TITLE

The evolution of pair-living, sexual monogamy, and cooperative infant care: Insights from research on wild owl monkeys, titis, sakis, and tamarins

SHORT RUNNING TITLE

Evolution of pair-living, monogamy, and infant care

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If it rained, then he would go to the movies
He went to the movies
Therefore, it rained.

If there were a high risk of infanticide, then they would be monogamous
They are monogamous
Therefore, there was a high risk of infanticide.

If there were a high risk of infant alien-abduction, then they would be monogamous
They are monogamous
Therefore, there was a high risk of infant alien-abduction.

And so begin many evolutionary explanations – the explanation of how the risk of infanticide as a reproductive strategy of males leads to "social monogamy", or the one that says that owl monkeys in Argentina evolved to be cathemeral because it was unusually cold in the Argentinean Chaco. Both explanations begin with a common fallacy, the fallacy of *affirming the consequent* (McCloskey & Ziliak, 2008).

In the conditional logic statements above, if the antecedent (the clause after the "if") is true, then, formally, so must be the consequent (the clause after the "then"). But it is clearly false to presume that if the consequent is true, then so must be the antecedent; yet, too many explanations in evolutionary biology rely on such inferential sleight-of-hand. There are many reasons why a person might go to the movies, and many reasons why certain taxa may have evolved to be monogamous or why owl monkeys in the Argentinean Chaco may be cathemeral. The risk of infanticide *might* be important, and temperature *might* play a role, but these possibilities need to be evaluated against, and along with, other factors that may yield the same outcome. Because much of what gets published implicitly begins with the fallacy of affirming the consequent, it is sometimes difficult to assess the robustness of the conclusions reached. It does not help that, too frequently, the "Methods" section – the single most defining component of our writing that sets apart a scientific piece of work from a blog – is relegated to the category of "Supplementary Material" in academic publications, as if those details were an afterthought and not an essential part of scientific work.

In the following pages, we explore a question that has driven our collective research interests for almost 30 years: why are some species of primates "monogamous"? It is not our goal to settle on an answer; we have known all along that we will never get "the" answer. Rather, we aim to examine the existing ideas, methods, and data that can help us reduce the uncertainty around causal inferences made to explain why and where we find "monogamy" in primates. We hope our work will encourage the biological anthropology community to consider steps we can all take so that our explanations are written following the highest possible standards of scientific rigor.

INTRODUCTION

"Monogamy": An Ambiguous Concept

"Monogamy" has been of interest for anthropological and primatological theory and research for many decades. Yet, terms like "monogamy" and "social monogamy" have been used by some authors to refer to a particular social organization, by others to describe a particular mating system, and by still others to evoke a vague construct that combines aspects of grouping patterns, sexual behavior, social relationships, and patterns of infant care. We have recently argued that such unclear, fuzzy terminology has led researchers to sometimes compare "apples with oranges" (Maren Huck, Di Fiore, & Fernandez-Duque, 2019). Below, we begin by clearly communicating the terminology we use, and, throughout the remainder of the manuscript, we use these particular terms and eschew the fuzzy terminology as much as possible.

Here, building on the contributions of others (e.g., Díaz-Muñoz & Bales, 2016; Jeffrey A. French, Cavanaugh, Mustoe, Carp, & Womack, 2018; P.M. Kappeler & van Schaik, 2002; U. Reichard, 2017; Tecot, Singletary, & Eadie, 2016), we suggest the use of the following terms and definitions (Figure 1), which we have developed more fully elsewhere (Maren Huck et al., 2019).

[INSERT FIGURE 1 ABOUT HERE]

We use **'pair-living'**, a type of social organization (i.e., "who lives with whom" sensu P.M. Kappeler & van Schaik, 2002), to refer to a male and a female living together within a common home range (possibly with their non-reproductive infants) and associating either continuously or intermittently.

We use '**pair bonded'** to refer to a male and a female manifesting an emotional attachment to one another, to the exclusion of other adults, as evidenced by their affiliative interactions, maintenance of spatial proximity, physiological distress upon separation from the pair-mate, and reduced anxiety following reunion with the pair-mate.

We use **'sexual monogamy'**, a type of social mating system (i.e., "who mates with whom"), to refer to an exclusive mating relationship between a female and a male during at least one reproductive season. We use **'genetic monogamy'**, a type of genetic mating system ("who has offspring with whom"), to refer to when a female and a male reproduce exclusively with one another over a set of multiple births, i.e. over at least one reproductive season for species that produce two or more infants per litter and over more than one consecutive reproductive season for species with singleton births.

We use '**biparental care**', a type of care system, to refer to both members of a putative sire-dam pair regularly performing behaviors with presumed positive effects on infant development, growth, well-being, or survival. Finally, we use '**cooperative infant care**' when other individuals, in addition to one or both of the putative parents, regularly perform behaviors with presumed positive effects on infant development, growth, well-being, or survival.

For consistency, in the remainder of the text, we write "monogamy" and "social monogamy" in quotation marks when referring to published literature that uses either of these terms, but where it is unclear if the authors are referring to a type of social organization or a type of mating system.

“Monogamy” and pair-bonding in humans

Regardless of the social, marriage, or mating system, the residential pair-bond is a ubiquitous feature of human mating relationships (Chapais, 2011, 2013; Lieberwirth & Wang, 2014) and is argued to be an integral component of human social behavior (Fletcher, Simpson, Campbell, & Overall, 2015; Schacht & Kramer, 2018). Despite extensive variation in marriage practices and sexual behavior across cultures, humans seem to consistently form special pairwise relationships, most often between opposite-sex individuals, based on persistent emotional attachments (Jankowiak & Fischer, 1992; Robert J. Quinlan, 2008; R. J. Quinlan & Quinlan, 2007; Strassman, 2003).

When and how pair-bonding evolved in the human lineage remains a controversial topic. The emergence of “monogamy” in humans has been proposed to extend back to some of the earliest hominins (Ardipithecus ramidus, Australopithecus afarensis, Lovejoy, 2009; P.L. Reno, McCollum, & Meindl, 2010; Philip L. Reno, Meindl, McCollum, & Lovejoy, 2003). The extent of sexual dimorphism in these hominins has been argued to suggest an early switch from polygyny or promiscuity to pair-bonded couples within groups in the human lineage (Gavrilets, 2012). Others, however, contend that the degree of dimorphism seen in these australopithecines is indicative of a male strategy of monopolizing groups of females (Adam, David, & Brian, 2008; Lockwood, Menter, J., & Keyser, 2007), with pair-bonding only evolving at a later stage. There is little direct evidence suggesting that a nuclear family of two adults was important in structuring early human societies; on the other hand, there is some consensus that pair-bonding may have been a fundamental adaptation of early hominins (Schacht & Kramer, 2018). Today, human societies are most often described as a multilevel structure in which long-lasting monogamous family unions form the smallest units (Rooker & Gavrilets, 2016).

An extensive literature has focused on the study of human pair-bonding, mating, marriage, and love. Approaches have ranged from cross-cultural studies of human behavior (R. J. Quinlan & Quinlan, 2007), to mathematical models of behavior (Gavrilets, 2012; Schacht & Bell, 2016), to sociobiological and psychological attempts to find an adaptive value for currently observed patterns (Borgerhoff Mulder, 2009; Fletcher et al., 2015; Robert J. Quinlan, 2008; Schacht & Bell, 2016). There are several recent reviews on the topic that offer a comprehensive point of entry to this literature (Carter & Perkeybile, 2018; Jeffrey A. French et al., 2018; Rooker & Gavrilets, 2016; Schacht, Davis, & Kramer, 2018; Schacht & Kramer, 2018). Thus, we will set aside the literature on humans, and instead focus our attention on the contributions that the investigation of non-human primates has made to our knowledge of the evolution, behavioral correlates, and biological underpinnings of pair-living, pair-bonding, sexual monogamy, genetic monogamy, biparental care, and cooperative infant care.

A focus on non-human primates allows us to explore the evolutionary basis of these phenomena more-or-less free from the cultural trappings that are associated with studies of human societies. The potential of this approach is made clear with examples from some non-human primates that show similar physiological responses to those observed in human pair-bonding behavior. For example, researchers have found that close contact in the form of frequent hugs between partners and spouses (defined as couples cohabiting for at least one year) was associated with lower blood pressure and higher levels of oxytocin (Grewen, Girdler, Amico, & Light, 2005; Light, Grewen, & Amico, 2005), similar to what has been described for tamarins where mutual contact and grooming explain most of the changes in levels of urinary oxytocin (Snowdon et al., 2010). The study of pair-living, pair-bonding, sexual monogamy, and genetic monogamy in extant primates continues to be an exciting research endeavor that contributes to our knowledge of evolutionary biology and human evolution. In fact, decades after the publication of several early and influential considerations of human "monogamy" and pair-bonding in an evolutionary framework (Alexander & Noonan, 1979; Kleiman, 1979; Lancaster & Lancaster, 1983), biological anthropologists and evolutionary biologists continue to search for satisfying explanations for the "paradox of monogamy" (Carter & Perkeybile, 2018). While, historically, few people questioned why females should mate only with a single partner, it was seen as paradoxically that males should restrict their mating to a single partner (Klug, 2018). This was supposed to result from females being more restricted in their reproductive success by access to resources like food and nesting sites, while males were seen to be restricted primarily by access to females (Bateman, 1948; Timothy H. Clutton-Brock, 2007; Trivers, 1972).

HISTORICAL AND RECENT THEORETICAL PERSPECTIVES ON "MONOGAMY" IN PRIMATES

The Main Hypotheses

Early hypotheses explaining the evolution and maintenance of "monogamy", which usually did not explicitly distinguish between pair-living, sexual monogamy, and genetic monogamy, tended to fall into one of two classes. Some suggested that "monogamy" was a default social system imposed upon males when either the spatial, or temporal, distribution of females made it difficult for single males to simultaneously defend access to more than one mate (Emlen & Oring, 1977; Gowaty, 1996; Rutberg, 1983; C. P. van Schaik & van Hooff, 1983). Other models proposed that it evolved in response to the need for obligate biparental care in order to successfully rear offspring (Kleiman, 1977; Wittenberger & Tilson, 1980; Woodroffe & Vincent, 1994). In both classes, the various elements of the "monogamy" behavioral repertoire – pair-living, mating exclusivity, and biparental care – were often conflated and presumed (Gowaty, 1996). For example, it was assumed that mating exclusivity was either an outcome or necessary correlate of pair-living. More recently, the focus has appropriately shifted to interpreting "monogamous" social systems and their behavioral correlates as the emergent result of a trade-off between male and female reproductive strategies (Hosken, Stockley, Tregenza, & Wedell, 2009). As Klug (Figure 1, 2018) nicely summarizes it: "It's complicated!"

Predation risk, infanticide risk, the cost of infant care, the distribution of resources, the spatial distribution of females, intrasexual intolerance, and female breeding seasonality are specific drivers considered in different hypotheses about the evolution of various components of the "monogamy" repertoire, including pair-living, sexual monogamy, genetic monogamy, and pair-bonding (Klug, 2018). Associated with these potential drivers are about seven hypotheses, although different authors combine or split these in different ways. We briefly review these hypotheses, and refer readers to previous work for more detail (e.g., Brotherton & Komers, 2003; Fuentes, 1998; U. H. Reichard, 2003a; Tecot et al., 2016). The seven hypotheses are [1] the **infant care hypothesis**, [2] the **predation prevention hypothesis**, [3] the **infanticide prevention hypothesis**, [4] the **mate-guarding hypothesis**, [5] the **female distribution hypothesis**, [6] the **resource defense hypothesis**, and [7] the **optimal group size hypothesis**. The last two of these hypotheses are developed from the same reasoning about potential drivers.

Before outlining these hypotheses in more detail, it is important to emphasize several points. First, these hypotheses are not necessarily mutually exclusive and some of them relate more to the current adaptive value of the feature of "monogamy" being explained, while others to their evolutionary origins. Second, some of them are more relevant for explaining pair-living, while others are more appropriate as explanations for sexual monogamy, for genetic monogamy, or for pair-bonding. Third, it is quite unlikely that the same hypothesis, or hypotheses, can be applied to all taxa considered to be "monogamous". Finally, a number of these hypotheses are "ultimate" explanations for the phenomenon, in the sense of Niko Tinbergen's four questions (Burkhardt, 2014; Taborsky, 2014; Tinbergen, 1963), while others can be viewed as "proximate" explanations that underpin ultimate hypotheses. Particularly, resource distribution, which is rarely measured or quantified, is presumed to be linked to female distribution, which in turn (along with predation and infanticide risk) underpins the relative benefits of mate-guarding, other types of mating effort, and optimal group size.

[1] Infant Care Hypothesis

This hypothesis states that because infant care is so costly for particular taxa, help from individuals other than the mother is required to successfully rear offspring, which increases the benefit to a male of remaining to care for the offspring of a partner rather than seeking further matings (Wittenberger & Tilson, 1980). Several studies have found a relationship between the need for male contribution to infant care and pair-living, sexual monogamy, or genetic monogamy (Arnold & Owens, 2002; M. Huck, Fernandez-Duque, Babb, & Schurr, 2014; Lambert, Sabol, & Solomon, 2018; Ribble, 2003). However, as traditionally stated, the hypothesis presents an inherent "hen-egg problem" with regards to the direction of causality. Thus, more recently, arguments have shifted from the view that the need for male care *leads* to a certain evolutionary trajectory to the view that once either pair-living or a trend to sexual or genetic monogamy has been established, male infant-care can *follow* (Dunbar, 1995; Komers & Brotherton, 1997; Lukas & Clutton-Brock, 2013; Opie, Atkinson, Dunbar, & Shultz, 2013). Then, once male care of infants has evolved, it stabilizes pair-living and sexual or genetic monogamy, leading to a positive feedback-loop (Kvarnemo, 2006; Stockley & Hobson, 2016).

The hypothesis assumes that, for some taxa, females are not capable of raising offspring on their own and that male care substantially improves an infant's fitness. If the need for care is a driver towards pair-living or sexual monogamy, then across a phylogenetic tree, costly offspring should appear evolutionarily before either of these traits arise. Alternatively, if one assumes that the need for care is merely a contributing or stabilizing factor to pair-living or sexual monogamy, then it is predicted that transitions from these conditions to other states should be rarer if associated with care than in the absence of care. Additionally, for pair-living species, extra-pair paternity rates are predicted to be lower in species where males contribute heavily to infant care in comparison to species where males are less involved. In some taxa with cooperative infant care, such as the callitrichines, this hypothesis seems less applicable. Males and other group members, whether related to the infant or not, provide substantial care; this occurs even when the modal mating system is not strictly monogamy and their social organization is group-living (Paul A. Garber, Porter, Spross, & Di Fiore, 2016).

[2] Female Distribution Hypothesis

This hypothesis states that when females do not aggregate and associate with one another, and their resulting ranges are either large or dispersed, it is not possible for a single male to defend access to the home ranges of more than one female. Under such a scenario, a male's home range is expected to map onto that of a single female, which leads to pair-living, either in associated or dispersed pairs (sensu C. P. van Schaik & Kappeler, 2003), and to sexual monogamy.

The key assumption of this hypothesis is that females have large or dispersed ranges because the resources they rely on are either so scarce, so low in quality, or so highly dispersed that intrasexual competition precludes the formation of female groups. Under this hypothesis, it is predicted that pair-living, sexual and genetic monogamy will occur when male space use (e.g., home range sizes, daily path lengths) does not allow individual males to cover and defend access to more than one female home range. It is predicted that the overlap among female ranges should be very low. Given that the assumptions are of an ecological nature, it predicts that under more favorable ecological conditions (e.g., in resource-rich environments), group-living or deviations from sexual monogamy (e.g., polygynandry, polygyny or promiscuity) will occur.

[3] Infanticide Prevention Hypothesis

This hypothesis states that the presence of a male deters other males from attacking and killing vulnerable infants, with fitness benefits for the male, mother and young. Infant protection could be considered a form of male parental care, but the lines of argument, and possibly also the relevance to various aspects of potential infanticide, are slightly different. The hypothesis has received much attention in the literature (Lukas & Huchard, 2014; C. van Schaik & Janson, 2000). And it has been invoked as a possible explanation for the observation of higher rates of "monogamy" in primates than in other mammals, possibly to an extent that it has compromised critical consideration of alternative hypotheses (Bartlett, Sussman, & Cheverud, 1993; A. F. Dixson, 2013; Jolly et al., 2000; Sussman, Cheverud, & Bartlett, 1995).

The hypothesis assumes that the protective male is the most likely father of his female partner's infants, such that both the mother of the infant and the father have an increased net fitness as a result of his presence. Implicit is also the assumption that a female will become receptive and fertile again sooner than expected if she loses a dependent offspring, such that by practicing infanticide a male can influence how quickly he might sire future offspring with her (Blaffer Hrdy, 1974). Such is the case if lactational amenorrhea prevents a female from conceiving another offspring while her current one is nursing. Therefore, in comparative studies, some researchers have used, as a proxy for the risk of infanticide, the relative length of the age at weaning (sometimes referred to as the lactation period, L) to the combined length of gestation (G) + weaning age – i.e., $L/(G+L)$. Opie et al. (2013) refer to this proxy as the "weaning proportion" (p. 13330). This proxy is valid only under the assumption that the species under consideration does not have post-partum estrus, has a long breeding season or breeds aseasonally, or has a period of infant dependency that lasts longer than one year. If those conditions are not met, then females will not resume typical estrous cycling immediately upon losing an offspring. Borries (1997) provides further assumptions and predictions related to the sexually selected infanticide hypothesis as a male mating strategy.

[4] Predation Prevention Hypothesis

This hypothesis states that infant, or female survival, are increased by the presence of a protective male. There is relatively little explicit consideration in the literature of predation as a driver of "monogamy" (Dolotovskaya, Flores Amasifuén, Haas, Nummert, & Heymann, 2019); and is usually subsumed under discussions of the infant care hypothesis (e.g. S. Sommer, 2000; S Sommer, 2003). While the connection between protection, infant survival and fitness of parents is obvious and implies that predation risk can be a driver for the evolution of a pair-bond between mating partners, it is less clear why and how this should be related to either pair-living or sexual monogamy, particularly from the male's perspective. What are, for example, the circumstances leading one or more males to focus on protecting the infant of a single female, as opposed to those of several females?

The hypothesis assumes that males are more effective than females at deterring predators. However, unless this assumption that males are better at predator detection or deterrence than females is true, the hypothesis does not explain why opposite-sex pairs would be more advantageous than same-sex dyads. It might be argued that in sexually dimorphic species where males are larger than females, the former might be more effective at anti-predator defense by virtue of their larger size; still, the fact that sexual dimorphism is minimal in many pair-living species runs counter to the idea that predation protection is an important driver. For species with biparental care, it is predicted that in the presence of a threat from predators, males will contribute more to the defense of an infant, for example by approaching the infant first and transporting it as they flee.

[5] Mate-Guarding Hypothesis

This hypothesis states that the balance of general benefits between securing paternity and gaining additional matings is shifted in sexually monogamous males towards the former. A male gains higher fitness preventing other males from gaining access to a female he has already mated with or expects to mate with, than by seeking matings with additional partners. The hypothesis is also known as the 'mate defense hypothesis' (Tecot et al., 2016). Three main conditions can favor mate-guarding and monogyny from the male's perspective: a strongly male-biased adult sex ratio (ASR) or operational sex ratio (OSR) (Harts & Kokko, 2013; Kokko & Morrell, 2005), a high degree of breeding synchrony amongst females in local populations, and a high cost of searching for additional females. While the argument might equally be applied to females, it is usually discussed specifically with reference to males, and thus for this review we will do the same.

Under this hypothesis, in contrast to the next, it is predicted that males will not seek to mate with other females even when it may be possible for them to range over more than one female's range. It is also predicted that females will show reproductive synchronicity that will limit the reproductive opportunities for males outside the pair. With regards to sex-specific predictions, females and males will show more aggression towards same-sex than opposite-sex intruders, and it is expected that those differences will be more pronounced during the mating than during the birth season.

[6] Resource Defense Hypothesis

This hypothesis states that pair-living and defense of the same set of resources – either separately or jointly – will evolve when the resources needed to support survival and reproduction, are low in quality, rare, or highly dispersed so that a given area cannot support more than two adults and a small number of immatures. The hypothesis does not necessarily state that the situation will lead to sexual monogamy.

Unless there are reasons to assume that the two sexes differ in their needs and reliance on specific resources, the prediction is that the defense of resources will not be sex-specific and that the defense will be of similar form and strength against same-sex intruders than it will be against members of the opposite sex. It is also expected that defense related behaviors will vary with changes in resource availability, not with regards to the mating season as predicted in the mate-guarding hypothesis.

[7] Optimal Group Size Hypothesis

This hypothesis, very similar to the resource defense one, states that pair-living (though not necessarily genetic or sexual monogamy) is the optimum group size given the costs and benefits of aggregating with conspecifics. The hypothesis proposes that living in a small social group is optimal for adults in some environments, and pair-living species will almost necessarily have such small group sizes, since, by definition, only the adult pair and non-reproducing offspring are present. However, strictly speaking, an optimal group size of two adults could also be achieved with two adults of the same sex, a situation not considered in this hypothesis.

It is predicted that, for example, an increase in resource availability, or predation pressure, will increase the optimal group size and be associated with shifts from pair-living to living in social groups with more than one adult of one or both sexes. It is also predicted that there will be no link between the social organization of pair-living and the mating system of sexual monogamy.

THE EVOLUTION OF "SOCIAL MONOGAMY" IN PRIMATES: CONTRIBUTIONS OF BROAD-SCALE COMPARATIVE ANALYSES

> *"Field studies on primates have blossomed in the present century, but surprisingly few have been comparative in nature. Therefore, much of the analysis of potential species differences in ecology and behavior, or in physiology for that matter, must be pieced together from different reports" (p.33 Groves, 2014)*

We present in this section some reflections on the contributions, limitations and problems associated with a number of comparative analyses, some of them order or class-wide, that have considered several of the hypotheses mentioned above. Given our research interest on pair-living, sexual and genetic monogamy, and cooperative infant care, we focus our attention on a set of studies that relate to these topics published in high impact journals several years ago (Lukas & Clutton-Brock, 2014; Lukas & Clutton-Brock, 2013; Opie et al., 2013; Shultz, Opie, & Atkinson, 2011; West & Capellini, 2016). Below, we summarize the contributions of these studies to the current state of thinking about the origins and evolution of "monogamy", identify some concerns we have regarding the limitations and problems associated with class and order-wide analyses, and ponder whether the amount of primatological and biological anthropological research and literature that has crystalized around the proposition that infanticide risk drives pair-living and sexual or genetic monogamy in primates may be unwarranted in view of the existing evidence.

Recent Comparative Studies: Overview and Concerns

We begin by focusing on two large-scale, and ambitious analyses that explored, using comparative phylogenetic methods, the evolutionary history of "monogamy" across mammals and across primates, respectively (Lukas & Clutton-Brock, 2013; Opie et al., 2013). Using trait data compiled from the literature and from published databases, coupled with composite phylogenies, these studies sought to analyze the correlated evolution between "social monogamy" and some of the candidate drivers of its evolution discussed above. A third study examined the potential role of infanticide in the evolution of social organization and mating system in mammals, including the role that infanticide may have played in the evolution of pair-living in primates (Lukas & Clutton-Brock, 2014).

The two studies that examined the evolution of "monogamy" found some consensus with respect to the sequence of the evolution of the character state of "social monogamy" and the character state of “presence of paternal care”. Across both mammalian and primate phylogenetic trees, transitions to pair-living, and possibly also a trend to sexual monogamy, often preceded or co-occurred with, rather than followed, an increase in male involvement in infant care (Lukas & Clutton-Brock, 2013; Opie et al., 2013). This result is perhaps not surprising. Once intense male care has evolved, it is assumed that the likelihood of lower rates of extra-pair paternity increases, potentially leading to more strict genetic monogamy (M. Huck et al., 2014); this evolutionary sequence may then contribute to the persistence of sexual monogamy once it has arisen (Lukas & Clutton-Brock, 2013). Likewise, the quality of the relationship between the pair, whether pair mates are associated or dispersed, can also influence the rates of extra-pair paternity (Cohas & Allainé, 2009; M. Huck et al., 2014). However, the two studies reached different conclusions with regard to the ultimate causes of the evolution of “monogamy”. Lukas and Clutton-Brock (2013) concluded that “social monogamy” has evolved most commonly when females are solitary and, presumably, when males are then unable to defend reproductive access to more than one of them. They additionally concluded that the evolution of “monogamy” does not seem to be associated with a high risk of infanticide by males. By contrast, Opie and colleagues {, 2013 #5079} claimed that their results provide strong support for the hypothesis that “social monogamy”, at least among primates, evolved in response to increased infanticide risk; indeed, they codified that position in the title of their article: “Male infanticide leads to social monogamy in primates”. In their follow-up study directly focusing on the potential role of infanticide as a driver of mammalian social evolution, Lukas and Huchard (2014) reached a different conclusion, arguing that the distribution of infanticide in mammals is best explained by variation in male-male contest competition, and that infanticide has not promoted major switches in primate social systems.

These studies generated a set of reply letters and commentaries on the validity of the data used, analytical methods, findings, and interpretations (de Waal & Gavrilets, 2013; A. F. Dixson, 2013; Lukas & Clutton-Brock, 2014; Opie, Atkinson, Dunbar, & Shultz, 2014). A problem repeatedly pointed out was about classifications, i.e., how different research groups classified each taxon with regard to traits of interest (e.g., does a taxon have paternal care or not). This is an issue that we have considered thoroughly before (Maren Huck et al., 2019) and is one that has been extensively commented upon in reference to other comparative analyses of a wide range of animal taxa (e.g., Griesser & Suzuki, 2016; Patterson, Sandel, Miller, & Mitani, 2014; Sandel et al., 2016; Stokes & Sandel, 2019; Taborsky et al., 2019; Tanaka et al., 2018; Valomy, Hayes, & Schradin, 2015). In addition to the doubts raised by de Waal and Gavrilets (2013) and Lukas and Huchard (2014) regarding the potential role of infanticide as a driver of “social monogamy”, there had already been earlier ones raised by other researchers who have first-hand experience with pair-living primates (U. H. Reichard, 2003b) and other mammals (Brotherton & Komers, 2003). As field primatologists working with a suite of taxa that has been characterized as “socially monogamous” in these comparative analyses, we are of course intimately interested in the questions being explored and the claims being disputed. We are of the opinion that, given continued uncertainty about phylogenetic reconstructions, the observational nature of most primate field work (R. J. Smith, 2019), numerous problems of definitions, data quantity, and data quality, and the inherent complexity of biological systems, any attempt to attribute a single causal explanation to the evolution of “social monogamy” across primates is a fraught one. Indeed, we think it is premature to put much stock in the results of these comparative analyses, or to try to compare or weigh the merits of their different conclusions, before considering the analytical choices made and the quality of the datasets used. It is because of the doubts we have about the definitions, datasets, and interpretations that we urge caution in the use of these studies as building blocks for new research.

Terminology Matters, or We May Be Comparing "Apples with Oranges"

We are concerned about how the muddled terminology used when discussing "monogamy" has hindered our understanding of both a rare social organization ("pair-living") and a rare social mating system ("sexual monogamy"). Most researchers are aware that there are various definitions of "monogamy" used in the literature and that, depending on the taxa being studied, a veritable menu of different terms are considered as part of the definition. Still, the terms "pair-living", "pair-bonded", "social monogamy", "sexual monogamy", and "monogamy" are seldom properly distinguished and are often used interchangeably. We are also guilty ourselves of using this terminological shorthand in less than a consistent manner (e.g., Di Fiore, Fernandez-Duque, & Hurst, 2007; Eduardo Fernandez-Duque, 2016; Eduardo Fernandez-Duque, Juárez, & Di Fiore, 2008; Maren Huck et al., 2014). And we are definitely not the first to call attention to this situation and to recommend suggestions for improvement (Jeffrey A. French et al., 2018; P. M. Kappeler & Pozzi, 2019; Klug, 2018; Lambert et al., 2018; U. Reichard, 2017; Tecot et al., 2016).

The potential problems derived from unclear terminology are well illustrated by the classification of callitrichid primates as "monogamous" in some studies (Lukas & Clutton-Brock, 2013; West & Capellini, 2016), but not others (Opie et al., 2013). This occurs because some researchers only classify pair-living taxa as "socially monogamous", whereas others classify certain taxa as "socially monogamous" when there are several potentially reproducing adults, as long as there is substantial monopolization of reproduction by one male and one female. The consequence of using those two different definitions is that 38% (N = 28 of 74) of the "monogamous" primate taxa that were included in the three comparative studies considered above are classified differently across these studies (Supplementary Table 1). Comparing the results from the two different datasets is problematic, akin to "comparing apples and oranges" (A. F. Dixson, 2013; Maren Huck et al., 2019)! It is therefore positive that Lukas and Clutton-Brock conducted subsequent analyses of Opie et al's data classifying the species following the criteria used by the latter (Lukas & Clutton-Brock, 2014, 2015).

Reviewing "The Literature"

> *"In comparing data from various authors collected under varying conditions with differing standards of reliability one must be somewhat selective. Not all of the columns are filled, since the methods of individual workers over a span of 17 year cannot be made uniform in the here and now." (p.219 Eisenberg, 1979)*

Eisenberg's quote is a good reminder that the expectation that a comparative study must rely on a thorough, systematic search and consideration of the literature is not new. Twenty years after his work, Smith and Jungers (1997), while reviewing the literature on body mass in primatology, identified many problems associated with the publishing and use of those data and eloquently showed the problems of using secondary sources. Their detailed tracking of the data on body mass for *Ateles spp*. as reported by Harvey and Clutton-Brock (1985) and then repeatedly used by so many researchers should be required reading material for anyone planning a comparative study. The three main problems they found were that [1] estimated data were treated as real data, [2] data from earlier sources were incorrectly attributed to particular species (a thorny issue as taxonomies become updated), and [3] review articles inadequately and incompletely reflected the state of knowledge at the time they were produced. They concluded that "the body masses provided by Clutton-Brock and Harvey (1977), Harvey and Clutton-Brock (1985) and Harvey *et al.* (1987) should not be used" (p.532). More recently, Borries and colleagues (2013) – concerned about the differences they found between their own literature-based assessments of gestation length estimates for various Asian colobines and macaques and those published in four "popular" life history compilations – attempted to reproduce the analyses in those compilations without success. Some of the problems they found, as well as other issues related to the transparency, usability and reproducibility of comparative analyses are discussed in more detail in a recent publication (Borries et al., 2016).

We have some familiarity with the situations described above through our own research. In fact, a major motivation for the work presented here is the mixture of surprise and disappointment we experienced when realizing that the data used in several reviews for owl monkeys (*Aotus*), sakis (*Pithecia*), tamarins (*Saguinus* and *Leontocebus*), and titis (Callicebinae) fall short of the quality standards we would like to see followed in comparative studies. Sometimes the data included in the analyses are incorrect, meaning that the numbers reported in a cited review manuscript, or included in a comparative study, are not those found in the original article. Other times, the data used are, in our opinion, a poor choice out of the set of numbers reported in the primary source, or the primary source and accompanying methods do not warrant the use of the data.

On the specific topics of pair-living, sexual and genetic monogamy, and pair-bonding, the problems usually begin with the continued reliance – both for data and terminology – on seminal work of profound historical importance (Kleiman, 1977; Kleiman & Malcolm, 1981; Lack, 1968), but of decreasing empirical value as more information is gathered. For example, the opening statement in Opie et al. (p.13328, 2013) that "Social monogamy, or pair-living, is much more common among birds (90% of species) (Lack 1968) than mammals (less than 3% of species) (Kleiman 1977)" made in this exact or similar forms in so many introductions is, given the current state of knowledge, an incorrect foundation upon which to rationalize a study. Although it is still accurate today, to say that there are more pair-living bird taxa than mammal ones, adding quantification (e.g., "90%", "3%") requires careful consideration of definitions and five decades of published research since those estimates were produced.

We more fully document the scope of the problem in a section below, where we discuss our own data and compare them to data used in recent comparative studies; here, we briefly provide two illustrative examples. One of these recent comparative studies examined the possible relationship between pair-living (termed "social monogamy" in the study) and infanticide (Opie et al., 2013). Given that "[i]t may be that infanticide is affected by sampling effort, such that it is more likely to have been observed in well-studies species, and may have been missed in less well-studied ones." (p. 1330 Opie et al., 2013), the authors were concerned with accounting for this potential problem, and did so in several ways. One was to include in the analyses only species "that had at least 20 publications" (p. 1330 Opie et al., 2013). It is certainly a laudable idea to consider the need to assess the extent of knowledge available on a given taxon before deciding whether or not it should be included in a comparative study; still, the criterion used is arbitrary and of questionable validity (Lukas & Clutton-Brock, 2014). The database they searched (*Web of Science*) indexes only a subset of "the literature" (mainly English language journals), and in defining their criterion the authors did not consider the type of publication (e.g., abstract, peer-reviewed article), the length and type of study (e.g., ecological field study vs. captive husbandry), or the quality of data reported. In their Supplementary Table (Dataset S1), the authors provide data for two species of titis, *Callicebus donacophilus* and *C. moloch*, with 20 and 192 publications, respectively; they classify the former as "Data Deficient" and the latter as "Low Risk" with regards to "risk of infanticide". We conducted a search, using the same database, on October 10, 2013, two months after the article by Opie et al. (2013) was published. Our search produced only nine publications for *C. donacophilus*, including seven published abstracts in the *American Journal of Physical Anthropology*, and one chromosomal study. A similar search for *C. moloch* conducted on July 11, 2019 produced 58 publications, far fewer than the 192 reported. Only seven of these involved field observations, and four of them focused on titi species that are now considered to be from species *other* than *C. moloch*. Of the three remaining publications, two were reports on population surveys, and one reported a predation on an infant titi by *Sapajus apella*, the subjects of the study (Sampaio & Ferrari, 2005). All told, we found **no field studies** that actually focused on *C. moloch*, the large number of "publications" produced by searches notwithstanding! Thus, it seems unwarranted to consider this taxon as "well-studied" and premature to characterize it as having a "low risk of infanticide".

We provide another example from *Aotus*, a second genus on which we have worked extensively. While developing the rationale for their study, Opie et al (2013) state in their introductory paragraphs that "....the females of socially monogamous New World primates (callitrichids and *Aotus*) typically give birth to twins and cannot cope with infant carrying without the help of a male (Kleiman 1977)." (p.13328). But, this statement is both factually incorrect and wrongly referenced. While it is true that callitrichids regularly produce twins, owl monkeys do not typically give birth to twins. As summarized by Fernandez-Duque (2011), for captive individuals of *A. nancymaae* twinning occurred in only one of 169 births at the Primate Center of Iquitos, Peru, in one of 287 births at the Batelle Primate Facility and in three of 365 births in a colony of unknown karyotypes (Gibson et al., 2008). In the wild, twinning has been reported only once in *A. vociferans* (Aquino, Puertas, & Encarnación, 1990) and twice out of 223 births in *A. azarae* (Maren Huck et al., 2014). Secondly, callitrichines are not pair-living (Opie et al. equates "social monogamy" with pair-living), and their modal mating system is not sexual monogamy, as clearly noted by several researchers (Paul A. Garber et al., 2016; Eckahard W. Heymann, 2000; A. Savage, Giraldo, Soto, & Snowdon, 1996). In addition, the statement is wrongly referenced because in the publication that the authors cite to substantiate the claim, Kleiman (1977) writes: "the [*Aotus*] female bears only a single young at a time" (p. 51). These mistakes might be considered trivial, were it not for their frequency and the fact that the rationale of the study is built on them.

The ease of access to information on the web and the mushrooming of web-based databases are likely to exacerbate the problems we are describing. We show below that there is evidence that the use of secondary and tertiary sources of information, or of information from databases, whether they are peer-reviewed or not, will likely affect the quality of comparative studies. The two examples we presented above are from an article published in *Proceedings of the National Academy of Sciences*, one of the scientific publications presumed to be setting quality standards. Lukas and Clutton-Brock, who published one of the other comparative studies we discuss here in the journal *Science* (2013), have explained that they "removed around 75% of [their] 2000+ sources" to comply with the request by the editors to reduce the associated reference list (Lukas & Clutton-Brock, 2017). We are failing as reviewers and editors by not demanding more rigor in the citing of references and the use of published data.

Biological anthropology has grown as a scientific discipline through the development of new ideas and the scientific evaluation of them. Our discipline values, encourages and welcomes new ideas, but for those ideas to become part of the discipline's scientific research they ought to be supported by actual data collected through rigorous methods. If methods and quality of data were not the foundations on which scientific ideas grow, what would be the difference between science and science fiction?

Not All Data are Created Equal… and Sometimes Data Have Not Yet Been Created

> *"A comparative study can be no more reliable than the data on which it is based" (p. 529, Richard J. Smith & Jungers, 1997)*

We have argued above that using unclear terminology can lead to ambiguity in the data upon which an analysis rests, which in turn calls into question the results and validity of the analyses. This is particularly true for comparative analyses that use large datasets for phylogenetic studies or for meta-analyses, where data from studies by different authors are compared. A second important issue to consider is that the quantitative combination and comparison of individual studies requires serious consideration of the data to be used.

Comparative analyses must be done on comparable data. Although this may seem obvious, it is our impression that most comparative analyses do not present detailed consideration of how data are selected for inclusion. Given that the number of primate field studies continues to increase, the aim of including all available and relevant data in a comprehensive analysis – which is already a challenging task – is likely to become even more challenging. Moreover, huge variation exists across primate field studies in their duration, the expertise of research team, and the methods used, among other factors, all of which will directly influence the quality of the data produced. We delve into data quality issues in the section below that discusses our own research; here, we provide just one example to illustrate a few key points.

First, it cannot be emphasized enough that for some recent comparative analyses, there are far fewer studies with adequate data than one is led to believe by titles and abstracts. For example, in their comparative study examining the evolution of social monogamy in primates, Opie et al. (2013) state in their abstract that they "combine trait data across 230 primate species". Yet, their supplementary table only reports 214 species for which data are presented on the mating system, and for only 134 of those taxa are data available to estimate the risk of infanticide. In other words, a key analysis was done on 134, not 230 species. Similarly, their claim that more than 25% of primates are "monogamous" is misleading; that calculation is only accurate if it includes taxa classified as having a variable system that can include monogamy; for those classified only as "monogamous", the proportion shrinks to 15%.

Comparative studies also often suffer if authors do not properly distinguish between absence of evidence and evidence of absence. Obviously, it is a very different situation when no information about a taxon is available because the taxon has not been well studied in the wild than the situation where there is no evidence for a given trait after extensive study of such taxon. Sometimes, authors seem to fill in gaps for some taxa by using data from related taxa. We think this should not be acceptable. For example, Pearce and colleagues (2013), in their evaluation of space use traits in primates, extracted body mass data from the PanTHERIA dataset (Jones et al., 2009). The dataset they used includes 13 species of *Callicebus*, and for six of them the same female body mass of 992 grams is reported. This seems to be a clear case where data from one species are presumed – inappropriately – to apply to additional species from the same genus. For *Aotus*, PanTHERIA reports body mass data on 10 species, but a comparison of those data with our own previous review of body mass data (Eduardo Fernandez-Duque, 2011) resulted in disagreement (defined as a difference ≤5%) in 10 out of 13 comparisons (Table 1).

The challenge of compiling comparable data for comparative analysis is further exacerbated by the proliferation of new taxa being recognized as a result of revised taxonomies proposed during the last 20 years (e.g. Byrne et al., 2016; Groves, 2014; Rylands et al., 2016; Silva Jr., Figuereido-Ready, & Ferrari, 2013), an issue that some researchers have already voiced concerns about (Isaac, Mallet, & Mace, 2004; Zachos, 2013; Zachos et al., 2013). Indeed, new taxonomies for four taxa previously considered to be genera on which we have worked extensively – *Plecturocebus* (formerly *Callicebus*)*, Pithecia, Saguinus*, and *Aotus* – have been proposed within the past 17 years. For *Callicebus* and *Pithecia*, these new proposals were published in *Neotropical Primates*, the journal and newsletter of the Neotropical section of the Primate Specialist Group of the IUCN, with the proposed number of saki species changing from 5 to 16 (Marsh, 2014) and of titi monkey species from 24 to 28 (van Roosmalen, van Roosmalen, & Mittermeier, 2002) without any consideration of genetic data. More recently, and based on genetic data, Byrne et al. (2016) proposed splitting the genus *Callicebus* into three genera (*Callicebus*, *Plecturocebus*, and *Cheracebus*) and a total of 33 species, and Buckner et al. (2015) proposed dividing the genus *Saguinus* into two genera (*Saguinus* for the "large-bodied" tamarins and *Leontocebus* for the "small-bodied" forms) with a total of 15 or more species. While we prefer not to take sides as either "splitters or lumpers", we do think that for the case of comparative studies it might be prudent to err on the "safe" side of considering more rather than fewer taxa. Subspecies, or even populations, might differ in the traits being considered, which might add valuable information if properly acknowledged. Still, this will require more field studies to collect comparable natural historical data from additional taxa. In this text, we generally adhere to the taxonomy outlined by Mitani et al. (2012) for owl monkeys, Byrne et al. (2016) for titis, Silva Jr. (2013) for sakis, and Rylands, Heymann et al. (2016) for tamarins, unless indicated otherwise for special reasons.

[INSERT TABLE 1 ABOUT HERE]

Similar to the problems outlined above around the PanTHERIA dataset (Jones et al., 2009) for body mass, the analysis of the role that infanticide may have played in the evolution of pair-living and sexual monogamy presents challenges with regards to the availability of data. Even some of the authors proposing the use of the infanticide risk index, discussed in the section above on the **infanticide prevention hypothesis**, have acknowledged a paucity of data to calculate this index. For example, van Schaik and Kappeler (2003) write, “unfortunately, data on the relative duration of lactation are not available for a critical set of primate species, so it is not certain whether all of the infant-cachers are below the infanticide-threshold value of relative lactation length and all infant carriers above it” (p. 60). The limited availability of adequate data from wild primates on the duration of lactation and age at weaning is so serious that one should question whether or not to use the index in the first place (Borries et al., 2013; Borries, Lu, Ossi-Lupo, Larney, & Koenig, 2014). But, since the index has been used, we illustrate here just how problematic its use can be, based on data for *Aotus*.

Five species of *Aotus* were included in Opie et al.’s (2013) comparative study on the evolution of “monogamy” in primates; for three of these species, the authors calculate indices of “infanticide risk” based on weaning age and gestation period length. A weaning age of 75 days is reported for *A. lemurinus griseimembra*, *A. nancymai*, and *A. trivirgatus*, while no data are reported for *A. azarae* and *A. infulatus*. Within the literature cited by Opie et al. (2013), we were able to find a value of 75 days listed in Table 11.2 of Ross (2003) and attributed to *A. trivirgatus*, which was formerly used as the species name for all currently recognized forms of owl monkeys. The chapter by Ross (2003) does not provide information on the original source of those weaning age data, but Ross (1991) also provides a value of 75 days for *A. trivirgatus* and indicates that these data come from captive individuals. Ross’ (Ross) description of the situation is worth quoting:

> *“The paucity of data for many species forced me to draw on a variety of sources, including field studies of varying lengths, laboratory studies, and zoo records. For this reason, much of the variation in the data may be caused by direct environmental influence on the life history parameters, e.g., animals in food-deprived conditions may grow slowly and have long interbirth intervals. Such factors are possible sources of error in the data and in the conclusions drawn therefrom”, (Ross, 1991, p.486)*

In summary, Opie et al. (2013) used the same age at weaning of 75 days for three species of owl monkeys, but not for two others, and without a traceable reference to original sources.

Even more problematic is that our own review of the literature on owl monkeys provides grossly different estimates of weaning age. For example, Wolovich (2008) estimated lactation as lasting 120-150 days for *A. lemurinus* in captivity. Moreover, to the best of our knowledge, data on age at weaning in the wild is available only for *Aotus azarae*, where it is estimated to be between 150 and 240 days (N = 7 infants, Rotundo, Fernandez-Duque, & Dixson, 2005). In summary, Opie et al. (2013) estimated the risk of infanticide in owl monkeys using one data point for weaning age, most likely from (a) captive animal(s), that cannot be tracked back to the original source, when there are other published estimates of between two and three times as long for captive and wild individuals, respectively.

We understand that, to some extent, mistakes and limitations are unavoidable when compiling comparative datasets. Therefore, we propose that when examining a given hypothesis, a more rigorous approach would require that researchers assess the sensitivity of the findings to data that counter the expected results. For example, in making our own estimates of infanticide risk below, we use both the minimum and maximum reported values for age at weaning; the former "favors" the hypothesis, while the latter "counters" it. We also suggest that, given the paucity of data, authors must make clear the definitions and criteria that are used for assigning data to a taxon, providing explicit and accurate reference to the primary literature where the original data were published (Borries et al., 2016).

OUR RESEARCH PROGRAM ON "MONOGAMY" IN WILD PLATYRRHINES

The comparative study of "monogamy" is no exception to our proposition that it requires judicious compilation and integration of data from a large number and a wide range of sources that vary in quality, length, scope, and sample size (Borries et al., 2016). The goal should be to produce research that [1] focuses on the natural history of the taxa of interest, [2] uses methods that are either standardized, or comparable, across research sites and taxa, and [3] yields data on the variables of interest and on variation in those traits. Motivated by that goal, we have developed our collective and collaborative research programs on four genera of neotropical primates that are often considered to be "socially monogamous" – *Pithecia*, *Plecturocebus* (one of the three currently recognized genera of Callicebinae), *Saguinus* (one of the two currently recognized genera of Amazonian tamarins), and *Aotus*. We have conducted such research at field sites in Ecuador, Peru, and Argentina (Figure 2), as well as in captivity, over the past 24 years.

The *Owl Monkey Project of Argentina* was started by EFD in 1996, to study the natural history of wild *Aotus azarae* at the very southern end of their natural geographic distribution where the taxon is not strictly nocturnal (Figure 2, Eduardo Fernandez-Duque & Bravo, 1997). MH joined the *Owl Monkey Project of Argentina* in 2010 and, since then, has collaborated on studies of infant development, floaters and pairmate relationships (Maren Huck & Fernandez-Duque, 2012, 2013, 2017; M. Huck et al., 2014; Maren Huck, Rotundo, & Fernandez-Duque, 2011).

[INSERT FIGURE 2 ABOUT HERE]

[INSERT FIGURE 3 ABOUT HERE]

The *Socioecology of Monogamous Primates Project* was started by AD and EFD in 2003 to study similarities and differences in the ecology and expression of pair-living, male-female social relationships, and patterns of parental care in three genera of pair-living and seemingly sexually monogamous platyrrhines (*Pithecia*, *Plecturocebus*, and *Aotus*) living in the same tropical environment, the lowland Amazon rainforest of the Yasuní Biosphere Reserve in Ecuador (Figure 2a and Figure 3). SVB joined this project in 2014 to work on aspects of range use and intergroup interactions, as well as on the genetic mating system of equatorial sakis (*Pithecia aequatorialis*) and red titis (*Plecturocebus discolor*) (Van Belle, Fernandez-Duque, & Di Fiore, 2016; Van Belle, Porter, Fernandez-Duque, & Di Fiore, 2018).

MH conducted 16 months of fieldwork in 2001 and 2002 in lowland Amazonian Peru (Figure 2b) on the mating system and reproductive biology of wild moustached tamarins (*Saguinus mystax mystax,* Figure 3). Her research was done as part of the long-term research program run by Dr. Eckhard Heymann of the German Primate Center and the University of Göttingen (Maren Huck, Löttker, Böhle, & Heymann, 2005; M. Huck, Löttker, & Heymann, 2004; Maren Huck, Löttker, Heymann, & Heistermann, 2005; M. Huck, Roos, & Heymann, 2007; A. C. Smith et al., 2007).

In addition to the fieldwork described above, EFD has also studied behavioral and physiological aspects of pair-bonding and parent-offspring relationships in captive titis as part of his dissertation research (Eduardo Fernandez-Duque, Mason, & Mendoza, 1997; Eduardo Fernandez-Duque, Valeggia, & Mason, 2000). Since 2008, he has conducted research on captive owl monkeys in collaboration with colleagues who manage captive colonies of several owl monkey species at the Michale Keeling Center for Comparative Medicine (M.D. Anderson, University of Texas, Bastrop) (Garcia de la Chica, Fernandez-Duque, & Williams, in press; Hopper, Fernandez-Duque, & Williams, 2019; Larson, Colchero, Jones, Williams, & Fernandez-Duque, 2016; Andrea Spence-Aizenberg, Kimball, Williams, & Fernandez-Duque, 2018; A. Spence-Aizenberg, Williams, & Fernandez-Duque, 2018) and the Dumond Conservancy for Tropical Forests (Miami, Florida) (Babb et al., 2011; Levenson, Fernandez-Duque, Evans, & Jacobs, 2007; Macdonald, Fernandez-Duque, Evans, & Hagey, 2008).

Over the years, our collective and collaborative field and captive research has made contributions to several topics related to the evolution of “monogamy”, including [1] the expression and biological basis of pair-living and pair-bonds in primates, [2] the importance of alloparental and paternal care as a possible influence on the evolution of primate mating and social systems, as well as life history, and [3] the relationship among mating systems, intra-sexual competition, and sexual dimorphism – a relationship that regularly informs our reconstructions of early human behavior. In the following sections, we briefly summarize some of the contributions that our own research programs have made to those topics, and we provide references to the published studies where further details are available.

Pair-Living and Pair-Bonds in Primates

The study of pair-living and pair-bonding is of particular interest to biological anthropologists. Using a combination of demographic and behavioral data, our research group has shown that the owl monkeys of Argentina and the titis of Ecuador always live in small social groups that contain only one reproductive adult male and one reproductive adult female (Eduardo Fernandez-Duque, 2016; Van Belle, Fernandez-Duque, et al., 2016). However, even when the adult male and female of an owl monkey or titi pair have a remarkably coordinated and close relationship, they do not necessarily pair for life, a finding which has implications for understanding the evolution of "pair-bonding". Among owl monkeys, who give birth to singletons, males and females are regularly replaced by intruding adult individuals, with both males and females being replaced equally often (E. Fernandez-Duque & Huck, 2013). These forced changes of partner reduced the reproductive success of the remaining pair-mate in the same group; an adult, male or female, who only had one partner throughout life produced ~25% more offspring per decade of tenure than one that was forced to switch partners (7.9 (N = 19) vs 6.3 (N = 27), E. Fernandez-Duque & Huck, 2013). Much of the observed reduction is explained by the fact that new pairs do not reproduce during their first season together, a possible indicator of the need to consolidate the relationship between pair mates.

In studying pair-living, sexual monogamy, and pair-bonding in wild primates, we have examined behavioral aspects of male-female social relationships, as has long been standard in field studies, and we have also conducted studies to explore the physiological processes that correlate with a behavioral manifestation of attachment. Using fecal samples collected noninvasively from seven reproductive females, we successfully detected ovarian function, conception, and pregnancy in wild owl monkeys (E. Fernandez-Duque, Burke, Schoenrock, Wolovich, & Valeggia, 2011). This preliminary study laid the foundations for subsequent ones on olfactory communication, behavioral coordination, mating, and reproduction of owl monkeys in both the laboratory and the field (Corley, Valeggia, & Fernandez-Duque, 2017; Andrea Spence-Aizenberg et al., 2018). For example, we were able to examine the behavioral and endocrinological mechanisms regulating natal dispersal (Corley et al., 2017) and the subsequent competition between dispersing sexually mature adults and pair-living sexually monogamous ones (E. Fernandez-Duque & Huck, 2013).

Our field studies of sakis have demonstrated that, contrary to their commonly being characterized as "socially monogamous", there can be substantial variation over time in grouping patterns and in both mating and reproductive behavior, even within the same social group (Porter, Grote, Isbell, Fernandez-Duque, & Di Fiore, 2015, 2017). For example, our examination of 12 years of data on group composition and demography for six social groups of sakis indicated that during 45% of group-months, groups contained two or more adult females and/or two or more adult males (Van Belle, Fernandez-Duque, et al., 2016). That is, groups of equatorial sakis were often not "pair-living", an observation that is consistent with observations for other pitheciines (C. L. Thompson, 2013; Cynthia L. Thompson & Norconk, 2011). Moreover, we have also documented several cases when more than one adult female (including mother-daughter pairs) reproduced in the same group at the same time, belying characterization of *Pithecia aequatorialis* as either sexually or genetically monogamous.

Finally, a large body of fieldwork on both small-bodied (*Leontocebus*) and large-bodied (*Saguinus*) Amazonian tamarins (Paul A. Garber et al., 2016; A. Goldizen, Mendelson, van Vlaardingen, & Terborgh, 1996) – to which we have contributed through our observations on *Saguinus mystax* (Maren Huck, Löttker, Böhle, et al., 2005; M. Huck et al., 2004; Maren Huck, Löttker, Heymann, et al., 2005; M. Huck et al., 2007) – highlights the considerable variation in tamarin grouping patterns, mating patterns, and the genetic mating system. This research adds to many other investigations on other Amazonian tamarin species that, collectively, indicate that tamarin groups routinely contain multiple adult females and/or multiple adult males (reviewed in Paul A. Garber et al., 2016). For example, among *Saguinus mystax* of Peru, the mean number of adult males and adult females in a group was 2.5 and 1.8, respectively (8 groups, 17 group-years P. Löttker, M. Huck, & E. W. Heymann, 2004). Importantly, dominant adult females are also routinely observed mating with all of the unrelated adult males in their group, while subordinate females – who are sometimes seen mating with males in neighboring groups, but not with their own group males – rarely reproduce (Culot et al., 2011; Maren Huck, Löttker, Böhle, et al., 2005). Thus, in this population of *Saguinus mystax*, neither is the social organization pair-living, nor is the mating system sexual monogamy. Still, a parentage study of two groups in the population suggested that paternity was somewhat monopolized, with 67-100% of infants being sired by a single male in each of the groups, during at least five consecutive years (Maren Huck, Löttker, Böhle, et al., 2005).

The Importance of Alloparental and Paternal Care

To further understand the evolution of pair-living, pair-bonding, and sexual or genetic monogamy, taking advantage of our research system that includes three predominantly pair-living taxa (titis, sakis, and owl monkeys), and three taxa where substantial levels of care are provided by nonmothers (titis, owl monkeys, and tamarins), we have also explored the behavioral, ecological, and physiological correlates of alloparental and paternal care. Nowhere among primates – or among other mammals for that matter – is "paternal care" (i.e., care by a resident adult male in a group, whether the biological father or a "stepfather") more extensive than among owl monkeys and titis (Eduardo Fernandez-Duque, Di Fiore, & de Luna, 2013; Eduardo Fernandez-Duque, Valeggia, & Mendoza, 2009).

When we first began our research on wild owl monkeys and titis, reports that males played an important role in infant care in these taxa were based primarily on one field study of owl monkeys (15 months, Patricia Chapple Wright, 1985) and two of titis (11 months, Mason, 1966; 15 months, Patricia Chapple Wright, 1985); the subjects in both of the latter studies were seemingly individuals of unknown age and sex. There was also more extensive work on pair-housed animals in captivity that likewise demonstrated males' involvement in infant care (A.F. Dixson, 1983; Alan F. Dixson, 1994; Alan F. Dixson & Fleming, 1981; Fragaszy, Schwarz, & Shimosaka, 1982; Mason, 1974, 1975; Mendoza & Mason, 1986; Moynihan, 1964). The remarkably reduced sexual dimorphism characteristic of these two genera made it important for us to focus on capturing and identifying adult individuals in wild groups of both taxa to accurately describe patterns of infant care and how those did or did not differ between the sexes. We found that in both Azara's owl monkeys (*Aotus azarae*) and red titis (*Plecturocebus discolor*), males carry infants most of the time (ca. 80-90%) from very soon after birth, and infants only transfer to the mother for brief periods usually around the time of active nursing bouts. This pattern has been documented for every group of owl monkey and titis we have studied in the field (owl monkeys N = 15, titis N = 5)(Eduardo Fernandez-Duque et al., 2013; Maren Huck & Fernandez-Duque, 2013; C. Juárez, Rotundo, & Fernandez-Duque, 2003; Rotundo, Fernandez-Duque, & Giménez, 2002; Andrea Spence-Aizenberg, Di Fiore, & Fernandez-Duque, 2015). Moreover, we found that adult owl monkey males share food with infants more frequently than do mothers (Wolovich, Perea-Rodriguez, & Fernandez-Duque, 2007) and are also the first source of support when an infant faces a challenging situation (e.g., crossing a canopy gap, Rotundo et al., 2005). Genetic analyses we have conducted (N = 35 putative father-infant dyads) also suggest that the resident adult male in an owl monkey group is almost invariably the biological father of the infant he carries (M. Huck et al., 2014). Similar ongoing paternity analyses for titis, however, tentatively suggest a more fluid system than in owl monkeys. Three of seventeen infants (18%) born in four different groups could not be assigned to the male that was in the group at the time of conception suggesting some possible extra-pair paternity (Van Belle, Martins, Fernandez-Duque, & Di Fiore, 2016). We have also described how, in both titis and owl monkeys, the presence of infants changes the dynamics between pair-mates. In both *Aotus azarae* and *Plecturocebus discolor,* pair-mates groom and huddle less after an infant is born, and sex differences in time budgets become accentuated (Boner et al., 2014; Andrea Spence-Aizenberg et al., 2015).

Among tamarins, males' contributions to infant care are reported to be more important for infant survival than females' (Paul A. Garber, 1997). Still, in a Peruvian population of *Saguinus mystax*, Huck et al. (2004) found that in the two study groups both male and female non-parents carried more than either the father or the mother did, while mothers provisioned their offspring more than nonparental helpers. There was also a negative association between infant carrying and food provisioning (M. Huck et al., 2004). Genetic relationships had been established using microsatellite analysis, and it was also shown that all males not-related to the breeding female copulated with her (Maren Huck, Löttker, Böhle, et al., 2005). At this point, clearly, quantifying the relative contributions and impact of potential fathers (i.e., males that had copulated with the female but were not sires), mothers, and nonparental helpers to infant survival in the wild is far from easy.

Our research on sakis illustrates a different situation with regards to the extent and importance of paternal care and other forms of allocare. Unlike titis, owl monkeys, and tamarins, all of which show minimal sexual dimorphism in body size (Eduardo Fernandez-Duque, 2011; Norconk, 2011; Soini & Soini, 1990), adult male sakis are 25 to 40% larger than adult females (Norconk, 2011), and, in some species, the sexes also show differences in coloration. During 17 years of fieldwork on sakis in lowland Ecuador, we have only rarely seen males provide direct infant care in the form of carrying of immatures, though food sharing is more common. Indeed, it was only recently (July 2018), that we observed for the first time male carrying behavior. The resident adult male in our best-studied focal group was seen carrying a small infant continuously over a period of several days. Interestingly, during the same period, we also noted that another infant in the group, which was no longer being carried by its mother, had disappeared. Subsequently, both the infant we saw being carried by the male and that infant's mother also disappeared from the group, and the mother's dead body was found several days later, in a seldom used portion of the group’s home range. This anecdotal observation is intriguing; the only time a male was seen carrying an infant for a prolonged period coincided with a period of demographic upheaval in the group, i.e., when there was a reduction in group size from six individuals (one adult male, his subadult son, and two adult females, each with an infant) to three (the adult male, his subadult son, and one remaining adult female). Still, and alluded to above, we have seen extensive evidence of more indirect care of infants by males over the past 17 years, particularly in the form of “tolerated theft”, a form of passive food sharing. And, we have also observed incidents of carrying of an immature individual by its older female sibling on two occasions that involved different pairs of siblings. By contrast, we have never observed direct care (e.g., carrying, food sharing) by siblings in titis. And in owl monkeys, the only time we have observed carrying by a sibling or a stepfather was associated with the replacement of the putative father by an intruding male (Eduardo Fernandez-Duque et al., 2008). The virtual absence of care by siblings among titis, owl monkeys, and sakis is in clear contrast to the patterns of infant care observed in tamarins, where adult siblings provide regular care of infants.

Collectively, these studies demonstrate the following for the four species we study: [1] presumably energetically-costly male care, in the form of carrying, is indeed a conspicuous part of the social system of wild titis, owl monkeys, and tamarins; [2] carrying by adult male sakis is rare, but males do participate in other potentially costly forms of direct care , such as food sharing (Eduardo Fernandez-Duque et al., 2009); and [3] alloparental care in the form of carrying is common in the cooperatively breeding tamarins, sometimes seen in sakis, and almost never seen or reported for titis or owl monkeys (except in the case of step-fathers if male replacement took place shortly before or after the birth of an infant). We think that is it important to stress that it is only through years of field study (more than two decades' worth, in the case of owl monkeys) that these patterns have come to light. The question remains as to how this kind of variation within and across taxa is best distilled into character states for use in comparative analyses. Which of the taxa we study, for example, show "high" versus "low" paternal care? How should this be accounted for when paternal care is defined, for example, as occurring only "where males provide for at least 30% of infant time (p.13330, Opie et al., 2013)? How is our understanding of the importance of paternal and alloparental care in the evolution of pair-living and sexual monogamy affected by considering nonmaternal care in these different taxa as a unitary and homologous trait?

Intra-Sexual Competition and Sexual Dimorphism

Anthropologists' inferences about early hominin social systems, grouping patterns, and mating patterns are regularly based upon consideration of the degree of sexual dimorphism present in, or inferred from, physical traits, such as stature, body size, and canine size (J. M. Plavcan, 2000; J.M. Plavcan & van Schaik, 1997). Although there may be robust comparative primate data from highly dimorphic species that broadly support the notion that sexual dimorphism in physical traits is correlated with behavioral sex differences (e.g., *Pan*, *Pongo*) (M. J. Plavcan, 1993), the situation is less clear for pair-living and sexually monogamous taxa. Behavioral, body mass, and canine size data from wild, pair-living, and sexually monogamous primates was rather limited when we started our field projects, and such data were often available only for individuals of unknown age, social status, and sometimes even unconfirmed sex.

Over the years, we have amassed information on ~300 wild owl monkeys, ~30 titis, and ~20 sakis from Argentina and Ecuador that speak to issues of dimorphism in morphology, behavior, and development. Our data on patterns of infant development in wild owl monkeys show little evidence of sexual dimorphism in developmental trajectories (Maren Huck et al., 2011). Owl monkey infants of both sexes are very dependent upon parents until roughly six months of age. Following weaning, both males and females continue to grow and remain in their natal groups. For example, a study of 104 individuals born in 24 groups found that all males and females dispersed from their natal groups when they were between 2.2 and 4.9

years of age (Eduardo Fernandez-Duque, 2009). Both males and females reproduce for the first time when they are approximately six years of age (males: 75 months, females: 73 months, Table 1, Maren Huck et al., 2011). Several wild owl monkeys in our study population have lived at least 14 to 15 years, and a few have lived to 18-19 years; analyses of mortality trajectories based on captive (25 males, 29 females) and wild (70 males, 73 females) owl monkeys suggest that females live longer (Larson et al., 2016). Among titis, infants also become increasingly independent from their parents at roughly six months of age, and both males and females disperse from their natal group when they are subadults or young adults (~ 2-3 years old, N = 3); individuals have lived at least 11-15 years (Van Belle, Fernandez-Duque, et al., 2016). In contrast to titis and owl monkeys, among sakis not all animals disperse from their natal groups before adulthood. In our main saki group, two daughters out of three born during the study period stayed and reproduced in their natal group, alongside their mother at the ages of 4.5 and 6.4 years old, respectively. Of seven other infants born in the same group since 2003, one male dispersed as a young adult to an adjacent range before disappearing, and another six (one male, one female, and four of unknown sex) disappeared as infants or juveniles (Van Belle, Fernandez-Duque, et al., 2016). Data on lifespan suggest that sakis can live to at least 9-16 years (Van Belle, Fernandez-Duque, et al., 2016). In moustached tamarins, which usually bear twins once a year, both males and females can either remain in their natal group or emigrate (Petra Löttker, Maren Huck, & Eckhard W Heymann, 2004). While no data were published on life-span reproductive rates, one male and female pair produced at least 5-6 sets of twins (Maren Huck, Löttker, Böhle, et al., 2005). If one assumes a minimum age of reproduction of 19 months (P. Löttker et al., 2004), and because we know (E. Heymann, personal communication) that both individuals lived at least another year, this means that both males and females can reach at least 8 years of age, producing at least 10 (9 for the male) infants, of which at least 6 reached adulthood (Maren Huck, Löttker, Böhle, et al., 2005; Petra Löttker, Maren Huck, & Eckhard W Heymann, 2004).

In 2002, we first seriously considered the possibility that a population of “floater” individuals might exist in the owl monkey population we study (Eduardo Fernandez-Duque & Huntington, 2002). "Floaters" are relatively young adults who have dispersed from their natal groups and are, presumably, seeking a reproductive opening in another group. We now have evidence that the frequent (27 female and 23 male replacements, 18 groups, 2001-2011) and sometimes intense intrasexual competition we observe in *Aotus azarae* originates from these floaters (E. Fernandez-Duque & Huck, 2013; Maren Huck & Fernandez-Duque, 2017). The implications of describing for the first time, for any pair-living sexually monogamous species, an intense and frequent source of competition cannot be underestimated, particularly since it is often presumed that species that are monomorphic in body size show a low level of intraspecific competition (e.g., Cheverud, Dow, & Leutenegger, 1985). Since then, we have begun to consider how the function and adaptive value of territoriality, mate guarding, pair-bonds, and reproduction may be influenced by the presence of an important number of solitary individuals in the population. Our studies of titis and sakis in Ecuador also suggest the potential presence of such solitary or “floater” individuals who can rapidly replace resident adults and, therefore, may constitute an important source of competition for those residents. For example, following the death of the original resident adult male in our best-studied saki group, several adult males were seen associating intermittently with the original resident female over a period of weeks before she established a stable association with one male, who remained the sole resident male for the next seven years (Di Fiore et al., 2007; Van Belle, Fernandez-Duque, et al., 2016). Future work will examine the role that floaters, in addition to same-sex residents of neighboring groups, have on intrasexual competition, selection, and the genetic structure of groups and populations.

In the End, It Is Only Data that Matter!

In the remainder of this article, we examine more fully how the data we have collected can be used to examine particular predictions about three of the important potential evolutionary drivers of "monogamy" outlined above. In particular, we examine how our data compare to those used in the broad-scale comparative analyses of mammalian and primate "monogamy" that we critique above when examining the three hypotheses most commonly addressed in comparative studies – the **infant care hypothesis**, the **female distribution hypothesis**, and the **infanticide prevention hypothesis**. Summary details about our study sites, study populations, and field methods, as well as about the methods we used to collate the variables of interest are provided below, along with an overview of our strategy for searching and reviewing the primary literature.

METHODS

Field Research

Study Sites

Our research is being conducted at two South-American field sites, one in the Argentinean Gran Chaco, where we study Azara's owl monkeys (*Aotus azarae*) and one in the Ecuadorian Amazon, where we study red titi monkeys (*Plecturocebus*, formerly *Callicebus*, *discolor*) and equatorial saki monkeys (*Pithecia aequatorialis*). The field site in Argentina is located within the Reserva Privada Mirikiná (named after the local term for owl monkeys), a 1,100 ha private reserve within the Guaycolec Ranch (58°11' W, 25°58' S). The climate is subtropical, with the lowest monthly mean temperatures from May through August (16 to 18 °C) and highest from October through March (23 to 27 °C). Mean annual precipitation is 1,436 ± SD 333 mm (1977 to 2017) with a drier period in June through August (Eduardo Fernandez-Duque, 2016). The field site in Ecuador – the Tiputini Biodiversity Station (76°08' W, 0°38' S) – encompasses approximately 650 ha of primary evergreen lowland rainforest and is located adjacent to the 9,820 km^2 Yasuní National Park and Biosphere Reserve in eastern Ecuador. The climate is hot and humid, with mean monthly temperatures of 24 – 27°C throughout the year (Van Belle, Fernandez-Duque, et al., 2016). Mean annual precipitation is 2,924 ± SD 267 mm (2009 to 2014) with the wettest period occurring from March through June (Snodderly et al., 2019). Additionally, between 2000 and 2001, one of us (MH) conducted a 16-month field study on wild moustached tamarins (*Saguinus mystax mystax*) at the Estación Biológica Quebrada Blanco (EBQB, 4°21’ S, 73°09’ W, about 120 m above sea level, encompassing ca. 100 ha), Peru, run by E. W. Heymann. The data we report below on tamarins is based on this study, complemented by results from more recent studies conducted at the field site by other researchers. In 2001, mean monthly minimum and maximum temperatures at the EBQB ranged from 21.4 to 23.3 °C and 25.0 to 27.7 °C, respectively. During that year, 2781 mm rain fell, with the dry season (precipitation < 200 mm) lasting from June through September (M Huck, 2004).

Study Subjects

In Argentina, we have collected demographic data from 27 different groups of owl monkeys over the course of our research program. The number of groups monitored for collecting behavioral data has been smaller and variable across periods and studies. In Ecuador, we have monitored seven titi groups for various lengths of time over the course of the project, with a main focus on three groups that have been studied for 12 to 15 years, with varying degrees of intensity. We have also monitored six saki groups, one of which has been studied for 17 years (Van Belle, Fernandez-Duque, et al., 2016). At the EBQB, we intensively observed two main study groups of tamarins and sampled six neighboring groups to collect additional demographic data and samples for genetic analysis.

Demographics and Group Size Data

Given their cryptic behavior, small body sizes, and (for owl monkeys and titis) the general difficulty of sexing and identifying individuals due to their lack of conspicuous sexual dimorphism, we have darted, captured, and fit with radiocollars, one or more individuals in most of our study groups of *Aotus*, *Plecturocebus*, and *Pithecia*, following procedures described previously (Eduardo Fernandez-Duque & Rotundo, 2003; M. Fernandez-Duque, Chapman, Glander, & Fernandez-Duque, 2017; C. P. Juárez, Rotundo, Berg, & Fernandez-Duque, 2011). The radiocollars have allowed us to consistently locate our study groups and has also facilitated the consistent identification of group members, which in turn has enabled us to record accurate data on group composition, pedigrees, age categories, and life history traits. The tamarins, who can be easily sexed through their conspicuous and large genitalia, were identified individually through natural markers such as pigmentation patterns on the genitals, notches in ears, or broken fingers, but were not radiocollared, and behavioral data were only recorded when the observers were confident in their identification (M Huck, 2004).

For the Ecuadorian and Argentinean species, each main study group was contacted, on average, about four days per month throughout their respective study periods to record changes in group composition and to collect behavioral data (Supplementary Table 3). During group contacts, we noted the presence or absence of expected group members and recorded observations of new infants. Dates of birth for new infants were estimated as the midpoint between the last day the group was seen without an infant and the first day a newborn was observed, aided by growth and behavioral characteristics (*Aotus*: N = 230; *Pithecia*: 2-23 days, N = 8 births; *Plecturocebus*: range: 0-38 days, N = 24 births). During group contacts, we also recorded the identity of all missing group members.

Over the course of our multi-year fieldwork, we have employed the same data collection protocol for three of our study taxa (*Aotus azarae*, *Pithecia aequatorialis*, and *Plecturocebus discolor*) explicitly to facilitate comparative analyses. Briefly, during group contacts, we collect data on the behavior and spatial associations of each group member during 20-min focal animal samples. During focal sampling, we recorded the behavior of the focal individual at 2-min intervals (instantaneous scan points) using ethograms that describe mutually exclusive behavioral categories that largely coincide across the three taxa, but with species-specific sections on vocalizations. In between instantaneous scan points, we recorded all occurrences of specific social, alloparental, vocal, and feeding behavior that involves the focal individual. In addition, during focal samples we conducted instantaneous group scans at 4-min intervals to record the estimated distance of all visible group members relative to the focal individual.

The field methods used to study *Saguinus mystax* were similar, but involved the quasi-continuous presence of observers during the activity times of the two study groups. At least one observer remained with the group from when they left a sleeping tree at dawn until they entered a sleeping tree in the afternoon, nearly every day, which resulted in 3,004 contact hours on 330 days for group W, and 3,257 contact hours on 351 days for group E (M. Huck et al., 2004; P. Löttker et al., 2004). Behavioral observations were conducted during 10-min focal sampling sessions with instantaneous recording of focal animal behavior at 1-min intervals. This was complemented by *ad libitum* sampling of behaviors of special interest such as social interactions or food sharing (M Huck, 2004; M. Huck et al., 2004). Additionally, fecal samples were collected for hormonal and genetic analyses (Maren Huck, Löttker, Böhle, et al., 2005; Maren Huck, Löttker, Heymann, et al., 2005; Löttker, Huck, Heymann, & Heistermann, 2004). For the latter, six neighboring groups, whose demography was also determined, were also sampled (P. Löttker et al., 2004).

Our multi-year research program has provided demographic histories of known individuals that enables us to propose both chronological and biologically defined age classes for *Aotus azarae*, *Pithecia aequatorialis*, and *Plecturocebus discolor*. As such, based on ontogeny patterns and field observations of age at dispersal and age at first reproduction, we have classified individuals of the three taxa as infants (0 – 6 months old), juveniles (6.1 – 24 months old), subadults (24.1 – 48 months old), or adults (>48 months old: Maren Huck et al., 2011; Van Belle, Fernandez-Duque, et al., 2016). For *Saguinus mystax*, individuals were considered infants up to three months of age, juveniles if they were 4 – 12 months old, sub-adults when they were 13 – 18 months old, and adults when they were 19 months of age or older (P. Löttker et al., 2004).

Ranging Patterns

Methods used to collect data on ranging and use of space by *Aotus azarae*, *Pithecia aequatorialis*, and *Plecturocebus discolor* were comparable. Briefly, every time we encountered a group or single individual, we recorded the location when encountered and when left or lost. During group follows, we supplemented these initial and final locations with positional information at 20-min intervals. This was done either by using a GPS unit, by measuring the distance and direction of the location of the group or individual in relation to a previously georeferenced location nearby (i.e., a mapped feeding or sleeping tree or a trail point), or by extracting the group's location from an observer's own GPS track record when following a group. A quantitative evaluation of the accuracy of these methods indicated that the mean distance between pairs of points (N = 4,451) obtained from the observers' GPS tracks and points taken with a GPS unit or measured relative to previously georeferenced markers was 9.0 m (SD = 12.4; range = 0–109 m; median = 5.0 m) (Van Belle et al., 2018). We used the fixed kernel density method (Seaman & Powell, 1996) to estimate home ranges as the 90 kernel isopleth of the set of location records (Figure 4, Maren Huck & Fernandez-Duque, 2017; Van Belle et al., 2018; Van Belle, Porter, Fernandez-Duque, & Di Fiore, in preparation; Wartmann, Juárez, & Fernandez-Duque, 2014). At the time we observed the moustached tamarins, no GPS locations were taken. However, the study site had a 100x100 m^2 path grid with intersection identifiers, and opportunistically, we noted the intersection locations if we saw a group within 10 m of such an intersection, which allowed a rough estimate of home range size (M Huck, 2004). Given these differences in methods of data collection, home range data for the tamarins cannot be directly compared with the results for the other three species and should be viewed as an approximation.

[INSERT FIGURE 4 ABOUT HERE]

Literature Review and Cross-Checking

To compare the data that Opie et al. (2013) and Lukas and Clutton-Brock (2013) used in their comparative analyses on male care of infants, population density, patterns of home range use, infanticide, and risk of infanticide, we examined the references that were cited in both articles to support the character state assignments made. We also searched the *Web of Science* database, as well as *Google Scholar* for additional articles, relevant book chapters, and theses from the primary literature in English as well as in Spanish, Portuguese and German. Given the upheaval in primate taxonomy that has occurred over the past 20 years, when searching for studies on "topic X in species Y" we only searched for the species' scientific name (rather than its common name), including also taxonomic synonyms, revised names, and alternative spellings. For example, for Nancy Ma's owl monkey, we used the search term "*Aotus nancyma**" (where * is a wildcard) because the species is sometimes referred to as *A. nancymae*, *A. nacymaae*, and even *A. nancymai*. We also checked how the species name provided in an article (especially older articles) relates to the currently accepted species name. In some cases, to make this assessment, we used the geographic information provided in an article (e.g., coordinate data) to compare it with contemporary species distribution maps as provided by the IUCN or recent publications on distributions. For species where the number of initial search results exceeded 100 publications, we refined our results by excluding articles we judged to be unrelated to evolutionary biology (e.g., those focused on veterinary, parasitological, immunological, or neurobiological topics). Each of the remaining articles was then read fully to determine whether it contained relevant data and whether those data were based on the authors' own data collection and analysis (i.e., the article was a primary source of information) or whether the authors were reporting values from reviews of previously published articles (i.e., the article was a secondary source). We also followed the references cited in secondary and review sources to find additional published materials that we might have missed through our searches of *Web of Science* and *Google Scholar*. We then used only the primary data sources to evaluate the strength of the evidence for character state assignments used in the comparative articles of Opie et al. (2013), and Lukas and Clutton-Brock (2013). We did not consider conference abstracts as primary sources, since abstracts would not provide sufficient details of the data and methodology to judge their value.

RESULTS

Infant Care Hypothesis

This hypothesis posits that infant care is sometimes so costly that mothers require help from others to successfully rear offspring. Such a situation creates a fitness benefit to males for remaining with and investing in the reproduction of a single female instead of seeking further mating opportunities elsewhere (Wittenberger & Tilson, 1980). The hypothesis received substantial consideration in the recent comparative studies by Lukas and Clutton-Brock (2013) and Opie et al. (2013), both of which concluded that "male care is probably a consequence rather than a cause of the evolution of social monogamy" (p. 527 Lukas & Clutton-Brock, 2013). Or, in the words of Opie et al. (2013),

> *"We find decisive support for correlated evolution between [pair-living] and paternal care… Paternal care only evolves after a switch to [pair living] and not in polygynous systems… Once paternal care evolves within [pair living] it is unlikely to be lost." (Opie et al., 2013 , p. 13329)*

In their analyses, Lukas and Clutton-Brock (2013) classified species as "showing paternal care if males regularly contribute to feeding or carrying offspring" (p. 526). However, is not clear what constitutes a "regular" contribution. By contrast, Opie et al. (2013) define "paternal care as occurring only where males provide care for at least 30% of infant time" (p. 13330). "Infant time", however, is not defined; presumably, this is the time spent carrying infants. Both studies take the same approach in dichotomizing paternal care as either "present" or "absent". The two studies differed in the number of species included from each of the four genera we worked with. Lukas and Clutton-Brock (2013) include eight owl monkey species, 27 titi species, five saki species, and 17 tamarin species in their dataset, while Opie et al.'s (2013) dataset includes information on five owl monkeys, two titi, no saki, and five tamarin species. Apart from one species, *Aotus infulatus*, which is not included in the other study, all species used by Opie et al. (2013) were also part of Lukas and Clutton-Brock's (2013) dataset.

In our own review of the literature, we found that the references cited to support the claim that specific species show paternal care are insufficient (Table 2). References in Lukas and Clutton-Brock's study (2013) for all eight owl monkey species, all 27 titis, all five sakis, and 15 out of 17 tamarins, and for three out of five owl monkeys, both titis, and four out of five tamarins in the study by Opie et al. (2013) do not provide appropriate evidence. For example, Lukas and Clutton-Brock (2013) provide a single reference to the encyclopedic secondary source, *Walker's Mammals of the World* (Nowak, 1999) for all eight species of *Aotus* included in their analysis. This reference, moreover, provides only general, genus-wide descriptions of the relative amounts of care provided by males and females and does not report any species-level data. Indeed, the only primary information published on patterns of parental care by either male or female owl monkeys cited by Opie et al. (2013) is Wright (1990), a study that reports findings from wild *A. nigriceps*, where the author concedes that it was not possible to distinguish between individuals or sexes (Supplementary Table 2).

[INSERT TABLE 2 ABOUT HERE]

Similarly, none of the references provided by Lukas and Clutton-Brock (2013) to support claims about the presence of male care of infants in any of the species of either titis or sakis included in their study is, in fact, suitable for this purpose. Only one appropriate reference is included for the tamarin species included in their dataset (*Leontocebus fuscicollis* and *Saguinus oedipus*); and even that one, which does mention relevant primary sources (Supplementary Table 2), is based on an article primarily addressing a different species (*Callimico goeldi*). With regards to references for *Leontocebus fuscicollis* the relevant study was conducted with captive individuals and it is not clear if it referred to the correct species (Gisela Epple, 1975).

In our view, there are seven problems with how the literature is being used and cited in these and other comparative studies (Table 2): [1] because primate taxonomy is in flux, the data "available" for character state assignment often come from a different species than the species name suggested in an older reference; [2] references on the behavior of captive animals often do not provide information on the provenance of the captive population, making it difficult to know the taxon of the population; [3] data from captive individuals are of limited value to assess the prevalence of a behavior in the wild because animals are frequently housed in ways that do not reflect the size and composition of wild groups; [4] abstracts are sometimes cited, even when they do not provide sufficient information to evaluate whether the claim made is actually supported; [5] summary data sources are used that themselves rely on other review sources, such that it is difficult to trace back character state assignments, or variable values, to the primary literature; [6] sources are often cited that are irrelevant to the subject at hand and instead pertain to a different topic, different species or both (e.g., a study on infanticide in Hanuman langurs (*Semnopithecus entellus)* being cited as providing support for parental care in *Saguinus* species: Vogel and Loch 1984); and [7] multiple sources are sometimes cited as being indicative of multiple studies, when they in fact all refer to the same study and data set. For example, there are seven published articles, or book chapters that are regularly cited as providing evidence of male infant care in owl monkeys or titis (Patricia C. Wright, 1978, 1981, 1984, 1986; P. C. Wright, 1990; Patricia C. Wright, 1994; P.C. Wright, 1997). However, all these publications, by the same author, refer to the same single study where the researcher candidly admits that, "for the most part [she] had to rely on [her] sense of hearing. Therefore, individuals often could not be identified, especially when there was no moon" (p. 27, Patricia Chapple Wright, 1985). Identification of who was the male and who the female was therefore not possible. By calling attention to this situation, we do not intend to diminish the importance of this particular foundational study of wild titi and owl monkey behavior, but simply to point out the need to be more thoughtful when considering published work. The use, in some comparative studies, of the number of publications about a topic that appear in a database as an indication of "research effort" gives an inappropriately inflated sense of the extent of knowledge we actually have.

It is likely that the numerous titi, saki, owl monkey, and callitrichine species for which there are no good data on male care available from field studies would indeed show generally similar (though not identical) patterns, to those from captive individuals or from closely related taxa in the wild. Still, our point is that we should not assume such a situation, and there is no excuse for assigning such "data" to unstudied taxa. Indeed, there is no shortage of examples in the history of science to demonstrate that such extrapolations cannot be taken for granted (e.g, Boinski, 2005; Mason, 1971). A more recent example – closely related to the central topics of our work here – offers a similarly critical evaluation of the way in which shrew species have been classified as either "solitary" or "social" in comparative studies and is a compelling reminder of the risks associated with assuming knowledge when there is none (Valomy et al., 2015). Much of the confusion generated by the comparative studies that we examine here is the consequence of assuming sexual monogamy, pair-living, and high levels of male care based on studies of captive marmosets and tamarins, which tend to be managed as monogamous pairs in captivity but in the wild live more commonly in small multimale-multifemale groups.

Those caveats noted, our own fieldwork does support general statements made about male care of infants in some of the respective genera we have studied. For our study taxa, we quantified "paternal care" as defined by Opie et al. (2013), i.e., by calculating the males' percent contribution to infant carrying as a value from the infant's perspective, where infant care by all care-givers adds up to 100%. By this criterion, in wild Azara's owl monkeys (*Aotus azarae azarae*), males carry infants at least 75% of the time (Maren Huck & Fernandez-Duque, 2013), and for a different subspecies (*A. a. boliviensis*), a value of 92% has been estimated in an 8-month study of captive individuals (Jantschke, Welker, & Klaiber-Schuh, 1996). In our study of two wild red titis groups (*Plecturocebus discolor*), males are clearly the main carriers of immature infants, responsible for 98% of carrying time (Andrea Spence-Aizenberg et al., 2015). Due to cooperative care, the pattern in moustached tamarins (*Saguinus mystax*) is more complicated. While fathers carried more than mothers (18% vs. 7% of the time, respectively, N = 2 groups), other adults of both sexes usually carried infants more than either fathers or mothers (M. Huck et al., 2004). These values are roughly supported by another study on one group of the same species, where male care (without distinguishing between fathers and non-fathers) ranged between 5 – 52%, (mother, 16 – 19%, other females 0 – 23%, sub-adult male 8.9%, Paul A. Garber, 1997). Further complicating the evaluation of infant care contributions by males and other alloparents in *S. mystax* is the fact that food sharing with infants is more frequent in this taxon (304 events, 424 hours of focal observations) than in either Azara's owl monkeys (77 events, ~2300 hours: Fernandez-Duque, et al., unpublished data) or red titis (20 events, 210 hs, 2 males, Andrea Spence-Aizenberg et al., 2015). There is also a negative association between the extent of food sharing by male tamarins and how frequently they carry infants (r = -0.52, p = 0.12: M. Huck et al., 2004). Despite some anecdotal evidence of infant carrying (Di Fiore, personal observation) and of occasional food sharing (Eduardo Fernandez-Duque et al., 2013) among equatorial sakis, extensive direct care by males is clearly not typical in this species (Norconk, 2011).

Overall, based on our own examination of published data, we tentatively agree with the assessments of previous comparative studies with respect to the presence or absence of “paternal care” for the various titi, owl monkey, saki, and tamarin species that we study. Still, we stress that actual data supporting the assignment of these character states to all species in those genera is much scarcer than the long list of references seems to suggest! In fact, for the vast majority of species in all of these genera, absolutely no data from the wild are available. Thus, any comparative study must be regarded as preliminary, at best.

Female Distribution Hypothesis

In their comparative study of the evolution of “social monogamy” in mammals (i.e., a combination of “pair-living” and “sexual monogamy”, sensu Maren Huck et al., 2019), Lukas and Clutton-Brock (2013) reported strong support for the hypothesis that “monogamy” occurs in response to the distribution of resources, which determines how individual females are distributed across a landscape. That is, under certain ecological conditions (possibly associated with habitats that provide only relatively scarce food), females are expected to space themselves out individually and with relatively little overlap among ranges in order to minimize competition with one another over food. Under such a scenario, the ranges of individual males map on to those of individual females, resulting in male-female pairs sharing a collective range and practicing sexual monogamy.

Lukas and Clutton-Brock’s (2013) conclusion was based on three main findings. First, they found that “monogamous” species occur at lower population densities than do species where animals live solitarily (median: 15 ind/km^2 versus 156 ind/km^2), which they considered to be the ancestral grouping pattern from which sexual monogamy evolved. Second, they found that home ranges of “monogamous” species were comparable in size to those of solitary species despite what seem to be some substantial differences in the median values (median: 21 ha and 53 ha, respectively). Third, they reported that home ranges among neighboring groups of “monogamous” species overlapped less than those of solitary ones (median: 17% and 58%, respectively).

[INSERT FIGURE 5 ABOUT HERE]

In making these comparisons, Lukas and Clutton-Brock (2013) used data obtained, not from primary sources, but from PanTHERIA (http://esapubs.org/archive/ecol/E090/184/), a species-level database of life history, ecology, and geography of mammals (Jones et al., 2009). Their use of this database was only stated in the article’s supplementary material. Notably, this database rarely references primary sources; perusal of the references for owl monkeys, for example, shows that none of 27 references is to a source in the primary literature, as was only two of 23 references for titis, three of 21 references for sakis, and five of 29 references for tamarins. Nonetheless, the database contains estimates of population density for all four genera of primates on which we work (owl monkeys: N = 6 species, titis: N = 4 species, sakis: N = 4 species, and tamarins: N = 9 species). Our own search of primary sources for information on population densities for these genera resulted in 58 publications (owl monkeys: N = 7 species, titis: N = 15 species, sakis: N = 6 species, and tamarins: N = 17 species).

The population density medians we calculated from primary sources were similar to those we obtained from PanTHERIA for owl monkeys, titis, and sakis (Figure 5 and Table 3). The medians for tamarins were markedly different.

[INSERT FIGURE 5 ABOUT HERE]

[INSERT TABLE 3 ABOUT HERE]

Traditional population census methods (e.g., line transects) can underestimate population densities of elusive and cryptic species, such as owl monkeys, titis, sakis, and, to a lesser extent, tamarins. For example, line transects provided estimates of 25 ind/km^2 (Arditi & Placci, 1990) for *Aotus azarae* at our field site in Formosa, Argentina. However, our complete counting of all individuals in a 70-ha area where our main study groups reside resulted in an estimate of 64 ind/km^2 (Fernandez-Duque, 2016). Similarly, at the Tiputini Biodiversity Station in Ecuador, population density estimates for *Plecturocebus discolor* obtained with line transects (11 ind/km^2 , Derby, 2008) were four times smaller than those obtained using playback experiments along transects (48 ind/km^2, Dacier, de Luna, Fernandez-Duque, & Di Fiore, 2011). Both of these improved alternative methods of estimating population density for these two well-studied species yield values outside the quartiles around the median for the genus (Fig. 5). Our findings suggest that the overall median population density for several of these genera might be underestimated when relying on secondary data sources as those frequently included in PanTHERIA, which for many taxa incorporates data based on rapid population censuses rather than extended autecological studies.

Lukas and Clutton-Brock (2013) also used PanTHERIA to obtain data on home range sizes of various species within each of these four genera (owl monkeys: N = 1 species, titis: N = 4 species, sakis: N = 1 species, and tamarins: N = 8 species). We compared their estimates as extracted from the PanTHERIA database with those as obtained from our own review of the primary literature (owl monkeys: N = 4 species, titis: N = 12 species, sakis: N = 6 species, and tamarins: N = 10 species).

The median home range sizes we estimated from primary sources were roughly twice (tamarins and owl monkeys), three times (titis), and six times (sakis) higher than those calculated using data in PanTHERIA (Figure 6 and Table 4). Our estimates again suggest that data in this database, which heavily relies on secondary data sources, inadequately and inaccurately reflects information on space use, at least for these four taxa that we know well.

[INSERT FIGURE 6 ABOUT HERE]

[INSERT TABLE 4 ABOUT HERE]

Because PanTHERIA does not include information on home range overlap, Lukas and Clutton-Brock (2013) used data available in Pearce et al. (2013), which examined home range overlap exclusively in primates. Lukas and Clutton Brock (2013) state that the Order Primates is “the only taxonomic group for which comparative data are available” on home range overlap (p. 528), but it is our impression that detailed information on home range overlap may, in fact, be available for many more mammalian taxa. As an example, in an earlier phylogenetic study of the evolution of sexual monogamy in mammals, Komers and Brotherton (1997) included in their analyses a binomial variable (yes/no) of home range overlap for 84 species, of which 82% (N = 69) were non-primate mammals.

The database in Pearce et al. (2013) includes estimates of home range overlap for only two of the four primate genera on which we work (titis: N = 3 species; tamarins: N = 6 species). Still, our own search for primary sources reporting information on home ranges yielded data for all four genera (owl monkeys, N = 1 species; titis, N = 3 species; sakis, N = 4 species; tamarins, N = 7 species). It is worth noting that six of these sources became available after Pearce et al.'s (2013) publication likely explaining the difference in the number of sources they found and we found.

The home range overlap medians we estimated from primary sources for titis and sakis are comparable to the median for the set of "socially monogamous" primates, as a whole, as calculated by Lukas and Clutton-Brock (2013). On the other hand, the medians for tamarins and owl monkeys are more similar to the median calculated by Lukas and Clutton-Brock (2013) for solitary primates (Figure 7 and Table 5).

[INSERT FIGURE 7 ABOUT HERE]

[INSERT TABLE 5 ABOUT HERE]

Notably, the only data available for owl monkeys come from our own study of *Aotus azarae*, where we calculated home range overlap for each of five groups as the percentage of area within their respective home ranges that was shared with any of the four other groups (Wartmann et al., 2014). Such a method – also used for *Pithecia irrorata* (Palminteri, Powell, & Peres, 2016) and *Leontocebus nigrifrons* (P. A. Garber, 1988) – results in a higher estimate for percent home range overlap than simply calculating overlap between pairs of neighbors, which is the method used in most studies. Neither Pearce et al. (2013) nor Lukas and Clutton-Brock (2013), however, addressed in their methods how they standardized such differences. The **female distribution hypothesis** assumes that females space themselves individually with limited overlap among ranges of *all* neighbors. As such, calculating the percentage of area within a home range that is shared with any neighbor is a more adequate approach for this particular research question. Yet, most studies only focus on a small number of study groups and may have limited knowledge of home range overlap with all neighbors of their focal groups. Indeed, our five study groups of *A. azarae* had additional neighboring groups with whom they shared other sections of their home ranges, but which were not included in the calculation because they were not systematically followed (Wartmann et al., 2014). Similarly, in our studies of *Plecturocebus discolor* and *Pithecia aequatorialis* in Ecuador, we have been unable to adequately estimate the full extent of home range overlap between our study groups and all their neighboring groups because of the difficulty of habituating and following individuals in neighboring groups not under study. For these two species, the mean annual home range overlap between pairs of groups (sakis: mean = 5.0%, range = 3 - 8%, Van Belle et al., 2018; titis: mean = 4.8%, range = 0 - 13%, Van Belle et al., in preparation) is well below the mean of 21% (median = 17%) home range overlap calculated by Lukas and

Clutton-Brock (2013) for "monogamous" mammals and of 49% (median = 58%) for solitary females.

Moreover, we would argue that a truly comprehensive comparative evaluation of the **female distribution hypothesis** is currently infeasible. Such evaluation would require a quantitative characterization of both the spatial and temporal distribution of resources, along with characterization of the individual ranging patterns of males and females. This is necessary because the hypothesis is based on the foundational assumption of a direct relationship between the use of space and the distribution of food that limits the ability of males to monopolize more than one female. Our research has revealed substantial variation in annual home range sizes for owl monkeys (3.6 – 10.9 ha, Wartmann et al., 2014), titis (2.0 – 8.5 ha, Van Belle et al., in preparation), and sakis (16 – 102 ha, Van Belle et al., 2018). This substantial range of variation suggests that, at least for these three populations, males occupying large home ranges should (in theory) be capable of ranging over areas that encompass two, or sometimes even three, females each living in smaller home ranges. That is, males may not be physically constrained to range beyond the area occupied by a single female, and thus other factors need to be explored to explain the nature of sexual monogamy.

If such variation in home range size among groups reflected local differences in the spatiotemporal distribution of food resources, then each group would have access to a comparable amount of food necessary for their survival and reproduction. However, that was not the case among four groups of our owl monkey population. The group that occupied the largest home range had more than double the total basal area of fruit producing trees than the smallest one (103 m^2 vs 44 m^2). The home ranges of the four groups also differed in their potential availability of flowers, leaves, and other edible vegetative parts with the largest home range being the most productive (largest: 54 m^2, smaller ones: 31 – 37 m^2)(van der Heide, Fernandez-Duque, Iriart, & Juárez, 2012).

However, fruit production in a dry season following an unusually dry rainy season was comparable across the four home ranges (and even more so across the four core areas)(see Fig 1a and 1b in Eduardo Fernandez-Duque & van der Heide, 2013). These findings suggest that during harsh, bottleneck ecological conditions, groups had access to a similar amount of food potentially irrespective of the size of their home range or core area. It is possible that it is the availability of food resources, particularly in core areas, during such harsh dry seasons that may be important in regulating female distribution in owl monkeys as they provide groups with the minimum nutritional requirements at times of unusual food scarcity (Eduardo Fernandez-Duque, 2016). Unfortunately, no such data on food availability in home ranges of different sizes are available for our titi or saki study population.

Infanticide Prevention Hypothesis

Evaluating the **infanticide prevention hypothesis** requires quantifying the risk of infanticide experienced by different taxa. Researchers then need to consider whether this estimated risk differs for those taxa that are pair-living or sexually monogamous (depending on whether they are looking at the social organization or the mating system) compared to either solitary or group living species, depending on the ancestral condition. Finally, such studies need to evaluate whether, across a phylogeny, pair-living or sexual monogamy arises more commonly than expected in lineages that show higher levels of infanticide risk. As noted above, defining and quantifying the risk of infanticide is a complex task, but there are several variables that might be informative. First, we might assess this risk by considering **whether infanticide occurs or not** in a particular taxon – presumably, if infanticide is sometimes seen, then the risk is there! However, the converse is not necessarily true; if infanticide is not observed presently this can be the result of successful counter-strategies despite a risk in the evolutionary past. We might also assume that relative infanticide risk in different taxa might be related to **breeding seasonality or synchrony**; if breeding is strongly seasonal, or synchronized among females, then the risk of infanticide is argued to be lower, as males may not be able to induce females to begin cycling again by killing their offspring. When considering the seasonality of breeding, it is thus necessary to evaluate if the taxon has a reproductive "time out", a period during lactation when they cannot conceive. Indices of infanticide risk that are commonly used in comparative studies consider the **lengths of the gestation (*G*) and lactation (*L*) periods** (with the latter being operationalized as weaning age). Opie et al. (2013), for example, used the ratio of $L/(G+L)$ as an index of risk, whereas Lukas and Clutton-Brock (2014) simply assessed whether lactation is longer than gestation. Thus, data on observations of infanticide, breeding seasonality, gestation length and weaning age are considered central to evaluating the infanticide prevention hypothesis.

In the abstract for their article, Opie et al. (2013) stated that they combined trait data across 230 primate taxa, a set which includes five owl monkey species, two titis, no sakis, and five tamarins. Relevant for consideration of the hypothesis is how many taxa actually contributed data to the comparative analyses of "infanticide risk" in "monogamous" primates. Of these 230 taxa, the authors classified 16 as "Data Deficient" (DD) for the character of mating system; of the remaining 214 taxa, 32 were classified as "monogamous", but of those, four were deemed DD for the character of infanticide, leaving 28 supposedly pair-living taxa for consideration. Opie et al. (2013) classified two of these as "High Infanticide" (i.e., "where infanticide has been widely documented") and 26 as "Low Infanticide" (i.e., "where infanticide has not been reported or is thought to be rare").

Opie et al. (2013) considered there is enough evidence for assessing the existence of infanticide in all five *Aotus* taxa included in their analysis, given the number of publications they found in the searches they conducted. We disagree with this assessment since there have been no studies of wild owl monkeys, besides *A. azarae*, that provide any information on the variables mentioned before. The only titi species that Opie et al. (2013) considered to be "well studied" is *Callicebus moloch* (or rather *Plecturocebus moloch*); it has indeed been studied, but primarily in the laboratory from which most publications arise, and this laboratory population is now attributed to *P. cupreus* rather than *P. moloch*. As noted above, there have been no field studies conducted on *P. moloch*. No saki taxa were included in Opie et al.'s (2013) dataset. We have no explanation for their lack of consideration of this genus, on which there have been definitely more than 20 publications, focusing on multiple aspects of their behavior, in both the wild and captivity (Norconk, 2006, 2011; Shideler, Savage, Ortuno, Moorman, & Lasley, 1994; C. L. Thompson, Norconk, & Whitten, 2012).

Regarding tamarins, Opie et al. (2013) classified all five *Saguinus* species in their dataset with regards to the existence of infanticide as "low risk". We disagree with this assessment; we deem that there is not enough data from wild populations to classify them all. There have been no studies of wild "*Saguinus" fuscicollis*; the populations formerly considered under this name are now considered *Leontocebus weddeli* or *L. nigrifrons*. Only one 9-month study on a wild population, concerned with sleeping site use, has been conducted on *Saguinus midas* (Day & Elwood, 1999). There have been studies of *S. geoffroyi, S. oedipus*, and *S. imperator* in the wild, but whether these taxa have been studied thoroughly enough to justify classifying them requires careful consideration of the primary literature. Furthermore, we cannot understand the omission from their analyses of *S. mystax*, which has studied extensively in the wild (Culot et al., 2011; P. A. Garber, 1988; P.A. Garber, Encarnacion, Moya, & Pruetz, 1993; Eckhard W. Heymann, 1990; Maren Huck, Löttker, Böhle, et al., 2005; M. Huck et al., 2004; P. Löttker et al., 2004; Norconk, 1990).

Lukas and Clutton-Brock (2014, 2015) classified all titis and all but one owl monkeys species as “Not Available” (NA) for data on "Male Infanticide", while sakis and *Aotus trivirgatus* were scored as showing no infanticide. For the tamarins, they classified all species apart from “*S. fuscicollis*” and *S. oedipus* as NA, while these two species were considered to show no male infanticide. Again, we cannot understand all of these decisions, as Lukas and Clutton-Brock (2014) state that they analyzed Opie et al.'s (2013) dataset, but the latter does not, in fact, include any *Pithecia* species.

Opie et al. (2013) also classified the owl monkey species we study (*A. azarae*) as “seasonal breeders with time out”, and the remainder of the owl monkey taxa as “seasonal breeders without time out”. “Time out” in this context refers to times when an individual is not available in the mating pool. We agree with the classification of our taxon of study (Eduardo Fernandez-Duque, Rotundo, & Ramírez-Llorens, 2002), but not with the classification of the other four *Aotus* taxa, for which there are extremely limited data from the wild (Eduardo Fernandez-Duque, 2011, 2012; E. Fernandez-Duque, Corley, & Spence-Aizenberg, 2013). Most publications on those four taxa come only from studies of captive colonies of owl monkeys (Garcia de la Chica et al., in press). We are also puzzled by their consideration on the existing data on tamarins to assess seasonality. The authors classify “*Saguinus fuscicollis*” and *S. oedipus* as non-seasonal breeders, even when *Leontocebus weddeli* (one of the species formerly considered *S. fuscicollis*) had 75% of births occurring within 4 months and a five-month period during which births never occurred (A. W. Goldizen, Terborgh, Cornejo, Porras, & Evans, 1988). Likewise, *L. nigrifrons* – another species formerly classified as *S. fuscicollis* – had numerous births concentrated during seven months and a five-month period with no births (Slana, 2019). They did not classify the three other tamarin species in their table. In the absence of information on birth seasonality for these three species, we do not understand why they included them in their evaluation of infanticide risk, providing values for the estimated infanticide risk index. The argument might be yet more complicated for tamarins (and callitrichines in general), since on the one hand there are several studies of captive individuals that have shown that they experience a postpartum estrous, which would allow females to conceive while lactating (Kholkute, 1984; Toni E Ziegler, Savage, Scheffler, & Snowdon, 1987; T. E. Ziegler, Snowdon, & Warneke, 1989), but on the other hand there are at least two studies from wild populations indicating that females might actually experience postpartum amenorrhea (Petra Löttker, Maren Huck, Eckhard W Heymann, et al., 2004; A Savage et al., 1997).

Of the 28 taxa they classified only as “monogamous” and not DD for infanticide, Opie et al. (2013) reported data on gestation length and weaning age for only 15 of them. Among those 15 species, five belong to genera we study. A gestation length of 133 days is reported for *A. lemurinus griseimembra* and *A. trivirgatus* and of 131 days for *A. nancymai*, while no data are reported for *A. azarae* and *A. infulatus*. The value of 133 days appears to correspond to a record for *A. griseimembra* (Hunter, Martin, Dixson, & Rudder, 1979); we could not find any other published account of a gestation length of 133 (or 131) days for any other species of owl monkey. There are, however, published accounts for other species that Opie et al. (2013) did not cite that provide values other than 133 days (Eduardo Fernandez-Duque, 2011; Málaga, Weller, Buschbom, Baer, & Kimsey, 1997; Montoya, Moro, Gozalo, & Samame, 1995; Wolovich et al., 2008).

Opie et al. (2013) reported data on gestation length for *Callicebus* (now *Plecturocebus*) *moloch* (164 days) citing Smuts et al. (1987), but no data are reported for *Plecturocebus donacophilus*. Smuts et al. (1987) listed 167 and 160 days (p. 49, Table 5-3), citing both Wright (1985) and D. Fragaszy (personal communication). Yet, Wright (1985) did not evaluate hormonally the individuals she studied, so it is unclear how she estimated gestation length in the wild. Nevertheless, there are estimates of 122-135 days (8 pregnancies) from captive animals that are now considered *P. cupreus* (Valeggia, Mendoza, Fernandez-Duque, Mason, & Lasley, 1999). Opie et al. (2013) did not provide data on *Pithecia*, even when there are data reported in the reference cited (164 days for Pithecia pithecia Ross, 2003, p. 271, Table 11.2). Similarly, Savage (1995) estimated 146 days for the same species. Lukas and Clutton Brock (2013), who coded species based only on whether lactation is longer than gestation length, indicated NA for all three of these taxa. For the tamarins, Opie et al. (2013) provided values of 150 days for the gestation length of "*Saguinus fuscicollis*", 145 days for *S. geoffroyi*, 127 days for *S. midas*, and 168 days for *S. oedipus*. The gestation length of *Leontocebus fuscicollis* (species identity confirmed by M. Heistermann, personal communication) has indeed been estimated as 148 – 152 days (N = 3 births) in captivity (Heistermann & Hodges, 1995). The value for *S. midas* seems to have been obtained from Harvey and Clutton-Brock (1985), who do not provide any references for the data. We were not able to find any published studies on gestation length for *S. midas*. For *S. oedipus*, we found an estimated gestation length of 184 days (6 captive females)(T. E. Ziegler, Bridson, Snowdon, & Eman, 1987). A captive study that briefly housed a pair of cotton-top tamarins together stated that the gestation length was between 166 and 202 days (Brand, 1981). We also do not know from where Opie et al. (2013) got the estimated value of 145 days for *S. geoffroyi*. They may have used Epple (1970) who states for one female that "the estimated gestation period is 140 – 150 days", without indicating on what this estimate is based, and furthermore for a female that was described to suffer from chronic illness with several abortions. The only primary source we found reported a rough estimate of 182 d for a captive population based on the difference between mean inter-birth intervals and an estimated cycle length using endocrine profiles of 23 days (Kuhar, Bettinger, Sironen, Shaw, & Lasley, 2003). Thus, we found agreement only for one of the four tamarin species, and reliable estimates for gestation lengths for only two species.

The data on weaning age reported from secondary sources are equally problematic, as discussed above (Table 6). A weaning age of 60 days is reported for *P. moloch* in the cited reference. Ross (2003, p. 271, Table 11.2) reported a weaning age of two months, citing Fragaszy (1982) and of nine weeks, citing Wright (1984). However, based on endocrine profiles, Valeggia and colleagues (1999) estimated it to be 195 days for captive *P. cupreus*. Similarly, we were not able to find the original sources for the weaning ages of the tamarin species. The values, ranging from 50 – 90 days for the four tamarin species provided by Opie et al. (2013) come from Harvey and Clutton-Brock (1985), who do not provide their sources, nor a definition of weaning. The weaning age of 50 days reported for *S. oedipus* likely stems from French (1983) who, without providing methodological details, states that "weaning is initiated around 50 days of age" – initiated, not weaned. In contrast, a study on captive cotton-top tamarins that lasted 20 weeks still recorded occasional nursing at 20 weeks of age (Cleveland & Snowdon, 1984).

[INSERT TABLE 6 ABOUT HERE]

Finally, for comparison with the data reported in these two comparative studies, we evaluate the data generated from our own research. We have studied owl monkeys, titis, and sakis for 23, 17, and 17 years respectively, and tamarins (*Saguinus mystax* and *Leontocebus nigrifrons*) have been studied at the EBQB for over 22 years, and we have absolutely **no evidence** that male infanticide occurs in any of these taxa. Thus, we do not consider our study taxa to be "Data Deficient" *sensu* Opie et al. (2013).

All four taxa we study can be considered "seasonal breeders with time out", with births being concentrated almost exclusively in a three-month period for *Aotus azarae* (Eduardo Fernandez-Duque et al., 2002), in five and seven months for *Plecturocebus discolor* and *Pithecia aequatorialis* (Van Belle, Fernandez-Duque, et al., 2016), and in eight months, with a clear peak in two, for *Saguinus mystax* (P. Löttker et al., 2004). Although we have no solid data from the field, research in captive individuals suggest that there is some evidence for lactational amenorrhea for *Aotus*, Callicebinae*,* and *Pithecia*; therefore classifying them as seasonal breeders with some "time out" seems reasonable. In the population of tamarins we have studied, the two reproducing females in two different groups showed hormonal profiles after birth that were "flat", resembling the profile of non-ovulating sub-adults, which suggests that these females did indeed experience lactational amenorrhea (Petra Löttker, Maren Huck, Eckhard W Heymann, et al., 2004).

We have estimated gestation length for *Aotus azarae* to be 120 – 140 days (N = 2 females, E. Fernandez-Duque et al., 2011), and this is the only owl monkey taxon for which there is information available on gestation length from wild individuals. We unfortunately have no information on gestation length for *P. discolor* and *P. aequatorialis* from wild individuals. Age at weaning, estimated as the age when individuals are not seen nursing, for wild *A. azarae* is between 150–240 days (N = 7 infants, Rotundo et al., 2005). For red titis, we have data suggesting that two infants were still nursing at 60 days and two were still nursing at 90 days of age. We unfortunately do not have any data from our field studies on weaning age in either *P. aequatorialis* or *S. mystax*, but the latter are usually considered to be weaned (and to be classified as juveniles rather than infants) by three months of age (A. Goldizen et al., 1996; see also P. Löttker et al., 2004; Soini & Soini, 1990). For example, three moustached tamarin infants from two litters in different groups were last seen carried at between 104 and 114 days (Maren Huck, Löttker, Heymann, & Heistermann, 2004).

The final step is to compute the proportion *of L/(G+L)* as a quantitative index of the risk of infanticide. Of the four genera that we study, Opie et al. (2013) obtained the same value of 0.36 for three owl monkey taxa, a value of 0.27 for one titi species, and four values ranging between 0.23 and 0.38 for four tamarin species. With the limited data we have on gestation length and weaning age from the taxa we study, we could compute the proportion for only *Aotus azarae*. Given the range of ages for weaning we documented (Table 6), we computed two proportions, one using the values to obtain the minimum possible proportion (i.e., biased in favor of the infanticide prevention ypothesis) and one for the maximum (counter to the hypothesis). The estimated minimum and maximum values (0.52 – 0.67) are almost twice as large as the value of 0.36 reported by Opie et al. (2013), and within the range of infanticide risk values reported for polygynous taxa (mean = 0.59, range: 0.36 – 0.83), and higher than the mean for monogamous taxa (mean = 0.49, range: 0.27 – 0.73).

CONCLUSIONS AND LOOKING FORWARD

In this work, our goal has been to present an overview of the progress our discipline of biological anthropology has made in understanding the evolution of "monogamy" in non-human primates. We found it necessary to begin such attempt on the solid foundations of a clearly defined terminology, leaving aside vague terms like "monogamy" or "social monogamy". Instead, we have relied on our proposed terminology (Figure 1) to briefly describe the set of hypotheses that are usually considered to explain pair-living, pair-bonding, sexual monogamy, genetic monogamy, biparental care, and cooperative infant care. We then reviewed and critiqued some recent comparative studies that focused on these issues, paying special attention to how these studies have characterized and analyzed data on four platyrrhine genera on which we have worked extensively in the field for almost three decades.

Our studies have convincingly shown that owl monkeys and titis are pair-living, sakis are sometimes pair-living, and tamarins are primarily not pair-living. Owl monkeys and titis are consistently sexually monogamous; for sakis, whether they are sexually monogamous or not depends on whether or not they are pair-living; and tamarins are not sexually monogamous. Information on genetic monogamy is much scarcer. We have reported genetic monogamy among owl monkeys, and some preliminary results indicate that titis are mostly genetically monogamous, as are sakis when they are pair-living. In tamarins, the picture is more complicated, with at least some populations showing a degree of monopolization of paternity, despite the occasional occurrence of multiple paternity even within litters. It is only for captive titi monkeys that there are solid data to suggest pair-bonding; whether titi monkeys or any of the other taxa show physiological evidence of pair-bonding in the field remains completely unexplored. Identifying and characterizing a "discernable attachment to one another" (i.e., evaluating pair-bonding) remains challenging under field conditions. We, therefore, cannot draw strong conclusions about pair-bonds in owl monkeys, sakis, and tamarins.

What may have been the important drivers that have shaped the social organization, social structure, mating system, and care patterns of owl monkeys, titis, sakis, and tamarins? We found only very limited support for the **infanticide prevention hypothesis** for the four species we have studied (*Aotus azarae*, *Plecturocebus discolor*, *Pithecia aequatorialis*, and *Saguinus mystax*). For starters, there is no evidence that infanticide occurs in any of the populations of these taxa that we have studied in Argentina, Ecuador, and Peru. Secondly, we expect that the risk of infanticide should be low because the populations of owl monkeys and titis, and to a lesser extent of sakis and tamarins at our field sites experience pronounced breeding seasonality, thus creating a reproductive “time out” during certain times of the year. Thirdly, our calculation of the infanticide risk index for owl monkeys, using the methods of Opie et al. (2013), provides a value comparable to that of polygynous primates rather than "monogamous" ones. Information on gestation and lactation length for titis, sakis, and tamarins is lacking, precluding calculation of the index for these species.

We also found inconsistent support for the **female distribution hypothesis** for the four species we studied. Both titis and sakis have limited home range overlap with neighboring groups, which is consistent with the hypothesis, while owl monkeys and tamarins have extensive overlap, which is inconsistent with the hypothesis. Home ranges within the owl monkey, titi, and saki populations vary considerably in size, suggesting that males might be able to range across the home ranges of more than one female, which is inconsistent with the hypothesis. Alternatively, the **mate-guarding hypothesis** predicts that males should not seek to mate with other females, even if they are able to cover the ranges of more than one female, and that female reproductive synchrony might limit the reproductive opportunities for males outside the pair. We observe both of these patterns in owl monkeys and titis, which supports this hypothesis.

In owl monkeys, female distribution might be driven by food availability during periods of extreme food scarcity, particularly in the frequently used core areas (Eduardo Fernandez-Duque, 2016). Thus, despite substantial overlap among home ranges, the minimal overlap among neighboring core areas is consistent with the **female distribution hypothesis**. No such data are available for the other species. If ecological factors mediate female distribution and, subsequently, social organization and mating system, we would expect to see deviations from pair-living and sexual monogamy when ecological conditions are more favorable. However, based on our review of the literature, it seems that throughout the geographic distribution of owl monkeys and titis, virtually all species are pair-living, making it unlikely that ecological factors are the sole or primary driver of that form of social organization in these two taxa. In contrast, *Pithecia aequatorialis*, as well as other saki species, deviate from pair-living, and groups sometimes contain multiple breeding females and mating males (Porter et al., 2017; C. L. Thompson, 2013; Van Belle, Fernandez-Duque, et al., 2016). It has not been investigated whether this variation is associated with fluctuations in food availability in space or time. *Saguinus mystax*, along with other tamarin species, also deviates from pair-living groups. In fact, tamarins in the wild rarely live in pairs, nor are they sexually or strictly genetically monogamous (Paul A. Garber et al., 2016).

Finally, there is evidence for a strong association between paternal care and pair-living for both owl monkeys and titis that is consistent with the **infant care hypothesis**. These species show some of the highest levels of paternal care in mammals and both live in strictly pair-living groups. Additionally, owl monkeys are strictly genetically monogamous, whereas our preliminary paternity results for titis suggest that, occasionally, an offspring lives in a group with an adult male who is not its sire. Whether this is due to extrapair breeding or to adult turnover is not yet conclusively known. Paternal care in the form of food sharing is present in sakis, but there is limited evidence of other forms of care. Despite the regular deviation from pair-living groups, tamarin males engage in paternal care, and extensive care is provided by other group members as well.

The examination of evolutionary hypotheses can certainly benefit from studies developed in a comparative framework. In fact, comparative studies are critical for advancing our understanding of the evolution of pair-living and sexual monogamy in mammals and primates, including humans. But, the quality of those comparative studies is wholly contingent on the quality of data they are based on. We of course expected to see some disagreement between the data presented in the large datasets used in the comparative studies we examined and specific data available in primary sources, in part due to challenges related to operationalizing variables of interest across studies conducted by different research groups at different times using disparate definitions and methods. Indeed, we are by no means the first to point to this as a serious issue in comparative research (e.g., Borries et al., 2016; Dey et al., 2019; Schradin, 2017; Stokes & Sandel, 2019; Taborsky et al., 2019; Valomy et al., 2015). Still, we are alarmed by the magnitude and frequency of the disagreements we have noted in our review of just four genera with which we have direct experience. Not least are we concerned with the unthinking classification of callitrichines, or even sakis, as pair-living or sexually monogamous. Based on our review of the *literature actually cited* in the two seminal comparative studies that have looked at the "evolution of monogamy", on our own search for and review of *further relevant literature*, and on primary data we have collected through more than 20 years of *fieldwork* on species of each of these genera, we would argue that there is little reason to put any stock in the conclusions of these studies. Further, we would argue that continuing to cite and refer to the results of these studies as somehow advancing our understanding of the evolution of pair-living and sexual monogamy in primates and mammals is simply unjustified. In saying this, we want to stress that we are not making any claims about the validity or lack thereof of the underlying hypotheses being examined. For example, in challenging Opie et al.'s (2013) assertion that "Male infanticide leads to social monogamy in primates" we are not discounting the potential importance of infanticide as a male reproductive strategy that may have shaped many aspects of primate behavioral biology, morphology, cognition, and the like – including, plausibly, the evolution of pair-living and sexual monogamy. Rather, we are saying that the comparative dataset mustered to "test" this idea is woefully inadequate.

Now, it is undoubtedly true that more **natural history data** on wild populations of pair-living species from across the primate radiation could potentially help this situation, and we would love to see granting agencies commit to supporting more long-term natural historical research on little-studied and, especially, at-risk primate taxa. Additionally, it would be valuable to also collect information on flexibility and variability in grouping patterns, social structure, mating behavior, female ranging patterns, and levels of male care in these taxa (Strier, 2017, 2018). Such variation within pair-living (e.g., owl monkeys and titi monkeys, and to a lesser extent sakis, but not tamarins) and sexually monogamous species (e.g., owl monkeys and possibly titi monkeys, less likely sakis, but again not tamarins) is rarely considered in broad-based comparative studies, where the need to distill information on traits of interest for a particular taxon to single data points can compromise confidence in an analysis and its results (Patterson et al., 2014; Sandel et al., 2016).

However, most of the problems we have identified will remain even if we had the largest dataset on all living taxa. It is not a matter of just adding more data. One solution that is already available and that does not require commitment of additional time and funding is to take certain steps that will make the most of existing data. We offer below a few suggestions we like to invite the biological anthropology community to consider:

[1] Commit to **transparency and reproducibility** in our research design, and methods of data collection and analysis (Martin, 2019; Turner & Mulligan, 2019). Fully developed, clearly presented methods should be included within the main article of every publication. Methodological details matter, and we think we should push back against the increasing tendency to relegate this important component of our work to "supplementary" information; information to be found, when lucky, after navigating uncountable links and pages. These details should also include exact locations of study populations, to facilitate determining which species the study was conducted on, in case of changing taxonomy.

[2] Consider conducting comparative studies **at a smaller scale**, limiting them to those taxa for which data are, demonstrably, comparable and of high quality (Borries et al., 2016). This will mean setting out and following clear criteria for what constitutes acceptable evidence for inclusion or exclusion of a datum.

[3] Explicitly **acknowledge the limitations** of our studies formally in our publications. For example, articles could include a fully developed section on "limitations and caveats". This is a common practice in some of the top journals in political science and economics, disciplines where, as in biological anthropology, observational (rather than structured experimental) data are the norm and research design and data analysis limitations are plentiful (Janson, 2012; R. J. Smith, 2019).

[4] Encourage researchers to present **alternative hypotheses**, both when outlining the conceptual models of our studies and when interpreting results. We have always known that most biological phenomena do not have a single cause (Hilborn & Stearns, 1982; Platt, 1964), still too much of our published work continues to have a "single cause" approach, from the design of the study to the interpretation of findings. Articles could include full subsections considering confounding effects, masking effects, and sampling biases when analyzing data and interpreting results (e.g., Hernán, Hernandez-Diaz, Werler, & Mitchell, 2002; Hernán & Robins, 2020; R. J. Smith, 2019).

[5] Explain and explore the **internal validity of the variables** used in our studies. Many variables in biological anthropology are not only measured with error, but are also defined with error (R. J. Smith, 2019). For example, in the study of pair-living it is common practice to identify, define and measure variables that we consider will be informative of the phenomenon of theoretical interest, in this case the existence and characteristics of a bond between pair-mates. Distance, proximity, approaches are some standard variables of such studies. Whereas "distance" can possibly be both defined and measured with little error, "proximity" and "approaches" not only are more difficult to quantify but require another level of expertise for both measuring it and defining it.

To conclude, we think that it is important to reiterate one hugely important point, which Smith (2019) has also stressed in a recent – often brilliant – "Theory and Synthesis" article published in the *American Journal of Physical Anthropology*. He emphasizes that in biological anthropology our data are *inherently observational*, and, as such, we in our field need to be much more conscientious and careful in our discussions of "effects", "evidence", and "causation". One of the wonderful features about our discipline – and one that has motivated our fieldwork personally – is that many of us engage with the **natural world**, in all its messiness and complexity. We typically do not find ourselves in situations where we can control for all sources of variation in who, what, or when we sample. To a large extent, the animals we might observe in the wild, the research sites where we might work, and the fossils that we might find are opportunistic and, in ways we may or may not understand, are biased subsets of subjects. We **do not** have the luxury of being able to appropriately control and randomize the samples we collect, which in most cases is a central prerequisite for robust causal inference. Moreover, many of our subjects (e.g., individual primates, fossil specimens) and many of the sites where we work share connections and histories that we are not privy to, connections that can be phylogenetic, involving common ancestry in either the recent or more distant past, as well as experiential (such as growing up in the same environment or in the same social group). All of this complicates the interpretation of patterns we may see and find interesting and makes it difficult – and often impossible – to attribute causation to those patterns and relationships. As a field, we can, and should acknowledge and embrace the uncertainty in our research (Wasserstein, Schirm, & Lazar, 2019).

Additionally, we also need to remain cognizant of what sources of variation we can "control for" and what that "control" means. In the best phylogenetic comparative methods, for example, "control for" phylogeny in the **statistical** sense only means that they are useful for correcting for one particular aspect of common history (the amount of evolutionary change measured on a particular scale that separates two taxa) and may not adequately control for other dimensions that those taxa have in common (e.g., living in similar versus divergent environments). To bring this back to the current issue, for example, even if we were convinced that pair-living or sexual monogamy is more common in taxa that have higher "weaning proportions", that finding would offer, at best, weak support for drawing a causal **inference** between the risk of infanticide and pair-living or sexual monogamy.

Why are some species of primates pair-living and sexually monogamous? We stated it at the beginning, but it is worth repeating here: it has never been our goal to find "an" answer, much less "the" answer. It is very unlikely that there will be any single unitary explanation for the kinds of phenomena that many of us are interested in, like the functional relevance of pair-bonding, or the distribution of sexual monogamy across the primate radiation, much as we would like to paint a convincing story. Social systems are complex, primates (and many other animals) are complex, and historical contingency and random chance matter.

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FIGURE LEGENDS

Figure 1. Preferred terms for referring to different components of "monogamous" social systems and brief definitions of those terms; see text and Huck et al. (2019) for additional details. Figure inspired by Reichard (2017) and Kappeler (2019).

Figure 2. Field sites where the authors have studied titi monkeys, sakis, owl monkeys and tamarins. Red rectangles in the map on the right indicate the regions of Ecuador, Peru, and Argentina where the field sites are located, with the three maps on the left showing details of these areas. Areas shaded in tan represent the countries of Ecuador, Peru, and Argentina. Rivers and bodies of water are shaded in blue. Roads and provincial and country boundaries are indicated in black. Green areas indicate national parks and other nominally protected areas. Field site locations are indicated by red diamonds in the detailed maps. Top (A): Tiputini Biodiversity Station (Yasuní National Park and Biosphere Reserve, Orellana and Sucumbios Provinces, Ecuador). Middle (B): Estación Biológica Quebrada Blanco (Loreto Province, Peru). Bottom (C): Reserva Privada Mirikiná, Estancia Guaycolec (Formosa Province, Argentina).

Figure 3. Owl monkeys (*Aotus azarae*) at Reserva Privada Mirikiná, Estancia Guaycolec, Formosa, Argentina (top left); sakis (*Pithecia aequatorialis*) and titis (*Plecturocebus discolor*) at the Tiputini Biodiversity Station (top right and bottom left), Yasuní National Park, Ecuador; and tamarins (*Saguinus mystax*) at the Estación Biológica Quebrada Blanco, Peru (bottom right). Photo credits (respectively): E. White/Owl Monkey Project, Formosa-Argentina; S. Van Belle/Proyecto Primates; S. van Kuijk/Proyecto Primates; P. Löttker.

Figure 4. Home ranges of owl monkeys (top left, *Aotus azarae*, N = 18 groups) in Reserva Privada Mirikiná, Estancia Guaycolec, Formosa, Argentina, of sakis (top right, *Pithecia aequatorialis*, N = 6 groups) and titis (bottom left, *Plecturocebus discolor*, N = 5 groups) at the Tiputini Biodiversity Station, Yasuní National Park, Ecuador, and of tamarins (bottom right, *Saguinus mystax*, N = 2 groups) at the Estación Biológica Quebrada Blanco, Peru.

Figure 5. Population densities for various species of owl monkeys, titis, sakis, and tamarins reported in the PanTHERIA database (orange, http://esapubs.org/archive/ecol/E090/184/) and found in the primary literature for this study (blue, see Table 3). The solid black line across the figure is the median population density reported for "socially monogamous" mammalian taxa, as calculated by Lukas and Clutton-Brock (2013). The box plots represent the median, 1st and 3rd quartiles with the lower whiskers including values ≥ 1st Q – 1.5 * IQR (interquartile range) and upper whiskers including values ≤ 3rd Q + 1.5 * IQR. Population density values >75 ind/km^2 are omitted from the figure. Population densities for *Aotus azarae* and *Plecturocebus discolor* from our studies are indicated with accompanying text next to the data point.

Figure 6. Home range sizes (ha) reported in the PanTHERIA database (orange, http://esapubs.org/archive/ecol/E090/184/) and found in the primary literature for this study (blue, see Table 4). The lower black line, across the figure, is the median home range for "socially monogamous" taxa, and the upper black line, across the figure, is the median home

range for solitary species, as calculated by Lukas and Clutton-Brock (2013). The box plots represent the median, 1st and 3rd quartiles with the lower whiskers including values ≥ 1st Q – 1.5 * IQR (interquartile range) and upper whiskers including values ≤ 3rd Q + 1.5 * IQR.

Figure 7. Percent home range overlap as reported in Pearce et al. (2013) (red) and in the primary literature (blue, see Table 5). The lower black line is the median home range overlap for "socially monogamous" taxa, and the upper black line is the median home range overlap for solitary species, as calculated by Lukas and Clutton-Brock (2013). The box plots represent the median, 1st and 3rd quartiles with the lower whiskers including values ≥ 1st Q – 1.5 * IQR (interquartile range) and upper whiskers including values ≤ 3rd Q + 1.5 * IQR.

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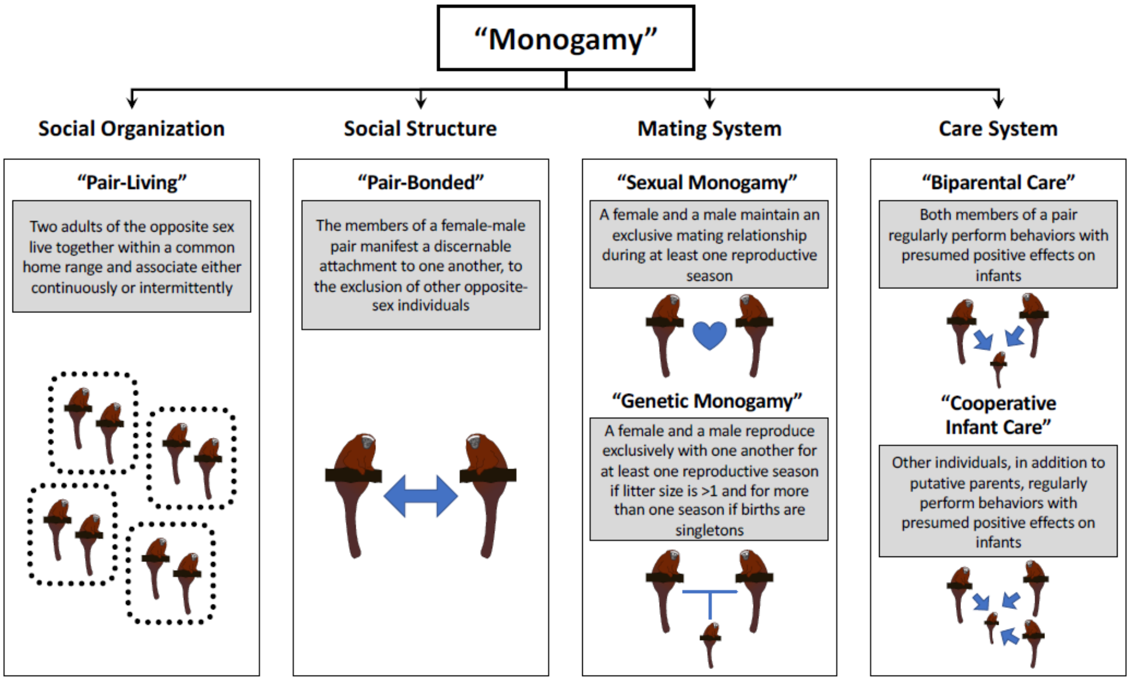
Figures



Two adults of the opposite sex live together within a common home range and associate either continuously or intermittently

The members of a female-male pair manifest a discernable attachment to one another, to the exclusion of other opposite-sex individuals

A female and a male maintain an exclusive mating relationship during at least one reproductive season

Both members of a pair regularly perform behaviors with presumed positive effects on infants

A female and a male reproduce exclusively with one another for at least one reproductive season if litter size is >1 and for more than one season if births are singletons

Other individuals, in addition to putative parents, regularly perform behaviors with presumed positive effects on infants

Fig. 1

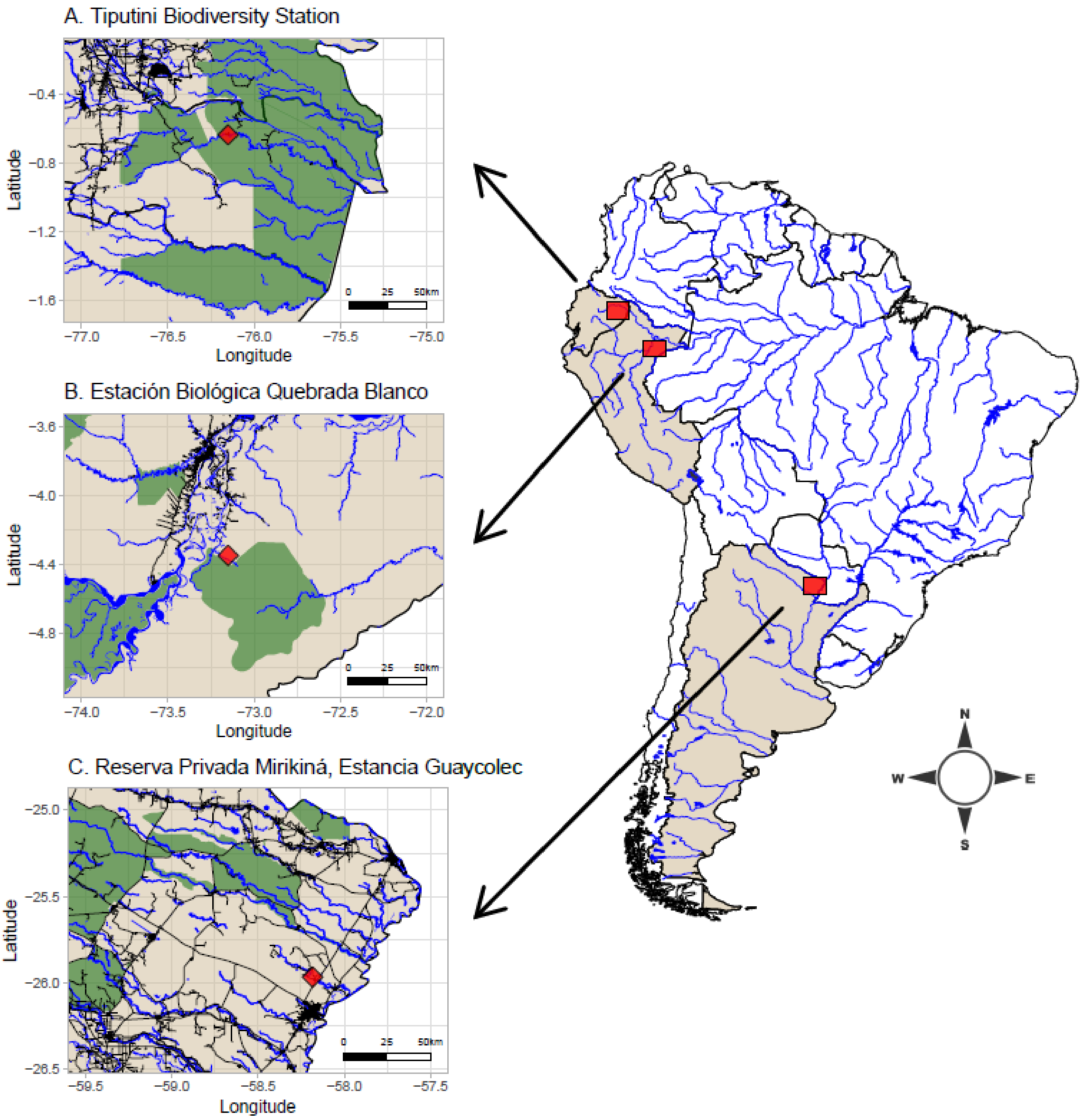

A. Tiputini Biodiversity Station
Latitude
−0.4
−0.8
−1.2
−1.6
−77.0
−76.5
−76.0
−75.5
−75.0
Longitude
0
25
50km
B. Estación Biológica Quebrada Blanco
Latitude
−3.6
−4.0
−4.4
−4.8
−74.0
−73.5
−73.0
−72.5
−72.0
Longitude
0
25
50km
C. Reserva Privada Mirikiná, Estancia Guaycolec
Latitude
−25.0
−25.5
−26.0
−26.5
−59.5
−59.0
−58.5
−58.0
−57.5
Longitude
0
25
50km
N
W
E
S

Fig 2.

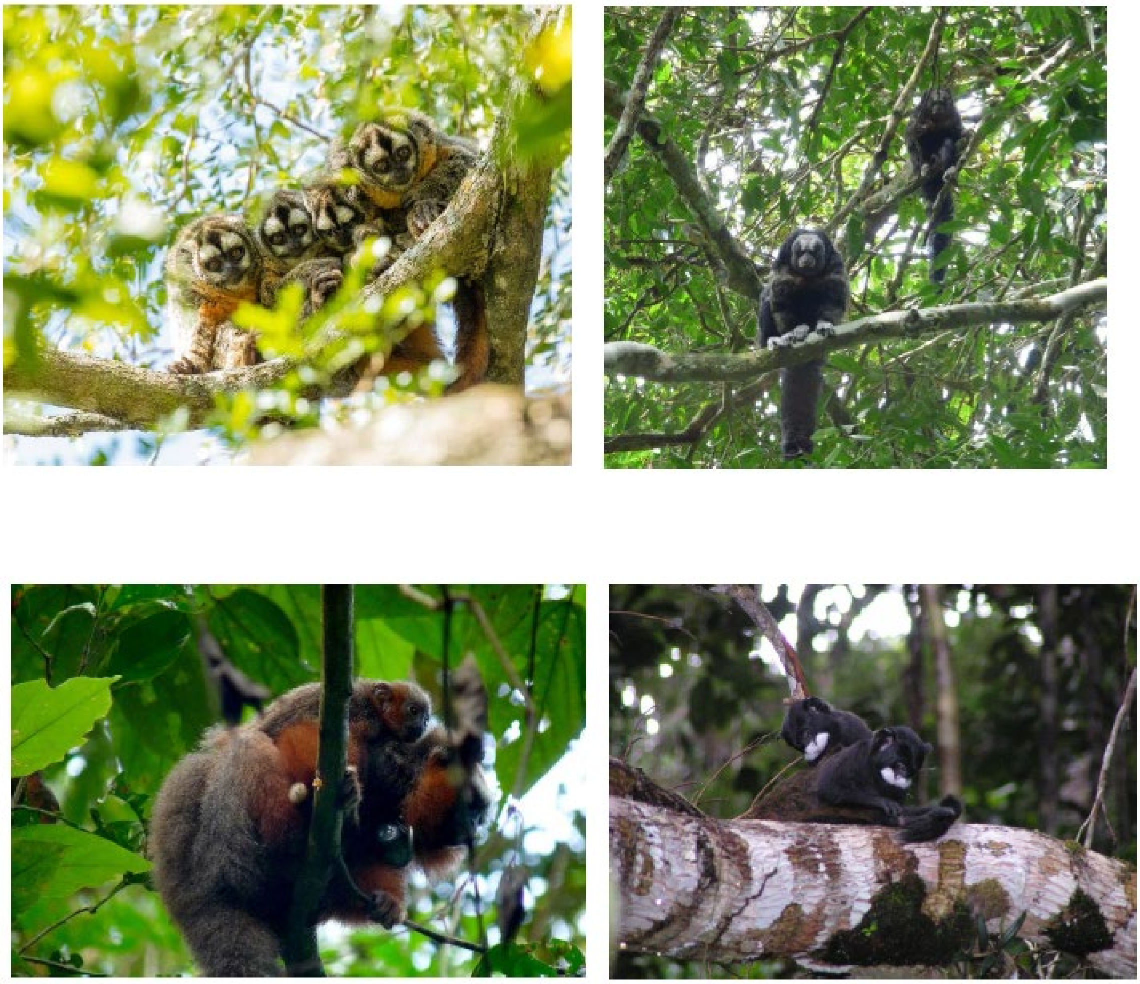


Fig. 3

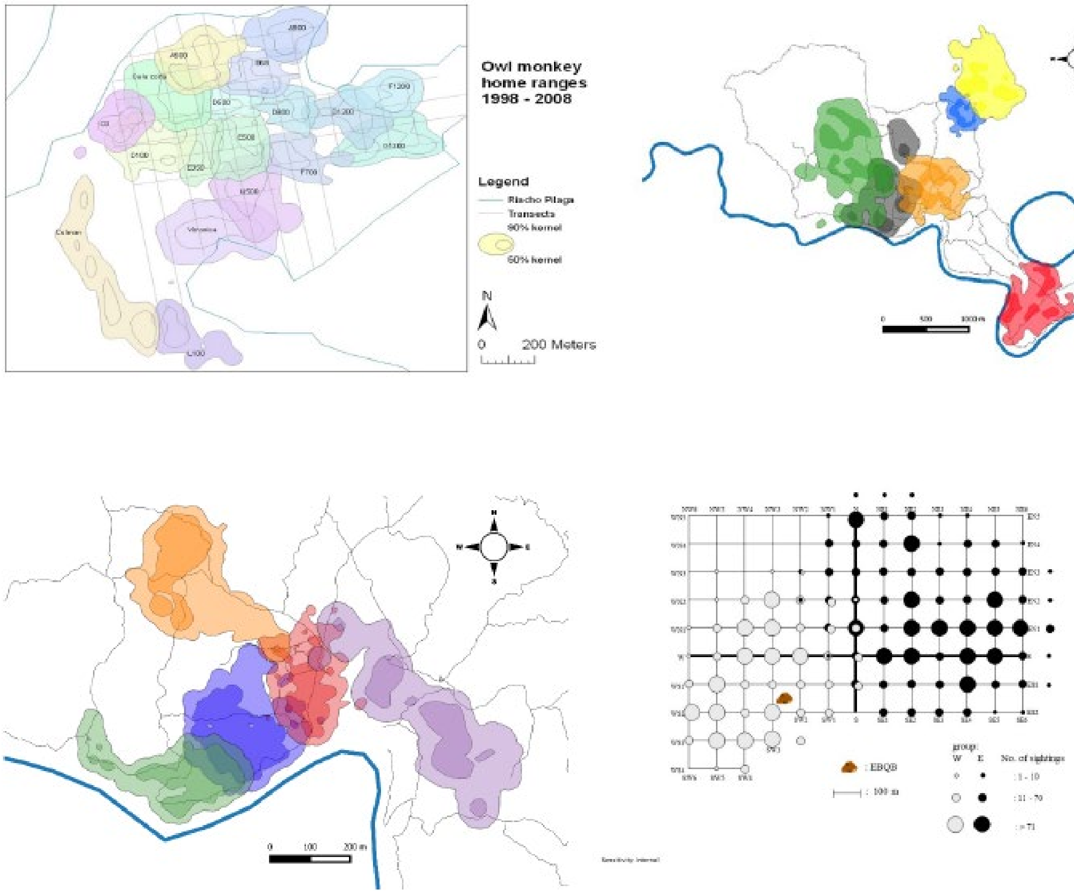

Owl monkey home ranges 1998 - 2008
Legend
Riacho Pilaga
Transects
90% kernel
50% kernel
N
0
200 Meters
A800
A900
Cola corta
D630
D900
D1200
F1200
D1300
E500
D1100
E350
F700
M500
Veronica
Coleman
L100
0
500
1000 m
0
100
200 m
: EBQB
: 100 m
group
W
E
No. of sightings
: 1 - 10
: 11 - 70
: > 71

Fig 4

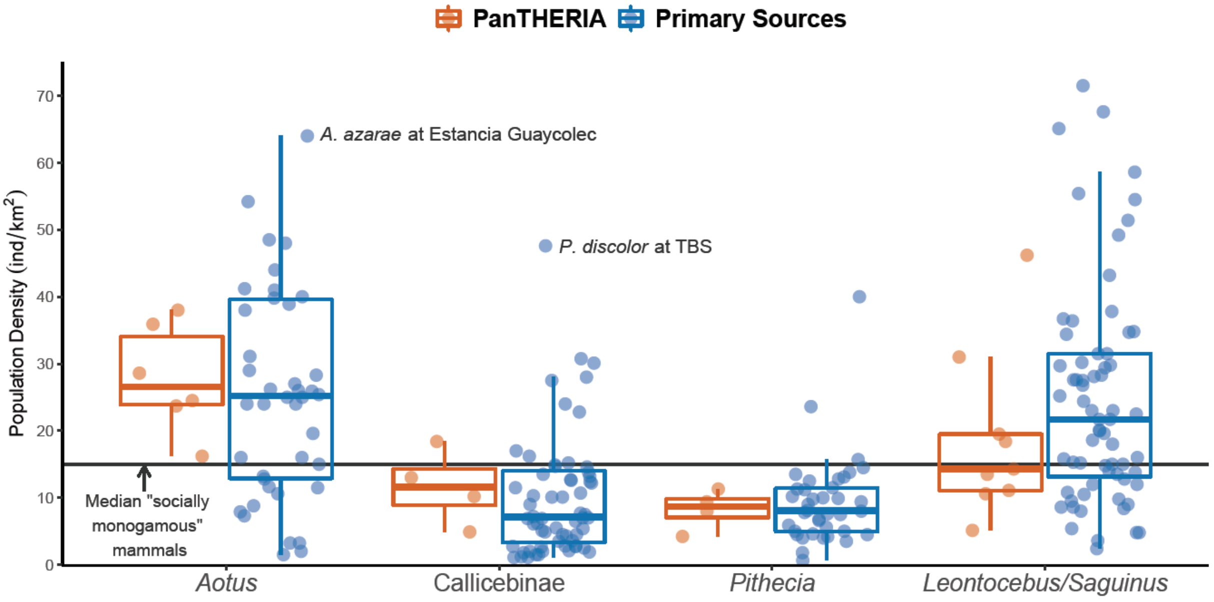

PanTHERIA
Primary Sources
Population Density (ind/km^2)
0
10
20
30
40
50
60
70
A. azarae at Estancia Guaycolec
P. discolor at TBS
Median "socially monogamous" mammals
Aotus
Callicebinae
Pithecia
Leontocebus/Saguinus

Fig 5.

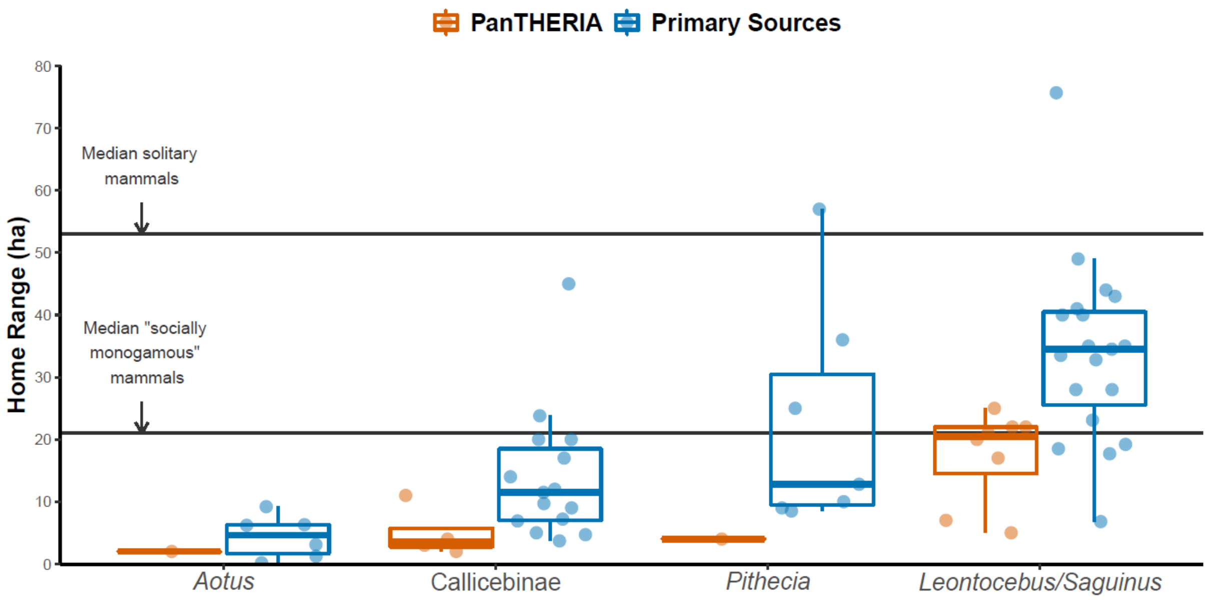

PanTHERIA
Primary Sources
Home Range (ha)
80
70
60
50
40
30
20
10
0
Median solitary mammals
Median "socially monogamous" mammals
Aotus
Callicebinae
Pithecia
Leontocebus/Saguinus

Fig 6.

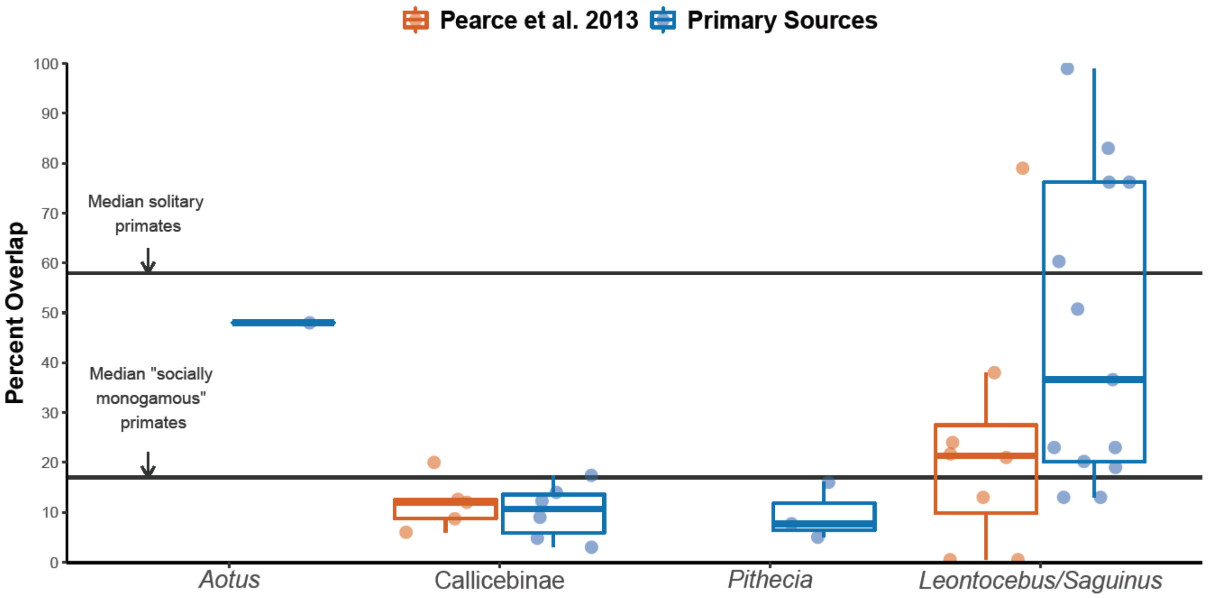

Pearce et al. 2013
Primary Sources
Percent Overlap
100
90
80
70
60
50
40
30
20
10
0
Median solitary primates
Median "socially monogamous" primates
Aotus
Callicebinae
Pithecia
Leontocebus/Saguinus

Fig 7.

Tables

Table 1. Agreement between body mass values (g) reported in the PanTHERIA database (Jones et al., 2009) for *Aotus* spp. and our own evaluation of body mass data available in primary sources (Fernandez-Duque, 2011). The % Difference column indicates how much larger or smaller the value in Jones et al. (2009) is when compared with our own assessment. For example, the PanTHERIA database reports for *A. brumbacki* a value of 603 grams that is 10% smaller than the one we found in the primary literature (665 grams). We considered to have agreement when the difference was ≤ 5%.

Species	(Jones et al., 2009)	Fernandez-Duque, (2011)		% Difference	Agreement?	Reference
	Median (grams)	Average (grams)	Range (min-max)			
Aotus brumbacki	603	665	455-875	-10	NO	(Hernández-Camacho & Defler, 1985)
Aotus nancymaae	795	930	760-1190	-17	NO	(Málaga, Weller, & Buschbom, 1991)
Aotus nancymaae	795	788.4		1	YES	(Aquino & Encarnación, 1986)
Aotus nancymaae	795	905.6	706-1055	-14	NO	Evans, S. (unpublished data)
Aotus hershkovitzi	800	no data			NO	
Aotus infulatus	800	1240		-55	NO	(Fernandes, 1993)
Aotus miconax	800	no data			NO	
Aotus vociferans	873	698		20	NO	(Montoya, Moro, Gozalo, & Samame, 1995)

Aotus lemurinus	881	889.8	578-1150	-1	YES	(Hernández-Camacho & Defler, 1985)
Aotus trivirgatus	912	736		19	NO	(Smith & Jungers, 1997)
Aotus trivirgatus	912	1000		-10	NO	(Fernandes, 1993)
Aotus azarae	963	1246	1010-1450	-29	NO	(Fernandez-Duque, 2004)
Aotus nigriceps	1060	1040		2	YES	(Peres, 1993)

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Table 2: Comparison of classification of male care behavior by two studies (Lukas & Clutton-Brock, 2013, LCB; Opie et al. 2013, OPIE) and evidence reported only in primary sources. Assessments that are not supported by the references provided in these studies are highlighted in gray, irrespective of whether supporting evidence is actually available or not. Numbers in superscript and between square brackets indicate the references listed in Supplementary Table 2. Dates provided in the "Comments" column indicate the date the species was searched for, using all recent synonyms, on Web of Science and Google Scholar. When the column "This Review" states between parentheses care as "(Present)", it indicates that the evidence for the assessment was judged as anecdotal, from captive studies only, or where methodology does not allow to conclude that researchers were really able to distinguish between adults.

	Male Care according to[0]				
Species	LCB	OPIE	This Review[1]	References this Review	Comments
Owl monkeys					
Aotus azarae	Present[1]	Present[2-4]	75%-92%	(Huck & Fernandez-Duque, 2012; Jantschke, Welker, & Klaiber-Schuh, 1998)	In a wild population of *A. a. azarae* with individually identified animals, infants were carried 75% of the time by males. However, the value is likely an underestimate, because some carrying observations occurred out of sight or when it was not possible to identify the carrying individual. The 92% relates to a captive population of *A. a. boliviensis.*
A. hershkovitzi	Present[1]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (28/Jul/2019).
A. miconax	Present[1]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (28/Jul/2019).
A. vociferans	Present[1]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (28/Jul/2019).
A. nancymaae	Present[1]	Present[2-4]	NA	NA	No relevant behavioral studies from the wild or captivity (28/Jul/2019).

A. infulatus	NA	Present[2-4]	NA	NA	No relevant behavioral studies from the wild or captivity (27/Jul/2019).
A. lemurinus griseimembra	Present[1]	Present[2-4]	(91%)	(Dixson & Fleming, 1981)	This refers to a captive study that ended after 18 weeks.
A. trivirgatus	Present[1]	Present[2-4]	NA	NA	While many studies claim to be on *A. trivirgatus*, these are all older studies before the revision of taxonomy (Hershkovitz, 1983). In most cases, it is not possible to determine from the information provided in the articles which species was actually used (e.g., Welker & Schäfer-Witt, 1987). In some other cases it is clearly referring to a different species (e.g. *A. zonalis* – see below). No relevant behavioral studies from the wild or captivity that is clearly on this species (27/Jul/2019).
A. nigriceps	Present[1]	NA	NA	NA	While Wright (1984)[5] studied *A. nigriceps* in the wild at Cocha Cashu National Park, Peru, the data on infant care behavior are from captivity from a presumably different species (from "Northern Colombia" origin, which could be one of several species). She must have assumed that males were main carriers in the wild, but she was not able to distinguish sexes. No relevant behavioral studies from the wild or captivity that is clearly on this species (28/Jul/2019).
A. zonalis	NA	NA	(Present)	(Moynihan, 1964)	The referenced study was conducted partly on captive (which mostly came from populations in

					Panama) and partly on wild individuals in Panama. While the study reports the species name as *A. trivirgatus*, it was most likely *A. zonalis*. The only text in the publication relating to male care states that by the time the infant was 3 weeks old, it was carried mostly by the father. For the wild it is unclear (and unlikely) whether it was possible to distinguish sexes.
Titi monkeys					
Callicebus barbarabrownae	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (25/Oct/2019).
C. coimbrai	Present[6]	NA	Present	(Santana, João Pedro, & Stephen, 2014)	A study on lactation in the species does not mention other infant care behavior (Souza-Alves, Caselli, Gestich, & Nagy-Reis, 2019). At the same study site, after the birth of twins (unusual for titi monkeys) the male carried the twins for the majority of time. The female carried the infants when nursing. A juvenile also carried occasionally but rather while resting (Santana et al., 2014). The author does not explicitly state how adults were individually recognized.
C. melanochir	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (10/Nov/2019).
C. nigrifrons	Present[6]	NA	(Present)	(Cäsar, Franco, de Castro Nogueira Soares, & Young, 2008;	One anecdotal report on a case of adoption mentions that "the adult male provid[ed] transport and care" (Cäsar & Young, 2008). The same research team (Cäsar et al., 2008) also

				Cäsar & Young, 2008)	refers to predominantly male carrying in the context of another anecdotal case study (different titi group). A study on lactation in the species does not mention other infant care behavior (Souza-Alves et al., 2019). No further (relevant) behavioral studies from the wild or captivity (10/Nov/2019).
C. personatus	Present[6]	NA	(Present)	(Kinzey & Becker, 1983)	The study mentions that "[t]he infant was usually carried by the adult male", but gives no indication how they distinguished between individuals (Kinzey & Becker, 1983). A circular argument is likely (i.e. male is identified as the individual carrying the infant). No further relevant studies (04/Dec/2019).
Cheracebus lucifer	Present[6]	NA	NA (Present for other care behaviours)	NA	The studies by Kinzey (1981; Kinzey, Rosenberger, Heisler, Prowse, & Trilling)[9, 10] are in fact on *Cheracebus lucifer*. **The articles therefore cannot be used as evidence for higher male carrying contribution in *Cheracebus torquatus*,** but as preliminary evidence for male participation in other infant care aspects such as grooming and play in *C. lucifer*, albeit lacking quantitative data (see Supplementary Table 2). Similarly, a study by Starin (1978) indicated more food transfer from the male to the infant than from the female. It is not clear how sexes were distinguished. No further relevant articles (04/Dec/2019).

C. lugens	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (12/Aug/2019).
C. medemi	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (10/Nov/2019).
C. purinus	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (10/Nov/2019).
C. regulus	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (10/Nov/2019).
C. torquatus	Present[11]	NA	NA	NA	See *Cheracebus lucifer*. No relevant behavioral studies from the wild or captivity (04/Dec/2019).
Plecturocebus aureipalatii	NA	NA	NA	NA	No relevant behavioral studies from the wild or captivity (10/Nov/2019).
P. baptista	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
P. bernhardi	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
P. brunneus	Present[6]	NA	NA	NA	Most studies supposedly conducted on *P. brunneus* (in Peru) are in fact on *P. toppini*. No relevant studies (06/Dec/2019).
P. caligatus	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
P. caquetensis	NA	NA	(Present)	(Acero-Murcia, Almario, García, Defler, & López, 2018)	No study on parental care available, but one study on the species' diet states "The newborn was constantly carried by the father" (Acero-Murcia et al., 2018). The study does not specify how, or whether individuals were identified and whether sexes could be distinguished, or

					whether the assignment of sexes was based on behavior patterns like carrying the infant, which would then result in a circular argument. No other relevant studies (10/Nov/2019).
P. cinerascens	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
P. cupreus	Present[6]	NA	Male main carrier	(Tirado Herrera & Heymann, 2004)	A study on the diet conducted at the Estación Biológica Quebrada Blanco, Loreto, Peru, states that, of the two infants born over the study period (1 group), “infants were exclusively carried by the male”, but no actual data are presented (Tirado Herrera & Heymann, 2004). In an intensive, ongoing study on 6 groups of titis (9 infants), with individually recognized adults, the male was the main carrier (>90% of time)(Dolotkovskaya & Heymann, pers. comm.). Additionally, during observations of a birth in the same study population, a juvenile was carrying the infant for several hours on its first day of life, but later it was again the male (Terrones Ruíz, Vela Diaz, Flores Amasifuén, & Heymann, 2004). The species studied by Mason and co-workers in captivity was at that time considered to be *Callicebus moloch*. Currently it is thought to be *P. cupreus*, though it seems to look rather differently from other *P. cupreus* populations.

P. discolor	Present[6]	NA	98%	(Spence-Aizenberg, Di Fiore, & Fernandez-Duque, 2016)	A study on two wild, habituated groups, with individually marked adults was carried out including 5 infants and 210h of behavioral data. Infants were carried 98% of the times by males. Additionally, males but not females were observed grooming infants (Spence-Aizenberg et al., 2016). This study was published after the study by Lukas and Clutton-Brock (2013) and is the only one reporting data on carrying behavior in the species (06/Dec/2019).
P. donacophilus	Present[6]	Present[2-4]	NA	NA	No relevant behavioral studies from the wild or captivity (11/Aug/2019).
P. hoffmannsi	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
P. miltoni	NA	NA	NA	NA	No relevant behavioral studies from the wild or captivity (13/Nov/2019).
P. modestus	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
P. moloch	Present[12]	Present[2-4]	NA	NA	Commonly cited studies for this species are [5, 12], both not suitable as reference for this species (see *P. cupreus*). Another recent study of captive individuals (Mayeaux, Mason, & Mendoza, 2002) does not directly examine carrying and other care behaviors. Additionally, the provenance of the breeding population is unclear, i.e. it cannot be confirmed that it is truly *P. moloch*. Generally, the titi monkey colony established by Mason (e.g., Mason) is not *P.*

					moloch. It might be *P. cupreus*, but even that is not clear. Some abstracts on titi monkeys at Cocha Cashu National Park, Peru, are in fact on *P. toppini*, not *P. moloch*. A further study (in German) on captive animals also states that the male was the main carrier, but because the animals were born in captivity and came from a different institution it is not possible to know whether the species was really *P. moloch* (Welker, Röber, & Lührmann, 1981). **Thus, there is NO information on parenting behavior from *Plecturocebus moloch* from the wild** (12/Aug/2019).
P. oenanthe	Present[6]	NA	Male main carrier	(DeLuycker, 2014)	The referenced study, based on one intensively observed group, found that "[t]he male carried the newborn the majority of the time, beginning within 24 h after birth." This study was published after the study by Lukas and Clutton-Brock (2013) and is the only one reporting data on carrying behavior in the species (12/Aug/2019).
P. olallae	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
P. ornatus	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
P. pallescens	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).

P. stephennashi	Present[6]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
P. toppini	NA	NA	Male main carrier	(Lawrence, 2007)	The titi species present in Cocha Cashu National Park and Madre de Dios Research Station, Peru, was originally considered to be *C. moloch*, then *P. brunneus*, but is now considered *P. toppini* (Vermeer & Tello-Alvarado, 2015). A Ph.D. thesis conducted at the Madre de Dios Research Station, Peru, on 5 groups (four with infants, including a pair of twins), stated that "only the adult male of each group was the exclusive infant carrier, transferring the infant to the female only for nursing. There was one exception: the adult female of Sm carried the infant throughout one day." (Lawrence, 2007).
P. urubambensis	NA	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
Saki monkeys					
Pithecia aequatorialis	Absent[13]	NA	Absent	(Fernandez-Duque, Di Fiore, & de Luna, 2013)	The only reference is from our own study site in Ecuador. Over the course of three years, a single group of saki monkeys (with individually marked adults) was observed, with one male replacement. During the 63h and 467h of observation on the two males, with two infants born during the residency of the second male, "saki males were never observed carrying infants". However, males were very occasionally observed sharing food with infants.

					We also checked for *P. napensis*, which is by some considered a separate species (Marsh, 2014; but see Silva Jr., 2013), but did not find relevant articles (04/Dec/2019).
P. albicans	Absent[13]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (03/Dec/2019).
P. chrysocephala	NA	NA	NA	NA	No relevant behavioral studies from the wild or captivity (03/Dec/2019).
P. irrorata	Absent[13]	NA	(Not present)	(Palminteri & Peres, 2012)	The referenced study on habitat selection of 5 groups did not explicitly address infant care behavior or explicitly state that males were *not* carrying infants, yet infants were defined as “carried by their mothers”. Sexual dimorphism in facial hair coloration makes identification of adult sexes easy. Thus, the statement implies that the female is the sole carrier. No directly relevant articles found (06/Dec/2019). We also searched for the following names, since these are sometimes considered to be different species (Marsh, 2014; but see Serrano-Villavicencio, Hurtado, Vendramel, & Nascimento, 2019): *P. mittermeieri*: (04/Dec/2019) *P. pissinattii*: (04/Dec/2019) *P. rylandsi*: (04/Dec/2019) *P. vanzolinii*: (04/Dec/2019)

P. monachus	Absent[13]	NA	(contradictory statements for two populations (or (sub-)species, but if present, then rare)	NA	*P. monachus* (s.s.): No relevant behavioral studies from the wild or captivity (06/Dec/2019). We also searched for the following names, since these are sometimes considered to be different species (Marsh, 2014; but see Serrano-Villavicencio et al., 2019): *P. catzuzai* (03/Dec/2019) *P. hirsuta*: within an article on the ecology of the species, the authors cite an anecdotal claim by non-scientist that “males [were seen] carrying infants on their back”, though the author of the study did not report seeing this herself (Happel, 1982). A study conducted by Soini (1986) was reported for *P. hirsuta*, but according to Marsh (2014) it would be considered *P. isabela.* No other relevant article (24/Nov/2019). *P. inusta*: (03/Dec/2019). *P. isabela*: Soini (1986) reports that in “*P. hirsuta*” infants were carried by mothers or perhaps occasionally by subadult females, but that males did not participate in carrying and only very few instances of other forms of direct care such as huddling or grooming were observed. No further relevant articles found (04/Dec/2019). *P. milleri*: (04/Dec/2019)

P. pithecia	Absent[14]	NA	Absent	(Homburg, 1997; Thompson, 2011)	The Ph.D. thesis of I. Homburg (1997; in German) specifically states that the offspring is not carried by males, whether adult or juvenile. The study was based on an isolated group on a small island. Another Ph.D. study on the social system of three groups of wild, individually identified animals, including infants, did not explicitly investigate infant care behavior, but states in Table 19 that male care is not present (Thompson, 2011).
Tamarins					
Leontocebus fuscicollis	Present[15]	Present[2-4]	(Present)	NA	Most studies supposedly done on "*Saguinus fuscicollis*" were done in Cocha Cashu National Park, Peru (now considered to be *Leontocebus weddelli*) or Loreto, Peru (now considered *L. nigrifrons*, *L. lagonatus*, *L. nigricollis* and *L. illigeri*, with only a very small population of *L. fuscicollis* s.s.). (Epple, 1975)[16] and (Vogt, 1978) report on parenting behavior in captive pairs of supposed "*S. fuscicollis*". Epple (1975) mentions two sub-species *S.f. fuscicollis* and *S. f. illigeri*. This would indicate that the species were *L. fuscicollis* and *L. illigeri*. As it is not clear throughout the 7 study groups which individual was from which (sub-)species, the provided percentage values are only tentative, but the study provides evidence of male (and cooperative) care for both species in captivity.

					There are no studies conducted on *L. fuscicollis* in the wild (06/Dec/2019).
L. nigricollis graellsi	Present[15]	NA	(anecdotal evidence for cooperative care)	(de la Torre, Campos, & de Vries, 1995)	A study related to home-range size and birth seasonality mentions that older infants were “only in cases of rapid movements … carried by the adults or subadults” (de la Torre et al., 1995). While this implies co-operative infant care, no data on the participation of the father, or males more generally, are available. No further relevant studies (03/Dec/2019).
L. nigricollis hernandezi	Present[15]	NA	(not present?)	(Izawa, 1978)	The referenced study[39] on *L. n. hernandezi* states: “At no time in the growth stages of a baby was the author able to see the so-called "infant-care", whereby an individual other than the mother actively carries a baby on its back to spend a certain part of its daily life.” This explicit statement by Izawa (1978) is rather astonishing. The author states that he was able to individually identify the animals in the study groups. While it might be possible that the author might have in some cases attributed identity of the carrying individual to “the mother” by a preconception, this warrants further investigation of this (sub-)species.
L. illigeri	NA	NA	(Present)	(Epple, 1975)	Epple (1975)[16] mentions two sub-species *S. f. fuscicollis* and *S. f. illigeri*. This would indicate that the species were *L. fuscicollis* and *L.*

					illigeri. As it is not clear throughout the 7 study groups which individual was from which sub-species, the provided percentage values are only tentative, but the study provides evidence of male (and cooperative) care for both species in captivity.
L. nigrifrons	NA	NA	Median carrying behavior by: Fathers: 20%, other males: 22%, Mothers: 18%, other females: 10%	(Slana, 2019)	In an intensive study on eight litters, with individually identified animals based on natural markings, cooperative care was studied. Numbers are based on the figures in the thesis.
L. tripartitus	Present[15]	NA	Infants carried by males 28-50%	(Kostrub, 2003)	Infants (N = 2 litters) were carried by males between ca. 28 – 50% of the time, while 24-48% by the single female in the group (mother), where nursing was included in carrying behavior. The numbers are based on the figures in the thesis. The fathers of the infants were not known (although the author distinguished between males that mated more or less with the female).
L. weddelli melanoleucus	Present[15]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (03/Dec/2019).
L. weddelli	NA	NA	During first month:	(Goldizen, 1987)	Detailed observations (more than 1100 observation hours on two habituated groups with

			Adult males: 37-43%, mothers: 20-23%, other females: 12-24%; subadults: 0.5-3%		marked individuals) clearly showed cooperative infant care. Paternity was not known[17].
Saguinus bicolor	Present[15]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (03/Dec/2019).
S. geoffroyi	Present[15]	Present[2-4]	(present)	(Díaz-Muñoz, 2010; Moynihan, 1970)	A study on captive animals held in pairs found that the "infants were carried by their mothers and fathers with approximately equal frequency" (Moynihan, 1970). Another intensive study on the species in the wild mentions casually co-operative infant care for the species, but did not study infant care behavior itself or provides data (Díaz-Muñoz, 2010).
S. imperator	Present[15]	Present[2-4]	Present	(Windfelder, 2000)	The assessment is based on one young, inexperienced, wild pair with no other group members.
S. inustus	Present[15]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (03/Dec/2019).
S. labiatus	Present[15]	NA	(Present: father after day 3: 45-	(Coates & Poole, 1983; Pryce, 1988)	Both captive studies kept individuals in pairs, so that contributions of other adults but parents were not possible (03/Dec/2019).

			55% of time per infant)		
S. leucopus	Present[15]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (03/Dec/2019).
S. martinsi	Present[15]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
S. midas	Present[15]	Present[2-4]	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
S. mystax	Present[15]	NA	Breeding male: 18%, other adult males: 27%, breeding female: 7.4%, other adult females: 16%	(Huck, Löttker, & Heymann, 2004)	Numbers are based on an intensive field study on two groups (one litter each; > 3000 contact hours/group) with individually identified animals, only one with more than one (i.e. three) females. Biological parents were known.
S. niger	Present[15]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).
S. oedipus	Present[15]	Present[2-4]	Mothers: 23%, ad. males: 50%, other females carried but no value given	(Savage, Snowdon, Giraldo, & Soto, 1996)	This study, on individually identified wild animals, is based on 12 litters.
S. pileatus	Present[15]	NA	NA	NA	No relevant behavioral studies from the wild or captivity (24/Nov/2019).

[0] The superscript numbers in brackets refer to references provided by LCB or OPIE, which are summarized in Supplementary Table 2.

[1] The value gives the percentage of carrying time the infant is carried by the social or biological father.

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Table 3. Population density estimates (individuals/km^2) for owl monkeys (*Aotus* spp.), titi monkeys (*Callicebus*, *Cheracebus*, and *Plecturocebus* spp.), sakis (*Pithecia* spp.), and tamarins (*Saguinus* and *Leontocebus* spp.) as reported in the PanTHERIA database (Jones et al., 2009) and in primary sources we reviewed. We report in the column "PanTHERIA" the numbers as provided in the database (http://esapubs.org/archive/ecol/E090/184/). In the column "This Review", we report the values we found in our own search of the primary literature or the mean of those values and the range between parentheses. A list of values indicates that different populations are reported in the same reference. In the column "References in this Review", we provide the references we consulted.

Species	PanTHERIA	This Review	References in this Review
Aotus azarae	16.2	64	(Fernandez-Duque, Rotundo, & Sloan, 2001)
A. azarae		29	(Rathbun & Gache, 1980)
A. azarae		12.8	(Zunino, Galliari, & Colillas, 1985)
A. azarae		8.9 - 14.4	(Stallings, West, Hahn, & Gamarra, 1989)
A. azarae		25.4	(Arditi & Placci, 1990)
A. azarae		15	(Brown & Zunino, 1994)
A. griseimembra		150	(Heltne, 1977)
A. griseimembra		1.5	(Green, 1978)
A. lemurinus	35.9	113	(Hirche, Jimenez, Roncancio-Duque, & Ansorge, 2017)
A. nancymaae	28.6	25	(Aquino & Encarnación, 1986)
A. nancymaae		48.5, 54.2, 48.0, 41.0, 39.8, 28.3, 27.0, 16.0, 26.2	(Aquino & Encarnación, 1988)
A. nancymaae		3.24, 24.0	(Maldonado & Peck, 2014)
A. nancymaae		24.0, 25.0	(Puertas, Bodmer, & Aquino, 1995)
A. nigriceps	38	36 - 40	(Wright, 1985)
A. nigriceps		40	(Janson & Emmons, 1990)
A. nigriceps		31.1	(Aquino, Cornejo, & Heymann, 2013)
A. nigriceps		8.8	(Peres, 1993)
A. trivirgatus	24.5		
A. vociferans	23.7	7.9	(Heltne, 1977)
A. vociferans		2.0, 7.3, 11.5, 10.6, 19.6, 38.9, 41.2	(Aquino & Encarnación, 1988)
A. vociferans		24.0, 25.9, 44.0	(Maldonado & Peck, 2014)
A. vociferans		26.0	(Aquino, López, García, & Heymann, 2014)

A. zonalis		13.2	(Svensson, Samudio, Bearder, & Nekaris, 2010)
Callicebus coimbrai		12.6	(Chagas & Ferrari, 2011)
C. melanochir		17.0	(Müller, 1995)
C. nigrifrons		14.9	(Oliviera, Coelho, & Melo, 2003)
C. nigrifrons		3.5	(Bernando & Galetti, 2004)
C. nigrifrons		12.2	(Trevelin, Port-Carvalho, Silviera, & Morell, 2007)
C. nigrifrons		10.3	(Cosenza & de Melo, 1998)
C. personatus	13	12.4 (12.3 - 12.6)	(Price, Piedade, & Wormell, 2002)
C. personatus		6.5 (1.3 - 10.2)	(Chiarello, 2000)
C. personatus		5.4 (2.4 - 40.0)	(Pinto, Costa, Strier, & da Fonseca, 1993)
Cheracebus lucifer		2.0, 15.2	(Freese, Heltne, Napoleon Castro, & Whitesides, 1982)
C. lucifer		1.5, 1.5, 1.9	(Aquino, Lopez, Arevalo, & Daza, 2016)
C. lucifer		28, 6.1, 9, 2.7, 12.7	(Defler, 2013)
C. purinus		7.7, 13.5	(Peres, 1997)
C. regulus		7.0, 2.8, 7.2, 6.9	(Peres, 1997)
C. torquatus	10.2	2.5 - 2.8	(Aquino, Terrones, Cornejo, & Heymann, 2008a)
C. torquatus		10.1	(Peres, 1993)
Plecturocebus aureipalatii		6.2	(Wallace, Gómez, Felton, & Felton, 2006)
P. brunneus		14.7	(Freese et al., 1982)
P. brunneus		11.5	(Aquino et al., 2013)
P. cupreus		5.1	(Peres, 1993)
P. cupreus	4.9	22.8, 1.1, 4.3, 4.9, 5.5, 10.7, 30.1, 4.5, 1.1, 1.2, 4.5	(Peres, 1997)
P. cupreus		14.6	(Bennett, Leonard, & Carter, 2001)
P. cupreus		13.2	(Freese et al., 1982)
P. cupreus		2.0, 2.5	(Puertas et al., 1995)
P. discolor		7.0	(Aquino, Terrones, Navarro, Terrones, & Cornejo, 2008b)
P. discolor		47.6	(Dacier, de Luna, Fernandez-Duque, & Di Fiore, 2011)
P. discolor		13.8	(Aquino et al., 2014)
P. discolor		1.8, 3.6, 7.5, 16.2	(Freese et al., 1982)
P. moloch	18.4		

P. oenanthe		113	(Aldrich, Molleson, & Nekaris, 2008) ***
P. oenanthe		12.0 - 49.5	(van Kuijk, García-Suikkanen, Tello-Alvarado, Vermeer, & Hill, 2016)
P. oenanthe		124	(Allgas et al., 2017)
P. ornatus		192 (60 - 369)	(Wagner, Castro, & Stevenson, 2009)
P. toppini		24	(Janson & Emmons, 1990)
P. toppini		2.1	(Freese et al., 1982)
P. toppini		20-26	(Wright, 1985)
Pithecia aequatorialis		5.6, 5.9, 7.8	(Aquino, Cornejo, Pezo Lozano, & Heymann, 2009)
P. aequatorialis		15.7, 11.5	(Aquino et al., 2014)
P. aequatorialis		4.0, 13.5	(Freese et al., 1982)
P. albicans		9.8	(Peres, 1993)
P. albicans	9.4	9.4	(Peres, 1997)
P. chrysocephala		40	(Oliviera, Lima, Bonvincino, Ayres, & Fleagle, 1985)
P. irrorata	11.3	11.2, 23.6, 9.9, 4.6, 11.3	(Peres, 1997)
P. irrorata		1.3 (ind/10 km)	(Ferrari et al., 1999)
P. irrorata		12.5	(Palminteri & Peres, 2012)
P. irrorata		6.6	(Freese et al., 1982)
P. monachus	8	12.8	(Soini, 1986)
P. monachus		8.0, 13.8, 8.1, 6.8, 7.5, 10.2	(Peres, 1997)
P. monachus		9 - 17.2	(Bennett et al., 2001)
P. monachus		1.8, 4.2, 5.0	(Aquino et al., 2016)
P. monachus		4.5, 4.5, 9.0	(Freese et al., 1982)
P. monachus		3.5, 5.0	(Puertas et al., 1995)
P. monachus		4, 10, 7.6, 14.5	(Defler, 2013)
P. pithecia	4.23	0.64	(Vié, Richard-Hansen, & Fournier-Chambrillon, 2001)
P. pithecia		14.1 (ind/10 km)	(Norconk et al., 2003)
Saguinus bicolor		6 - 18	(Gordo, Calleia, Vasconcelos, Leite, & Ferrari, 2013)
S. geoffroyi	5.13	27 - 36	(Dawson, 1979)
S. imperator	18.4	58.6, 25.2	(Peres, 1997)
S. imperator		20.1	(Aquino et al., 2013)
S. imperator		5.4	(Freese et al., 1982)
S. imperator		12	(Janson & Emmons, 1990)
S. inustus		19.6	(Castillo-Ayala & C. I., 2007)

S. labiatus	14.3	8.6	(Yoneda, 1981)
S. labiatus		27.6	(Freese et al., 1982)
S. leucopus	10.6	15.2	(Green, 1978)
S. midas	11.1	34.7 (ind/10 km)	(Norconk et al., 2003)
S. mystax	31	33.2	(Garber & Teaford, 1986)
S. mystax		87.8, 54.5, 71.5, 29.8, 34.7, 49.2, 55.4, 34.4, 36.4	(Peres, 1997)
S. mystax		15.3	(Peres, 1993)
S. mystax		23	(Soini & Soini, 1990)
S. mystax		8.4, 21.7	(Puertas et al., 1995)
S. oedipus	46.2		
*Leontocebus fuscicollis**	19.5	51.4, 43.2, 20.0, 29.7, 28.1, 24.4, 31.5, 30.2	(Peres, 1997)
*L. fuscicollis**		9.8	(Peres, 1993)
*L. fuscicolis graellsi**		22 - 33	(de la Torre, Campos, & de Vries, 1995)
*L. fuscus**		8	(Defler, 2013)
*L. illigeri**		18	(Soini & Soini, 1990)
*L. lagonotus**		10.5	(Aquino et al., 2008b)
*L. lagonotus**		34.8	(Aquino et al., 2014)
*L. lagonotus**		14.8	(Kolowski & Alonso, 2012)
*L. lagonotus**		4.8, 15.0, 29.4	(Freese et al., 1982)
*L. leucogenys**		2.4, 13.8	(Freese et al., 1982)
*L. nigricollis**		15.8, 18.6, 22.5	(Aquino et al., 2016)
*L. nigricollis**		14, 15, 9.5	(Defler, 2013)
*L. nigrifrons**	13.5	23	(Soini & Soini, 1990)
*L. nigrifrons**		28.3	(Garber & Teaford, 1986)
*L. nigrifrons**		9.0	(Freese et al., 1982)
*L. nigrifrons**		21.7, 37.8	(Puertas et al., 1995)
L. tripartitus		13.5	(Aquino, Ique, & Gálvez, 2005)
L. tripartitus		26.8	(Aquino et al., 2014)
*L. weddelli**		12.8	(Yoneda, 1981)
*L. weddelli**		3.6, 4.8, 10.8, 27.6	(Freese et al., 1982)
*L. weddelli**		16	(Janson & Emmons, 1990)
*L. weddelli melanoleucus***		65.1, 36.7, 67.6,	(Peres, 1997)

* formerly known as *Saguinus fuscicollis*

** formerly known as *Saguinus melanoleucus*

*** Authors provide inconsistent information (in text (p3): 1.40 ind/ha; in Table 1: 113 ind/km^2).

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Table 4. Home range size estimates (ha) for owl monkeys (*Aotus* spp.), titi monkeys (*Callicebus*, *Cheracebus*, and *Plecturocebus* spp.), saki monkeys (*Pithecia* spp.), and tamarins (*Saguinus* and *Leontocebus* spp.) as reported in the PanTHERIA database (Jones et al., 2009) and in primary sources we reviewed. We report in the column "PanTHERIA" the numbers as provided in the database (http://esapubs.org/archive/ecol/E090/184/). In the column "This Review", we report the values we found in our own search of the primary literature or the mean of those values and the range between parentheses. In the column "References in this Review", we provide the references we found and consulted.

Species	PanTHERIA	This Review	References in this Review
Aotus azarae		6.2 (3.6 - 10.9)	(Wartmann, Juárez, & Fernandez-Duque, 2014)
A. azarae		0.18	(García & Braza, 1987)
A. miconax		1.23	(Shanee, Algass, & Shanee, 2013)
A. nigriceps		9.2 (4 - 14)	(Wright, 1994)
A. nigriceps		3.1	(Wright, 1978)
A. trivirgatus	2	No Data	
A. vociferans		6.3	(Fernandez-Duque, Di Fiore, & Carrillo-Bilbao, 2008)
Callicebus melanochir		23.8 (23.3 - 24.3)	(Heiduck, 2002; Müller, 1995)
C. nigrifrons		17	(Nagy-Reis & Setz, 2017)
C. personatus	3	11.5 (10.7 - 12.3)	(Price & Piedade, 2001)
C. personatus		4.7	(Warren & Becker, 1983)
Cheracebus lucifer		20	(Easley & Kinzey, 1986)
C. torquatus	11	45	(Peres, 1993)
Plecturocebus brunneus	4	6.9 (6 - 8)	(Wright, 1986)
P. cupreus		9.0 (6.7 - 11.4)	(Kulp & Heymann, 2015)
P. cupreus		20	(Peres, 1993)
P. discolor		5.0 (2.0 - 8.5)	(Van Belle, Porter, Fernandez-Duque, & Di Fiore, in preparation)
P. modestus		9.7 (9.6 - 9.8)	(Martinez & Wallace, 2016)
P. moloch	2		
P. olallae		7.2 (6.5 - 7.8)	(Martinez & Wallace, 2016)
P. ornatus		3.7 (3.3 - 4.2)	(Robinson, 1979)
P. ornatus		< 1	(Mason, 1968)
P. ornatus		14	(Polanco-Ochoa, 1993)
P. toppini		12 (6 - 18)	(Bossuyt, 2002)
Pithecia aequatorialis		57 (16 - 102)	(Van Belle, Porter, Fernandez-Duque, & Di Fiore, 2018)

P. albicans		172 (147 - 204)	(Peres, 1993)
P. chrysocephala		10	(Setz & Gaspar, 1997)
P. chrysocephala		8.5	(Oliviera, Lima, Bonvincino, Ayres, & Fleagle, 1985)
P. irrorata		36 (16 - 60)	(Palminteri, Powell, & Peres, 2016)
P. monachus		9	(Oliviera et al., 1985)
P. monachus		25 (10 - ca. 42)	(Soini, 1986)
P. pithecia	4	108 (68 - 148)	(Vié, Richard-Hansen, & Fournier-Chambrillon, 2001)
P. pithecia		12.8	(Cunningham & Janson, 2007)
*Leontocebus fuscicollis**		145	(Peres, 1993)
*L. fuscicollis graellsi**		49 (41.7 - 56.2)	(de la Torre, Campos, & de Vries, 1995)
*L. nigricollis**	25	41	(Izawa, 1987)
*L. nigrifrons**	21	40	(Garber, 1988)
*L. weddelli **		32.8 (25.9 - 40.1)	(Yoneda, 1981)
*L. weddelli **		44	(Lopes & Ferrari, 1994)
Saguinus geoffroyi	17	26 - 43	(Dawson, 1979)
S. imperator	22		
S. labiatus	20	33.5 (23.2 - 40.7)	(Yoneda, 1981)
S. labiatus		19.2 (16.8 - 23)	(Buchanan-Smith, 1991)
S. leucopus		17.7	(Poveda K & Sánchez-Palomino, 2004)
S. leucopus		75.7 (53.6 - 94.9)	(Alba-Mejia, Caillaud, Montenegro, Sánchez-Palomino, & Crofoot, 2013)
S. leucopus		23.1 (15.0 - 32.1)	(de Luna, García-Morera, & Link, 2016)
S. midas	5	35.0 (31.1 - 42.5)	(Day & Elwood, 1999)
S. midas		28	
S. mystax	22	40	(Garber, 1988)
S. mystax		6.8	(Garber, Pruetz, & Isaacson, 1993)
S. mystax		43 (41 - 45)	(Heymann, 2000)
S. mystax		145	(Peres, 1993)
S. niger		28	(Oliveira & Ferrari, 2000)
S. niger		35	(Veracini, 2000)
S. oedipus	7		

* formerly known as *Saguinus fuscicollis*

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Table 5. Percentage of home range overlap among neighboring groups of owl monkeys (*Aotus* spp.), titi monkeys (*Callicebus*, *Cheracebus*, and *Plecturocebus* spp.), saki monkeys (*Pithecia* spp.), and tamarins (*Saguinus* and *Leontocebus* spp.) as provided by Pearce et al. (2013) and in primary sources we reviewed. We report in the column "Pearce et al. 2013" the numbers as provided in their supplementary file or the mean of those values and the range between parentheses when they came from the same population/field site. For example, they report three values for *S. oedipus* (20, 25, 27) from Tolu, we present the mean and the range of those values (24, 20-27). In the column "This Review", we report the values we found in our own search of the primary literature since Pearce et al. 2013 do not provide the references they consulted. In the column "References in this Review" we provide the references we found and consulted.

Species	Pearce et al. 2013	This review	References in this Review
Aotus azarae		48 (41 - 56)	(Wartmann, Juárez, and Fernandez-Duque 2014)
Callicebus melanochir	12.3 – 12.9	12.3	(Müller 1995, Heiduck 2002)
C. personatus	20	17.4 (16 -19)	(Price and Piedade 2001)
Plecturocebus discolor		4.8 (0 - 13)	(Van Belle et al. in preparation)
P. modestus		3	(Martinez and Wallace 2016)
P. olallae		14	(Martinez and Wallace 2016)
P. ornatus	9.4 (1.4 - 18)	9 (0.9 - 16.6)	(Robinson 1979)
P. ornatus	6		
Pithecia aequatorialis		5 (3 - 8)	(Van Belle et al. 2018)
P. irrorata		16 (0 - 33)	(Palminteri, Powell, and Peres 2016)
P. monachus		2 – 70	(Soini 1986)
P. pithecia		7.7 (5.5 - 9.0)	(Thompson, Norconk, and Whitten 2012)
*Leontocebus fuscicollis**		76.2	(Peres 1992)
*L. fuscicollis graellsi**		83 (81.6 - 84.4)	(de la Torre, Campos, and de Vries 1995)
*L. nigrifrons**	79	23	(Garber 1988)
*L. weddelli**	0.5 (0 - 1)	60.3 (44 - 79)	(Yoneda 1981)
*L. weddelli**	21		
Saguinus geoffroyi	13	19 (13 - 25)	(Dawson 1979)
S. imperator	0.5 (0 - 1)		
S. leucopus		50.8 (33.2 - 69.6)	(Alba-Mejia et al. 2013)
S. leucopus		13 (9 - 20)	(de Luna, García-Morera, and Link 2016)
S. mystax	38	23	(Garber 1988)

S. mystax		76.2	(Peres 1992)
S. mystax		20.2	(Garber, Pruetz, and Isaacson 1993)
S. mystax		36.6	(Heymann 2000)
S. niger	21.7	100	(Veracini 2000)
S. oedipus	24 (20 - 27)		

* formerly known as *Saguinus fuscicollis*

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Table 6: Comparison between evidence for seasonal breeding, infanticide risk, gestation length (days), and weaning age (days) of owl monkeys (*Aotus* spp.), titi monkeys (*Plecturocebus* spp.), and saki monkeys (*Pithecia* spp.) as it is provided by Opie et al. (2013) and in primary sources we reviewed. We report in the columns "Opie et al. 2013" the classification assigned by the authors or the data they provide. In the columns "This Review", we report the values we found in our own search of the primary literature. In the column "Reference", we provide the references we consulted. DD: data deficient; ND: no data; Blank cells: no information provided at all; C: captivity.

Species	**Seasonal breeders**			**Infanticide**		**Gestation (days)**			**Weaning age (days)**		
	Opie et al. 2013	This Review	Reference	Opie et al. 2013	This Review	Opie et al. 2013	This Review	Reference	Opie et al. 2013	This Review	Reference
Aotus azarai	Yes	Yes: Sep-Nov (62% of births, N=24/39)	(Fernandez-Duque, Rotundo, & Ramírez-Llorens, 2002)	Low	Well studied, no evidence		121 (N=1) (C) / est. 120-126 & 132-140 (N=2)	(Fernandez-Duque, 2011)		150-240 (N=7)	(Rotundo, Fernandez-Duque, & Dixson, 2005; Wolovich, Evans, & French, 2008)
A. infulatus		ND		Low	ND						

A. lemurinus griseimembra	No	ND		Low	ND	133	117 ± 8 (N=4) (C)		75	120-150 (C)	(Wolovich et al., 2008)
A. nancymaae	No	Yes: Dec-Mar		Low	ND	131	122-141 (C)		75		
A. nigriceps		Yes: Aug-Feb (100% births,N=9/ 9); Nov-Jan	(Wright, 1985)		DD						
A. trivirgatus	No			Low	ND	133	126/ 138/ 148-159		75	75 (C)	
Plecturocebus cupreus		Yes: 60% Dec-Mar (C)	(Valeggia, Mendoza, Fernandez-Duque, Mason, & Lasley, 1999)				122-135 (N=8) (C)	(Valeggia et al., 1999)		Anovulatory Period: 194 ± 25.1 (C)	(Valeggia et al., 1999)

P. discolor		Y: Sep-Jan (N=20/24)	(Van Belle, Fernandez-Duque, & Di Fiore, 2016)		Well studied, no evidence		ND			90	
P. donacophilus	DD			DD	ND						
P. moloch	Yes				ND	164			60		
Pithecia aequatorialis		Yes: Mar-Apr + Oct-Dec (N=8/8)	(Van Belle et al., 2016)		Well studied, no evidence		ND				
P. albicans		N: Nov-Jun (N=5)	(Johns, 1986)		DD						
P. chrysocephala		Y: Sep-Apr (N=6)	(Setz & Gaspar, 1997)		DD						

P. irrorata					Well studied?, no evidence						
P. monachus		Y: Sep-Dec	(Soini, 1986)		DD						
P. pithecia		Y: Nov-April (N=10/12); Oct-Jan, Suriname	(Norconk, 2006)		Well studied, no evidence		164 / 146.1 ± 5.2 (C)	(Savage, Lasley, Vecchio, Miller, & Shideler, 1995)		Anovulatory Period: 163 ± 40.6 (C)	(Savage et al., 1995)

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Supplements

Supplementary Table 1. Classifications of primate species across four comparative studies and the number of times each species is included in either of these four studies. S: Solitary; PL: Pair Living; UM: Uni-male Groups; MMMF: Multimale-multifemale Groups

Species	(Opie et al., 2013)	(Lukas & Clutton-Brock, 2013)	(West & Capellini, 2016)	(Shultz et al., 2011)	N Studies
Allocebus trichotis	Monogamous	Solitary		S, PL	3
Avahi laniger	Monogamous	Social Monogamy	Social Monogamy	PL	4
Avahi occidentalis	Monogamous	Social Monogamy		PL	3
Avahi unicolor		Social Monogamy			1
Cheirogaleus crossleyi	Monogamous	Social Monogamy	Social Monogamy	NA	4
Cheirogaleus major	Monogamous	Social Monogamy	Social Monogamy	S	4
Cheirogaleus medius	Polygynous/ Monogamous	Social Monogamy	Social Monogamy	S, PL	4
Cheirogaleus sibreei		Social Monogamy			1
Cheirogaleus adipicaudatus		Social Monogamy			1
Cheirogaleus minusculus		Social Monogamy			1
Eulemur mongoz	Monogamous	Social Monogamy	Social Monogamy	PL, MMMF	4
Eulemur rubriventer	Monogamous	Social Monogamy	Social Monogamy	PL	4
Hapalemur aureus	Monogamous	Group Living	Not Social Monogamy	PL, MMMF	4
Hapalemur griseus			Not Social Monogamy		1
Hapalemur griseus alaotrensis	Polygynous/ Monogamous			PL	2
Hapalemur griseus griseus	Polygynous/ Monogamous	Group Living		PL	3
Hapalemur griseus meridionalis	Polygynous/ Monogamous			PL	2

Hapalemur griseus occidentalis	Polygynous/ Monogamous	Group Living		PL	3
Indri indri	Monogamous	Social Monogamy		PL	3
Lepilemur edwardsi	Monogamous	Solitary		S	3
Lepilemur ruficaudatus	Monogamous	Solitary	Social Monogamy	S	4
Propithecus diadema	Polygynandrous/ Monogamous	Group Living		PL, UM, MMMF	3
Propithecus coquereli	Polygynandrous	Group Living		PL, UM, MMMF	3
Propithecus verreauxi verreauxi	Polygynandrous	Group Living	Not Social Monogamy	PL, UM, MMMF	4
Propithecus edwardsi	Polygynandrous	Group Living		PL, UM, MMMF	3
Phaner parienti		Social Monogamy			1
Phaner furcifer		Social Monogamy	Social Monogamy		2
Varecia rubra	Polygynandrous/ Monogamous	Group Living	Not Social Monogamy	MMMF	4
Varecia variegata variegata	Polygynandrous/ Monogamous	Group Living	Not Social Monogamy	MMMF	4
Loris lydekkerianus malabaricus				S, PL	1
Loris tardigradus	Polygynandrous/ Monogamous	Solitary	Not Social Monogamy	S, PL	4
Galago demidoff	Polygynous/ Monogamous	Solitary	Not Social Monogamy	S, PL, UM	4
Galago zanzibaricus	Polygynous/ Monogamous	Solitary	Not Social Monogamy	S, PL, UM	4
Otolemur crassicaudatus		Solitary	Not Social Monogamy	S, PL, UM	3
Tarsius bancanus	Polygynous/ Monogamous	Solitary	Not Social Monogamy	S	4
Tarsius syrichta	Polygynous/ Monogamous	Solitary		S	3

Callicebus baptista		Social Monogamy			1
Callicebus barbarabrownae		Social Monogamy			1
Callicebus bernhardi		Social Monogamy			1
Callicebus brunneus		Social Monogamy			1
Callicebus caligatus		Social Monogamy			1
Callicebus cinerascens		Social Monogamy			1
Callicebus coimbrai		Social Monogamy			1
Callicebus cupreus		Social Monogamy			1
Callicebus discolor		Social Monogamy			1
Callicebus donacophilus	Monogamous	Social Monogamy		PL	3
Callicebus dubius		Social Monogamy			1
Callicebus hoffmannsi		Social Monogamy			1
Callicebus lucifer		Social Monogamy			1
Callicebus lugens		Social Monogamy			1
Callicebus medemi		Social Monogamy			1
Callicebus melanochir		Social Monogamy			1
Callicebus modestus		Social Monogamy			1
Callicebus moloch	Monogamous	Social Monogamy	Social Monogamy	PL	4
Callicebus nigrifrons		Social Monogamy			1
Callicebus oenanthe		Social Monogamy			1
Callicebus olallae		Social Monogamy			1
Callicebus ornatus		Social Monogamy	Social Monogamy		2

Callicebus pallescens		Social Monogamy			1
Callicebus personatus		Social Monogamy			1
Callicebus purinus		Social Monogamy			1
Callicebus regulus		Social Monogamy			1
Callicebus stephennashi		Social Monogamy			1
Callicebus torquatus		Social Monogamy	Social Monogamy		2
Pithecia pithecia		Social Monogamy			1
Pithecia monachus		Social Monogamy			1
Pithecia irrorata		Social Monogamy			1
Pithecia albicans		Social Monogamy			1
Pithecia aequatorialis		Social Monogamy			1
Aotus azarae	Monogamous	Social Monogamy	Social Monogamy	PL	4
Aotus infulatus	Monogamous			PL	2
Aotus lemurinus griseimembra	Monogamous	Social Monogamy	Social Monogamy	PL	4
Aotus nancymaae	Monogamous	Social Monogamy	Social Monogamy	PL	4
Aotus trivirgatus	Monogamous	Social Monogamy	Social Monogamy	PL	4
Aotus hershkovitzi		Social Monogamy			1
Aotus miconax		Social Monogamy			1
Aotus nigriceps		Social Monogamy			1
Aotus vociferans		Social Monogamy			1
Callimico goeldii	Polygynous/ Monogamous	Group Living	Not Social Monogamy	PL, UM, MMMF	4
Callithrix acariensis		Social Monogamy			1
Callithrix argentata	Polygynous/ Monogamous	Social Monogamy	Social Monogamy	PL, UM, MMMF	4
Callithrix aurita	Polygynous/ Monogamous	Social Monogamy	Social Monogamy	PL, UM, MMMF	4

Callithrix chrysoleuca		Social Monogamy			1
Callithrix emiliae	Polygynous/ Monogamous	Social Monogamy		PL, UM, MMMF	3
Callithrix flaviceps		Social Monogamy			1
Callithrix geoffroyi	Polyandrous/ Monogamous	Social Monogamy	Social Monogamy	PL, UM, MMMF	4
Callithrix humeralifera	Polygynous/ Monogamous	Social Monogamy		PL, UM, MMMF	3
Callithrix humilis		Social Monogamy			1
Callithrix intermedia		Social Monogamy			1
Callithrix jacchus	Polyandrous/ Monogamous	Social Monogamy	Social Monogamy	PL, UM, MMMF	4
Callithrix kuhli	Polygynous/ Monogamous	Social Monogamy	Social Monogamy	PL, UM, MMMF	4
Callithrix leucippe		Social Monogamy			1
Callithrix manicorensis		Social Monogamy			1
Callithrix marcai		Social Monogamy			1
Callithrix mauesi		Social Monogamy			1
Callithrix melanura		Social Monogamy			1
Callithrix nigriceps		Social Monogamy			1
Callithrix penicillata	Polygynous/ Monogamous	Social Monogamy		PL, UM, MMMF	3
Callithrix pygmaea	Monogamous	Social Monogamy	Social Monogamy	PL, UM, MMMF	4
Callithrix saterei		Social Monogamy			1
Leontopithecus chrysomelas	Polygynous/ Monogamous	Social Monogamy		PL, UM, MMMF	3
Leontopithecus chrysopygus	Monogamous	Social Monogamy	Social Monogamy	PL, UM, MMMF	4
Leontopithecus rosalia	Polygynous/ Monogamous	Social Monogamy	Social Monogamy	PL, UM, MMMF	4
Leontopithecus caissara		Social Monogamy	Social Monogamy		2

Saguinus bicolor		Social Monogamy	Social Monogamy		2
Saguinus fuscicollis	Polgynous/ Polyandrous/ Monogamous	Social Monogamy		PL, UM, MMMF	3
Saguinus geoffroyi	Polygynous/ Monogamous	Social Monogamy		PL, UM, MMMF	3
Saguinus graellsi		Social Monogamy			1
Saguinus imperator	Polgynous/ Polyandrous/ Monogamous	Social Monogamy		PL, UM, MMMF	3
Saguinus inustus		Social Monogamy			1
Saguinus labiatus		Social Monogamy			1
Saguinus leucopus		Social Monogamy			1
Saguinus martinsi		Social Monogamy			1
Saguinus melanoleucus		Social Monogamy			1
Saguinus midas	Monogamous	Social Monogamy	Social Monogamy	PL, UM, MMMF	4
Saguinus mystax		Social Monogamy	Social Monogamy		2
Saguinus niger		Social Monogamy			1
Saguinus nigricollis		Social Monogamy	Social Monogamy		2
Saguinus oedipus	Polygynandrous/ Monogamous	Social Monogamy	Social Monogamy	PL, UM, MMMF	4
Saguinus pileatus		Social Monogamy			1
Saguinus tripartitus		Social Monogamy			1
Cercopithecus neglectus	Polygynous/ Monogamous	Group Living		UM, PL	3
Colobus angolensis	Polygynandrous	Group Living	Not Social Monogamy	PL, UM, MMMF	4
Colobus guereza	Polygynous	Group Living	Not Social Monogamy	PL, UM, MMMF	4
Bunopithecus hoolock	Monogamous	Social Monogamy	Social Monogamy	PL	4

Homo sapiens	Polygynous/Monogamous				1
Hylobates agilis	Monogamous	Social Monogamy		PL	3
Hylobates klossii	Monogamous	Social Monogamy		PL	3
Hylobates lar	Monogamous	Social Monogamy	Social Monogamy	PL	4
Hylobates moloch	Monogamous	Social Monogamy		PL	3
Hylobates muelleri	Monogamous	Social Monogamy		PL	3
Hylobates pileatus	Monogamous	Social Monogamy		PL	3
Hylobates albibarbis		Social Monogamy			1
Nomascus concolor	Monogamous			PL	2
Nomascus gabriellae	Monogamous			PL	2
Nomascus leucogenys	Monogamous			PL	2
Symphalangus syndactylus	Monogamous	Social Monogamy	Social Monogamy	PL	4

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Supplementary Table 2: Evaluation of the pertinence of references provided by Lukas & Clutton-Brock (2013) and Opie et al. (2013) in connection to statements on male care behavior in owl monkeys, titis, sakis and tamarins. This includes also references provided within reviews used by these authors. References are color-coded as follows. Beige: not a suitable reference, yellow: suitable reference for the species in question from captivity, green: suitable reference for the species in question from the wild (but could be limited in scope), blue: review article that refers at least to some relevant sources for at least some of the species in question, gray: suitable for some species, but might have been originally supposed to be on a different species (due to changes in taxonomy) or reference is suitable for some species but not others. When we state that an article is not a suitable reference for a claim, or more generally a suitable source, we do NOT imply that the claimed fact concerning the presence or absence of male care is incorrect. We also do not imply that the author of that source might not have elsewhere provided better support for a statement or that that particular study was not well conducted. We simply state that for a given statement a given reference is not appropriate.

	Reference	Comment
[1]	(Nowak, 1999)	The section on owl monkeys provides general genus-wide descriptions and rarely provides species-level information. The only statement on parental care refers to [18]. That chapter reports "findings" from the wild on *A. nigriceps*, but the actual methods are given in [5, 19]. All data in those references comes from a field study where it was not possible to distinguish between individuals (sexes). **This reference is therefore not sufficient to support the claim of male care in ANY of the owl monkey species.**
[2]	(Fernandez-Duque, 2007)	The chapter on Aotinae cites [5, 20-24] as evidence for paternal care in **captive** owl monkeys and it cites [5, 18, 25-30] for male care in wild *A. azarae*. It cites [26] for other care behaviors in the wild, and for *A. nancymae* and *A. lemurinus* [5, 31]. **If one accepts reviews citing relevant primary sources as evidence, this review is relevant to support claims on male care in *A. azarae*** [26, 27] **and for captive *A.* (*lemurinus*) *griseimembra*** [20]**.**
[3]	(Ross & MacLarnon, 2000)	For the species considered here, [3]'s Table 2 **reviews** literature on "*Aotus trivirgatus*" (citing [5, 20]), "*Callicebus moloch*" (citing [5, 12]), *Pithecia monachus* (citing Bode, 1952, 1953; these two articles are published in Zoonooz, a magazine of the San Diego Zoo. Given that both articles are cited to have only one or two pages, they clearly do not provide citable primary data), *P. pithecia* [32, 33], "*Saguinus fuscicollis*" (citing [34-36]), *S. labiatus* [37, 38], *Leontocebus nigricollis* [39], and *S. oedipus* [40]. **If one accepts reviews citing relevant primary sources as evidence, and if one accepts captive studies as evidence for the presence or absence of male care, this review is relevant to support claims on male care in *A.* (*lemurinus*) *griseimembra (but not A. trivirgatus!*)** [20], ***Saguinus labiatus*** [37, 38] **and *Saguinus oedipus***

		[40]. **The references cited are not adequate for *Plecturocebus moloch*. It does not make statements on *Plecturocebus donacophilus*, *Saguinus imperator*, *S. geoffroyi*, or *S. midas, or Leontocebus nigricollis.***
[4]	(Wright, 1990)	This study is comparative, using data collected in earlier work by the same author on *Aotus nigriceps* and *Callicebus toppini* [5]. Further details on data collection make it clear that infants were the focal animals and that for owl monkeys, it was not possible to distinguish between sexes. The study does not provide any information beyond [5] and **is not suitable to support claims on male care behavior**.
[5]	(Wright, 1984)	Wright studied *A nigriceps* (not *A. trivirgatus*) in the wild at Cocha Cashu, Peru; the data on infant care behavior are from captivity from a presumably different species (from "Northern Colombia" origin, which could be one of several species). She assumed that males were main carrier in the wild, but was actually not able to distinguish between the sexes. Therefore, many statements on infant care behavior must have been retrospectively assigned to sexes or formulated using a circular argument ("We see in captivity (in other species) that males carry more, so if in the wild an individual carries an infant it must be the male."). For the supposed *Callicebus moloch* (now considered *C. toppini*) it is also not clear on what basis sexes were distinguished in the wild. The study makes the statement that "the father carried the infant 92% of the time by the third week". **The reference is not suitable to make statements on sex specific contributions to infant care** (other than suckling) **in *Aotus nigriceps* (or *A. trivirgatus*). It might be considered as evidence for male care in *Callicebus toppini*, but not *Callicebus moloch***.
[6]	(Kappeler, 1999)	This article does not deal with parental care, and only mentions the topic very briefly. **This article is not suitable to support claims on infant care behavior, either in titi monkeys or any other species.**
[9]	(Kinzey, 1981)	This is mainly a review article on various titi monkey species, not based on primary data. It contains some apparently primary data on diet (though not specifying the methods used for the study). The article states that "within 48 hours after birth *C. moloch* males generally start carrying the infant (R. Lorenz, pers. comm)." Neither is it clear which species this really refers to, nor are data provided to support it. The article also states "*C. torquatus* males have been observed in the wild carrying infants (Miller, in Allen, 1916; Kinzey, pers. obs)" and also provides some further own observations on "*C. torquatus torquatus*". Given the distribution of *Cheracebus torquatus* (IUCN 2019), it is unlikely that the species studied in Peru by Kinzey was *C. torquatus*, but rather *C. lucifer* [10], and since the article does not specify in which part of Peru the observations were made, no statement

		can be made. The article refers also to [10] with respect to, for example, play behavior and other sex-specific roles. **This article could be tentatively used as evidence for *C. lucifer* (though not specifically for carrying behavior), but not for *C. moloch* or *C. torquatus.***
[10]	(Kinzey, Rosenberger, Heisler, Prowse, & Trilling, 1977)	The study is in fact on *Cheracebus lucifer*. A single study group with one already independently moving infant was studied for about three weeks (25 d, 138h). The study makes qualitative statements on more frequent close proximity (including play and grooming) between the male and the infant, compared to the female with the infant. The article states: "When we first observed Gr. 1 the infant already moved independently from its parents, BUT WE PRESUME THAT AT AN EARLIER AGE, as in *C. moloch*, he was carried by the adult male" (our emphasis). **The article therefore cannot be used as evidence for higher male carrying contribution in *Cheracebus lucifer*, but as preliminary evidence for male dominance in other infant care aspects such as grooming and play, albeit lacking quantitative data.**
[11]	(Kinzey & Wright, 1982)	While at the time of the study the species was considered *Callicebus torquatus*, the only titi monkey species of the *torquatus* group ranging in Peru is ***Cheracebus lucifer***, that ranges in Loreto, the Peruvian department in which the study took place (Byrne et al. 2016). The study did not investigate carrying behavior but only grooming, based on a single group and only 18 days of observation. While the total amount of grooming by the male directed towards either of the two juveniles (mean 28.2% over both juveniles) was slightly higher than by the female (mean 21.5%), this difference is rather slight, was not statistically tested, and **is overall not enough to make the statement that the male grooms infants more than the female and does not allow any statement on male care behavior in general and *C. torquatus* in particular.**
[12]	(Fragaszy, Schwarz, & Shimosaka, 1982)	This study was on two captive pairs . The assignation of species as *C. moloch* (or *Plecturocebus moloch*) cannot be confirmed since at that time only two species of titi monkey were commonly recognized (e.g. , Hershkovitz, 1990). Although two of the individuals were wild-born, the article does not state the origin of the animals. The study found a higher contribution of male carrying compared to females, but **due to the uncertainty of species, it is not adequate as a reference for a statement on *P. moloch*.**
[13]	(Norconk, 2007)	The chapter on sakis, uakaris (not included here) and titi monkeys cites [9, 12, 41-47] as evidence for paternal care in the titis. For sakis (genus *Pithecia*) it cites [48-51] in relation to infant care behavior. Additionally, their table 8.2 provides references on various aspects of social and reproductive characteristics of the pitheciines, including paternal care [9, 30, 41, 52-60]. **If one accepts reviews citing relevant primary sources as**

		evidence, and that this evidence can be from captive studies, this review is relevant to support claims on male care in *Plecturocebus cupreus* (with the caveat that the species' identiy in [47] is not 100% sure) **and *Pithecia pithecia*** [48]. **It is not a suitable reference for *P. aequatorialis.***
[14]	(Lehman, Prince, & Mayor, 2001)	This article is concerned with census data and **does not provide any information about infant care or the lack thereof** by either male or female *Pithecia pithecia.*
[15]	(Porter, 2001)	This article is only on a single group of *Callimico goeldii*. It provides evidence that all group members participate in transporting the infant in the species, but not for *S. oedipus*. It cites further articles for cooperative infant care in callitrichines in general: [61-66]. **The reference is not suitable as primary source for any of the tamarin species, but as review article cites a relevant primary source** [66] **and a relevant older review** [63], both relating to *Leontocebus weddeli*, Concerning the species mentioned by Lukas & Clutton-Brock (1993) it is a review that cites a review [63] that provides some relevant data from captivity (*L. fuscicollis*) [16, 68] and the wild *S. oedipus* [40].
[16]	(Epple, 1975)	Epple studied captive animals of "*Saguinus fuscicollis*", but using different "subspecies" (*S. f. fuscicollis* and *S. f. illigeri*) – in some cases even within groups. Individuals were kept in pairs with "subordinate" individuals (where the age class of these subordinates is not quite clear, but they seem to be sub-adults). The dominant male was not always the father of the offspring. Based on her Table II, the mean percentage of carrying effort of mothers was 32.8%, for dominant males 52.5% (which was not significantly different from mothers), and for "subdominant" 10.5% . **This reference is evidence for male and cooperative care in captive *L. fuscicollis* and *L. illigeri*, though the percentage values must be considered tentative.**
[17]	(Goldizen, 1987a)	Detailed observations (more than 1100 observation hours on two habituated groups with marked individuals) clearly showed cooperative infant care. Paternity was not known. **This study provides evidence for male and cooperative care in wild *L. weddeli*** (but evidence is not independent of [66]).
[18]	(Wright, 1994)	The time-period and other methods for behavioral data collection are not explicitly mentioned, but it appears to be the same study as detailed in [5], i.e., it was actually not possible to distinguish confidently between the sexes. **The reference is not suitable to support statements on male care.**

[19]	(Wright, 1989)	Field study on *A. nigriceps* at Cocha Cashu, Peru, and on *A. azarae* at Golondrina Ranch, Paraguay. Care behavior is not explicitly investigated, but refers to [5, 20]. **The reference is not suitable to support statements on male care.**
[20]	(Dixson & Fleming, 1981)	This **captive** study is in fact not on *A. trivirgatus*, but on *A.* (*lemurinus*) *griseimembra*. **The reference can be tentatively used to support claims on male care in *A. griseimembra*, but studies from the wild are needed to further support it.**
[21]	(Jantschke, Welker, & Klaiber-Schuh, 1998)	This study includes data on captive *A. azarae boliviensis* (N=34) infants. The mean value provided in Table 2 is recalculated from their Fig. 1. **The reference can be tentatively used to support claims on male care in *A. azarae*, and is in line with findings from a wild population of *A. azarae azarae*.**
[22]	(Málaga, Weller, Buschbom, Baer, & Kimsey, 1997)	The study deals with reproduction in a breeding colony of various species of owl monkeys, but **does not make any statements on infant care behavior**.
[23]	(Meritt Jr., 1980)	The article is essentially a review article on captive populations. While it makes the statement that "young of both genera [i.e. owl and titi monkeys] are usually carried by the male", no direct evidence is provided, and it is not clear to which species it refers in any case. **The reference is not suitable to make statements on sex specific contributions to infant care.**
[24]	(Robinson, Wright, & Kinzey, 1987)	This is a review on owl monkeys, titis and sakis. The review states that *“Callicebus* and *Aotus* have extensive paternal care”, citing [5, 12, 20]. It also states that in sakis “carrying is done by the female (Buchanan et al. 1981; van Roosmalen et al. 1981), although Hicks (1973) mentions male carrying”. We were not able to access these three articles ourselves. We doubt that Buchanan et al. 1981 and van Roosmalen et al. 1981 provide relevant primary data, because they are review chapters in a book. We also have some doubts whether Robinson et al. (1987) have actually read the German article by Hick (1973), since the reference gives as the title of this article “Wir sind umgezogen”, which means “We have moved” – an unlikely title for a supposed study on saki behavior.

		The article does not provide suitable primary evidence to make claims on parental care in any of the species.
[25]	(Juárez, Rotundo, & Fernandez-Duque, 2003)	**This is a conference abstract which should not be used as evidence.** If reviews resort to citing abstracts this already indicates that few primary data are published.
[26]	(Rotundo, Fernandez-Duque, & Dixon, 2005)	This study was conducted on 6 infant *A. azarae*, but did not distinguish between the sexes. **It therefore cannot be used as evidence for the predominance of male care behavior. However, given that transfers of infants between adults were observed, it shows that males do participate.**
[27]	(Rotundo, Fernandez-Duque, & Giménez, 2002)	(Article in Spanish) This is the first study on any wild species of *Aotus* where adult males and females were distinguished, but rather preliminary, studying infant development of 9 infants and care behaviour on a single infant. **It clearly shows the preponderance of male carrying compared to the female for *Aotus azarae*, but should be viewed as preliminary evidence due to the low sample size.**
[28]	(Schwindt, Carrillo, Bravo, Di Fiore, & Fernandez-Duque, 2004)	**This is a conference abstract which should not be used as evidence.** If reviews resort to citing abstracts this already indicates that few primary data are published.
[29]	(Wright, 1981)	This study uses the same data (or absence thereof) as specified in [5]. **The reference is not suitable to make statements on sex specific contributions to infant care in either *Aotus nigriceps* (or *A. trivirgatus*) or *Plecturocebus brunneus* (or *Callicebus moloch*)**.

[30]	(Wright, 1986)	This study uses the same data (or absence thereof) as specified in [5]. **The reference is not suitable to make statements on sex specific contributions to infant care in either *Aotus nigriceps* (or *A. trivirgatus*) or *Plecturocebus brunneus* (or *Callicebus moloch*)**.
[31]	(Feged, Wolowich, & Evans, 2002)	**This is a conference abstract and therefore not sufficient for claims on which further analyses should be based.**
[32]	(Hanif, 1967)	This study on one pair of wild-caught, captive *Pithecia pithecia* states that for almost the whole of the nearly four months the infant was nursed it did not leave the female. **This study therefore supports for captive *P. pithecia* that the female is the only carrier.**
[33]	(Trivers, 1974)	This seminal article developed a theory for parent offspring conflict. **It does not provide primary data and cannot be used as evidence for male care or absence thereof in any species.**
[34]	(Goldizen, 1987b)	This study was supposed to be on *Saguinus fuscicollis*, but the species at Manu National Park, Peru, is now considered *Leontocebus weddelli weddelli*. This book chapter is more of a review, but also contains some previously unpublished data showing that adult males (father and other males) carry more than adult females (mother and other females), and that young individuals contribute to infant care. **This study is suitable to provide evidence on male care in *L. weddelli*, but not *S. fuscicollis*.**
[35]	(Vogt, 1978)	This **captive** study on a single group does not specify the origin of the captive colony. It is therefore **not possible to verify whether the species is *Leontocebus fuscicollis* or a different species**. While the study clearly shows that the father carries more than the mother and that other group members participate, the artificial group composition that would not necessarily reflect conditions in the wild do not allow to make strong statements about relative contributions of specific age-sex classes.
[36]	(Vogel & Loch, 1984)	This book chapter uses primary data on Hanuman langur infanticide and is not concerned with parental care in any *Saguinus* species.
[37]	(Kohda, 1985)	This study observed 24 species of primates in captivity in various locations in Japan. Observations were restricted to the first month of life of infants. The study does not state were the founding individuals of the various populations were originally caught in the wild, so the taxonomy cannot be taken for granted for all species. Of the taxa considered in our review, the study by Kohda deals with *Saguinus labiatus* and "*Aotus trivirgatus*". Given

		the upheaval in owl monkey taxonomy, the species of owl monkey must be considered as undetermined. For both these species "aunting" behavior is mentioned, but for *S. labiatus* it is not stated who the "aunt" is, but the group composition for the observed group indicates the presence of the adult breeding pair and two younger males, i.e. the "aunts" must have been male for this species. **If one accepts evidence from captive populations, the study can therefore be taken as evidence for male participation in infant care in *S. labiatus*.**
[38]	(Pryce, 1988)	This study on 10 captive family groups of *Saguinus labiatus* (incl. an adult pair, older offspring and twin infants) showed that father carried infants from their third day of life for 45-55% of the time. As no other adult individuals were living in the group, contributions of other adults cannot be determined. **If one accepts evidence from captive populations, the study provides evidence for male carrying behavior.**
[39]	(Izawa, 1978)	This study on what would now be considered *Leontocebus nigricollis hernandezi* does explicitly state that "[a]t no time in the growth stages of a baby, … , was the author able to see the so-called "infant-care", whereby an individual other than the mother actively carries a baby on its back to spend a certain part of its daily life." The study does mention that infants climbed for short periods of times on the backs of other individuals, and that other individuals might perform behaviors such as grooming or food sharing. **On the whole, the article rather argues AGAINST male care in *Leontocebus nigricollis*** (although we are skeptical that this is a true representation of the species – see Table 2).
[40]	(Tardif, Carson, & Gangaware, 1986)	This **captive** study on 4 groups each of *Callithrix jacchus* and *Saguinus oedipus* indicates that **in captivity both mothers and fathers carry infants, as well as younger individuals**. It was not tested whether fathers carried significantly more than males, but at least in the latter half of the carrying period the mean carrying time for males was larger than for females. Due to unnatural group compositions it is, however, not possible to make inferences on relative contributions of specific age-sex classes.
[41]	(Mason, 1968)	The species was regarded as *Callicebus moloch ornatus*, now considered *Plecturocebus ornatus* (based on the location within Colombia). The article is concerned with spatial use patterns, travel lengths etc., not with care behavior. While it makes the statement that "the male carries the infant at most times", this is not substantiated with data. **This reference is not suitable to make statements on infant care behavior in any titi monkey species.**
[42]	(Mason, 1971)	While this study includes some information from the wild population investigated in [41] , it is mainly concerned with a captive population (which might be *P. cupreus*, see Table 3), for which pair-bonding between

		adults was investigated. Again, while male care is mentioned, t**his reference is not suitable to make statements on infant care behavior in any titi monkey species.**
[43]	(Menzel, 1986)	Two groups of captive titi monkeys in captivity were studied regarding their territorial behavior. The species is named as *C. moloch*, but the provenance of the individuals is not specified, and thus **it is not possible to establish which species was actually studied. The study does not deal with parental care behavior.**
[44]	(Mendoza & Mason, 1986b)	This book chapter seems to **repeat essentially the same data as presented in Mendoza and Mason 1986a** and **is therefore not independent evidence. The study demonstrates higher levels of carrying by the father compared to the mother for a captive population of an unknown titi monkey species and can therefore not be used as evidence for a specific species.**
[45]	(Mason & Mendoza, 1998)	This is a review article on attachment in primates. It does not provide any primary data and **can therefore not be used as evidence for parenting behavior in any species.**
[46]	(Mendoza & Mason, 1986a)	This captive study on 5-7 triads (probably same study and individuals as in[44] claims to be on *Callicebus moloch* . The study does not mention were the captive colony founders came from, so it is not possible to determine which species was observed. The study showed an increase in cortisol levels in both adult male and adult female when separated from each other, but not upon separation from the infant. In preference tests it also showed preference of adults towards each other compared to the infant, and of the infant towards the father compared to the mother. However, the study also explicitly states that the infant directed behaviors shown by the father were relatively rare, with no grooming or cradling. **The study demonstrates higher levels of carrying by the father compared to the mother for a captive population of an unknown titi monkey species and can therefore not be used as evidence for a specific species.**
[47]	(Schradin, Reeder, Mendoza, & Anzenberger, 2003)	This study was mainly concerned with prolactin levels in fathers in three species, including titi monkey species of the captive colony established by Mason, which is currently considered to be *P. cupreus*, although there is some doubt on that. The study also collected data on carrying behavior in 8 titi monkey families. While data on the carrying behavior itself are not presented, the study reports a lack of correlation between paternal carrying effort and prolactin levels, and states that 6 of the 8 fathers carried infants from day 1 of the infant's birth. **If one accepts evidence from captive studies, this study supports claims on male care in *P. cupreus*** (as well as *Callithrix jacchus* and *Callimico goeldii*).

[48]	(Homburg, 1997)	The PhD thesis of I. Homburg (1997; in German) on *Pithecia pithecia* specifically states that the offspring is not carried by males, whether adult or juvenile. The study was based on an isolated group on a small island. **This is suitable, though preliminary, evidence for the absence of male care in *P. pithecia*.**
[49]	(Brush & Norconk, 1999)	**This is a conference abstract which should not be used as evidence.** If reviews resort to citing abstracts this already indicates that few primary data are published.
[50]	(Buzzell & Brush, 2000)	**This is a conference abstract which should not be used as evidence.** If reviews resort to citing abstracts this already indicates that few primary data are published.
[51]	(Ryan, 1995)	**This is a conference abstract which should not be used as evidence.** If reviews resort to citing abstracts this already indicates that few primary data are published.
[52]	(Wright, 1985)	This is the PhD thesis that led to various publications. **The reference is not suitable to make statements on sex specific contributions to infant care** (other than suckling) **in *Aotus nigriceps* (or *A. trivirgatus*). It might be considered as evidence for male care in *Callicebus toppini* (but not *Callicebus moloch*)**.
[53]	(Hershkovitz, 1990)	This is a taxonomic review of the titi monkeys, providing morphological evidence for taxonomy. It is not concerned with behavior and **does not support any claims of male care in any species.**
[54]	(Kinzey & Robinson, 1983)	This study was concerned with range size and inter-group vocalizations in *Callicebus lucifer* (then called *C. torquatus*). **It does not deal with parental care at all.**
[55]	(Easley & Kinzey, 1986)	This study investigated ranging patterns in one group of *Callicebus lucifer* (then called *C. torquatus*). **It does not deal with parental care at all.**
[56]	(Hershkovitz, 1987)	This is a taxonomic review of the saki monkeys, providing morphological evidence for taxonomy. It is not concerned with behavior and **does not support any claims of male care in any species.**
[57]	(Ford, 1994)	This study was a review on the evolution of sexual dimorphism in primates and **does not deal with parental care at all.**
[58]	(Norconk, 2006)	This article summarizes 11 years of data on a single, habituated, group of *Pithecia pithecia*, inhabiting a very small island. Animals were identified individually. Relating to maternal carrying behavior (and thus implying, but

		not explicitly stating, that males do not carry), she refers to [48, 50]. No primary data are presented. **If one accepts that this article cites a relevant source** [48]**, it provides evidence for absence of male care in *P. pithecia.***
[59]	(Savage et al., 1992)	**This is a conference abstract which should not be used as evidence.** If reviews resort to citing abstracts this already indicates that few primary data are published.
[60]	(Shideler, Savage, Ortuno, Moorman, & Lasley, 1994)	This study monitored estrogen and progesterone profiles of captive female *Pithecia pithecia* (note: given that the study does not report where the animals from the colony originally came from, the identity of the species cannot be confirmed for sure). **It is not concerned with parental care.**
[61]	(Sussman & Garber, 1987)	This study is primarily concerned with the social organization, i.e. showing clearly that tamarins are not normally pair-living. While it mentions cooperative care, no data are provided, although a table shows a relationship between the number of surviving offspring and the number of adult males in groups. **This study is therefore not suitable to make claims about infant care.**
[62]	(Garber, 1994)	This study is concerned with a phylogenetic reconstruction of the social organization and mating system (as well as other aspects of the social system) of callitrichids. While it mentions cooperative care, no data are provided. **This study is therefore not suitable to make claims about infant care.**
[63]	(Goldizen, 1990)	This is a review citing for wild populations of *Leontocebus weddeli* (then considered *S. fuscicollis*): [17, 66] and *Saguinus mystax*: [67]. Additionally, for captive populations they cite for "*S. fuscicollis*": [16, 35, 68] and for *S. oedipus* [40]. **If one accepts reviews that cite relevant primary sources and that these might be from captivity, this makes relevant claims for *L. weddeli* [17, 66], possibly also from captivity for *L. fuscicollis* [16, 68] and for *S. oedipus* [40].**
[64]	(Tardif, Harrison, & Simek, 1993)	This is a study that draws on data from other studies, including two tamarin species: "*S. fuscicollis*" [16, 35] and *S. oedipus* [40, 69], as well as talking about additional observations (without providing details on methodology). **If one accepts reviews, this article provides evidence for male care behavior in *S. oedipus* and more tentatively for some tamarin species in the *Leontocebus* genus** (possibly *L. fuscicollis* and *L. illigeri*, see [16]).

[65]	(Ferrari & Lopes Ferrari, 1989)	This review is concerned with various aspects of the ecology, home-range use and social organization of the callitrichines, but does not deal with male or cooperative care. **This study is therefore not suitable to make claims about infant care.**
[66]	(Terborgh & Goldizen, 1985)	This study was conducted on 7 groups of wild, habituated individually marked *Leontocebus weddeli* (then named *S. fuscicollis*). Infant carrying was studied in 2 multi-male groups. In both groups all individuals in the group were seen carrying infants. **This study provides evidence for male and cooperative care in wild *L. weddeli*** (but not independent of the evidence provided in [17]).
[67]	(Garber, 1986)	This is a single page short report published in the "house journal" of the German Primate Centre, which is not peer-reviewed. **This is not a suitable source of scientific evidence.**
[68]	(Cebul & Epple, 1984)	We were not able to get access to this book chapter. The chapter is concerned with captive animals - and given the recent revision of the taxonomy of the "saddle-back" tamarins, it is doubtful whether the species is really *Saguinus fuscicollis.* Furthermore, traditionally, captive populations of callitrichines are kept in pairs, which is not the typical social organization for most species (and clearly not for saddle-back tamarins). **The reference is therefore not suitable to make claims on wild populations, but might be evidence for captive *L. fuscicollis* and *L. illigeri* (see** [16]**).**
[69]	(Cleveland & Snowdon, 1984)	This study on captive *Saguinus oedipus* states that during the first four weeks of an infant's life males carried more than females. **If one accepts evidence from captive studies, this study supports that male carrying and other forms of care are present in the species.**

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Supplementary Table 3. Number of observation days across study years for all study groups of owl monkeys (*Aotus azarae*) at the Reserva Privada Mirikina, Guaycolec Ranch, Argentina, titi monkeys (*Plecturocebus discolor*) and sakis (*Pithecia aequatorialis*) at the Tiputini Biodiversity Station, Ecuador.

Group	**‘97**	**‘98**	**‘99**	**‘00**	**‘01**	**‘02**	**‘03**	**‘04**	**‘05**	**‘06**	**‘07**	**‘08**	**‘09**	**‘10**	**‘11**	**‘12**	**‘13**	**‘14**	**‘15**	**‘16**	**‘17**	**‘18**	**N Yrs**
Aotus																							
D500	29	32	44	48	86	106	64	80	71	20	20	89	128	95	102	90	161	22	24	18	45	49	22
E500	7	20	44	36	50	82	36	42	47	11	22	134	140	52	114	157	130	21	112	16	46	45	22
E350	52	58	118	21	27	129	129	43	37	43	39	16	12	59					146	16	30	16	18
CC	18	24	70	36	33	80	45	69	46	11	24	90	95	102	45	39	151	14	53	17	46	44	22
C0	20	31	63	32	50	57	45	57	83	11	24	88	43	37	133	91	34	15	158	20	76	55	22
D100	11	25	78	41	55	21	40	59	92	18	27	100	105	67	18	15	50						17
Colman	28	77	50	65	35	7	13	67	27	29	69	23	16	2	14	36			3	10	7	3	20
D800	8	1	35	51	26	14	16	66	34	7	12	49	40	31	54	66	113	17	95	9	15	37	22
F1200	6	13	21	11	38	50	48	61	9	11	52	27	35	23	15	25	3	17	3	4	4	3	22
F700	5	1	36	30	30	16	9	4	36	18	15	22	6	117	4	15	23		90	11	16	35	21
P300	18	17	14	9	32	21	17	25	19	72	2	11	22						8	7	8	4	17
B68	19	16	41	32	39	44	33	21	17	6	11	9	9	32	17	14	15	7	6	10	9	7	22
D1200	9	5	12	18	36	57	24	35	8	3	5	7	10	3	32	86	10	3			2		19
G1300	22	37	37	47	9	10	16	10	14	10	5	5	2	13	17				3				16
L100	2	6	13	31	10	10	28	13	14	17	11	6	2	13	13				1	4	1		18
Parrilla	41	11	8	3	5	13	4	7	12														9
A500	3	2	2	1	2	7	14	13	23	24	19	8	5	13	9				1	3	5		18
IJ500	1	10	6	3	5	30	18	6	1	3	19	9	15	10	6	11	4	17	4	2	3	4	22
CAMP	2	18	15	4	21	17	12	3	1	2	1	11	9								1		14
A900	1	14	6	3	7	22	14	5	6	13	1	13	4	2	14	8							16
Aranda	13	5	3	3	7																		5
Fauna	2	28	12	4	2	3	5	3	6	1	10	7											12
Pic Camp	2	1	1	3	5	4	9	2	9	9	4								1				12
H900	10	1	1	3	4																		5

F1400	6	4	1	1	1	2	9	2	8	3									1				11
Pic Casco	2	5	4	1	5	1	6	3															8
D1400	5	1	2	2	1	5	2												1				8
Plecturocebus																							
Group K								12	77	56	71	70	79	37	41	49	13	27	67	23	1	13	15
Group L										10	31	50	77	42	33	46	20	21	58	58	30	21	13
Group B										5	44	34	31	32	45	59	16	17	21	9		9	12
Group H										13	45	40	30	9									5
Group G									16							54	25	4	2				5
Group P								4	6														2
Pithecia																							
Group M								73	115	52	44	60	57	43	67	59	24	37	60	41	27	35	15
Group S																	24	32	50	31	33	16	6
Group D											15	13		12	16								4
Group H																39	10						2
Group P																	18	17	47	34	30	3	6
Group T																20							1