The influence of ecology on social behavior and mating strategies is one of the central questions in behavioral ecology and primatology. Callitrichines are New World primates that exhibit high behavioral variability, which is widely acknowledged, but not always systematically researched. Here, I examine the hypothesis that differences in the cost of infant care among genera help explain variation in reproductive traits. I present an integrative approach to generate and evaluate predictions from this hypothesis. I first identify callitrichine traits that vary minimally and traits that are more flexible (e.g., have greater variance or norm of reaction), including the number of males that mate with a breeding female, mechanisms of male reproductive competition, number of natal young retained, and the extent of female reproductive suppression. I outline how these more labile traits should vary along a continuum of infant care costs according to individual reproductive strategies. At one end of the spectrum, I predict that groups with higher infant care costs will show multiple adult males mating and providing infant care, high subordinate female reproductive suppression, few natal individuals delaying dispersal, and increased reproductive output by the dominant female—with opposite predictions under low infant costs. I derive an estimate of the differences in ecological and physiological infant care costs that suggest an order of ascending costs in the wild: *Cebuella*, *Callithrix*, *Mico*, *Callimico*, *Saguinus*, and *Leontopithecus*. I examine the literature on each genus for the most variable traits and evaluate a) where they fall along the continuum of infant care costs according to their reproductive strategies, and b) whether these costs correspond to the ecophysiological estimates of infant care costs. I conclude that infant care costs can provide a unifying explanation for the most variable reproductive traits among callitrichine genera. The approach presented can be used to generate predictions and motivate researchers to unravel complexity in callitrichine social and reproductive behavior. Am. J. Primatol. © 2015 Wiley Periodicals, Inc.

Key words: cooperation; sexual selection; ecology; mating systems; phenotypic plasticity

INTRODUCTION

The influence of ecology on social and reproductive behavior is one of the central questions in behavioral ecology, with deep roots in primatology [Crook & Gartlan, 1966]. Recent studies on primates and other species have highlighted the influence of ecology on variability in social and reproductive behavior [Bertran et al., 2009; Savini et al., 2009; Thompson, 2013; Morino in press; Porter et al. in press]. For example, white-handed gibbons (*Hylobates lar*) are thought to be socially monogamous, but groups exploiting smaller home ranges—defined as lower quality territories by phenology surveys quantifying monthly productivity of trees per hectare—were associated with a socially polyandrous (i.e., two-male) configuration. In highly social species, variability in mating patterns, social bonds, and parental care is not readily explained using the traditional mating systems concept, which assumes a low potential for long-lasting, reciprocal interactions between group members [Emlen & Oring, 1977], a condition not found in most primates. Instead, social, mating, and caregiving behaviors in group-living taxa are best viewed as emerging from the actions of individuals attempting to balance cooperation and conflict to maximize their reproductive success [Caine, 1993; Davies et al., 1995; Digby & Saltzman, 2009; Sussman & Garber, 2011]. The assets required...
for offspring production, which may vary across species and include ecological factors (e.g., food availability and distribution, habitat structure, predation risk, access to refuges, and sleeping sites) and social factors (individuals to assist in rearing young or protecting group, infanticide risk, collective action, and long-term partner preferences), influence the costs and benefits of reproduction for individuals [Koenig et al., 1992], and thus, emergent patterns of social behavior [Curry, 1989; Helms & Helms Cahan, 2012; Kocher et al., 2014; Rubenstein, 2007, 2011].

Callitrichines are a subfamily of diminutive anthropoids that have been characterized as exhibiting high variability in social and reproductive behavior [Goldizen, 1988], including number of breeding adults, mating patterns, dispersal, and strategies of reproductive suppression. Callitrichine cooperative infant caregiving, lack of sexual dimorphism, and possible evidence of a male-female pair bond in captivity were originally understood within the framework of a monogamous mating system [Kleiman, 1977]. However, field and captive studies that revealed behaviors such as frequent migration, multiple reproductively active males and females per group, and reproductively inactive resident adult females, provided evidence that an exclusive and long-term mating relationship between a single male and a single female is not the modal pattern [Epple, 1975; Garber et al., 1984; Hampton et al., 1966; Garber et al., 2015]. Thus, a debate regarding the “true” mating system of callitrichines ensued [Anzenberger & Falk, 2012; Baker et al., 1993; Goldizen, 1989; Sussman & Garber, 1987]. However, a failure to identify callitrichine behaviors that vary minimally from those that vary more widely, and the limits of such variability across different callitrichine taxa has resulted in a reduced understanding of the role of specific ecological factors in shaping callitrichine behavioral variability.

A number of synthetic reviews in the 1980’s and 1990’s presented diverse approaches to explain reproductive and social behavior in callitrichines. Caine [1993] focused on the importance of predation as a promoter of cooperation and behavioral flexibility. Garber [1994] presented a phylogenetic approach to study variation in callitrichine behaviors. Dunbar [1995a,b] used game theory models highlighting the role of individual decision-making in shaping behavior. Rylands [1996] focused on ecological differences in the habitat and dietary niche in which each of the major callitrichine lineages likely evolved. These explanations and approaches are not necessarily mutually exclusive [Tinbergen, 1963], and represent different levels of analysis [Sherman, 1988]. For example, whereas Caine [1993] focused on the origin of twinning and cooperative breeding, Dunbar [1995b] focused on the maintenance and current function of this behavior. In contrast, Ferrari and Lopes [1989] took an integrative approach, proposing that specific ecological differences in exudate feeding between divergent lineages (Saguinus and Callithrix) offered the strongest explanation for differences in reproductive output and social organization compared to tamarins. Since these reviews, notable advances in the study of callitrichines –long-term field studies, genetic studies examining relatedness and paternity [Diaz-Munoz, 2011; Garber et al., 2015; Huck et al., 2005b; Nievergelt et al., 2000; Suarez, 2007], new phylogenetic information [Buckner et al., 2014; Perelman et al., 2011,], and the recent analysis [Harris et al., 2014] of the marmoset genome [Marmoset Genome Consortium, 2014]—have resulted in new data and avenues of analysis that warrant a renewed attempt to produce an explanatory framework for variability in callitrichine reproductive and social behaviors.

In this paper, I present the hypothesis that the costs of infant rearing offer a strong explanation for differences in the most variable social and reproductive traits among callitrichine genera. I first identify callitrichine traits that vary minimally and traits that are more variable in their expression, including, number of breeding adults, mating patterns, dispersal, and strategies of reproductive suppression. Second, I outline how these more labile traits should vary along a continuum of infant care costs according to individual reproductive strategies. I then estimate differences in infant care costs among genera based on ecological and physiological proxy measurements. Finally, I examine the literature of each genus for the most variable traits and evaluate a) where they fall along the continuum of reproductive strategies according to infant care costs, and b) whether these costs correspond to ecophysiological estimates of infant care costs.

**CALLITRICHINE EVOLUTION**

Callitrichines share a unique set of traits, among them twinning (except Callimico), small body size, large maternal-infant mass ratios, post-partum estrus, female reproductive suppression, and extensive alloparental care of infants. Disentangling the order of appearance of these traits during the evolutionary history of callitrichines is critical for determining how traits that evolved earlier in callitrichine evolution impacted traits that evolved later in callitrichine evolution. Based on analyses of the newly released marmoset genome and genetic data from other New World monkeys, Harris et al. [2014] argue that small size, twinning, postpartum estrus, and ecological specialization to edge habitats [Rylands, 1996] may have co-evolved endowing ancestral callitrichines with the ability to rapidly colonize newly emerging habitats associated with forest contraction due to flooding cycles during the creation of the Amazonian drainage [Buckner et al., 2014]. The maternal demands of rapid reproduction
(twining and short interbirth intervals) then constituted a strong selection pressure for alloparenting and female reproductive suppression [Goldizen, 1990; Harris et al., 2014; Ross, 1991]. Regardless of the particular sequence of events, the high costs to mothers of caring for twin infants appears to be the key to understanding callitrichine social and reproductive behavior [Goldizen, 1988; Tardif, 1997].

THE IMPACT OF INFANT CARE COSTS ON SOCIAL BEHAVIOR

The costs of callitrichine infant care on mothers, i.e., twining and short interbirth intervals, serve to shape the social and reproductive dynamics of callitrichine groups [Goldizen, 1990; Harris et al., 2014; Ross, 1991]. This key cost leaves a footprint on callitrichine social organization and reproductive behavior, wherein some traits are characterized by limited variability—skewed female breeding, male-biased group composition, alloparental care [Digby et al., 2007; Ferrari & Lopes, 1989; Koenig, 1995; Sussman & Garber, 1987]—and other traits exhibit greater variability including the number of males that mate and sire young, mechanisms of male reproductive competition, number of natal young that delay dispersal into adulthood, extent of female reproductive suppression, and dominant female reproductive output. Callitrichine taxa show considerable variability in the latter traits, and given the importance of the cost of infant care to reproductive success, variability in these traits is likely to respond to differences in the costs of infant care [Digby et al., 2007; Digby & Barreto, 1996; Ferrari & Lopes, 1989; Goldizen, 2003; Heymann, 2000; Tardif et al., 1993].

The key question then is the extent of variability in infant care costs across taxa, as well as its correlates and potential causes. The costs of infant care arise from the energetic expenditures that callitrichines must incur to successfully rear twin young, which can roughly be separated into physiological and ecological components [Tardif, 1994]. Parameters such as maternal-infant mass ratios, infant development rate, and litter size constitute the physiological components of the cost of infant production and care [French, 1997; Tardif et al., 1993]. However, the environment necessarily affects these physiological costs, and therefore different habitats will vary in the assets required for infant rearing. These assets include the social environment (e.g., group size and composition, reproductive competition, kinship, predation risk, intergroup encounters with neighboring groups) and the ecological context (e.g., home range size, resource seasonality, daily path length, population demography) [Digby et al., 2007; Tardif, 1994]. Callitrichines show evidence of responding to these social and ecological assets by manipulating offspring production. For instance, in captivity the number of ovulations are higher in common marmoset mothers with increased body mass [Tardif & Jaquish, 1997]. In wild S. mystax and S. fuscicolis, maternal infanticide has been documented on two occasions, apparently in response to a shortage of infant caregivers [Culot et al., 2011; Herrera et al., 2000;]. Demographic conditions also appear to affect pregnancy rates for wild L. rosalia females; the presence of additional group members increases the likelihood of successful pregnancy, independent of female dominance status [Henry et al., 2013]. Importantly, there can be complex interactions between the ecological conditions and group demography, such that ecological conditions can drive demographic changes and patterns of natal migration that influence infant care costs, with feedbacks possible in both directions.

An example of the interplay of the social and ecological context comes from marmosets, which are characterized by modifications of dentition [Eng et al., 2009] and digestion [Power & Oftedal, 1996] that allow them to exploit tree exudates, which for many species represent a year-round resource. This stable resource has been hypothesized to enable marmosets to have smaller home ranges, larger group size, and persist in more highly seasonal environments compared to Saguinus or Leontopithecus [Ferrari & Lopes, 1989].

The ability of marmosets to control the availability and production of exudates suggests that reproduction may be less nutritionally constrained [Ferrari & Lopes, 1989; Tardif et al., 1993; Tardif, 1994] and accordingly, breeding females more regularly produce two litters of twins a year. Thus, increased exudate availability, especially during periods of increased nutritional demands may relax the constraints of infant care either directly via increased food resources, or indirectly through changes in group demography (larger group sizes, more alloparents, less frequent natal migration).

Changes in reproductive output between wild and captive callitrichines represent another line of evidence indicating that the environment can affect infant care costs and variation in reproductive behavior. If captivity is viewed as an ecological manipulation that reduces travel costs, predation risk, and exposure to pathogens, while increasing food resources, this may explain why marmoset females regularly produce triplets—and sometimes larger litters—in captivity [Tardif et al., 2003; Windle et al., 1999], albeit with reduced survival rates [Tardif et al., 2003]. Similarly, given that captive callitrichines are kept as breeding pairs, there is considerable evidence that in the confines of cages that generally measure 2–11 m³, a single male and a single female can form a strong social bond and reproduce successfully without the assistance of alloparents. Collectively, these observations suggest...
that callitrichine reproductive biology exhibits phenotypic plasticity in the number of offspring per litter and interbirth interval across genera, consistent with requirements for rapid colonization of new environments [Harris et al., 2014].

Given that differences in the social and ecological environments can lead to differences in infant care costs [French, 1997; Tardif, 1994] two important questions arise. How is variability in traits such as mating patterns, social bonds, and parental care defined, constrained, and characterized? Can the costs of infant care be estimated using ecophysiological measurements and do these correspond to expected variability in these traits?

### ESTIMATING INFANT CARE COSTS: PHYSIOLOGY AND ECOLOGY

Fine-grained data on the costs of infant care are not widely available across all callitrichine genera; nevertheless the use of proxy measures –incomplete as they may be– can serve to estimate the relative physiological and ecological costs of caregiving across species [French, 1997; Tardif, 1994]. French [1997] and Tardif [1994] employed this approach to predict the incidence of reproductive suppression among females and infant care costs (respectively) across different callitrichine taxa. I have adopted their general approach to estimate infant care costs. Specifically, following Tardif [1994], I use relative infant weight (defined as the neonate to adult body mass ratio) and spatial movement patterns (home range area) to rank callitrichine lineages in terms of their effective costs of infant care. I use home range area rather than daily path length, which was used by Tardif [1994], for several reasons. First, by definition, home range area includes the entire set of resources exploited by group members over some predetermined period, i.e., the “area traversed by the individual in its normal activities of food gathering, mating, and caring for young” [Burt, 1943: 351]. I argue that this measure represents a reasonable starting point when the specific ecological factors influencing infant care costs are unknown. Second, home ranges show considerable variation among and within different callitrichine lineages [Fig. 1 and Digby et al., 2007], suggesting that, at least statistically, they will have more power than daily path lengths—which are less variable [Digby et al., 2007]– to explain the variation observed in reproductive behavior. Third, while home range size scales allometrically, body size explains a relatively small proportion of the variation between species (~30%, Fig. 1), suggesting home range area may reflect important ecological differences. Here I use home range area [from Digby et al., 2007] multiplied by neonate:adult mass ratios [from Hartwig, 1996] as a proxy for quantifying relative infant care costs (Fig. 2). I restrict myself to these sources, which are the most complete and recent, for simplicity and to avoid selection bias in these two variables. Importantly, I do not propose that mass ratios and home ranges are causal factors underlying infant care costs. Instead, because these variables are among the most well documented across taxa, they serve the purpose of estimating relative differences among genera. Undoubtedly, future studies will identify more relevant causal factors to estimate infant care costs.

There is relatively little variation in adult: neonate mass ratios across callitrichine taxa [Fig. 2 and as noted by French, 1997] and home range area explains ~90% of the variance in ecophysiological costs in this calculation (Fig. 2). However, adult-infant mass ratios set an important baseline of infant care costs that interacts with the home range area (Fig. 2). I propose a relative ordering of infant care costs across the major callitrichine lineages based on this proxy measure with: *Cebuella* exhibiting the lowest costs, followed by *Callithrix, Mico, Callimico, Saguinus*, and *Leontopithecus* (Fig. 2). The relative order of infant care costs presented here is a hypothesis to be tested. Importantly, this order can be rearranged when considering intraspecific variation in factors that can affect home range area such as group demography, food resources, sleeping sites, and predation pressure (Fig. 2).
INDIVIDUAL REPRODUCTIVE STRATEGIES UNDER DIFFERENT INFANT CARE COSTS

To describe the impact of infant care costs on variability in behavior, it is necessary to define the social and reproductive characters that vary minimally, from those that vary more widely across different callitrichine taxa, and examine the individual reproductive strategies that arise as a consequence [Davies et al., 1995; Sussman & Garber, 2011]. This approach views callitrichines as cooperative breeders [Digby & Saltzman, 2009; Garber et al., 1984; Henry et al., 2013], in contrast to the more traditional view that variability arises from a “deviation” from an idealized “mating system” [e.g., Anzenberger & Falk, 2012]. Under this view mating (individuals who copulate) and breeding (individuals who donate genes to the next generation) patterns are assumed to be identical, and certain behavioral and morphological traits are assumed to be co-evolved or invariably linked (e.g., for monogamy: exclusive mating, pair bond, territoriality, size monomorphism) as intrinsic to a given mating system [Fuentes, 1998].

There is a general agreement that all or virtually all callitrichine species are characterized by highly skewed female breeding, a male-biased group composition, allopasternal care, and twinning (except Callimico) [Digby et al., 2007; Ferrari & Lopes, 1989; Koenig, 1995; Sussman & Garber, 1987]. Traits that are more variable across species include: number of males that mate and sire young, mechanisms of male reproductive competition, number of natal young retained to adulthood, extent of female reproductive suppression, and reproductive output of the dominant female. Infant care costs will affect the relative

Fig. 2. Estimates of ecophysiological costs of infant rearing vary among and within Callitrichine lineages. Each bar represents ecophysiological cost (median home range size multiplied by average neonate:adult body mass ratio), the point represents the median value and the ends of the line the minimum and maximum values. The yellow star indicates the value for Leontopithecus rosalia at the Poco das Antas site. Bottom graphs represent ecological (median home range size in hectares) and physiological (average neonate:adult body mass ratio) costs among lineages on the left and right, respectively. Note the relative similarity between the ecological and ecophysiological costs graphs. Data on home range from [Digby et al., 2007] and body size from [Hartwig, 1996]. Data and code available in the Figshare repository (doi:10.6084/m9.figshare.1393430).
costs and benefits of individual reproductive strategies, which may alter the patterns of variability expressed in these traits. Thus, I outline a heuristic categorization scheme to predict the reproductive strategies individuals in a group will adopt along a continuum of infant care costs. Many of these categories have been widely used in the callitrichine literature, so I only briefly define each category and examine differences in individual behavioral status (e.g., social dominance relationships) vs. individual breeding status (e.g., successful mating). I use these categories to predict the reproductive strategies that individuals will adopt under conditions of low and high infant care costs, based on models of individual fitness [Chao, 1997; Dunbar, 1995b; Stacey, 1982].

**Dominant Female**

The presence of a single breeding female per group is characteristic of most callitrichine species [Sussman & Garber, 1987]. However, there are many exceptions to this “rule” [Garber et al., 2015], and a second female may mate, conceive, and occasionally produce twin offspring. This has led some to question the idea of a sovereign breeding female [Henry et al., 2013]. However, it is generally possible to designate a single dominant female per group [French, 1997] based on behavioral dominance, hormonal profiles indicating active reproductive cycling, and age, with the older females tending to be breeders [Garber, 1997]. Female dominance status and age, in this regard, are highly correlated with reproductive success.

A dominant callitrichine female appears to increase her reproductive success by limiting the reproductive success of other resident females, presumably to secure assistance with rearing young. The dominant female’s fitness also may be increased by the preferential use of particular adult male caregivers, assuming significant differences in male caregiving behavior and effectiveness. If caregiving competence is highly variable among males, then even under conditions in which infant care costs are relaxed, the fitness of the dominant female may increase by suppressing other females, to minimize competitive over access to competent caregivers. Alternatively, dominant females may be less effective at suppressing (chemically or socially) subordinate females when food availability is high or the number of alloparents is not limiting [Digby & Saltzman, 2009]. For instance, in wild *L. rosalia*, an increase in group members increases the likelihood of females becoming pregnant, independent of dominance status [Henry et al., 2013].

**Adult Male Groupmates (Non-Natal)**

The presence of multiple adult males is common in wild callitrichine groups [reviewed by Garber et al., 2015; Sussman & Garber, 1987], and in many studies females mate with more than one male. In some studies dominance hierarchies based on agonistic interactions have been used to designate one male as a socially dominant male [Baker et al., 1993; Soini, 1987; Yamamoto et al., 2009], whereas in other studies there were no clear behavioral or hormonal signatures of male dominance [Diaz-Munoz, 2011; Goldizen, 1989; Huck et al., 2005a]. I refer to these males as groupmates, which does not assume differences in mating or breeding behavior.

In some callitrichine studies [e.g., Baker et al., 1993; Yamamoto et al., 2014], one male has been assumed to be the sole breeder and the “extra” resident males are often assumed to serve as non-breeding helpers of the breeding pair; however, this assumption is rarely tested. When testing hypotheses stemming from the cooperative breeding literature, the use of the term helper for these males is inappropriate because in that literature, helpers are non-breeders by definition [Skutch, 1935], and in virtually all callitrichine studies paternity is unknown [Garber et al., 2015 but see Diaz-Munoz, 2011; Huck et al., 2005b; Suarez, 2007]. Within the frame of testing hypotheses of cooperative breeding, designating males as helpers when they also mate with the breeding female(s) during fertile periods can lead to premature rejection of relevant explanations for mating and parental care patterns. In the absence of paternity data, it is most conservative to consider adult males—that are unrelated to the breeding female (and possibly those also related to the breeding female)—as potential breeders, independent of the degree of reproductive monopolization [Stacey, 1982].

When infant care costs are high, two or more adult males may depend on each other for successful reproduction, because lone male-female pairs cannot breed in the wild [Goldizen, 1988]. Males may be advantaged by acting cooperatively with other males, provided they have some expectation of siring young or are related [Diaz-Munoz, 2011]. The age of a male also may influence the benefits of cooperation, as younger adult males may have an increased chance of inheriting a breeding position—assuming a multiple male situation where the main breeders are older. Males also may derive indirect fitness benefits by cooperating with adult male kin [Diaz-Munoz, 2011; Huck et al., 2005b; Suarez, 2007]. In groups in which multiple adult males copulate with the same female during their ovulatory period, males may compete via sperm competition. Resident males also have been observed to mate with females from neighboring groups [Digby, 1999; Yamamoto et al., 2009], which may also contribute to their reproductive success. Under conditions in which the costs of rearing twin infants are reduced (e.g., due to an increased group size with more alloparents, exploiting a home range.
with abundant nutritional resources, or both), an increased effort by a single male to limit the reproductive opportunities of other resident males may be expected, if they have sufficient assistance to rear young. Under conditions in which the costs of rearing twins is lowest (for example, when extensive infant carrying is not required, see pygmy marmosets below), each male might be expected to maximize his individual fitness by attempting to eject other males from the group or producing offspring with more than one resident female.

**Subordinate Adult Females**

In addition to the dominant female there are often other adult females present in callitrichine groups. In most cases, these females are reproduc-tively subordinate to the dominant female and fail to produce offspring. However, in some cases these females mate with resident or neighboring males and produce offspring [Arruda et al., 2005; Yamamoto et al., 2009]. For example, in golden lion tamarins 10% of groups contain subordinate adult females who are successful breeders [Dietz & Baker, 1993], and a review by Garber et al. [2015] reports that 23 of 52 Saguinus groups (44%) in the wild contained multiple breeding females.

When subordinate females successfully breed, their reproductive success is generally lower than that of the dominant female [Digby, 1995]. In general, the breeding success of subordinates is expected to be higher under conditions in which infant care costs are low, such as when there are more alloparents to assist in rearing two litters of young [Henry et al., 2013]. However, when infant care costs are too high to permit subordinate females to breed, these females may attempt to disperse to find new breeding opportunities [Koenig et al., 1992]. Alternatively, when subordinate adult females are genetically related to the group’s dominant female, individuals may delay dispersal and potentially gain indirect fitness by successfully caring for related young until a breeding vacancy arises.

**Natal Individuals**

When offspring delay dispersal and remain in the natal group into adulthood, the breeding status of natal individuals may depend strongly on group composition. The costs of inbreeding in callitrichines include severely reduced infant survival to weaning [Dietz & Baker, 1993; Dietz et al., 2000] and there exist strong inbreeding avoidance mechanisms such as endocrine modulation (higher progesterone levels in natal groups) and ovulation suppression in subordinate females [French, 1997; Saltzman et al., 1997]. Assuming inbreeding avoidance, a change in the breeding female can turn inhibited natal males that have reached maturity into potential co-breeders. Similarly, a change in breeding males can potentially open reproductive opportunities for natal subordinate females.

The conditions influencing the dispersal or retention of natal individuals in cooperatively breeding groups remain unclear. Dispersal patterns will exert a strong influence on group demography and consequently infant care costs. For instance, when infant care costs are high, and the number of adult alloparents are limited, juvenile males may be retained preferentially due to the positive impact of adult males on offspring rearing success [Garber et al., 1993; Heymann, 2000]. However when opportunities for reproduction in their natal group are low, most natal individuals (males and females) are expected to disperse. In contrast when infant care costs are low (for example, when groups occupy small and highly productive home ranges, need for parental care is reduced by an abundance of alloparents) there may be more opportunities for breeding within the natal group. This may explain the high incidence of two breeding females in common marmosets [Garber et al., 2015].

In sum, for the most labile callitrichine traits, such as the number of males that mate and sire young, male cooperation and tolerance in caring for young, mechanisms and effectiveness of female reproductive suppression, the number and sex of natal individuals that delay dispersal, and the reproductive output of dominant females (Table 1), I expect that under high infant care costs: a) dominant females’ reproductive output is low (1 litter per year) and subordinate females are reproductive suppressed; b) >2 adult males mate with the dominant female, care for her offspring, and exhibit low reproductive competition; and c) most natal individuals disperse owing to severely reduced breeding opportunities within the group. In contrast, under low infant care costs, a) dominant females have increased reproductive output (>1 litter per year) and suppression of subordinate females is either incomplete or absent; b) male reproductive competition will vary according to their ability to breed with subordinate females: b1) it may increase if there are few or no subordinate females to breed with and a single male may attempt to monopolize matings with the lone breeding female, b2) or it could decrease if reproductive suppression is low, because more males will have mating opportunities c) natal individuals will have more breeding opportunities within the group, so more may delay dispersal. However, natal individuals may increase dispersal rates depending on the presence of their parents in the group: c1) fathers limit opportunities for natal females, c2) mothers do the same for males, and c3) both parents may limit opportunities for all natal individuals.

<table>
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<tr>
<th>Category</th>
<th>Infancy care costs</th>
<th>Subordinate care costs</th>
<th>Natal care costs</th>
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<td>Dominant female</td>
<td>Low infant care costs</td>
<td>Intermediate infant care costs</td>
<td>High infant care costs</td>
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<td><em>Cebuella, Callithrix, Mico</em></td>
<td><em>Callimico, Leontopithecus rosalia</em></td>
<td><em>Saguinus</em></td>
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<td></td>
<td>--Infanticide of sub♂ offspring common [Digby and Saltzman, 2009; Yamamoto et al., 2009]</td>
<td>--Infanticide of sub♂ offspring rare</td>
<td>--Maternal infanticide in unfavorable conditions [Herrera et al., 2000]</td>
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<td></td>
<td>--Two litters a year [Digby et al., 2007]</td>
<td>--Maternal infanticide in unfavorable conditions</td>
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<td></td>
<td>--More groups with successful subordinate breeders [Digby and Saltzman, 2009]</td>
<td>--Few groups with successful subordinate breeders [Porter, 2001; Dietz and Baker, 1993]</td>
<td>--Groups with successful subordinate breeders rare [Garber et al., 2015; Lottker et al., 2004; Diaz-Muñoz, 2011; Garber et al., 1993]</td>
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<td>Non-natal adult males</td>
<td>--More groups with single adult male</td>
<td>--More groups with single adult male [Porter, 2001; Garber, 2004]</td>
<td>--Few groups with single adult male [Garber et al., 2015; Goldizen et al., 1996]</td>
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<td></td>
<td>--Monopolization of paternity frequent</td>
<td>--More monopolization of paternity [Baker et al., 1993]</td>
<td>--No monopolization of paternity</td>
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<td></td>
<td>--Number does not correlate with infant survival [Heymann and Soini, 1999]</td>
<td>--Number correlates with infant survival [Bales et al., 2000]</td>
<td>--Number correlates with infant survival [Koenig, 1995]</td>
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<td>Natal delayed dispersal offspring</td>
<td>--Number correlates with infant survival [Heymann and Soini, 1999; Koenig, 1995]</td>
<td>--Number does not correlate with infant survival</td>
<td>--Number does not correlate with infant survival [Koenig, 1995]</td>
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<td>--More retained in group and providing allocare [Koenig, 1995; Digby and Barreto, 1993]</td>
<td>--Fewer retained in group and providing allocare [Porter, 2001]</td>
<td>--None retained in group and providing allocare [Garber et al., 1993; Lottker et al., 2004; Diaz-Muñoz, 2011]</td>
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EVALUATING PREDICTED INFANT CARE COSTS BASED ON OBSERVED REPRODUCTIVE STRATEGIES

I have outlined predictions for how infant care costs will influence the expression of variation in certain labile callitrichine traits associated with individual reproductive strategies. I also have separately estimated infant care costs for each callitrichine lineage based on ecophysiological costs calculated using the proxy measurements of home range area and neonate:adult body mass ratios. Here, I bring these two predictions together by using published findings from the wild and captivity to evaluate: a) where each genus falls along the continuum of high to low infant care costs according to male and female reproductive strategies (see also Table I); and b) how closely these predicted infant care costs correspond to the ecophysiological estimates of infant care costs (Fig. 2). Finally, I briefly discuss some of the potential causes underlying the proposed differences in infant care costs across genera.

*Saguinus* Tamarins

Reproductive and social behavior of *Saguinus* has been the most well-characterized among callitrichines, thanks to long-term field studies [Garber...
et al., 1993; Goldizen et al., 1996; Huck et al., 2005b; Lottker et al., 2004) and studies using molecular genetics to determine relatedness and paternity patterns [Diaz-Muñoz, 2011; Garber et al., 2015; Huck et al., 2005b; Suarez, 2007]. Based on predictions from individual reproductive strategies, Saguinus groups appear to conform to expectations under high infant care costs.

First, examining reproductive suppression among females, field evidence suggests that successful breeding by two females is rare, except in saddleback tamarins (Saginus weddelli) in which approximately 12% of groups contain two breeding females [Garber et al., 1993; Garber et al., 2015; Goldizen & Terborgh, 1989; Huck et al., 2005b; Lottker et al., 2004]. Dominant females generally produce only one twin litter per year [Goldizen & Terborgh, 1989; Lottker et al., 2004]. Potential maternal infanticide has been reported in only two cases; both instances were interpreted as postnatal termination in maternal investment under conditions of too few alloparents [Culot et al., 2011; Herrera et al., 2000]. However, the number of potential alloparents in these two groups ranged from two to four, which in many instances is sufficient for the successful rearing of tamarin twins. In the single group of mustached tamarins studied by Culot et al. [2011] over 4 years, when the group contained ≥3 males infant survival was 75% whereas when there were two adult males, infant survival was 42% with only one or two males.

Second, examining patterns of male mating, field and genetic data suggest that multiple non-natal adult males mate with the dominant female [Diaz-Muñoz, 2011; Garber et al., 1993; Garber et al., 2015; Goldizen, 1987], and in some cases share paternity, albeit to a different extent in different groups [Diaz-Muñoz, 2011; Huck et al., 2005b; Suarez, 2007]. This pattern is consistent with high infant care costs, because adult males can share matings and reproduction with a single female without production of additional young that would further increase infant care costs [Chao, 1997]. As expected under high infant care costs, Saguinus tamarin males also exhibit little overt reproductive competition in the form of dominance relationships [Diaz-Muñoz, 2011; Goldizen, 1989; Huck et al., 2004] or hormonal profiles [Huck et al., 2005a]. Finally, there is only one documented case in the wild of a lone female-male pair producing offspring [Diaz-Muñoz, 2011; Garber et al., 1993; Goldizen et al., 1996; Goldizen & Terborgh, 1989; Lottker et al., 2004; Winfielder, 2000] and the number of adult males in tamarin groups correlates with increased offspring productivity [Garber et al., 1993; Heymann, 2000].

Third, examining patterns of natal dispersal, high infant care costs would suggest that both males and females experience reduced breeding opportunities in their natal group. Accordingly, demographic [Garber et al., 1993; Goldizen et al., 1996] and genetic [Diaz-Muñoz & Ribeiro, 2014; Garber et al., 2015] evidence suggest that both sexes regularly disperse.

In sum, Saguinus tamarin groups exhibit behavioral patterns expected under high infant care costs, consistent with calculated ecophysiological costs (Fig. 2). Large home ranges, generally 30–100 ha [Digby et al., 2007; Garber et al., 1993; Goldizen & Terborgh, 1989], and increased resource seasonality (e.g., due to inability to gouge the bark of trees to use exudates as a food source) may be some factors influencing group demographics, the likely proximate driver of infant care costs.

Lion Tamarins

Data on lion tamarin individual reproductive strategies are based principally from studies conducted on L. rosalia (golden lion tamarins, GLT) at Poço das Antas, Brazil, a highly disturbed site. These data suggest that golden lion tamarin infant care costs are intermediate between Saguinus and Callitrichis (Table 1). As many as 83% of golden lion tamarin groups contain more than one pregnant female [Henry et al., 2013], suggesting that subordinate females frequently attempt to reproduce. However, only 10% of L. rosalia groups have two successful breeding females [Dietz & Baker, 1993] suggesting that subordinate females often abort during gestation.

Male reproductive strategies suggest high infant care costs, but perhaps lower than that of Saguinus due to the fact that mating by multiple males is reported in approximately 57% of groups [Baker et al., 1993] and non-natal male duos (related in 40–60% of cases) remain together for several years, and may act jointly and take over new groups [Baker, 1991]. However, in golden lion tamarin groups a single non-natal adult male frequently attempts to monopolize mating attempts with the breeding female(s) [Baker et al., 1993] – a strategy expected under lower infant care costs. The presence of multiple resident adult male GLTs increases offspring survivorship, as expected for higher infant care costs, but this has only been reported for newly formed groups [Bales et al., 2000]. In GLTs 60% of natal individuals disperse by 3 years of age and 90% disperse by 4 years of age [Baker et al., 2002]. This high degree of natal dispersal is expected when infant care costs are high.

In sum, an analysis of reproductive strategies in L. rosalia groups suggests that infant care costs are intermediate between Saguinus and Callitrichis. However, estimates of these costs based on ecophysiological suggest that Leontopithecus should experience the highest cost among callitrichines. This is due to the fact that Leontopithecus exhibits extreme variation in home range size: from 20–73 ha, in L. rosalia at Poço das Antas a highly disturbed
forest fragment, to 125.5–300 ha in *L. cassairae* in Superagüí, Brazil, a well-preserved portion of coastal Atlantic forest [Digby et al., 2007]. The predictions based on reproductive strategies and ecophysiological costs for *Leontopithecus* appear to be at odds, but the costs calculated for *L. rosalia* in Poço das Antas specifically are in between those calculated for *Saguinus* and *Callithrix* (see Fig. 2). More data are needed to resolve the within-genus differences in reproductive strategies and infant care costs for *Leontopithecus*.

**Goeldi’s Monkeys**

Recent field studies have shed considerable light on the ecology, habitat, and behavior of *Callimico goeldii* [Porter & Garber, 2009; Porter & Garber, 2010; Rehg, 2009], the only callitrichine species with single births [Porter & Garber, 2004]. Phylogenetic analyses consistently have nested *Callimico* within the subfamily callitrichine, [Buckner et al., 2014; Perelman et al., 2011] and as a close relative to marmosets. These characteristics make this species of special interest regarding the impact of infant care costs on social and reproductive behavior.

Despite single births, which may suggest the lowest infant care costs among callitrichines, *Callimico* exhibits infant care costs intermediate between *Saguinus* and *Callithrix*. Female reproductive strategies suggest low infant care costs, with breeding and synchronous births by subordinate females common in the wild. Two of four intensively studied groups in the wild contained evidence of two breeding females [Christen, 1999; Pook & Pook, 1981; Porter, 2001]. This synchronous breeding is consistent with a lack of physiological reproductive suppression of subordinate females in captivity, as also observed for *Leontopithecus* [Dettling & Pryce, 1999]. Dominant females can successfully produce a second (singleton) litter in the same year, but it is unclear how often this occurs [Porter, 2001].

*Callimico* groups have multiple males, but there is evidence that males mate guard females [Porter, 2001], consistent with lower infant care costs compared to *Saguinus*. At present there is no genetic evidence to indicate whether one or more males mate with the a breeding female [Porter, 2001; Porter & Garber, 2010]. Finally, consistent with increased breeding opportunities under low infant care costs, in 2 of 4 groups, natal females remained in the group as breeders [Porter, 2001].

In sum, contrary to the expectation that reduced little size in *Callimico* has resulted in reduced infant costs or that large infant costs led to reduced litter size, ecophysiological cost calculations (see Fig. 2) indicate that *Callimico* have infant care costs intermediate between *Saguinus* and *Callithrix*. Thus, despite lower infant care costs resulting from a change in litter size from two to one, the presence of two breeding females in some groups, and the presence of 1–7 alloparents [Porter 2001], home range size is relatively large (>100 ha) suggesting that infant care costs remain high. While *Callimico* produces singleton litters, it can produce a second litter in the same year, matching the output of *Saguinus* species [Porter, 2001]. Singleton births once or twice during the year may spread the prenatal and postnatal costs of reproduction across a longer time period allowing females to build up resources for gestation [Porter & Garber, 2004, 2009].

One of the putative underlying causes for *Callimico*’s large home range sizes is the dependence on fungi as a crucial food resource [Porter & Garber, 2004, 2010]. Future research examining home range size, the extent of fungivory, and reproductive behavior within *Callimico*, and comparison with other fungal specialists (e.g., *Callithrix flavigaeta* [Hilário & Ferrari, 2010]), will clarify the importance of fungi consumption in shaping callitrichine behavior.

**Callithrix and Mico Marmosets**

Marmosets of the genera *Callithrix* and *Mico* have lower ecophysiological costs of infant care than *Saguinus, Leontopithecus*, but higher than *Cebuella* (Fig. 2). Dominant female marmosets are the main breeders in their group, but subordinate females have increased breeding opportunities compared to *Saguinus, Leontopithecus*, and *Cebuella*. For example, subordinate females attempted breeding in seven groups of *C. jaccus* [Arruda et al., 2005; Digby & Ferrari, 1994]. In these studies, subordinate females, however, were less successful than the dominant female. Based on a study of infant survival of 19 infants of six females, there is evidence in *Callithrix jaccus* that dominant females can have, on average, four times as many offspring [Digby, 1995] as subordinate females over the course of 11 months. Overall, these breeding attempts resulted in stable groups with two parous females. Further evidence for relatively low infant care costs, comes from the fact that *Callithrix* dominant females regularly produce two litters of twins a year compared to tamarins and lion tamarins [reviewed in Digby et al., 2007].

Second, there is indirect evidence of increased male reproductive competition, as expected under lower infant care costs. Single male breeders attempt to monopolize matings with the dominant female in several marmosets groups, with behavioral observations suggesting that most groups contain a male-female pair that mates preferentially [Arruda et al., 2005; Lazaro-Perea et al., 2000; Yamamoto et al., 2009, 2014]. Furthermore, in at least one study, a single male was reported to mate with two females in
all three study groups [Digby & Ferrari, 1994]. However, there are no definitive genetic data on paternity in these marmoset groups, multiple adult males are typically present, and multiple males may mate with the main breeding female [Ferrari, 1992; Ferrari & Digby, 1996; Nievergelt et al., 2000], although this has not been directly observed in the wild. In captivity C. kuhlii groups with multiple related adult males and a single female have been formed and are stable [Schaffner & French, 2004]. In these groups, both males mated and neither attempted to monopolize mating opportunities [Schaffner & French, 2004]. In a study of group composition and reproductive success by Koenig [1995], as in the case of tamarins, there is evidence of a positive relationship between the number of adult males present in the group and the number of surviving offspring [Koenig, 1995] in C. jaccus. However, this result does not preclude a breeding monopoly by a single male or paternity by two different males. The single study examining paternity using genetic methods in Callithrix [Nievergelt et al., 2000] did not have sufficient power to exclude the possibility of males sharing paternity, thus the question of whether males are co-breeders remains open. In the absence of paternity studies it remains unclear whether there are multiple males in marmoset groups that breed (analogous to subordinate females that breed with limited success) or whether these males are true non-breeders.

Finally, natal individuals may be more likely to be retained in the group if infant care costs are low and breeding opportunities in the natal group are high. Demographic data suggest that the Callithrix has larger average group size than Saguinus, Leontopithecus, and Cebuella, however, whether this results from the retention of natal individuals remains to be confirmed.

In sum, an evaluation of reproductive strategies and estimates of ecophysiological costs support the idea of low infant care costs in Callithrix marmosets. The ability of marmosets to control the availability and production of exudates may result in reproduction that may be under fewer nutritional constraints [Ferrari & Lopes, 1989; Tardif et al., 1993; Tardif, 1994]. However, some well-studied Callithrix species can have much larger home ranges than common marmosets: a mycophagous C. flaviceps group had a reported home range of 138 ha [Hilário & Ferrari, 2010]. Hilario and Ferrari [2010] suggest that this exceptionally large home range may be due to C. flaviceps less specialized dentition for exudativity, but future study is needed to rule out other possibilities.

The Amazonian marmosets, Mico appear to inhabit larger home ranges [Digby et al., 2007] than Callithrix marmosets (ca. 24 ha vs. 14 ha, respectively) and therefore based on ecophysiological cost estimates, are expected to have higher infant care costs. However, little is known about their ecology or social and reproductive behavior [Goçalves et al., 2009], precluding an analysis on the basis of reproductive strategies. However, if Mico has higher infant care costs, I expect its reproductive strategies should incorporate more elements that characterize Saguinus and Leontopithecus rather than Callithrix.

**Pygmy Marmosets**

*Cebuella pygmea*, the smallest bodied callitrichine, has the lowest infant care costs based on ecophysiological estimates (Fig. 2) and reproductive strategies. Female reproductive strategies also are consistent with relatively low infant care costs, including parking infants while foraging and feeding. Dominant females can frequently produce two twin litters per year, with a frequency ranging from four of five study groups [de La Torre et al., 2000] to 84% of 14 study groups [Soini, 1982]. Subordinate female reproduction can occur, but appears to be rare: none of 21 groups in two studies had more than one breeding female [Soini, 1988; Heymann & Soini, 1999] and one of seven groups in a separate study contained two breeding females [de La Torre et al., 2000]. In fact, most groups (71–80%) contained only one adult male and female and their offspring [Heymann & Soini, 1999; de La Torre et al., 2000], indicating that infant care costs may be so low that preadult alloparents are sufficient to care for young and, thus, a single breeding pair may be able to monopolize reproduction within a group. However, there are no genetic data available on parentage in any Cebuella group.

Male reproductive strategies also suggest low infant care costs. In all 21 Cebuella groups observed by Heymann and Soini [1999], only one adult male was present. In one case in which multiple males were present in a studied Cebuella group, males exhibited ritualized displays mediating aggression [Soini, 1987, 1988]. The dominant male also intervened and attempted to disrupt copulations with the other resident male [Soini, 1987].

Finally, the strategies of natal males and females also suggest low infant care costs. Intriguingly, the relationship between the number of adult male caregivers and increased offspring survivorship reported in other callitrichines may not hold in Cebuella. A study by Heymann and Soini based on 21 groups found a significant relationship between the total number of adults and subadults, but not adult males, and infant survivorship [Heymann & Soini, 1999]. It is possible that, unlike other callitrichines, subadults or females contribute sufficiently to infant care that adult males are not essential for infant survivorship. Consistent with expectations under low infant care costs, Cebuella groups can retain up
to 4 litters of young in their group, with 10 of 14 groups having at least 2 successive litters in the same year [Soini, 1982].

There are two main factors proposed to explain the very low infant care costs in Cebuella pygmea. First, Cebuella are arguably the most specialized callitrichine exudate feeders [Harrison & Tardif, 1994; Nash, 1986; Soini, 1982]. This stable, defensible, year-round resource, is presumably what allows pygmy marmoset groups to inhabit exceptionally small home ranges (commonly <1 ha) [Soini, 1982, 1988]. It is notable that while Cebuella are the smallest callitrichines in body mass and have the smallest home ranges, body size explains only a small proportion of the variation in home range sizes (Fig. 1). Pygmy marmosets are three to four times smaller than marmosets, yet their home ranges are between one to two orders of magnitude smaller. Second, pygmy marmosets further reduce the cost of infant care by “parking” infants while foraging and feeding. This results in potential caregivers reducing the proportion of the time caregiving.

BEYOND THE CALLITRICHINAE: MONOGAMY AND THE MATING SYSTEMS CONCEPT

The foregoing discussion on infant care and social and breeding systems in callitrichines is directly relevant to questions concerning monogamy and single female breeding systems in primates [Garber et al., 2015]. First, studies of several species of callitrichines, such as lion tamarins [Baker et al., 1993], common marmosets [Yamamoto et al., 2014], and pygmy marmosets [Heymann & Soini, 1999] have claimed that individual groups that in the wild exhibit a social or breeding system consistent with monogamy. Second, many species of primates traditionally characterized as monogamous have variable patterns of social and breeding patterns in which more than one adult male and more than one adult female are reproductively active. These findings potentially call into question the validity and ubiquity of monogamy as a breeding system [Garber et al., 2015; Morino, 2015; Savini et al., 2009; Thompson, 2013]. In this paper, I identified some of the more variable reproductive traits among callitrichines, including the extent of reproductive suppression among females and the number of adult males that are present and mate in a group, which in the vast majority of cases (with the possible exception of Cebuella), directly contradict monogamy as a common or modal mating and breeding system in these primates.

More broadly, the study of behavior in callitrichines raises questions regarding the general utility of the “mating systems” concept. Mating systems are a heuristic device that scientists have devised and used to aggregate a range of reproductive and social behaviors that are likely to have evolved in different order, under different social and ecological conditions, and for different functions across taxa. Mating systems represent a set of component traits [Emlen & Oring, 1977] and do not exist in the sense of being organismal traits subject to selection. However, in practice, mating systems are routinely treated as a single fixed trait, often obscuring patterns and processes that reflect a range of alternative behavioral strategies adopted by individual males and females under changing social and ecological conditions. For instance, the classic hypothesis linking differences in sex-biased dispersal as a response to differences in “mating systems” [Greenwood, 1980] has limited predictive power [Mabry et al., 2013] due, in part, to greater within species variability in reproductive and social behaviors than was previously appreciated [Dobson, 2013]. Similarly, recent empirical studies on the evolution of monogamy reached very different conclusions [Lukas & Clutton-Brock, 2013; Opie et al., 2013] due in part to the ways they classified species as monogamous. Thus, treating a “mating system” as a single, fixed trait risks ignoring the set of social and ecological factors that drive variation within and between species. Grouping of behavioral traits can be a useful scientific tool, but it should not be assumed these traits invariably co-occur just because scientists have added a label to them [e.g., pair-bonding, mating exclusivity, and territoriality as part of the “monogamy package” Fuentes, 1998]. Mating systems are our own creation and as limitations in the concept arise it may be reformed, redefined, or abandoned altogether.

CONCLUSIONS

Across all callitrichine groups some traits are almost universally shared – highly skewed female breeding, a male-biased group composition, alloparental care– and others are more variable, such as number of males that mate and sire young, mechanisms of male reproductive competition, number of natal young retained, and extent of female reproductive suppression. Variability in these labile traits reflects individual reproductive strategies that are expected to arise under different infant care cost scenarios. Specifically, under high infant care costs I predict: a) dominant females’ reproductive output is low (1 litter per year) and dominant females attempt to suppress reproduction by other females; b) multiple adult males mate with the dominant female, care for her offspring, and are characterized by high levels of social tolerance and limited direct reproductive competition; c) the majority of natal individuals are expected to disperse owing to severely reduced breeding opportunities within the group. I present an alternative set of predictions under conditions favoring low infant care costs.
Infant care costs can be estimated using data on neonate:adult mass ratios and home range size (referred to as ecophysiological cost) and suggest an ascending order of infant care costs: *Cebuella*, *Callithrix*, *Mico*, *Callimico*, *Saguinus*, and *Lentopithecus*. I argue that these ecophysiological costs correspond well with expected infant care costs inferred from male and female reproductive strategies across these genera. The precise ecological, physiological, behavioral, and genetic data needed to adequately test these predictions are unavailable. The ultimate goal of this paper is to put forward an integrative framework to generate predictions and tools to evaluate the drivers of “variability”, so that we may not confuse variation for noise when it is a signal.

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