

MSc Essay

Adult Sex Ratio in Social Systems: Causes and Consequences in  
Primates

University of Groningen

Student: Tommaso Saccà

Supervisors: prof. dr. Charlotte K. Hemelrijk and Lauren Seex (PhD)

## Abstract

Adult sex ratio is a central topic in sociobiology and has been hypothesized to be linked to social behavior and population dynamics. This essay aims to survey the literature on the general theory concerning which factors cause skewed adult sex ratio and how this influences social systems, specifically in primates. Shifts in adult sex ratio are bound to specific proximate causations, namely changes in birth sex ratio and sex-biased mortality. In primates, while biases in birth sex ratio are present, the main drivers of biases in adult sex ratio are sex-specific behaviors (i.e. male-biased risky behaviors) and physiological differences (male-biased sexual dimorphism), and the resulting male-biased mortality results in the typical female-biased adult sex ratio observed in most species. Consequences of different adult sex ratio on social systems mainly revolve around mating systems, specifically in the relationship between decreasing mating skew and increasing female proportion in groups. Also, an increased male proportion in primate groups influence dominance hierarchies, increasing female dominance over males. Among primates, lemurs show an unusual, even adult sex ratio, and their case is explored in the discussion to identify the possible causes of it and the consequences on their social systems.

## Introduction

Across and within different taxa, adult sex ratio presents great variety; however, it is still unclear which demographic processes cause this variation and how this variation affects social behavior (Eberhart-Phillips et al. 2018). Theoretical models show that adult sex ratio is expected to influence the evolution of mating competition, mating systems and parental care, with the less abundant sex selected to provide less care to its offspring and increase mating competition. The less abundant sex experience less mating competition due to the lower number of same-sex competitors, while the more abundant sex gains more benefits from investing in parental care of successful mating than in competing for additional mating opportunities, due to the increased mating competition (McNamara et al. 2000, Kokko and Jennions 2008). Differences in behavior between sexes are the norm in sexually reproducing organisms and mainly revolve around the intensity of competition with other same sex individuals for reproduction and the level of parental care that each sex show. The most commonly found pattern, deemed the 'conventional' sex roles, is that of female care for offspring, and male-male competition for mates (Queller 1997). Sex-role reversal (male caring and female competing) is commonly seen in insects, fish, amphibia and birds (*see* Liker et al. 2013), and there is direct (Fritzsche et al. 2016) and correlational (e.g. Liker et al. 2013) evidence that in these taxa sex role reversal is linked to adult sex ratio, with caring males linked to populations with male-biased sex ratio, and caring females (conventional role) to female-biased populations. Comparative analyses on 18 shorebird species showed how a male-biased adult sex ratio was linked to female polygamy, female-female competition for mates and male parental care, while species with a female-biased adult sex ratio showed more conventional sex roles (Liker et al. 2013). Evidence for the role of adult sex ratio on parental care has also been found in humans, with the assumption that marriage is a form of parental investment; when a male-biased adult sex ratio was recorded, men were more likely to marry (Schacht and Kramer 2016), while when a female-biased adult sex ratio was present, males were more likely to have short-term relationships with lower investment than females (Schacht and Mulder 2015). Correlational support for the prediction that adult sex ratio influences mating competition comes again from birds; a

comparative analysis of 201 avian species found that a bias in adult sex ratio resulted in later maturation for the less abundant sex, a result that was found linked to increase in sexual selection, through phylogenetic path analyses (Ancona et al. 2020). Adult sex ratio shows great variation in different taxa, although the direction of the bias change; for birds, the ratio is usually male-biased, while for mammals it is typically female biased (Donald 2007); what are the possible causes of this variation?

## Causes

A biased adult sex ratio can result from different factors, namely a biased sex ratio at birth (birth sex ratio), sexual differences in the juvenile and/or adult survival, and sex-biased dispersal (Veran and Beissinger 2009, Székely et al. 2014). A bias in sex ratio can arise from a difference in how many males and females are born; a bias in giving birth to offspring of a specific sex can be adaptive if there are differential costs and benefits in raising either a male or a female. One sex can be philopatric and, with a local scarcity of resources, investing in it could be more detrimental than investing in the sex that disperse (“local resource competition hypothesis”; Hamilton 1967, Clark 1978). In cooperative breeders, one sex can be more beneficial than the other in its ability to provide help in raising offspring, resulting in a preference for it over offspring of the other sex (“local resource enhancement hypothesis”; Gowaty and Lennartz 1985). A bias in birth sex ratio could also be connected to parental condition; Trivers and Willard (1973) proposed that a mother in good condition was expected to invest in the sex which shows more variable reproductive success (i.e. males in polygynous, sexually dimorphic species; Brown and Silk 2002) as its good physical condition allowed for a greater parental investment, and as the potential for an increase in the reproductive success was greater for that sex than the other. This hypothesis has strong empirical support in some taxa, while its predictive power in mammals is controversial; nonetheless, there are studies that support this theory (Cameron 2004, Sheldon and West 2004). Different conclusions can be reached when considering different values of fitness; Leimar (1996) modeled the relation between maternal quality and offspring quality considering the reproductive value of offspring instead of immediate reproductive success; the model showed that in species in which there is a strong maternal transmission of conditions to their daughters (e.g. through the inheritance of territories or rank, such as in species that show female philopatry and female dominance) females in good conditions are expected to receive more fitness benefits in investing in daughters than in sons. This is because the fitness of sons’ offspring depends on the quality of the female they mate with, while the fitness of the daughters’ offspring only depends on her quality. This results in greater benefits for females in investing in daughters even if their sons’ reproductive success is higher than their daughters’. Frequently, a skewed adult sex ratio is the result of sex differences in survival (Clutton-Brock et al. 1977), both during youth and adulthood, and in multiple bird and mammal species has been observed to be linked with a bias in juvenile survival (Clutton-Brock et al. 1997, Veran and Beissinger 2009, Eberhart-Phillips et al. 2018). Male bias in juvenile mortality is most often present in sexually dimorphic mammals, where males are the larger sex (Clutton-Brock et al. 1985). In 45% of mammal (Lindenfors et al. 2007) and 66% of bird (Székely et al. 2007) species, sexual size dimorphism is biased towards males, since for females reproductive costs increase with body size, and for males competitive ability increase with size (see Kappeler et al. 2019). In order to reach a larger body size males have to grow faster and/or grow for an increased period of time than females; in both cases, an

increase in energetic requirements and an increase in metabolic rate can expose juvenile males to an increased nutritional stress (“fragile males hypothesis”; Clutton-Brock et al. 1985), which has been observed in empirical studies on mammals (Clutton-Brock et al. 1992, Loison et al. 1999). Also, there is evidence for increased juvenile mortality in males when they are the larger sex in multiple mammal species (Promislow 1992). The presence of sexual size dimorphism can be a cause of bias in mortality also in adults for bird and mammal species (Promislow 1992, Promislow et al. 1992, Kalmbach and Benito 2007), with the larger sex showing increased mortality, possibly due to: (i) the increased vulnerability to food shortages that larger body size impose (Kalmbach and Benito 2007), (ii) shifts from ecological optimum, where males increase their sizes exceeding what would be their ecological optimum in order to increase their reproductive success (Owen-smith 1993), or (iii) increased susceptibility to parasitic and infective diseases caused by a larger and more energy-consuming investment in growth than the other sex and by androgens such as testosterone, that hinders immunocompetence (Zuk and McKean 1996, Moore and Wilson 2002, Hau 2007). Other factors that can result in sex-biased mortality in adults; as males, in general, have a higher potential reproductive rate and show a higher reproductive success (Clutton-Brock and Vincent 1991), they are more prone to undertake risky behavior (e.g. physical combat, male-male competition, and dispersal) to increase their reproductive output (“high risk, high gain hypothesis”; Magnhagen 1991, Rajpurohit and Sommer 1991, Alberts and Altmann 1995, Zuk and McKean 1996).. This propensity for risky behaviors could also result in an increased susceptibility to predation. In a comparative analysis of 81 predator-prey interactions of different taxa, males were 2.3 times more likely to be predated than females (Boukal et al. 2008). A survey of literature for bird predator species confirmed that sex-biased predation is very common, as all of them exhibited a sex bias in their predation; sex bias was significant for 27 of the 32 prey species analyzed. Also, in the vast majority of cases (26 out of 27), the bias was towards male individuals (Christe et al. 2006). This could mean that predators have a bias towards males, or that they encounter males more often than females (Magnhagen 1991). One of the behaviors that could result in an increased exposition to predators for one sex is sex-biased dispersal. While sex-biased dispersal patterns could result in local imbalances in open populations (i.e. that are linked to other populations through immigration and emigration of individuals), with immigration and emigration, in closed populations (i.e. that are isolated from other populations) these differences even out, assuming the survival of the dispersing individuals (Székely et al. 2014, Kappeler 2017). However, dispersal is often linked to increased mortality, due to higher vulnerability to predation or diseases, and to aggressive encounters with resident individuals of surrounding territories (Rajpurohit and Sommer 1991, Alberts and Altmann 1995, Rödel et al. 2004). Interestingly, while morphological differences between sexes result in pregnant, incubating or nursing females having reduced fleeing capabilities and having to invest more time eating in order to meet their energy demands, making them generally more vulnerable (Székely et al. 2014), this doesn’t offset the other sources of male-biased mortalities in mammals. with the effect that in this taxa male-biased mortality is seen as a general rule and consistently observed, phenomenon that can be linked to male-biases in body size dimorphism, dispersal, and mating competition (Clutton-Brock et al. 1985, Promislow 1992). In birds, on the other hand, the opposite seems to be the case; on average, populations are male-biased, and since birth sex ratio did not generally differ from equality, this was linked to sex-biased mortality, which was found to be systematically higher for females (Donald 2007). This has been attributed to

many possible factors, such as female-bias in dispersal, female bias in parental investment through incubation that increases predation risk and metabolic demands, the exclusion from better territories by males (who are generally larger than females) and the tendency in migratory species of females to migrate further, increasing energy costs and risks (reviewed in Donald 2007).

## Primates

Primate species commonly form groups, and there is a possible between adult sex ratio of a population and adult sex ratio of the groups that form that population; however, the adult sex ratio of a population is usually calculated as the average of the adult sex ratio of the study groups of that populations (Kappeler 2017); since only a few primate species form all-male groups and is difficult to keep track of floaters (Kappeler 2017), this links the two measures and allow to discuss them at approximately the same time. Notably, for the species that form all-male groups, it is not possible to generalize the population adult sex ratio to the specific cases of groups.

Primate species commonly present female bias in adult sex ratio (Kappeler 2017), and, according to the theory, show a male-bias in mortality (e.g. Fedigan and Zohar 1997). An additional source of bias in adult sex ratio could be a bias in birth sex ratio; a comparative analysis on 102 primate species found evidence for biases in birth sex ratio accordingly to the local resource hypothesis in species without cooperative breeding, where there was a bias in birth sex ratio towards offspring of the dispersing sex to reduce competition over resources, and accordingly to the local enhancement hypothesis in species with cooperative breeding, where there was a bias towards the offspring of the most cooperative sex (Silk and Brown 2008). However, the bias observed in birth sex ratio in primate species is generally only small (Brown and Silk 2002, Kappeler 2017). Additionally, Trivers and Willard (1973) hypothesis that maternal condition will influence the sex of the offspring has been found lacking empirical support in a meta-analysis on 15 primate species (Brown and Silk 2002).

The “high risk, high gain” hypothesis, that predicts lower survival in male adolescent and adults due to risky behaviors, have been found presenting empirical support in a variety of species (yellow baboons, *Papio cynocephalus*: Alberts and Altmann 1995; vervet monkeys, *Chlorocebus aethiops*: Fairbanks et al. 2004; gray mouse lemurs, *Microcebus murinus*: Kraus et al. 2008; Japanese macaque, *Macaca fuscata*: Fedigan and Zohar 1997; langurs, *Presbytis entellus*: Rajpurohit and Sommer 1991). The act of dispersal, commonly male-biased in most primate species, was found to be a significant source of mortality in multiple species (Rajpurohit and Sommer 1991, Alberts and Altmann 1995, Fedigan and Zohar 1997). As a last source of male-biased mortality, primates present cases of the strongest sexual dimorphism registered in mammals, with males commonly being the larger sex (Plavcan 2001). However, while generally mortality is male-biased, juvenile mortality doesn't follow the “fragile male hypothesis”, with female juveniles that are usually less viable than male juveniles (van Schaik and de Visser 1990). The decreased survival of female juveniles has been linked to local resource competition, where adult females acted to prevent the recruitment of unrelated females in female bonded species through direct aggression and harassment (van Schaik and de Visser 1990).

All of these factors could interact to result in a skewed adult sex ratio in the population; when diving into the

different interests that each sex has in the sex ratio of the group, we can analyze additional dynamics shaping adult sex ratio in groups.

## Conflict between sexes

Male infanticide is a central dynamic affecting primate social systems as it has been argued to be one of the most fundamental constraints on female reproduction (Kappeler 2012, Palombit 2012), and results in a consistent conflict of interests between sexes. Among mammals, male infanticide is most common in species characterized by prolonged infant dependency and altricial young (van Schaik 2000a). Therefore, due to their reproductive physiology, primates are particularly susceptible to this phenomenon. Females are occupied with gestation and lactation for a consistent part of their life, being at that same time unavailable to be fertilized, while males are always available to mate (Palombit 2012). Male infanticide increase male fitness when three conditions are met: (1) he is not likely the sire of the infant, (2) after the death of its offspring the female return to be fertilizable before than what would be expected with her offspring alive and (3) the male who committed the infanticide is more likely than before to fertilize the female who had her offspring killed (Hrdy 1979). This has been later called the sexual selection hypothesis. These conditions are usually met after a change in the dominant individual(s) after a take-over from external or subordinate males. This is particularly true when the new dominant individual(s) is not related to the previous, in which case infanticide would be less favorite due to the portion of inclusive fitness that closely related offspring have on the new dominant (e.g. Robbins et al. 2013). Among the hypothesis explaining infanticide, the sexual selection hypothesis is the most supported as a general explanation for male infanticide (Palombit 2012), even though other studies point out additional adaptive functions in specific conditions for certain taxa (reviewed in Palombit 2012). The emergence of this behavior results in intense intersexual conflict; while for females, who invest substantially in offspring through gestation and lactation, such an occurrence is extremely costly, for males is adaptive (Pradhan and Van Schaik 2008). Females are, then, expected to develop counterstrategies to prevent its occurrence (van Schaik 2000b). One of the main counterstrategies has been suggested to be to encourage multimale grouping, based on the analysis of infanticide rates in multiple species (Janson and Van Schaik 2000). In multimale groups, it has been theorized that females can focus on polyandrous mating (to expand the distribution of paternity among a larger pool of mates) and on manipulating information about paternity, creating uncertainty that bring males to estimate to be the sire of a higher number of infants than they actually are (Pradhan and Van Schaik 2008). Both strategies results in a higher number of potential fathers that will protect the female's offspring and in a lower number of unrelated individuals that will threaten it, particularly during the change in the dominant individual (Robbins et al. 2013). Additionally, a larger number of males makes external takeovers more difficult, as the newcomer(s) is faced with multiple male residents (van Schaik 1996). Empirical studies show how with an increased percentage of males in the group, female fecundity has been seen to increase (Mantled howlers (*Alouatta palliata*): Ryan et al. 2008; Black howlers (*Alouatta caraya*): Van Belle and Estrada 2008; White-faced capuchins (*Cebus capucinus*): Fedigan and Jack 2011). Lastly, the increased proportional presence of males affords better protection from predation, as seen in a comparative study of 39 species of cercopithecoid primates, where under high predation

risk the proportion of males was higher than expected by the number of females or group size, while under low predation risk the proportion of males was lower than predicted (Hill and Lee 1998). This could be due to more vigilant behavior that males show compared to females (van Schaik and Hörstermann 1994) or better physical defense of the group due to males' larger body size and possible counter-attacks against the predator (Willems and van Schaik 2017).

In general, both sexes could gain benefits from an increased proportion of males in the form of inter-group competitive ability to access high-quality food resources (Treves 2001), predator defence (Willems and van Schaik 2017) and defence from takeover from external male individuals (Grueter et al. 2012, Snyder-Mackler et al. 2012, Gilby et al. 2013, Chowdhury et al. 2015). However, males theoretically prefer to live in uni-male/multi-female groups, where they do not have to share paternity and can monopolize reproduction (van Schaik and van Hooff 1994, Kappeler 1999). Empirically, male fecundity has indeed been seen to decrease with increasing proportion of males in the group (Comparative study: Cowlshaw and Dunbar 1991; Mantled howlers (*Alouatta palliata*): Ryan et al. 2008; White-faced capuchins (*Cebus capucinus*): Fedigan and Jack 2011), arguably due to the limitation of finite breeding opportunities (Ryan et al. 2008). Interestingly, under certain conditions single male groups could be beneficial also to females. A mathematical model, which confirmed the general prediction that females prefer to live in multimale groups, it also predicted that female preference for multimale groups against single-male groups would decline, even when infanticide is present, when a specific set of conditions are met.; if dominant males in both types of groups are much stronger than subordinate or solitary males, the preference of females for multimale groups decline (Pradhan and Van Schaik 2008). Under this scenario, preference would even shift to uni-male groups when any unspecified extra costs were added to multimale grouping in the model (Pradhan and Van Schaik 2008), that can be coherent with increased intragroup food competition, as an example. Lastly, the model predicts that females could prefer one-male groups if the dominant males in those groups were much stronger than the dominant males in multi male groups (Pradhan and Van Schaik 2008). Stronger males were defined as males having a longer tenure, which offset the higher risk of infanticide that females in one-male groups incurred after the dominant was replaced (Pradhan and Van Schaik 2008). The alternative scenarios that would result in increasing female preference for uni-male groups have been observed in the wild for certain species. In ursine colobus (*Colobus vellerosus*) males in uni-male groups are better at defending from male immigration, they perform more energetically expensive displays and show dominance over males in multi-male groups during intergroup encounters (reviewed in Sicotte et al. 2017). In mountain gorillas (*Gorilla beringei beringei*), dominant males in uni-male groups had significantly longer tenures than dominant individuals in multi-male groups (Robbins et al. 2013). Even though in uni-male groups the overall rates of infanticide were higher, infant mortality was not significantly different between group types and there were no significant fitness benefits for females to prefer multimale groups over uni-male groups (Robbins et al. 2013).

## Influences of females on spatial distribution of males

Male and female individuals differ in the main factors underlying their distribution in the environment; females are expected to react to the landscape of risks and resources (Wrangham 1980), while males make decisions based on

the spatial distribution of females (Altmann 1990). These different preferences mirror the difference in the principal limiting factor that each sex has concerning reproduction; access to receptive females for males (Glutton-Brock and Parker 1992), and access to resources for females (Wrangham 1980). There is consistent evidence from comparative studies that the distribution of females influences the distribution of males in primates, where a larger female group size results on average on a larger male group size (Mitani et al. 1996, Nunn 1999, Carnes et al. 2011). This has been suggested to reflect the increasing inability of males to monopolize individuals of the other sex as the number of females increase (Mitani et al. 1996, Nunn 1999). A comparative study on 71 primate species (49 haplorhine species and 22 strepsirrhine species) has found evidence that corroborates this explanation (Carnes et al. 2011). Female estrous synchrony (i.e. female temporal overlap during fertile periods) has been found to be one of the most important factors influencing male group size, second in importance after female group size (Carnes et al. 2011). Female estrous synchrony is expected to result in a decrease in male monopolization potential, as it makes it more difficult for a single male to exclude rivals from the simultaneous reproductive opportunities from different females (Nunn 1999). Indeed, an increase in female receptive synchrony has been linked to a decrease in reproductive skew (a proxy used to estimate monopolization ability of males, e.g. Kokko and Johnstone 1999) in two comparative analyses (Ostner et al. 2008, Gogarten and Koenig 2013), while a third did not find any correlation between the two (Kutsukake and Nunn 2006). Even in light of the importance of female receptive synchrony on primate social systems, females' ability to synchronize their estruses has been found generally lacking empirical evidence in multiple studies (Assamese macaques (*Macaca assamensis*): Fürtbauer et al. 2011, mandrills (*Mandrillus sphinx*): Setchell et al. 2011; chacma baboons (*Papio ursinus*): Clarke et al. 2012; olive baboons (*Papio anubis*): Ihara et al. 2016). The only two studies that reported estrus synchrony in non-human primates (Wallis 1985, French and Stribley 1987), were criticized on their statistical procedures, which were argued to have resulted in statistical artifacts (Schank 2001). Instead, some species actively avoid synchronization (chimpanzees (*Pan troglodytes schweinfurthii*): Matsumoto-Oda et al. 2007; Verreaux's sifakas (*Propithecus verreauxi*): Mass et al. 2009). However, in primates, mating can happen outside the ovulatory periods, a phenomenon that has been attributed to the need to increase paternity confusion as a protection from infanticide (van Noordwijk and van Schaik 2000). As it has been seen for Assamese macaques, this can lead to female synchronising mating events without any synchronization in estrus cycles (Fürtbauer et al. 2011). Additionally, concealed ovulation and polygamous mating from females might result in males not being able to clearly identify fertile periods, being lead to consider female to be receptively synchronous even when they are not; as an example, in redfronted lemurs (*Eulemur fulvus rufus*) all females copulated with multiple partners several days before and after the likely days of ovulation, resulting apparently more synchronous with each other than they effectively were (Ostner and Kappeler 1999). Breeding seasonality is another possible explanation for female receptive synchrony, as in shorter breeding season females are expected to come into estrous more synchronously; both breeding seasonality and shorter breeding seasons were found to affect male group size in the comparative analysis of Carnes et al. (2011), the latter more than the former.



## Adult sex ratio and social systems

Adult sex ratio in groups also feeds back on different aspects of social systems, such as the mating system; reproductive skew has been seen to decrease with larger male group size in multi-male groups (Kutsukake and Nunn 2006, Gogarten and Koenig 2013), and a higher number of males is correlated with a higher number of females (Carnes et al. 2011). A clear example of the effect that female spatial distribution, dependent on resources, can have on male numbers and on mating system can be seen in the bonnet macaque (*Macaca radiata*: Sinha et al. 2005). This species usually lives in large multi-male/multi-female groups (8-60 individuals), with female philopatry, male dispersal, and strong, linear matrilineal dominance hierarchies (Sinha 2001). However, in places in which the monkey received irregular and unpredictable food handouts by tourists, group composition shifted to small uni-male/multi-female groups (Sinha et al. 2005). This was argued to be a result of the reliance on food provided by tourists' handouts, that could sustain only small groups and resulted in high competition for food, since the single food items were highly nutritious, unsharable and unpredictable in their availability. This resulted in smaller groups of highly related females, and males reacted, each in accordance with their potential to monopolize the new females' spatial distribution. While usually males in multi-male groups were tolerant of each other, males in single-male groups were aggressive toward external males, probably due to their newfound ability to better monopolize the smaller groups of females (Sinha et al. 2005). In the population most reliant on tourist handouts, female dispersal was also observed, with relatively more female emigrating out of uni-male groups compared to multi-male groups. This has been proposed to be due to the decreased mate choice that females experienced in this recently formed social organization. (Sinha et al. 2005).

Another way in which adult sex ratio could influence social systems is through changes in dominance hierarchies, with an increase in female dominance; an agent-based model shows that, in groups with a high intensity of aggression, a larger proportion of males in group resulted in an even higher average intensity of aggressive interactions, and a higher number of interactions with males, which in turn differentiated more strongly the individuals alongside the dominance hierarchy, increasing the proportion of female dominance over males (Hemelrijk et al. 2008). These results were significant only when the intensity of aggression was not even between sexes, with females showing less intense aggression than males, while for groups that present low initial intensity of aggression the results were still significant, but too small to have an impact on hierarchies (Hemelrijk et al. 2008). Empirical analyses on multiple primate taxa support that female dominance increases with a larger proportion of males in groups, and when focusing on the genus *Macaca*, the effect of male proportion on female dominance was found significant in despotic species, but not in egalitarian species, as found in the model (Hemelrijk et al. 2008).

## Discussion

Biases in adult sex ratio influences multiple aspects of social living, such as mating system and parental care, disentangling the components of each sex-related causes of death, that can range from specific behaviors (e.g. dispersal, aggressive interactions) to physiological constraints (i.e. higher susceptibility to food shortages for the larger sex in dimorphic species, differences in the costs of reproductive effort) would increase our understanding of sociality. Lemurs, due to their particular characteristics, can be an interesting case study for what concerns causes

and consequences of adult sex ratio in social systems. Lemurs present a set of traits (female dominance, even adult sex ratio and female genital masculinization) usually linked to the lack of sexual dimorphism, which are collectively referred to as the “lemur syndrome” (Kappeler et al. 2019). One of the arguable causes that could result in the unusual, even adult sex ratio is a specific set of sex-biased mortalities that differentiates lemurs from the more general pattern of biases observed in primates. There is evidence for a lack of sex-biased mortality in lemur species (e.g. Ostner and Kappeler 2004, Tecot et al. 2013). The typical lack of sexual size dimorphism is the first factor that reduces male-biased mortality, and sets apart lemurs from other primates. Monomorphism in lemurs has been proposed to be linked to the specific characteristic of Madagascar. Low plant productivity, limited number of reliable year-round food sources, drought and cyclones, all concur in defining Madagascar’s environment as harsh and unpredictable, which is argued to be an ecological constrain on male and female body size (Pochron and Wright 2003). Kappeler et al. (2019) found that sexual dimorphism is generally absent among all Madagascar mammals, and found partial support for the role of Madagascar environment in this observed pattern through phylogenetic analyses. Whether the effect of monomorphism on sex-related mortality is quantitatively enough to result in an unbiased-mortality and an equal sex ratio, is worth investigating. Especially since examples from lemurs (grey mouse lemur, *Microcebus murinus*: Kraus et al. 2008), and other monomorphic mammals (European rabbit, *Oryctolagus cuniculus*: Rödel et al. 2004) suggests how even with monomorphism sex-biased mortality can still consistently occurs.

A review of Erhart and Overdorff (2008) on lemur species highlights other possible causes of decreased male-biased mortality. Among group-living, diurnal lemurs, only *Lemur catta* show consistent female philopatry; in other species, females may stay, but can also decide to leave, or can be forced to leave through targeted aggression (Erhart and Overdorff 2008). This increase in female dispersal will likely increase their sex specific mortality rates, while in primates in general males are the main dispersing sex and the subsequent mortality linked with the risks of dispersal is limited to them. Even though the rate of aggression of females was generally comparable with other primates, targeted aggression towards other females can be intense and severe in some species (Erhart and Overdorff 2008), increasing costs of aggression that usually are attributed predominantly to males. Additionally, the harsh environment of Madagascar, with low plant productivity and extremely variable food availability in reproductive seasons (Pochron and Wright 2003), might exacerbate female costs of pregnancy and lactation. Empirically, an absence of sex-biased mortality has indeed been recorded in multiple lemur species (e.g. Ostner and Kappeler 2004, Tecot et al. 2013). How and with which intensity each of these factors contributed - with possible, unforeseen factors not covered in this discussion – is still a matter of debate, as is the generality of this lack of sex-biased mortality. Lastly, as hormonal masculinization’s role in female dominance has been examined and found significant (Petty and Drea 2015), the effect that masculinization can have on sex-biased mortality - from both a behavioral (e.g. aggressivity) and a physiological point of view (e.g. immunodeficiency)- is worth further investigation.

Regarding the effect that adult sex ratio can have on social systems, lemurs could show an interesting interaction between even adult sex ratio and polyandrous mating, that have the theoretical possibility to result in another characteristic of lemurs, which is the lack of male monopolization of small groups of females (<5) (Kappeler 2000, Pochron and Wright 2003). In apparent contrast to the observed lack of this behavior, Kappeler and Schäffler (2008)

found for Verreaux's sifakas (*Propithecus verreauxi*) a strong reproductive skew biased towards the dominant male. However, during their fertility period female sifakas mate with multiple males, including neighbors males from adjacent groups and roaming males; this behavior is also typical of many other lemur species (e.g. Ostner and Kappeler 1999; Kappeler and Schaffler 2008). Therefore, for all practical purposes males could perceived the monopolization of females as unfeasible, and this could be aided by the high number of possible mates with which the female could mate, due to the even adult sex ratio in the population. In other cases, specifically in species in which females show more consistent dominance over males, reproductive asynchrony might be retained (e.g., *Lemur catta*: Pereira 1991; *Propithecus diadema edwardsi*: Pochron and Wright 2003) and mechanisms for confounding paternity might not be selected to incite male-male competition, thus providing useful information to females in selecting males (Pereira 1991).

The effect of number of females on reproductive skew has been found to follow general theoretical predictions, at least in redfronted lemurs (*Eulemur fulvus rufus*); female group size positively covaried with the probability of a male subordinate to sire infants (Kappeler and Port 2008). However, studies on this topic conducted on other lemur species seem to be lacking. In other cases, contrary to general theory, the number of females did not influence the number of males in groups of *Propithecus diadema edwardsi* (Pochron and Wright 2003); this was argued to be due to the female's habit of mating with both group males and neighbor males, which resulted in a difference between "feeding groups", which are the spatial groups, and "mating groups", which are the neighborhood. Consequently, males may not necessarily prefer groups with a higher number of females, as they would not gain preferential access to fertile females. In general, in species that present extra-group mating, the group composition could not accurately represent the mating system of the species. In that context, female cryptic choice can have a significant effect on mating systems, yet this mechanism remains poorly explored in mammals and primates (Kappeler and Schaffler 2008).

## References

- Alberts, S. C., and J. Altmann. 1995. Balancing Costs and Opportunities: Dispersal in Male Baboons. *The American Naturalist* 145:279–306.
- Altmann, J. 1990. Primate males go where the females are. *Animal Behaviour* 39:193–195.
- Ancona, S., A. Liker, M. C. Carmona-Isunza, and T. Székely. 2020. Sex differences in age-to-maturation relate to sexual selection and adult sex ratios in birds. *Evolution Letters* 4:44–53.
- Van Belle, S., and A. Estrada. 2008. Group size and composition influence male and female reproductive success in black howler monkeys (*Alouatta pigra*). *American Journal of Primatology* 70:613–619.
- Boukal, D. S., L. Berec, and V. Krivan. 2008. Does Sex-Selective Predation Stabilize or Destabilize Predator-Prey Dynamics? *PloS one* 3:1–10.
- Brown, G. R., and J. B. Silk. 2002. Reconsidering the null hypothesis: Is maternal rank associated with birth sex ratios in primate groups? *Proceedings of the National Academy of Sciences of the United States of America* 99:11252–11255.
- Cameron, E. Z. 2004. Facultative adjustment of mammalian sex ratios in support of the Trivers-Willard hypothesis: Evidence for a mechanism. *Proceedings of the Royal Society B: Biological Sciences* 271:1723–1728.
- Carnes, L. M., C. L. Nunn, and R. J. Lewis. 2011. Effects of the distribution of female primates on the number of

males. PLoS ONE 6.

- Chowdhury, S., M. Pines, J. Saunders, and L. Swedell. 2015. The adaptive value of secondary males in the polygynous multi-level society of hamadryas baboons. *American Journal of Physical Anthropology* 158:501–513.
- Christe, P., L. Keller, and A. Roulin. 2006. The predation cost of being a male: Implications for sex-specific rates of ageing. *Oikos* 114:381–384.
- Clark, A. B. 1978. Sex ratio and local resource competition in a prosimian primate. *Science* 201:163–165.
- Clarke, P. M. R., S. P. Henzi, and L. Barrett. 2012. Estrous synchrony in a nonseasonal breeder: Adaptive strategy or population process? *Behavioral Ecology* 23:573–581.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313:131–133.
- Clutton-Brock, T. H., P. H. Harvey, and B. Rudder. 1977. Sexual dimorphism, sociometric sex ratio and body weight in primates. *Nature* 269:797–800.
- Clutton-Brock, T. H., O. F. Price, S. D. Albon, and P. A. Jewell. 1992. Early Development and Population Fluctuations in Soay Sheep. *Journal of Animal Ecology* 61:381–396.
- Clutton-Brock, T. H., K. E. Rose, and F. E. Guinness. 1997. Density-related changes in sexual selection in red deer. *Proceedings of the Royal Society B: Biological Sciences* 264:1509–1516.
- Clutton-Brock, T. H., and A. C. J. Vincent. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature* 351:58–60.
- Cowlshaw, G., and R. I. M. Dunbar. 1991. Dominance rank and mating success in male primates. *Animal Behaviour* 41:1045–1056.
- Donald, P. F. 2007. Adult sex ratios in wild bird populations. *Ibis* 149:671–692.
- Eberhart-Phillips, L. J., C. Küpper, M. C. Carmona-Isunza, O. Vincze, S. Zefania, M. Cruz-López, A. Kosztolányi, T. E. X. Miller, Z. Barta, I. C. Cuthill, T. Burke, T. Székely, J. I. Hoffman, and O. Krüger. 2018. Demographic causes of adult sex ratio variation and their consequences for parental cooperation. *Nature Communications* 9.
- Erhart, E. M., and D. J. Overdorff. 2008. Rates of agonism by diurnal lemuroids: Implications for female social relationships. *International Journal of Primatology* 29:1227–1247.
- Fairbanks, L. A., M. J. Jorgensen, A. Huff, K. Blau, Y. Y. Hung, and J. J. Mann. 2004. Adolescent impulsivity predicts adult dominance attainment in male vervet monkeys. *American Journal of Primatology* 64:1–17.
- Fedigan, L. M., and K. M. Jack. 2011. Two girls for every boy: The effects of group size and composition on the reproductive success of male and female white-faced capuchins. *American Journal of Physical Anthropology* 144:317–326.
- Fedigan, L. M., and S. Zohar. 1997. Sex differences in mortality of Japanese macaques: Twenty-one years of data from the Arashiyama West population. *American Journal of Physical Anthropology* 102:161–175.
- French, J. A., and J. A. Stribley. 1987. Synchronization of ovarian cycles within and between social groups in golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology* 12:469–478.
- Fritzsche, K., I. Booksmythe, and G. Arnqvist. 2016. Sex Ratio Bias Leads to the Evolution of Sex Role Reversal in Honey Locust Beetles. *Current Biology* 26:2522–2526.
- Fürtbauer, I., R. Mundry, M. Heistermann, O. Schülke, and J. Ostner. 2011. You mate, I mate: Macaque females synchronize sex not cycles. *PLoS ONE* 6:6–11.
- Gilby, I. C., L. J. N. Brent, E. E. Wroblewski, R. S. Rudicell, B. H. Hahn, J. Goodall, and A. E. Pusey. 2013. Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology* 67:373–381.

- Glutton-Brock, T. H., and G. A. Parker. 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology* 67:437–456.
- Gogarten, J. F., and A. Koenig. 2013. Reproductive seasonality is a poor predictor of receptive synchrony and male reproductive skew among nonhuman primates. *Behavioral Ecology and Sociobiology* 67:123–134.
- Gowaty, P. A., and M. R. Lennartz. 1985. Sex ratios of nestling and fledgling red-cockaded woodpeckers (*Picoides borealis*) favor males. *American Naturalist* 126:347–353.
- Grueter, C. C., B. Chapais, and D. Zinner. 2012. Evolution of Multilevel Social Systems in Nonhuman Primates and Humans. *International Journal of Primatology* 33:1002–1037.
- Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156:477–488.
- Hau, M. 2007. Regulation of male traits by testosterone: Implications for the evolution of vertebrate life histories. *BioEssays* 29:133–144.
- Hemelrijk, C. K., J. Wantia, and K. Isler. 2008. Female dominance over males in primates: Self-organisation and sexual dimorphism. *PLoS ONE* 3.
- Hill, R. A., and P. C. Lee. 1998. Predation risk as an influence on group size in cercopithecoid primates: Implications for social structure. *Journal of Zoology* 245:447–456.
- Hrdy, S. B. 1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* 1:13–40.
- Ihara, Y., D. A. Collins, R. Oda, and A. Matsumoto-Oda. 2016. Testing socially mediated estrous synchrony or asynchrony in wild baboons. *Behavioral Ecology and Sociobiology* 70:1921–1930.
- Janson, C. H., and C. P. Van Schaik. 2000. The behavioral ecology of infanticide by males. Pages 469–494 in C. H. Janson and C. P. Van Schaik, editors. *Infanticide by males and its implications*. Cambridge University Press, Cambridge.
- Kalmbach, E., and M. M. Benito. 2007. Sexual size dimorphism and offspring vulnerability in birds. Pages 133–142 in D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely, editors. *Sex, Size and Gender Roles*. Oxford University Press, Oxford.
- Kappeler, P. M. 1999. Primate socioecology: New insights from males. *Naturwissenschaften* 86:18–29.
- Kappeler, P. M. 2000. Causes and consequences of unusual sex ratios among lemurs. Pages 55–63 in P. M. Kappeler, editor. *Primate males: causes and consequences of variation in group composition*. Cambridge University Press, Cambridge.
- Kappeler, P. M. 2012. Mate Choice. Pages 367–387 in J. C. Mitani, J. Call, Peter M. Kappeler, R. A. Palombit, and J. B. Silk, editors. *The evolution of primate societies*. The University of Chicago Press, Chicago and London.
- Kappeler, P. M. 2017. Sex roles and adult sex ratios: Insights from mammalian biology and consequences for primate behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372.
- Kappeler, P. M., C. L. Nunn, A. Q. Vining, and S. M. Goodman. 2019. Evolutionary dynamics of sexual size dimorphism in non-volant mammals following their independent colonization of Madagascar. *Scientific Reports* 9:1–14.
- Kappeler, P. M., and M. Port. 2008. Mutual tolerance or reproductive competition? Patterns of reproductive skew among male redfronted lemurs (*Eulemur fulvus rufus*). *Behavioral Ecology and Sociobiology* 62:1477–1488.
- Kappeler, P. M., and L. Schaffler. 2008. The lemur syndrome unresolved: Extreme male reproductive skew in sifakas (*Propithecus verreauxi*), a sexually monomorphic primate with female dominance. *Behavioral Ecology and Sociobiology* 62:1007–1015.
- Kokko, H., and M. D. Jennions. 2008. Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology* 21:919–948.

- Kokko, H., and R. A. Johnstone. 1999. Social queuing in animal societies: A dynamic model of reproductive skew. *Proceedings of the Royal Society B: Biological Sciences* 266:571–578.
- Kraus, C., M. Eberle, and P. M. Kappeler. 2008. The costs of risky male behaviour: Sex differences in seasonal survival in a small sexually monomorphic primate. *Proceedings of the Royal Society B: Biological Sciences* 275:1635–1644.
- Kutsukake, N., and C. L. Nunn. 2006. Comparative tests of reproductive skew in male primates: The roles of demographic factors and incomplete control. *Behavioral Ecology and Sociobiology* 60:695–706.
- Leimar, O. 1996. Life-history analysis of the Trivers and Willard sex-ratio problem. *Behavioral Ecology* 7:316–325.
- Liker, A., R. P. Freckleton, and T. Székely. 2013. The evolution of sex roles in birds is related to adult sex ratio. *Nature Communications* 4:1–6.
- Lindfors, P., J. L. Gittleman, and K. E. Jones. 2007. Sexual size dimorphism in mammals. Pages 16–26 *in* D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely, editors. *Sex, size and gender roles: Evolutionary studies of sexual size dimorphism*. Oxford University Press, Oxford.
- Loison, A., R. Langvatn, and E. J. Solberg. 1999. Body mass and winter mortality in red deer calves: Disentangling sex and climate effects. *Ecography* 22:20–30.
- Magnhagen, C. 1991. Predation risk as a cost of reproduction. *Trends in Ecology and Evolution* 6:183–186.
- Mass, V., M. Heistermann, and P. M. Kappeler. 2009. Mate-Guarding as a male reproductive tactic in *Propithecus verreauxi*. *International Journal of Primatology* 30:389–409.
- Matsumoto-Oda, A., M. Hamai, H. Hayaki, K. Hosaka, K. D. Hunt, E. Kasuya, K. Kawanaka, J. C. Mitani, H. Takasaki, and Y. Takahata. 2007. Estrus cycle asynchrony in wild female chimpanzees, *Pan troglodytes schweinfurthii*. *Behavioral Ecology and Sociobiology* 61:661–668.
- McNamara, J. M., T. Székely, J. N. Webb, and A. I. Houston. 2000. A dynamic game-theoretic model of parental care. *Journal of Theoretical Biology* 205:605–623.
- Mitani, J. C., J. Gros-Louis, and J. H. Manson. 1996. Number of males in primate groups: Comparative tests of competing hypotheses. *American Journal of Primatology* 38:315–332.
- Moore, S. L., and K. Wilson. 2002. Parasites as a viability cost of sexual selection in natural populations of mammals. *Science* 297:2015–2018.
- van Noordwijk, M. A., and C. P. van Schaik. 2000. Reproductive patterns in eutherian mammals: adaptations against infanticide? Pages 322–360 *in* C. P. van Schaik and C. H. Janson, editors. *Infanticide by males and its implications*. Cambridge University Press, Cambridge.
- Nunn, C. L. 1999. The number of males in primate social groups: A comparative test of the socioecological model. *Behavioral Ecology and Sociobiology* 46:1–13.
- Ostner, J., and P. M. Kappeler. 1999. Central males instead of multiple pairs in redfronted lemurs, *Eulemur fulvus rufus* (Primates, Lemuridae)? *Animal Behaviour* 58:1069–1078.
- Ostner, J., and P. M. Kappeler. 2004. Male life history and the unusual adult sex ratios of redfronted lemur, *Eulemur fulvus rufus*, groups. *Animal Behaviour* 67:249–259.
- Ostner, J., C. L. Nunn, and O. Schülke. 2008. Female reproductive synchrony predicts skewed paternity across primates. *Behavioral Ecology* 19:1150–1158.
- Owen-smith, N. 1993. Comparative Mortality Rates of Male and Female Kudus: The Costs of Sexual Size Dimorphism. *Journal of Animal Ecology* 62:428–440.
- Palombit, R. A. 2012. Infanticide: Male Strategies and Female Counterstrategies. Pages 432–469 *in* J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, and J. B. Silk, editors. *The evolution of primate societies*. The University of Chicago Press, Chicago and London.

- Pereira, M. E. 1991. Asynchrony within estrous synchrony among ringtailed lemurs (Primates: Lemuridae). *Physiology and Behavior* 49:47–52.
- Petty, J. M. A., and C. M. Drea. 2015. Female rule in lemurs is ancestral and hormonally mediated. *Scientific Reports* 5:1–5.
- Plavcan, J. M. 2001. Sexual dimorphism in primate evolution. *American Journal of Physical Anthropology* 116:25–53.
- Pochron, S. T., and P. C. Wright. 2003. Variability in adult group compositions of a prosimian primate. *Behavioral Ecology and Sociobiology* 54:285–293.
- Pradhan, G. R., and C. Van Schaik. 2008. Infanticide-driven intersexual conflict over matings in primates and its effects on social organization. *Behaviour* 145:251–275.
- Promislow, D. E. L. 1992. Costs of Sexual Selection in Natural Populations of Mammals. *Proceedings of the Royal Society B: Biological Sciences* 247:203–210.
- Promislow, D. E. L., R. Montgomerie, and T. E. Martin. 1992. Mortality costs of sexual dimorphism in birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 250:143–150.
- Queller, D. C. 1997. Why do females care more than males? *Proceedings of the Royal Society B: Biological Sciences* 264:1555–1557.
- Rajpurohit, L. S., and V. Sommer. 1991. Sex Differences in Mortality among Langurs (*Presbytis entellus*) of Jodhpur, Rajasthan. *Folia Primatologica* 56:17–27.
- Robbins, A. M., M. Gray, A. Basabose, P. Uwingeli, I. Mburanumwe, E. Kagoda, and M. M. Robbins. 2013. Impact of male infanticide on the social structure of mountain gorillas. *PLoS ONE* 8.
- Rödel, H. G., A. Bora, P. Kaetzke, M. Khaschei, H. Hutzelmeyer, and D. Von Holst. 2004. Over-winter survival in subadult European rabbits: Weather effects, density dependence, and the impact of individual characteristics. *Oecologia* 140:566–576.
- Ryan, S. J., P. T. Starks, K. Milton, and W. M. Getz. 2008. Intersexual conflict and group size in *Alo uatta palliata*: A 23-year evaluation. *International Journal of Primatology* 29:405–420.
- Schacht, R., and K. L. Kramer. 2016. Patterns of family formation in response to sex ratio variation. *PLoS ONE* 11:1–14.
- Schacht, R., and M. B. Mulder. 2015. Sex ratio effects on reproductive strategies in humans. *Royal Society Open Science* 2.
- van Schaik, C. P. 2000a. Vulnerability to infanticide by males: Patterns among mammals. Pages 61–71 in C. van Schaik and C. H. Janson, editors. *Infanticide by Males and Its Implications*. Cambridge University Press, Cambridge.
- van Schaik, C. P., and J. A. R. A. M. van Hooff. 1994. Male Bonds: Affiliative Relationships Among Nonhuman Primate Males. *Behaviour* 130:309–337.
- van Schaik, C. P., and M. Hörstermann. 1994. Predation risk and the number of adult males in a primate group: a comparative test. *Behavioral Ecology and Sociobiology* 35:261–272.
- van Schaik, C. P., and J. de Visser. 1990. Fragile sons or harassed daughters? Sex differences in mortality among juvenile primates. *Folia Primatologica* 55:10–23.
- van Schaik, C. 2000b. Social counterstrategies against infanticide by males in primates and other mammals. Pages 34–52 in P. M. Kappeler, editor. *Primate Males*. Cambridge University Press, Cambridge.
- Schank, J. C. 2001. Measurement and cycle variability: Reexamining the case for ovarian-cycle synchrony in primates. *Behavioural Processes* 56:131–146.

- Setchell, J. M., J. Kendal, and P. Tynieć. 2011. Do non-human primates synchronise their menstrual cycles? A test in mandrills. *Psychoneuroendocrinology* 36:51–59.
- Sheldon, B. C., and S. A. West. 2004. Maternal Dominance, Maternal Condition, and Offspring Sex Ratio in Ungulate Mammals. *American Naturalist* 163:40–54.
- Sicotte, P., J. A. Teichroeb, J. V. Vayro, S. A. Fox, I. Bădescu, and E. C. Wikberg. 2017. The influence of male takeovers on female dispersal in *Colobus vellerosus*. *American Journal of Primatology* 79.
- Silk, J. B., and G. R. Brown. 2008. Local resource competition and local resource enhancement shape primate birth sex ratios. *Proceedings of the Royal Society B: Biological Sciences* 275:1761–1765.
- Sinha, A. 2001. The Bonnet Macaque Revisited: Ecology, Demography and Behaviour. *ENVIS Bull Wildl Prot Areas* 1:30–39.
- Sinha, A., K. Mukhopadhyay, A. Datta-Roy, and S. Ram. 2005. Ecology proposes, behaviour disposes: Ecological variability in social organization and male behavioural strategies among wild bonnet macaques. *Current Science* 89:1166–1179.
- Snyder-Mackler, N., S. C. Alberts, and T. J. Bergman. 2012. Concessions of an alpha male? Cooperative defence and shared reproduction in multi-male primate groups. *Proceedings of the Royal Society B: Biological Sciences* 279:3788–3795.
- Székely, T., T. Lislevand, and J. Figuerola. 2007. Sexual size dimorphism in birds. Pages 27–37 in D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely, editors. *Sex, size and gender roles: Evolutionary studies of sexual size dimorphism*. Oxford University Press, Oxford.
- Székely, T., F. J. Weissing, and J. Komdeur. 2014. Adult sex ratio variation: Implications for breeding system evolution. *Journal of Evolutionary Biology* 27:1500–1512.
- Tecot, S. R., B. D. Gerber, S. J. King, J. L. Verdolin, and P. C. Wright. 2013. Risky business: sex differences in mortality and dispersal in a polygynous, monomorphic lemur. *Behavioral Ecology* 24:987–996.
- Treves, A. 2001. Reproductive consequences of variation in the composition of howler monkey (*Alouatta* spp.) groups. *Behavioral Ecology and Sociobiology* 50:61–71.
- Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90–92.
- Veran, S., and S. R. Beissinger. 2009. Demographic origins of skewed operational and adult sex ratios: Perturbation analyses of two-sex models. *Ecology Letters* 12:129–143.
- Wallis, J. 1985. Synchrony of estrous swelling in captive group-living chimpanzees (*Pan troglodytes*). *International Journal of Primatology* 6:335–350.
- Willems, E. P., and C. P. van Schaik. 2017. The social organization of *Homo ergaster*: Inferences from anti-predator responses in extant primates. *Journal of Human Evolution* 109:11–21.
- Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262–300.
- Zuk, M., and K. A. McKean. 1996. Sex differences in parasite infections: Patterns and processes. *International Journal for Parasitology* 26:1009–1024.