REVIEW ARTICLE

To Pair or Not to Pair: Sources of Social Variability With White-Faced Saki Monkeys (*Pithecia pithecia*) As a Case Study

CYNTHIA L. THOMPSON*
Department of Biomedical Sciences, Grand Valley State University, Allendale, Michigan

Intraspecific variability in social systems is gaining increased recognition in primatology. Many primate species display variability in pair-living social organizations through incorporating extra adults into the group. While numerous models exist to explain primate pair-living, our tools to assess how and why variation in this trait occurs are currently limited. Here I outline an approach which: (i) utilizes conceptual models to identify the selective forces driving pair-living; (ii) outlines novel possible causes for variability in social organization; and (iii) conducts a holistic species-level analysis of social behavior to determine the factors contributing to variation in pair-living. A case study on white-faced sakis (*Pithecia pithecia*) is used to exemplify this approach. This species lives in either male-female pairs or groups incorporating "extra" adult males and/or females. Various conceptual models of pair-living suggest that high same-sex aggression toward extra-group individuals is a key component of the white-faced saki social system. Variable pair-living in white-faced sakis likely represents alternative strategies to achieve competency in this competition, in which animals experience conflicting selection pressures between achieving successful group defense and maintaining sole reproductive access to mates. Additionally, independent decisions by individuals may generate social variation by preventing other animals from adopting a social organization that maximizes fitness. White-faced saki inter-individual relationships and demographic patterns also lend conciliatory support to this conclusion. By utilizing both model-level and species-level approaches, with a consideration for potential sources of variation, researchers can gain insight into the factors generating variation in pair-living social organizations. Am. J. Primatol. 78:561–572, 2016.   © 2015 The Authors, *American Journal of Primatology*. published by Wiley Periodicals, Inc.

INTRODUCTION

Sociality is a pervasive feature of anthropoid primates. Primates are considered to have a relatively high number of pair-living species, with reports of 10–29% of primate species displaying this pattern, compared to only 3–9% of all mammals [Fuentes, 1998; Lukas & Clutton-Brock, 2013; van Schaik & Dunbar, 1990]. However, these estimates do not always take into account species that may sometimes live in pairs, but also display variation in grouping patterns. Although pair-living has long been an area of intense investigation, recent and increasing recognition has been given to the plasticity primates can display in social organization [Chapman & Rothman, 2009; Reichard, 2009; Setchell, 2013; Strier, 2003,2009; Struhsaker, 2000]. For pair-living primates, plasticity in social organization entails incorporating extra adult males and/or females into the group, which could lead to greater potential for promiscuous matings, within-group competition, or cooperative behavior [e.g., Digby, 1995; Savini et al., 2009]. While many models for the evolution of pair-living and

monogamy exist [reviewed in Brotherton & Komers, 2003; Fuentes, 2002; van Schaik & Dunbar, 1990; van Schaik & Kappeler, 2003], the conceptual framework for understanding how and when variations occur (and what factors constrain this variation) is currently lacking. Additionally, many discussions of intraspecific social variation have focused on differing demographic structures in larger groups [Chapman & Rothman, 2009; Struhsaker, 2000, 2008; Struhsaker et al., 2004; Yamagiwa & Hill, 1998], although variation in the grouping patterns of uni- and bi-male harems has also been well documented [Pope, 1990; Robbins, 1995; Watts, 2000; Yamagiwa et al., 2003]. Socioecological models for large multi-male, multi-female groups are usually based on competitive interactions between individuals of the same sex [e.g., Isbell, 2004; Sterck et al., 1997; Wrangham, 1980; van Schaik, 1989 but see Sussman & Garber, 2011 for a discussion of the advantages of living in a larger group]. These models are difficult to apply to small groups with only 1–3 members of each sex and their accuracy has also come under scrutiny due to their lack of fit to currently available data [Koenig & Borries, 2009; Lawler, 2010; Sussman et al., 2011; Thierry, 2008]. Understanding social variation is a critical area to improve upon since many 'pair-living' species have been reported to incorporate extra adults into the group [galagos (*Galago, Galagoides*): Harcourt & Nash, 1986; Müller & Thalmann, 2000; lemurs (*Eulemur, Varecia, Hapalemur, Propithecus*): Jolly, 1998; Kappeler, 1997, 2000; tarsiers (*Tarsius*): Gursky, 2000; MacKinnon & MacKinnon, 1980; owl monkeys (*Aotus*): Aquino et al., 1990; white-faced sakis (*Pithecia*): Norconk, 2011; callitrichines (*Saguinus, Leontopithecus*): Goldizen, 2003; Digby et al., 2011; pig-tailed langurs (*Simias*): Tenaza & Fuentes, 1995; gibbons and siamangs (*Hylobates, Nomascus, Symphalangus*): Fan & Jiang, 2010; Fan et al., 2010; Fuentes, 2000; Lappan, 2007; Reichard, 2003, 2009]. While primates will inevitably have some stochastic variation in the size and composition of groups, many of the above species have demonstrated consistent tendencies to form small multi-adult groups. Despite this social variation, conceptual models can still provide valuable insight into pair-living social systems by identifying the relative importance of selective pressures acting on a species.

To better assess the appearance of consistent variability in pair-living behavior, I advocate an approach that: (i) utilizes conceptual models to identify the selective forces driving pair-living; (ii) acknowledges possible causes for variability in social organization in light of said selective forces; and (iii) considers a holistic species-level analysis of social behavior. These steps will allow researchers to make testable predictions and draw conclusions about how and when animals adopt pair-living versus multi-adult scenarios. Here I use the social system of white-faced saki monkeys (*Pithecia pithecia*) as a case study to demonstrate the utility of this approach.

Describing Social Systems

The complexity of primate social behavior has often been parceled down by researchers into smaller, discrete components that can be easily analyzed. These components of sociality can be helpful in identifying interconnected themes at the species level. A variety of terminologies have been applied for these variables [Eisenberg et al., 1972; Müller & Thalmann, 2000; van Schaik & van Hooff, 1983; Whitehead & Dufault, 1999]. Here, I adopt the nomenclature from Kappeler & van Schaik [2002] to characterize social systems:

Social organization
A group's number of individuals, sex composition, and spatiotemporal relationships. This category describes whether individuals are gregarious, and if so, which sex(es) permanently associate with one another. Kappeler & van Schaik [2002] outlined three fundamental types of social organization: solitary, pair-living, and group-living.

Mating system
The number of mating males and females in a group and the sexual relationships present (e.g., monogamous, polygamous). This component can be dissected into two discrete, but related, traits: (i) the behavioral mating system (observed copulations, sexual behavior); and (ii) the genetic mating system (which animals actually produce offspring). While the genetic mating system will be more informative as to patterns of reproductive success and evolution, reports on primate behavioral mating systems are more widespread in the literature. Knowledge of both components is ideal for characterizing a species' mating system. Studies assessing both components are currently small in number, yet increasing [Di Fiore, 2009; Huck et al., 2014].

Social structure
The character of social relationships between conspecifics, including inter- and intrasexual relationships within and between groups. This aspect describes which individuals exhibit affiliative and agonistic social interactions.

Parceling these separate components into discrete entities has an obvious utility for describing and comparing primate species. However, it is important to note that these components are highly interrelated. For instance, mating system often roughly corresponds to social organization [Kappeler

& van Schaik, 2002] and female-female bonded social structures are not possible in social organizations lacking multiple females. Yet all components are needed to provide a complete picture of a species' social system. As an example, pair-living groups can display varying social structures, such as strong reciprocal pair-bonds, asymmetrical bonds maintained solely by one member, or infrequent social interactions between pair members [Fuentes, 1998, 2002; Mock & Fujioka, 1990]. In these cases, knowing the selective forces leading to social organization alone will tell us little about the social structure dominating these groups. Group history can also provide vital insight into variation in social systems [e.g., Bartlett, 2003]. For instance, incorporating multiple adults into the pair via retained offspring versus immigration of unrelated individuals will lead to similar social organizations, but will likely yield quite disparate social structures and mating systems. Intraspecific variation can further complicate characterization of these components, as species can display multiple social organizations, mating systems, or social structures. Using the case study of variable pair-living in white-faced saki monkeys, I aim to demonstrate that considering these three components holistically can provide insight into the factors generating intraspecific social variability.

The Evolution of Pair-Living

The evolution of pair-living in primates benefits from a strong and well developed background. Since these models have been reviewed extensively elsewhere [Brotherton & Komers, 2003; Fuentes, 2002; van Schaik & Dunbar, 1990; van Schaik & Kappeler, 2003] I only briefly outline them here: (i) Widely dispersed females [Rutberg, 1983; van Schaik & van Hooff, 1983; Wrangham, 1980]. Females are distributed such that males can only monopolize one at a time and males gain more reproductive success through associating with one female than ranging widely and mating promiscuously; (ii) Obligate paternal care [Kleiman, 1977; Wittenberger & Tilson, 1980]. Male assistance is required to successfully rear offspring, leading males to remain with one female to assure paternity of reared offspring; (iii) Male defense against predators or defense against resource competition [van Schaik & Dunbar, 1990; Wittenberger & Tilson, 1980]. Females choose to associate with males that provide protection from predation and/or access to greater amounts of food (i.e., allow females to avoid the costs of resource competition); (iv) Mate guarding [Brotherton & Manser, 1997; Palombit, 1996, 1999]. Males maintain pair-bonds with females to ensure they sire offspring and prevent copulations with competing males; (v) Bodyguard hypothesis [Emlen & Wrege, 1986; Mesnick, 1997; Smuts & Smuts, 1993]. Females choose to pair with males that provide protection from harassment and coercion by conspecific males; (vi) Infanticide prevention hypothesis [Palombit, 2000; van Schaik, 2000; van Schaik & Dunbar, 1990; van Schaik & Kappeler, 1997]. Females maintain pair-bonds with males to acquire protection from infanticidal males.

Analyses have found conflicting support for these hypotheses as selective forces leading to primate and mammalian pair-living. There is consistent evidence supporting paternal care as a pressure that maintains, but did not initially generate, pair-living [Komers et al., 1997; Lukas & Clutton-Brock, 2013; Opie et al., 2013a]. However, the roles of the infanticide prevention and widely dispersed female hypotheses have been under intense dispute. Several studies have supported infanticide as the main selective pressure leading to pair-living in primates [Opie et al., 2013a,b, 2014; van Schaik & Dunbar, 1990; van Schaik & Kappeler, 2003], but others have failed to support it [Fuentes, 2002; Lukas & Clutton-Brock, 2014], instead favoring the widely dispersed female hypothesis [Komers et al., 1997; Lukas & Clutton-Brock, 2013]. Another study by Dobson et al. [2010] concluded that there was not a single predominate selective pressure leading to pair-living for all mammals. Given this ongoing lack of consensus (despite decades of research on primate and mammalian pair-living), in addition to the high ecological and physiological diversity of primates displaying pair-living, it is seems prudent to begin incorporating species-specific approaches into our examinations of pair-living.

Sources of Intraspecific Variation

The above conceptual models outline selective forces that favor pair-living. However, the dynamics shaping realized social phenotypes are more numerous and complex. For pair-living primates, a number of factors could impact whether additional adults are incorporated into the group. Here, I put forth three selective factors that may lead to variability in pair-living social organizations: (i) A battle of the sexes [Arnqvist & Rowe, 2005; Davies, 1992; Parker, 2006]. It is notable that many of the basic selective pressures proposed in the conceptual models above only explain why one sex benefits from a pair-living scenario. Since males and females maximize reproductive success differently (males by gaining access to females, females by gaining access to food or infant caregivers), both sexes may not share a common benefit from a pair-living arrangement. For instance, in the mate guarding and bodyguard hypotheses, females benefit from associating with one male, but males will still benefit from incorporating multiple females into the group, if possible. Alternately, under an obligate paternal care scenario, females will benefit from the presence of more than one male in the group, to the detriment of these males'

reproductive success [e.g., Goldizen, 1990, 2003]. Stronger selective pressures favoring pair-living for one sex but not the other could lead to a tug-of-war scenario in which the displayed social organization represents a compromise between differing male and female fitness optima; (ii) Decisions are made on the individual level [Clutton-Brock, 1989; Kenrick et al., 2003; Parrish & Edelstein-Keshet, 1999]. The actions of individuals can prevent other animals from achieving their optimal social organization. As an example, sharing mating access to a female would reduce the reproductive success of a male already in an established breeding pair. However, this shared access would represent a potential increase in reproductive success for a solitary floater male. If a solitary male joins a breeding pair (and perhaps has support of the female to do so), the established male may be unable to exclude this new immigrant. In such a case, animals are not able to reach their fitness optima due to the decisions of other animals [e.g., Clutton-Brock, 1998]; (iii) Conflicting selection pressures [Schluter et al., 1991]. Primates are subject to a wide range of selective forces, which may or may not favor pair-living. For instance, to gain sole reproductive access to females, established males should exclude extra-group males. Yet incorporating extra males into the group could provide alternate benefits such as more successful resource defense, increased protection from predators (through increased vigilance and selfish herd/dilution effects), or additional help rearing offspring [Nunn, 2000; van Schaik & Kappeler, 2006]. The social organization adopted by animals may represent a compromise between these competing selective forces [e.g., Savini et al., 2009]. In addition to the above factors, it has also been previously acknowledged that environmental variation can impact social organization [Chapman & Rothman, 2009; Savini et al., 2009]. Differences in habitat quality, population density, presence and abundance of predators, or interspecific competition can all impact which social strategy best enables animals to reach their fitness optima in specific localities. While not exhaustive, this list outlines major themes to consider when analyzing sources of variation in sociality. Considering these pressures in conjunction with the above pair-living models can assist in reconstructing the selective pressures generating variably pair-living social systems.

WHITE-FACED SAKIS AS A CASE STUDY IN VARIABLE PAIR-LIVING

White-Faced Saki Social System

White-faced sakis (*Pithecia pithecia*) provide an intriguing case to assess variable pair-living. While the pitheciines have traditionally been an understudied group, continued research has allowed us to gain a more substantial understanding of white-faced saki social behavior. *Pithecia* represents an evolutionary intermediate in a large-scale phylogenetic shift in social organization, being sister taxa to both the consistently pair-living titi monkeys (*Callicebus*) and the large grouped multi-male, multi-female bearded sakis (*Chiropotes*) and uakaris (*Cacajao*) [Thompson & Norconk, 2011]. White-faced sakis also display a unique mix of traits both indicative and non-indicative of 'typical' monogamous primates [i.e., Fuentes, 1998], having strong male-female social bonds and territoriality, yet lacking sexual monomorphism and paternal care (see below). Given our present knowledge, the three components outlined by Kappeler & van Schaik [2002] can be used to characterize this species' social system. While research has been published on several aspects of white-faced saki social behavior independently, the current work represents the first integrative characterization of this species' social system as a whole. This research adhered to legal and ethical standards outlined by the American Society of Primatologists.

Social organization

Several long-term and census studies have now reported that white-faced sakis naturally occur in both male-female pairs and small multi-male, multi-female groups [Kessler, 1998; Lehman et al., 2001; Mittermeier, 1977; Muckenhirn et al., 1975; Norconk et al., 2003; Oliveira et al., 1985; Thompson & Norconk, 2011; Vié et al., 2001]. White-faced saki groups average 3.2 individuals (range = 2–12) [Norconk, 2011] and a survey in Guyana reported that roughly 26% (N = 19 observed bisexual groups) of groups were pair-living, while 74% contained more than one adult male and/or female [Lehman et al., 2001]. These small multi-male, multi-female groups likely form via two means: (i) the maturation and subsequent breeding of offspring within their natal group, and/or; (ii) immigration of unrelated adults into established groups [Norconk, 2006; Soini, 1986; Thompson et al., 2010]. These mechanisms likely lead to differing social dynamics within the group, reinforcing that group history can be an important factor shaping social structure and mating systems. The factors constraining groups to small sizes are unclear, however white-faced sakis' cryptic strategy suggests predator avoidance may be a factor [Gleason & Norconk, 2002]. Although this review focuses on white-faced sakis (due to the relatively larger amount known about their social behavior), similar variation has also been reported for other *Pithecia* sp. [reviewed in Norconk & Setz, 2013].

In addition to pairs and small multi-adult groups, the presence of solitary floater individuals (of both sexes) has been reported in multiple populations from both censuses and studies with sustained observation [Mittermeier et al., 1977; Muckenhirn, 1975; Thompson et al., 2010; Vié

et al., 2001; for similar data on other *Pithecia* sp. see Di Fiore et al., 2007; Soini, 1986].

Mating system

Two studies have now documented concurrent pregnancies of >1 white-faced saki females within a single group [Norconk, 2006; Thompson, 2013]. Reports of copulations from a 17-month study in Suriname have shown that both pair-living and multi-adult groups can exhibit monogamous copulation patterns [Thompson, 2013]. However multi-adult groups can also display polygamous copulations, with both males and females copulating with more than one partner. Behaviors indicative of within-group mating competition (copulation interference, female-directed sexual aggression) have also been reported for multi-adult groups [Thompson, 2013]. White-faced sakis continuously cycle and births occur throughout the year, although there is a slight peak in births November through April [Norconk, 2006; Savage et al., 1995]. Both birth and group membership sex ratios are male biased [Norconk, 2006]. No published studies to date have measured mating success from genetic data to determine if observed copulations correspond to actual siring of offspring.

Social structure

Details regarding social structure have emerged from long-term studies of white-faced sakis in Venezuela [Harrison & Norconk, 1997, 1999; Norconk et al., 1999; Norconk, 2006] and Suriname [Norconk et al., 2003; Thompson & Norconk, 2011; Thompson et al., 2012]. The strongest social bonds in white-faced saki groups are between a single male-female reproductive pair (with females being responsible for grooming and maintaining proximity to males), regardless of the presence of same-sex kin or other sexually active dyads [Thompson & Norconk, 2011]. This affiliative male-female bond lies in stark contrast to the consistent same-sex aggression exhibited between groups [Norconk, 2006; Thompson et al., 2012; Thompson & Norconk, 2013]. Encounter rates range from almost daily by one report, to an average of one encounter per 7.5 days and can be intense, involving chases, animals biting one another, and falling from trees [Norconk, 2006; Thompson et al., 2012; Thompson & Norconk, 2013]. Although males are the primary participants in this aggression, females have also been reported to participate [Norconk, 2006]. There is evidence this aggression is tied to both mate guarding of females and resource defense [Cunningham & Janson, 2007; Thompson et al., 2012]. Within-group aggression is relatively low [Harrison & Norconk, 1997; Norconk et al., 1999], exhibited between members of the same-sex, and generally directed toward older members of the group by younger individuals [Norconk, 2006]. Male-male aggression in sexual contexts is also directed

from younger toward older males [Thompson, 2013]. Norconk [2006] proposed that this same-sex aggression may reflect efforts by younger group members to dispose older individuals from breeding positions.

Applying the Models

Evaluating the specific evolutionary pressures driving pair-living in white-faced sakis may help elucidate the factors underlying social variation. However, comparing available data with each models' expectations yields only partial support for most models (Table I). Given the deviation of white-faced sakis from a rigidly pair-living social system, this mixed result is not entirely unexpected. Yet some clear trends do result from this exercise. Our currently available data show more superficial support for the infanticide hypothesis than others (Table I), however there are some justified reservations to fully accepting this hypothesis. Namely, infanticide has never been observed in wild white-faced sakis. It is notable that there have been relatively few long-term studies on *Pithecia* sp., decreasing the chances infanticide would have been observed if it is a rare behavior. As outlined above, infanticide has been proposed as a main factor contributing to both pair-living and other permanent male-female associations in primates [Opie et al., 2013a; Palombit, 2000; van Schaik & Kappeler, 1997, 2003]. Accordingly, it may be tempting to invoke past infanticidal pressures as a selective force that shaped the currently observed social system (i.e., 'ghost of selection past') [Fuentes, 2002; Opie et al., 2013a; van Schaik & Dunbar, 1990]. While this may be a plausible explanation, empirically testing for past selection pressures is often either very difficult or unfeasible, putting researchers in an uncomfortable position of accepting an explanation without hard evidence. Yet, pair-living primates do tend to have lower levels of infanticide than species exhibiting other social organizations [Opie et al., 2013a], consistent with the idea that pair-living is an effective infanticide prevention strategy. If a similar strategy is occurring in white-faced sakis as in other variably uni- or bi-male groups such as gorillas, the presence of extra males may help further reduce infanticide risk [Robbins, 1995; Yamagiwa et al., 2003]. This is consistent with the idea that a greater number of white-faced saki groups are multi-adult, compared to pair-living [statistics provided above; Lehman et al., 2001]. Despite ongoing debate over the role of infanticide in primate and mammalian pair-living (see above), these larger taxonomic trends don't preclude a role for infanticide in shaping white-faced saki social organization specifically, since separate selective pressures may be acting on different primate species. However there are currently no data to support infanticide as a direct motivation for between-group aggression in white-

TABLE I. Expectations of Models Explaining Pair-living and an Assessment for White-Faced Sakis

Model	Predictions[a]	Supported?
Females as a widely dispersed resource	1) females exhibit range defense	N[b]
	2) males cannot achieve more copulations under a roving male strategy	?
	3) species occur exclusively in two-adult groups	N
	4) females are more energetically limited than males	?[c]
Obligate paternal care	1) males display caretaking of immature	N[d]
	2) females without males will have lowered reproductive success	?
Male defense against predators/conspecifics	1) predation is a significant selective pressure	?[e]
	2) vigilance behavior is costly & males are more vigilant	?[e]
	3) males exhibit predator defense	N
	4) there is intergroup competition for resources	Y
	5) group size is small	Y
	6) both sexes actively defend range from conspecifics	N[b]
	7) solitary females will have smaller ranges and lose interspecific contests	?
Mate guarding	1) males will be primarily responsible for maintaining the pair-bond	N
	2) male-male aggression should be high	Intergroup: Y; Intragroup: N
	3) females should be dispersed/limited	N
Bodyguard	1) females are responsible for maintaining the pair-bond	Y
	2) males direct substantial aggression to females	N
	3) males are larger or somehow more capable of inflicting damage to females	?[f]
Infanticide prevention	1) infanticide occurs in the species	N[d]
	2) male-female associations last longer than one interbirth interval	Y
	3) females are unable to defend young from infanticidal males	?[g]
	4) male floater population and/or skewed sex ratio exists	Y
	5) females are responsible for maintaining the pair-bond	Y
	6) adults should be wary of extra-group males	Y[h]
	7) adults should not be wary of extra-group females	?[h]

[a]Models' predictions are from Fuentes [2002].
[b]Males are the primary participants in between-group aggression, but females do participate in a limited number of cases [Norconk, 2006; Thompson et al., 2012; Thompson & Norconk, 2013].
[c]Female mammals are presumed to be more energetically limited than males due to the constraints of internal gestation and lactation, however there is no reason to believe this is more exacerbated in white-faced sakis than other primates. Male white-faced sakis are slightly larger in body size than females (see footnotes e, f below), which may increase their absolute energy requirements.
[d]No cases have been reported in the literature.
[e]Although their relatively small body size [$\bar{x}$ = 1.68 kg: Ford & Davis, 1992] makes white-faced sakis susceptible to a variety of predators, it in unknown whether predation pressure is higher than expected for an arboreal primate. The cost of vigilance behavior has not been evaluated in white-faced sakis. Cunningham et al. [2013] found that males often assumed more vulnerable positions while traveling, but not while feeding. Males are more vigilant than females before entering the sleeping tree, although reactions to predator sightings (mobbing, alarm calls) are more often initiated by females [Thompson, pers. obs.]. See Gleason & Norconk [2002] for a review of anti-predator behavior.
[f]Body size dimorphism: 1.14 (M:F); canine size dimorphism: 1.24 [Hershkovitz, 1987; Ford & Davis, 1992; Ford, 1994].
[g]No evidence exists on defensive ability of females against males. Although body size dimorphism exists (see f above), it is relatively small.
[h]During intergroup encounters, females generally hang back from the encounter area and avoid the males at the front of the encounter, indicating that both sexes are wary of males approaching from the opposing group. However, since females avoid interactions with the opposing group, the reaction of either sex to an unknown female is currently unknown [Thompson et al., 2012; Thompson & Norconk, 2013].
In addition to the above citations, the table was based on these additional references: [Buchanan et al., 1981; Cunningham & Janson, 2007; Lehman et al., 2001; Norconk, 2006; Norconk et al., 1999; Thompson, 2013; Thompson & Norconk, 2011, 2013; Thompson et al., 2010; Vié, et al., 2001].

faced sakis [Thompson et al., 2012]. The risk of infanticide posed from within white-faced groups is low given the overall low levels of aggression, low number of males per group, and potential relatedness of males [although recent unrelated male immigrants may pose a more viable threat: e.g., Cheney et al., 2004; Fedigan et al., 2003; Knopff et al., 2004]. It is also possible that multiple competing females within the group could present a risk of female infanticide, as seen in marmosets [Digby, 1995; Lazaro-Perea et al., 2000]. Lastly, floater populations could pose a high risk of infanticide. In three observed instances of interactions between floaters and established groups, established males were always aggressive toward floater males [Thompson, pers. obs.]. Unfortunately, there is not currently enough data to investigate whether floaters target groups during times of infant vulnerability

and aggression towards floaters can serve multiple functions other than infanticide. It is also worth considering that the mixed support for the infanticide hypothesis (Table I) may result from unfit predictions or because predictions do not mutually exclude hypotheses.

The partial support for the infanticide hypothesis rests on data indicating that male-male between-group aggression plays a central role in white-faced saki behavior. This trait emerges as a common theme with other partially supported hypotheses, namely defense against resource competition from conspecifics and mate guarding (Table I). There is additional evidence for these partially supported models, as between-group aggression has been linked to both female reproductive status and resource defense in white-faced sakis [Cunningham & Janson, 2007; Thompson et al., 2012]. This commonality suggests that male defense from extra-group individuals, whether for infanticide prevention, mate-guarding, or resource defense, is a key component in the white-faced saki social system. These motivations are not mutually exclusive and selection pressures from all three may influence the social patterns of white-faced sakis to greater or lesser degrees. The influence of multiple, concurrent selection pressures on social organization has also been noted in other primates [Kappeler, 1997; Hill & Lee, 1998; Hilgartner et al., 2012]. For instance in *Lepilemur*, there is concurrent selection for males to monopolize single females in order to gain information on females' relatively short estrus period and to minimize the energy expenditure posed by a roving-male strategy [Hilgartner et al., 2012]. It is additionally worth noting (as above) that the original selective pressure favoring these behaviors could differ from the selective pressure currently maintaining them [Dobson et al., 2010; Opie et al., 2013a]. This mix of selective pressures may actually warrant reconsideration of the infanticide hypothesis, as year-round defense for resources or mate guarding should functionally provide protection from infanticide, without leaving a clear, detectable signal of defense only when infants are present.

Thus, a systematic assessment of models has given us insight into the central themes shaping pair-living in white-faced sakis. Primarily, that high between-group aggression is a central factor in their social organization (although the ultimate drive(s) for this aggression are unresolved). Examining potential sources of variation within this framework can provide additional perspective. If excluding extra-group males is a key component of white-faced saki social strategy (regardless of the selective pressure(s) favoring it), then these high levels of same sex and between-group aggression should prevent immigration into the group. Yet males may still experience competing advantages of including versus excluding extra adults into/from the group

[Savini et al., 2009]. In pair-living or uni-male groups, males will benefit from sole reproductive access to females, especially under conditions when other resident males do not provide beneficial services such as infant caregiving or resource and mate defense. On the other hand, adding extra males to the group may increase established males' competitive ability through cooperative defense [Savini et al., 2009; Port et al., 2011]. It is also worth noting that if extra group members are not reproductively active (as may be the case for retained adult offspring if their parents are still active breeders in the group), there will be lower costs of incorporating them into the pair. This is likely the case with *Cebus capucinus* groups, in which the dominant male sires most of the offspring regardless of other males being present [Jack & Fedigan, 2005]. A similar phenomenon has been well demonstrated for variably uni- or bi-male harems in howler monkeys (*Alouatta*) and gorillas (*Gorilla*), in which extra adult males stabilize the group and extend the tenure of the alpha male [Pope, 1990; Robbins, 1995; Snyder-Mackler et al., 2012; Watts, 2000; Yamagiwa et al., 2003]. In this scenario there are multiple ways for animals to maximize their fitness, either through: (i) less effective defense, but exclusive reproductive access in a pair-living scenario, or (ii) more effective defense, but shared reproductive access in a multi-adult group. Additionally, the opportunity to adopt cooperative group defense likely varies on an individual basis. For example, males may not have a suitable coalitionary partner until they have surviving adult offspring that choose to stay in the group. Alternately, established males may be unable to exclude males that chose to immigrate into the group. These types of individual decisions and group history scenarios undoubtedly affect the social organization (pair-living or multi-adult) exhibited by white-faced saki groups.

A Holistic Approach to Sociality

Analyzing the three components of sociality (social organization, mating system, and social structure) in conjunction can provide a more complete picture of the forces generating variation in pair-living. For white-faced sakis these elements fit together congruously (Fig. 1). Figure 1 shows the dynamics in which variable pair-living could be maintained as an evolutionarily stable strategy in white-faced sakis. By analyzing social structures, it is revealed that high between-group aggression can strengthen the male-female affiliation observed in this species. Females have an incentive to remain and form bonds with males who will protect access to feeding resources. Female choice for high quality males should also reinforce high male-male competition and aggression. Since this aggression provides exclusive or near-exclusive sexual access to
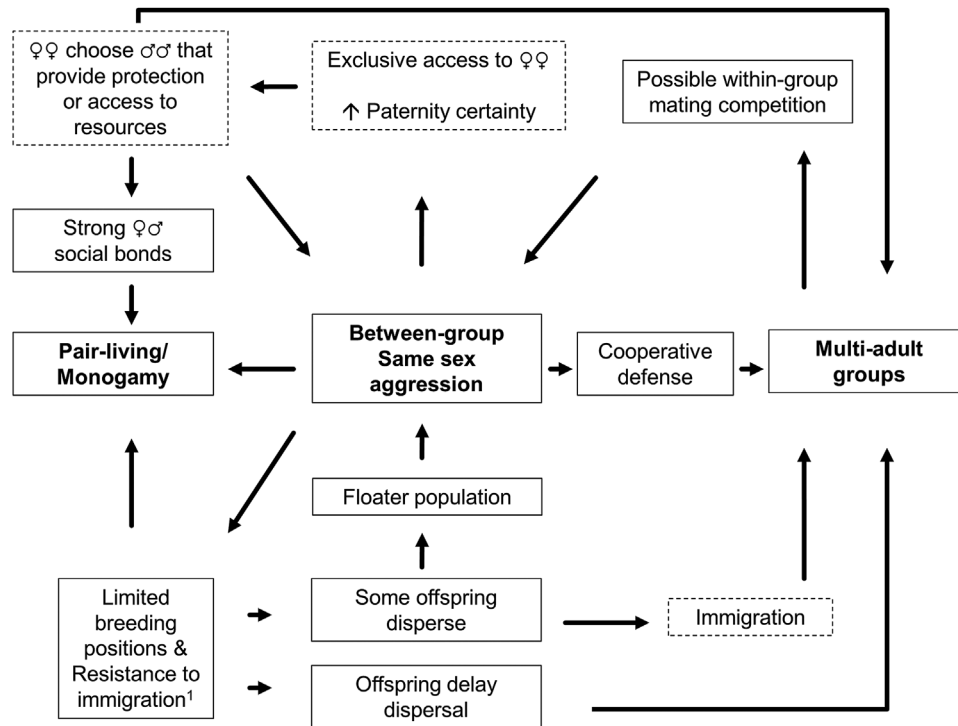
Fig. 1. Interrelationships between components of the white-faced saki social system. **Bold** lettering indicates the three components of social system. Boxes with solid borders indicate traits reported in the literature; dotted borders represent proposed relationships between traits. Arrows indicate direction of impact. [1]The presence of floater populations and aggression toward extra-group members implies that breeding positions are limited.

female(s), it should also reinforce the male's commitment to the female by increasing paternity certainty, further enabling strong male-female bonds. High levels of male-male aggression may also make a roving male strategy unfeasible, if females are guarded. On the other hand, if a single male is unable to provide adequate defense, females should favor incorporating additional males into the group (Fig. 1). However, factors such as heightened within-group feeding competition may ultimately limit overall group size. Additionally, if females mate with a large number of males (and thus reduce paternity certainty), these males will have little incentive to defend resources for females. Lastly, although the same-sex aggression displayed by white-faced sakis (both male and female) may promote pair-living via excluding new members, this force may also lead to multi-adult groups when offspring delay dispersal and attempt to establish a reproductive role within the group (if the potential for non-incestuous mating arises) (Fig. 1). Thus, some portion of multi-male white-faced saki groups are likely comprised of related father-son pairs, although the documentation of polygamous mating suggests this may not be true for all groups. In sum, white-faced saki social organization appears to result from the interaction between the selective benefits of pair-living versus incorporating extra adults into the group.

This analysis suggests that the primary white-faced saki strategy is for males to limit access to females by non-group members, but also possibly tolerate minimal within-group mating and/or feeding competition, if it achieves better group defense. This may occur when the threat posed by floater animals is high, when between-group feeding competition is high, or when males are unable to exclude extra adult males from the group (either from immigration or delayed dispersal by offspring). This cooperative defense likely provides benefits to females through reducing infanticide risk, reducing harassment from floaters, or increasing access to resources. Receiving these advantages provides a testable explanation for why females choose to cultivate close social bonds with (presumably) high-quality males. If the current assertion is correct, then: (i) multi-adult groups should be more effective in home range and infanticide defense than pairs; (ii) females should have or attempt to cultivate stronger bonds with males that participate in defense and/or are more effective in group defense; (iii) females in multi-adult groups should receive greater benefits of defense (increased access to resources or protection) than those in pairs [see Santos & Nakagawa, 2013].

Analyzing these separate components of social behavior has provided corroboratory evidence to the insights gained from our conceptual models regarding variable pair-living in white-faced sakis. This

species-level approach has utility across a range of social animals, since: (i) an overarching model for the variability displayed in social and mating patterns of pair-living is currently lacking, and (ii) factors selecting for pair-living versus small multi-adult groups may differ between species and likewise the stimuli for variation will also be species-specific. In addition to helping generate species-specific models of social system (i.e., Fig. 1) this approach can supply testable predictions to assess the accuracy of these models and guide future research.

Species such as white-faced sakis that exhibit variable social organizations present an ideal natural experimental design to directly compare the factors, pressures, and advantages driving pair-living and multi-adult groups. The current exercise has demonstrated how conceptual models, a consideration of sources of variation, and a holistic examination of social systems can provide insight into the selective forces driving variation in pair-living.

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