Argentina. We use these data to thoroughly describe dispersal patterns and evaluate proximate factors that may be influencing variation in the age and timing of natal dispersal in this socially monogamous primate. Our specific objectives are to first determine the average dispersal age and the characteristics of the social groups from which offspring disperse, and quantify the extent of variation present in these variables. We then evaluate how social and ecological variables (group size, infant births, adult

replacements, rainfall, etc.) contribute to variation in the age and timing of dispersal to evaluate explanations for why some individuals delay dispersal. Finally, we discuss our results in the context of evolutionary explanations that have been advanced to explain dispersal patterns in pair-living monogamous primates and other taxa. Specifically, we assess the extent to which our results support inbreeding, mate competition, and resource competition avoidance hypotheses as explanations for dispersal.

The correlational nature of data collected during observational field studies, such as ours, does not allow us to infer causality between proximate factors and dispersal. Rather than confirmatory testing, our goal is to examine which factors best explain variation in observed patterns of dispersal in order to evaluate which factors are *most likely* to influence dispersal decisions. Similarly, inbreeding, mate competition and resource competition avoidance hypotheses are broad and non-exclusive to one another, and multiple forces may work simultaneously to shape patterns of dispersal. Our goal in placing our results in the context of these hypotheses is therefore to evaluate the plausibility of each and the relative importance that they have in shaping owl monkey dispersal.

## **Methods**

### **Study site, subjects, and data collection**

We conducted the study at the Reserva Mirikiná, a 1,500 ha reserve on the private cattle ranch, Estancia Guaycolec, in Formosa, Argentina (58°13'W, 25°54'S). This location is part of the humid portion of the South American Gran Chaco, which consists of a mosaic of gallery forest, grasslands, savannahs, and isolated patches of dry forest [Juárez et al., 2012; Placci, 1995; van der Heide et al., 2012]. Owl monkeys (*A. azarae*) in this area reside in both

gallery forest and forest patches, but the data reported here come from groups residing primarily in gallery forest. The climate in this area is highly seasonal, with a dry season (June-August) and peaks of rain in April and November. Temperature and food productivity also show substantial season variation, with maximum average temperatures in December-March, and peaks of fruit occurring in November-December. Both the amount of insects and the percentage of tree species producing new leaves, fruits, or flowers are lowest in the fall/winter period, from April to August, and begin to increase in September [Fernandez-Duque, 2003; Fernandez-Duque, 2009]. Additional details about climate and seasonality at the Reserva Mirikiná are described elsewhere [Fernandez-Duque, 2009; Fernandez-Duque et al., 2002; van der Heide et al., 2012].

Within the reserve, a 300 ha area of gallery forest along the banks of the Riacho Pilagá has been mapped and groups within this core area have been habituated and are monitored by the Owl Monkey Project (OMP) [Fernandez-Duque, 2016; Fernandez-Duque et al., 2001]. Since 2000, the OMP has also been capturing and fitting some individuals in this area with radiocollars, which allows researchers to consistently locate identified groups, and bead collars, which facilitate the reliable identification of specific individuals [Juárez et al., 2011]. We collected all data reported here from habituated groups, in which members could be discriminated from one another by collars or natural distinguishing markings. When necessary, we utilized body size and the relative amount of subcaudal scent gland secretions to distinguish non-captured, and thus uncollared, subadults and juveniles from adults and from one another [Huck et al., 2011]. We classified individuals as infants (< 6 months), juveniles (6 < 24 months), subadults (predispersed individuals > 24 months), or adults

(dispersed individuals > 48 months), following the age categories recommended in Huck et al. [2011].

Continued and regular monitoring of identified, habituated individuals in our study population allowed us to determine demographic changes in groups. Since 1997, we have regularly contacted a core set of approximately ten groups, at least once every week or every second week. Groups within the reserve but outside of the core area are also contacted at least several times per year [Fernandez-Duque, 2016]. Every time we contacted a group, the observer recorded group size, age structure, the identities of previously identified individuals, and noted any changes to group composition since the previous sighting. This monitoring has allowed us to identify dates of births, deaths, and other demographic changes, such as dispersals and adult replacements, within a range of a few weeks in our core study area [Huck and Fernandez-Duque, 2012]. We entered all data on dates of births, deaths, disappearances, dispersals, and adult replacements into the Owl Monkey Project's Microsoft Access database.

We recorded the births of 253 individuals from 26 different social groups between September 1996 and September 2016 (Table 2.1). We did not include offspring that were already present at the onset of the study (births prior to 1996), since the year of birth for these individuals could only be estimated. We also did not include births that occurred in peripheral groups that we monitored for less than four consecutive years, as our ability to detect demographic changes (especially adult replacements) in these groups was diminished. When the *exact date* of a birth, disappearance, dispersal, or adult replacement could not be pinpointed, we estimated the event to have occurred on the average between the date on which the demographic change was first observed and the most recent date on which the



**Table 2.1.** Number of births and fates (disappearance, dispersal, death, still in natal group, or unknown) of offspring in each of 26 social group of owl monkeys between 1996 and 2015.

Group	Range of years with recorded births	Births				Offspring Fates				
		Total births	U	M	F	Disappearances	Dispersals	Deaths	Still in group	Unknown
A500	1998-2012	8	8	0	0	5	0	0	1	2
A900	1997-2012	10	8	2	0	5	1	2	1	1
B68	1998-2014	11	10	0	1	5	1	4	1	0
C0	1996-2015	10	6	2	2	6	1	1	2	0
Camp	1997-2003	6	3	3	0	2	1	3	0	0
CC	1996-2015	13	6	2	5	5	3	4	1	0
Colman	1999-2015	15	8	3	4	5	3	6	1	0
Corredor	1999-2015	11	9	0	2	4	1	4	2	0
D100	1996-2004	4	3	0	1	3	0	1	0	0
D1200	1996-2014	16	12	3	1	8	3	3	2	0
D1400	2003-2011	5	4	0	0	0	0	0	1	4
D500	1996-2015	15	8	3	4	3	5	6	1	0
D800	1998-2015	9	7	2	0	3	1	3	2	0
E350	1996-2015	13	7	3	3	3	2	5	3	0
E500	1997-2015	13	7	3	3	5	2	4	2	0
F1200	1997-2014	15	10	2	3	6	2	5	2	0
F700	2000-2015	12	9	2	1	5	2	3	2	0
Fauna	2001-2008	8	6	1	1	3	1	2	0	2
G1300	2001-2014	9	8	0	1	1	1	5	2	0
IJ500	1997-2014	10	9	1	0	3	1	4	2	0
L100	1998-2014	9	8	1	0	4	0	0	2	3
P300	2001-2015	10	9	0	1	5	1	3	1	0
Parrilla	2001-2006	5	4	1	0	3	0	2	0	0
Picada C.	2000-2008	4	3	0	1	1	0	0	0	3
Soldado	2004-2008	4	4	0	0	0	0	0	0	4
Veronica	2000-2013	8	7	0	1	3	1	1	2	1
<b>Total</b>	<b>1996-2015</b>	<b>253</b>	<b>183</b>	<b>34</b>	<b>35</b>	<b>96</b>	<b>33</b>	<b>71</b>	<b>33</b>	<b>20</b>

U = sex unknown, M = male, F = female.

“Range of years with recorded births” is the span of years over which each social group was monitored and all births that occurred during this period were recorded.

Disappearances and Dispersals are defined in the text. “Deaths” includes both confirmed and presumed deaths (all disappearances of individuals at  $\leq 19$  months)

group had previously been sighted prior to that demographic change. We excluded all individuals (N=33) for which the date of birth, disappearance, or dispersal could not be estimated with an accuracy of at least six months. For analyses examining the seasonality of dispersal (part three, as described below; Table 2.2), we included only individuals for whom the date of the disappearance or dispersal could be determined to have occurred within a particular season (i.e., the range of all possible dates fell entirely within a single season) (N=121).

For the purposes of this study, we use the term “dispersal” to refer only to a permanent departure of an individual from the group into which it was born. Thus, dispersals in our analyses exclude temporary departures or “prospecting” events [Danchin et al., 2001; Mares et al., 2014; Ponchon et al., 2013] and secondary dispersals of adults (which are rare in our population) [Fernandez-Duque and Huck, 2013].

We classified all departures of offspring from their group between 1997 and 2016 as a “death”, a “disappearance”, or a “dispersal” (Table 2.1). We use the term “disappearance” to refer to any offspring that vanished from its natal group at the age of 20 months or older, but that we did not see again outside of the natal group. We reserve the term “dispersal” for an offspring that we observed ranging solitarily or as an adult in a new social group after leaving its natal group. We make this distinction because, while we generally presume the disappearance of any offspring  $\geq 20$  months to be the result of dispersing, it is possible that some “disappearing” individuals died before leaving their natal groups.

Including individuals who died prior to dispersing could skew estimates of the age at dispersal, so we analyzed our data in two ways. We first included dispersed and disappeared individuals together and then performed a more conservative analysis in which disappeared

individuals were censored. For all analyses, we presumed any offspring that vanished from its natal group at < 20 months to have died rather than dispersed. We chose 20 months as the minimum age for a potential dispersal because this is the youngest age at which any offspring in our study population has ever been confirmed to successfully disperse, and to be consistent with previous studies [Fernandez-Duque, 2009; Huck and Fernandez-Duque, 2012]. In the few cases when observers found the remains of an offspring within that offspring's home range, we classified this as a death for that individual, as well.

### **Data analyses**

To assess the potential influence of social and ecological factors on dispersal age and timing of dispersal, we organized our analyses into three major parts. Part one examines the relationship between variables associated with the social composition of the natal group and age at dispersal. In part two, we investigate in more detail the relationship between factors related to adult replacements and dispersal. In part three, we explore the relationships between social, abiotic/ecological factors known to vary seasonally and the time of year (i.e., season) in which an individual dispersed. We provide detailed descriptions of variables utilized in each of the three parts of our analyses in Table 2.2.

**Table 2.2.** List and description of variables utilized in each part of the analysis.

<b>Explanatory variables</b>			
<b>Variable name</b>	<b>Type of variable</b>	<b>Analyses used in</b>	<b>Description</b>
Group size	Count	Parts 1, 3	Number of individuals in the group (range 2-6) at the time of the dispersal, not including the dispersing individual
Time since last birth	Continuous numerical	Part 1	Number of months the dispersing individual was in the natal group since the last birth in the group (equal to the age of the dispersing individual if there were no younger offspring born prior to dispersal)
Replacement	Categorical	Parts 1, 3	Whether a dispersing individual had experienced the replacement of an adult prior to the dispersal (yes or no)
Sex	Categorical	Parts 2	Sex of the dispersing individual (male, female or unknown)
Age at replacement	Continuous numerical	Part 2	Age (in months) of the dispersing individual when the replacement occurred
Same sex	Categorical	Part 2	Whether the adult replaced was the same sex as the dispersing individual (yes or no)
Dispersal age	Continuous numerical	Part 3	Age (in months) when the dispersal occurred
Recent birth	Categorical	Part 3	Whether there was a birth in the natal group within the past 12 months (yes or no)
High Rainfall	Categorical	Part 3	Whether the amount of rainfall between April and August was above average ("high") in the year that an offspring dispersed
<b>Outcome (dependent) variables</b>			
Age at dispersal	Continuous numerical	Part 1	Age (in months) when an individual permanently dispersed from the natal group
Time to dispersal	Continuous numerical	Part 2	Time (in months) after a replacement that an individual remained in the natal group before dispersing
Birth Season	Categorical	Part 3	Whether an individual dispersed between mid-September and early January (the birth season)
Fall/Winter Season	Categorical	Part 3	Whether an individual dispersed between April and August (the period of low resource abundance)

We analyzed our data using an information theoretic approach [Burnham and Anderson, 2002; Symonds and Moussalli, 2011]. We first defined an *a priori* set of models for each of the three parts of our analysis (Cox regression models for parts 1-2; generalized linear regression models for part 3) based on our previous knowledge of dispersal in this population of owl monkeys [[Fernandez-Duque, 2009], personal observations]. We discuss in detail our reasoning for including each explanatory variable and methods for constructing these variables in the following section.

We report all candidate models constructed in Tables 2.3-2.5. Within each of our three model sets, we calculated corrected Akaike information criteria (AICc) and utilized delta AICc and cumulative Akaike weights (AICc weights) to assess the plausibility of each candidate model [Burnham and Anderson, 2004; Long, 2012; Mazerolle, 2016]. Prior to fitting models, we set criteria for selecting the model(s) from each set that would be used in making inferences. We considered there to be a single best approximating model only if the model with the lowest AICc had an Akaike weight of  $> 0.9$ . Even if one best model was supported, in making inferences from our models we considered all those with a delta AICc  $\leq 6$  and report their results, following recommendations that models within this delta AICc range should not be completely discounted [Richards, 2005; Symonds and Moussalli, 2011]. When a single best approximating model could *not* be identified, we made our inferences utilizing multiple models by calculating model-averaged parameters [Burnham and Anderson, 2004; Symonds and Moussalli, 2011]. We report characteristics [e.g., number of parameters (K), AICc, delta AICc, cumulative Akaike weights, log likelihood] for all candidate models, so that readers can assess the plausibility of each of our candidate models for themselves (Tables 2.3-2.5).

We performed all statistical analyses in R 3.3.2 [R Core Development Team, 2016]. We utilized the package AICcmodavg (v. 2.1-0) to calculate AICc and other model characteristics, as well as for calculating model-averaged parameter estimates, their standard errors, and 95% unconditional confidence intervals [Mazerolle, 2016] (Tables 2.6-2.8). For descriptive statistics, we report the mean  $\pm$  one standard error, unless otherwise specified.

*Selection of response and explanatory variables and construction of candidate models*

The explanatory variables that we included in our models (Tables 2.3-2.5) were chosen by carefully considering which potential factors were likely to be *biologically relevant*, based on our previous knowledge of owl monkey dispersal and dispersal and social dynamics in other socially monogamous taxa [Eikenaar et al., 2007; Emlen, 1997; Huck and Fernandez-Duque, 2012; Piper and Slater, 1993]. For example, previous observations and an earlier analysis of dispersal data from the same population showed that both the median age and range of variation in dispersal age are extremely similar for males and females [Fernandez-Duque, 2009; Fernandez-Duque and Huntington, 2002]. The sex of dispersing individuals was also unknown for the majority of individuals in our data set (63%). Therefore, to maximize our sample size and to avoid overfitting our data, we did not include sex in our candidate models for analyses unless otherwise specified.

In part one, to examine how factors associated with the social group may influence age at dispersal, we conducted statistical “survival” analyses that considered censored data using Cox-proportional hazard models. Variation in group size, which in monogamous groups is largely determined by the presence of infants or younger individuals, is likely to influence the amount of competition within a disperser’s natal group. Adult replacements

also are likely to influence social dynamics, particularly between adults and older individuals (juveniles and subadults) that are undergoing sexual maturity. Therefore, in this part, we included group size, time since last birth, and adult replacements as potential explanatory variables. We used these variables to construct eleven candidate models for explaining the variation of age at dispersal (Table 2.3). We first ran these eleven candidate models on our entire data set (n=138 individuals), censoring only individuals still in their natal groups (n=16). For comparison, we repeated our analyses using a more conservative definition of dispersal, which treated as confirmed dispersals only individuals seen as solitaries or in a new group after leaving the natal group (n=33). In this conservative analysis, we ran our eleven candidate models again, but this time censoring all individuals who disappeared (n=89), as well as those still in their natal groups.

In part two, we utilized Cox-proportional hazard models to further investigate the potential influence of adult replacements on dispersal. We considered as potential explanatory variables the age at which an individual experienced a replacement and whether the sex of the adult replaced was the same as the disperser's sex, since these factors are likely to influence social interactions between adults and offspring [Emlen, 1997]. There is preliminary evidence that females may begin to develop mature hormone profiles at a somewhat earlier age than males [Corley et al., 2016]. We therefore also included the disperser's sex in interaction terms in candidate models. In total, we constructed nine candidate models (Table 2.4) to examine how these explanatory variables relate to how long an offspring remains in the natal group after experiencing a replacement ("time to dispersal", Table 2.2). For these analyses, we utilized data only from the subset of individuals who experienced a replacement and met our criteria of having dates of birth and

disappearance/dispersal that could be estimated with an accuracy of at least six months. There were 50 individuals (28 disappeared, 21 dispersed, 1 still in the natal group) for analyses. Some offspring experienced more than one adult replacement. Since an individual can only disperse once, we only considered the most recent replacement (the one that occurred most immediately before dispersal). In the model set for part two, potential explanatory variables included the age at which an individual experienced a replacement and whether the sex of the adult replaced was the same as the disperser's sex, since these factors are likely to influence social interactions between adults and offspring [Emlen, 1997]. There is preliminary evidence that females may begin to develop mature hormone profiles at a somewhat earlier age than males [Corley et al., 2016]. We therefore also included the disperser's sex in interaction terms in candidate models. In total, we used these potential variables to construct nine candidate models (Table 2.4).

We also performed a separate analysis that included only the subset of individuals in the data set for part two that were subadults ( $\geq 24$  months old). One of the reasons that we predicted that the age at which an individual experienced an adult replacement would be important is that replacements would expose older offspring (e.g., subadults) to potential mating competition or opportunities to mate with an unrelated adult. We thus expected that adult replacements might influence subadults, who were approaching sexual maturity, differently than younger offspring. We had a relatively small number of individuals who had experienced replacements as subadults (N=7 with same sex replacements, N=9 with opposite sex replacements). To avoid overfitting our data, we did not create a full set of models for this small subset. Instead, we calculated the mean number of months that individuals who experienced the replacement of a same, or opposite, sex adult remained in the natal group



after a replacement. We used a non-parametric Wilcoxon rank-sum test to evaluate the statistical significance of the difference.

In part three, we examined the potential influence of several explanatory variables on the seasonality of dispersal. Previous observations indicate that dispersals occur throughout the year, but are concentrated between September and January, with a peak in October [Fernandez-Duque, 2009]. This preferred dispersal period corresponds roughly to a period when group composition frequently changes (i.e., the season when births occur) and to a period of relative resource abundance (i.e., the spring/early summer). We thus defined seasonality in two ways and performed separate analyses on each. First, we constructed 15 candidate models for which the outcome variable was whether dispersal occurred during the birth season (mid-September to early January) or another time of the year. In the birth season model set, potential explanatory variables included dispersal age, group size, adult replacement, and whether a birth had occurred in the natal group within the past year (Table 2.2). We did not use time since last birth, as in parts one and two, because births are highly seasonal and thus correlated with our outcome variable.

Next, we performed analyses in which we defined seasonality based on abiotic proxies of resource abundance. Specifically, we constructed 15 candidate models for which the outcome variable was whether dispersal occurred during the fall/winter, when resource abundance is relatively low, or another time of year. We chose this season to focus on because of our interest in examining which variables might explain the reason that individuals sometimes disperse during times when ranging solitarily is presumably most difficult (due to limited food resources and colder temperatures). The amount of rainfall during the fall/winter season is a relatively good proxy for food abundance during this

season. We know that “wet” years, such as those related to El Niño Southern Oscillation (ENSO) events, are associated with heavy rain and higher fruit production in the region [Fernandez-Duque, 2009]. We divided the 20 years (1997-2016) in our study into two categories, based on the amount of rain that occurred between April and August. Specifically, we considered years with an amount of rainfall that was more than one standard error above the average fall/winter rainfall (>450 mm) to be “high rainfall” years (N=10), and we presumed that these years had relatively high fall/winter resource abundance. We considered years that had average or lower than average rainfall (<450 mm) to have relatively low fall/winter resource abundance (N=10). We did not include temperature as a variable because it is correlated with both the birth season and the fall/winter season [Fernandez-Duque, 2009]. In the abiotic season model set, potential explanatory variables included whether there was high rainfall during the fall/winter season in the year in which the dispersal occurred, dispersal age, adult replacement, and whether a birth had occurred in the natal group within the past year (Table 2.2).

Although many groups were represented more than once in our data set (i.e., observations of the same groups over many years), we did not include group ID as a random factor in any of our candidate models. The characteristics and composition of owl monkey groups are not stable over multiple years: the demographic structure frequently changes due to births and deaths, the identities of “parents” (due to adult replacements) often changes, and even the home ranges held by a particular group fluctuate over time. Thus, there are not strong reasons to include group ID in our models when considering 20 years of data. To provide support for this assumption, we re-constructed model set 1 to include *Group ID* as a random factor in each candidate model. *Group ID* did not improve our models or

substantially change our results; *Group ID* accounted for almost none of the variance in dispersal age (for each candidate model, all or almost all of the variance was in the residual for this variable). We therefore report only results from models that do not include *Group ID* as a random effect (Tables 2.3-2.5).

**Table 2.3.** Models of age at dispersal, as explained by characteristics of the social group, ranked according to their AICc values (Part One).

Model name	Model parameters	K	AICc	delta AICc	AICc weight	Cum. weight	Log Likelihood
M1.2	birth	1	967.78	0	0.40	0.40	-482.88
M1.4	group size + birth	2	969.25	1.47	0.19	0.59	-482.58
M1.1	group size	1	970.10	2.32	0.12	0.71	-484.04
M1.10	birth * replacement	5	971.29	3.51	0.07	0.78	-480.42
M1.8	group size * birth	3	971.34	3.55	0.07	0.85	-482.58
M1.6	birth + replacement	3	971.69	3.91	0.06	0.90	-482.76
M1.3	replacement	2	972.13	4.35	0.05	0.95	-484.02
M1.7	group size + birth + replacement	4	973.24	5.46	0.03	0.97	-482.47
M1.5	group size + replacement	3	974.19	6.41	0.02	0.99	-484.01
M1.11	group size * birth + replacement	5	975.39	7.61	0.01	1.00	-482.47
M1.9	group size * replacement	5	978.34	10.56	0	1.00	-483.94

Model name	Model parameters	K	AICc	delta AICc	AICc weight	Cum. weight	Log Likelihood
C1.6	birth + replacement	2	229.93	0	0.44	0.44	-112.92
C1.10	birth * replacement	3	231.79	1.85	0.17	0.61	-112.80
C1.7	group size + birth + replacement	3	231.91	1.98	0.16	0.77	-112.87
C1.11	group size * birth + replacement	4	232.99	3.05	0.09	0.86	-112.34
C1.2	birth	1	234.45	4.52	0.05	0.91	-116.21
C1.5	group size + replacement	2	235.82	5.88	0.02	0.93	-115.86
C1.3	replacement	1	235.90	5.97	0.02	0.95	-116.94
C1.4	group size + birth	2	236.23	6.29	0.02	0.97	-116.07
C1.8	group size * birth	3	236.36	6.43	0.02	0.99	-115.09
C1.9	group size * replacement	3	237.83	7.89	0.01	1.00	-115.82
C1.1	group size	1	241.54	11.61	0.00	1.00	-119.76

-Model names beginning with M (top) refer to models run using the full data set (n=138 individuals), while those beginning with C (bottom) refer to conservative models run using the more conservative definition of dispersal (n=35 uncensored individuals). The model numbers (1.1 – 1.11) were randomly assigned to the 11 candidate models in Part 1, and are used as shorthand throughout the results to refer to the models with the parameters specified here.

-Models with delta AICc > 6, which accounted for relatively little of the cumulative Akaike weight, are shaded in gray.

-“K” = number of parameters contained in each model, as calculated by the AICcmodavg package [Mazerolle, 2016].

-“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].

**Table 2.4.** Models of time to dispersal after an adult replacement, ranked according to their AICc values (Part Two).

Model name	Fixed effects	K	AICc	delta AICc	AICc weight	Cumulative weight	Log Likelihood
M2.1	age at replacement	1	148.41	0.00	0.43	0.43	-73.14
M2.3	age at replacement + same sex replacement	2	148.86	0.45	0.34	0.77	-72.22
M2.4	age at replacement * same sex replacement	3	150.92	2.51	0.12	0.90	-72.03
M2.5	age at replacement * sex	3	152.93	4.52	0.04	0.94	-73.04
M2.9	same sex replacement * sex + age at replacement	4	153.61	5.20	0.03	0.97	-72.07
M2.6	age at replacement * sex + same sex replacement	4	153.91	5.50	0.03	1.00	-72.21
M2.7	sex	1	164.44	16.03	0	1.00	-81.15
M2.2	same sex replacement	1	165.12	16.71	0	1.00	-81.49
M2.8	same sex replacement * sex	3	169.00	20.59	0	1.00	-81.07

-The model numbers (2.1 – 2.8) were randomly assigned to the eight candidate models in Part 2 are used as shorthand throughout the results to refer to the models with the parameters specified here.

-Models with delta AICc > 6, which accounted for relatively little of the cumulative Akaike weight, are shaded in gray.

-“K” = number of parameters contained in each model, as calculated by the AICcmodavg package [Mazerolle, 2016].

-“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].

**Table 2.5.** Models of season of dispersal, ranked according to their AICc values (Part Three).

Model name	Model parameters	K	AICc	delta AICc	AICc weight	Cumulative weight	Log Likelihood
B3.9	recent birth + adult replacement	3	165.24	0	0.27	0.27	-79.52
B3.2	recent birth	2	166.09	0.85	0.18	0.45	-81.00
B3.11	dispersal age + recent birth + adult replacement	4	166.97	1.73	0.11	0.56	-79.31
B3.14	recent birth + group size + adult replacement	4	167.37	2.13	0.09	0.65	-79.51
B3.8	recent birth + group size	3	168.00	2.76	0.07	0.72	-80.90
B3.5	dispersal age + recent birth	3	168.04	2.80	0.07	0.79	-80.92
B3.4	adult replacement	2	168.79	3.54	0.05	0.83	-82.34
B3.15	dispersal age + recent birth + group size + adult replacement	5	169.09	3.85	0.04	0.87	-79.29
B3.3	group size	2	169.82	4.57	0.02	0.90	-82.86
B3.10	group size + adult replacement	3	170.01	4.76	0.02	0.92	-81.90
B3.13	dispersal age + recent birth + group size	4	170.02	4.78	0.02	0.95	-80.84
B3.7	dispersal age + adult replacement	3	170.40	5.15	0.01	0.97	-82.10
B3.1	dispersal age	2	171.62	6.38	0.01	0.98	-83.76
B3.6	dispersal age + group size	3	171.84	6.59	0.01	0.99	-82.82
B3.12	dispersal age + group size + adult replacement	4	171.84	6.6	0.01	1	-81.75

Model name	Model parameters	K	AICc	delta AICc	AICc weight	Cumulative weight	Log Likelihood
A3.1	high rainfall	2	140.69	0.00	1.00	0.25	-68.29
A3.6	high rainfall + recent birth	3	140.73	0.04	0.98	0.49	-67.26
A3.5	high rainfall + replacement	3	142.76	2.07	0.36	0.57	-68.28
A3.7	high rainfall + dispersal age	3	142.79	2.10	0.35	0.66	-68.29
A3.11	high rainfall + replacement + recent birth	4	142.86	2.17	0.34	0.74	-67.26
A3.13	high rainfall + recent birth + dispersal age	4	142.87	2.18	0.34	0.82	-67.26
A3.3	recent birth	2	144.25	3.56	0.17	0.86	-70.07
A3.12	high rainfall + replacement + dispersal age	4	144.89	4.20	0.12	0.90	-68.27
A3.15	high rainfall + replacement + recent birth + dispersal age	5	145.03	4.34	0.11	0.92	-67.26
A3.2	replacement	2	145.88	5.19	0.07	0.94	-70.89
A3.4	dispersal age	2	145.89	5.20	0.07	0.96	-70.90
A3.8	recent birth + replacement	3	146.34	5.65	0.06	0.97	-70.07
A3.9	recent birth + dispersal age	3	146.35	5.66	0.06	0.99	-70.07
A3.10	replacement + dispersal age	3	147.97	7.28	0.03	0.99	-70.88
A3.14	replacement + recent birth + dispersal age	4	148.48	7.78	0.02	1.00	-70.07

-Model names beginning with B (top) refer to models for which the outcome variable was whether or not dispersal occurred during the “birth season” (mid-Sep to early Jan), while those beginning with A (bottom) refer to models for which the outcome variable was whether or not dispersal occurred during the period of low resource abundance during the fall/winter (“abiotically defined season”). The model numbers 3.1 – 3.15) were randomly assigned to the candidate models in Part 3 are used as shorthand throughout the results to refer to the models with the parameters specified here.

-Models with delta AICc > 6, which accounted for relatively little of the cumulative Akaike weight, are shaded in gray.

-“K” = number of parameters contained in each model, as calculated by the AICcmodavg package [Mazerolle, 2016].

-“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].

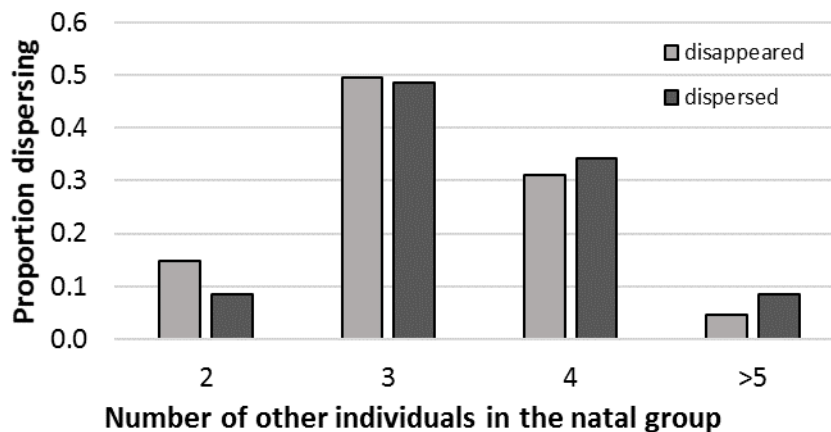
## Results

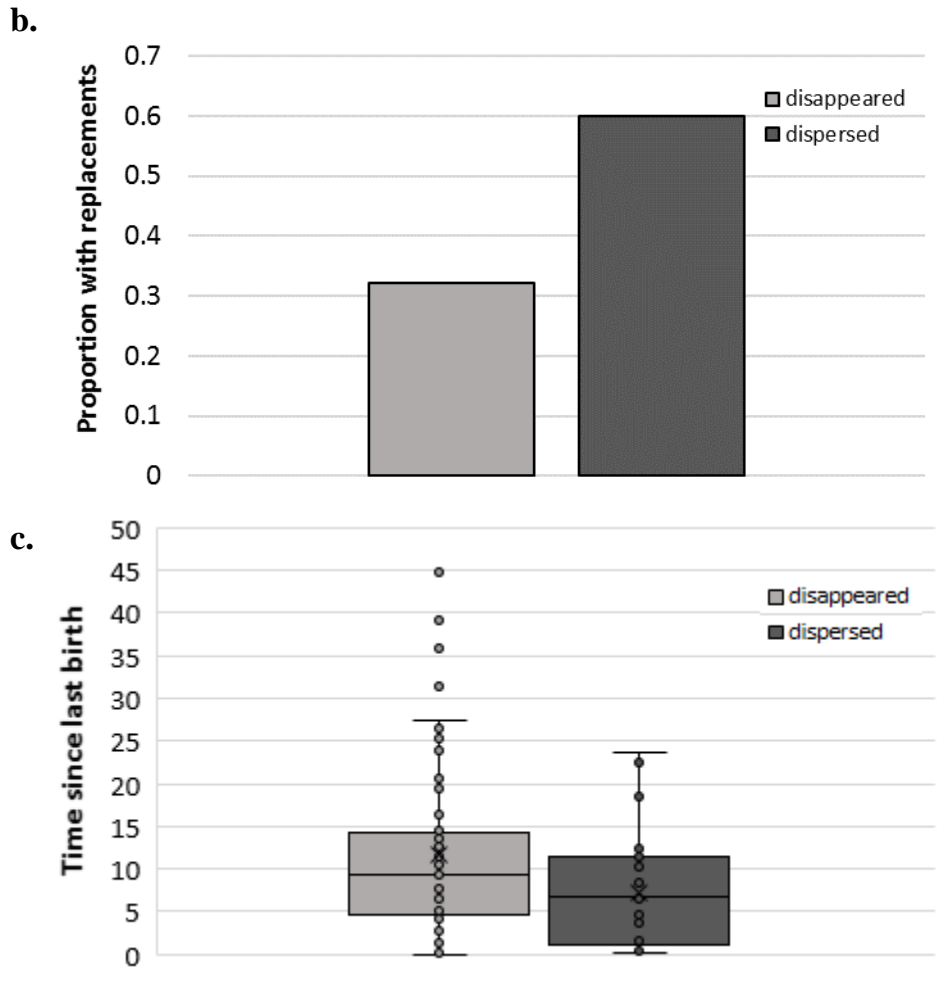
### Characteristics of the natal group and age at dispersal

No individuals reproduced in their natal groups; all dispersed, disappeared, or died. Approximately one third of the offspring (70/220) with dates of birth and departure from the natal group known with an accuracy of  $\leq 6$  months, died or were presumed to have died before they were old enough to disperse. Another 40% (N=89) disappeared, 15% (N=33) were confirmed to have dispersed, and 11% (N=25) were still living in their natal groups at the end of the study.

At the time of dispersal the natal groups showed variation in the number of other group members present, whether there had been a replacement, and the time since the most recent infant birth. At the time of disappearance or dispersal, there was a mean of 3.3 other individuals present (range 2-6, Figure 2.1a), 40% of individuals had experienced an adult replacement (Figure 2.1b), and a mean of  $11 \pm 1$  months (range 0-46) had passed since the last infant was born in the natal group (Figure 2.1c). We report the characteristics of the natal group for individuals who disappeared and individuals who were confirmed to have dispersed separately, for comparison, in Figure 2.1.

**a.**





**Figure 2.1.** Characteristics of the natal groups from which individuals disappeared (N=89) or dispersed (N=33): a) Proportion of individuals leaving natal groups containing 2 to > 5 other individuals; b) Proportion of individuals leaving a natal group; c) Time since the most recent infant birth (in months) when an individual departed from its natal group. “X” indicates the mean.

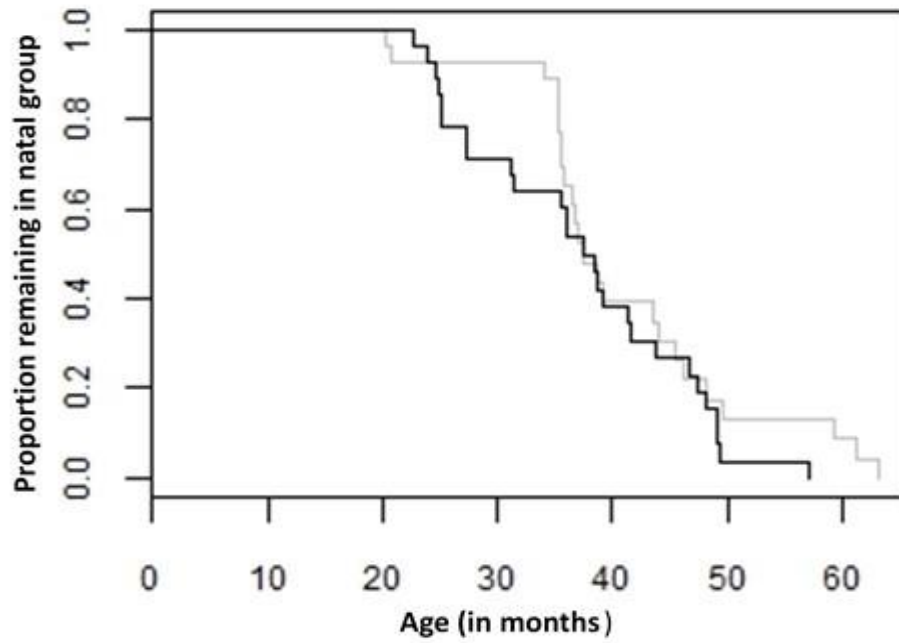
There was substantial variation in the age when individuals disappeared and dispersed from the natal group. Offspring departed from the natal group when they were between 1.7 and 5.3 years old (i.e., 20-63 months; median = 35 months; mean  $\pm$  SE = 35  $\pm$  1 months). Males and females had very similar ages of dispersal [median (mean  $\pm$  SE): males = 37 (37  $\pm$  2) months, females = 37 (40  $\pm$  2) months], and had similar probabilities of dispersing at most ages (Figure 2.2a). There was a tendency for more females than males to



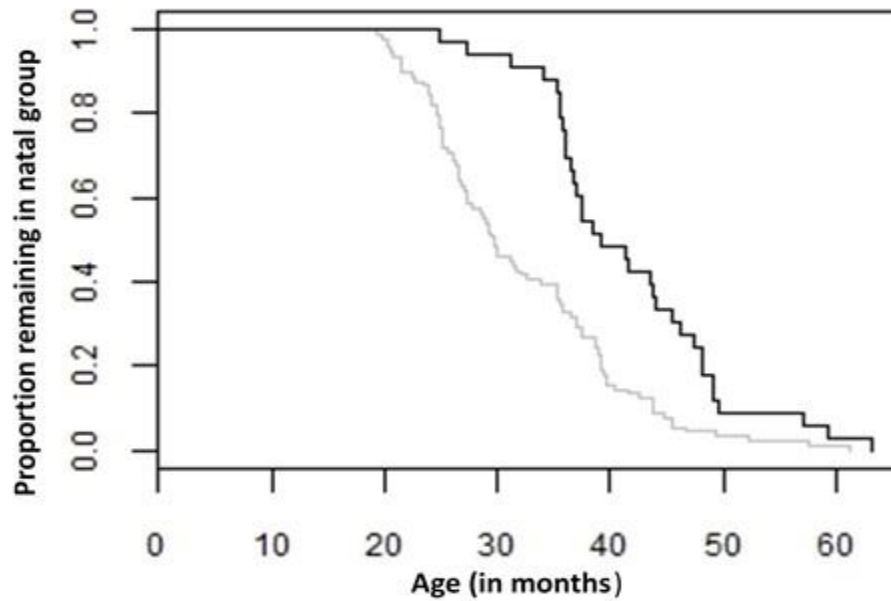
delay dispersal until 35 months of age. Of the 14 individuals of known sex that dispersed prior to reaching 35 months, ten were male and only four were female. However, after 35 months, this sex difference tendency disappeared, and the age-specific probabilities of dispersing were otherwise similar for males and females (Figure 2.2a; G-rho test for differences in survival:  $X^2 = 1.3$ ,  $df = 1$ ,  $p = 0.3$ ). When we limited our analyses to individuals for which dispersal had been confirmed, the mean and median age at dispersal was higher than when we included individuals that had disappeared (Figure 2.2b; G-rho test for differences in survival:  $X^2 = 14.9$ ,  $df = 1$ ,  $p < 0.01$ ). Specifically, dispersed individuals' median age at dispersal was 39 months, compared to 30 months for disappeared individuals (mean age =  $42 \pm 2$  months versus  $32 \pm 1$  months, respectively). For individuals with confirmed dispersals, age at dispersal was again similar for males and females [median (mean  $\pm$  SE): 40 ( $41 \pm 2$ ) and 38 ( $43 \pm 2$ ) months, respectively].

For models in part one, our results differed depending on whether we considered disappearances to be dispersals (Figure 2.2b). Our analyses utilizing the full data set ( $n=122$  uncensored individuals that either dispersed or disappeared) differed from those utilizing the more conservative data set ( $n=33$  confirmed dispersals) (Tables 2.3 and 2.6). With the full data set, eight of our 11 models had a delta AICc of  $\leq 6$ , and together these accounted for 97% of the cumulate weight (Table 2.3). However, for the full data set, none of our potential explanatory variables (adult replacement, birth, and group size) explained much of the variation in age at dispersal, and all model-averaged parameters had confidence intervals that included zero (Table 2.6).

a.



b.



**Figure 2.2.** Survival curves (i.e., age-specific probabilities of dispersal) for disappearing and dispersing offspring: a) survival curve for male (black; N=28) and female (gray; N=27) offspring; b) survival curve for offspring that disappeared (gray; N=89) and offspring confirmed to have dispersed (black; N=33).

On the other hand, results from our more conservative analyses suggested that adult replacement is an important factor for explaining age at dispersal. When we limited our definition of dispersal to include only confirmed dispersals, seven out of our 11 models had a delta AICc of  $\leq 6$ , and together these accounted for 95% of the cumulate weight (Table 2.3). Six of these seven best models (including the best model, C1.6, which alone accounted for 59% of the cumulative weight) included adult replacement as a factor. Of the three explanatory variables included in our candidate models (adult replacement, time since a birth, and group size), having an adult replacement was the only one with a model-averaged parameter estimate whose confidence interval did not include zero ( $0.9 \pm 0.4$ , 95% CI = 0.2-1.6). Specifically, an offspring had a hazard of dispersing 2.5 times greater (95% CI: 1.2-5.0) if they had experienced an adult replacement. Additionally, this parameter reached statistical significance at a level of  $p \leq 0.05$  in all the candidate models in which it was included as a factor (Table 2.6). We present parameter estimates and standard errors for each model included in our model-averaged estimates for both full and conservative analyses in Table 2.6.

**Table 2.6.** Details of the models used in multimodel inference for each model-averaged parameter in Part One (age at dispersal models).

Parameter	Model	AICc	AICc weight	Estimate (Coeff.)	SE
<b>Adult replacement</b>	M1.6	971.69	0.37	0.12	0.25
	M1.3	972.13	0.30	0.05	0.25
	M1.7	973.24	0.17	0.08	0.26
	M1.5	974.19	0.11	0.06	0.26
	M1.11	975.39	0.06	0.08	0.26
<b>Average = 0.08 ± 0.26; 95% Unconditional confidence interval: -0.42 - 0.58</b>					
<b>Births</b>	M1.2	967.78	0.53	-0.01	0.01
	M1.4	969.25	0.26	-0.02	0.01
	M1.8	971.34	0.09	-0.02	0.04
	M1.6	971.69	0.08	-0.01	0.01
	M1.7	973.24	0.03	-0.02	0.01
	M1.11	975.39	0.01	-0.02	0.04
<b>Average = -0.02 ± 0.02 (SE); 95% Unconditional confidence interval: -0.05 - 0.01</b>					
<b>Group size</b>	M1.4	969.25	0.44	-0.09	0.12
	M1.1	970.10	0.29	0.01	0.10
	M1.8	971.34	0.16	-0.10	0.15
	M1.7	973.24	0.06	-0.09	0.13
	M1.5	974.19	0.04	0.02	0.11
	M1.11	975.39	0.02	-0.10	0.15
<b>Average = -0.06 ± 0.13 (SE); 95% Unconditional confidence interval: -0.32 - 0.20</b>					

Parameter	Model	AICc	AICc weight	Estimate (Coeff.)	SE
<b>Adult replacement</b>	C1.6	229.93	0.59	0.89	0.35
	C.17	231.91	0.22	0.93	0.38
	C1,11	232.99	0.13	0.86	0.37
	C1.5	235.82	0.03	1.01	0.37
	C1.3	235.9	0.03	0.87	0.35
<b>Average = 0.90 ± 0.36 (SE); 95% Unconditional confidence interval: 0.19 - 1.61 Hazard ratio with 95% confidence interval = 2.46 (1.21-5.00)</b>					
<b>Births</b>	C1.6	229.93	0.56	-0.06	0.02
	C1.7	231.91	0.21	-0.06	0.03
	C1.11	232.99	0.12	-0.18	0.13
	C1.2	234.45	0.06	-0.06	0.02
	C1.4	236.23	0.02	-0.06	0.02
	C1.8	236.36	0.02	-0.23	0.14
<b>Average = -0.08 ± 0.07 (SE); 95% Unconditional confidence interval: -0.22 - 0.06</b>					
<b>Group size</b>	C1.7	231.91	0.51	0.07	0.21
	C1.11	232.99	0.3	-0.19	0.35
	C1.5	235.82	0.07	0.28	0.19
	C1.4	236.23	0.06	-0.11	0.21
	C1.8	236.36	0.06	-0.43	0.34
	C1.1	241.54	0	0.14	0.18
<b>Average = -0.03 ± 0.32 (SE); 95% Unconditional confidence interval: -0.65 - 0.59</b>					

-Models beginning with M (top) refer to models run using the full data set (n=138 individuals), while those beginning with C (bottom) refer to models run using the more conservative definition of dispersal (n=35 uncensored individuals) (see Table 3).

-Only models containing the parameter of interest were utilized in calculating the model-averaged parameters. All models utilized are ranked by AICc values.

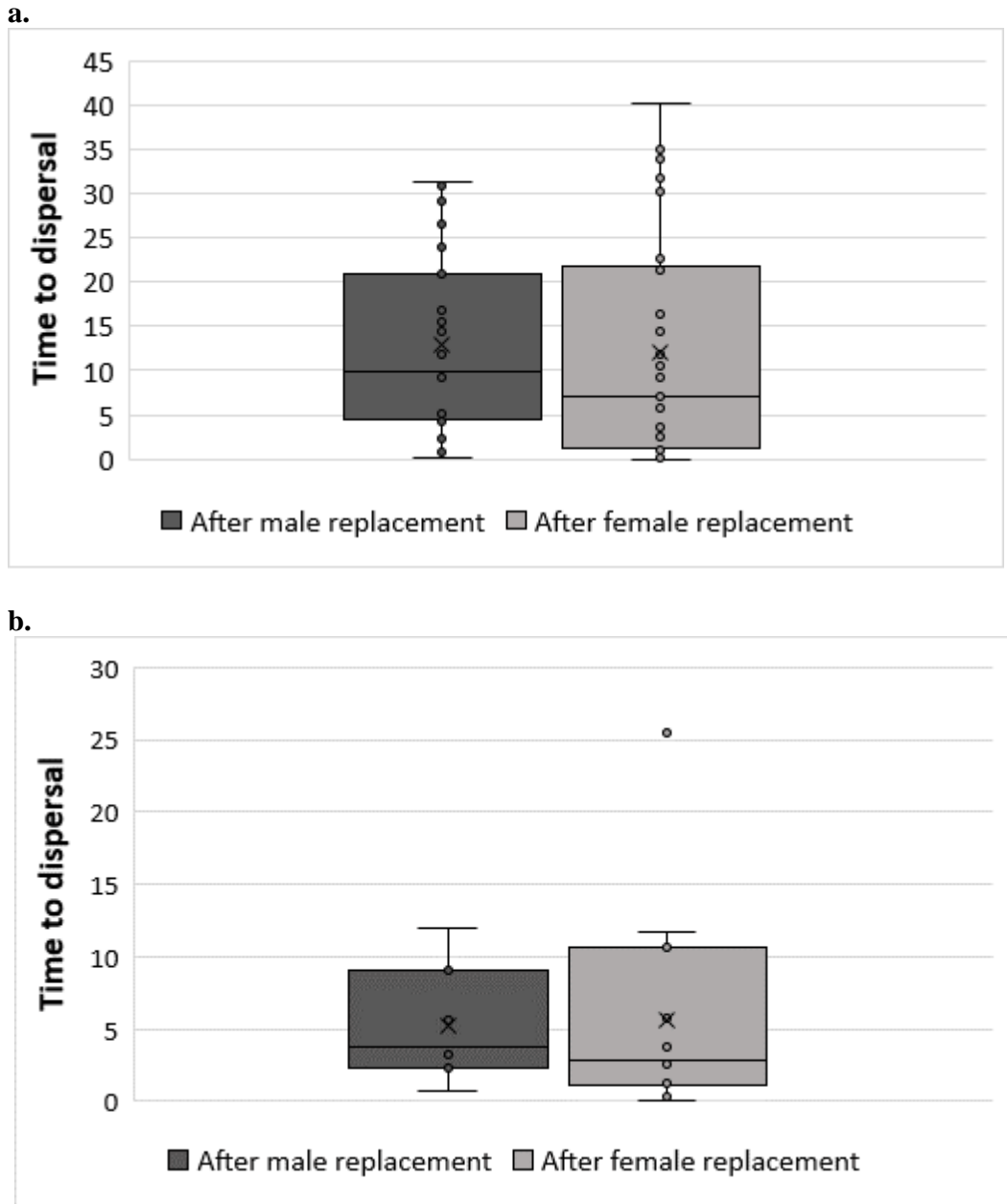
-Estimate = the coefficient for each model; SE = standard error for the estimate for each model

### Adult replacements and dispersal

Of the 253 individuals born between 1996 and 2015 (Table 2.1), at least 63 (25%) of them experienced the replacement of a resident adult. When we exclude individuals still in their natal groups, who could potentially still experience a replacement before dispersing (N=32), 29% of dispersed/disappeared individuals experienced a replacement. Offspring

experienced the replacement of adults of both sexes with equal frequency: 36 experienced the replacement of an adult female and 36 experienced the replacement of an adult male. Some offspring experienced more than one adult replacement (mean = 2.3, range 2-4 replacements). Nine individuals experienced the replacement of both a male and female adult, and eight experienced an additional replacement of an adult of the sex that had already been replaced earlier during the offspring's lifetime (four experienced multiple replacements of the adult male, five experienced multiple replacements of the adult female).

Offspring experienced adult replacements at all ages ( $20.0 \pm 1.8$  months; range 2 months before birth to 57 months). On average, an offspring remained in the natal group for  $12.4 \pm 1.5$  months after experiencing the replacement of an adult, and they remained in the natal group for a similar amount of time when the replacement involved an adult male ( $12.8 \pm 1.9$  months) or an adult female ( $12.0 \pm 2.3$  months; Wilcoxon Rank-Sum test:  $W = 478$ ,  $p = 0.4$ ). However, there was much variation, with some individuals dispersing within a day of experiencing a replacement, while one remained in the natal group for 40 months after a replacement (Figure 2.3a). When we consider just individuals that experienced an adult replacement as older juveniles or subadults (i.e.,  $>20$  months, when they were old enough to potentially disperse;  $N=17$ ), they remained in their natal group for  $5.5 \pm 1.3$  months. The time that older juveniles and subadults remained in their natal group was also similar after experiencing the replacement of an adult male ( $5.2 \pm 1.5$  months) or an adult female ( $5.6 \pm 1.9$  months; Wilcoxon Rank-Sum test:  $W = 57.5$ ,  $p = 0.6$ ; Figure 2.3b).



**Figure 2.3.** Box plots showing the time (in months) that offspring remained in the natal group after experiencing the replacement of an adult male or adult female, for: a) all offspring who experienced replacements, and b) offspring who experienced replacements at an age when they were old enough to disperse (>20 months). “X” indicates the mean.

Our part two models indicate that the age at which an offspring experienced an adult replacement was the most important factor for explaining the amount of time that an

individual remained in the natal group before dispersing. Six of our nine candidate models had a delta AICc of  $\leq 6$ , and together they accounted for 100% of the cumulative weight of our models (Table 2.4). Age at replacement was the only variable included in all six of these models, and it was the only variable included in the very best model (M2.1, which accounted for 43% of the cumulative weight). Specifically, an offspring had a hazard of dispersing 1.1 times greater (95% CI: 1.0-1.1) for every month older they were at the time of an adult replacement. The variable “same sex as replacement” was in four of the six best models, suggesting that offspring who experienced a replacement of the adult that was the same sex as themselves had a somewhat increased risk of dispersing. However, this variable’s effect did not reach statistical significance at a level of  $p \leq 0.1$  in any of the models in which it was included and the model-averaged parameter (0.53) had a 95% confidence interval that included zero (-0.2-1.3; Table 2.7). The sex of the dispersing individual did not explain much of the variance in age at dispersal either, and no interaction terms including sex were significant at a level of  $p \leq 0.1$  in any of the four models in which they were included. We present details of our models and model-averaged parameters in Table 2.7.

When we limited our analysis only to offspring who had experienced an adult replacement as a subadult ( $\geq 24$  months), there was a difference in the amount of time they remained in the natal group, depending on whether the adult replaced was the same or opposite sex as themselves (Figure 2.4). Individuals who experienced the replacement of the same sex adult dispersed sooner after the replacement (mean time remained =  $1.7 \pm 0.5$  months) than those that experienced the replacement of an opposite sex adult (mean time remained =  $5.8 \pm 1.4$  months), and this difference was statistically significant (Wilcoxon Rank-Sum:  $W = 12.5$ ,  $p = 0.05$ ). Furthermore, all seven individuals that experienced a same-



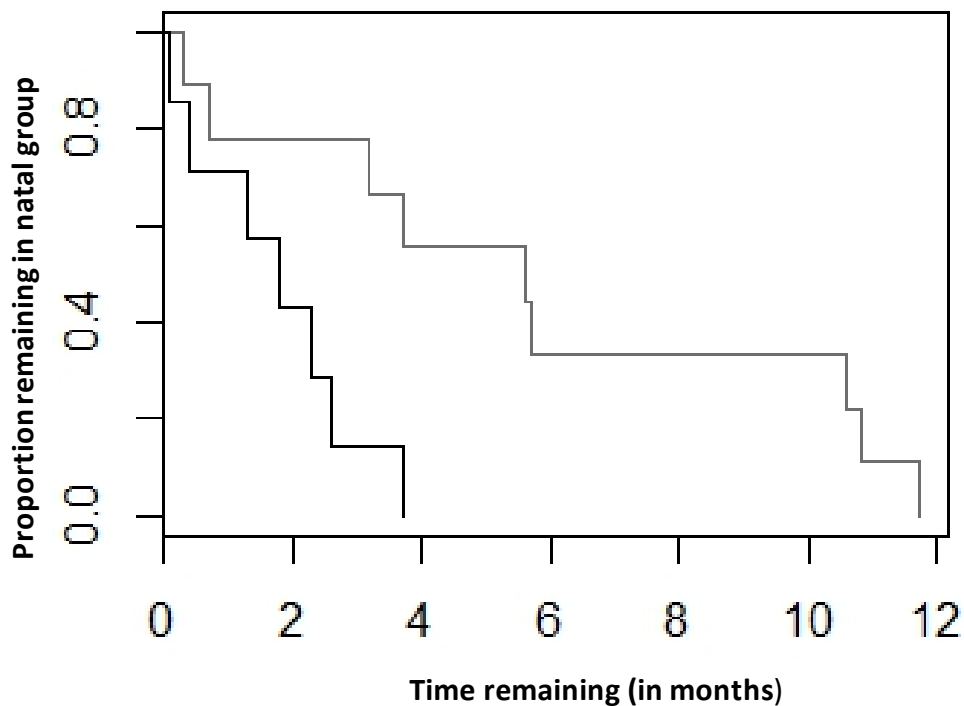
sex replacement dispersed within four months, while more than half of the nine that experienced an opposite-sex replacement remained in the natal group for more than four months (Figure 2.4).

**Table 2.7.** Details of the models used in multimodel inference for each model-averaged parameter in Part Two (time until dispersal).

Parameter	Model #	AICc	AICc weight	Estimate (Coeff.)	SE
<b>Age at replacement</b>	1	148.41	0.46	0.06	0.02
	3	148.86	0.37	0.07	0.02
	4	150.92	0.13	0.08	0.02
	9	153.61	0.03	0.07	0.02
<b>Average = 0.07 ± 0.02 (SE); 95% Unconditional confidence interval: 0.03 - 0.10</b> <b>Hazard ratio with 95% confidence interval = 1.07 (1.03 - 1.1)</b>					
<b>Same Sex</b>	3	148.86	0.93	0.53	0.39
	6	153.91	0.07	0.55	0.44
	2	165.12	0.00	0.14	0.38
<b>Average = 0.53 ± 0.39 (SE); 95% Unconditional confidence interval: -0.24 - 1.30</b>					
<b>Sex</b>	7	164.44	1	-0.33	0.36
<b>Estimate = -0.33 ± 0.36; 95% Unconditional confidence interval: -1.04 - 0.38</b>					

-Only models containing the parameter of interest were utilized in calculating the model-averaged parameters. All models utilized are ranked by AICc values.

-Estimate = the coefficient for each model; SE = standard error for the estimate in each model



**Figure 2.4.** Proportion of subadults that remained in the natal group after experiencing a replacement of the same sex (black) or opposite sex (gray) adult over one year.

### Timing of dispersal throughout the year

Individuals disappeared and dispersed in all months, but these events were concentrated in the birth season: approximately 50% (60/121) occurred mid-September to mid-January. Since the birth season constitutes only four months of the year, disappearance/dispersal during the birth season occurred more frequently than expected by chance and this difference was statistically significant (50% observed versus 33% expected;  $X^2 = 6.61$ ,  $df = 1$ ,  $p = 0.01$ ). Disappearances/dispersals were most frequent during October (N=24) (20% observed versus 8% expected;  $X^2 = 6.59$ ,  $df = 1$ ,  $p = 0.01$ ), though many also occurred in November (N=14) and December (N=12). They were least frequent in April

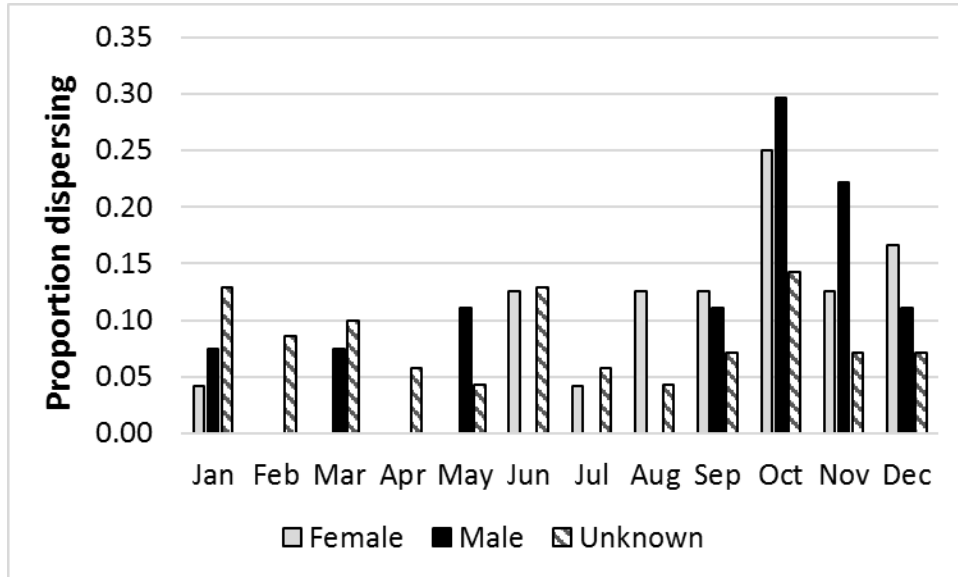
(N=4; 3% observed versus 8% expected;  $X^2 = 2.80$ ,  $df = 1$ ,  $p = 0.09$ ; Figure 2.5a), and occurred much less frequently than expected by chance in the fall/winter season (N=33/121; 27% observed versus 42% expected;  $X^2 = 5.54$ ,  $df = 1$ ,  $p = 0.02$ ).

The annual distribution of dispersal was also more skewed towards the birth season when we considered only individuals with confirmed dispersals: 61% (20/33) occurred mid-September to mid-January (61% observed versus 33% expected;  $X^2 = 4.93$ ,  $df = 1$ ,  $p = 0.03$ ). Dispersal were most frequent during October (30% observed versus 8% expected;  $X^2 = 5.11$ ,  $df = 1$ ,  $p = 0.02$ ), while none occurred during February or April (Figure 2.5b). Confirmed dispersals also occurred less frequently than expected by chance in the fall/winter season (N=7/33; 21% observed versus 42% expected;  $X^2 = 3.20$ ,  $df = 1$ ,  $p = 0.07$ ).

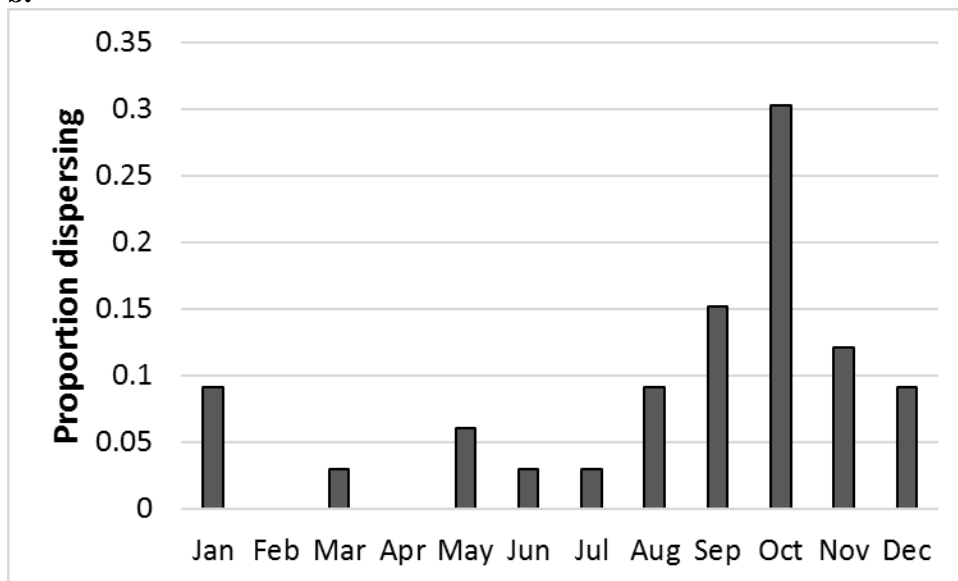
Our part three models indicate that a recent birth in the natal group was the factor most important in explaining whether an individual dispersed during the birth season. Twelve of the 15 candidate models had a delta AICc of  $\leq 6$ , and these accounted for 97% of the cumulative weight of our models. The six models with the best AICc ranking all included recent birth as a factor and recent birth was the only model-averaged parameter whose confidence interval did not include 0. Specifically, the odds of dispersing during the non-birth season increased by 2.6 (95% CI = 1.1-5.8) if there was a birth in the natal group within the past year. The model-average estimate for the effect of adult replacement was  $-0.7 \pm 0.4$  (SE), but the 95% confidence interval (-1.4-0.1) included zero (Table 2.8). However, the estimate for adult replacement was negative in all models in which it was included as a factor, and this parameter reached significance at the level of  $p \leq 0.1$  in the five best models (Table 2.8). This suggests that experiencing an adult replacement may be associated with a somewhat decreased chance of dispersing outside of the birth/dispersal season (odds ratio =

0.5, 95% CI = 0.2-1.1). Neither group size nor dispersal age were important in explaining variation in season of dispersal (Table 2.8).

a.



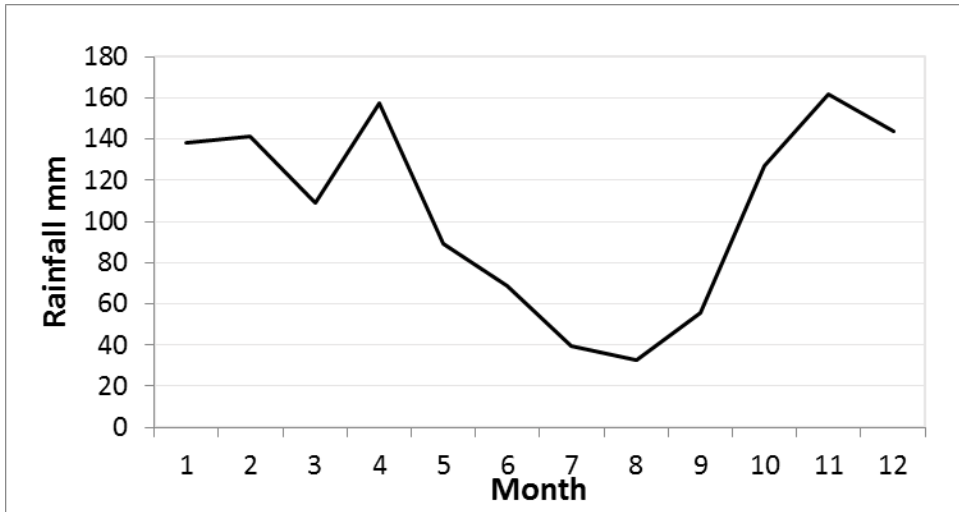
b.



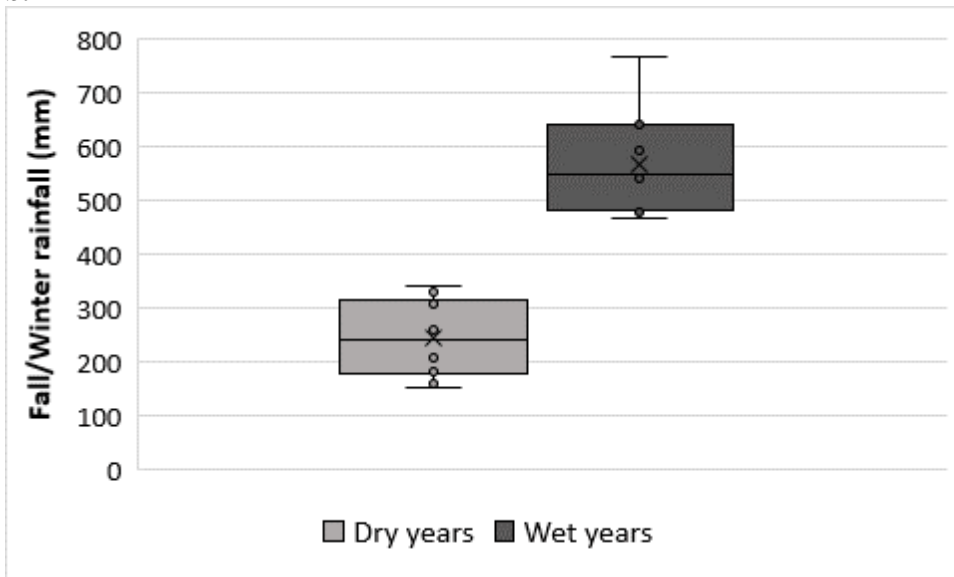
**Figure 2.5.** a) Proportion of males (N=27), females (N=24), and offspring of unknown sex (N=70) dispersing or disappearing in each month. b) Proportion of confirmed dispersals (N=33) occurring in each month.

Rainfall was the factor most important in explaining whether an individual dispersed during the fall/winter season (Figure 2.6). Thirteen of the 15 candidate models had a delta AICc of  $\leq 6$ , and these accounted for 100% of the cumulative weight of our models (Table 2.5). Eight of these models included high rainfall as a factor and this factor reached significance at level of  $p \leq 0.05$  in all eight of the models in which it was included. Model averaging indicated that high rainfall decreased the odds of dispersing during the fall/winter season by a factor of 2.7 (odds ratio: 0.4, 95% CI = 0.2-0.9). Rainfall was the only model-averaged parameter whose confidence interval did not include zero (model-averaged estimate =  $-1.0 \pm 0.5$ ), indicating that recent births, adult replacements, and age at dispersal were relatively unimportant in explaining whether dispersal occurred during the fall/winter season (Table 2.8). We present details of our models for birth season and fall/winter season and their model-averaged parameters in Table 2.8.

a.



b.



**Figure 2.6.** Rainfall at Guaycolec Ranch between 1997 and 2016: a) Mean monthly rainfall (in mm) for all months of the year; b) Mean rainfall (mm) between April and August for 10 “wet” years and 10 years with average or below average rainfall during the fall/winter (“dry years”).

**Table 2.8.** Details of the models used in multimodel inference for each model-averaged parameter in Part Three (season of dispersal).

Parameter	Model #	AICc	AICc wt	Estimate	SE
<b>Adult replacement</b>	B3.9	165.24	0.44	-0.66	0.38
	B3.11	166.97	0.18	-0.69	0.39
	B3.14	167.37	0.15	-0.67	0.41
	B3.4	168.79	0.07	-0.65	0.38
	B3.15	169.09	0.06	-0.73	0.42
	B3.10	170.01	0.04	-0.54	0.39
	B3.7	170.40	0.03	-0.69	0.38
	B3.12	171.84	0.02	-0.58	0.40
<b>Average = -0.66 ± 0.39 (SE); 95% unconditional confidence interval: -1.43 - 0.1</b>					
<b>Recent birth</b>	B3.9	165.24	0.32	0.95	0.41
	B3.2	166.09	0.21	0.94	0.40
	B3.11	166.97	0.13	0.94	0.41
	B3.14	167.37	0.11	0.97	0.45
	B3.8	168.00	0.08	0.86	0.44
	B3.5	168.04	0.08	0.94	0.40
	B3.15	169.09	0.05	0.99	0.45
	B3.13	170.02	0.03	0.87	0.44
<b>Average = 0.94 ± 0.42 (SE); 95% unconditional confidence interval: 0.12 - 1.76</b> <b>Odds ratio with 95% confidence interval = 2.56 (1.13 - 5.81)</b>					
<b>Group size</b>	B3.14	167.37	0.31	-0.03	0.27
	B3.8	168.00	0.23	0.11	0.25
	B3.15	169.09	0.13	-0.07	0.27
	B3.3	169.82	0.09	0.32	0.23
	B3.10	170.01	0.08	0.22	0.24
	B3.13	170.02	0.08	0.10	0.26
	B3.6	171.84	0.03	0.31	0.23
	B3.12	171.84	0.03	0.20	0.24
<b>Average = 0.08 ± 0.29 (SE); 95% unconditional confidence interval: -0.48 - 0.65</b>					
<b>Dispersal Age</b>	B3.11	166.97	0.38	0.01	0.02
	B3.5	168.04	0.23	0.01	0.02
	B3.15	169.09	0.13	0.01	0.02
	B3.13	170.02	0.08	0.01	0.02
	B3.7	170.40	0.07	0.01	0.02
	B3.1	171.62	0.04	0.01	0.02
	B3.6	171.84	0.03	0.01	0.02
	B3.12	171.84	0.03	0.01	0.02
<b>Average = 0.01 ± 0.02 (SE); 95% unconditional confidence interval: -0.03 - 0.05</b>					

Parameter	Model #	AICc	AICc wt.	Estimate	SE
<b>Adult replacement</b>	A3.5	142.76	0.32	-0.08	0.43
	A3.11	142.86	0.30	-0.05	0.43
	A3.12	144.89	0.11	-0.09	0.43
	A3.15	145.03	0.10	-0.05	0.43
	A3.2	145.88	0.07	-0.06	0.42
	A3.8	146.34	0.05	-0.05	0.42
	A3.10	147.97	0.02	-0.07	0.42
	A3.14	148.48	0.02	-0.05	0.42
<b>Average = -0.06 ± 0.43 (SE); 95% unconditional confidence interval: - 0.9 - 0.77</b>					
<b>Recent birth</b>	A3.6	140.73	0.00	0.66	0.47
	A3.11	142.86	2.13	0.66	0.47
	A3.13	142.87	2.14	0.66	0.47
	A3.3	144.25	3.52	0.58	0.46
	A3.15	145.03	4.30	0.66	0.47
	A3.8	146.34	5.61	0.58	0.46
	A3.9	146.35	5.62	0.58	0.46
	A3.14	148.48	7.74	0.58	0.46
<b>Average = 0.65 ± 0.47 (SE); 95% unconditional confidence interval: - 0.28 - 1.58</b>					
<b>Rainfall</b>	A3.1	140.69	0.00	-0.98	0.45
	A3.6	140.73	0.04	-1.03	0.45
	A3.5	142.76	2.07	-0.98	0.45
	A3.7	142.79	2.10	-0.98	0.45
	A3.11	142.86	2.17	-1.03	0.45
	A3.13	142.87	2.18	-1.03	0.45
	A3.12	144.89	4.20	-0.98	0.45
	A3.15	145.03	4.34	-1.03	0.45
<b>Average = -1.00 ± 0.45 (SE); 95% uncond. confidence interval: -1.88 - 0.13</b> <b>Odds ratio with 95% confidence interval = 0.37 (0.15-0.88)</b>					
<b>Dispersal Age</b>	A3.7	142.79	0.00	0.00	0.02
	A3.13	142.87	0.08	0.00	0.02
	A3.12	144.89	2.10	0.00	0.02
	A3.15	145.03	2.24	0.00	0.02
	A3.4	145.89	3.10	0.00	0.02
	A3.9	146.35	3.56	0.00	0.02
	A3.10	147.97	5.18	0.00	0.02
	A3.14	148.48	5.68	0.00	0.02
<b>Average = 0.00 ± 0.02 (SE); 95% unconditional confidence interval: -0.04 - 0.04</b>					

-Model names beginning with B (top) refer to models for which the outcome variable was whether or not dispersal occurred during the “birth season” (mid-Sep to early Jan). Model names beginning with A



(bottom) refer to models for which the outcome was whether dispersal occurred during the period of low resource abundance during the fall/winter (“abiotically defined season”).  
-Only models containing the parameter of interest were utilizing in calculating the model-averaged parameters. All models utilized are ranked by AICc values.  
-Estimate = the coefficient for each model; SE = standard error for the estimate for each model

## Discussion

Owl monkey dispersal strategies are flexible: variation in age and timing of dispersal is explained by several proximate social and ecological factors. The flexibility in age at dispersal that we found is consistent with previous observations of dispersal in Azara’s owl monkeys [Fernandez-Duque, 2009], and is similar to that observed in a variety of other primate taxa [Alberts and Altmann, 1995; Cheney, 1983; Fernandez-Duque, 2009; Jack and Fedigan, 2004; Morelli et al., 2009]. Our results underscore the importance of incorporating intraspecific variation into descriptions of species’ dispersal patterns.

In the remainder of this section, we first discuss our results related to the influence that social and ecological variables have on the age and timing of natal dispersal, and consider how these results inform our understanding of why some individuals delay dispersal. We then discuss our results in the context of evolutionary explanations for dispersal in pair-living monogamous taxa by assessing the extent to which our results support inbreeding, mate competition, and resource competition avoidance hypotheses. These hypotheses are broad and are not mutually exclusive, and the correlational nature of our data does not allow us to infer causality between proximate factors and dispersal. Therefore, what we do is evaluate how the associations between various factors and dispersal *most likely* influence dispersal patterns in owl monkeys, and evaluate which evolutionary explanations are most plausible, based on the associations we found.

Variation in the age at which owl monkeys dispersed was best explained by adult replacements. The replacement of a parent by an unrelated adult is expected to increase the chance of dispersal if access to nepotistic benefits is influencing dispersers' decisions to stay. This is because adult replacements reduce potential nepotistic benefits available to offspring in the natal group [Ekman and Griesser, 2002]. Models using data from individuals with confirmed dispersals found that, at a given age, individuals that experienced an adult replacement had an increased risk of dispersing approximately 2.5 times higher than those who did not experience a replacement (Table 2.6). Our results are consistent with the "safe haven" hypothesis, which suggests that offspring delay dispersal when their natal group consists of close kin, to maintain access to nepotistic benefits [Kokko and Ekman, 2002].

The proportion of offspring experiencing adult replacement was higher for individuals with confirmed dispersals compared to individuals that disappeared (Figure 2.1b). This is likely a consequence of our enhanced ability to detect adult replacements in groups that were more closely monitored. We capture individuals from our core study groups, which we contact almost every week, much more frequently than individuals in non-core groups. Individuals with confirmed dispersals had all been captured and radiocollared prior to their dispersal, and generally came from one of our core groups. Owl monkeys are sexually monomorphic and lack obvious distinguishing markings, and it is not typically possible to distinguish one adult from another adult, unless the individuals have been captured and collared or marked [Fernandez-Duque and Rotundo, 2003; Juárez et al., 2011]. We suspect that our detection rate for replacements in core groups, and thus for individuals with confirmed dispersal, was higher than for non-core groups. The difficulty in detecting adult replacements in groups in which one or both adults have not been captured and identified

likely resulted in us underestimating the proportion of offspring in these groups that experienced an adult replacement. This may, at least in part, explain why we did not find that adult replacement explained a significant amount of variation in our part one models that included disappeared individuals (Table 2.6). However, it is also possible that some of the disappearances that we observed were due to deaths, and thus should not be considered dispersals at all. This may also have contributed to the differences between our analyses that used disappeared individuals and our more conservative analyses.

Variation in the amount of time that an individual remained in the natal group after experiencing a replacement was best explained by the offspring's age (Table 2.7). This is unsurprising as the costs of dispersal and benefits of philopatry are expected to depend on characteristics of the predispersing offspring that change with age, such as size and physical condition, foraging skills and competitive ability, and sexual maturity [Bonte et al., 2012]. It follows that the benefits of remaining in the natal group after a replacement likely also change with age. Four of our six best models also contained the variable "same sex as replacement", suggesting that offspring who experienced a replacement of the adult that was the same sex as themselves had a somewhat increased risk of dispersing. The effect of the same sex variable was not statistically significant in our models that included individuals of all ages, but subadults who experienced the replacement of the same sex adult remained in the natal group for less time than those that experienced the replacement of an opposite sex adult (Figure 2.4). The fact that this effect was stronger in subadults, who had likely already experienced the onset of sexual maturity at the time of the replacement [Corley et al., 2016; Chapter 4], suggests that mating competition with the new same sex adult may increase the costs of delaying dispersal.

Variation in the timing of dispersal during the year was not well-explained by adult replacements. According to our models, individuals did *not* have a decreased chance of dispersing outside of the preferred dispersal season if they had experienced an adult replacement nor did they have an increased chance of dispersing during the fall/winter season (Table 2.8). One might expect that replacements could force individuals to disperse at a non-preferred time, when the relative costs of dispersal were high. In fact, our previous examination of owl monkey dispersal provided preliminary support for this prediction [Fernandez-Duque, 2009]. However, our models were not consistent with this prediction: the data actually suggest that there was a slight (though non-significant) *decreased* chance of dispersing during a non-preferred season for individuals that had experienced a replacement (Table 2.8). While replacements were associated with an increased risk of dispersing at a given age, the factors that influence offspring to remain in the natal group until the preferred dispersal season may outweigh the costs of delaying dispersal after a replacement. This “benefit” could prevent replacements from having a substantial effect on the time of year at which a dispersal occurs. Thus, the benefits of delaying dispersal until the preferred dispersal season may be more important than the costs of remaining in the natal group (whether due to risk of inbreeding or risk of aggression related to mating competition in the natal group).

Other demographic factors, particularly infant births, were also important in explaining variation in the timing of dispersals. Specifically, individuals were more likely to disperse outside of the preferred dispersal season if a birth had taken place within that past year. If infant births were a mechanism for triggering dispersal, we would expect dispersals to be more likely immediately or shortly after the birth of an infant. In other words, we would expect recent births to be associated with increased odds of dispersing during the preferred

dispersal season, since it overlaps with the birth season. Our results do not support this expectation. Furthermore, time since the most recent infant birth also did not explain much variation in the age at dispersal (Table 2.6). Together, these results suggest that infant births in the natal group do not immediately trigger dispersals. Instead, it is possible that the presence of an infant or young juvenile (< 1 year old) alters social interactions within the natal group in a way that decreases potential nepotistic benefits available to the dispersing offspring. Decreased benefits from philopatry that begin to manifest in the months after an infant birth could explain why individuals had increased chances of dispersing outside of the preferred dispersal season if a birth had occurred in their natal group within the past year. The precise mechanisms that underlie this increased risk of dispersing at non-preferred times of the year require investigations into how social interactions may differ during times when infants are present compared to when they are not.

The distribution of dispersals throughout the year was also explained by ecological factors. Specifically, increased rainfall, which is linked to increased resource availability, during the fall/winter months was associated with a decreased chance of dispersing during the fall/winter (Table 2.8). Our results thus suggest an association between increased resource availability during periods typically marked by relative scarcity and delaying dispersal until the preferred dispersal season. The inverse of this finding is that individuals are more likely to disperse during the fall/winter when conditions are relatively harsher (e.g., drier years with lower resource availability). Years during which fall/winter season resources are more scarce likely correspond to higher resource competition within the natal group. This may influence social interactions between adults and dispersers and reduce the value of the natal group as a safe haven [Kokko and Ekman, 2002]. Our results are therefore again consistent with the

“safe haven” hypothesis, as they suggest that offspring will continue to utilize their natal groups as safe havens while resources are relatively abundant, but may disperse when increased scarcity or resource competition reduces the benefits of philopatry.

Our results provide limited support for the inbreeding avoidance hypothesis. Replacement of the same sex parent is predicted to increase the chances of inbreeding (i.e., mating with the remaining opposite-sex parent), potentially leading to earlier dispersal. Consistent with this idea, we found that subadults who experienced a replacement of the same sex adult did disperse sooner than subadults who experienced an opposite sex adult replacement. However, inbreeding avoidance is not the only possible explanation for this difference. Replacement of the opposite sex parent also introduces an unrelated potential mate to the natal group. The fact that subadults who experienced an opposite sex adult replacement remained in the natal group longer could suggest that these individuals delayed dispersal due to interest in the new opposite sex adult as a potential mate.

Our results cannot distinguish between these two alternatives, but we can gain insight by considering behavioral observations. Over 20 years we have observed almost no sexual interactions between predispersing individuals and adults, even unrelated adults who have entered the group as the result of an opposite sex replacement (Huck et al., 2012; personal observations). These observations suggest that inbreeding avoidance may be a more important than mating competition avoidance as a force underlying dispersal in owl monkeys, at least for dispersals associated with adult replacements.

If inbreeding avoidance is the mechanism primarily driving natal dispersal, then individuals should disperse around the time of sexual maturation. The median age at dispersal for both sexes was 37 months. On average, females begin to establish ovulatory cycles at 36

months of age (median 32 months), though they may undergo at least several months of adolescent subfecundity (Corley et al., 2016, Chapter 4). Based on the median ages alone, the age at sexual maturation and the age at dispersal are similar, which would support the inbreeding avoidance hypothesis. However, both male and female owl monkeys dispersed at a wide range of ages, both before and after the likely onset of sexual maturity. It is possible that some of the variation in age at dispersal may be associated with intra-individual variation in the timing of sexual maturation. However, behavioral observations suggest that at least some individuals achieve sexual maturity prior to dispersing and are capable of being perceived as potential mates by others in the natal group. For example, we observed an adult male mount a four-year-old predispersed female after we had tranquilized her with a dart during an attempt to capture her. This male was the putative father of the female, and we had not observed any previous sexual interactions between the two of them prior to this event [Fernandez-Duque, 2009]. In another case, on the first day after a male replacement occurred, we observed a four-year-old predispersed female being mounted multiple times by the new male that had replaced her putative father. We did not observe any additional instances of mounting between the new male and the subadult female after this initial day, and this is the only case in which we have observed an adult male copulating with an individual other than the adult female after a replacement (Corley personal observation, Chapter 5). While the anesthetic likely played a role in the first incident described, together these examples indicate that subadult females can be perceived as potential mates by adult males in the natal group, even their own fathers, at least under certain circumstances.

The fact that some offspring remained in the natal group after the onset of sexual maturity is consistent with the mating competition avoidance hypothesis. However, the

mating competition hypothesis predicts that dispersals will more frequently occur during the mating season (April-July/August), when mating competition is most intense [Fernandez-Duque, 2009]. Our results did not support this prediction, as dispersals were actually least frequent during the mating season (Figure 2.5). Furthermore, as discussed in the previous paragraph, sexual interactions between predispersing offspring and adults in the natal group, such as mountings, are rare [Huck and Fernandez-Duque, 2012; Chapter 5]. This suggests that behavioral or other mechanisms may typically be in place to prevent predispersed offspring from mating with adults in the natal group, even though they may be sexually mature. Thus, mating competition seems unlikely to be the primary force driving dispersal. Subadults remained in the natal group for less time after experiencing the replacement of a same sex adult compared to an opposite sex adult. This finding might implicate a role for mating competition in regulating natal dispersal. However, an increased risk of inbreeding with the remaining opposite sex parent could also explain this finding.

Our results do not generally support the resource competition avoidance hypothesis, but there is evidence that resource abundance may influence dispersal under certain circumstances. The resource competition avoidance hypothesis predicts that dispersals should occur during or shortly after periods of food scarcity and that there should be an increased chance of dispersal in larger groups, where competition is presumably higher. In disagreement with these predictions, neither age at dispersal nor timing of dispersal was well-explained by the size of the natal group (Tables 2.6 and 2.8). Most offspring dispersed during the spring or early summer, when resources abundance is generally increasing or at its peak. This contrasts with predictions of the resource competition hypothesis, and suggests instead that individuals may time dispersals to take advantage of relatively high resource abundance



during the time that the disperser is adjusting to ranging solitarily and searching for a new group to join. This strategy may help newly solitarily individuals buffer the costs of ranging solitarily [Bonte et al., 2012]. However, our results suggest that this preference for dispersing during times of relative abundance may be over-ridden during times of very low resource availability (i.e., when conditions are relatively dry during the already generally resource-poor fall/winter season). Individuals were 2.7 times more likely to disperse during the fall/winter season if there was lower than average rainfall, and thus likely lower resource abundance, during the fall/winter of the year in which they dispersed (Table 2.8).

There is more than one plausible explanation for why dispersal during the fall/winter was most likely during years with lower resource abundance. Competition for resources with natal groups members could intensify the costs of philopatry by increasing the amount of aggression offspring receive during foraging. Alternatively, offspring may leave on their own accord in order to seek out habitats with higher resource availability [Kennedy and Ward, 2003; Schneider et al., 2003]. Whether individuals that disperse during resource-poor periods leave voluntarily or are expelled by adults remains unclear, and additional behavior data is needed to explore this question (Chapter 3). Nonetheless, from the evidence currently available, resource competition seems to be the most likely explanation for increased dispersal during the fall/winter during years with lower resource availability. One important caveat is we did not measure resource abundance directly during all 20 years of our study, and we thus used rainfall as a proxy. While there is evidence to support the link between high amounts of rain and higher forest productivity [Fernandez-Duque, 2009], a better understanding of exactly how resource availability changes with rainfall and other factors would improve our ability to investigate how dispersal is related to resource abundance.

In summary, multiple hypotheses about dispersal patterns are supported to some extent. As mentioned previously, our goal in placing results in the context of these hypotheses is to evaluate the plausibility of each and the relative importance that they have in shaping owl monkey dispersal patterns. Just as variation in the age and timing of dispersal exists in owl monkeys, the proximate mechanisms and evolutionary forces shaping dispersal patterns are also varied, and different mechanisms seems to operate in different situations. Our results support the “safe haven” hypothesis as a general explanation for much of the variation in the age and timing of dispersal in owl monkeys. While inbreeding avoidance seems to be the most likely force driving dispersal after the replacement of the same sex adult, variation in the age at dispersal means that some individuals remain in the natal group with genetic parents of the opposite sex after reaching sexual maturity. This finding suggests that inbreeding avoidance alone cannot explain the timing of dispersal under all circumstances. Resource competition avoidance is implicated as a force underlying the increased likelihood of dispersing during years when there is higher intragroup competition during the fall/winter seasons due to lower rainfall and resource abundance.

Our results highlight the importance that close, long-term monitoring of wild populations has for developing a detailed understanding of dispersal patterns. The age-specific probabilities of survival differed for individuals that were confirmed to have dispersed and those that disappeared (Figure 2.2b). This may explain why the results of our models in part one differed, depending on whether we included disappeared individuals in our analyses (Table 2.6). The fact that individuals that disappeared were, on average, younger than those that dispersed suggests that it is likely that at least some individuals that disappeared died rather than successfully dispersed. Our results suggest that claims about

dispersal based on data primarily from disappeared individuals should be interpreted with care.

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### **Chapter 3. The role of intragroup agonism in parent-offspring relationships and natal dispersal in monogamous owl monkeys (*Aotus azarae*) of Argentina**

#### **Abstract**

Agonistic behaviors are common in many group-living taxa and may serve a variety of functions, ranging from regulating conflicts over reproduction to defending food resources. However, high rates of agonism are not expected to occur among close relatives or individuals in established mating relationships, which are characteristics of monogamous groups. To contribute to our understanding of agonism within socially monogamous groups, we collected behavioral and demographic data from Azara's owl monkeys (*Aotus azarae*) in the Gran Chaco of Argentina over 14 years. We examined factors related to age, sex, kinship, and behavioral context to evaluate predictions of the hypotheses that agonism functions to regulate dispersal and that it mediates competition for food and/or mates. Intragroup agonism was relatively rare, with the group rate being approximately one event every three and a half hours. Rates of agonism were generally similar for both sexes, although there were marked differences among age categories. Agonism was most frequently performed by adults and directed at offspring, particularly subadults. In contrast, agonistic interactions involving infants were very rare. Subadults also received more agonism in the six months immediately preceding dispersal than they did prior to this peri-dispersal period, suggesting that agonistic interactions may regulate natal dispersal patterns. Agonistic events were most frequent during foraging, but also regularly occurred during non-foraging contexts, particularly during bouts of social behavior. In owl monkey groups agonism seems to serve as an important mechanism for regulating dispersal, and possibly also plays a role in mediating mating and feeding competition amongst adults and subadults.

## **Introduction**

Agonistic interactions are a part of social life for all group-living taxa, and primates are no exception. All primates are known to engage in overt aggression against conspecifics, at least on occasion [Bernstein, 1976; Holloway, 1974; Sussman and Garber, 2004; Sussman et al., 2005; Wrangham and Peterson, 1996; Zinner and Wheeler, 2012]. What constitutes agonistic behavior may vary from species to species [Klein, 1974], but agonism is generally considered to encompass behaviors ranging from aggressive physical contact to more passive actions, such as displacements. Often resulting from competition for limited resources, agonism has important consequences for dominance [Drews, 1993], and thus fitness [Cowlshaw and Dunbar, 1991; Fedigan, 1983; Harcourt, 1987; Majolo et al., 2012; Pusey, 2012]. Therefore, explaining patterns of agonism is important for understanding the mechanisms regulating primate societies [Sterck et al., 1997; van Schaik, 1989; Wheeler et al., 2013; Wrangham, 1980].

Rates of agonism vary substantially among primate species [Sussman et al., 2005]. There is both theoretical and empirical work suggesting that variation in agonism rates may be best explained by factors such as resource distribution, social organization, or kinship [Isbell, 1991; Koenig, 2002; Koenig et al., 2013; Vehrencamp, 1983; Wheeler et al., 2013]. For example, female agonism rates are positively correlated with the number of adult female primates in a group when examined across taxa [Wheeler et al., 2013].

Among monogamous taxa, agonism towards extra-pair adults has been proposed to be a proximate mechanism that maintains the relationship between pair-mates [Kleiman, 1977]. Supporting this hypothesis, studies of socially monogamous species suggest that paired individuals commonly display agonistic behavior towards unfamiliar conspecifics,

particularly strangers of the same sex (e.g., titi monkeys (*Callicebus spp.*): [Fisher-Phelps et al., 2015; Mason and Mendoza, 1998]. In captive owl monkeys (*Aotus lemurinus*), most aggression occurred when “intruders” were introduced to established groups, or when unfamiliar individuals of the same sex were introduced to one another. In these cases, aggression was sometimes extreme, resulting in injury or even death if individuals were not separated [Evans et al., 2009; Hunter and Dixson, 1983].

The extreme aggression towards extra-group individuals in captivity is concordant with observations of monogamous owl monkeys in the wild. Encounters between neighboring groups are often characterized by agonistic behaviors, such as vocalizations and displays, sometimes chasing, but rarely fighting [Fernandez-Duque, 2011; Wright, 1994]. On the other hand, both male and female reproductive adults experience intense intra-sexual aggression in interactions with solitary floaters [Fernandez-Duque, 2004; Fernandez-Duque and Huck, 2013]. Data from other free-ranging socially monogamous species are limited, but pairs of dusky titi monkeys (*Callicebus moloch*) have also been observed to engage in aggressive interactions with extra-group conspecifics [Mason, 1966]. Likewise, black-fronted titi monkeys (*Callicebus nigrifrons*) respond agonistically to playbacks of both simulated solitary and paired intruders in a manner consistent with joint territorial defense [Caselli et al., 2015]. Several species of gibbon respond to conspecifics’ calls in ways that suggest that both sexes defend territories from intruders (Bornean gibbons: *Hylobates muelleri* [Mitani, 1984]; Agile gibbons: *H. agilis* [Mitani, 1988]). The majority of intergroup encounters among white-handed gibbons (*H. lar*) also involve at least some agonistic behaviors, such as chasing [Bartlett, 2003; Reichard and Sommer, 1997].

In addition to agonism towards extra-group individuals, agonistic interactions also

occur *within* groups in taxa where there is only one reproducing pair (i.e., monogamous) or one pair of adults that monopolizes most of the mating (e.g., callitrichids). In the latter case, this behavior is often directed towards same-sex individuals in the group (cooperative breeding callitrichids: e.g., [Abbott, 1984; Baker et al., 1993; Ferrari, 2009; Rothe, 1975; Soini, 1987], sakis: [Thompson, 2013; Thompson, 2015], siamangs: [Morino, 2015]). In some cases, aggression from the dominant, reproductive female may even induce reproductive suppression in subordinate females [Abbott and Hearn, 1978; Abbott, 1993; Wasser and Barash, 1983; Young, 2009].

While competition for mating opportunities can explain intragroup agonism in groups with multiple mature animals of the same sex, such as cooperative breeders, it cannot readily explain why it occurs in monogamous species in which groups consist of only an adult male, an adult female, and their putative offspring. Yet, among monogamous taxa, intragroup agonism has been described for captive [Dixson, 1983; Evans et al., 2009] and wild owl monkeys [Huck and Fernandez-Duque, 2012], wild titi monkeys (*Callicebus discolor*) [Mason, 1966; Spence-Aizenberg et al., 2016], and titi monkeys housed in a one-hectare field enclosure [Menzel, 1993].

In Azara's owl monkeys (*Aotus azarae*), intense intrasexual competition with solitary floaters results in relatively frequent adult turn-overs [Fernandez-Duque and Huck, 2013]. Adult replacements are predicted to have social consequences for offspring, as replacements introduce a "step-parent", who may represent either a competitor or a potential breeding partner [Emlen, 1995; Emlen, 1997]. Indeed, among callitrichids, changes in group composition, such as the loss of the breeding female, were found to be associated with increased rates of intragroup agonism [Lazaro-Perea et al., 2000]. Data on inter-individual

distances and identity of the nearest neighbor further provided some evidence that the quality of the relationship between owl monkey parents and their same-sex offspring may deteriorate prior to dispersal, particularly after the replacement of the opposite-sex adult [Huck and Fernandez-Duque, 2012].

The Azara's owl monkey (*A. azarae*) [Huck et al., 2014] constitutes a well-suited model for exploring hypotheses about the function of within group agonism in monogamous taxa. In the Gran Chaco region of Argentina, groups consist of one pair of reproductive adults and their putative offspring (mean group size = 4, range: 2-6) [Fernandez-Duque et al., 2001]. Owl monkeys display remarkably little sexual dimorphism: male and female adults are similar in size, coloration, and markings, and male and female offspring develop at similar rates and both disperse at similar ages [Chapter 2, Fernandez-Duque, 2009; Fernandez-Duque, 2011; Fernandez-Duque, 2016; Huck et al., 2011]. While offspring do not typically participate in sibling care, adult males engage in high levels of paternal care and often behave affiliatively towards offspring [Fernandez-Duque, 2011; Rotundo et al., 2005]. Unlike the strictly nocturnal tropical species of owl monkeys, *A. azarae* is cathemeral [Fernandez-Duque and Erkert, 2006], and its activity patterns allow for detailed behavioral data to be collected from identified individuals during the daytime.

In this study, we quantified intragroup agonism in wild Azara's owl monkeys to examine three main hypotheses that explain its potential functions (Table 3.1). We first examined the general hypothesis that agonism between adults and offspring, particularly older offspring (i.e., subadults), acts as a dispersal mechanism. We then explored two more specific hypotheses related to within-group competition. The "food competition hypothesis" proposes that the primary function of agonism is resolving conflicts over food resources

among adults and offspring. The “mate competition hypothesis” suggests that it allow adults to avoid competition over mates with offspring in the group. We considered factors related to age, kinship, sex, and behavioral context to construct predictions for these three hypotheses. These hypotheses are not mutually exclusive, as agonism may function, to some extent, for a variety of purposes simultaneously. We distinguished between them primarily as a heuristic to assess the potential relative importance of various functions of agonism.

**Table 3.1.** Hypotheses<sup>1</sup> and predictions.

<b>Hypotheses</b>	<b>Prediction</b>	<b>Description</b>
<b>1. Dispersal</b>	P1.1	If adults minimize competition by expelling/encouraging subadults to disperse from their natal group, the frequency at which subadults are engaged in agonistic behaviors will be higher in the period just prior to dispersal, than at younger ages.
	P1.2	Within agonistic events involving both adults and subadults, adults will be the actors (and subadults the recipients) more frequently than subadults will be the actors.
	P1.3	If adults are less tolerant of unrelated offspring (i.e., step-offspring) than their own offspring, there will be higher rates of agonism between adults and their step-offspring than between adults and their own offspring.
<b>2. Food competition</b>	P2.1	Assuming that food is a resource over which individuals compete, agonistic behaviors will occur more frequently in feeding contexts (i.e., while individuals are foraging) than expected based on the proportion of time individuals spend foraging.
	P2.2	As offspring of both sexes likely present equal levels of competition for food resources, adults will direct agonistic behavior towards males and females at similar rates.
<b>3. Mate competition</b>	P3.1	Adults will engage in agonistic behaviors more often with subadults than younger offspring, since the former represent potential competitors for mates.
	P3.2	Adults of both sexes will direct agonistic behavior primarily towards subadults of the same sex as themselves.

<sup>1</sup>As noted in the text, these hypotheses are not mutually exclusive: the removal of a subadult offspring from the group via dispersal can potentially reduce *both* feeding and mating competition. We distinguish between them as a heuristic and to assess the relative contributions of food competition or mating competition to explaining patterns of intragroup agonism.

## **Methods**

### **Study site and subjects**

Our study was conducted at the Reserva Mirikiná, a 1500 ha reserve of gallery forest in the ranch Estancia Guaycolec, in Formosa, Argentina (58°13'W, 25°54'S). The region is part of the South American Gran Chaco, a mosaic of gallery forest, grasslands, savannahs, and isolated patches of dry forest [Placci, 1995; van der Heide et al., 2012]. Climate and seasonality at this site have been described previously [Fernandez-Duque, 2009].

Within the reserve, a 300 ha area of gallery forest along the banks of the Riacho Pilagá has been mapped. Groups within this core area have been habituated and monitored by the Owl Monkey Project (OMP) since 1997 [Fernandez-Duque, 2016; Fernandez-Duque et al., 2001]. All data we report here were collected from habituated groups, in which members could be discriminated from one another by collars or natural distinguishing markings. When necessary, we utilized body size and the relative amount of subcaudal scent gland secretions to distinguish non-captured, and thus uncollared, subadults and juveniles from adults and from one another [Huck et al., 2011]. We classified individuals as infants ( $\leq 6$  months), juveniles ( $6 < 24$  months), subadults ( $\geq 24$  months), or adults (dispersed individuals  $> 48$  months), following Huck et al. [2011].

### **Data collection**

Demographic changes in groups were determined through close monitoring of the study population. Since 1997, a core set of approximately 10 groups has been regularly contacted, at least once every week or every second week. Every time that a group was contacted, the observer recorded the presence of identified individuals and noted any changes to group composition since the previous sighting. This monitoring has allowed us to identify

dates of births, deaths, dispersals, and adult replacements within a range of a few weeks [Huck and Fernandez-Duque, 2012]. In the rare cases when the exact date of a birth, disappearance, dispersal, or replacement could not be determined to have occurred within a period of < 30 days, we estimated the event to have occurred on the average between the date on which the demographic change was first observed and the most recent date on which the group had previously been sighted.

Behavioral data were collected following research protocols (available in English and Spanish upon request) that are utilized for comparative purposes in studies of owl monkeys in Argentina [Fernandez-Duque and Huck, 2013; Fernandez-Duque and van der Heide, 2013; Huck and Fernandez-Duque, 2012; Huck and Fernandez-Duque, 2013], as well as studies of titis (*C. discolor*) and sakis (*Pithecia aequatorialis*) in Yasuní National Park in Ecuador [Porter et al., 2015; Spence-Aizenberg et al., 2016; Van Belle et al., 2016]. In brief, each focal sample consisted of a 20-minute period during which all behavioral events (e.g., movements, social interactions, foraging) were recorded and the behavioral state of the focal individual (resting, foraging, moving, socializing, other, or out of view) was recorded every two minutes (i.e., focal sampling point). Additionally, after every four minutes, the instantaneous behavioral state and distance to the focal individual were recorded for each non-focal member of the group.

Focal samples utilized in this study were collected, by trained observers, over 14 years (August, 2001 to August, 2015). To ensure the quality of behavioral observations, all new observers were trained by experienced observers and inter-observer reliability was regularly evaluated. Behavioral data were only collected by observers who worked in the field for longer than two months, usually only by those who stayed at least four months.



Each observer goes through a period of training during which they collect “practice” focal samples, not used in analyses, simultaneously (i.e., standing side by side) with the staff member for later comparison. For analyses, we excluded the first 20 focal samples collected by each trained observer, as we deemed this to be the amount of practice needed for observers to become sufficiently familiar with the protocol and reliably identify behaviors at levels similar to more experienced observers.

### **Data analyses**

We considered a behavior to be agonistic if it fell into one of the following behavioral categories listed in the protocol’s ethogram: aggression, food robbing, chasing, or displacing (Table 3.S1). These behaviors may not represent equivalent magnitudes of agonism. For example, displacing another individual could be considered a milder form than aggression involving biting or shoving. However, displacements have been useful for determining dominance hierarchies, particularly when other forms of agonism are rare [Borries et al., 1991; Sterck and Steenbeek, 1997], and are typically included in analyses for other primates [Erhart and Overdorff, 2008; Koenig et al., 2004; Ramanankirahina et al., 2011; Sussman et al., 2005; Wheeler et al., 2013].

Since the goal of our study was to examine rates and potential functions of intragroup agonism, we excluded behaviors that were observed in the context of intergroup encounters, or encounters between groups and solitary individuals. Additionally, to determine if we should exclude milder types of agonism (food robbing and/or displacing), we performed analyses that included only what we considered to be the most extreme forms (aggression and chasing). The pattern of results from analyses that excluded milder behaviors

were similar to those from analyses that include all agonistic behaviors. For that reason, and to produce results more comparable to the existing literature, our analyses pooled all four categories of agonism.

We extracted all data from the Owl Monkey Project Database stored in Microsoft Access, and organized and cleaned the data in Microsoft Excel. We performed all statistical analyses in R version 3.0.2 [R Development Core Team, 2008]. We only included in analyses groups with more than 20 focal samples. The resulting dataset included 15 groups, 169 individuals, and 6430 focal samples collected during 2124 hours of focal behavioral observations (Table 3.2). Some individuals contributed data to multiple age categories, as they aged over the course of the study.

**Table 3.2.** Number of individuals and observation effort for 15 groups of owl monkeys observed in the Reserva Mirikiná in Formosa, Argentina between 2001 and 2015.

<b>Group Name</b>	<b>Total Individuals</b>	<b>Adult males</b>	<b>Adult females</b>	<b>Male off-spring</b>	<b>Female off-spring</b>	<b>Off-spring sex unknown</b>	<b>Focal samples</b>	<b>Sampling points</b>
B68	10	2	3	0	1	4	36	360
C0	12	2	2	2	2	4	456	4511
CC	18	4	5	2	5	2	741	7360
Colman	14	1	2	3	4	4	495	4950
Corredor	6	1	1	0	2	2	170	1654
D100	8	3	2	0	2	1	326	3258
D1200	12	1	2	3	1	5	153	1524
D500	17	2	3	3	4	5	1170	11612
D800	11	2	4	1	0	4	611	5925
E350	14	2	3	3	3	3	687	6776
E500	18	2	4	2	3	7	1094	10887
F1200	10	1	1	2	3	3	218	2180
F700	14	4	2	2	1	5	100	989
G1300	8	2	3	0	1	2	130	1300
P300	4	1	1	0	1	1	43	428
<b>Total</b>	<b>176<sup>1</sup></b>	<b>30</b>	<b>38</b>	<b>23</b>	<b>33</b>	<b>52</b>	<b>6430</b>	<b>63714</b>

“Individuals” indicates the total number of unique owl monkeys observed in each group over the entire study period. Group composition changed during the study and only 2-6 individuals were present in a group at any given time.

“Focal samples” refers to the number of 20-minute focal samples collected on individuals in each group.

“Sampling points” refers to the number of times that 2-minute instantaneous behavioral states of individuals were recorded during focal samples in each group.

<sup>1</sup>Seven individuals transferred from one group to another during the observing periods and are counted twice in the table (once in each group). There were 169 distinct individuals.

We did not find a strong relationship between the number of focal sampling points for each group and the mean individual rate of agonism in groups (Figure 3.S1;  $r = 3.03 \times 10^{-5}$ ,  $P = 0.98$ ). We did not control for group size in any of the analyses because there was no strong relationship between group size and the proportion of focal samples containing agonistic events (Figure 3.S2;  $b = -2.59 \times 10^{-6}$ ,  $t = -1.16$ , Adjusted  $R^2 = 0.01$ ,  $F(49) = 1.34$ ,  $P = 0.25$ ). While this was unexpected, the small amount of variation in group size (2-6) and the relatively few groups with more than four individuals may have prevented any strong, detectable correlation.

We calculated an individual rate of agonism for each of the 169 individuals. We first computed the proportion of two-minute intervals during which the animal was engaged in agonism (as actor or recipient), within 20-minute focal samples, and then used this per focal sample estimate to produce an individual rate per hour. We used the estimates of individual rates for all members in a group to calculate an average rate for each group. Using the individual rates, we also calculated the mean rate of agonism for each age-sex category and used Wilcoxon rank-sum tests to assess the statistical significance of the differences found.

**Table 3.3.** a) Candidate model set for explaining the variation in rates of agonistic behavior (as an actor/initiator); b) Comparison of all models for explaining the variation in rates of agonistic behavior (as an actor/initiator); c) Full results of best model (Model 1) for rate of agonism as actor).

**a.**

Candidate model	Fixed and Random effects
Model 1	Age category + (1 Group/Individual ID)
Model 2	Age category + sex + (1 Group/Individual ID)
Model 3	Age category * sex + (1 Group/Individual ID)

Age category = infant, juvenile, subadult, adult (classified as described in the text).

**b.**

	K	AICc	Delta AICc	AICc Wt	Cum. Wt	Conditional R <sup>2</sup>
<b>Model 1</b>	7	-468	0	1	1	0.1
<b>Model 2</b>	9	-452	15	0	1	0.1
<b>Model 3</b>	15	-41	52	0	1	0.1

AICc, rather than AIC, was utilized to select the best approximating model due to our relatively small sample size (Burnham and Anderson 2002).

K = number of estimated parameters; AICc Wt = AICc weight, Cum. Wt = cumulative weight.

**c.**

Random effects	Variance	Standard Deviation			
ID: Group (Intercept)	0.00	0.00			
Group (Intercept)	0.00	0.01			
Residual	0.01	0.08			
Fixed effects	Estimate	Std. Error	df	t value	Pr(> t )
(Intercept)	0.08	0.01	30.30	7.71	<0.01
Infant	-0.06	0.02	219.21	-4.16	<0.01
Juvenile	-0.04	0.01	216.7	-2.68	<0.01
Subadult	-0.05	0.02	225.06	-3.09	<0.01

To examine the potential influence of age and sex on the rate of being an actor (i.e., initiator) in agonism, while also accounting for dependence among observations from the same group and subject, we constructed three linear mixed models with age, or age and sex, as fixed effects, and individual identity nested within group identity as random effects (Table 3.3a). 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 three candidate models (Burnham and Anderson 2004; Mazerolle 2016; Symonds and Moussalli 2011). The model containing only age as a fixed effect was far better than those containing only sex or an interaction between age and sex (AICc weight = 1; Delta AICc from second best model = 15.4; Table 3.3). Therefore, we report full results of only this best approximating model (Burnham and Anderson, 2002).

To further assess the relative frequency at which individuals were the actors in agonistic behavior, we calculated the mean proportion of agonistic events in which an individual was an actor (as opposed to recipient) for individuals in each age-sex category. Since variances within each age-sex category were relatively homogenous across groups (Bartlett's K-squared = 6.28, df = 3, P = 0.10), a one-way ANOVA was used to test for statistical significance. We then pooled individuals in each age-sex category for dyad-based analyses, and determined the frequency and the proportion of events in which individuals were actors between each pair of age categories.

To evaluate the potential relationship between adult replacements and rates of agonism, we compared the rates among each offspring and the adult(s) with which it had co-resided since the time of its birth (“adults and own-offspring” dyads) with the rates among each offspring and any adult(s) that had entered the offspring’s natal group since its birth

(“adults and step-offspring” dyads). Due to the relative rarity of agonism (see results), and the short time that many adults resided in groups with step-offspring, there were no agonistic events for most adult-step-offspring dyads. Thus, we limited our analyses to those dyads for which the particular offspring and adult had been observed together during at least 10 focal samples (N=25). The differences in rates were evaluated statistically using a Wilcoxon rank-sum test.

We classified each event as occurring during a foraging, non-foraging related moving, resting, socializing, or other context (Table 3.S1) by assigning each event to the behavioral category in which the actor was engaged immediately preceding the agonistic act. If the behavioral category could not be determined, the context was categorized as “unknown”. We also calculated the number of all two-minute focal sampling points in which the behavioral state of the focal animal could be characterized as foraging, moving, resting, socializing, or other. Since behavioral contexts were not observed at equal frequencies, we determined the proportion of sampling points in which agonism occurred for each context. We also determined the proportion of sampling points for the subset of agonistic events that occurred between adults and offspring and between adults and subadults in each context. We then compared the proportion of agonistic events that occurred during each behavioral context to the proportion of total focal data points within each behavioral context. For each context, differences were evaluated statistically using non-parametric two-sample  $\chi^2$  tests for equality of proportions.

To assess the frequency of agonism during periods preceding dispersals, we compared each individual’s rates during two periods: 1) the six months immediately preceding the date of natal dispersal (“peri-dispersal period”), and 2) the time as a juvenile or

subadult prior to the “dispersal period” (“pre-dispersal period”). We chose six months as the peri-dispersal period because it allowed us to maximize the number of focal samples per individual, while still limiting observations to a relatively brief window preceding dispersal, during which events were most likely to influence dispersal decisions. For this analysis, we included only individuals who had been observed for at least 10 focal samples during each of the two time periods (N=18).

All behavioral observations, as well as protocols for the capturing and collaring of owl monkeys, were approved by the ethics committees (IACUC) of the Zoological Society of San Diego (2000-2005), the University of Pennsylvania (2006-2014), Yale University (2014-2015), and the National Wildlife Directorate in Argentina. All research adhered to the American Society of Primatologists’ Principles for the Ethical Treatment of Non-Human Primates and the Argentine Society for Mammalian Studies guidelines [Giannoni et al., 2003].

## **Results**

### **Rate and distribution of agonistic behavior among age and sex categories**

On average, there was an agonistic event in a group about once every three and a half hours (group rate of agonism  $\pm$  SE:  $0.3 \pm 0.1$  events per hour, N=15 groups) and in only  $5.7 \pm 0.01\%$  of focal samples (492/6430 focal samples, 614/63714 two-minute sampling points). About half of the individuals (56%, 95/169) engaged in agonism at least once. With one exception, individual rates of agonism were fairly similar across groups (Table 3.4, Figure 3.1): the mean rate across groups was  $0.11 \pm 0.03$  times/hr (95% CI = 0.09-0.18 time/hr, or approximately once every 9 hours [95% CI: 5.5 – 11.5 hours]). Group P300 had a rate that was more than twice that of any other group. However, this group was unusual in that it had

only 43 focal samples, which were collected from three individuals over three months. Most agonistic events (71%) in this group occurred within a single week, four weeks before the dispersal of a subadult.

**Table 3.4.** Number of agonistic events and hourly rates of agonism in 15 groups of owl monkeys observed in the Reserva Mirikiná in Formosa, Argentina between 2001 and 2015.

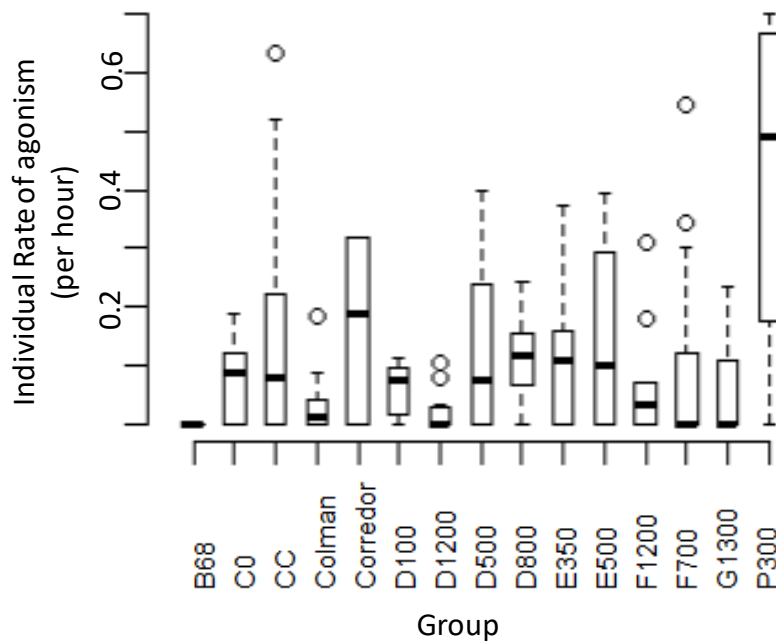
<b>Group Name</b>	<b>Agonistic events</b>	<b>Sampling points with <math>\geq 1</math> agonistic events</b>	<b>Group rate (per hour)</b>	<b>Mean individual rate (per hour)</b>	<b>SE of individual rate (per hour)</b>
B68	0	0	0.00	0.00	0.00
C0	29	25	0.17	0.10	0.02
CC	96	78	0.32	0.15	0.04
Colman	10	9	0.05	0.03	0.01
Corredor	32	25	0.45	0.17	0.06
D100	11	11	0.10	0.06	0.02
D1200	8	8	0.16	0.03	0.01
D500	164	138	0.36	0.13	0.04
D800	58	52	0.26	0.12	0.02
E350	87	75	0.33	0.12	0.03
E500	175	151	0.42	0.14	0.03
F1200	9	8	0.11	0.07	0.03
F700	18	12	0.36	0.09	0.05
G1300	10	10	0.23	0.06	0.03
P300	14	12	0.84	0.42	0.16
<b>Total/ Mean</b>	<b>721</b>	<b>614</b>	<b>0.28</b>	<b>0.11</b>	<b>0.03</b>

“Group rate (per hour)” indicates the number of sampling points containing agonistic events that took place among individuals in a particular group per hour of focal sample observation time for that group.

“Mean individual rate (per hour)” indicates the number of agonistic events in which an individual was involved (as either actor or recipient) per hour of focal observations in which that particular individual was observed (group means calculated for all 177 individuals in the data set).

The mean values listed in the bottom row are the means of the 15 group means (of individual rates/SEs). No agonistic events were observed in group B68 so it was excluded from subsequent analyses.





**Figure 3.1.** Variation in the individual rates of agonism for all members of 15 groups of owl monkeys. Horizontal black lines indicate medians, boxes indicate the interquartile range, and dotted lines span from the minimum values, at the bottom, to the maximum values (or maximum values of the third quartiles plus 1.5 times the interquartile range, whichever is smaller) at the top.

The most frequent type of agonism was overt aggression (number of events, mean percentage across groups  $\pm$  SE:  $N=306$ ,  $51 \pm 5.9\%$ ), followed by displacing ( $N=208$ ,  $26 \pm 3.5\%$ ), chasing ( $N=78$ ,  $16 \pm 4.5\%$ ), and food robbing ( $N=67$ ,  $7.8 \pm 2.6\%$ ) (Table 3.S2).

The rate of agonism differed between age groups (Tables 3.5, 3.S3). Infants ( $N=55$ ) were rarely involved, with a rate of about one event every 24 hours ( $0.04 \pm 0.02$  events/hr), which was much lower than the rates of other age groups (Wilcoxon rank-sum tests:  $W = 140$ ,  $P = 0.05$  [Juvenile];  $W = 177$ ,  $P < 0.01$  [Subadult];  $W = 178$ ,  $P < 0.01$  [Adult]). Subadults had the highest mean rate ( $0.17 \pm 0.05$  events/hr): 44% higher than for adults ( $0.12 \pm 0.03$  events/hr) and 116% higher than juveniles ( $0.08 \pm 0.02$  events/hr). Differences among

subadults and adults or juveniles were not statistically significant (Wilcoxon rank-sum tests:  $W = 91, P = 0.38$  [Subadult-Adult];  $W = 129, P = 0.15$  [Subadult-Juvenile];  $W = 117, P = 0.38$  [Adult-Juvenile]).

**Table 3.5.** Mean  $\pm$  SE individual hourly rates of involvement in agonistic events, mean  $\pm$  SE percent of agonistic interactions in which the focal owl monkeys were actors, comparison of males and females, and results of Wilcoxon Rank-sum tests for all four age categories of owl monkeys.

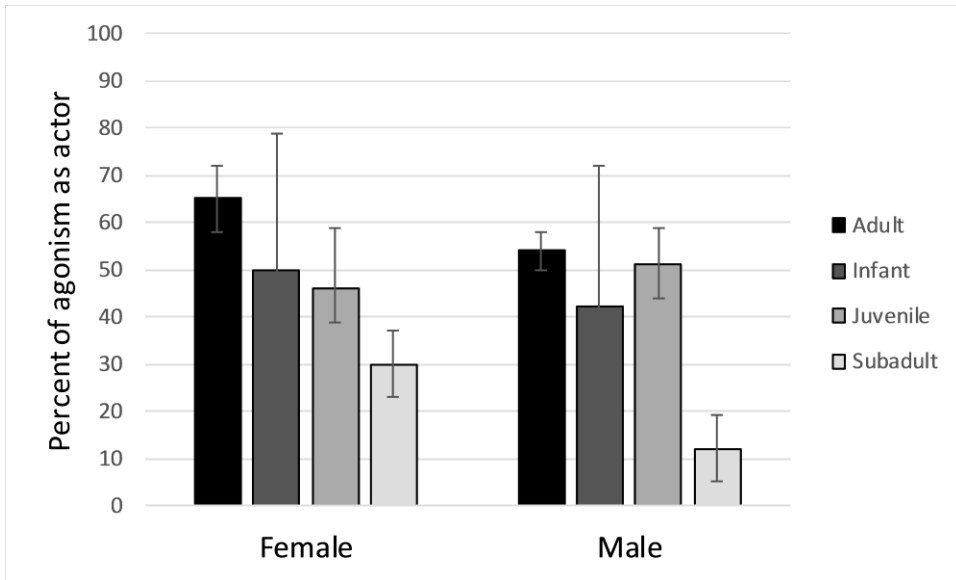
Age group	Individual Hourly Rates of Agonism				Percent of Agonistic Interactions as Actor				
	Female	Male	Statistic (W)	P	All Individuals <sup>1</sup>	Female	Male	Statistic (W)	P
Infant	0.02 $\pm$ 0.01	0.09 $\pm$ 0.06	30	0.73	36% $\pm$ 12%	50% $\pm$ 29%	42% $\pm$ 30%	5	1.00
Juvenile	0.07 $\pm$ 0.02	0.12 $\pm$ 0.04	53	0.56	42% $\pm$ 7%	46% $\pm$ 13%	51% $\pm$ 8%	53	0.64
Subadult	0.19 $\pm$ 0.05	0.13 $\pm$ 0.06	47	0.44	23% $\pm$ 5%	30% $\pm$ 7%	12% $\pm$ 7%	73	0.15
Adult	0.12 $\pm$ 0.04	0.12 $\pm$ 0.03	121	0.72	62% $\pm$ 4%	65% $\pm$ 7%	54% $\pm$ 4%	292	0.72

<sup>1</sup>The “All Individuals” column includes those classified as females, males, or unknown sex. We classified individuals following the age categories defined in Huck et al. [2011]: infants ( $\leq 6$  months), juveniles ( $6 < 24$  months), subadults ( $>24$  months), or adults (individuals  $> 48$  months who had dispersed from their natal group). Some individuals contributed data to multiple age categories (as they aged over the years of observation included in our results).

Rates were calculated as follows: Individual rates were found by dividing the number of focal sampling points in which a particular individual engaged in agonism by the number of focal sampling points during which that individual was observed. Then the mean individual rate was determined for each age-sex category and used to find the overall mean rates (“All individuals”).

The probability of an individual being an actor in an agonistic event also varied with age (Figure 3.2, Table 3.5, One-way ANOVA:  $F = 9.19, \text{num df} = 3, \text{denom df} = 18, P < 0.05$ ). Adults tended to be the initiators more often than other age groups ( $62 \pm 4\%$ ). Specifically, the proportion of times that adults were actors was 72% higher than infants, 48% higher than juveniles, and 170% higher than subadults. Subadults were initiators in a

lower proportion ( $23 \pm 5\%$ ) than infants or juveniles (57% and 83% lower, respectively), (Figure 3.2, Table 3.5).



**Figure 3.2.** Percentage of agonistic events in which individual owl monkeys in each age and sex category were actors/initiators in agonistic interactions. Error bars represent one standard error (SE) from the mean.

Males and females, of all ages, showed similar rates of agonism. The proportion of events in which individuals were actors was also similar for males and females within each age category (Tables 3.5, 3.S3). Likewise, male and female offspring in each age category received similar rates of agonism from adult males and adult females, and were the actors in a similar proportion of interactions with adults of each sex (Table 3.6). Subadult females received slightly higher rates of agonism from adult females than from adult males, but the difference was not statistically significant (Table 3.6, Wilcoxon rank-sum tests:  $W = 244$ ,  $P = 0.29$ ). Further suggesting that sex does not explain much of the variance in the rate of being an actor in agonism, comparisons of our candidate models using AICc indicated that the

model that included only age as a fixed effect was substantially better than either of the models that included sex as a factor. According to this best model (Model 1), the rate as an actor was 0.04-0.06 events per hour lower (about 1 less event per day) for offspring compared to adults. However, the  $R^2$  for this “best” model was relatively small (Table 3.3).

Adult agonism towards juveniles and subadults was the most frequent type (Table 3.6). When interacting with subadults, adult males were actors 4.9 times more often than recipients [83% of 87 interactions] and adult females 4.0 times more [80% of 85 interactions]. There was a similar pattern between adults and juveniles, with adults behaving agonistically towards juvenile males 1.3 times more and toward juvenile females 2.6 times more frequently than juveniles towards adults. Both sexes of offspring received aggression from adult males and females at similar frequencies (Table 3.6). Agonistic interactions between adult pairmates were not symmetrical; males were actors 1.8 times more frequently than females. In interactions between adults, males were actors 63% of the time, and an exact binomial test indicated that this differed statistically from the expected 50% (71/112 events;  $P = 0.01$ ; 95% CI: 0.54-0.72; Table 3.6).

Agonism among adults and step-offspring ( $N=25$  dyads) was more frequent than among adults and their own offspring ( $N=78$  dyads). Adults and step-offspring interacted agonistically about once every seven hours, while adults and their own offspring interacted only once every 18 hours (Table 3.7; adults and step-offspring:  $0.14 \pm 0.04$  vs adults and their own offspring:  $0.06 \pm 0.01$  times per hour; Effect Size:  $\theta = 0.32$ ; Wilcoxon Rank-Sum test:  $W = 89$ ,  $P = 0.07$ ).

**Table 3.6.** a) Percentage and number of agonistic events for each dyad of age categories in which individuals were the actors and recipients. b) Mean hourly rate of agonism (+ SE) received from adult males and adult females for each age-sex category of offspring and percentage and number of agonistic events in which individuals in each age-sex category were the actors.

**a.**

		Recipients				
		Inf	Juv	Sub	AF	AM
<b>A c t o r s</b>	Infant	NA (3)	0% (0)	33% (1)	18% (2)	30% (3)
	Juvenile	100% (1)	NA (7)	54% (14)	30% (34)*	47% (47)
	Subadult	67% (2)	46% (12)	NA (0)	20% (17)*	17% (15)*
	Adult Female	82% (9)	70% (81)*	80% (68)*	NA (0)	37% (41)*
	Adult Male	70% (7)	53% (54)	83% (72)*	63% (71)*	NA (0)

**b.**

	N	Rate of agonism received from AM	Rate of agonism received from AF	Proportion Actor with AM	Proportion Actor with AF
<b>Inf M</b>	8	0	0.01 ± 0.01	100% (1)	0% (0)
<b>Inf F</b>	13	0.01 ± 0.01	0.01 ± 0.01	50% (1)	0% (0)
<b>Juv M</b>	18	0.03 ± 0.02	0.03 ± 0.01	47% (16)	41% (11)
<b>Juv F</b>	24	0.02 ± 0.01	0.02 ± 0.01	38% (9)	30% (9)*
<b>Sub M</b>	17	0.03 ± 0.01	0.02 ± 0.01	20% (8)*	26% (7)*
<b>Sub F</b>	24	0.04 ± 0.01	0.08 ± 0.03	18% (6)*	18% (9)*

Inf = Infant, Juv = Juvenile, Sub = Subadult, AF = Adult Female, AM = Adult Male.

Number of interactions observed (as actor) is listed in parentheses after the %.

“\*” signifies that an exact binomial test indicated that the proportion of interactions as actors differed from the 0.5 expected by chance at  $P < 0.05$ .

N = number of offspring in each age-sex category.

Part a shows results for males, females, and offspring of unknown sex combined within each age category of offspring. Part b includes data only from offspring whose sex could be determined.

**Table 3.7.** Mean hourly rates of agonism for adult male and female owl monkeys with their own offspring and step-offspring for each of 12 social groups.

Group	Number of adult-offspring dyads	Mean Rate for AMs and step-offspring	Mean Rate for AMs and their own offspring	AM-offspring dyads: time observed (step/own)	Mean Rate for AFs and step-offspring	Mean Rate for AFs and their own offspring	AF-offspring dyads: time observed (step/own)
<b>C0</b>	7	0.00	0.07	110/ 2083	0.15	0.05	1373/ 790
<b>CC</b>	15	0.21	0.01	1596/ 10004	0.13	0.04	897/ 9897
<b>Colman</b>	10	NA	0.05	NA/ 3180	NA	0.03	NA/ 3180
<b>D100</b>	5	NA	0.03	NA/ 2870	0.00	0.04	30/ 2430
<b>D500</b>	21	0.04	0.07	2420/ 15323	0.15	0.04	5907/ 11836
<b>D800</b>	8	NA	0.06	NA/ 6346	0.10	0.09	4539/ 1807
<b>E350</b>	8	NA	0.06	NA/ 7206	NA	0.13	NA/ 7206
<b>E500</b>	14	0.35	0.10	868/ 11627	0.00	0.07	1369/ 8293
<b>F700</b>	2	0.17	NA	130/ 862	NA	NA	NA/ NA
<b>F1200</b>	8	NA	0.01	NA/ 2880	NA	0.03	NA/ 2880
<b>G1300</b>	3	0.00	0.06	110/ 980	0.14	NA	1070/ NA
<b>P300</b>	2	0.21	NA	428/ NA	0.49	NA	428/ NA
<b>Mean</b>	<b>8.6</b>	<b>0.14</b>	<b>0.05</b>	<b>809/5760</b>	<b>0.15</b>	<b>0.06</b>	<b>1952/5369</b>
<b>SE</b>	<b>1.65</b>	<b>0.05</b>	<b>0.01</b>	<b>338/1446</b>	<b>0.05</b>	<b>0.01</b>	<b>743/1331</b>

“AM” = Adult males, “AF” = Adult females. “NA” indicates that there were no well-sampled dyads.

“Well-sampled” refers to adult-offspring pairs that were observed in >100 sampling points (i.e., 10 focal samples) together in this group.

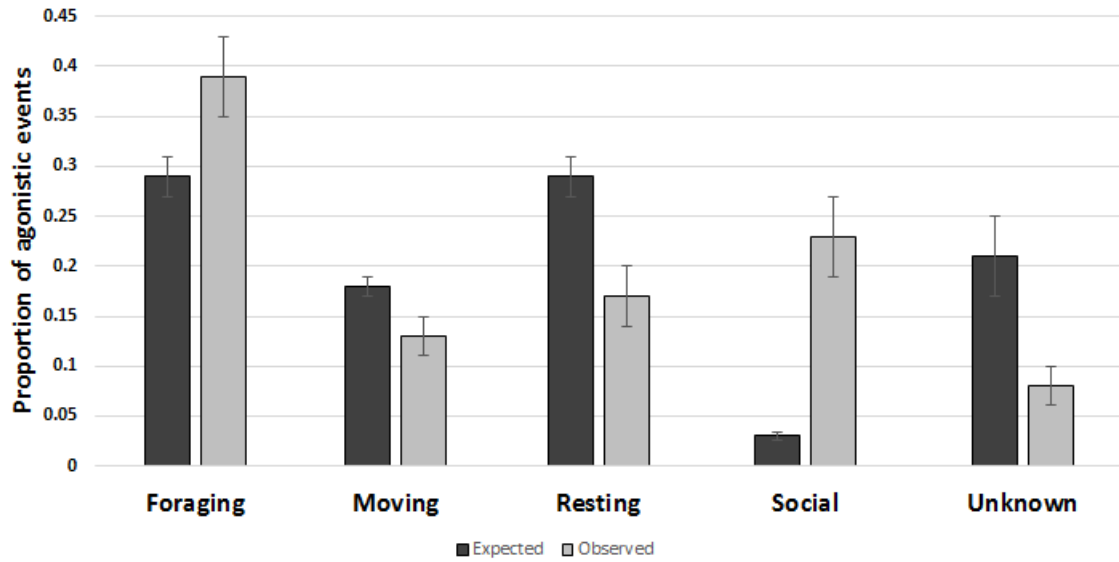
“Own Offspring” refers to young that were born while the adult was present in the group. “Step-offspring” refers to young that had already been born before the adult joined the group.

“Offspring dyads: time observed” refers to the total amount of focal sampling points during which the dyads of adults and their step or own offspring were observed together/had the opportunity to interact. These were used to calculate the rate of agonism for each type of dyad in the group.

### Context of agonism

Agonistic events were most frequent during foraging, but also regularly occurred during non-foraging contexts, particularly during bouts of social behavior with other group members. Agonism occurred more frequently in the context of social behavior (two-sample  $\chi^2$  test for equality of proportions, %  $\pm$  SE observed vs expected:  $23 \pm 4$  vs  $3 \pm 0.4$ ;  $\chi^2 = 755.54$ ,  $df = 1$ ,  $P < 0.001$ ) and during foraging contexts ( $39 \pm 4$  vs  $29 \pm 2$ ;  $\chi^2 = 64.17$ ,  $df = 1$ ,  $P < 0.001$ ), but less frequently during resting ( $17 \pm 3$  vs  $29 \pm 2$ ;  $\chi^2 = 86.66$ ,  $df = 1$ ,  $P < 0.001$ ) and moving ( $13 \pm 2$  vs  $18 \pm 1$ ;  $\chi^2 = 14.34$ ,  $df = 1$ ,  $P < 0.001$ ) (Table 3.8, Figure 3.3).

Agonistic events between adults and young and between adults and subadults showed a pattern similar to that observed when agonistic events among all individuals were considered. Agonism between adults and young occurred more frequently while foraging (%  $\pm$  SE observed vs expected:  $47 \pm 4$  vs  $29 \pm 2$ ) and socializing ( $19 \pm 3$  vs  $3 \pm 0.4$ ), and less frequently while resting ( $17 \pm 3$  vs  $29 \pm 2$ ) and moving ( $11 \pm 1$  vs  $18 \pm 1$ ). Adult-subadult agonism showed a similar pattern, with agonism being more likely while foraging and socializing ( $35 \pm 8$  and  $30 \pm 7$ , respectively) than while resting and moving ( $18 \pm 5$  and  $13 \pm 4$ , respectively; Table 3.8).



**Figure 3.3.** Proportion of all agonistic events observed in each context (light) compared to proportion of focal sampling points observed in each context (dark), shown with standard error bars. Expected: proportion of sampling points in which the behavioral state was observed; Observed: proportion of agonism occurring in each behavioral context.



**Table 3.8.** Number and mean proportion  $\pm$  SE of agonistic events in focal samples during each category of behavioral context.

Context	Foraging	Moving	Resting	Social	Other
Total # of agonistic events	327	95	92	157	50
Total # of behavioral states in focals	20011	11936	18170	2025	11695
Mean ( $\pm$ SE) proportion of sampling points in which the behavioral state was observed	0.29 ( $\pm$ 0.02)	0.18 ( $\pm$ 0.01)	0.29 ( $\pm$ 0.02)	0.03 ( $\pm$ 0.004)	0.21 ( $\pm$ 0.04)
Mean ( $\pm$ SE) proportion of agonism occurring in each behavioral context	0.39 ( $\pm$ 0.04)	0.13 ( $\pm$ 0.02)	0.17 ( $\pm$ 0.03)	0.23 ( $\pm$ 0.04)	0.08 ( $\pm$ 0.02)
# of agonistic interactions between adults and offspring <sup>1</sup>	225	51	57	92	22
<i>Adults <math>\rightarrow</math> offspring</i>	170	30	43	63	15
<i>Offspring <math>\rightarrow</math> adults</i>	55	21	14	29	7
Proportion of agonism occurring in each context for adult-offspring interactions	0.47 ( $\pm$ 0.04)	0.11 ( $\pm$ 0.01)	0.17 ( $\pm$ 0.03)	0.19 ( $\pm$ 0.03)	0.04 ( $\pm$ 0.02)
# of agonistic interactions between adults and subadults	95	18	23	40	12
<i>Adult <math>\rightarrow</math> subadult</i>	83	10	20	31	8
<i>Subadult <math>\rightarrow</math> adult</i>	12	8	3	9	4
Proportion of agonism occurring in each context for adult-subadult interactions	0.35 ( $\pm$ 0.08)	0.13 ( $\pm$ 0.04)	0.18 ( $\pm$ 0.05)	0.30 ( $\pm$ 0.07)	0.04 ( $\pm$ 0.02)

<sup>1</sup>“Offspring” refers to young in all age-categories other than adults (infants, juveniles, and subadults), regardless of whether the individual was a “step-offspring” or “own offspring”.

“Total # of events” is the number of times an agonistic event was observed during the context. The “Total # of behavioral states in focals” is the number of two-minute focal sampling points (over all 6430 focal samples) in which the behavioral state of the focal animal could be characterized as each context.

The proportions listed in the table are the means (with standard errors) calculated for the 14 groups in which agonism occurred (we excluded group “B68”, since no agonism was observed in this group).

Results of two-sample test for equality of proportions for the proportion of adult-offspring agonistic interactions in each context and the proportion of focal data in which each context was observed are as follows: Foraging:  $\chi^2 = 74.202$ ,  $df = 1$ ,  $P < 2.2e-16$ ; Moving:  $\chi^2 = 15.543$ ,  $df = 1$ ,  $P = 8.064e-05$ ; Resting:  $\chi^2 = 53.939$ ,  $df = 1$ ,  $P = 2.068e-13$ ; Socializing:  $\chi^2 = 422.45$ ,  $df = 1$ ,  $P < 2.2e-16$ ; Unknown:  $\chi^2 = 53.464$ ,  $df = 1$ ,  $P = 2.634e-13$ .

Results of two-sample test for equality of proportions for proportion of adult-subadult agonistic events in each context and the proportion of focal data in which each context was observed are as follows: Foraging:  $\chi^2 = 32.027$ ,  $df = 1$ ,  $P = 1.52e-08$ ; Moving:  $\chi^2 = 10.274$ ,  $df = 1$ ,  $P = 0.001349$ ; Resting:  $\chi^2 = 24.271$ ,  $df = 1$ ,  $P = 8.367e-07$ ; Socializing:  $\chi^2 = 196.84$ ,  $df = 1$ ,  $P < 2.2e-16$ ; Unknown:  $\chi^2 = 17.876$ ,  $df = 1$ ,  $P = 2.357e-05$ .

### **Agonism and dispersal**

Subadults were involved in agonism at higher rates in the six month peri-dispersal period than they were in the pre-dispersal period. For the 18 well-sampled offspring included in the analysis, individuals engaged in an agonistic event approximately once every 2.8 hours (mean:  $0.35 \pm 0.14$ ) during the six-months immediately preceding their dispersal, compared to only once every 8.2 hours ( $0.12 \pm 0.03$ ) at other times (Table 3.9; Effect Size:  $\theta = 0.36$ ; Wilcoxon Rank-Sum test:  $W = 114$ ,  $P = 0.1$ ). It should be noted that, while there was an overall trend for more agonism to occur within the six months immediately preceding natal dispersal, there was also considerable variation among groups. Of the 18 offspring analyzed, 13 had higher rates of agonism during the six months immediately preceding dispersal, while five actually had somewhat higher rates of agonism *before* the six-month period preceding dispersal (Table 3.9).

**Table 3.9.** Number of agonistic events, sampling points, and hourly rates of agonism for each dispersing owl monkey offspring in two periods prior to natal dispersal

Group	Individual	Sex	Pre-dispersal period (# of agonistic events)	Pre-dispersal period (# of sampling points)	Peri-Dispersal period (# of agonistic events)	Peri-Dispersal period (# of sampling points)	Hourly rate in pre-dispersal Period	Hourly rate in peri-dispersal period
C0	Celeste	F	7	1093	1	260	0.19	0.12
CC	Cata	F	0	130	9	1030	0.00	0.26
CC	CC_06	U	5	1720	1	290	0.09	0.10
Colman	Andre	M	0	130	1	500	0.00	0.06
Colman	Colman_09	U	0	270	1	480	0.00	0.06
Corredor	Betty	F	0	964	12	170	0.00	2.12
D500	Diafano	M	0	120	4	890	0.00	0.14
D500	Dionisio	M	5	1010	3	710	0.15	0.13
D500	Diosa	F	0	1180	3	380	0.00	0.24
D500	Discoteca	F	22	1352	25	1838	0.49	0.41
D500	Diuresis	F	0	2850	1	360	0.00	0.08
D500	Dixi	M	7	1100	13	1042	0.19	0.37
D800	Donovan	M	32	3359	4	720	0.29	0.17
E350	Eusebia	F	10	2127	0	639	0.14	0.00
E500	E500_11	U	5	540	26	458	0.28	1.70
E500	E500_08	U	6	1050	3	959	0.17	0.09
F1200	Fuerte	M	0	190	2	610	0.00	0.10
G1300	Gargara	F	6	840	3	310	0.21	0.29
<b>Mean</b>			<b>5.83</b>	<b>1113</b>	<b>6.22</b>	<b>647</b>	<b>0.12</b>	<b>0.36</b>
<b>Standard Error</b>			<b>2.01</b>	<b>217</b>	<b>1.87</b>	<b>95</b>	<b>0.03</b>	<b>0.14</b>

Pre-dispersal period = The time post-infancy (as juvenile and/or subadult) prior to the six months immediately preceding an individual's natal dispersal.

Peri-dispersal period = The time period starting six months prior to an individual's dispersal through the date of natal dispersal.

F = Female, M = Male, U = Sex unknown.

## Discussion

Intragroup agonistic behavior is not very common in wild Azara's owl monkeys at our site. Agonistic events occur in a variety of contexts and can involve any member of the social group, but our data distinctly show that age is an important factor influencing the distribution of agonistic events. First, as an example, infants experienced very low rates of agonism compared to other age categories. This is consistent with the absence of reported infanticide and intense paternal care observed in owl monkeys [Fernandez-Duque, 2011; Rotundo et al., 2005]. Second, within interactions between adults and subadults, subadults were much more frequently the recipients than the actors. This pattern held across contexts, with subadults receiving agonism from adults more frequently than initiating it towards them whether they were foraging, moving, resting, socializing, or engaged in any other behavior. Third, subadults were initiators in a lower proportion of events than younger offspring (juveniles or infants).

Taken together, our results strongly suggest that adults are utilizing agonism to mitigate competition with *older* offspring (i.e., subadults approaching adulthood/maturity). These findings are consistent with our first hypothesis, that agonism directed at subadults is a mechanism regulating dispersal. While juveniles and subadults did not differ much in the overall frequency at which they received agonism from adults, subadults did *initiate* agonistic interactions with adults less frequently than did juveniles (Table 3.6). This is *not* the pattern expected if agonistic behavior towards adults increased as offspring aged. This could indicate that older offspring (subadults) are avoiding agonism with adults more than younger offspring, possibly due to decreased tolerance by adults that subadults may face. Some of the most severe instances of intragroup aggression that we have observed involved adults attacking and expelling subadults [Huck and Fernandez-Duque, 2012]. Reduced initiation of

agonism may be a strategy that subadults use to minimize the likelihood that they will become involved in severe aggression with adults. This may allow them to delay dispersal and maintain access to philopatric benefits that the natal group may provide (Kokko and Ekman, 2002).

Our results differ from observations of captive owl monkeys, in which male subadult owl monkeys (*Aotus* spp.) were often the aggressors, and no adult males were observed acting aggressively toward their male offspring (Evans et al 2009). It is possible that the subadult-driven agonism observed in captivity may be a consequence of the captive setting, which may prevent offspring from maintaining their desired distances from adult group members. Additional data on patterns of social behavior in captivity are needed to provide insight into this apparent difference in agonism between individuals in the wild and in captivity.

Subadults experienced more agonism with adults in the six months prior to dispersing than they did at younger ages. This provides further support for a prediction of our first hypothesis (P1.1). This trend was observed for the majority, but not all, subadults in the study. It may be that the large amount of variation among groups during the six months preceding dispersals, and the relatively small number of groups from which we had sufficient focal data both before and after the time surrounding dispersal prevented us from detecting a more pronounced increase in agonism prior to dispersal. It is also possible that a severe bout of aggression (rather than a general increase in agonism) may trigger natal dispersal. This would be consistent with extremely aggressive behaviors, from adults to subadults, sometimes observed once the predispersing individual had begun to range independently for hours or days at a time [Corley and Fernandez-Duque, personal observations; Huck and

Fernandez-Duque, 2012].

Our results provide mixed support for the mating competition hypothesis. The finding that subadults are recipients of agonism from adults in a higher proportion of events than are younger offspring is consistent with the hypothesis that agonism functions to minimize mating competition (P3.1). Importantly, wild owl monkey subadult females begin experiencing sporadic ovulatory cycles at two to three years of age, while still in their natal group [Chapter 4, Corley et al., 2016]. The fact that hormonal sexual maturity seems to coincide with an increase in an offspring's rate of agonism and an increase in the proportion of events in which subadults receive agonism from adults suggests that, when offspring reach sexual maturity, adults begin to perceive them as potential mating competitors.

In contrast to age, sex does *not* appear to be strongly related to patterns of agonism. Within each age category, males and females participated in events at similar rates, and the proportion of agonistic events initiated by offspring were similar for both sexes. This is consistent with what we might expect for a largely monomorphic socially monogamous species. However, these data do not support our second prediction of the mating competition hypothesis (P3.2), that adults will be more aggressive towards offspring of the same sex as themselves.

Sex differences were only prominent in agonistic interactions between adults. Between adults, males were more often the actor and females the recipient. Buffy-headed marmosets (*Callithrix flaviceps*) showed a similar, but more pronounced, pattern, with male to female aggression being five times more frequent than female to male aggression [Ferrari, 2009]. Additional research is required to elucidate the potential function of this higher rate of male agonism within monogamous pairs.

Our results also provide some support for the idea that patterns of agonism are related to food competition. The facts that sex was not strongly related to patterns of agonism among offspring and adults and that agonism was more frequent during foraging are both consistent with predictions of the food competition hypothesis (P2.1 and P2.2). More than half of the agonistic interactions between subadults and adults took place during foraging. However, agonism also occurred more frequently than expected in non-foraging contexts, especially while socializing. Thus, while agonistic events may sometimes be motivated by competition or conflict over food resources, food competition *alone* cannot explain patterns of agonism.

The relationship between agonism and age is somewhat difficult to interpret in the context of the food competition hypothesis. While it could be argued that older, and larger, offspring may pose somewhat greater competition for food resources than smaller, younger infants or juveniles, the consistent pattern of agonism being directed by adults towards subadults across *all contexts* (socializing, resting, moving, etc.) suggests that this trend cannot be attributed exclusively to direct competition over food. Dispersal reduces the number of group members, and thus, ultimately intragroup competition for resources. Agonism in any context, if it encourages dispersal, could therefore be viewed as an indirect means of reducing feeding competition. While some of our data, which show a relationship between agonism and age, more directly support the mating competition avoidance hypothesis, it remains possible that mitigating food competition also contributes to the patterns of agonism observed.

Our data suggest that parent-offspring relatedness may also be an important factor influencing intragroup agonism. Kinship is known to influence many aspects of social behavior, and relationships between close kin are often characterized by increased

cooperation and reduced agonism due to inclusive fitness benefits [Hamilton, 1964]. In our population, owl monkey offspring are typically born into groups in which the adults present are their genetic parents [Huck et al., 2014]. However, due to frequent replacements of adults, offspring may often reside in a group, for some period before they disperse, in which one or both adults are “step-parents” [Fernandez-Duque and Huck, 2013; Huck and Fernandez-Duque, 2012]. The Evolutionary Theory of the Family [Emlen, 1995; Emlen, 1997] predicts that relationships between offspring and adults, particularly the same-sex adult, will tend to deteriorate after an adult replacement occurs. Consistent with this prediction, there were higher rates of agonism between adults and their step-offspring than between adults and their own offspring in groups in which a replacement had occurred.

While we did observe an overall trend for adults to have higher rates of agonism with step-offspring, there was variation in this behavior among individuals, with particularly high amounts of variation observed among the rates from step-parents to step-offspring. The high variation in rates with step-offspring may stem from the fact that adults may interact more agonistically with step-offspring of specific age or sex classes, although our data set was not large enough for us to formally consider these factors. There was also no strong evidence that experiencing a parental replacement influenced an offspring’s rate of agonism, or the proportion of interactions in which an offspring was the actor. Overall, our results indicate that adult replacement does not have a consistent effect on rates across all circumstances. We suggest that rates of agonism between offspring and their step-parents likely depend on a variety of factors (e.g., age of offspring at time of the replacement), and may only be elevated in certain cases, such as when a sexually maturing subadult experiences a replacement [Huck and Fernandez-Duque, 2012].



Inclusive fitness theory predicts that “families” of closely related individuals will differ from other forms of social groups [Emlen, 1997]. Specifically, kinship could be expected to mediate agonism such that taxa living in groups composed primarily of closely related kin (e.g., owl monkeys) behave agonistically towards one another less frequently than taxa that commonly reside in groups containing many individuals to which they are *not* closely related. Our results are consistent with this general prediction: a group rate of  $0.3 \pm 0.1$  agonistic events/hr is relatively low when compared to the average rate of 0.6 events/hr estimated for mostly non-monogamous New and Old World monkey species overall [Sussman et al., 2005].

Whether it is related more to competition over food or mates, agonism appears to be an important mechanism for regulating natal dispersal. This differs somewhat from what has been found among cooperative breeders. In captive cotton-top tamarins (*Saguinus oedipus*), most fights occur between siblings, and parent-offspring conflict is rare [Snowdon and Pickhard, 1999]. In wild buffy-headed marmosets (*C. flaviceps*), intragroup agonism also does not appear to be associated with dispersal [Ferrari, 2009]. However, since cooperative breeding is thought to mediate tolerance of mature, non-reproductive “helpers” in social groups, the finding that adults do not frequently behave aggressively towards helpers or utilize agonism to encourage individuals to disperse is not necessarily unexpected. Owl monkey groups do not contain “helpers”: offspring care is typically provided exclusively by the reproductive pair (the putative parents) [Fernandez-Duque, 2011; Rotundo et al., 2005]. Thus, because adults are not relying on subadult group members to provide infant care, adult owl monkeys may not be constrained from acting agonistically towards mature offspring.

There is evidence from other pair-living primates without “helpers” that agonistic

behavior from adults may sometimes assist in regulating dispersal. For example, though a variety of mechanisms appear to be involved in the peripheralization and eventual dispersal of subadult gibbons (*Hylobates klossii*), the rate of aggression from adults towards their same-sex offspring was observed to increase prior to dispersal in at least some groups [Tilson, 1981]. Similarly, aggression between adults and subadults was sometimes observed prior to dispersal in flexibly pair-living white-handed gibbons (*Hylobates lar*) [Brockelman et al., 1998].

It is important to acknowledge the limitations of our study when attempting to make generalizations. Collecting behavioral data from Azara's owl monkeys is challenging: they are relatively small and arboreal primates with cathemeral habits, which means that detailed focal data can only be collected during relatively short bouts of activity when there is adequate light. Additionally, males and females are not conspicuously different to the observer, and adult males and females can only be unequivocally identified after they have been marked/collared. The result of this work is a 14-year data set which, although rather unique for the number of groups, individuals, and years sampled, still has limitations for examining all of the factors that could be informative for assessing hypotheses for the function of intragroup agonism.

In summary, our results indicate that intragroup agonism likely serves multiple functions within groups of wild owl monkeys, but frequently it is associated with conflicts between adults and offspring. While intragroup agonism appears to play a role in mediating competition among group members for food resources, the overall trend for offspring to experience increased agonism as they age and mature is also consistent with the mating competition hypothesis. To an extent, our results could be considered consistent with the

hypothesis that adults use agonism to expel sexually maturing subadults in order to avoid inbreeding. However, the fact that subadults received agonism from unrelated step-parents, as well as putative genetic parents, suggests that mitigating mating competition is likely an important function of agonism, as well. Ultimately, adults seem to utilize agonism to encourage subadults to disperse, thus eliminating competition, of all types, with their older offspring.

While we did not find support for just one of our hypotheses, this is likely a reflection of the multifaceted role that intragroup agonism plays in owl monkey social life. Our study highlights the fact that agonism can play diverse and important roles, even in a monogamous taxon like owl monkeys, in which aggression is typically considered to be rare.

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### Supplementary Tables and Figures for Chapter 3

**Table 3.S1.** Ethogram used by the Owl Monkey Project for the collection of agonistic behavioral data (2001-2015).

<b>Behavior</b>	<b>Definition</b>
Aggression Actor	The focal individual is grabbing, hitting or biting another individual, it can include vigorous grasping, pulling or slapping at another, this may occur together with biting.
Aggression Recipient	Another individual is grabbing, hitting or biting the focal, it can include vigorous grasping, pulling or slapping at the focal, this may occur together with biting.
Aggression Mutual	The focal individual is aggressive and receives aggression simultaneously.
Aggression Undetermined	It is not known whether the focal individual gives or receives aggression.
Food Rob Actor Successful	The focal grabs a piece of food from another individual with the other individual offering resistance or trying to keep the food away from the focal with some form of aggression.
Food Rob Actor Unsuccessful	The focal tries, but fails, to grab a piece of food from another individual with the other individual offering resistance or trying to keep the food away from the focal with some form of aggression.
Food Rob Recipient Successful	Another individual grabs a piece of food from the focal with the focal offering resistance or trying to keep the food away from the individual with some form of aggression.
Food Rob Recipient Unsuccessful	Another individual tries, but fails, to grab a piece of food from the focal with the focal offering resistance or trying to keep the food away from the individual with some form of aggression.
Chase Actor	The focal moves rapidly (i.e., runs) reducing the distance between itself and another animal which at the same time runs away increasing the distance between itself and the first animal.
Chase Recipient	Another individual moves rapidly (i.e., runs) reducing the distance between itself and the focal which at the same time runs away increasing the distance between itself and the first animal.
Displace Actor	The focal moves to within 0.5 m of another animal and stays put while the other animal moves to more than 0.5m within 3 sec.
Displace Recipient	Another animal moves within 0.5 m of the focal and stays put and the focal moves to more than 0.5 m within 3 sec.

Ethogram is based on the Monogamous Primates Protocol:

<http://www.sas.upenn.edu/~eduardof/Protocols%20English/Protocols%20Main%20Menu.htm>

**Table 3.S2.** Number of events of each type of agonistic behavior observed in each group of owl monkeys and mean proportion of them across groups.

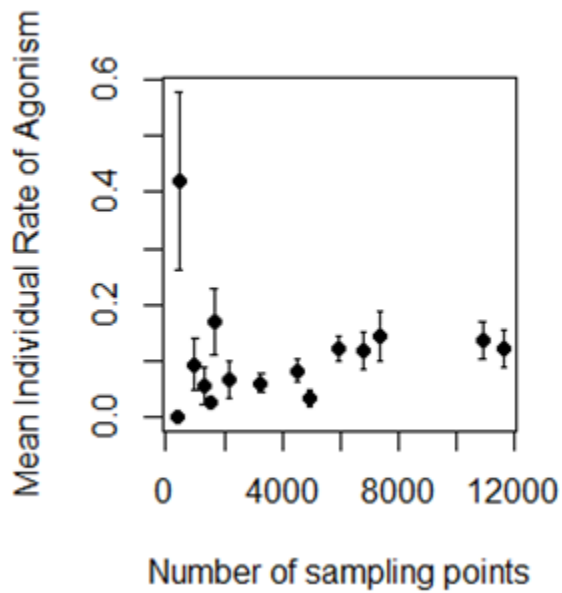
<b>Group</b>	<b>Aggression</b>	<b>Chase</b>	<b>Food Rob</b>	<b>Displace</b>
B68	0	0	0	0
C0	14	1	5	8
CC	36	10	8	35
Colman	6	0	0	3
Corredor	10	1	9	6
D100	7	1	0	3
D1200	8	0	0	0
D500	77	13	6	57
D800	18	10	5	22
E350	44	9	11	14
E500	70	18	22	51
F1200	4	4	0	0
F700	0	7	1	5
G1300	6	2	0	2
P300	6	2	0	2
<b>Total</b>	<b>306</b>	<b>78</b>	<b>67</b>	<b>208</b>
<b>Mean Proportion of events</b>	<b>0.51</b>	<b>0.16</b>	<b>0.08</b>	<b>0.26</b>
<b>SE of Mean Proportion</b>	<b>0.06</b>	<b>0.05</b>	<b>0.03</b>	<b>0.04</b>

**Table 3.S3.** Mean hourly rates, standard errors (SE) and 95% confidence intervals (CI) of involvement in agonistic events for each age-sex category of owl monkeys.

<b>Sex</b>	<b>Age</b>	<b>Individuals<sup>1</sup></b>	<b>Rate<sup>2</sup></b>	<b>SE</b>	<b>Lower limit of 95% CI</b>	<b>Upper limit of 95% CI</b>
Female	Infant	16	0.02	0.01	0.00	0.05
Male	Infant	14	0.08	0.05	0.00	0.19
Unknown	Infant	26	0.05	0.03	0.01	0.11
Female	Juvenile	21	0.14	0.05	0.06	0.26
Male	Juvenile	22	0.33	0.10	0.15	0.54
Unknown	Juvenile	25	0.06	0.02	0.02	0.11
Female	Subadult	23	0.31	0.07	0.17	0.46
Male	Subadult	18	0.19	0.08	0.06	0.35
Unknown	Subadult	11	0.18	0.11	0.02	0.42
Female	Adult	33	0.16	0.04	0.09	0.25
Male	Adult	25	0.15	0.04	0.09	0.24
Unknown	Adult	2	0.00	0.00	0.00	0.00

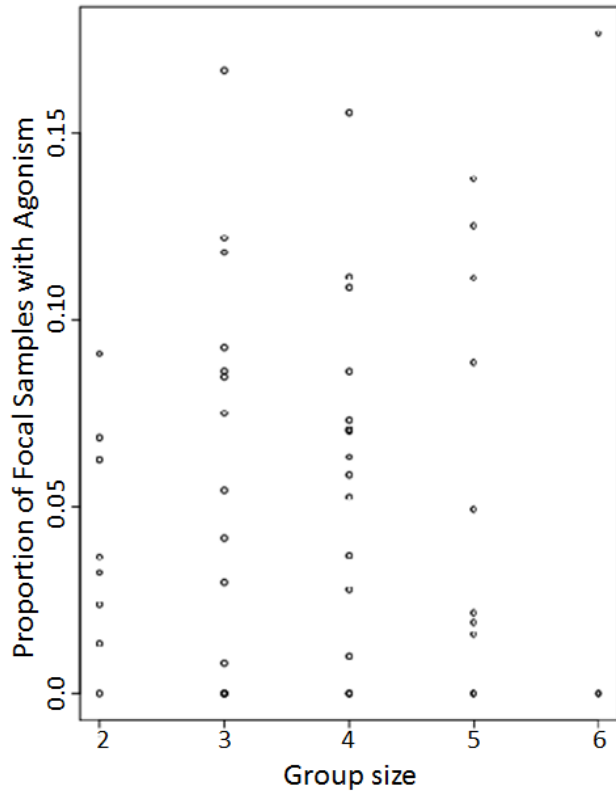
<sup>1</sup> Number of distinct individuals in each age-sex category

<sup>2</sup> Mean individual rates of agonistic events per hour for each age-sex category



**Figure 3.S1.** Relationship between the mean individual rate of agonism ( $\pm$  SE) and the number of sampling points for each of the 15 owl monkey groups considered. Bars represent standard errors<sup>1</sup>.

<sup>1</sup>See text for discussion of the outlying point (group P300) in the upper left of the figure.



**Figure 3.S2.** Relationship between the proportion of focal samples containing one or more agonistic events and group size. Since group composition changed during the period of study, most of the 15 groups in the study appear more than once in the figure.

## **Chapter 4. Hormonal correlates of development and natal dispersal in a socially monogamous primate, *Aotus azarae***

### **Abstract**

Reproductive suppression is a means through which intragroup conflict over reproduction may be resolved. Pair-living and socially monogamous primates typically do not reproduce before dispersing, but unlike cooperatively breeding taxa, neither inclusive fitness benefits nor inbreeding avoidance hypotheses can adequately explain their lack of reproduction prior to leaving the natal group. Examining the mechanisms underlying reproductive suppression in pair-living primates is important for understanding the evolution and functioning of this phenomenon in these taxa. In this study, we determined whether wild Azara's owl monkeys (*Aotus azarae*) in the Argentinean Chaco establish reproductive maturity prior to dispersing. We utilized 635 fecal extracts to characterize reproductive hormone profiles of 11 wild juvenile and subadult females using enzyme immunoassays. Subadult females showed hormone profiles indicative of ovulatory cycling and had mean PdG and E1G concentrations approximately five times higher than juveniles. Contrary to the inbreeding avoidance hypothesis, female owl monkeys do not delay puberty, but rather commence ovarian cycling while residing in their natal group. Even so, subadults appear to have a period during which they experience irregular, non-conceptive cycles prior to reproducing. Commencing these irregular cycles in the natal group may allow them to develop a state of suspended readiness, which could be essential to securing a mate, while avoiding the costs of ranging solitarily. Our results indicate that reproductive suppression in female owl monkeys is not due to endocrine suppression, and suggest that adults likely use behavioral mechanisms to prevent subadults from reproducing with unrelated adult males in their natal group.

## Introduction

Any time that multiple individuals of the same sex co-reside within the same group, conflicts over which member(s) of a group will reproduce may arise. Both the degree to which group members partition reproduction and the mechanisms regulating reproductive partitioning appear to vary widely among taxa [Hager and Jones, 2009; Johnstone, 2000; Keller and Reeve, 1994]. For example, high reproductive skew, when one or a few individuals monopolize reproduction in a group, occurs in diverse taxa, ranging from eusocial insects to brown jays (*Cyanocorax morio*) to meerkats (*Suricata suricatta*) [Bell et al., 2014; Reeve and Keller, 2001; Williams, 2004]. On the other hand, similar levels of skew may be the result of vastly different mechanisms (e.g., worker caste sterility vs. behavioral inhibition) [Heinze, 2004], and the degree of skew can vary vastly even among related species with similar ecologies [e.g., dwarf mongooses (*Helogale parvula*) vs. banded mongooses (*Mungos mungo*)] [Cant, 2000; Johnstone and Cant, 2009].

A potential means through which intragroup conflict over reproduction may be resolved, is reproductive suppression. It has been proposed that suppressing subordinates' reproduction benefits dominants in some way [Hodge, 2009; Vehrencamp, 1983], though few studies have tested this assumption empirically [though see [Bell et al., 2014; Cant et al., 2010]]. Lifetime reproductive success can be increased by beginning reproduction early [Altmann et al., 1988]. It is therefore expected that suppression must negatively impact subordinates. While forgoing reproduction may at first seem counter to maximizing fitness, it can be an adaptive strategy [Beehner and Lu, 2013]. Among cooperatively breeding species, explanations for why subordinates forgo their own reproduction have historically been based on kin selection arguments; providing allocare to dominant relatives allows subordinate



helpers to maximize their inclusive fitness [Emlen, 1995; Hamilton, 1964]. In fact, high levels of average relatedness between group members have been hypothesized to play important roles in the evolution of reproductive suppression of subordinates and cooperative breeding [Lukas and Clutton-Brock, 2012].

Alternatively, rather than benefitting dominants or providing inclusive fitness benefits to subordinates, suppression of reproduction may be a mechanism to avoid inbreeding [Hamilton, 2004]. Inbreeding avoidance is likely to be important in taxa where social groups have high degrees of average relatedness, such as socially monogamous or cooperatively breeding species. This seems to be the case among cooperatively breeding mole-rats (*Cryptomys damarensis*) [Bennett et al., 1996; Clarke et al., 2001; Cooney and Bennett, 2000] and meerkats (*S. suricatta*) [O’Riain et al., 2000]. Inbreeding avoidance mediated by reproduction suppression can be enforced or self-imposed. Self-imposed suppression may occur when group members are closely related, the opportunities for independent breeding are poor, the costs of assessing reproductive status and eviction are relatively high, and the chance of being detected when cheating is high [Hamilton, 2004].

The mechanisms underlying reproductive suppression vary across taxa. In some cases, reproductive suppression may be mediated by the induction of physiological changes, such as the endocrine inhibition of gonadal function [Hamilton, 2004; Wasser and Barash, 1983; Wasser and Starling, 1988]. In other cases, non-breeding individuals may be physically capable of reproducing, but still forgo their own reproduction through the influence of behaviors directed at them (e.g., mate guarding, agonism, or eviction) by reproductive individuals in the group [Cant et al., 2010; Hager and Jones, 2009; Kutsukake and Nunn, 2006].

Much of our knowledge about the hormonal suppression of reproduction in primates comes from studies of captive, cooperatively breeding callitrichids [Abbott et al., 1990; Saltzman et al., 2009; Ziegler et al., 1990]. In captive marmosets and tamarins, generally only one dominant female reproduces, while the gonadal function of other females in the group, including the offspring of the dominant female, is suppressed and non-dominant females do not ovulate [Abbott and Hearn, 1978; Abbott, 1993; Ziegler et al., 1987]. However, this mechanism of ovulatory inhibition does not always occur among all subordinate females in captivity [Abbott, 1984; Hubrecht, 1989; Smith et al., 1997; Ziegler and Sousa, 2002] and it may not consistently occur in wild populations [Albuquerque et al., 2001; Digby and Ferrari, 1994; French et al., 2003; Lottker et al., 2004; Savage et al., 1997]. Fertility in female callitrichid offspring is regulated by a complex combination of behavioral and endocrine factors [Albuquerque et al., 2001; Smith et al., 1997; Ziegler et al., 1990]. The higher frequency of inhibition of gonadal function observed in subordinate females in captivity compared to the wild may be a consequence of specific social conditions, such as forced close proximity to (dominant) female conspecifics or a lack of access to unrelated males, which frequently occur in captive settings [French et al., 2003; Lottker et al., 2004; Widowski et al., 1990]. Given that their social and mating system is neither pair-living nor primarily monogamous [Garber et al., 2016], studying reproductive suppression in callitrichids may not be particularly useful when trying to understand pair-living and socially monogamous taxa.

Reproductive suppression of female primates has also been documented in pair-living taxa without cooperative breeding. In both captive and wild pair-living primates, females typically do not reproduce while in their natal groups. For example, among wild New World

primates, neither red titi monkeys (*Callicebus discolor*) nor Azara's owl monkeys (*Aotus azarae*) have ever been observed to breed prior to dispersing [Fernandez-Duque, 2009; Van Belle et al., 2016], and captive dusky titi monkey (*Callicebus moloch*) females do not breed while in their natal groups, even after reaching sexual maturity [Valeggia et al., 1999; Valeggia, 1996; Van Belle et al., 2016]. Suppression is not restricted to New World primates though, as data from pair-living lemurs [Tecot et al., 2016], wild siamang (*Symphalangus syndactylus*), and white-handed gibbons (*Hylobates lar*) also suggest that females must typically disperse from their natal groups before they reproduce [Palombit, 1995; Reichard and Barelli, 2008].

Socially monogamous groups are usually defined as containing one adult male, one adult female, and their offspring, and have been historically been referred to as “family groups”. Under these considerations, it is hypothesized that females in monogamous taxa do not reproduce prior to dispersal due to a lack of unrelated males. However, in the last two decades, a number of studies have challenged the notion that pair-living taxa live in “nuclear family groups” in which parents and offspring are always genetically related [Fuentes, 1998; Garber et al., 2016]. For a variety of reasons, and in a range of socially monogamous taxa, offspring often encounter situations in which they are residing in their natal groups with unrelated adults of the opposite sex. It is now clear that several taxa categorized as “monogamous” would be better described as serially monogamous or pair-living [Fuentes, 1998; Palombit, 1994; Sommer and Reichard, 2000; Tecot et al., 2016]. In support of this, the replacement of reproductive adults is frequent in owl monkeys (*A. azarae*) [Fernandez-Duque and Huck, 2013], equatorial saki monkeys (*Pithecia aequatorialis*) [Di Fiore et al., 2007], and several species of gibbon [Brockelman et al., 1998; Koda et al., 2012; Palombit, 1994].

Social structures among gibbons and sakis are also more flexible than traditionally viewed [Norconk, 2011; Sommer and Reichard, 2000], with groups of white-faced sakis (*Pithecia pithecia*) [Thompson and Norconk, 2011] and white-handed gibbons (*H. lar*) at some sites frequently containing more than one adult male [Barelli et al., 2008; Reichard and Barelli, 2008].

The presence of unrelated adults in these groups makes the inbreeding avoidance hypothesis for reproduction suppression unlikely. These pair-living primate taxa are also characterized by the absence of alloparental care; nonreproductive individuals do not assist in the care of the young. Thus, the absence of cooperative breeding makes the inclusive fitness hypothesis for reproductive suppression unlikely, as well. Generating and evaluating alternative explanations for the widespread presence of reproductive suppression in these taxa and the mechanisms underlying it thus require empirical investigations of wild pair-living primates.

Azara's owl monkey (*A. azarae*) provides a good model to examine reproductive suppression in wild pair-living primates. Owl monkeys are a pair-living, serially and genetically monogamous taxon [Huck et al., 2014] in which predispersing non-reproducing individuals do not provide infant care. Adults reside with their offspring for several years (2-5) before the offspring disperse from their natal groups, allowing the potential for conflicts over reproduction, particularly when the replacement of a genetic parent has occurred [Fernandez-Duque, 2009; Huck and Fernandez-Duque, 2012]. Since offspring never reproduce in their natal group, dispersal is an extremely important step towards achieving reproductive success. Once offspring disperse, individuals of both sexes become solitary "floaters" for a variable period. Floaters typically need to fight with members of established

social groups in order to gain a reproductive position. While severe intragroup aggression is not frequent, adults of both sexes frequently act aggressively towards intruding floaters. These aggressive encounters can be deadly, and eviction from the group is likely highly risky for the evicted individual [Bonte et al., 2012; Fernandez-Duque and Huck, 2013].

To better understand reproductive suppression and how it relates to natal dispersal in owl monkeys and other pair-living primates, it is essential to determine the mechanisms through which reproduction is inhibited. As explained above, the richest literature on reproductive suppression of primates is based on studies of captive individuals, where predispersing individuals obviously cannot disperse, nor distance themselves from reproducing adults more than one or two meters. There is currently very limited evidence with which to evaluate whether suppression of reproduction in wild pair-living primates may result from inhibition of endocrine function. For pair-living socially monogamous taxa, urinary hormone profiles of captive titi monkeys (*C. moloch*) indicate that females experience occasional adult-like ovarian cycles while residing with parents in their natal groups [Valeggia, 1996]. In a study utilizing fecal samples from wild white-faced saki monkeys (*P. pithecia*), at least one subadult began cycling while in her natal group [Thompson et al., 2011]. In contrast, fecal samples from three wild subadult white-handed gibbons (*H. lar*) did not show progesterone profiles indicative of ovulatory cycling [Barelli et al., 2007]. Thus, for pair-living primates, evidence for the inhibition of endocrine function in predispersed females is mixed.

Little is known about the development and sexual maturation of wild predispersing owl monkeys, though ovulatory cycles of wild adult females have been described (Fernandez-Duque et al., 2011). In captivity, conception leading to successful offspring

production occurred in a 20.5 month old female, and also following mating with a 23.5 month old male [Gozalo and Montoya, 1990]. However, the pace of growth and reproductive maturation in captive and provisioned primates is substantially different than in the wild [Alberts and Altmann, 1995; Altmann and Alberts, 1987; Altmann et al., 1981; Altmann et al., 1977; Dunbar, 1990; Durgavich, 2013; Milton, 1981; Mori, 1979; Rowell and Richards, 1979].

Our objectives in this study were to determine the age at which wild female owl monkeys typically experience the onset of reproductive maturity and establish whether this typically occurs prior to dispersing from the natal group. By reproductive maturity, we are referring to an individual being physiologically capable of reproducing (e.g., increases in levels of reproductive hormones and establishment of ovulatory cycles similar to reproducing adults), not the first successful copulation or parturition. We characterized the reproductive hormone profiles of wild juvenile and subadult female owl monkeys to 1) determine the mean concentrations of female reproductive hormones (PdG and E1G) in feces of juvenile, predispersed subadult, and solitary dispersed subadult females; 2) describe patterns of fluctuations in reproductive hormones and determine if they constitute evidence for ovulatory cycling; and 3) compare profiles of reproductive hormones detected in juveniles or subadults to those previously described for wild adult owl monkeys.

## **Methods**

### **Study site and subjects**

We conducted this study at the Reserva Mirikiná, a 1500 ha reserve of gallery forest within the private cattle ranch Estancia Guaycolec, in Formosa, Argentina (58°13'W,

25°54'S). Owl monkeys (*A. azarae*) at this site, which is within the South American Gran Chaco region, reside in both gallery forest and forest patches, which are separated from one another by grasslands and savannahs [Juárez et al., 2012; Placci, 1995; van der Heide et al., 2012]. We have described climate and seasonality in the area previously [Fernandez-Duque, 2009].

Within the Reserva Mirikiná, the Owl Monkey Project (OMP) has mapped a 300 ha area of gallery forest along the banks of the Riacho Pilagá, and established a system of intersecting transects. Groups within this mapped area were habituated and are monitored consistently (contacted at least once every week or every second week) since 1997 [Fernandez-Duque, 2016; Fernandez-Duque et al., 2001]. This monitoring has allowed us to identify dates of births, deaths, and other demographic changes, such as dispersals, within a range of a few weeks [Huck and Fernandez-Duque, 2012]. Reproduction is highly seasonal: almost all births occur between late September and December, and 80% occur in either October or November [Fernandez-Duque, 2012; Fernandez-Duque et al., 2002].

The Owl Monkey Project (OMP) also captures and fits some individuals with radio-collars, which allows us to consistently locate identified groups, and bead collars, which facilitate the reliable identification of specific individuals [Juárez et al., 2011]. We collected all data reported here from individuals in well-habituated groups within the mapped area. It was possible to discriminate all group members from one another by collars or natural distinguishing markings. We classified individuals as infants (< 6 months), juveniles (6 < 24 months), subadults (> 24 months), or adults (a dispersed individual which has become a member of a reproductive pair in group), following the age categories defined in Huck et al.

[2011]. We classified subadults as predispersed or solitary, based on whether they had permanently dispersed from their natal group (Table 4.1).

**Table 4.1.** Juvenile, predispersed subadult, and solitary dispersed subadult owl monkey females sampled in Formosa, Argentina between 2011 and 2015.

Category	Age	Group	Individual ID	Year Sampled	Adult Male Replacement
juvenile	<1 yr	Corredor	Bella	2014	No
juvenile	<1 yr	E350	Estupenda	2014	Unknown
juvenile	<2 yrs	C0	Cebollita	2015	No
<i>juvenile</i>	<i>&lt;2 yrs</i>	<i>Corredor</i>	<i>Bella</i>	<i>2015</i>	No
juvenile	<2 yrs	D500	Discoteca	2013	No
juvenile	<2 yrs	E350	Eusebia	2014	Unknown
<i>juvenile</i>	<i>&lt;2 yrs</i>	<i>E350</i>	<i>Estupenda</i>	<i>2015</i>	Unknown
subadult	<3 yrs	C0	Celeste	2011	No
<i>subadult</i>	<i>&lt;3 yrs</i>	<i>D500</i>	<i>Discoteca</i>	<i>2014</i>	No
<i>subadult</i>	<i>&lt;3 yrs</i>	<i>E350</i>	<i>Eusebia</i>	<i>2015</i>	Unknown
subadult	<3 yrs	F700	Felicia	2013	Yes
subadult	<3 yrs	P300	Petisa	2013	Yes
subadult	<4 yrs	CC	Cordelia	2013	Yes
subadult	<4 yrs	Corredor	Betty	2014	No
<i>solitary subadult</i>	<i>&lt;4 yrs</i>	<i>NA</i>	<i>Cansada</i>	<i>2011</i>	No
<i>solitary subadult</i>	<i>&lt;4 yrs</i>	<i>NA</i>	<i>Discoteca</i>	<i>2015</i>	No
<i>solitary subadult</i>	<i>&lt;5 yrs</i>	<i>NA</i>	<i>Betty</i>	<i>2014</i>	No
<i>solitary subadult</i>	<i>&lt;5 yrs</i>	<i>NA</i>	<i>Celeste</i>	<i>2013</i>	No

*Italics indicate that the individual was sampled previously in another (younger) age category as well.* “Adult Male Replacement” refers to whether or not the individual had experienced the replacement of the reproductive adult male in their group prior to being sampled (i.e., their genetic father had been replaced by an unrelated male). “Unknown” indicates that the identity of the male present at the time of the individual’s birth was unknown, and thus it could not be determined whether a replacement had occurred.

Owl monkeys do not show obvious visual signals of ovulatory cycling, so changes in reproductive hormone levels must be monitored in order to determine reproductive status [Bonney et al., 1979; Bonney et al., 1980; Wolovich and Evans, 2007]. We utilized feces to monitor reproductive hormones, because feces are the only medium that we can reliably obtain from wild individuals without repeated captures [Fernandez-Duque et al., 2011]. We



collected fecal samples systematically from five juveniles, seven subadults that had not yet dispersed from their natal groups, and four subadults that had dispersed from their natal groups within the previous 12 months and were ranging solitarily. These represent 11 unique individuals, as some were sampled in multiple categories over several years (Table 4.1). We used a fecal sample to confirm the genetic sex of each of our subjects prior to conducting hormone analyses, following established methods [Di Fiore, 2006].

We followed a sampling schedule previously utilized to monitor the reproductive status of adult female owl monkeys at our field site [Fernandez-Duque et al., 2011]. Under this schedule, we sampled each female, on average, every 3.5 days (typically 2-4 days (85% of samples), absolute range: 5-7 days). We monitored individuals an average of  $129 \pm 16$  consecutive days (range: 31-220 days) between May and December in three consecutive years (2013, 2014, 2015), with the exception of two females who were sampled during July and August in 2011 (Table 4.1). The average cycle length for wild adult reproductive *A. azarae* females is approximately  $22 \pm 3$  days (range 18–25 days) when computed using consecutive peaks in E1C from 12 cycles, and  $24.0 \pm 1.6$  days (range 20–26 days) when computed using E1C nadirs from 10 cycles [Fernandez-Duque et al., 2011]. Thus, the time when each female was monitored encompassed at least one full potential ovulatory cycle. In sum, we collected 635 fecal samples, and analyzed an average of  $33 \pm 5$  SE samples per female.

### **Fecal sample processing**

We obtained fecal samples non-invasively through the collection of feces from the forest floor immediately after the target individual defecated. For each sample, we placed the

fecal material directly into an 8 mL screw-cap tube containing 5 mL of a 1:1 solution of ethanol and deionized (DI) water, secured the cap with a Parafilm® strip, and then shook the tube for one minute to homogenize the sample. We transferred the sample tubes from the field site to a freezer in the city of Formosa as soon as possible (within 5 days during the winter, within 1-2 days during periods of warm weather). For each fecal sample collected, we recorded the date, time, and GPS location of collection, as well as the group, identity, and sex of the animal sampled. We transported samples back to the US following all shipping regulations and immediately placed tubes in a -20°C freezer once they reached the laboratory. We transported samples collected prior to 2013 to the Reproductive Ecology Lab at the University of Pennsylvania (Penn REL) and extracted them there before shipping them to the Yale Reproductive Ecology Laboratory (YREL) for analysis. We transported samples collected in 2013 or later directly from Argentina to the YREL. We followed all necessary local, national, and international regulations for the collection and transportation of biological samples and obtained all necessary permits.

We utilized the same protocols for samples processed at both the Penn REL and YREL. To extract samples, we allowed sample tubes to stand undisturbed overnight, and then centrifuged them if necessary, to separate the solid fecal material portion from the liquid portion in each tube. We set aside a 1 mL aliquot of the liquid portion for subsequent hormone extraction, and then transferred the remaining liquid to 1 mL tubes, which we stored at -20°C in a YREL freezer as backups. We then air-dried the fecal material portion of each sample and recorded the dry weight to the nearest 0.001 gram.

We performed diethyl ether extractions on all samples using established methods [Fernandez-Duque et al., 2011; Strier and Ziegler, 1994]. Briefly, we transferred 1 mL of the

liquid portion of each sample into a glass culture tube and then added 1 mL of DI water and 5 mL of diethyl ether to the tube. We vortexed tubes for 1 minute and then left them undisturbed for 5 minutes to allow for separation into aqueous and ether layers. We used a Pasteur pipette to decant the top ether layer into a clean glass tube, in which we completely evaporated the ether. We then re-suspended the sample in 2 mL of phosphate buffer and froze 1 mL aliquots of the extracts at  $-20^{\circ}\text{C}$ .

### **Pregnanediol-3-Glucuronide (PdG) and Estrone-3-Glucuronide (E1G) assays**

We assayed all fecal extracts for progesterone metabolites (PdG) and secreted estradiol (E1G), in order to determine whether females showed hormone profiles indicative of ovulatory cycling. PdG assays are a reliable means of monitoring progesterone excretion during the ovulatory cycle in owl monkeys [Dixson, 1983]. Fecal PdG levels have also previously been used to successfully monitor ovarian cycles in adult females from the same population of wild *A. azarae* sampled in this study [Fernandez-Duque et al., 2011].

We used DetectX Enzyme Immunoassay (EIA) kits from Arbor Assays (K037-H5 and K036-H5, Ann Arbor, MI) to measure the levels of PdG and E1G. These kits have been validated by the manufacturer for use on fecal extracts. The PdG kits have cross reactivity of 100% for PdG, 44.8% for 20 $\alpha$ -hydroxyprogesterone, and <4% with other reactants at the 50% binding point. The E1G kits have cross reactivity of 100% for E1G, 238% for estrone, 66.6% for estrone-3-sulfate (E1S), 7.8% with 17 $\beta$ -Estradiol, and <4% with other reactants at the 50% binding point, as determined by the manufacturer. Thus, we can say with certainty that our assay results truly reflect levels of PdG and E1G, or closely related metabolites. We performed all hormone assays at the YREL following the manufacturer's protocols.

We diluted all extracts at least 1:8 with assay buffer and assayed in duplicate. We express the mean concentration of each set of duplicates as micrograms of PdG per gram of feces and nanograms of E1G per gram of feces. As quality control measures, we reran all samples for which the difference between duplicates was  $\geq$  twice the amount of non-specific binding (NSB) and we re-diluted and re-assayed samples for which binding was  $>90\%$  or  $<20\%$  of the maximum binding. Mean inter-assay coefficients of variation (CVs) were 15.6% for PdG ( $15.3 \pm 0.25\%$  SD = high control;  $15.8 \pm 0.15\%$  SD = low control) and 10.4% for E1G ( $10.7 \pm 0.06\%$  SD = high control;  $10.1 \pm 0.11\%$  = low control). The mean intra-assay CVs were  $11.6 \pm 3.1\%$  SD for PdG and  $9.5 \pm 3.4\%$  SD for E1G.

### **Data Analyses**

We determined the mean concentration of each hormone for each individual and then used these means to calculate mean hormone levels for each category of individuals (juvenile, predispersed subadult, and solitary dispersed subadult). We used Wilcoxon rank-sum tests to assess the statistical significance of differences between categories. We visually inspected the hormonal profile of each individual to identify the possible presence of ovarian cycles. For each cycling individual, we also calculated the mean concentration of each hormone during peaks and the mean concentration of each hormone during troughs between peaks (baseline levels). We calculated baseline levels as the mean PdG or E1G levels during the follicular phase(s) (i.e., the parts of the profile without a clear PdG peak). We report the mean  $\pm$  standard error (SE) unless otherwise noted.

In addition to considering mean PdG levels in each broad category, we examined the potential influence of age (in days), season (mating vs. birth), and year of sampling on the

mean monthly PdG concentrations through the evaluation of GLM models. We defined four candidate models, with mean monthly PdG level as the outcome variable. Each model contained a random intercept for subject ID and one or more fixed effects/predictor variables: Model 1 contained just the predictor variable age, Model 2 contained age and year, Model 3 contained age and season, and Model 4 contained all three variables. We provide details of candidate model sets in the Supplementary Information (Table S4.1). All GLMMs were estimated with restricted maximum likelihood, using the function *lmer* in R (ver. 3.2.3) [Bates et al., 2014; R Core Development Team, 2016], and we chose the best approximating models on the basis of AICc [Mazerolle, 2016] and parsimony (Table S4.2).

To identify ovulatory cycles, we used the criteria of progesterone-defined ovulation. A previous study on adult owl monkeys considered any rise in PdG that was 50% above baseline follicular levels to be indicative of ovulatory peaks [Fernandez-Duque et al., 2011]. Since it was vital to our objective to be able to distinguish between PdG increases indicative of ovulation and non-cyclic fluctuations, we chose to use an even stricter criterion for classifying ovulatory peaks. We considered a cycle to be ovulatory only when PdG peaks reached a level at least two standard deviations higher than the individual's mean PdG level. Thus, if juveniles or subadults in our study showed peaks using this more conservative criterion, we considered them to have experienced the onset of reproductive maturity.

Captive owl monkeys, like some other New World monkeys, have profiles of progesterone and estrogen that are nearly superimposed [Bonney et al., 1979; Preslock et al., 1973]. In concordance with this, we observed more or less concurrent rises in fecal PdG and E1G in samples from wild adult owl monkeys (Fernandez-Duque et al., 2011). Following previous studies, we utilized E1G profiles to estimate cycle length. Specifically, we estimated

cycle length by counting the days between 1) two consecutive E1G peaks, and 2) the lowest points in the profile (the nadir). We considered cycles to be consecutive if peaks occurred within 25 days of one another (based on estimates of cycle lengths of adult owl monkeys), and excluded from our calculations of cycle length any peaks that occurred more than 25 days apart. We then computed the average cycle length over all individuals that had more than one peak. These methods are consistent with the way that a previous study determined ovulation and cycle lengths for adult female owl monkeys [Fernandez-Duque et al., 2011]. Thus, our methods allow us to compare cycle lengths of subadult females to those previously established for wild adults.

We also determined the age when each female showed evidence for the onset of PdG peaks indicating ovulation. For all individuals, dates of birth were either known exactly or could be estimated to have occurred within a period of  $\pm 22$  days.

Ovulatory cycles of wild adult owl monkeys seem to lack strong seasonality. Females may resume cycling as soon as three months after giving birth, and may cycle for several months prior to the mating season and for at least four months before conceiving [Fernandez-Duque et al., 2011]. To examine the potential influence of season on reproductive hormones of female subadults and juveniles, we determined the mean PdG and E1G levels for individuals and number of PdG peaks that occurred during each of two seasons: the mating/pregnancy season (May-August) and the birth season (September-December).

### **Ethical statement**

The ethics committees (IACUC) of the University of Pennsylvania (2006-2014), Yale University (2014-2015), and the National Wildlife Directorate in Argentina approved all

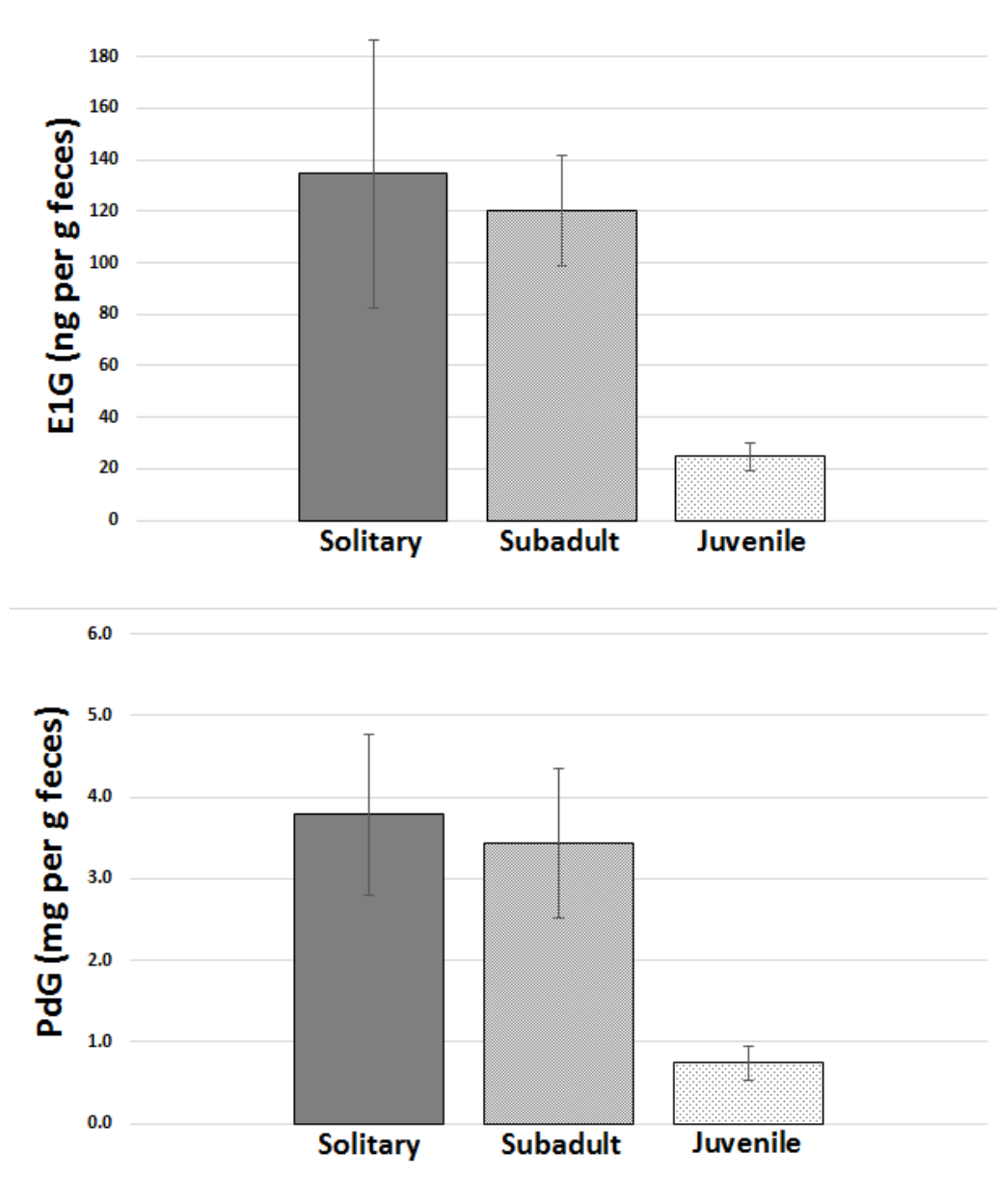
behavioral observations, sample collection, and protocols for the capturing and collaring of owl monkeys for identification. All research also adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Non-Human Primates and the Argentine Society for Mammalian Studies guidelines [Giannoni et al., 2003].

## Results

Solitary dispersed and predispersed subadults had very similar mean PdG and mean E1G levels (Figure 4.1, Wilcoxon Rank Sum Test:  $W = 15$ ,  $p = 0.93$ ). In contrast, juveniles had mean levels of both hormones that were substantially lower than those of predispersed and solitary dispersed subadults. Specifically, the mean PdG value in juveniles was only 20% and 22% of the values of solitary and predispersed subadult levels, respectively. Similarly, the mean E1G value in juveniles was only 19% and 21% of the values of solitary and predispersed subadult levels, respectively (Figure 4.1). The differences were statistically significant between solitary subadults and juveniles (Wilcoxon Rank Sum Tests:  $W = 19$ ,  $p = 0.03$  for PdG,  $W = 19$ ,  $p = 0.03$  for E1G) and between predispersed subadults and juveniles (Wilcoxon Rank Sum Tests:  $W = 33$ ,  $p = 0.01$  for PdG,  $W = 35$ ,  $p < 0.01$  for E1G).

Age was the most important factor for explaining mean PdG in our models. The variation in mean PdG was best explained by the approximating model that contained only age and sampling year as explanatory variables (Model 2). The AICc for this model was only marginally lower than for the more parsimonious model which contained only age (Model 1) (Delta AICc = 1.41; Supplementary Information: Table S4.2), so we report parameters from both models (Table 4.2). Season was not contained in either of these two models. Both of our best models estimated mean PdG increases of  $0.004 \pm 0.001$  mg/g for each day that an

individual ages, which is equivalent to an increase of  $1.5 \pm 0.4$  mg/g PdG per year. This estimate is fairly consistent with the mean PdG concentrations observed in 1-2 year-old subjects vs. 4-5 year-old subjects ( $0.7 \pm 0.2$  and  $3.8 \pm 1.0$  mg/g in juveniles and solitary dispersed subadults, respectively; Figure 4.1).



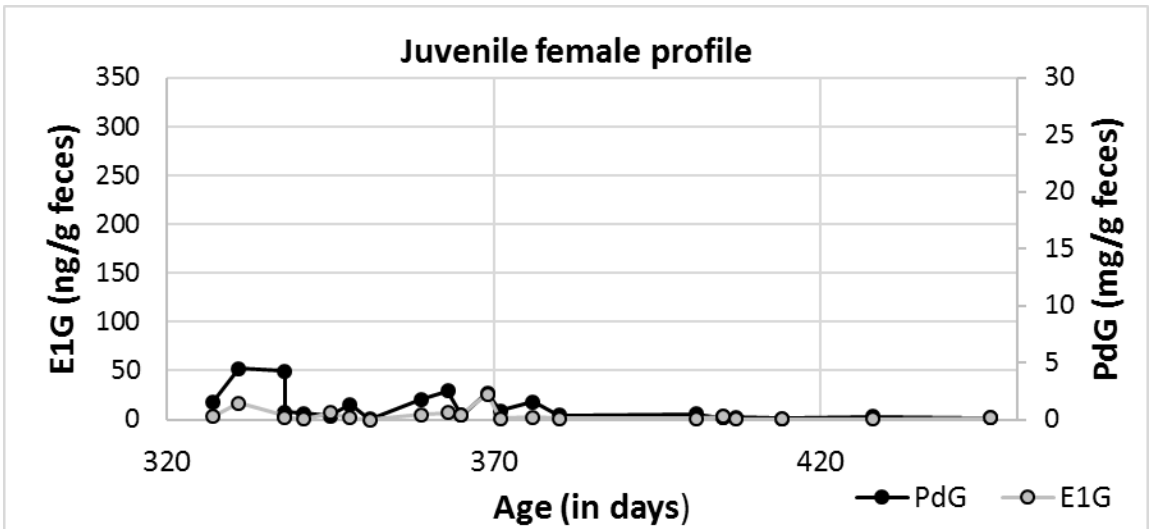
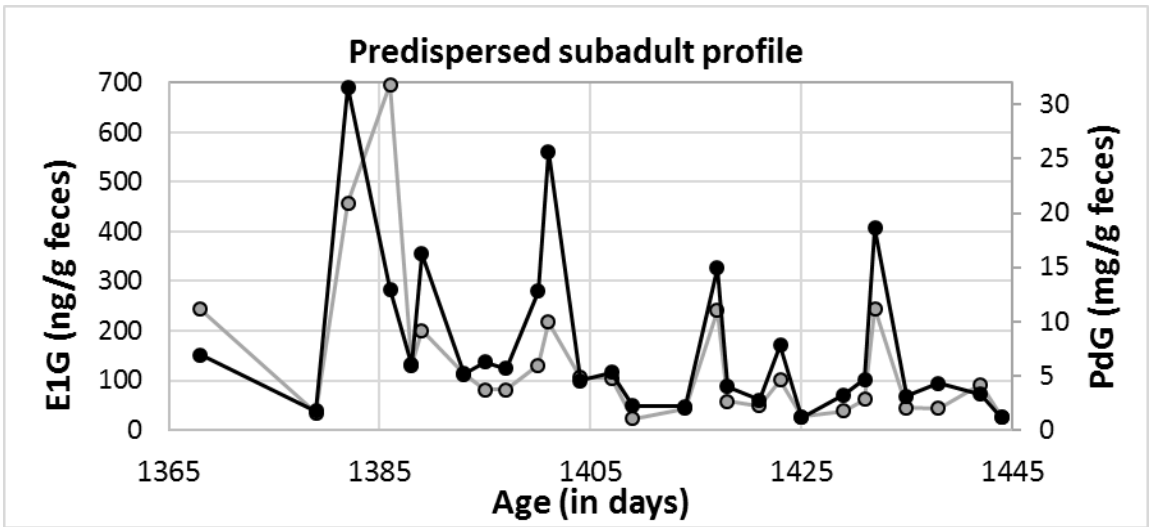
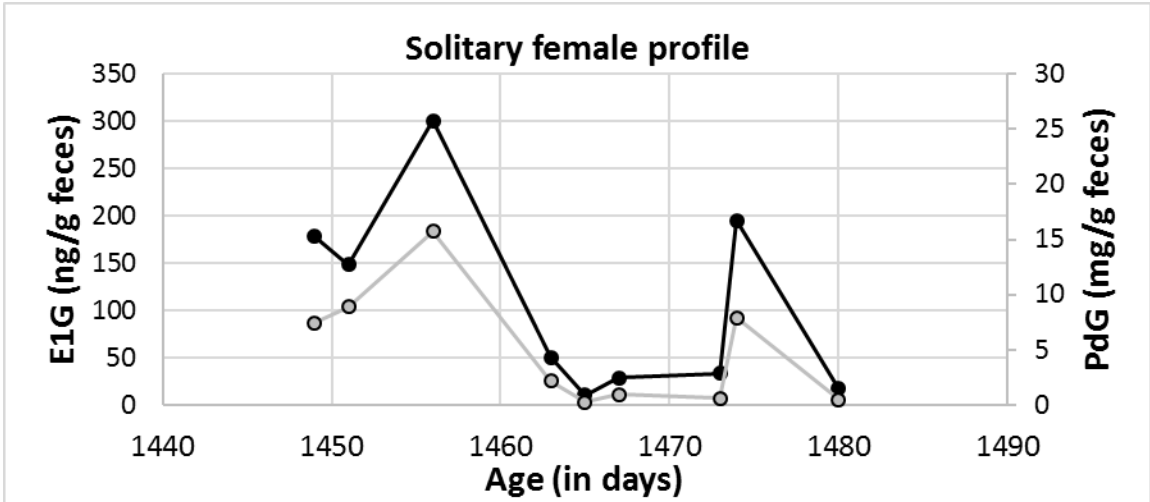
**Figure 4.1.** Mean levels of PdG (top) and E1G (bottom) in solitary and predispersing subadult and juvenile owl monkeys' fecal samples, shown with standard error bars.



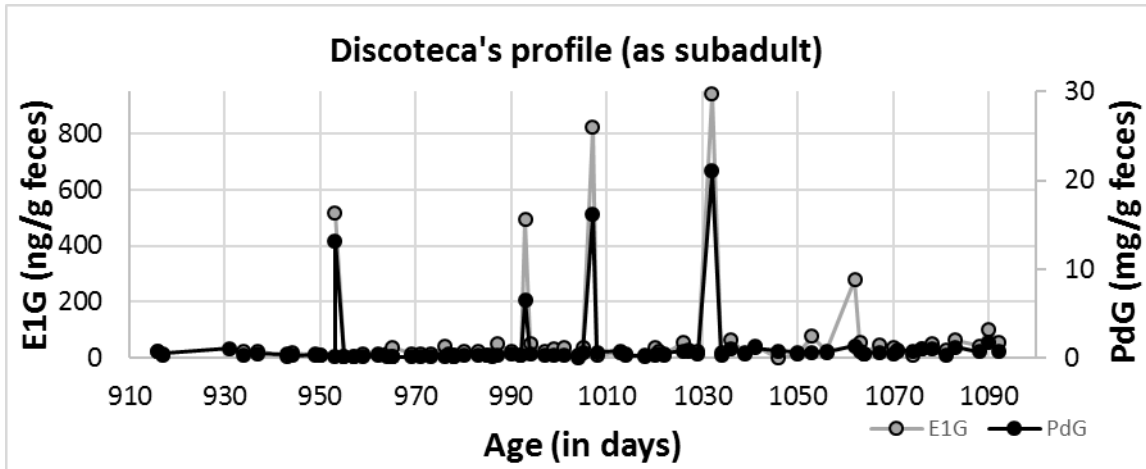
**Table 4.2.** Summary table of the two (out of four models in the a priori set) best-approximate generalized linear mixed-effects models for mean monthly PdG concentration.

Parameter		Estimate	Std. Error	95% CI
<b>Model 2</b>				
<i>Fixed Effects</i>				
Intercept		0.561	1.772	-1.978- 4.850
Age (in days)		0.004	0.001	0.002-0.006
Year	2013	-1.6953	1.607	-4.758-1.353
	2014	-1.480	1.648	-4.548-1.740
	2015	-2.416	1.650	-5.499-1.742
<i>Random Effects</i>				
ID	Intercept	1.197	1.094	
	Residual	3.894	1.973	
Marginal R <sup>2</sup> = 0.34				
Conditional R <sup>2</sup> = 0.49				
<b>Model 1</b>				
Parameter				
<i>Fixed Effects</i>				
Intercept		-0.749	0.941	-1.755-2.377
Age (in days)		0.004	0.001	0.002-0.005
<i>Random Effects</i>				
ID	Intercept	1.381	1.175	
	Residual	3.885	1.971	
Marginal R <sup>2</sup> = 0.24				
Conditional R <sup>2</sup> = 0.44				

Both solitary and predispersed subadults showed clear peaks of PdG and E1G during the luteal phase consistent with ovulatory cycling (Figure 4.2). Fecal PdG and E1G followed similar patterns, rising almost in parallel with one another during peaks. Peaks were generally separated by spans of consistently low levels (troughs) for both hormones, though intermediate activity was observed in some individual's profiles (Figure 4.2). Peaks were typically represented by 1-3 consecutive samples with relatively higher PdG and E1G levels, before hormone levels returned to baseline (Figure 4.2). Subadults' mean PdG levels varied between  $16.8 \pm 2.4$  mg PdG/g feces during peaks and  $2.0 \pm 0.4$  (SE) mg PdG/g feces in



**Figure 4.2.** Sample profiles of PdG (black) and E1G (gray) levels. Top: Example of a typical profile with ovulatory peaks from a solitary dispersed subadult (Betty, sampled 1 month). Middle: Example of a typical profile with ovulatory peaks from a predispersed subadult (Betty, sampled >2.5 months). Bottom: Example of a typical profile, lacking substantial hormonal peaks, from a juvenile (Bella, sampled >4 months).



**Figure 4.3.** PdG (black) and E1G (gray) profiles from a four-year old predispersed subadult to illustrate sporadic ovulatory peaks that were present in five of six subadults.

troughs, and mean E1G levels varied between  $410.9 \pm 73.7$  ng E1G/g feces during peaks and  $69.0 \pm 11.0$  ng E1G/g feces in troughs (Table 4.3).

We observed 21 distinct peaks in total (mean = 2.1 peaks per individual, range 1 - 4). All seven predispersed subadults showed at least one set of correlated PdG and E1G peaks (n = 18 total peaks). Similarly, all but one of the solitary dispersed subadults showed a PdG peak. The solitary dispersed subadult for which no peak was detected (Cansada, Table 4.1) was sampled only during 16 consecutive days (a much shorter period than other individuals), still her PdG and E1G baseline levels were within the range of other cycling solitary subadults (Table 4.3).

While the general appearance of peaks was similar among all subadult individuals, there was substantial interindividual variation in the absolute concentrations of PdG (maximum during peaks ranged from 5.3-31.7 mg/g) and E1G (maximum during peaks ranged from 181.3-841.8 ng/g) (Table 4.3). One solitary dispersed subadult had a maximum PdG level during a peak that was relatively low compared to other subadults' peak levels ("Discoteca" in Table 4.3). However, this peak met our strict criteria (>100% higher than SD from the baseline mean), and the peak PdG level was six times higher than mean trough levels, suggesting that this individual may have experienced an ovulatory cycle even though her PdG and E1G levels were relatively low compared to other subadults.

**Table 4.3.** Mean PdG and E1G concentrations ( $\pm$  SD) in peaks and troughs and the number of samples used to calculate means for each cycling owl monkey.

			PdG				E1G			
ID	Category	# of PdG peaks	mean PdG $\pm$ SD in peaks	N for peaks	mean PdG $\pm$ SD in troughs	N for troughs	mean E1G $\pm$ SD in peaks	N for peaks	mean E1G $\pm$ SD in troughs	N for troughs
Betty	predispersed	3	18.2 $\pm$ 6.9	8	3.9 $\pm$ 2.0	20	350.3 $\pm$ 191.7	6	73.7 $\pm$ 45.1	22
Celeste	predispersed	1	31.7	1	2.1 $\pm$ 1.9	7	528.1 $\pm$ 318.9	2	142.2 $\pm$ 126.6	6
Cordelia	predispersed	2	16.4 $\pm$ 7.1	4	2.0 $\pm$ 1.6	53	266.4 $\pm$ 94.9	4	78.0 $\pm$ 59.7	53
Discoteca	predispersed	3	16.9 $\pm$ 4.0	3	0.6 $\pm$ 0.8	70	695.5 $\pm$ 224.4	4	30.0 $\pm$ 36.6	67
Eusebia	predispersed	4	9.9 $\pm$ 2.5	6	1.9 $\pm$ 1.5	46	250.2 $\pm$ 113.9	5	68.2 $\pm$ 54.8	47
Felicia	predispersed	2	13.8 $\pm$ 1.1	2	0.9 $\pm$ 1.1	39	841.8 $\pm$ 709.7	2	80.8 $\pm$ 96.9	39
Petisa	predispersed	3	13.8 $\pm$ 3.5	3	1.1 $\pm$ 1.6	44	572.9 $\pm$ 250.6	4	67.7 $\pm$ 76.0	44
Betty	dispersed	1	15.7	1	3.6 $\pm$ 3.8	8	205.6 $\pm$ 66.2	4	28.1 $\pm$ 15.4	5
Celeste	dispersed	1	26.1	1	3.3 $\pm$ 2.4	11	181.3 $\pm$ 28.4	3	92.3 $\pm$ 55.1	8
<i>Discoteca</i>	<i>dispersed</i>	<i>1</i>	<i>5.3</i>	<i>1</i>	<i>0.9 <math>\pm</math> 0.8</i>	<i>32</i>	<i>217.1</i>	<i>1</i>	<i>28.6 <math>\pm</math> 26.5</i>	<i>32</i>
<i>Cebollita</i>	<i>juvenile</i>	<i>4</i>	<i>8.7 <math>\pm</math> 2.9</i>	<i>4</i>	<i>0.8 <math>\pm</math> 1.3</i>	<i>41</i>	<i>269.0 <math>\pm</math> 90.5</i>	<i>5</i>	<i>16.1 <math>\pm</math> 31.8</i>	<i>40</i>

N = the number of samples used to calculate the mean hormone concentration.

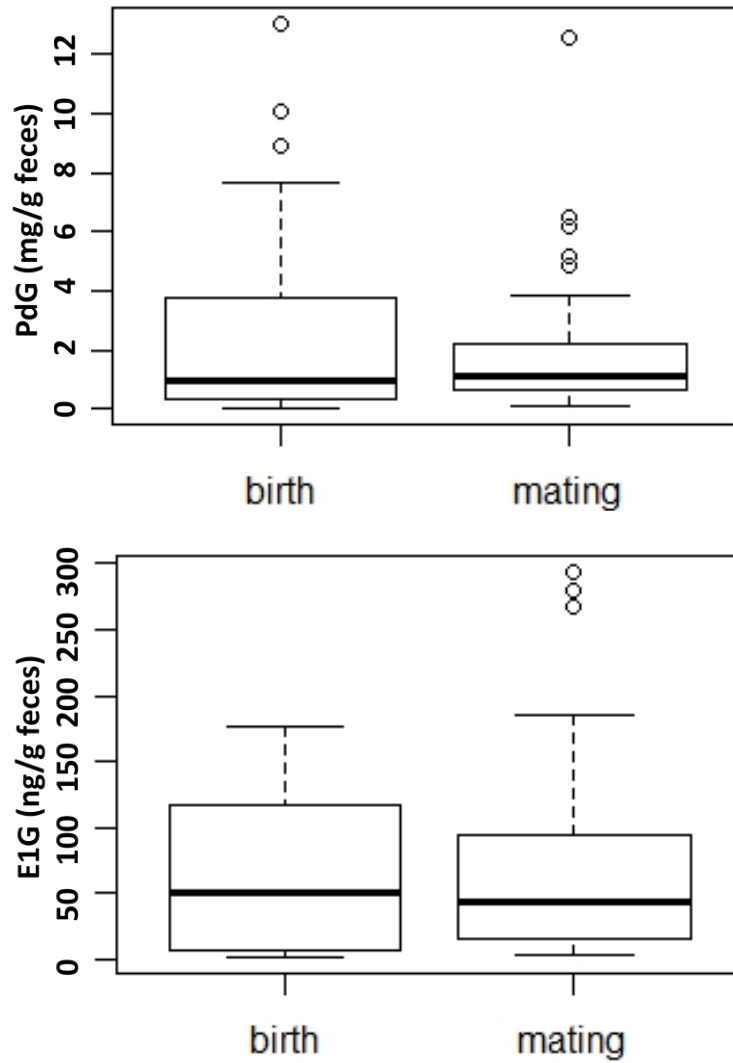
PdG values are in mg/g feces. E1G values are in ng/g feces.

*Italics indicate that the individual's hormone profile had one of more sections that qualified as peaks under our criteria (2 SD higher than the mean), but the maxima of these peaks were relatively low and they should not necessarily be interpreted as evidence of ovulation.*

Six predispersed or solitary dispersed subadults showed multiple PdG peaks. All but one of these six individuals had at least one gap longer than 25 days between the peaks of two or more of their cycles (Figure 4.3). In three cases, an individual's peaks occurred several months apart (up to 167 days between peaks). We monitored one solitary, Discoteca, who had previously cycled while in her natal group, for three months before we detected another ovulatory peak in her profile. Using distances between consecutive cycles without large gaps (>25 days) between peaks, the average number of days between E1G peaks was  $16.5 \pm 3.6$  (range 14-25 days, n= 4 subadults, 8 peaks) and the average number of days between E1G nadirs was  $17.9 \pm 2.4$  (range 15-22 days, n=4 subadults, 7 nadirs).

On average, subadults were approximately 36 months ( $1080 \pm 70$  days) old when we detected their first PdG peak indicative of ovulatory cycling. The youngest predispersed subadult was 31 months (953 days) old at the time of her first peak. The mean age at first peak was virtually the same for the three females who had experienced adult male replacements and the three who had not ( $1100 \pm 93$  and  $1098 \pm 142$  days, respectively). There was one individual, Cebollita, whose profile indicated several relatively small peaks in PdG, starting when she was still a juvenile (610 days of age). The mean maximum value of this individual's PdG peaks was considerably lower than the average of PdG during subadults' peaks ( $8.7 \pm 2.9$  vs.  $16.8 \pm 2.4$  mg PdG/g feces), so it is unclear whether these "peaks" can be considered equivalent to the ovulatory peaks observed in subadults. None of the other four juvenile females showed evidence of PdG or E1G peaks. No females showed any evidence of conception (as suggested by sustained increases in PdG) in their hormone profiles.

The distribution of PdG peaks over time does not suggest that ovulation was seasonal. Peaks occurred in all months during which sampling occurred (June-December). Of the 21 peaks, 10 occurred during the mating/pregnancy season (May-August) and 11 during the birth season (September-December), and the median concentrations were similar in both seasons for PdG and for E1G (Figure 4.4). The mean monthly PdG in both seasons was also similar ( $3.5 \pm 0.5$  vs.  $2.9 \pm 0.3$  mg PdG/g feces in mating and birth season, respectively; Wilcoxon Rank Sum test:  $W = 919$ ,  $p = 0.7$ ). Mean monthly E1G was slightly higher in the mating season compared to the birth season ( $98.4 \pm 35.9$  vs.  $68.0 \pm 10.6$  ng E1G/g feces), but the difference was not statistically significant (Wilcoxon Rank Sum test:  $W = 888$ ,  $p = 0.9$ ).



**Figure 4.4.** Box plots showing median of PdG and E1G concentrations during the birth and mating season (based on monthly means) in solitary and predispersed female owl monkeys' fecal samples.

## Discussion

This study provides the first description of reproductive hormone profiles and reproductive capacity in wild subadult owl monkeys. Female Azara's owl monkeys consistently experienced the onset of reproductive maturity prior to dispersing. Our results suggest that the reproductive suppression observed in female owl monkeys while in their natal group is not due to an inhibition of ovarian function.

Females were, on average, 36 months old when they experienced the onset of PdG peaks, which is substantially older than the onset of reproductive maturity observed in captive *Aotus* females [Gozalo and Montoya, 1990]. However, this finding is consistent with a later onset of reproductive maturity typically observed in wild primates when compared to captive ones [Dunbar, 1990]. Since we did not continuously monitor all individuals from birth, there is a possibility that some subadults may have begun cycling prior to the age when we first detected hormonal peaks. The fact that one juvenile (Cebollita, Table 4.3) may have had cyclic increases in PdG and E1G when she was 20 months suggests that our estimate of 36 months may be an overestimate. However, none of the other four individuals sampled as juveniles (<2 years of age) showed evidence of cycling, indicating that reaching sexual maturity prior to 2.5 years of age is likely atypical.

The hormone cycles in subadults were generally similar to those described for wild adult females at our field site [Fernandez-Duque et al., 2011]. That previous study of adults performed hormone assays at a different laboratory and utilized slightly different protocols than we employed in this study. We therefore refrained from making formal statistical comparisons of our data to adult hormone concentrations. However, it is worth noting that subadults in our study had mean PdG peak concentrations similar to those found in wild



adults ( $17.3 \pm 6.9$  vs.  $18.1 \pm 9.1$  mg PdG/g feces). The general pattern for E1G, which typically rose and fell in parallel with PdG in subadults, was also similar to the pattern observed for estrone conjugates (E1C) in adult females' cycles [Fernandez-Duque et al., 2011].

The average cycle length for subadults was somewhat shorter than expected. We anticipated that subadults' cycle lengths would be similar to those previously estimated for five wild adult *A. azarae* females, which had an average cycle length between  $22.2 \pm 2.7$  and  $24.0 \pm 1.6$  days [Fernandez-Duque et al., 2011]. Average cycle length in captive owl monkeys of Colombian origin is somewhat shorter, at  $16.09 \pm 0.15$  days (range 13-19 days) when computed using consecutive troughs of urinary PdG from 11 cycles in four adults [Bonney et al., 1979], and  $15.5 \pm 0.6$  days when computed using consecutive peaks in estradiol in four adults [Bonney et al., 1980]. Cycles of subadult owl monkeys thus seem to be of lengths intermediate ( $16.5 \pm 3.6$  -  $17.9 \pm 2.4$  days) to the average cycle lengths of wild and captive individuals.

Our estimates of cycle length are not as precise as those that could be computed from daily monitoring. Our sampling method did not necessarily allow us to detect the date of the absolute maximum or minimum hormone concentration reached in each ovulatory cycle. Since we collected feces only every 2-4 days, it is likely that for some cycles the days of the true maximum peak in PdG and E1G were often not sampled. This may account for the relatively wide range of days between consecutive cycles that we detected and for the somewhat shorter average cycle length compared to the previous estimates for adults at our study site.

The apparent brevity of the PdG peaks is also likely a consequence of our sampling paradigm, and should not be taken as evidence that subadults had an extremely short luteal phase. Peaks typically consisted of elevations in PdG in just one to three consecutive samples. It is possible that elevations in progesterone and its metabolites persist for a relatively short period during the ovulatory cycle of owl monkeys [Bonney et al., 1979]. However, we want to emphasize that while PdG peaks are sometimes represented by substantial elevations of PdG in just one sample, this does not necessarily imply that PdG (or E1G) levels are elevated for just one day. With gaps between samples averaging 3 days (with longer lapses on a few occasions), elevations in PdG lasting up to 6-7 days could be detectable in only one sample. It is possible that, if we had been able to sample individuals more frequently, we would have detected a more sustained elevation in luteal PdG.

Subadults displayed peaks in PdG somewhat irregularly, indicating that their cycles may be less regular than those of adults. One explanation for this observation is that our sampling schedule resulted in an inability to detect all peaks that occurred. However, our data strongly suggest that at least some individuals did not consistently ovulate after their first detected ovulatory cycle. For example, one predisposed subadult female, Discoteca, demonstrated hormone peaks consistent with ovulation at the age of 953 days (47 months). We subsequently monitored her consistently, without a gap of more than two days between any two samples, and she did not show any peaks in PdG or E1G until 40 days later (Figure 4.3). This inconsistent cycling suggests that owl monkey subadults may undergo a period of adolescent subfecundity, during which they may have irregular cycles and ovulate sporadically for several months or longer. This pattern is similar to what has been observed in captive adolescent titi monkeys (*C. moloch*), whose first cycles were typically followed by an

anovulatory period, ranging 2-4 months, before the next cycle was observed [Valeggia, 1996]. Irregular cycle lengths occurred in owl monkey subadults both before and after dispersal, suggesting that females may not establish more regular cycles until after pairing with an adult male in a non-natal group. At the very least, we can conclude that the development of fully mature ovarian function in wild owl monkeys generally takes at least several months, and may continue after dispersal.

Our results suggest that owl monkeys have a period of adolescent subfecundity, like that reported to occur in humans and some non-human primates, such as apes and macaques [Bercovitch and Ziegler, 2002; Metcalf et al., 1983; Nishida et al., 2003; Resko et al., 1982; Wallis, 1997; Young and Yerkes, 1943]. Hormone data from humans and captive macaques [Foster, 1977; Metcalf et al., 1983; Resko et al., 1982] indicate that adolescent subfecundity is typically characterized by a combination of anovulatory and ovulatory cycles [Vihko and Apter, 1984]. However, in wild primates, the presence of adolescent subfecundity is almost always inferred from observations of a delay between the onset of sexual behavior or sexual swellings and first conception, rather than from a direct examination of hormonal data [Knott, 2001]. The physiological basis for this delay in wild primates is often proposed to be hormonal, but is rarely verified. Our results support the suggestion that hormonal patterns of wild subadult owl monkeys may be consistent with patterns characteristic of adolescent subfecundity in human and captive non-human primates.

Season did not substantially influence the mean monthly levels of PdG or E1G (Figure 4.4). Subadults appeared to cycle in both the mating/pregnancy and birth seasons. We cannot say with certainty if subadults cycle throughout the entire year, since we did not sample individuals from January to April. Births are very seasonal at our field site, and we

have observed no successful pregnancies that could have resulted from cycles occurring outside of the mating season [Fernandez-Duque et al., 2002]. Thus, it is unclear why females would cycle in other seasons. However, wild adult females experienced non-conceptive cycles before becoming pregnant and at least one adult cycled outside of the mating season [Fernandez-Duque et al., 2011]. Given that subadults seem to require at least several months to establish consecutive regular cycles, it is possible that sporadically cycling throughout the year allows subadults time to fully establish adult-like, consistent reproductive cycles by the time the mating season arrives. This may allow them to be physiological ready to mate and conceive if an opportunity to do so arises (i.e., if they have successfully dispersed and established themselves as part of a pair in a new group by the next mating season). The extension of cycling outside of the mating season in adult females is something that requires further investigation.

Our findings do not support the inbreeding avoidance hypothesis [Pusey and Wolf, 1996]. Remaining in the natal group with reproductive adults, including the presumed father, does not appear to suppress ovulation in subadults over the age of 2.5-3 years. Yet, while subadult females apparently have the *capacity* to reproduce, we have never observed them to do so before dispersing. This is true even for subadults residing in natal groups with unrelated step-fathers, as three of our predispersed subadults were (Table 4.1).

Replacements of adult males did not appear to influence the timing of sexual maturity. If predispersing subadult females refrain from mating with the adult male in their natal group due to inbreeding avoidance, rather than behavioral inhibition by the adult male or other mechanism, we would not expect suppression of reproduction to continue once an unrelated male is introduced through an adult replacement. In some species, the introduction

of an unfamiliar adult male to the natal group may be associated with earlier onset of reproductive maturity [Cooney and Bennett, 2000; Hanby and Bygott, 1987; Wolff, 1992] and can stimulate predispersed females to breed [Saltzman et al., 2004]. However, we did not find any evidence to suggest that females residing in groups with step-fathers matured any earlier than females in groups that had not experienced an adult male replacement. To the contrary, the youngest predispersed subadult observed to cycle and the only juvenile that showed evidence of PdG peaks both resided in stable groups that had *not* experienced an adult male replacement (Discoteca and Cebollita, Table 4.1).

The mechanisms that prevent predispersed subadult females from reproducing with unrelated males in their natal groups remain unclear. One caveat is that, while subadults appear to have ovulatory cycles like those of adult females, we cannot say with certainty that cycling predispersed subadults are physiologically capable of sustaining a pregnancy even if they were to mate with an unrelated male. However, 20 years of observations of wild owl monkey behavior suggest that there are likely behavioral mechanisms that prevent cycling subadults from reproducing. Owl monkey groups are small and highly cohesive [Fernandez-Duque et al., 2001], which provides very few opportunities for individuals to copulate or reproduce without attracting the attention of other group members. Furthermore, neither juvenile nor female subadults typically engage in copulations with males in their natal groups, whether they are related or not (authors' personal observation). While adults generally tolerate sexually mature subadults in the natal group, they do target agonistic behavior at predispersed subadults more frequently than at younger offspring or pair-mates, and a subadult may be violently expelled if they attempt to copulate with a natal group member [Corley et al., in review; Huck and Fernandez-Duque, 2012]. Together, these

observations suggest that agonism may play a role in inhibiting sexually mature predispersed subadults' reproduction.

Our results raise questions as to why females would invest energy into developing and maintaining reproductive capacity prior to dispersal if they have no chance of reproducing until after they disperse and secure a mate. As has been suggested for titi monkeys [Valeggia, 1996], subadult wild owl monkeys may be developing a state of reproductive "suspended readiness", which could enable them to conceive upon entering the appropriate social environment (i.e., finding an available mate in a non-natal group).

Behavioral observations from our field site support this explanation. We have observed predispersed subadults temporarily separating from other members of their natal group to range solitarily, also known as "prospecting" [Mares et al., 2014; Reed et al., 1999], for several hours or even days. One function of these prospecting excursions may be for predispersed subadults to monitor the composition of neighboring social groups and evaluate potential opportunities for reproductive openings [Fernandez-Duque, 2009]. The relatively large amount of variation in the age at which individuals disperse and the variation in the amount of time that individuals may spend as solitaries after dispersing suggest that it is likely difficult for predispersed subadults to anticipate when mating opportunities will arise. Difficulty in anticipating reproductive opportunities is likely exacerbated by the fact that solitary floaters often need to engage in fights with adults in established social groups, the outcomes of which may be unpredictable, in order to gain a reproductive position [Fernandez-Duque and Huck, 2013]. Achieving reproductive maturity prior to dispersal may therefore physiologically prepare female subadults to reproduce whenever they are finally successful in securing a reproductive position.

It is also possible that establishing mature reproductive function could be a quality that is important in mate choice. For genetically monogamous species, like owl monkeys at our site, an individual may frequently only produce offspring with one mate, with whom they remain until their either die or are expelled by a solitary individual (after which they most likely will expire without gaining another opportunity to mate or reproduce) [Fernandez-Duque and Huck, 2013]. Obtaining a high-quality mate rapidly after dispersing from their natal group allows individuals to minimize the costs of dispersal and likely has an immense impact on lifetime fitness [Bonte and Dahiriel, 2016; Bonte et al., 2012]. Traits that allow subadults to acquire a high-quality mate and reproduce earlier will be selected for, as long as the benefits of early reproduction are not outweighed by costs [Altmann et al., 1988].

Ovulatory cycling may be a prerequisite to females gaining a reproductive position, if males can detect signals of ovulation and prefer to pair with already cycling females. In support of this view, there is emerging evidence that captive owl monkey males can detect if a female is sexually mature and cycling through olfactory mechanism (Spence-Aizenberg et al., in prep). Therefore, readying their reproductive systems (i.e., commencing ovulatory cycles) before dispersing may allow females to take advantage of unpredictable mating opportunities in their community. Mate selection, specifically the traits and signals preferred by each sex, is a topic on which further investigation is needed in owl monkeys and other monogamous species, to evaluate this hypothesis.

In summary, female owl monkeys do not delay puberty, but rather commence ovarian cycling as predispersed subadults, while still residing in their natal group. Subadults appear to have a period during which they experience irregular, non-conceptive cycles prior to reproducing. Commencing these irregular cycles while still in the natal group may allow

subadults to develop a state of suspended readiness, which may be essential to securing a mate, while avoiding the costs of ranging solitary. Our results indicate that reproductive suppression in owl monkeys is not due to a lack of reproductive capacity, although the specific mechanisms that prevent females from reproducing with unrelated adult males in their natal group require further investigation.

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The authors have no conflict of interest to declare.

## Supplementary Tables for Chapter 4

**Table S4.1.** Candidate model set for mean monthly PdG concentrations. Age = average age (in days) of the individual during the month she was sampled; Season = mating/pregnancy (May-Aug) vs. birth (Sep-Dec), Year = year in which sampling occurred (2011, 2013, 2014 or 2015).

Candidate model	Fixed and Random effects
Model 1	Age + (1 ID)
Model 2	Age + Year + (1 ID)
Model 3	Age + Season + (1 ID)
Model 4	Age + Season + Year + (1 ID)

**Table S4.2.** Comparison of the four candidate models for explaining variation in monthly PdG concentrations (most parsimonious best approximating models are highlighted in grey).

	K	AICc	Delta AICc	AIC weight	Cumulative Weight
<b>Model 2</b>	7	383.11	0	0.59	0.48
<b>Model 1</b>	4	384.52	1.41	0.29	0.71
<b>Model 4</b>	8	384.98	1.86	0.19	0.90
<b>Model 3</b>	5	386.23	3.11	0.12	1

K = number of parameters in the model

AICc = Akaike information criteria corrected for small sample size.

AICc weights, also termed model probabilities, indicate the level of support (i.e., weight of evidence) in favor of any given model within the candidate model set.

**Table S4.3.** Number of fecal samples, mean PdG (mg/g) and E1G (ng/g) values, and number of solitary dispersed subadults, predispersed subadults and juvenile female owl monkeys from which we collected samples in Formosa, Argentina between 2011 and 2015.

Category	N samples	Mean PdG $\pm$ SE	E1G Mean $\pm$ SE	N individuals
<b>Solitary Dispersed Subadult</b>	58	3.79 $\pm$ 0.98	134.42 $\pm$ 51.83	4
<b>Predispersed Subadult</b>	305	3.44 $\pm$ 0.91	120.30 $\pm$ 21.35	7
<b>Juvenile</b>	268	0.74 $\pm$ 0.20	24.85 $\pm$ 5.41	5
<b>TOTAL</b>	631	1.87 $\pm$ 0.15	65.25 $\pm$ 4.88	11*

\*Number of unique individuals. This is less than the sum of the number of individuals in each category because some individuals were sampled in multiple categories, as explained in Table 4.1.

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## **Chapter 5. Variation in dispersal strategies and the fates of dispersing individuals**

### **Abstract**

Dispersal is a key life-history stage, and understanding the factors that influence individuals to disperse from their natal groups is essential for evaluating hypotheses for the evolution of dispersal patterns. However, the complete process of dispersal involves more than leaving the natal group. Dispersal also entails a transient phase of movement, while searching for a new place to live, followed by settlement in a new area. Fully understanding the evolutionary forces that drive dispersal strategies requires data on the ultimate *outcomes* of dispersal decisions (e.g., mortality and reproductive success of dispersing individuals). In this study, I review what we have learned about the fate of dispersing individuals from observing a community of owl monkeys for over 20 years in the Argentinean Chaco. We observed 36% (21/58) of identified predispersed offspring prospecting at least once. Of the 34 individuals that we followed after dispersal, we observed 88% of them ranging solitarily at least once. Only ten individuals paired with an adult in a new group, and only seven of these remained in their new breeding positions for more than a year. Case studies of dispersing individuals, based on *ad libitum* observations, suggest that dispersal is an extremely varied process in owl monkeys. Both males and females follow a variety of strategies, which may involve prospecting and/or forming temporary associations with individuals outside of their natal groups before ultimately disappearing from the study area or finding a breeding position. Our data highlights the degree of heterogeneity among individuals within a single community and emphasizes the need to consider all stages of the dispersal process.

## **Introduction**

Natal dispersal is a multi-phase life-history process that can be classified into three main stages. These stages are departure from the natal area, a transient phase of movement while searching for a new place to live, and finally settlement in a new area [Bonte et al., 2012; Clobert et al., 2009; Ronce, 2007; Travis et al., 2012]. Each of these stages may be under selection to reduce the overall cost of dispersal [Bonte and Doherty, 2016; Travis et al., 2012]. Unfortunately, empirical studies often do not investigate all stages or distinguish between stages, which can confound our understanding of the influences that social or ecological factors have on dispersal [Cote et al., 2010].

Documenting the entire process of natal dispersal may be difficult for many reasons. The first stage, leaving the natal group, is typically a one-time event that researchers may easily miss, even if they are frequently monitoring a group. Even when researchers do witness an individual leave its natal group, they often have not been monitoring the group long enough to know the identity or date of birth of the dispersing individual [Jack and Isbell, 2009]. Dispersed individuals often range solitarily during the transient phase, which may make them difficult to find or follow. Researchers may also feel that their efforts and resources are better spent on observing groups, from which data on multiple individuals can be collected simultaneously. As a result, animals leaving their natal groups are rarely followed, unless dispersal is the primary focus of the study. This means that when an individual disappears from their natal group it is usually difficult to determine whether that individual has died or truly dispersed [Waser et al., 1994]. When researchers do attempt to follow individuals during the transient phase of dispersal, they may be unable to follow them outside of the study area, which limits their ability to determine the distance travelled during

dispersal and the ultimate fates of dispersing individuals [Clutton-Brock and Lukas, 2012; Koenig et al., 1996]. Studying long-lived animals, such as primates, which are generally slow to develop and mature, only increases the challenges associated with observing the entire dispersal process [Jack and Isbell, 2009].

Developing a better understanding of how long individuals spend ranging solitary and what challenges they face while doing so is essential for understanding the costs of dispersal. Of the three stages of dispersal, the solitary transient phase is typically the least well-studied and least understood in most taxa [Grabowska-Zhang et al., 2016; Ronce, 2007]. Being a solitary transient individual, or “floater”, presents individuals with many ecological and social challenges, which can have important consequences for their survival and fitness [Bélichon et al., 1996; Bonte et al., 2012; Ridley et al., 2008; Yoder et al., 2004]. For example, solitary dispersing male baboons (*Papio cynocephalus*) have mortality rates at least twice as high as group-living males [Alberts and Altmann, 1995]. In addition to mortality costs, floaters may have decreased foraging efficiency and experience a deterioration in body condition which may impede their ability to find a breeding position [Ridley et al., 2008]. A better understanding of the costs of the solitary life-history stage requires more data on the behavior of solitary floaters and their attempts to immigrate into established groups.

One way that individuals may reduce the costs of ranging solitary is through “prospecting”. Prospecting is when an individual separates from its natal group and explores extra-territorial areas prior to permanently dispersing. This behavior appears to be common in a variety of birds and mammals, and may provide predispersed individuals with information that helps them time their dispersal to coincide with conditions favorable for ranging solitary or finding a breeding position [Kingma et al., 2016; Mares, 2012; Raihani

et al., 2010; Reed et al., 1999; Ridley et al., 2008; Solomon, 2003]. For example, prospecting may allow individuals to gather information about the availability of potential mates or assess the quality of nearby territories [Dittmann et al., 2005; Selonen and Hanski, 2010]. In some taxa, it can also provide males with opportunities to engage in extra-group breeding prior to dispersing [Eikenaar et al., 2008; Griffin et al., 2003; Young et al., 2007]. Collecting data on prospecting or tracking prospecting movements can thus provide insight into dispersal decisions [Ponchon et al., 2013].

Taxa may often display intraspecific variation in both dispersal and pre-dispersal behaviors, like prospecting. For example, the frequency of prospecting may vary from year to year or from site to site, as environmental variables change [Quinn et al., 2011]. It may also vary from one individual to another, based on underlying differences in personality and the willingness to engage in exploratory behavior [Cote et al., 2010]. Understanding intraspecific variation is important not only for developing and evaluating theoretical frameworks, but also for assessing population viabilities and informing conservation management programs [Strier, 2017]. A better understanding of dispersal and its consequences therefore requires assessing variation during each of the three stages of dispersal.

In Azara's owl monkeys (*Aotus azarae*) in the Argentinean Gran Chaco, all offspring leave their natal groups prior to reproducing. Both males and females disperse between the ages of 2 and 5, and typically spend some time ranging solitarily before becoming a breeding adult in a non-natal group [Chapter 2; Fernandez-Duque, 2009]. Predispersed owl monkeys sometimes engage in prospecting [Fernandez-Duque, 2009]. While engaging in prospecting events and while ranging solitarily after dispersal, individuals will sometimes make vocalizations, known as hoots (Moynihan 1964; personal observations). Hoots are low-

frequency calls that convey information over long distances [Wright, 1989]. There is sexual dimorphism in the hoot-call vocalizations given by males and females (males produce deeper dog-like bark/"gruff" hoots, while females produce higher-pitched "tonal" hoots), which suggests that hoot calls may play an important role in mate attraction [Depeine et al., 2008]. Almost everything we know about owl monkey dispersal comes from studies of Azara's owl monkeys in the Gran Chaco of Argentina conducted by the Owl Monkey Project. While we have previously reported anecdotal observations of prospecting in owl monkeys [Fernandez-Duque, 2009], we have not quantified the prevalence of prospecting nor have we systematically reported the behaviors and other social interactions displayed by prospecting individuals. Similarly, while we have investigated various social and ecological factors associated with the timing of natal dispersal [Chapter 2; Fernandez-Duque, 2009], we have not previously provided detailed data on the entire dispersal process for individual owl monkeys.

This chapter provides an individual-based perspective on dispersal, by describing the entire dispersal process for a subset of identified owl monkeys. I have examined the social, hormonal, and ecological variables associated with dispersal in the other chapters of this dissertation. Here, I review what we have learned about all three stages of dispersal and the fates of dispersing individuals from observing a community of owl monkeys over 20 years in the Argentinean Chaco. I first present the frequencies at which we have observed prospecting and dispersal events, and provide details about the individuals that we have been able to follow after they dispersed from their natal groups. I then summarize the data that we have collected by following individuals during the solitary transient stage, and report the frequency at which we observed various fates (dying, disappearing, or becoming part of a

breeding pair). I then present a series of seven detailed case studies based on *ad libitum* observations, which describe the entire process of dispersal for individuals. Finally, I synthesize these data to identify common tendencies in dispersal in owl monkeys and discuss the variability of individual dispersal strategies. I also assess the limitations of our methods and suggest directions that future research should explore to enhance our understanding of owl monkey dispersal.

## **Methods**

The Owl Monkey Project (OMP) has been collecting data from a population of Azara's owl monkeys (*Aotus azarae*) at the Reserva Mirikiná, in the Argentinean Gran Chaco, since 1997. This site is located on Guaycolec Ranch, 25 km from the city of Formosa, and consists of 1500 ha of gallery forest along the Riacho Pilagá (58°11 W, 25°58 S). We closely monitor groups within a core area of this site (central groups) by contacting them at least once every week or second week and recording all changes in group composition (e.g., births, deaths, dispersals, adult replacements). The exact number of central groups that we monitor closely varies from year to year, but typically includes at least 10 groups. An additional 10-15 peripheral groups are contacted monthly to semi-annually (see Table III in [Fernandez-Duque, 2016] for a full report of our monitoring effort). Every time a group is contacted, observers record the presence of identified individuals and note any changes to group composition. Observers also collect *ad libitum* records on extreme aggression among group members, intergroup encounters, and interactions between social groups and solitary individuals. We enter all data into the Owl Monkey Project database, a Microsoft Access file.



Since 2000, the OMP has been capturing animals and fitting them with radio or bead collars to facilitate locating and identifying individuals [Fernandez-Duque and Rotundo, 2003; Juárez et al., 2011]. When capturing, we never target infants (< 6 months) or small juveniles, so the only animals routinely captured are adults and adult-sized (or nearly adult-sized) subadults ( $\geq 24$  months) and older juveniles (>18-24 months). The priority during most years of the study has been to target resident adults, who will not disperse, so that we can employ radiotelemetry to consistently locate and monitor the demographic changes within social groups. As a result of these practices, most offspring disappear or disperse from their natal groups without being captured, and we have only been able to follow a relatively small subset of offspring after they dispersed (25% of the 84 offspring that survived infancy in central groups from 1997-2014 [Fernandez-Duque, 2016]).

We report data here only on identified (i.e., captured) offspring who were wearing functioning radio-collars at the time they dispersed from a central or peripheral group (N = 34, Table 5.1). We were unable to follow the post-dispersal movements of any uncollared individuals. For each of these collared individuals, the sex, date of birth, and date of dispersal (with an accuracy of  $\pm 40$  days) were known, unless otherwise specified in Table 5.1. This allowed us to estimate the age at dispersal for each individual. We also recorded the composition of the natal group at the time of dispersal (e.g., number of other individuals of each age and sex category present) and noted if either of the resident adults in the natal group had been replaced at any point between the disperser's birth and date of dispersal. We then calculated summary statistics (e.g., average age at dispersal, percent of individuals dispersing from natal groups with a step-parent present, etc.) over all subjects. We report the mean  $\pm$  one standard error unless otherwise indicated.

We also quantified the number of times that we observed individuals “prospecting” prior to permanently dispersing. We quantified prospecting events for each of the 58 individuals that were captured and radio-collared while still in their natal group: the 34 individuals that we followed after dispersal and 23 additional individuals that we captured, but were unable to follow after they dispersed (e.g., individuals that died or disappeared from the natal group). We calculated the proportion of individuals of each sex that prospected and the mean number of prospecting events per individual (Figure 5.1). In our analysis of prospecting events, we included all instances when we observed a predispersed individual ranging solitarily, apart from all other members of their natal group. We also included all instances in which observers confirmed that the predispersed individual was absent from its natal group (Table 5.2). We considered an individual to be missing from its natal group only in cases in which an observer stayed with the group for at least half an hour and noted in the database’s comments or demography section that they could clearly see and identify all other members of the natal group. This means that we excluded all instances in which the observer noted that an individual appeared to be missing, but could not say with certainty which individuals in the group were present. Also excluded are all instances in which a group was observed for only a brief amount of time (< 30 minutes), because it is possible that during a brief observation period the observer may have overlooked a predispersed individual that may have been temporarily out of sight, but nearby. Thus, the absences from the natal group that we report are likely to represent true instances in which predispersed individuals were missing because they were ranging solitarily (i.e., prospecting). When we refer to “prospecting events”, we are referring to the number of observed solitary and missing events combined, unless otherwise specified.

For those individuals that we observed ranging solitarily *after* dispersing, we recorded the number of times that we observed the individual as a solitary and calculated the length of time that they spent as a solitary. We categorized each dispersing individual as having one of three ultimate dispersal outcomes: “paired”, “died” or “unknown” (Table 5.1). In many cases, we lost contact with an individual suddenly, because its radio-collar fell off or we could no longer detect a signal from the collar anywhere in or around our study area. If our last observation of an individual was as a solitary, we considered the outcome of that individual’s dispersal to be “unknown”, because we had no way of knowing whether the individual eventually died or joined a group after we lost track of it. For those individuals that became part of a pair in a non-natal group, we calculated the length of time that they spent in the new group (Table 5.1). When an individual was still solitary or still paired in its new group at the time when we last observed it, we report the length of time as being  $\geq$  the number of months we observed it in this state. We then calculated the average length of time individuals of each sex spent as solitaires and in a pair in a non-natal group (Figures 5.2 and 5.3).

To develop a more detailed understanding of the entire natal dispersal process, we utilized notes collected *ad libitum* to compile descriptive “case studies” for dispersed individuals. In each case study of a dispersing individual we include a description of 1) all instances of “prospecting” and all interactions with individuals outside of the natal group prior to permanently dispersing, 2) all instances of social interactions with adults that involved extreme aggression or copulations that occurred within the six months immediately preceding the dispersal, and 3) all changes in group composition (e.g., adult replacements, births, other dispersals) that occurred within the six months immediately preceding the

dispersal. We then describe any interactions with social groups or other solitaires that the individual had once they were a solitary, and describe the circumstances in which they joined a new group. While we provide information on the fates all 34 individuals followed after dispersal (Table 5.1), we do not report detailed descriptions of the full dispersal process for each of these individuals. Instead, the seven case studies that we present represent a subset of these individuals, which we selected because they covered a range of dispersal experiences. The individuals described in case studies are thus representative of the diversity in experiences that individuals faced before, during, and after dispersing.

The ethics committees (IACUC) of the Zoological Society of San Diego (2000-2005), the University of Pennsylvania (2006-2014), Yale University (2014-2015), and the National Wildlife Directorate in Argentina approved all capturing and data collection protocols. All research adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Non-Human Primates and the Argentine Society for Mammalian Studies guidelines [Giannoni et al., 2003].

## **Results**

### **Age at dispersal and characteristics of the natal group**

We observed 34 identified individuals after they dispersed from their natal groups (17 males, 17 females). The mean age at dispersal for these 34 individuals was  $41.3 \pm 1.5$  months ( $40.8 \pm 2.2$  for males,  $41.8 \pm 2.1$  for females). Unsurprisingly, all individuals dispersed from groups that contained one adult male and one adult female. Individuals' natal groups contained a mean of  $3.4 \pm 0.1$  other individuals at the time that they dispersed. Natal group

size was similar for dispersers that joined a non-natal group and dispersers that did not (mean =  $3.1 \pm 0.9$  and  $3.4 \pm 0.6$  individuals, respectively; median for both groups = 3 individuals).

Most individuals dispersed from a group in which at least one other offspring was present: 35% contained two or more younger offspring, while only two contained no other offspring. Half (50%) of individuals left natal groups in which one or both adults were a step-parent (i.e., had been replaced during the disperser's lifetime). Dispersers that joined a non-natal group (paired) were approximately equally likely to have experienced an adult replacement prior to dispersing (50%, 5/10 individuals, experienced a replacement) when compared to dispersers whose fates were unknown (54%, 13/24 individuals, experienced a replacement). Details of natal group compositions at the time of dispersal are reported in Table 5.1. Additional data on characteristics of the natal group from which offspring disappeared or dispersed are reported in chapter 2 of this dissertation (Figure 2.1).

**Table 5.1.** Sex, age and natal group composition at time of dispersal, time spent as solitary and/or in a new group after dispersal, the ultimate outcome of dispersal, and the dates of observation for 34 owl monkeys that we followed after they dispersed.

Group	Disperser	Sex	Dis. Age	Natal group composition	Time as solitary (mo.)	N as solit.	Observation period after dispersing	Outcome	Time in new group
A900	Apolo	M	40	AM, AF, SM, IU	$\geq 7$	6	23-Apr-04 – 11-Nov-04	Unk	NA
B68	Mony	F	43	AM, AF	$\leq 1$ week	0	31-Jul-02 – 9-Jun-11	Paired (CC)	107
C0	Celeste	F	45	AM, AF*, JU	$\geq 13$	31	19-Sep-12 – 16-Oct-13	Unk	NA
Camp	Camilo	M	48	AM, AF, IU	$\geq 4$	10	12-Oct-03 – 13-Apr-04	Unk	NA
CC	Cansada	F	43	AM, AF*?, JF	$\geq 3$	27	29-Jun-11 – 23-Sep-11	Unk	NA
CC	Cata	F	46	AM*, AF, JF, JU	$\geq 10$	4	6-Aug-08 – 24-Jun-09	Unk	NA
CC	Conchita	F	35	AM, AF*, JM, JF	$\geq 11$	45	1-Oct-02 – 26-Sep-03	Unk	NA
Colman	Andre	M	36	AM, AF, SU, JF, IU	$\geq 4$	7	21-Nov-11 – 30-Mar-12	Unk	NA

Colman	Anibal	M	36	AM, AF, SF	3	17	3-Nov-03 – 10-Feb-04	Paired (P300)	74
Colman	Anita	F	36	AM, AF, JM, JU	$\geq 1$	2	8-Oct-08 – 7-Nov-08	Unk	NA
Corredor	Betty	F	47	AM, AF, JF	$\leq 2$	32	24-Oct-14 – 30-Dec-14	Paired ? <sup>1</sup>	5
D1200	Dante	M	48	AM, AF*, JU	$\geq 1$	3	28-Oct-04 – 1-Nov-04	Unk	NA
D1200	Dardo	M	43	AM, AF, SM, JM, JU	5	29	16-Jul-02 – 7-Nov-16	Paired (F1200)	$\geq 171^2$
D1200	Dartagnan	M	41	AM, AF*, SM	$\geq 1$	7	1-Apr-03 – 29-May-03	Unk	NA
D500	Dionisio	M	35	AM*, AF, IU	$< 1$	0	19-Nov-05 – 23-Dec-16	Paired (D800)	$\geq 135^2$
D500	Diosa	F	35	AM*, AF, JM	$< 1$ week	0	6-Sep-04 – 24-Jun-05	Paired <sup>3</sup> (D800)	$< 10$
D500	Discoteca	F	36	AM, AF*, IU	$\geq 9$	59	3-Nov-14 – 13-Aug-15	Unk	NA
D500	Diuresis	F	58	AM*, AF, SF, JM	$< 15$	0	18-Aug-04 – 23-Mar-15	Paired (G1300)	$\geq 113^2$
D500	Dixi	M	39	AM, AF*, SF, IU	$\geq 14$	58	7-Jan-14 – 20-May-15	Unk	NA
D800	Donovan	M	47	AM, AF*, JU	$< 3$	3	29-Sep-15 – 23-Dec-16	Paired (D500)	$\geq 12^2$
E350	Eusebia	F	36	AM, AF, SF, IU	$\geq 9$	2	10-Nov-15 – 10-Aug-16	Unk	NA
E350	Evaristo	M	46	AM, AF, JF	$\geq 9$	28	11-Nov-07 – 21-Aug-08	Unk	NA
E500	Elino <sup>3</sup>	M	60	AM*, AF*	13	55	11-Oct-02 – 20-Apr-04	Paired <sup>4</sup> (D500)	5
E500	Emma	F	37	AM, AF, SM, IU	$\geq 7$	25	21-Jan-08 – 13-Aug-08	Unk	NA
E500	Enrique	M	51	AM, AF, JU	$\leq 9$ (3 + $\leq 6$ ) <sup>5</sup>	19	25-Mar-10 – 21-Jun-10 & 10-Sep-10 – 8-Mar-11	Died	NA
F1200	Fulera	F	33	AM, AF, JF	$\geq 1$	2	8-Oct-09 – 13-Oct-09	Unk	NA
F1200	Fugado	M	31	AM, AF, 2 JF	$\geq 2$	5	18-Nov-08 – 16-Jan-09	Unk	NA
F700	Felicia	F	35	AM*, AF, SM	$\geq 1$	7	8-Nov-13 – 27-Nov-13	Unk	NA
F700	Felix	M	26	AM, AF, IU	$\leq 10$	2	25-Dec-02 – 23-Nov-11	Paired (L100)	98
Fauna	Fidel	M	24	AM, AF, JF	$\geq 2$	3	19-Oct-03 – 11-Dec-03	Unk	NA
G1300	Gargara	F	48	AM*, AF*, IU	$\geq 4$	7	27-Oct-05 – 14-Mar-06	Unk	NA
IJ500	Idiota	M	42	AM*, AF*, IU	$\geq 1$	1	18-Apr-05 <sup>6</sup> – 08-Sep-05	Unk	NA

P300	Petisa	F	36	AM*, AF*, IU	≥ 1	2	29-Oct-13 – 7-Nov-13	Unk	NA
Veronica	Vilma	F	62	AM, AF, JU, IU	≥ 6	4	10-Dec-05 <sup>7</sup> – 10-Aug-06	Unk	NA

Age categories are abbreviated as A = Adult, S = subadult, J = juvenile, I = infant. Sexes are abbreviated as M = male, F = female, and U = sex unknown.

“Dis. Age” is the age (in months) of the individual at the time of natal dispersal.

“Natal group composition” is a list of the individuals present in the disperser’s natal group at the time of dispersal (not including the disperser). \* indicates that the adult present at the time of dispersal had replaced the presumed genetic parent of the dispersing individual.

“Time as solitary” is the length of time the disperser spent as a solitary prior to dying, disappearing, or pairing/joining a group (in months, unless otherwise indicated).

“Observation period” is the range of dates for which an individual was observed *after* dispersing from their natal group.

“Outcome” after dispersing is whether the individual was confirmed to have died, become a resident adult in a group (“Paired”), or was still solitary when last sighted (“Unk.”). If paired, the group in which it took up residence as an adult is reported in parentheses.

“Time in new group” is the number of months the dispersing individual was observed to reside a non-natal group as a paired adult.

<sup>1</sup>See Case study 2 for description of Betty’s fate.

<sup>2</sup>Still paired in group at time of last sighting before the study ended (31 December, 2016)

<sup>3</sup>Elino was already present when we first started observing the group E500 and he was not captured until he was an adult-sized individual. Observers assigned him an estimated date of birth as October 1997, but we cannot be 100% certain if this was his natal group or whether he was the adult male who later underwent secondary dispersal.

<sup>4</sup>Paired after dispersing, but expelled from new group before reproducing.

<sup>5</sup>See Case study 7 for a description of Enrique’s two dispersals and times as a solitary.

<sup>6</sup>Idiota’s natal group was not well-monitored at the time he dispersed. The estimated date of dispersal is the average between the day last seen in natal group and the day first seen as solitary (uncertainty of  $\pm 125$  days).

<sup>7</sup>The individual was seen solitarily or with an unknown adult several times prior to this date of permanent dispersal (see Case study 7 for details).

## Prospecting behavior of predispersed individuals

We observed evidence of prospecting for approximately 36% of predispersed individuals. Of the 58 individuals that were radio-collared while still in their natal groups, we observed 16 predispersed individuals ranging solitary at least once and 11 missing from their natal groups at least once. We observed six predispersed individuals both ranging solitarily and missing from their natal groups on different occasions, meaning that 21 unique individuals (36%) prospected or were presumed to prospect (Table 5.2).

**Table 5.2.** Number of observations, age, and time before dispersal/disappearance (in months) for all 21 individuals that exhibited prospecting behavior.

Name	Group	Sex	# of times S	# of times M	# of times P	Age at first S	Age at first M	Age at first P	Months before dispersal first S	Months before dispersal first M	Months before dispersal first P
Apolo/	A900	M	1	0	1	36.8	na	36.8	4.3	na	4.3
Celedonio/	C0	M	0	1	1	na	30.3	30.3	na	0.9	0.9
Camilo/	Camp	M	1	0	1	28.1	na	28.1	20.6	na	20.6
Cata/	CC	F	0	1	1	na	36.8	36.8	na	9.0	9.0
Constanza/	CC	F	1	1	2	20.5	20.5	20.5	0.0	<0.1	<0.1
<i>Cordelia/</i>	<i>CC</i>	<i>F</i>	<i>8</i>	<i>1</i>	<i>9</i>	<i>41.7</i>	<i>42.3</i>	<i>41.7</i>	<i>na</i>	<i>na</i>	<i>na</i>
Andre/	Colman	M	1	0	1	33.7	na	33.7	2.1	na	2.1
<i>Angelita/</i>	<i>Colman</i>	<i>F</i>	<i>2</i>	<i>0</i>	<i>2</i>	<i>24.7</i>	<i>na</i>	<i>24.7</i>	<i>na</i>	<i>na</i>	<i>na</i>
Anita/	Colman	F	0	2	2	na	23.2	23.2	na	13.3	13.3
Betty/	Corredor	F	5	1	6	45.2	44.7	44.7	2.6	3.1	3.1
Duana/	D100	F	5	3	8	39.5	43.6	39.5	21.1	17.1	21.1
Dante/	D1200	M	1	0	1	36.2	na	36.2	12.5	na	12.5
Diuresis/	D500	F	5	2	7	46.3	46.3	46.3	12.6	12.6	12.6
<i>Emilia/</i>	<i>E350</i>	<i>F</i>	<i>1</i>	<i>0</i>	<i>1</i>	<i>28.1</i>	<i>na</i>	<i>28.1</i>	<i>na</i>	<i>na</i>	<i>na</i>
Eusebia	E350	F	0	1	1	na	25.1	25.1	na	10.3	10.3
Evaristo/	E350	M	0	1	1	na	26.8	26.8	na	20.2	20.2
Enrique/	E500	M	1	0	1	36.2	na	36.2	20.5	na	20.5
Fugado/	F1200	M	1	0	1	30.0	na	30.0	1.0	na	1.0
Fuxia/	F1200	F	1	0	1	37.1	na	37.1	1.2	na	1.2
Gargara/	G1300	F	4	0	4	27.1	na	27.1	22.1	na	22.1
Vilma/	Veronica	F	9	1	10	26.5	27.8	26.5	36.1	34.8	36.1

“S” = solitary ranging, “M” = missing from the natal group, and “P” = presumed prospecting (sum of the times observed either ranging solitarily or missing from the natal group)

“# of times” refers to the number of observations in each of the three categories (S, M, and P).

“Age at first” refers to the age (in months) at which the individual was first observed to engage in prospecting behavior.

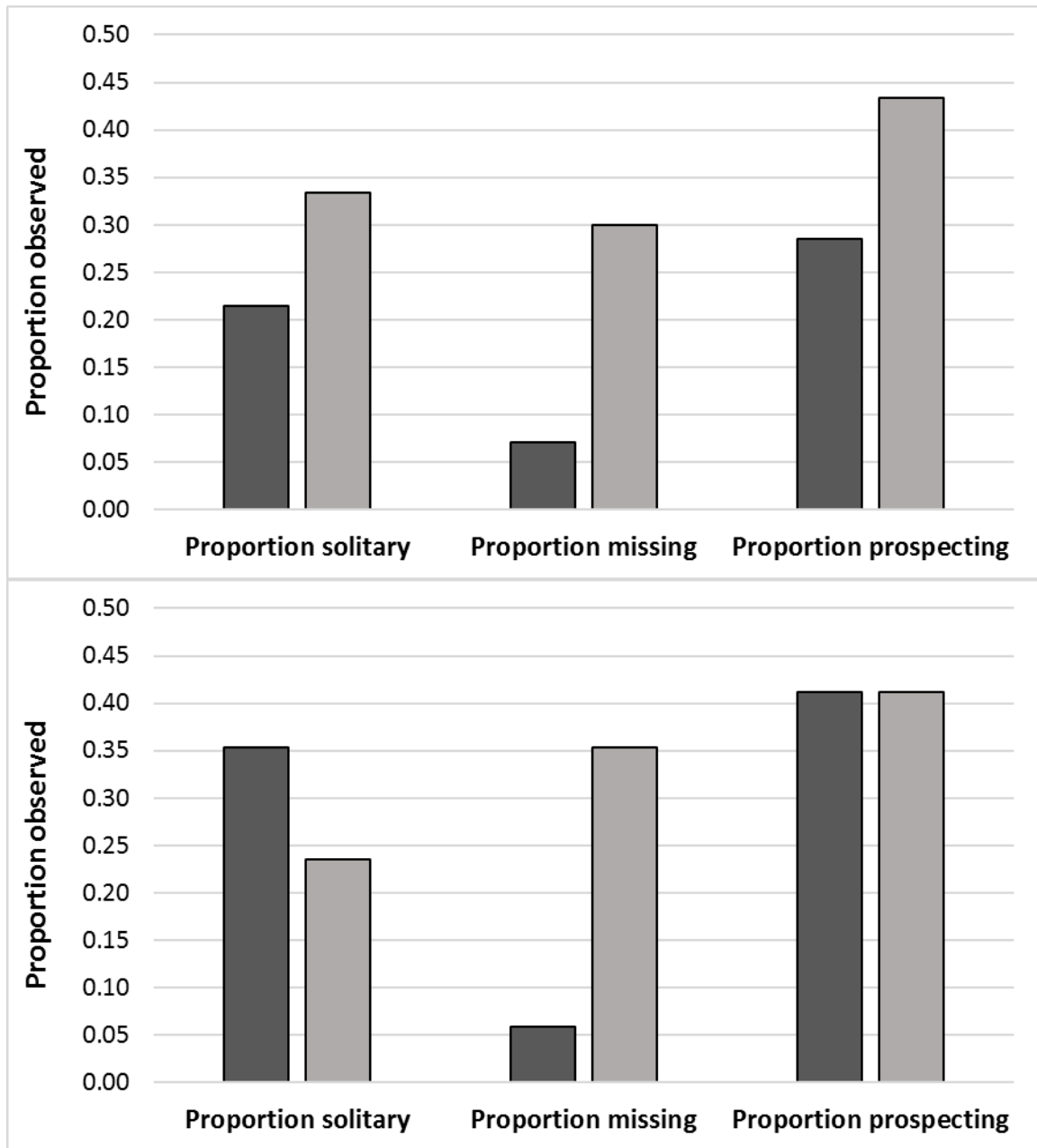
*Italics* indicate that the individual died while still in the natal group, and thus no estimate for “months before dispersal” could be determined.

Of these 21 individuals, 13 were females and eight were males, and we observed more females (N=9) than males (N=2) missing from their natal groups (Figure 5.1a). When we combined observations of solitary ranging and absences from natal groups, a somewhat



larger proportion of females (43%, 13/30) prospected than males (29%, 8/28), but this difference was not statistically significant (2-sample test for equality of proportions:  $X^2 = 0.8$ ,  $df = 1$ ,  $p = 0.4$ ; Figure 5.1a). When we limited analysis to the 34 predispersed individuals that were confirmed to have eventually dispersed, 41% (14 unique individuals) prospected on at least one occasion: ten were observed ranging solitarily, seven were observed to be missing from their group, and three were observed both solitarily and missing. We observed more males than females ranging solitarily (6 vs. 4) and more females than males missing from their natal groups (6 vs. 1), but overall the same number of females (7/17) and males (7/17) prospected (Figure 5.1b).

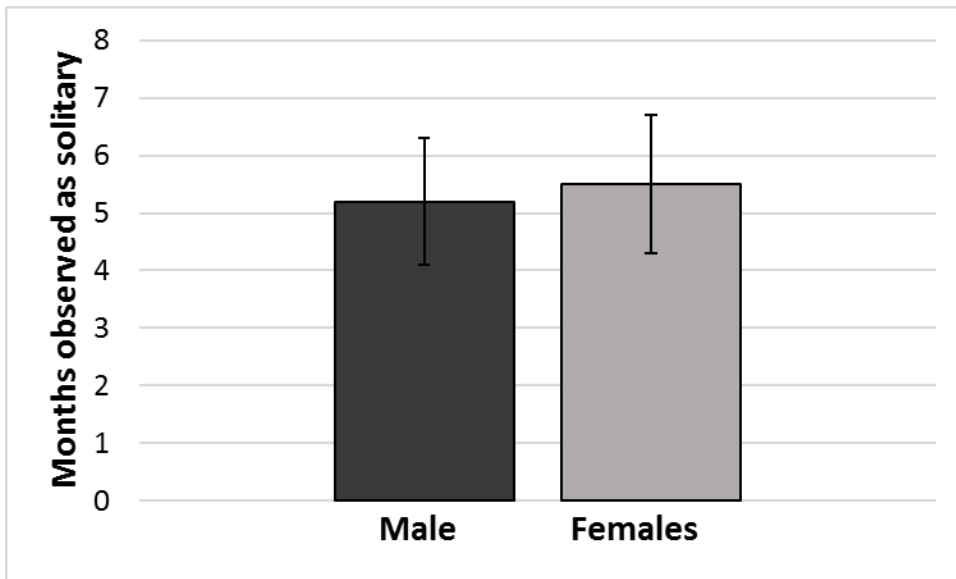
The frequency and timing of prospecting behaviors were very variable. Individuals who prospected did so an average of three times (range 1-10), but most individuals were observed prospecting just once (median = 1). We first observed individuals prospecting at a mean age of  $32.3 \pm 1.6$  months (range 20.5-46.3 months). Prospecting events occurred a median of 11 months prior to the date on which an individual permanently dispersed or disappeared from the natal group (range 1 day to 36 months). The median time before dispersal that we first observed individuals prospecting was similar whether evidence of solitary ranging or absences from the natal group were considered (median = 8 vs. 10 months prior to dispersing, respectively).



**Figure 5.1.** Proportion of males (dark bars) and females (light bars) observed prospecting, for a) 58 individuals captured and identified while in their natal groups (28 males, 30 females), and b) a subset of 34 of these 58 individuals with confirmed dispersals (17 males, 17 females). “Proportion solitary” refers to those observed ranging solitary, “proportion missing” refers to those observed to be missing from their natal group, and “proportion prospecting” refers to those who were observed either ranging solitary *or* missing from their natal group, at least once prior to permanently dispersing.

### Solitary ranging and fates of individuals after dispersal

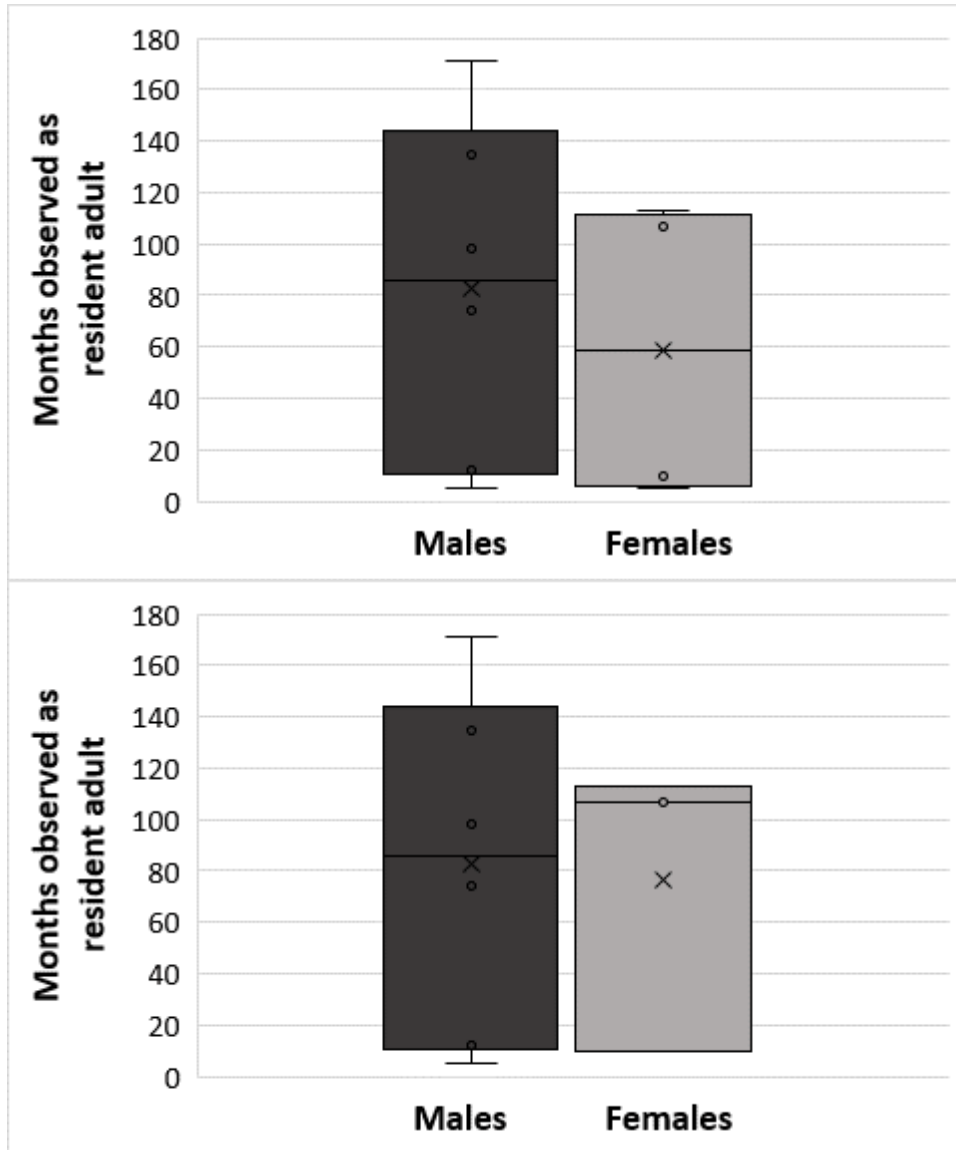
After dispersal, all but four subjects were observed as solitaires on at least one occasion (30/34 individuals, 88%). The remaining four were observed already paired in a new group by the first time that we observed them after their dispersal (1 male, 3 females). For those individuals that spent time as solitaires, we observed each a mean of  $17 \pm 3$  times, and the mean length of time observed as a solitary was  $5.4 \pm 0.8$  months ( $5.2 \pm 1.1$  for males, for  $5.5 \pm 1.2$  females, Figure 5.2). However, there was substantial variation in the number of months that we observed individuals as solitaires (from  $< 1$  month to more than 14 months; Table 5.1).



**Figure 5.2.** Mean number of months that we observed males and females ranging solitary after they permanently dispersed. Error bars show standard errors.

Ten of the 34 individuals paired with another adult after permanently dispersing (6 males, 4 females). Of these ten, nine paired with an adult in a group that our project was already monitoring. Five of these nine joined a group that was immediately adjacent to their

natal territory. We observed the tenth individual, Betty, with an unknown individual in the periphery of our study area. Since we were not monitoring this area before we followed Betty to it, we cannot say whether this individual was a resident adult with a territory or another solitary with which Betty was temporarily associating. We therefore report results for paired individuals both including and excluding Betty's case (Figure 5.3).



**Figure 5.3.** Number of months that we observed males and females paired with a resident adult in a non-natal group after dispersing, for: top = ten individuals (6 males, 4 females), and bottom = nine individuals, excluding Betty (6 males, 3 females). The “X” indicates the mean and the vertical line indicates the median.

We observed the ten individuals that paired in their new groups for a mean of  $73 \pm 19$  months (males =  $83 \pm 27$ , females =  $59 \pm 30$  months; Figure 5.3). When we exclude Betty, the length of time that we observed females paired in their new group ( $77 \pm 33$  months) was more similar to the length of time that we observed males (Figure 5.3). Seven of the nine individuals that joined a monitored group remained in their new group for at least 1 year, with one remaining as the resident adult for over 14 years (Dardo, Table 5.1). The remaining two subjects (1 male and 1 female) underwent a secondary dispersal from the group that they had joined after their natal dispersal. These two individuals maintained residence in their new group for only 5-10 months and did not reproduce. Both of these individuals were observed as solitaires after leaving or being expelled from their non-natal group and one (Elino) was eventually found dead. On several occasions, we have observed a resident adult that departed a monitored group find a second breeding position in a new group [Fernandez-Duque and Huck, 2013], but this was not the case for either of the two individuals that underwent secondary dispersal in this study.

## **Case studies**

### *Case 1. Ranging solitarily shortly after experiencing an adult replacement*

*Cansada (female, dispersed at age 43 months, from group “CC”, in June 2011)*

We never witnessed Cansada prospecting or missing from her natal group, CC, prior to dispersal. Three days before Cansada dispersed, the adult female (Cansada’s genetic mother), disappeared from CC. For two days after this, the group consisted of just Cansada, her presumed genetic father, and her 18-month-old female sibling (Cordelia). On the third day after her mother’s disappearance, a new adult (presumably a female) joined CC. Later

that same day, Cansada dispersed and was never seen with her natal group again. Observers were not with CC after 10:00 am the day of her dispersal, so we do not know the exact circumstances of Cansada's departure from her group (e.g., whether or not the new adult or her father aggressively expelled her). She did not have any visible injuries when she was sighted alone at 17:00 later that day, but the following day we observed both adults in CC acting aggressively towards Cordelia, the juvenile female that remained in the group. Cansada spent the next three months ranging solitarily as a floater within the study area. We did not observe her interacting with any groups or other solitaries during this time. After three months, observers were no longer able to detect her radio-collar's signal and did not see her again. Her ultimate fate is unknown.

*Case 2. Prospecting, ranging solitarily, and affiliatively associating with other individuals*

*Betty (female, dispersed at age 47 months, from group "Corredor", in October 2014)*

We first observed Betty missing from her natal group, Corredor, in July of 2014, 3.1 months before she dispersed. After this, she made at least five solitary expeditions away from her natal group during the three months immediately preceding her dispersal (Table 2). On two of these occasions, observers found Betty alone at dusk near the edge of her natal group's home range making vocalizations (tonal hoots). On another occasion, two months before she dispersed, we observed her moving in the direction of gruff hoots, but she did not leave her natal territory and rejoined the other members of her natal group after a few minutes. Sixteen days before her dispersal, we found her alone over 1 km away from her natal group in the morning, but she returned to Corredor's home range by that evening. The following morning we found her again in her natal group's home range, resting in contact

with the 12-month-old juvenile female from Corredor, but neither the adult male nor female were observed nearby. Betty and the juvenile female remained alone together, resting and foraging within Corredor's home range, for five hours before the adult pair from Corredor joined them. Two days later, we observed Betty ranging alone within her natal home range for > 5 hours. She remained with all three members of her natal group during all sightings for the next 12 days, and then permanently dispersed on October 22, 2014. We did not witness her leave her natal group, so we do not know if she left voluntarily or was aggressively expelled. There were no demographic changes in the six months leading up to her dispersal.

We found Betty ranging solitarily in the periphery of our core study area four times in the first week after she dispersed. After this, we observed her interacting with other individuals on at least six occasions. First, eight days after her dispersal, we observed her within the home range of group P300, resting in contact with an unknown individual that was carrying a small infant. Three days after this we found her resting in contact with a different individual, an unidentified adult with a torn left ear, across the river from group P300's home range. The very next day, we once again found Betty within P300's home range and observed her playing, sniffing, and resting with a juvenile-sized individual (believed to be the 1-year old juvenile from group P300) for about six minutes. She fled when two adult-sized individuals (presumed to be the adults from P300) entered the area. The next day we found her again with an unidentified adult with a torn left ear, which we believe was the same adult with whom she was observed two days prior. During the next week, we observed Betty ranging solitarily twice, and then observed her vocalizing (making tonal hoots) in the presence of an unidentified individual that observers could not see clearly. We then observed her ranging solitarily on six occasions over the next two weeks, before finding her once again

with an unidentified adult across the river from our study area, near P300's home range. We detected her signal in this same area six times over the next six months (until 9 June, 2015), which suggests that she may have established herself as a resident female in a group in this area. However, we were not able to get close enough to see her or any other individual(s) that she may have been with during this time due to flooding in the area. We tentatively classify her as paired, but we do not know how long she remained with the adult with whom we last observed her.

*Case 3. Temporarily associating with solitary and other group members after dispersing*

*Evaristo (male, dispersed at 46 months, from group "E350", in October 2007)*

Evaristo dispersed from his natal group, E350, sometime between 13 October and 11 November, 2007. Prior to this, we never observed him prospecting or missing from E350. We did not witness his departure from the natal group, so we do not know if he departed voluntarily or was aggressively expelled. There were no demographic changes in the group in the six months leading up to his dispersal.

We observed Evaristo ranging solitarily nine times over the next five months. Then on 6 April, 2008, we observed him with an unidentified individual, presumably another solitary. They rested and foraged together all morning, but separated by that afternoon. The entire time that they were together, they remained within the home range of E500, a group that neighbors Evaristo's natal group (E350). We observed Evaristo ranging solitarily in the study area ten more times before 26 July, when we observed him running away from group CC, after he had been resting in their home range. He continued ranging solitarily until 5 August, when we found him with an unknown female, again presumed to be a solitary. We



do not know if this was the same solitary with whom we observed him previously, but we found him resting with her within the home range of E500, not far from where we had observed him interacting with the solitary four months prior. On this occasion, we observed him mounting the solitary female and inspecting her genital area. About 30 minutes later, she acted aggressively towards him and then moved away to feed in another tree. However, he followed her, and we observed them resting in contact and tail twining with her for several more hours after this. In total, we observed them together for over six hours on this day.

When the solitary female left Evaristo, she twice made tonal hoot vocalizations as she moved away. Three and a half hours after she separated from Evaristo, around dusk, we heard tonal hoots coming from the direction in which the female solitary was last seen travelling. Evaristo moved towards the directions of the hoots, but stopped to forage after a few minutes, and we did not observe him approaching any closer to the source of the hooting after this. Evaristo was observed alone twice during the next two days, but on the third day after this, he was observed once again resting in contact with an unknown individual within D500's home range (a group that neighbors both E500's and his natal group's home range). After about an hour, group D500 approached and chased the unknown individual away. Evaristo remained in D500's home range and we briefly observed him resting within 5 m of group D500 as they rested in contact with one another. After several minutes, members of D500 chased Evaristo out of the tree in which they had been resting, but he remained in the area and rested on a branch only a few trees away from D500 for the next four hours, before departing from their home range. We saw Evaristo twice more as a solitary, but he did not interact with any other groups or solitaires on these occasions. His ultimate fate is unknown.

Case 4. A case of (almost) inheriting the natal territory

*Cordelia (female, died at 49 months, before dispersing from group “CC”, in December 2013)*

Cordelia’s case is difficult to classify. Although she never permanently dispersed from her natal group’s home range, she was residing alone with an unrelated adult male at the time of her death. She also engaged in many pre-dispersal behaviors that we believe are worth describing here.

We first observed Cordelia prospecting seven months before her death. We observed her missing from CC once, on 24 June, 2013, and as a solitary seven times between 4 June and 8 August, 2013. On both 3 July and 14 July, we observed an adult in CC chasing Cordelia, but outside of these two events she continued to act affiliatively with all members of her natal group (engaging in grooming and huddling on many occasions).

Up until 25 July, group CC consisted of Cordelia, an adult male (her presumed genetic father), an adult female (her step-mother), and an 8-month-old juvenile male. On 26 July, we observed that Cordelia’s father was missing from the group, and for almost two weeks the only individuals observed in CC were Cordelia, the adult female, and the juvenile male. On 8 August, we followed Cordelia at dusk as she rapidly moved more than 0.5 km away from her natal group, while making tonal hoot vocalizations. On this occasion, Cordelia was moving in the direction of gruff hoots being made by an unseen male when it became too dark for the observer to follow her. The next morning, we observed both Cordelia and a new adult male back in CC's home range, socializing with the adult female and male juvenile. On this morning (9 August), we observed the new male mounting/attempting to copulate with Cordelia six times within one hour. In the afternoon, we observed him mounting Cordelia

once again and the adult female in CC once. He also inspected the genital regions of both Cordelia and the adult female several times. Twice during the following week, we observed the new adult male and the adult female chasing and fighting with one another. We did not observe either Cordelia or the juvenile male participating in these aggressive interactions.

We observed all four individuals in CC (Cordelia, the new male, the adult female, and the juvenile) together until 10 December, 2013. On this day, we observed the adult male chasing another adult-sized individual, but observers could not determine whether it was Cordelia or the adult female. On 11 December, Cordelia and the adult male were found together within CC's home range, without the adult female or the juvenile male. We never observed the adult female or juvenile with the group again. Over the next week, we observed Cordelia and the adult male consistently together and observed no aggressive interactions between them during the four times that we observed them. After 19 December, 2013, we were unable to contact the group. We detected a mortality signal from Cordelia's radio-collar on 7 January, 2014, and found her remains this same day within CC's home range. The adult male from CC was never captured or marked, so we do not know his fate.

*Case 5. Siblings reunited, as solitaries, after dispersing*

*Dixi (male, dispersed at age 39 months from "D500", in January 2014)*

*Discoteca (female, dispersed at age 36 months from "D500", in November 2014)*

Dixi and Discoteca were born to the same parents in group D500, approximately one year apart from one another, and are presumed to be full siblings. A new adult female replaced their genetic mother when Dixi was 23 months and Discoteca was 10 months old. We did not observe either Dixi or Discoteca missing from D500 nor did we observe either of

them prospecting prior to their permanent dispersals. The only demographic change that occurred in the six months prior to Dixi's dispersal was the birth of an infant (19 September, 2013). We did not witness Dixi leaving his natal group, so we cannot say whether he dispersed voluntarily or was aggressively expelled. After Dixi dispersed, on 7 January, 2014, we observed him ranging solitarily 56 times during the next year. Once, about ten months after he dispersed, we observed him running away from the adults in group CC, after he had been resting alone within their home range. We did not observe him interacting with any other groups or solitaries in 2014.

Ten months after Dixi dispersed from D500, Discoteca was expelled from the group. The only demographic change that occurred in the six months prior to her expulsion was the birth of an infant, on 1 October, 2014. On 3 November, 2014, we witnessed Discoteca receiving extreme aggression from the adult female in D500 (her step-mother). The adult female chased and fought with Discoteca, repeatedly forcing her to retreat low to the ground many times over the course of one hour. The adult male (her father, carrying an infant) joined the adult female in attacking her on one occasion, about 30 minutes into the aggressive incident. The female eventually knocked Discoteca to the ground, shortly after which Discoteca separated from the D500 adults. Discoteca was never observed with the group D500 again after this incident. After dispersing, we observed Discoteca ranging solitarily 37 times over the next 6.5 months. About two weeks after her dispersal we observed adults in group CC chasing her out of their home range. This is the only time we observed Discoteca interacting with any other solitaries or groups during these 37 sightings.

On 20 May, 2015, we found Discoteca resting in contact with Dixi. Dixi's radio-collar had stopped functioning several months prior, but had not yet detached, which allowed

us to identify him. The two stayed together all day, for > 9 hours, during which we observed them resting in contact and occasionally grooming one another. At dusk, both individuals left the area rapidly, when the group in whose home range they had been resting, IJ500, approached. After this incident, we never saw Dixi again, but we observed Discoteca ranging solitarily an additional 20 times over the next 12 months. Only once during this time did we see her interact with any other individuals: she ran away when the group CC entered the area in their home range in which she had been resting. She was still solitary when we last detected a signal from her radio-collar (3 May, 2016). Her ultimate fate is unknown.

*Case 6. Related individuals disperse to a neighboring group: adult turn-overs prevent them from inbreeding*

*Diosa (female, dispersed at age 35 months, from “D500” to “D800”, in September 2004)*

*Dionisio (male, dispersed at age 35 months, from “D500” to “D800”, in October 2005)*

*Donovan (male, dispersed at age 47 months from “D800” to “D500”, in September 2015)*

Diosa and Dionisio were born to the same parents in group D500, approximately one year apart from one another, and were confirmed to be genetic full siblings [Huck et al., 2014]. Less than one year apart, both of them dispersed from D500 and became a resident adult in the group D800, which has a home range adjacent to their natal group. Ten years later, Dionisio’s son, Donovan, dispersed from D800 into his father’s natal group, D500. However, both adults in D500 had been replaced since Dionisio’s birth.

We never observed either Diosa or Dionisio prospecting or missing from their natal group prior to permanently dispersing. In the six months leading up to Diosa’s dispersal there were several demographic changes to her natal group. About 4.5 months before her dispersal,

the D500 adult male (Diosa's step-father) disappeared. Then just two weeks before her dispersal, Diosa's older genetic sister (who was 58 months old at the time) dispersed from D500.

Between 27 August and 6 September, 2014, Diosa dispersed from D500 and replaced the former resident adult female in D800. We did not observe her depart from her natal group, so we do not know whether she left voluntarily or was expelled. We also did not observe her ranging solitarily: she was already with her new group, D800, the first time we saw her after dispersing. She remained in D800 with an adult male, Donatello, and a juvenile that had been born in October 2003 (J03), for 6.5 months. Sometime between 15 March and 9 May, 2005, an unidentified male with a short tail replaced Donatello as the resident male in D800. We observed this male together with Diosa and the J03 until the end of May. By 23 June, 2005, the short-tailed adult male had disappeared from the group, and only Diosa and the J03 remained together. On 24 June, 2005, Diosa was observed ranging alone within D800's home range. The next day, June 25, 2005, we observed two unidentified adults with the J03 in D800's home range, indicating that Diosa had been replaced/expelled from D800. We only observed her ranging solitarily after this date. We observed her as a solitary 20 times before we lost contact with her in March, 2006, but her fate after this point is unknown.

Sometime between 18 October and 10 November, 2005, Dionisio dispersed from D500 and replaced the unidentified adult male in D800. As in Diosa's case, we did not observe him depart from his natal group, so we do not know whether he left voluntarily or was expelled. We also did not observe him ranging solitarily: he was already with his new group, D800, the first time we saw him after dispersing. The only demographic change in the six months before Dionisio's dispersal was the birth of an infant, 1.5 months prior to his

dispersal. His new mate in D800, was captured and identified as “Doly” two weeks after Dionisio entered the group. Thus, while he dispersed to the same group as his genetic older sister, we can confirm that the two siblings were never present in group D800 at the same time. Dionisio has remained the resident adult male in D800 since this time and was still paired with an adult female in this group at the end of our study period. Six infants have been born during his tenure, thus far.

Dionisio’s presumed genetic son, Donovan, dispersed from group D800 between 21 and 29 September, 2015. We never observed Donovan missing from his natal group or prospecting. However, we did observe him interacting with an individual from the neighboring group D500, about 11 months before he dispersed (22 October, 2014). During an intergroup encounter at the border between their groups’ home ranges, Donovan approached the subadult female in D500, Discoteca, and followed her repeatedly, such that he remained within three meters of her for about five minutes. We observed Donovan and Discoteca vocalizing, but observed no aggression or physical contact between them. There were no demographic changes to D800 in the six months before Donovan dispersed. We did not witness Donovan depart from his natal group, so we do not know if he left voluntarily or was expelled. After dispersing, we observed Donovan ranging solitarily three times between 29, September and 14 October, 2015. The next time we found him, Donovan had replaced the adult male in D500. At the end of our study period Donovan was still paired with an adult female in D500, “Dilema”, but this pair had not yet produced any offspring. Dilema is not the same adult female that was present when his father, Dionisio, dispersed from this group.

*Case 7. Returning to the natal group after “dispersing”*

*Vilma (female, dispersed at age 62 months from group “Veronica”, in December 2005)*

*Enrique (male, dispersed at 51 and again at 57 months from “E500”, in March and September 2010)*

Vilma and Enrique represent the only two cases that we have observed in which an individual appeared to permanently disperse, but then returned to the natal group before dispersing again. Unlike typical cases of prospecting, during which predispersed individuals are observed ranging solitarily for a few hours to one day, both Vilma’s and Enrique’s excursions outside of their natal groups lasted three or more days, so we consider them to be distinct from other prospecting events that we have witnessed and report their cases in detail.

Before permanently dispersing, Vilma repeatedly spent time socializing with individuals outside of her natal group. On 11 August, 2005, four months before her permanent dispersal, we observed Vilma alone outside of her natal group’s home range. She was vocalizing (tonal hoots) and moving in the direction of hooting vocalizations being made by an unseen male at dusk when we lost sight of her. She returned to her natal group by the following day. Less than one month later, on 2 September, we again observed Vilma ranging solitarily while hooting, but she returned to her natal group within three days and remained with them during all sightings until 23 September, when we again found her ranging solitarily. The next time we saw her, on 26 September, Vilma was still apart from her natal group, but this time, she was with an adult-sized individual not from her natal group. She remained with this individual throughout the day, and we observed her grooming, exchanging food, and sniffing this other individual. However, the next day we observed her back with her natal group. We consistently observed her with her natal group through early November. On 28 November, we again observed her with an unidentified adult-size individual that was not



from her natal group. She returned to her natal group again by 8 December, but after this date, we only observed her ranging solitarily. In the six months prior to the final time Vilma was sighted with her natal group, the only demographic change that occurred was the birth of an infant, about two months prior. We did not witness Vilma depart, so we do not know if she left voluntarily or was expelled. We last observed Vilma as a solitary on 10 August, 2006, after which we could no longer locate a signal for her radio-collar. Her ultimate fate is unknown.

Enrique is the only owl monkey that we have observed returning to the natal group after ranging solitarily for approximately three months. On 28 December, 2008, 20 months prior to his initial dispersal, we first observed Enrique ranging solitarily. We did not observe him prospecting or missing from his natal group again until two days prior to his initial dispersal, when he was not seen with the other members of E500. The day after this (one day before his dispersal), we observed him in his natal group with his father and 18-month-old younger sibling. His presumed genetic mother, Estrella, was not seen with the group at this time and we never saw her again after this date. Other than the disappearance of Estrella, there were no demographic changes in the six months prior to Enrique's initial dispersal. On 26 March, 2010, we found him ranging solitarily and presumed him to have permanently dispersed. We did not see him depart from the natal group, so we are unsure whether he left voluntarily or experienced aggression before dispersing. After his initial dispersal, we observed him ranging solitarily six times, during which he never interacted with his natal group or any other individuals. Then, on 22 June, 2010 we observed him back with his natal group, E500.

The details of Enrique's return to his natal group have been previously described [Huck and Fernandez-Duque, 2012]. Briefly, Enrique's presumed genetic mother, Estrella, was replaced by a new female during his three-month absence. After he returned to E500, he remained there for three additional months. At the end of this time, we observed Enrique copulating with his step-mother twice, on two successive days. After the second copulation, his father attacked him (biting, wounding, and chasing him to the ground). Enrique departed from E500 on this same afternoon (10 September, 2010), and we never observed him interacting with members of his natal group after this second dispersal. We observed Enrique ranging solitarily 13 more times after he was expelled from E500, the last of which was on 25 November, 2010. He ultimately died before joining a new group: we found his remains, within E500's home range, on 10 March, 2011.

## **Discussion**

There are a variety of potential strategies available to owl monkeys across all stages of natal dispersal. Consistent with previous findings, which suggest that owl monkeys follow flexible dispersal strategies [Fernandez-Duque, 2009], our results confirm that variation is present in the behavior of individuals before and after dispersal, in the amount of time spent as a solitary, and in the ultimate fate of dispersing individuals.

Males and females had relatively similar propensities to prospect (Table 5.2, Figure 5.1). We observed only 36% of radio-collared predispersed offspring engaging in prospecting behavior. However, this number should be considered an estimate of the *minimum* percentage of individuals that prospected. We did not attempt to contact or follow each predispersing individual every day. We also typically only attempted to contact groups and individuals

between dawn and dusk, and were thus unable to detect any instances of prospecting that occurred during the night. Azara's owl monkeys are cathemeral and have substantial amounts of activity during the nighttime, particularly during the full moon phase of the lunar cycle [Fernandez-Duque and Erkert, 2006]. Therefore, it is extremely likely that observers were not present during all instances of prospecting. We also have very limited data on *where* individuals who prospected went during prospecting expeditions. On multiple occasions, we observed predispersed offspring embarking on prospecting expeditions at dusk, but were unable to follow these individuals after the sun set (e.g., Case studies 2 and 4). Without detailed data on ranging behavior during prospecting events, we can only speculate about how far away from their natal home ranges individuals may travel and what kind of information about the availability of mates and/or resources they might obtain during prospecting.

Knowing the areas in which individuals spent time during all prospecting expeditions would allow us to evaluate potential functions of prospecting behavior in owl monkeys. For example, researchers were able to gain insight into how flying squirrels (*Pteromys volans*) utilize comparative decision rules during short-distance dispersal, by quantifying how frequently the squirrels revisited sites in which they previously prospected [Selonen and Hanski, 2010]. Methods that would allow us to track predispersed offspring at all times, such as fitting individuals with GPS-equipped collars, would enable us to carry out a much more thorough assessment of prospecting behavior and improve our understanding of how prospecting relates to dispersal decisions and outcomes.

While our data on prospecting behaviors are limited, we can draw a few tentative conclusions from the patterns we observed. We never witnessed any prospecting individual

engage in mating behavior with any other solitary or non-natal group member. Combined with genetic data, which revealed no cases of extrapair paternity among the 35 infants sampled [Huck et al., 2014], we can rule out the possibility that predispersed individuals frequently prospect to engage in extra-group breeding, as individuals do in some other taxa [Eikenaar et al., 2008; Griffin et al., 2003; Young et al., 2007]. However, we frequently observed prospecting individuals either making hooting vocalizations or moving in the direction of hoots being made by an unseen individual of the opposite sex (Case studies 2, 3, 4, 7). Hoot calls are one of the few sexually dimorphic characteristics displayed by owl monkeys and are hypothesized to serve an important role in mate attraction [Depeine et al., 2008]. The occurrence of hoots during prospecting suggests that one function of prospecting may be to provide predispersed individuals the opportunity to assess the local availability of potential mates.

Individuals did not begin prospecting until they were old enough to disperse (> 20 months old). This implies that prospecting is related, at least in some way, to dispersal. Individuals of some taxa, like meerkats (*Suricata suricatta*), are more likely to prospect when they are older and have stronger body condition [Mares et al., 2014]. This may be because prospecting is costly; in some taxa it can decrease body mass and negatively affect endocrine state [Young et al., 2005; Young and Monfort, 2009]. The timing of prospecting events may also vary with season and other ecological factors, like food availability [Mares et al., 2014]. Since our observations of prospecting were opportunistic and our observation efforts varied with season, we are unable to assess correlations between prospecting and ecological conditions in our dataset. Tracking individuals with GPS-collars could supply data on

correlations between these factors and prospecting, providing insight into how ecological and social factors influence prospecting and dispersal decisions.

Individuals sometimes began to prospect long before they dispersed. On average, we observed the first evidence of prospecting almost one year before an individual permanently left their natal group (Table 5.2). This indicates that while individuals may begin prospecting once they reach the minimum age of dispersal, few actually disperse around the time these prospecting forays commence. This makes sense if individuals are utilizing prospecting expeditions to gather information about local ecological and/or social conditions. If favorable conditions are not encountered, we expect individuals to return to their natal groups and remain there until subsequent prospecting events reveal improved conditions or mating opportunities. Even though we observed the majority of individuals prospecting only once, as discussed in the paragraphs above, the events that we observed represent the bare minimum frequency of prospecting. We observed ten individuals prospecting multiple times and three of these individuals prospected eight or more times (Table 5.2). Our data are thus consistent with the supposition that some predispersed owl monkey offspring may prospect repeatedly, and disperse opportunistically, when prospecting reveals a potential mating opportunity or conditions relatively favorable for ranging solitarily.

Overall, our data do not suggest strong sex differences in dispersal strategies or distances. The amount of time that we observed males and females ranging solitarily after dispersing was similar (Figure 5.2). Males and females also had relatively similar likelihoods of pairing in a non-natal group in our study area and spent similar amounts of time in their new groups after pairing (Table 5.1, Figure 5.3). When we exclude the one individual, Betty, that appeared to pair with an adult outside of our regularly monitored study area, only three

females, compared to six males, paired in a group *within* our study area. We avoid drawing conclusions about the mean dispersal distance of male and female owl monkeys in general based on our small sample, but it is possible that males may have somewhat shorter mean dispersal distances than females. On the other hand, ranging patterns of solitary dispersed individuals seem to be similar for both sexes [Fernandez-Duque, 2009; Huck and Fernandez-Duque, in press]. Genetic data from males and females in our population could be used to test this hypothesis in future studies. If verified, a sex-difference in mean dispersal distance could be a mechanism that allows related individuals dispersing from the same group (e.g., siblings and half-siblings) to avoid inbreeding [Kappeler et al., 2002; Wimmer et al., 2002].

Our data suggest that other mechanisms for inbreeding avoidance are likely operating in our population. Whether or not males disperse further than females *on average*, our observations provide evidence that both sexes may, at least on occasion, disperse to groups that share a border with their natal group. Even in our small sample of ten individuals, a male and female sibling both dispersed to the same neighboring group within a year of one another (Diosa and Dionisio, Case study 6). Rapid turn-over in the adults of this group prevented these siblings from having an opportunity to risk inbreeding. Additionally, the only time that we observed two siblings interacting after dispersal (Dixi and Discoteca, Case study 5), they did not engage in any sexual behaviors (e.g., genital inspections, copulations, etc.) with one another. In fact, we have never seen closely related individuals from the same natal group pair with one another in a residential group or behave in a way that suggests they perceive each other as potential mates. This suggests that owl monkeys may have mechanisms that allow them to recognize kin or familiar individuals from their natal group if they encounter them again after dispersal. The basis of these mechanisms may be olfactory, as family groups

of captive owl monkeys have been found to have distinct scent profiles unique from other families [Macdonald et al., 2008]. Additional research utilizing genetic and scent-gland data could provide insight into the mechanisms that prevent dispersing owl monkeys from pairing with close relatives.

Dispersed solitaries sometimes sought out social contact with other floaters or members of non-natal social groups (Cases 2, 3, 5, 7). Our observations indicate that while some social interactions may be related to finding a potential mate (e.g., Evaristo, Case 3), at other times floaters engaged in affiliative social interactions with individuals who were juveniles (Betty, Case 2) or relatives (Dixi and Discoteca, Case 5), and thus could not be potential mates. In great tits (*Parus major*), solitary floaters that were siblings associated more frequently than expected by chance [Grabowska-Zhang et al., 2016]. We only once observed siblings associating with one another as floaters, but taken together our case studies suggest that “solitary” floaters may actually engage in social behaviors more frequently than we have previously recognized. Dispersed individuals sought out social contact, even though they sometimes received aggression during these social interactions (Cases 2, 3). Evidence from ranging patterns of floaters indicates that they typically attempt to maintain relatively close proximity to groups while avoiding their core home ranges [Huck and Fernandez-Duque, in press]. This may allow individuals to opportunistically interact with individuals in groups that may be less likely to act aggressively towards them (e.g., juveniles or members of the opposite sex), while avoiding or being able to escape from resident adults that act aggressively towards them. Our data do not allow us to assess the reasons why solitaries may sometimes seek out social contact with individuals other than potential mates. Tracking multiple floaters and social groups at the same time would allow us to determine how

frequently dispersing individuals engage in social interactions during the otherwise “solitary” transient stage, and assess the costs and benefits associated with these social interactions.

We never observed a dispersing individual permanently pair with another solitary individual. While floaters sometimes formed temporary associations with other solitaires that lasted less than one day (Cases 2, 3, 5, 7), the only way in which dispersing individuals successfully mated and reproduced was by replacing a same-sex adult and pairing with a mate who was already part of a group with an established home range. Our observations are consistent with previous studies suggesting that floaters constitute intense mating competition for resident adults [Fernandez-Duque and Huck, 2013]. Monitoring the floater population more closely could supply valuable information on the local operational sex-ratio, and provide insight into competition in owl monkeys and other monogamous taxa [Fernandez-Duque and Huck, 2013; Huck and Fernandez-Duque, in press].

Predispersed owl monkeys do not reproduce and typically do not engage in any sexual behaviors while in their natal groups [Chapters 2, 3, 4; Fernandez-Duque, 2009]. We observed two exceptions in which individuals interacted sexually with a resident adult in their natal group (Cordelia and Enrique, Cases 4 and 7). In the case of Enrique, who we observed copulating with his step-mother after he returned to his natal group, there were immediate severe negative consequences (i.e., his father violently expelled him from the group). We did not observe Cordelia experiencing aggression immediately after copulating multiple times with the new male in her natal group. However, she did ultimately die prior to dispersing from her group’s home range. In fact, both Cordelia and Enrique died before reproducing, which suggests that attempting to mate with an adult in the natal group is a rare strategy that is generally unsuccessful.



Our data make it clear that owl monkeys can follow a variety of different strategies throughout the dispersal process. The opportunistic nature of our observations limits our ability to draw firm conclusions about the frequency of different dispersal strategies. However, we can infer that substantial variation exists and that individuals seem to respond flexibly to the specific set of conditions with which they are presented. Individuals may prospect once or many times prior to permanently dispersing. They may leave voluntarily or be forced to leave after experiencing severe aggression from adult(s) in their natal group. Sex differences in dispersal are not prominent and it seems likely that factors other than sex, such as individual body condition and/or the local social and ecological environment, influence aspects of all stages of dispersal.

The complete process of dispersal entails a lot more than just leaving one group for another [Bonte et al., 2012; Clobert et al., 2009; Ronce, 2007; Travis et al., 2012]. Very few owl monkeys transfer directly to a new group; most spend time as solitary floaters. Floaters may interact with other solitaries or members of non-natal social groups. They may end up as the resident adult in a social group bordering their own natal group or they may leave the study area altogether. Many questions remain about the factors underlying the variation in dispersal that we observed. Nonetheless, our descriptions of pre-dispersal and dispersal behaviors provide insight into the variety of different strategies available to owl monkeys. They also provide a basis for generating hypotheses that can be tested in future studies to increase our understanding of dispersal in owl monkeys and socially monogamous taxa in general.

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## Chapter 6. Summary and Conclusions

This dissertation has explored natal dispersal in socially monogamous Azara's owl monkeys (*Aotus azarae*) in the Argentinean Gran Chaco. After summarizing the theoretical frameworks that researchers have utilized to study and understand dispersal patterns, each subsequent chapter described an investigation into one or more aspects of natal dispersal. Together, these investigations provide insight into both proximate and ultimate causes for dispersal, and allow for the development of a multifaceted understanding dispersal patterns in this socially monogamous primate species.

Chapter two examined dispersal at the level of the community by exploring how demographic changes and environmental variables are associated with dispersal patterns. In this chapter, I investigated the social and ecological factors associated with the age and timing of natal dispersal in owl monkeys. Specifically, I examined how proximate factors, such as adult replacements, births, group size, and rainfall (as a proxy of resource abundance), explained variation in the age and timing of dispersal. The timing of owl monkey dispersal was highly flexible, but all individuals dispersed prior to reproducing. Both demographic changes and ecological factors explained variation in dispersal to some extent. Experiencing an adult replacement, and especially the replacement of a same sex adult, was associated with subadult dispersal. In general, dispersals were concentrated in the spring and early summer. However, individuals were more likely to disperse outside of this preferred season if there had been a recent infant birth in their natal group and if there was less than average rainfall, and thus increased resource scarcity, during the fall/winter season.

The results from Chapter two implicate both resource competition and inbreeding avoidance as forces influencing dispersal under different circumstances. Additionally, the variation in timing of dispersal suggests that delaying dispersal may be an adaptive strategy that owl monkeys utilize to minimize dispersal costs and maintain access to benefits provided by the natal group. These findings differed somewhat when we included individuals who disappeared from the natal group, but were not confirmed to disperse, in analyses. This finding suggests that disappearances of dispersal-aged individuals should not necessarily be assumed to be the result of dispersal, and results from analyses that include data on disappeared individuals should be interpreted with caution.

Chapter three narrowed the focus to the level of the group, and investigated how behavior, particularly agonism, among group members may function to regulate dispersal. High rates of agonism are not expected to occur amongst close relatives or individuals in established mating relationships, which are characteristics of monogamous groups. Using 14 years of owl monkey behavioral data, I examined factors related to age, sex, kinship, and behavioral context to evaluate predictions of the hypotheses that agonism functions to regulate dispersal and that it mediates competition for food and/or mates. As expected, intragroup agonism was relatively rare and rates of agonism were generally similar for both sexes. However, there were marked differences among age categories. Agonism was most frequently performed by adults and directed at offspring, particularly subadults. In contrast, agonistic interactions involving infants were very rare. Agonistic events were most frequent during foraging, but also regularly occurred during non-foraging contexts, particularly during bouts of social behavior. Finally, subadults also received more agonism in the six-month

period immediately preceding dispersal, further suggesting that agonistic interactions are a mechanism regulating natal dispersal.

Results from Chapter three suggest that, in owl monkeys, agonism appears to serve as an important mechanism for regulating dispersal, but it also serves other functions. Specifically, agonistic behaviors are also utilized in conflicts over food resources and may play a role in mediating mating competition amongst adults and subadults.

Chapter four narrowed the focus even further, to the level of the individual. This chapter examined hormonal correlates of development and dispersal in juvenile and subadult females to evaluate potential proximate mechanisms regulating reproductive suppression in owl monkeys. Since owl monkeys are not cooperative breeders, neither inclusive fitness benefits nor inbreeding avoidance hypotheses can adequately explain their lack of reproduction prior to leaving the natal group. In this chapter, I analyzed hormonal extracts from fecal samples in juvenile and subadult females to determine whether wild Azara's owl monkeys typically establish reproductive maturity prior to dispersing. Subadult females showed hormone profiles indicative of ovulatory cycling and had mean reproductive hormone concentrations much higher than juveniles.

The results from Chapter four indicate that reproductive suppression in female owl monkeys is not due to endocrine suppression. Contrary to the inbreeding avoidance hypothesis, female owl monkeys do *not* delay puberty while in their natal groups. However, subadults appear to have a period during which they experience irregular, non-conceptive ovarian cycles prior to reproducing. Commencing these irregular cycles in the natal group may allow them to develop a state of suspended readiness, which could be essential to securing a mate, while avoiding the costs of ranging solitary. It is likely that adults use



behavioral mechanisms to prevent subadults from reproducing with unrelated adult males in their natal group.

Finally, Chapter five kept the focus on the individual level by following individuals through the entire dispersal process, and describing what we have learned about the ultimate fates of dispersers. The complete process of dispersal entails a transient phase of movement, while individuals search for a new place to live, followed by settlement in a new area. In this chapter, I reviewed data on the *outcomes* of dispersal decisions (e.g., the mortality and ultimate fates of dispersing individuals). We observed 36% of identified predispersed offspring prospecting at least once, and 88% of dispersed individuals ranging solitarily at least once. Case studies of dispersing individuals, based on *ad libitum* observations, suggest that dispersal is an extremely varied process in owl monkeys. Both males and females follow a variety of strategies that may involve prospecting and/or forming temporary associations with individuals outside of their natal groups before ultimately disappearing from the study area or finding a breeding position. Results from Chapter five highlight the high degree of variation among individuals within a single community and emphasize the need to consider all stages of the dispersal process to develop a more complete understanding of dispersal.

Each of the preceding chapters took a different approach to studying dispersal. While each approach informs our understanding of dispersal in its own way, this dissertation has demonstrated that combining multiple types of data is necessary for developing a deeper understanding of owl monkey dispersal. For example, information about behavior, specifically the general absence of sexual behaviors between adults and predispersed subadults, is essential for interpreting findings from hormonal analyses. Similarly, information about the timing of sexual maturity, which was provided by hormonal data, is

essential for evaluating findings related to agonistic behavior and the potential effects of demographic changes, such as adult replacements, on dispersal.

Nonetheless, developing a complete understanding of owl monkey dispersal still requires additional research. Investigations into prospecting behavior and the solitary itinerant stage of dispersal would be particularly useful, as these remain relatively poorly understood aspects of this process. Individuals who can use information about their local environments to inform dispersal decisions should be favored by natural selection [Bowler and Benton, 2005; Clobert et al., 2009]. Chapter five demonstrated that owl monkey offspring often engage in prospecting behavior, but the type of information that individuals gather during prospecting expeditions and the way this information influences when and to where they disperse requires further examination. Tracking the prospecting movements of predispersed individuals and comparing them to post-dispersal ranging patterns could increase our understanding of the means by which dispersing individuals utilize information from their environment to make dispersal decisions [Selonen and Hanski, 2010].

All data presented in this dissertation were collected at a long-term field site of the Owl Monkey Project (OMP) in the Gran Chaco region of Formosa Province, Argentina. Continuous monitoring of wild primate populations can provide indispensable information on the behavior of a species that is impossible to get from short-term studies or captive research [Kappeler and Watts, 2012]. However, focusing in depth on one population typically requires sacrificing breadth. While long-term studies of a single site can reveal temporal variation in dispersal and other behaviors, these studies do not reveal variation that may exist across populations [Strier, 2017]. Examining owl monkey populations at other locations would therefore provide valuable insight into how aspects of the social and ecological environment

are associated with dispersal patterns and pre-dispersal behaviors. For example, at the OMP site, evidence suggests that the habitat is more or less “saturated” and competition for reproductive positions is likely high [Fernandez-Duque and Huck, 2013]. There is empirical evidence from a variety of taxa which indicates that dispersal decisions may depend on population density [Matthysen, 2005; Nowicki and Vrabec, 2011; Poethke et al., 2016], and density may also affect aggression [Knell, 2009]. Examining dispersal at additional sites, where population density and other factors differ from those at the OMP’s site, would thus provide insight into the degree of inter-population variation in dispersal behavior, and contribute to our general understanding of spatial variation in dispersal patterns.

In conclusion, this dissertation has investigated dispersal at population, group, and individual levels. The holistic approach to understanding dispersal taken in this project is one that could be useful for increasing our understanding of dispersal in many other taxa. This approach allowed me to develop a multifaceted exploration owl monkey dispersal, which provides insight into the role of various proximate mechanisms as well as evolutionary explanations for dispersal patterns. The data presented in this dissertation can also be utilized to refine hypotheses and stimulate additional empirical research, which is needed to provide a better understanding of dispersal in primates and other organisms.

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