



Sexual selection in the Kinda baboon

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ABSTRACT

Due to wide variation in the presence and degree of expression of a diverse suite of sexually-selected traits, the tribe Papionini represents an outstanding model for understanding how variation in sexual selection pressures and mechanisms leads to trait evolution. Here, we discuss the particular value of *Papio* as a model genus for studies of sexual selection, emphasizing the presence of multiple mating systems, and differences in the expression of sexually-selected traits among closely-related species. We draw particular attention to the Kinda baboon (*Papio kindae*), a comparatively less-studied baboon species, by providing a primer to Kinda baboon morphology, genetics, physiology, and behavior. Based on observations of large group sizes, combined with low degrees of sexual dimorphism and large relative testis size relative to other baboon species, we test the hypothesis that Kinda baboons have evolved under reduced direct, and increased indirect, male–male competition. We present the first long-term data on wild Kinda baboons in Zambia. Kinda baboon females show seasonal peaks in births and reproductive receptivity, and males exhibit a queuing-rather than contest-based dominance acquisition with long alpha-male tenure lengths. We finish by making a number of explicit testable predictions about Kinda baboon sexual signals and behaviors, and suggest that Kinda baboons have potential to offer new insights into the selective environments that may have been experienced during hominization.

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1. Introduction

Baboons are a canonical model for human evolution (Washburn, 1961; Jolly, 1970, 2001; Strum and Mitchell, 1987; Elton, 2006; Fischer et al., in review). Kinda baboons (*Papio kindae*) were long regarded as sub-species of yellow baboons, though recent evidence suggests they are genetically distinct enough to represent their own species (Burrell, 2009; Zinner et al., 2011, 2013; Burrell et al., 2013). Consistent with this genetic determination, Kinda baboons exhibit a number of morphologically (Frost et al., 2003; Leigh, 2006; Singleton et al., 2017) and behaviorally (Weyher et al., 2014) distinctive features that are consistent with recognition as a full ‘phylogenetic’ species (Jolly, 1993; Jolly et al., 2011). Interestingly, many of these distinctive features suggest that Kinda baboons might have evolved under a different dynamic of sexual selection compared to other baboon species.

Here, we examine Kinda baboon sexually-selected traits in the context of the well-studied genus *Papio*. Since little is known about

Kinda baboons, we first present a primer on the species detailing their taxonomy, morphology, genetics, physiology, and behavior. We then provide an overview of sexual selection in primates and how this has resulted in vast diversity in sexual traits among papionins. We then make the case for using *Papio* as a model genus for understanding the causes and consequences of this variation. We suggest that Kinda baboons might have evolved under a different dynamic of sexual selection compared to other baboons by highlighting some of their unique traits, and making specific predictions about correlative patterns. We present the first long-term data from a wild population of Kinda baboons in Zambia to address our predictions. We then suggest future directions of research that we hope will further add to our understanding of sexual selection in baboons.

2. Review

2.1. The Kinda baboon

Taxonomy and phenotype The Kinda (pronounced “kihn-dah,” not “kine-dah”) baboon, named after the type locality in Democratic

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Republic of Congo (Lönnberg, 1919), is found distributed across Angola, Democratic Republic of Congo, northern Zambia, and extreme southwest Tanzania, mainly in miombo woodland habitat with >1,000 mm mean annual rainfall (Ansell, 1960, 1978). The Kinda baboon range comes into contact with that of the grayfoot chacma baboon between the Zambezi floodplain and Kafue Flats in south-central Zambia (Jolly et al., 2011), and the yellow baboon in north-western Zambia (Burrell, 2009). Both contact zones have morphological and genetic signatures of introgression (Burrell, 2009; Jolly et al., 2011; Chiou et al., 2019). Kinda baboons exhibit pelage that is similar in coloration to the yellow baboon, although softer in texture (Ansell, 1978; Jolly, 1993). Compared to other baboons they are of smaller size, more gracile, longer limbed, lack white facial hair patches, have distinctive circumorbital skin coloration, and well-developed sagittal hair crests (Fig. 1) (Jolly et al., 2011). Kinda baboon infants exhibit polymorphic natal coats (white, grey, black, or patchy combinations) for the first 4–6 months of their lives, in contrast with the black natal coat observed in all other baboon species.

Kinda baboons are currently accepted as morphologically, genetically, and behaviorally distinct enough to be considered a full species under the phylogenetic species concept, however, until recently they were generally classified as a sub-species of the yellow baboon (*Papio cynocephalus kindae*). Despite early recognition that Kinda baboons expressed a distinct morphotype (e.g. Lönnberg, 1919; Hill, 1970; Szalay and Delson, 1979; Dechow, 1983;

Jolly, 1993), namely their small size, they were generally not considered different enough from yellow baboons given the observed morphocline in cranial size across the Kinda/yellow baboon distribution in northeastern Zambia (Freedman, 1963; Grubb et al., 2003). However, outside of this cline, the Kinda baboon morphotype is stable throughout its range (Burrell, 2009). Despite differences in species concept philosophy among researchers, the Kinda baboon's distinctive morphotype led to its consideration as a unique allotaxa by some early on (Szalay and Delson, 1979; Jolly, 1993), with more inclusion as one six major baboon types in the literature in the early 2000s (e.g. Delson et al., 2000; Frost et al., 2003), and consistent acceptance stemming from molecular phylogenetics studies by 2011 (e.g. Zinner et al., 2009, 2011; Keller et al., 2010; Jolly et al., 2011). Prior to this time, morphological and genetic specimens attributed to Kinda baboons were often characterized in the literature subsumed under yellow baboons (e.g. Hayes et al., 1990; Plavcan and van Schaik, 1992), such that assessing the locality of the source data is necessary for a historical understanding of Kinda and yellow baboons.

The type specimen description for Kinda baboons was based on three adult females and several immatures from the town of Kinda in Democratic Republic of Congo (Lönnberg, 1919). Even in this first description, Lönnberg notes their small size and short snout relative to other baboons, and states that “the Kinda Baboon appears to differ very much from other yellow baboons in proportion and color” (Lönnberg, 1919). By the 1960s, more morphological studies



Figure 1. The Kinda baboon phenotype. Top L: adult female being inspected by an adult male (note low sexual dimorphism in body size, and very small swelling size). Top R: adult female (with sperm plug) with adult male (note large male testis volume). Bottom L: adult female and infant with white natal coat. Bottom C: adult male. Bottom R: adult male yawning (note small canine size). Top R image taken by AHW, all other images taken by MP.

emerged on *Zambian Kinda baboons* (considered then a yellow baboon), noting their smaller cranio-dental size compared to other yellow baboons and chacma baboons (Freedman, 1963; Jolly, 1965). Early studies also noted cranial similarities to fossil baboon *Papio angusticeps* from South Africa (Simons et al., 1978; Delson, 1984, 1988; McKee, 1993; Williams et al., 2012; Gilbert, 2013; Gilbert et al., 2015, 2018). More recent morphological studies also confirm the diminutive cranial size and shape of *Kinda baboons* relative to other baboons (Frost et al., 2003; Leigh, 2006; Dunn et al., 2013; Singleton et al., 2017). Across all baboons, cranial shape co-varies with cranial size, and largely reflects species' biogeography (Frost et al., 2003; Dunn et al., 2013). *Kinda baboons* are outliers in cranial size, however, their size-controlled cranial shape simply reflects allometric scaling (Dunn et al., 2013; Singleton et al., 2017). *Kinda baboons* share a size-independent cranial shape with chacma and yellow baboons ('southern clade'), characterized by a narrower crania and more inferiorly flexed rostra (Frost et al., 2003; Dunn et al., 2013). Notably, adult *Kinda baboon* cranial size and shape are similar to subadults of other baboon species, and diverge from the shared *Papio* ontogenetic trajectory with accelerated shape changes occurring at smaller sizes in development (Leigh, 2006). This results in adult sexual dimorphism in cranial size and shape that is significantly lower than other baboon species (Singleton et al., 2017). Additionally, size-controlled facial shape is slightly masculinized in *Kinda* compared to other baboon species, especially in females (Singleton et al., 2017).

In line with their more moderate facial prognathism, *Kinda baboon* canines are also smaller in overall size and dimorphism. Although not the subject of the paper, Washburn and Ciochon (1974) report the small canine size of *Kinda* males compared to chacma and olive baboons. Basal canine area is significantly lower in wild-trapped *Kinda baboons* compared to all other species, driven by lower-than-predicted canine size in males (Table 1; Jolly et al., in review). However, canine height dimorphism, as measured from museum samples, is not smaller than predicted for their body size (Singleton et al., 2017), suggesting male canines are long but thin. Body size shows a similar pattern to cranio-dental

morphology, with *Kinda baboons* as the smallest of all baboon taxa. The earliest reported body mass (females: 9.8 kg, males: 16 kg) came from a small sample of young adults (Compère, 1971), with later body mass estimates from cranio-dental measurements estimated as 10.0 kg for females and 14.1 kg for males (Dechow, 1983). A recent study of a larger sample of wild-trapped *Kinda baboons* reports 10.3 kg for females and 16.0 kg for males (Table 1; Rogers et al., 2019; Jolly et al., in review). This body mass reflects a significantly smaller degree of sexual dimorphism compared to the other five baboon species (Table 1, Jolly et al., in review). Finally, *Kinda baboon* males exhibit larger relative testis size than other baboons, even when controlling for scaled allometry in body size (Table 1, Jolly et al., in review).

Genetics, physiology, and behavior *Kinda baboons* were included in molecular phylogenetics analyses of *Papio* beginning in 2009 (Burrell, 2009; Zinner et al., 2009). Phylogenies reconstructed from mitochondrial DNA show that *Kinda baboons* form a well-supported monophyletic clade, diverging from the rest of the 'southern' baboon clade (e.g. southern yellows, *Kindas*, chacmas) roughly ~1.4 mya (Burrell, 2009; Zinner et al., 2009, 2011, 2013; Keller et al., 2010). Phylogenies based on whole genome analysis of *Alu* polymorphisms show the same northern/southern baboon split, however, differ from mtDNA phylogenies on the relationship of *Kinda baboons* relative to yellow and chacma baboons within the southern clade, with either *Kinda baboons* (mtDNA, Zinner et al., 2013) or yellow baboons (*Alu*, Jordan et al., 2018) splitting from the southern clade first. Recent genome-wide analyses of *Papio* differ in whether *Kinda baboons* fall into the northern or southern clade, and suggest that *Kinda baboons* might have evolved as a result of admixture between the two clades (Rogers et al., 2019). Despite historic debate on the species-status of *Kinda baboons*, their morphotype concurs with their mitochondrial haplotype (Burrell, 2009; Zinner et al., 2009, 2011, 2013; Keller et al., 2010), and they have the largest number of species-specific *Alu* elements relative to the other species (Jordan et al., 2018), supporting their distinction as a separate taxon to yellow baboons.

Table 1
Distribution of sexually-selected traits among male and female *Papio*.

Species	Mating System ^a	Degree of Reproductive Synchrony	Sexual Swellings ^a	Copulation Calls	Degree of Dimorphism		Relative Testis Size ^c (mm ³ /kg)	Male Status Signals
					Body mass ^b (male:female)	Canine basal area ^c (male:female)		
<i>P. hamadryas</i>	Multi-level, base of OMUs	Low	Large	In females ^d and males ^e	1.75	2.84	1.34	Loud calls ^g Large cape ^a Red rump ^a
<i>P. papio</i>	Multi-level, base of OMUs	Low	Medium	In females ^d and males ^e	1.71	2.94	0.78	Loud calls ^h Large cape ^a
<i>P. anubis</i>	Polygynandry	Low/intermediate	Large	In females ^d and males of some populations ^e	1.83	2.89	2.16	Loud calls ^h Small cape ^a
<i>P. cynocephalus</i>	Polygynandry	Low/intermediate	Medium-large	In females ^d	1.82	2.75	1.61	Loud calls ⁱ
<i>P. ursinus</i>	Polygynandry	Low	Large	In females ^d and males ^f	1.77	3.14	1.62	Loud calls ^h
<i>P. kindae</i>	Polygynandry ^j	High ^j	Small ^j	In females and males ^j	1.55	1.96	2.28	Loud calls ^k

^a Dixon (2012).

^b Rogers et al. (2019).

^c Jolly et al. (in review).

^d Maestripieri and Roney (2005).

^e This paper (from pers. comm.), see text.

^f Hamilton and Arrowood (1978).

^g Estes (1991).

^h Hammerschmidt and Fischer (2019).

ⁱ Waser (1982).

^j This paper.

^k Chiou (2013).

Molecular research has also provided insight into socio-ecological variables such as a population structure and sex-biased dispersal. Kinda baboon mtDNA variation is higher among groups, whereas their autosomal variation is higher within groups, a typical signature of a social system characterized by female philopatry and male-biased dispersal (Burrell, 2009), as seen in chacma, yellow, and olive baboons. However, *Alu* insertion polymorphisms suggest that Kinda baboons might be characterized by less frequent male dispersal than expected when compared to yellow baboons (Steely et al., 2017).

Preliminary work has also been undertaken on various aspects of Kinda baboon physiology. Both sexes show significantly lower levels of insulin-like growth factor 1 (IGF-I) across development than hamadryas and olive baboons, which tracks their significantly smaller body mass (Drought et al., 2013). Across development, Kinda baboon males show significantly higher concentrations of serum testosterone than hamadryas or olive baboons with trajectories diverging around 8 years: hamadryas and olive baboon testosterone levels off whereas that of Kinda baboons continues to increase in high concentrations across adult life (Drought et al., 2013). Similar results are found when looking at fecal testosterone profiles: Kinda baboons exhibit adult testosterone levels at younger ages that they sustain throughout adulthood, when compared to chacma and yellow baboons (Beehner et al., 2013). Relatedly, Kinda baboon males exhibit high concentrations of serum prolactin that remain high in adulthood, in contrast to olive and hamadryas baboon males who show low concentrations that level off in adulthood or discrete peaks in subadulthood, respectively (Phillips-Conroy et al., 2013). Prolactin may reflect species-specific male social behavior, such that high levels in Kinda baboons are reflective of the uniquely high degree of male-directed grooming behavior (Weyher et al., 2014).

Kinda baboons live in a multimale–multifemale social system, with group sizes often including over 200 members (MP, pers. obs. from multiple localities). Long-term observations support the population genetic evidence for female philopatry and male-biased dispersal (AHW, pers. obs.). The few behavioral studies that have been undertaken suggest a unique suite of behaviors compared to other baboons. Notably, in multiple wild populations (Weyher and Chiou, 2013; Weyher et al., 2014), inter-sexual grooming interactions are characterized by higher proportions of male-driven grooming across all reproductive states (Fig. 2, Weyher et al., 2014). Males more often initiate these grooming bouts, whereas females terminate them (Weyher et al., 2014). Male–female proximity is also more common than female–female proximity

(Weyher and Chiou, 2013), in contrast to what is observed in other multimale–multifemale baboons. Kinda baboons exhibit a vocal repertoire similar to other baboon species including grunts, barks, screams, and loud calls (Chiou, 2013), although male loud calls are notably less frequent than in other baboons (MP, pers. obs.). Despite preliminary reports that female Kinda baboons do not make copulation calls (Chiou, 2013), longer-term observations suggest they do, although they are often not very conspicuous (MP, pers. obs.).

Collectively, the above review suggests an unusual (for a baboon) suite of traits, making the Kinda baboon an intriguing model for studies of socio-ecology, inter-specific variation, and evolution by natural and sexual selection.

2.2. Sexual selection and its implications for sexually-selected traits

Darwin proposed two main mechanisms of sexual selection – intra-sexual selection, based around competition between members of the same sex, and inter-sexual selection, based around mate choice between the sexes (Darwin, 1871; Andersson, 1994). Among vertebrate clades, typically one or the other process has predominated. For example, among large mammals (Class: Mammalia), male–male competition is stronger, whereas clades like birds (Class: Aves) and some classes of fish seem to have evolved under greater inter-sexual selection and processes of female mate choice (Clutton-Brock and McAuliffe, 2009).

Anthropoid primates, however, exhibit an unusual mix of traits related to mutual mate choice, male–male competition, or both (reviewed in Dixson, 2012). These traits are divergent in their presence and degree of expression even among closely-related taxa, suggesting that they are subject to particularly interesting combinations of sexual selection pressures that have produced highly different outcomes (Hunt et al., 2009). Consistent with this, they also exhibit an unusual backdrop for a mammalian group, including: i) the presence of polygynandrous mating systems in which multiple males reproduce; ii) female proceptivity and receptivity outside of fertile phases, extending the time periods over which males compete over access to females, and increasing female–female competition for males; and iii) vast inter-specific variation in the degree of female estrus synchrony.

Forms of sexual selection mechanisms among the primates include direct competition, i.e. fights among rivals (contest competition), indirect competition, i.e. efficiency in detection of potential mates (scramble competition), ability to sustain periods of competition and sexual activity (endurance rivalry) (Andersson,

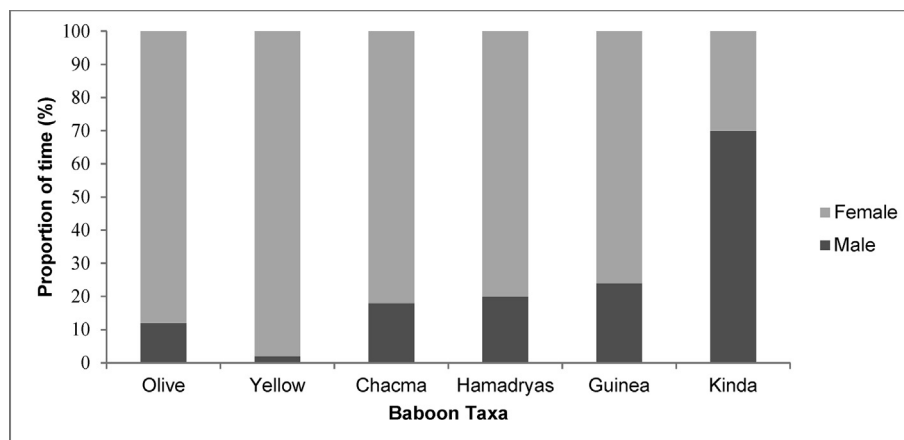


Figure 2. Proportion of time each sex spends grooming the other during intersexual grooming interactions across baboon taxa. Modified from Weyher et al. (2014) by addition of Guinea baboon data from Goffe et al. (2016).

1994), competition over the fertilizing of eggs (sperm competition) (Parker, 1970), and direct, indirect, and cryptic mate choice, i.e. the ability to select the best potential mating partner or ejaculate (Eberhard, 1996; Wiley and Poston, 1996). Although we have some understanding of how different forms of sexual selection mechanisms shape trait evolution, most work has focused on one form, mechanism, or trait at a time, and comparatively less is known about how mechanisms interact to create the overall direction in which sexual selection drives evolution (Wong and Candolin, 2005; Hunt et al., 2009). However, several mechanisms can act on several traits at the same time in reinforcing or opposing directions. As such, an understanding of the dynamic of all selective mechanisms is needed to understand the evolution of any given trait (Hunt et al., 2009). One excellent model system for evaluating such processes is the papionin primates.

2.3. Papionin sexual selection

The papionin tribe is an excellent group in which to examine the complex dynamics of sexual selection and the interaction of its various mechanisms because closely-related species show particularly marked variation in sexually-selected traits (reviewed in Dixon, 2012). These species show varying sexual dimorphism in body weight and canine size, ranging from males being three times the mass of females (e.g. mandrills, *Mandrillus sphinx*: Setchell et al., 2001; Leigh et al., 2008) to low/moderate sexual size dimorphism where males are one-third larger than females (e.g. rhesus macaques, *Macaca mulatta*: Plavcan, 2004). Males of some species also exhibit conspicuous color ornaments, a type of sexually-selected trait otherwise virtually absent among mammals (Bradley and Mundy, 2008; Pradhan and van Schaik, 2009). At the behavioral level, females are characterized by a loss of estrus and extended receptive behaviors (Hrdy and Whitten, 1987). Even more strikingly, conspicuous visual and acoustic sexual signals are more common among females than males. While some work has aimed to explain the inter-specific variation of such traits in papionin primates, the focus has been only on a few specific traits (e.g. sexual swellings (Nunn, 1999; van Schaik et al., 1999; Zinner et al., 2004); copulation calls (van Schaik et al., 1999; Maestripieri and Roney, 2005; Pradhan et al., 2006); relative testis weight (Harcourt et al., 1981, 1995); sexual dimorphism (Clutton-Brock et al., 1977; Plavcan, 2011)). However, among the tribe, there remain key questions about the overall causes of inter-specific variability in the number, development, and co-occurrence of male and female sexually-selected traits despite living in similar social and mating systems.

At first glance, the variation in sexually-selected traits among papionin primates is surprising because it occurs even between closely-related species with the same multimale-multifemale social organization, the ancestral state in this clade (Shultz et al., 2011). Such a social organization, in which several males live year-round with unrelated females and have the opportunity to reproduce, is rare among large mammals. This social organization is typically expected to lead to a similar mating system, polygynandry or promiscuity, with males of these species forming dominance hierarchies presumed to provide priority-of-access to fertile females (Altmann, 1962). However, there is great inter-specific variation in the extent to which reproductive success is correlated to dominance rank among papionins. While in some species one male monopolizes reproduction almost perfectly, in others, reproduction appears to be close to a random distribution (Dewsbury, 1982; Ellis, 1995; van Noordwijk and van Schaik, 2004; Ostner et al., 2008; Rodríguez-Llanes et al., 2009; Gogarten and Koenig, 2013).

Comparative studies have revealed that the main factor influencing within-group male reproductive skew in species forming

multimale-multifemale groups is the degree of synchrony of female mating activity. While there is some debate in the literature about the relative strength of the primary factors influencing the degree of synchrony, most comparative studies agree that the key variables relate to the degree of breeding seasonality (see van Schaik and Brockman, 2005 and Brockman and van Schaik, 2005 for consideration of ways of defining seasonality and seasonal breeding), and the number of females in the group (Paul, 1997, 2004; Kutsukake and Nunn, 2006; Ostner et al., 2008; Gogarten and Koenig, 2013). Increasing the number of females leads to an increased likelihood of synchrony, and reproductive seasonality further enhances this effect. In turn, the effect of mating synchrony on male monopolization of female mating has been explained by the Priority-of-Access (PoA) model (Altmann, 1962). This model posits that since males are able to monopolize only one female at a time, only when more than one female is sexually active do males other than the highest-ranking male of the group have access to females. Thus, the higher the number of sexually active females, the lower the rank of the males able to have mating access. However, empirical work among papionins has revealed substantial deviation from predictions of the PoA model (yellow baboons, *Papio cynocephalus* (Alberts et al., 2003, 2006); chacma baboons, *Papio ursinus* (Weingrill et al., 2003); mandrill, *M. sphinx* (Setchell et al., 2005)), especially in more seasonally breeding species (rhesus macaques, *M. mulatta* (Chapais, 1983; Dubuc et al., 2011); Barbary macaques, *Macaca sylvanus* (Bissonnette et al., 2011)), with high-ranking males mating or fathering less offspring than predicted. Together with the observed inter-specific variation in sexually-selected traits, this suggests that papionin primates forming multimale-multifemale groups have evolved under significantly different combinations of sexual selection mechanisms.

The degree of female mating synchrony may not only influence priority-of-access to mates, but ultimately select for the co-evolution of different forms of male–male competition and female mate choice. When a single male can monopolize female reproduction due to low female mating synchrony (e.g. small group sizes and/or aseasonal breeding), males undergo contest competition over females and fight for dominance rank (van Noordwijk and van Schaik, 2004), resulting in dominance rank that reflects competitive ability and stronger selection for morphological characteristics that assist in direct male–male competition (e.g. increased sexual dimorphism, weaponry) (Dubuc et al., 2011, 2013). Females might be selected to increase their monopolizability by such males with highly accurate sexual signals of ovulation. This ultimately may function as a type of indirect female choice to ensure paternity to the most competitive male (Higham et al., 2012; Higham and Dubuc, 2015). The co-occurrence of stronger direct male–male competition with indirect female mate choice in favor of the alpha male can result in high reproductive skew. When males cannot monopolize reproduction due to high female mating synchrony (e.g. large group sizes and/or seasonal breeding), they may queue instead of contest for dominance (van Noordwijk and van Schaik, 2004), resulting in dominance rank that reflects group tenure length rather than competitive ability, and stronger selection for male morphological features to assist in indirect competition (e.g. larger testicles for sperm competition) (Dubuc et al., 2011, 2013). When dominance rank is no longer surrogate for male competitiveness, females in these taxa might be selected to decrease their monopolizability to the alpha male with the evolution of less accurate signals of ovulation (Higham et al., 2012; Higham and Dubuc, 2015). Instead, mate choice may be more direct and related to factors other than male dominance such as indirect (e.g. signals of genetic quality: Charpentier et al., 2010) or direct (e.g. friendships: Smuts, 1985) benefits. The co-occurrence of stronger indirect male–male competition with direct female mate

choice may thus result in low reproductive skew and/or deviations from the PoA model (Dubuc et al., 2011, 2013).

Within the Papionini, the most-commonly studied test clades are *Macaca* and *Papio*. These two test genera represent ≈ 25 and 6 species respectively, which enable analysis within the context of a shared phylogenetic history of: (i) the inter-specific variation in occurrence of male and female sexually-selected traits, (ii) the overall diversity in form and function of sexually-selected traits in this clade, and (iii) the complex association and co-occurrence of several traits and signals in some species. While *Macaca* has received the most attention in this regard, new developments offer new promise for *Papio* as a model system.

2.4. Baboons as a model system

Papio is an excellent genus for testing ideas about the forms and mechanisms of sexual selection, and the underlying causes and consequences of variation in mating systems. A highly diverse and adaptable genus, they are found across a broad range of sub-Saharan Africa, occupying all areas and habitats aside from the closed canopy rainforests of the Congo basin. Baboon species are among the best-known of all primate species and a great deal is known about their socio-ecology. New research sites established since 2000 have expanded the taxonomic and geographic range in which baboon behavioral studies are being undertaken, increasing the breadth of data that are available across taxa, including many studies of sexually-selected traits.

Baboons exhibit great diversity in both social and mating systems, with Guinea and hamadryas baboons exhibiting multi-level societies which feature one-male units (OMUs) as the base component, whereas olive, yellow, chacma, and Kinda baboons are thought to exhibit multimale-multifemale social systems with true polygynandrous mating systems (Table 1; Henzi and Barrett, 2003; Barrett and Henzi, 2008). However, even within the same mating system, these baboon species exhibit great variation in the degree of sexual dimorphism in body and canine size, and relative testis size (Table 1), reflecting variation in the strength of direct versus indirect male–male competition, and in turn, direct versus indirect female mate choice.

Concurrently, there is marked inter-specific variation within the genus in the presence and degree of expression of other sexually-selected traits (Table 1; reviewed in Dixon, 2012). For example, adult males of both Guinea and hamadryas baboons exhibit large fur capes, which are moderately present in olive baboons, and absent in yellow, chacma, and Kinda baboons. Sexual swellings vary from extremely large in olive baboons, covering the whole anogenital region and the paracallosal areas, to small genital swellings in Kinda baboons. Copulation calls are present in females in all species (reviewed in Maestripieri and Roney, 2005; Dixon, 2012), although the percentage of copulations that occur with a call varies among taxa (Swedell and Saunders, 2006). Copulation calls in males have been observed in chacma (Saayman, 1970; Hamilton and Arrowood, 1978; A Baniel, pers. comm.), hamadryas (L Swedell, pers. comm.), Guinea (K Hammerschmidt, pers. comm.), and some populations of olive baboons (e.g. Gombe: J Walz, pers. comm.; Uaso Ngiro: J Gunson, pers. comm.), but not in other populations of olive (Gashaka: Inglis, 2013; Laikipia: A Pritchard, pers. comm.) or yellow baboons (C Fitzpatrick, pers. comm.). These individually-distinctive ‘rhythmical low-frequency vocalizations’ (Hamilton and Arrowood, 1978) are acoustically similar to grunts and ‘echs’ made in other contexts (Saayman, 1970). While they have been reported to occur with every adult male copulation in chacma (Hamilton and Arrowood, 1978), anecdotal reports suggest their presence is variable across populations and species. While female copulation calls have been the subject of multiple studies (chacma:

Saayman, 1970; Crockford et al., 2007; yellow: Semple, 2001; Semple et al., 2002; olive: Rigai et al., 2013; Walz, 2014; Guinea: Boese, 1975; Maestripieri et al., 2005; hamadryas: Swedell and Saunders, 2006), systematic analysis of male copulation calls has yet to be undertaken.

New developments offer great prospects for baboons as a model system for studying variation in sexually-selected traits. Firstly, the baboon genome consortium has published a well-annotated reference genome for one *Papio anubis* individual (Panu_3.0; GenBank accession GCA_000264685.2), and a further 15 lower-quality genomes from individuals of all 6 species, offering unprecedented genomic information across the whole genus (Rogers et al., 2019). The recent establishment of long-term field sites for the study of Guinea and Kinda baboons offers the potential for great new insights and enhances our capacity to understand how variation in underlying socio-ecology affects the evolution of sexually-selected traits. Such developments provide great promise for new studies of genotypic and phenotypic variation. Baboons also have the excellent advantage of being a group in which such traits have been generally well-studied for the other 4 of the 6 species. This includes the relationship between signals related to ovarian cycling and mating, such as sexual swellings and copulation calls, particularly true for those baboons with polygynandrous mating systems (e.g. yellow: Gesquiere et al., 2007; olive: Higham et al., 2008a; b; 2009; chacma: Gillmann and Gilbert, 1946, Saayman, 1970).

Baboon species are thought to generally conform to a pattern in which reproductive asynchrony creates female monopolizability, whereby males contest over dominance rank gaining priority of access to female reproduction (Altmann, 1962; van Noordwijk and van Schaik, 2004). This creates a dynamic of strong male–male direct competition, which precludes strong direct mate choice by females, and instead selects for forms of indirect mate choice in females. Consistent with this, females express a variety of sexual signals including exaggerated sexual swellings, behavioral signals, and copulation calls that advertise intra- and inter-cycle fertility relatively accurately (reviewed in Dixon, 2012). These signals are hypothesized to enable females to select for high quality males indirectly, by inciting male–male competition. Despite this wealth of information available on baboons, comparably little is known about one species: the Kinda baboon.

2.5. Kinda baboons: a new model for primate sexual selection

Kinda baboons represent an ideal case study of our comparative understanding of how divergent sexually-selected traits can occur in closely related species for several reasons. Firstly, they come from a well-described and well-studied genus, providing a great deal of comparative data and evolutionary context. Secondly, they have been little-studied. This is significant because the best tests of our understanding of comparative variation in evolutionary selective pressures, and how these lead to variation in phenotypes, are species that have themselves been little-studied, but for which we are well-placed to make specific predictions. Finally, Kinda baboons, particularly males, exhibit a marked departure from other species within the genus in a number of key morphological, physiological, and behavioral characteristics relevant to sexual selection (Table 1, Fig. 1).

In particular, they live in large group sizes up to 200 members, which increases the potential for spatially-based overlap in female reproduction. Compared to other baboon species, they are characterized by smaller degrees of sexual dimorphism in body and canine size, driven by the smaller-than-predicted size of males (Jolly et al., in review). Interestingly, while their canine basal area dimorphism is significantly smaller (Jolly et al., in review), their canine height dimorphism is not smaller than other baboon

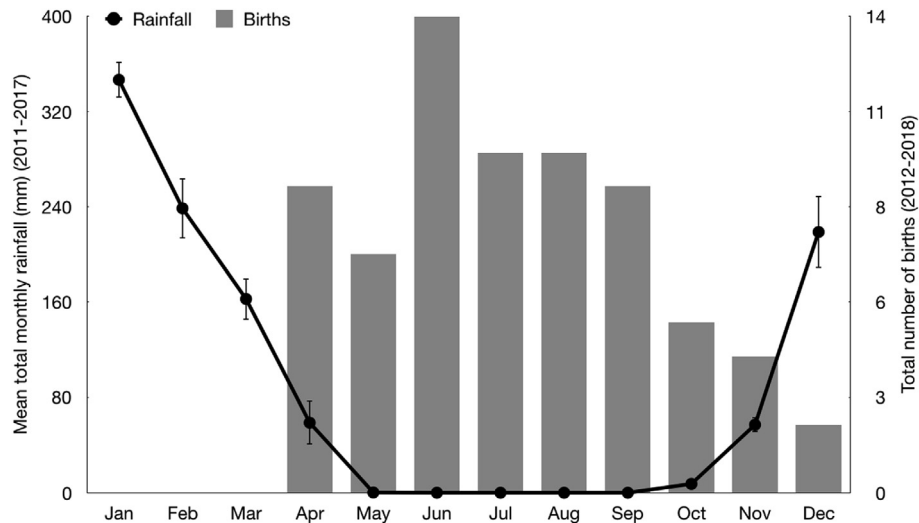


Figure 3. Total number of births per month (2012–2018) and mean total monthly rainfall \pm SEM (2011–2017) at the Kasanka Baboon Project.

species (Singleton et al., 2017), suggesting that while male canines might be long, they are much thinner. This might preclude them from use in direct physical combat and possibly function more behaviorally as a threat display. Males are also characterized by larger relative testis size (Jolly et al., in review), suggesting increased importance of sperm competition relative to contest competition. Sustained levels of testosterone throughout adulthood suggest males might reproduce throughout adulthood beyond 'prime age' (Beehner et al., 2013; Drought et al., 2013). Relatedly, *Alu* insertion polymorphisms suggest males might disperse among groups less often compared to other baboons (Steely et al., 2017). Finally, males appear to invest in social relationships with females much more than other baboon species, across all reproductive stages (Weyher and Chiou, 2013; Weyher et al., 2014). These traits increase the amount of intra-genus variation for comparison, and suggests that Kinda baboons are likely to have experienced selective pressures that are relatively unusual when compared to their sister taxa.

Here, we evaluate the hypothesis that Kinda baboons have evolved a mating system characterized by weaker direct and stronger indirect male–male competition relative to other baboons. This distinctive type and strength of male–male competition might have evolved due to increased female reproductive synchrony in space and time. Combined with observations of large group sizes (space), we predict that females will exhibit higher degrees of reproductive synchrony (time) in regards to: 1) birth seasonality; and 2) sexual swelling expression. Additionally, consistent with the unique morphology, physiology, genetics, and behavior observed in males, we predict that; 3) males do not compete directly over dominance rank, and instead acquire rank through succession over time.

3. Methods

We test our predictions using the habituated study population of the Kasanka Baboon Project (KBP) in Kasanka National Park (KNP). KNP is located in the central province of Zambia and is bounded by the coordinates S12.40° and 12.66° latitude and E30.05° and E30.38° longitude (Willems, 2014). KNP is 450 km² in area and is located 30 km east from the southwestern border of the Democratic Republic of Congo (The World Fact Book, 2014). The park lies within the belt of miombo-mopane woodland that

stretches from Mozambique to Angola (Campbell, 1996), with an altitude that varies from 1160 m to 1286 m above sea level (Willems, 2014) and an annual rainfall of ~1100 mm (KNP).

One habituated group of baboons ($N_{\min} = 54$, $N_{\max} = 83$) has been studied by AHW and her research assistants continuously since 2011, with the baboons followed roughly 20 days per month. Each follow day, a group census was undertaken, allowing for daily monitoring of births, deaths, immigrations, and emigrations. Accurate birth records are available beginning in 2012 from 27 adult females. The seasonality of births was quantified by summing the total number of births for each month between 2012 and 2018. Additionally, rainfall (mm) was recorded daily at 1900h from a rain gauge at the research camp. The monthly sum of rainfall was averaged across years between 2011 and 2017 to track environmental seasonality.

To compare birth seasonality to possible mating seasonality, and to monitor synchrony in reproductive receptivity, we looked at the distribution of sexual swellings across one year. Nine parous adult females were followed daily between April 2017 and April 2018. (Nulliparous females, which often show unusual patterns of swelling and reproductive cycling, were excluded.) The presence of female sexual swellings was recorded each day, noting whether the swelling was inflating or deflating. The total duration of the swelling period was determined as all days that a visible swelling was present, regardless of inflation or deflation.

To determine whether males had top- or bottom-entry immigration, we assessed dominance hierarchy ranks and changes over time. *Ad libitum* data were collected on clear displacements ($N = 149$ displacements) between all non-natal adult males present in the group between 2011 and 2018 ($N = 13$ males). Note that males who were adults when the group was originally habituated were assumed to be non-natal. A displacement was defined as one individual A (loser) moving out of the way of another individual B (winner). We calculated the dominance hierarchy with EloRatings (Neumann et al., 2011) to look at how dominance rank changed over time among males, particularly for those which we have definite immigration dates. In total, 6 males immigrated to the group during the study period, but one male, who was poached relatively soon after arrival, is excluded. We calculated alpha male tenure length as the number of months for which the male(s) maintained the highest EloRating compared to other males in the population at the same time.

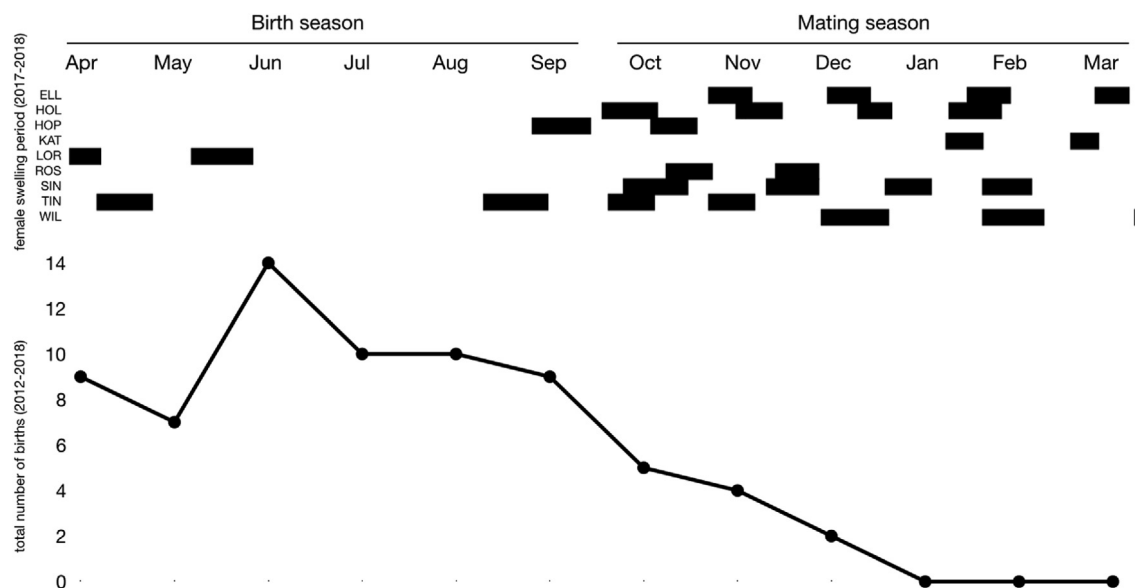


Figure 4. Distribution of sexual swelling expression ($n = 9$ females) from April 2017–March 2018 (top), and monthly distribution of total births ($n = 27$ females) from 2012 to 2018 (bottom), suggesting a high degree of reproductive seasonality in this population.

4. Results

Mean annual rainfall between 2011 and 2017 was 1089 mm, with mean monthly rainfall ranging from 0 mm (June–September) to 346.7 mm (January) (Fig. 3). 70 births from 27 adult females were recorded between 2012 and 2018, ranging from 0 to 14 births per month (Figs. 3, 4). 84% ($n = 59$) of births occurred between April and September and 16% of births ($n = 11$) between October and March (Figs. 3, 4). Rainfall and births were inversely correlated (Spearman's $\rho = -0.92$, $p < 0.001$).

Over the course of 12 months between April 2017 and 2018, nine females expressed 27 cycles representing 10 conceptions (based on 9 resulting births, and one presumed miscarriage, assessed by the absence of swelling and the presence of the pregnancy sign, followed by subsequent swelling resumption after 3 months) (Fig. 4). 19% ($n = 5$ cycles) occurred between April 2017 and September 2017, and 81% ($n = 22$ cycles) occurred between October 2017 and March 2018, showing an opposite pattern to birth timing (Fig. 4).

Our dominance data show that males in our study group exhibited bottom-entry upon immigration. No males entered in high-ranking positions, and all males entered the group in low ranks (Table 2). There was little physical aggression among males during these immigrations and in no instance was male-perpetrated infanticide suspected to be associated with a new non-natal male. Two of the males that immigrated into the group during this period have remained in the group for more than four years, and one of them achieved the rank of alpha male in September 2015, and is still alpha at the end of 2018 (Table 2). This coincides with our observation that alpha male tenure lengths tend to be long, averaging over two years during the study period.

5. Discussion

Our data show that Kinda baboons do indeed exhibit phenotypes that are consistent with the suggestion that they may have evolved under weaker direct, and stronger indirect male–male competition relative to other baboons. First, our data on the exhibition of sexual swellings, and on birth seasonality, indicate a strong degree of reproductive seasonality. In particular, long-term

Table 2

Alpha males and immigrant males from 2011 to 2018. All ranks based on Elo-ratings using displacement data, combining data collected by MP with data collected by AHW (Weyher and Kamilar, 2018). Note that no immigrant male has entered in the alpha position, and all have entered low-ranking (so-called “bottom-entry”; van Noordwijk and van Schaik, 2004).

Alpha males	Tenure length (mo.)
MRC	26–36*
MUM	25*
MRW	16
GAF	40
Immigrant males (immigration date)	Rank on entry (current rank)
GAF (August 2013)	5/6 (1/4)
SIM (August 2013)	6/6 (2/4)
KEN (May 2015)	4/4 (3/4)
LEA (November 2016)	4/5 (4/4)
ALF (November 2016)	5/5 (dead)

* These two males shared alpha status for at least some of this time, or at least, our data are insufficient to resolve their dominance status.

data from 2012 to 2018 show a highly seasonal peak in births. When combined with observations of very large group sizes, this indicates a relatively large amount of fertile-phase synchrony among females. With many females fertile at the same time, males are unlikely to be able to monopolize multiple female fertile phases via direct competition, and instead may copulate with multiple fertile females and compete indirectly at the level of sperm. This interpretation is strongly consistent with aspects of their morphology, such as relatively low body and canine size dimorphism, and large relative testis volume (Table 1).

In addition, our long-term data show that male Kinda baboons show non-aggressive immigrations into the bottom of dominance hierarchies, in contrast to the top-entry aggressive arrivals of males in other baboon species. Our data show that since 2011, six adult non-natal males immigrated into the group. Interestingly, none of them entered with alpha status. These observations are consistent with a “bottom-entry” queuing system for males, such as that seen in the mulatta macaque clade (van Noordwijk and van Schaik, 2004). Bottom-entry and dominance queuing are again consistent

with an interpretation that Kinda baboons may be in a selective environment of reduced direct, and increased indirect, male–male competition. In addition, the high proportion of male-driven grooming in inter-sexual relationships (Weyher et al., 2014) (Fig. 2) suggests that males might be offering direct benefits to females and be subject to greater direct female mate choice. When combined, the available evidence suggests that Kinda baboons represent an ideal species to test our comparative understanding of evolutionary models of reproduction and sexual signaling, as they may be under different selective dynamics than other baboons, which can be investigated within the context of a generally well-studied genus.

5.1. Further tests and predictions

The strong breeding seasonality and large group sizes of Kinda baboons, combined with their relatively small body and canine size dimorphism, and large relative testis volume, is strongly consistent with the hypothesis that relative to other baboons, they have evolved under mechanisms of weaker direct, and stronger indirect male–male competition, in addition to stronger mechanisms of direct female mate choice. This enables us, in turn, to make a number of predictions about their other sexually-selected traits.

Reduced direct and increased indirect male–male competition relative to other baboons may lead to a shallower degree of reproductive skew based on expectations from the PoA model (Altmann, 1962; Dubuc et al., 2011). Reduced direct male–male competition over dominance combined with a reduction in sexual size dimorphism may also lead to deviations from the PoA model, if females are able to and actively solicit non-dominant males as mating partners (Dubuc et al., 2011). Specifically, we predict that Kinda baboon male reproductive skew will be lower than other baboon taxa, such that male dominance rank will weakly or not influence i) mating success; and/or ii) genetic paternity success. We also predict that iii) alpha male paternity concentration (β) will be low-medium (≤ 0.5) compared to other baboon species (usually $\beta > 0.5$; van Noordwijk and van Schaik, 2004), and that Kinda baboons will differ from other baboons in that iv) mating success may not reflect genetic paternity success, similar to the pattern observed in rhesus macaques (Dubuc et al., 2011), another species with reduced direct and increased indirect competition relative to other papionins.

In the absence of strong competition over male dominance, Kinda baboon females may not benefit from reliably signaling ovulation to males, which would make them more monopolizable to high-ranking but not necessarily high-quality males. Females have small, less exaggerated sexual swellings (Fig. 1), copulation calls of lower amplitude, and less frequent proceptive behaviors compared to other baboon species (MP, pers. obs.). We predict that female sexual signals will indicate the timing of ovulation less accurately in Kinda baboons than in other baboon species, thus functioning as a female reproductive strategy to reduce their own monopolization potential. Specifically, we predict that female i) sexual swelling morphology (e.g. size, shape, and color); ii) copulation calls; and iii) proceptive behavior will not indicate ovulation or will do so less precisely when compared to other baboon species. This raises the question: if female sexual signals are less accurate indicators of the fertile phase and ovulation as predicted, are males informed about this timing, such that they bias mating effort? In olive baboons, males use changes in sexual swelling size to determine their consortship but not copulation effort, but consorting males still time their copulations more precisely to the fertile phase, suggesting they are informed about its timing (Higham et al., 2009). In contrast, in Assamese macaques, whose sexual swellings are not accurate indicators of fertility (Fürtbauer et al., 2010), males

still maintain consortships with females, but neither consortship nor copulations are timed to the fertile phase, suggesting that males are not informed about its timing (Fürtbauer et al., 2011). We predict that males time their mating effort to the female fertile-phase less accurately than in other baboon taxa.

5.2. The Kinda baboon as a hominization model

The mating system of modern humans (*Homo sapiens sapiens*) greatly differs from that of other primate species. While we do live in large multimale-multifemale groups like most anthropoids, human groups contain sub-units consisting of small long-term family units (Chapais, 2008, 2011). At first glance, this system resembles the multilevel societies of hamadryas and Guinea baboons and geladas (*Theropithecus gelada*) (Jolly, 1970; Swedell and Plummer, 2012). However, the sexual dimorphism in body size is much less pronounced in humans than in these species where males can be as much as twice the size of females (Dixon, 2012), which indicates a reduced level of direct male–male competition, and a concurrent increase in direct female mate choice. Sexual dimorphism is also less pronounced in humans than in chimpanzees, a close relative where direct male–male competition is known to be intense, suggesting that the change in mating system occurred during hominization. When this occurred during hominization, however, is unclear. Sexual dimorphism is generally considered to be very pronounced among australopiths (Brace, 1973; Plavcan, 2012; Gordon, 2013), which are inferred from this to have exhibited a polygynous or polygynandrous mating system. Indeed, the evolution of the hominin lineage is generally characterized by increased climatic fluctuations leading to marked environmental seasonality (Foley, 1993; Potts, 1998a; b). Combined with larger group sizes possibly due to range expansion and extractive foraging (Antón, 2003), either or both of these may have influenced the monopolization potential of male mating opportunities in hominin evolution.

The selective pressures of reduced direct male–male competition and a concurrent increase in direct female mate choice that may have acted during hominization are the very same selective pressures that we here postulate to be operating on Kinda baboons. As an adaptable African savannah species from a genus that has long been proposed as a putative model for australopiths and hominin evolution (Jolly, 2001), the selective dynamic of Kinda baboons may be more similar to that experienced during hominization than the dynamic experienced by any other member of *Papio*. Kinda baboons live in a distinctive ecological niche (Fuchs et al., 2018), characterized by a more seasonal and heterogeneous environment than other baboon species, similar to how early hominins were living in a range of habitats (Behrensmeyer and Reed, 2013). Their reduced sexual dimorphism in body size and increased male investment in female partners (Fig. 2) are indeed traits that are more reminiscent of modern humans. As such, Kinda baboons offer the potential for new insight into how selective pressures can affect polygynous and polygynandrous mating systems such as those perhaps exhibited by early hominins, and begin to select for similar traits, such as reduced body and canine size dimorphism, that emerged during hominization.

6. Conclusion

The species of the genus *Papio* are highly variable in their mating systems (from multi-male multi-female polygynandry, to multi-level societies with one-male units as the base level), and also in the presence and degree of expression of different kinds of sexually-selected traits. This includes marked variation in: the degree of sexual dimorphism in body and canine size, relative testis volume,

the size, shape, and color of sexual swellings, the rate, frequency, and amplitude of copulation calls, the presence of male fur capes, the steepness of dominance hierarchies, and mating behavior. Although not discussed here, they also vary greatly in patterns of dispersal, infanticide, kidnapping and coercion of females by males, and degree of male–male and female–female aggression, female and male mate choice, extent of male–female consortships, and in dominance styles. The Kinda baboon is relatively little-studied compared to the other baboon species (especially compared to the other polygynandrous baboons, olive, chacma, and yellow). As such, studies of the Kinda baboon represent a fascinating case study of our comparative understanding of variation in sexual selection pressures, and the effects that variation in such pressures can have on the evolution of sexually-selected traits. Differences in the Kinda baboon compared to other baboon species is further evidence of the evolutionary lability of such traits. It further highlights the relevance and importance of studies of papionin primates as an exemplary and canonical model clade for understanding processes of sexual selection and communication.

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