The Adaptive Value of Secondary Males in the Polygynous Multi-level Society of Hamadryas Baboons

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ABSTRACT *OBJECTIVES:* One-male social systems are usually characterized by polygyny and reproductive exclusion by a single resident male. Sometimes, however, secondary males join these groups, and this may carry fitness costs and/or benefits to the resident male. In hamadryas baboons (*Papio hamadryas hamadryas*), which live in one-male units (OMUs) with female defense polygyny within a multi-level social system, secondary "follower" males often reside in OMUs. Our aim here is to examine possible benefits of these secondary males to hamadryas resident males.

MATERIALS AND METHODS: Using 6 years of data from 65 OMUs in a band of wild hamadryas baboons in Ethiopia, we compared demographic and reproductive parameters of OMUs with and without secondary "follower" males to assess whether their presence conferred any reproductive benefits to resident "leader" males.

RESULTS: Leaders with followers had tenure lengths almost twice as long, acquired more than twice as many females, retained females longer, and had three times as many infants during their tenure compared to leaders without followers.

DISCUSSION: Hamadryas follower males enabled leaders to retain females for longer periods of time—likely through unit defense, social relationships with OMU members, and/or infant protection. Hamadryas leaders appear to be able to monopolize access to females despite the presence of followers, and as such any enhanced reproduction derived from the presence of followers likely increases the fitness of the leader rather than the follower. Thus the relationship between leaders and followers in hamadryas society appears to be a mutually beneficial one and tolerance of secondary males may be an adaptive reproductive strategy characterizing hamadryas leader males. Am J Phys Anthropol 158:501–513, 2015. © 2015 Wiley Periodicals, Inc.

In most animals, males and females differ in the way they can maximize fitness. Males generally achieve higher reproductive success by mating with as many females as possible, whereas females, constrained by pregnancy and lactation, benefit more from mate selectivity and maternal investment rather than mate quantity (Trivers, 1972; Emlen and Oring, 1977). Consequently, males will try to monopolize as many females as they can defend, which depends on the spatial and temporal distribution of fertile females (Emlen and Oring, 1977; Bissonnette et al., 2011). In many social animals, these efforts manifest themselves as female defense polygyny, in which a single male controls reproductive access to one or more females in a social unit.

One-male social systems can be found in a wide variety of mammals, including equids (Klingel, 1975), red deer (*Cervus elaphus*, Gibson and Guinness, 1980), yellow-bellied marmots (*Marmota flaviventris*, Allaine, 2000), black-tailed prairie dogs (*Cynomys ludovicianus*, Hoogland and Foltz, 1982), Indian fruit bats (*Cynopterus sphinx*, Storz et al., 2001), and grey seals (*Halichoerus grypus*, Worthington Wilmer et al., 1999). They also characterize many primates, including guenons (*Cercopithecus* species, Cords, 2010), snub-nosed monkeys (*Rhinopithecus roxellana*, Zhang et al., 2003), geladas (*Theropithecus gelada*, Dunbar and Dunbar, 1975), proboscis monkeys (*Nasalis larvatus*, Murai et al., 2007), mountain gorillas (*Gorilla gorilla beringei*, Robbins, 1995), and western gorillas (*Gorilla gorilla gorilla*, Parnell, 2002).

These one-male social systems are usually characterized by intense mate competition whereby one resident male aggressively excludes all other males, leading to polygyny and a high degree of reproductive skew among males (Emlen and Oring, 1977; Wade, 1979; Andersson, 1994). When no females are present, however, males may display higher degrees of inter-male tolerance, as exemplified by the presence of all-male groups in many of these systems, both primates (Cords, 1987; Dunbar, 1988; Rowell, 1988; Newton and Dunbar, 1994; Sterck, 2012) and non-primates (e.g., equids: Rubenstein, 1981;

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vicuñas, *Vicugna vicugna*: Vila, 1995; sperm whales, *Physeter macrocephalus*: Lettevall et al., 2002).

In some typically one-male systems, resident males do not attempt or are unable to exclude other males from a group, and secondary males may join for variable amounts of time. This may result in part from the difficulties of defending a group of females over the entire length of a male's tenure, especially if the group is a large one. The number of males in polygynous societies is typically a function of group size (Wade and Shuster, 2004) and, in primates in particular, the number of males is positively related to the number of females (Mitani et al., 1996; Altmann, 2000; Carnes et al., 2011), suggesting that it becomes more difficult for resident males to exclude secondary males as the number of females increases. The number of males and group size may also be related to predation risk such that under high predation risk, single-male groups are found to not be very feasible, whereas the number of males in multimale groups is disproportionately high (Hill and Lee, 1998).

In some taxa, the presence of secondary males can be fairly directly predicted by the number of females in the group. Andelman (1986) calculated threshold numbers of females for single-male and multi-male groups of cercopithecines, and showed that both single-male and multimale groups occurred at intermediate group sizes of between 6 and 10 females, with one-male groups being the norm in groups of 6 or fewer females and multiple males in groups of 10 or more. Altmann (2000), for example, showed that in (savanna) baboons, females tend to form large groups, and this leads to multi-male social systems. In the multi-level social system of geladas in which "one-male units" (OMUs) coalesce to form larger groups, multiple males most commonly occur in OMUs containing seven to eight females, and bachelor male strategies depend on female group size such that at larger sizes males attempt complete takeovers of entire units of females whereas at small sizes males attempt to join rather than take over the unit (Dunbar 1984). In part due to this dependence of male number on female number and the underlying variable ecological factors, we see the co-occurrence of both types of groups in several primate taxa, including hanuman langurs (*Semnopithecus entellus*: Newton, 1988), black and white colobus monkeys (*Colobus guereza*: Dunbar and Dunbar, 1976), mountain gorillas (Robbins, 1995), Phayre's leaf monkeys (*Trachypithecus phayrei*: Koenig and Borries, 2012), geladas (Snyder-Mackler et al., 2012), and hamadryas baboons (*Papio hamadryas hamadryas*: Swedell, 2006).

Secondary males in social groups may carry both costs and benefits for resident males. On the one hand, they pose obvious risks to a resident male as they can oust him or rise in rank, and they may also engage in sexual behavior with females. On the other hand, they may be beneficial as they may help in group defense (Pope, 1990; Cowlishaw, 1995) or resource defense (Pope, 2000), as evidenced by a direct link between the presence of secondary males and a lower probability of group takeover and longer resident male tenure lengths in red-fronted lemurs (*Eulemur fulvus rufus*: Port et al., 2010) and geladas (Snyder-Mackler et al., 2012). Moreover, in many multi-male groups the resident male, i.e., the male who was there first and occupies the highest dominance rank, has been found to sire the majority of offspring, leaving only a small proportion of the group's paternity for secondary males (e.g., Launhardt et al., 2001; Bradley et al., 2005). In such cases, the resident male ensures maximum paternity while simultaneously gaining benefits from secondary males by conceding just enough reproduction to these males to make it beneficial for them to stay. From the secondary male's perspective, while it may not always be in a bachelor male's best interest to join a one-male group as a secondary male, social options are often limited and it may be prohibitively difficult to form his own one-male group, thus a bachelor male may be making the best of a bad situation by joining another male's group as a secondary male.

The social system of hamadryas baboons provides an especially interesting model for this interplay between resident males and secondary males, as the basal unit in hamadryas society is an apparently exclusive reproductive unit that often contains secondary males who are typically assumed to be non-reproductive. The hamadryas system includes several nested layers, the smallest of which is the one-male unit or OMU, a spatially and socially cohesive grouping. The OMU consists of a resident "leader" male, one or more females and their offspring, and sometimes one or more secondary "follower" males that may in some cases be younger relatives of the leader (Kummer, 1968; Abegglen, 1984; Swedell, 2006). Cohesion of OMUs is based on long-term sociosexual bonds between the leader male and each female, and social interaction is generally limited to within the OMU (Kummer, 1968; Swedell, 2006). Females are transferred among OMUs by leader males (Swedell et al., 2011), who aggressively take over females from other males and condition females to change their allegiance from one male to another (Kummer, 1968; Swedell and Schreier, 2009). Outside of OMUs are bachelor "solitary males" that associate loosely with one another but are not attached to any particular OMU.

Unlike other primates with multi-level social systems, the bachelor "solitary males" in hamadryas society do not form all-male groups, but instead associate loosely with several OMUs into a layer of social organization known as a *clan*, which may be an outcome of kin relationships among solitary, follower, and leader males (Abegglen, 1984; Schreier and Swedell, 2009; Städele et al., 2015a). Two or more clans that remain together in permanent association form a band, the ecologically most equivalent unit to the troops formed by other baboons; and multiple bands may temporarily aggregate together at sleeping sites to form a troop. Thus, males within a hamadryas band (Hapke et al., 2001; Hammond et al., 2006), and particularly within a clan (Abegglen, 1984; Städele et al., 2015a), are typically close kin due to male philopatry.

The life cycle of post-adolescent hamadryas males is quite dynamic. Sub-adult males can become leaders right away, or, if they are unable to acquire females, become solitary or followers (Pines et al., 2011). Both solitary and follower males may acquire females over time and become leaders of OMUs. Conversely, leaders may be deposed and lose all of their females to become solitary or follower for the rest of their lives or, more rarely, they may acquire females and become leaders again. The general pattern is that males accumulate females into their OMUs one at a time. Thus, every OMU begins with a single female and the leader gradually takes over additional females from other males using a variety of behavioral strategies until he reaches a competitive peak, at which point he begins losing females and, upon loss of all females, returns to follower or solitary status

(Pines et al., 2011, 2015). Follower males may be part of these OMUs on and off, and leaders may gain and lose followers over time. Thus a hamadryas male can be solitary, leader, and follower at different stages of his life cycle, and the social organization of an OMU can change between one-male and multi-male several times as follower males join and leave OMUs.

For a species in which males are otherwise highly aggressive and intolerant of interactions of their females with other males, hamadryas leaders are generally not aggressive towards their followers and are exceptionally tolerant of social (though not sexual) interactions between their followers and females (Kummer, 1968; Abegglen, 1984; Swedell, 2006). Kin selection is a likely explanatory factor underlying this tolerance, as hamadryas followers and leaders are probably closely related due to male philopatry. Followers do not appear to pose a reproductive threat to leaders, even though they may take over females at a future time (as per Pines et al., 2011), as no more than 4-5% of copulations by OMU females involve non-leader males (Nitch et al., 2011; Swedell, unpublished data).

The tolerance shown by leader males towards followers may stem from the fact that followers provide tangible fitness benefits to leaders. Follower males often interact with infants in their OMUs and may contribute to infant survival via caretaking and protective behaviors, which would supplement the limited caretaking provided by the leader male (Kummer, 1968; Swedell, 2006). Infanticide following takeovers is a pervasive threat for primate females (Hrdy, 1979; van Schaik and Kappeler, 1997), including hamadryas baboons (Swedell et al., 2014). It is less common in hamadryas, however, compared to other baboons (Palombit, 2003; Cheney et al., 2004; Lemasson et al., 2008; Henzi et al., 2010), and this may be a result of the protection that hamadryas females and their infants receive from both leader and follower males (Kummer, 1968; Swedell and Saunders, 2006). In geladas, which experience high infant mortality after takeovers (Beehner and Bergman, 2008), the presence of follower males has been associated with a lower probability of takeovers (Dunbar 1984) through active defense of units (Snyder-Mackler et al., 2012). Followers in gelada units thus allow leader males to enjoy longer tenures and higher birth rates (Dunbar, 1984; Synder-Mackler et al., 2012), and this may be the case for hamadryas as well. Additionally, followers, by developing and maintaining social relationships with OMU females, may encourage females to remain longer in that unit and therefore help prolong female tenures.

Here we examine the benefits that these secondary "follower" males may provide to resident "leader" males within the one-male polygynous units of the multi-level social system of hamadryas baboons. We compare OMUs with and without followers and examine differences in parameters that both indirectly (tenure length, number of females acquired, female tenure length) and directly (birth rates) affect leader male reproductive success. We also examine whether the presence of followers influences the length of time it takes a leader male to acquire his maximum number of females and the length of time he is able to simultaneously retain the maximum number of females in his unit. We compare reproductive rates of leader males with and without followers to determine if leaders with followers achieve higher overall reproductive success. Ultimately we seek to examine the benefits that the presence of follower males in hamadryas society may endow to the leader male or his OMU, so as to better understand why leader males tolerate followers despite being so protective of their females from all other males.

MATERIALS AND METHODS

Study site and subjects

The data for this study derive from a population of wild baboons at the Filoha site in the north of Awash National Park located in central lowland Ethiopia. There are at least five bands of hamadryas baboons that range in the Filoha area, which consists of semi-arid acacia scrubland and doum palm trees among natural hot springs. The subjects of this study belong to Band 1, which has been studied intermittently since 1996 and continuously since 2002 (Swedell, 2006; Swedell et al., 2011). Here we used demographic data from 65 OMUs collected between March 1, 2005 and December 31, 2011. Some OMUs had formed before 2005 and continued to exist past 2011. We knew the dates of demographic changes for some OMUs before 2005 and, for certain analyses, we provide results using pre-2005 data to give an idea of the real lengths of the parameters in addition to the censored results.

During the study period Band 1 was observed for about 15 days a month for 2–12 h a day. We follow baboons on foot and record the presence of identified individuals opportunistically. All adult and sub-adult members of Band 1 are known from natural markings and features. Disappearances and deaths are often determined retroactively, as not all individuals are seen on every day and the band sometimes splits into clans for periods of days or even weeks (Schreier and Swedell, 2009). There have been some unavoidable gaps in data collection due to shifts in the natural ranging of the baboons as a result of environmental and anthropogenic changes within the national park. Most such gaps lasted less than a month, averaging 16 days (Pines et al., 2011).

Band 1 varied in size from 180 to 250 individuals during the study period. The number of OMUs (and thus leader males) ranged from 24 to 41, the number of reproductive females from 65 to 105, and the number of follower males from 10 to 19.

Membership in all or most OMUs within Band 1 was known from censuses conducted at every contact with the band. Any changes in OMU membership and all demographic events (births, deaths and transfers) were recorded as and when they happened. If an event occurred during a gap in observation, we estimated its date of occurrence as the mid-way point in the gap. Thus we knew or estimated when females were taken over by leader males and when they were lost. It is possible that we missed a leader male's acquisition and loss of some females if female tenure with a male spanned very short periods of time during the gaps in observation. However, the likelihood that there were many missed female tenures is low because very few tenures (2.6% of 305 female tenures) were shorter than 30 days.

We defined a follower male as a sub-adult (usually aged 6–9 years) or adult male (aged 10 years and older) who was within 5 m of an OMU for 25% or more of the observation time on that OMU and who had occasional physical contact with OMU members. The presence of follower males in OMUs is dynamic and so is the relationship between follower and leader males. A leader male may have more than one follower at a time in his OMU or different follower males may join a particular OMU at different times, with variable periods of temporal overlap among followers, from weeks to months. Similarly, a follower male may associate with more than one OMU at the same time. In such cases, the follower's association with one particular OMU is usually more long-lasting and involves social relationships with the OMU as a whole (i.e., the females as well as the leader male), whereas his association with other OMUs is usually more short-term and in such cases his association may only extend to his relationship with the leader male and not beyond (Pines, pers. obs.). In our analyses, we used data from males who were both short- and long-term followers, residing in an OMU from a few weeks to a few years.

Data analyses

We compared differences in several variables between OMUs that had one or more followers at any point during the male's tenure as leader of that OMU ($N = 36$) and OMUs that never had a follower ($N = 29$). We included all completely known (uncensored) tenures as well as incompletely known (censored) tenures, i.e., tenures whose start or end dates were not known. We tested all data for normal distribution using Kolmogorov–Smirnov tests and then used parametric or nonparametric tests as appropriate. We analyzed all data in the statistical package IBM SPSS Statistics 20. We report means with standard errors and medians with interquartile ranges. We set alpha at 0.05.

Follower male score

For each leader male we calculated a follower-male score. Using our observational data as described above, we recorded changes over time in the number and identity of follower males in OMUs and determined the average number of follower males per OMU for a given year as a proportion of total observation time for that year that a particular follower male was observed in association with that OMU. We could not calculate the exact number of months in each year that followers were present in OMUs because we do not have precise dates for their entry and exit from OMUs. Rather, we knew the number of followers present in an OMU based on bandwide censuses conducted one to three times every year (except for 2006, when we did not collect data on followers). From the number of follower males present at each census, we calculated the average number of follower males per year for each OMU. We then assigned a follower-male score to each OMU or leader male derived from the mean of the annual average numbers of followers.

Leader male tenure

A male was considered leader of an OMU from the acquisition of his first female until the loss of his last female. In our comparisons of tenure lengths of leaders with and without followers, we examined the effects of both the total number of follower males present throughout a leader's entire tenure and the number of followers present simultaneously in an OMU. For leader males with multiple followers, we analyzed their tenure lengths in two ways: tenure length of leaders who had multiple followers at different times in their tenure, and tenure length when multiple followers were present simultaneously in the OMU. Of the 65 leader tenures used in our analyses, 15 tenures were left-censored, meaning these tenures had actually started before the study start date of March 1, 2005. There were 39 right-censored tenures, i.e., the males were still leaders at the end of the study period on December 31, 2011.

For comparison purposes, we also calculated tenure lengths using the real start date of tenures that started before 2005 (left-censored data) and provided estimates of the real tenure lengths. Because most tenures were under-estimated given right-censoring, i.e., the fact that many tenures were not complete at the end of the study, we performed a survival analysis with right-censoring using the Kaplan-Meier estimator (Kaplan and Meier, 1958) in SPSS to compare the survival curves for tenure lengths in OMUs with followers versus those without. We used the real start dates of the tenures that started before March 1, 2005 to avoid the problem of having to exclude all left-censored data from the Kaplan-Meier analysis and to generate a better estimate of survival based on actual rather than shortened tenure lengths. We used the Wilcoxon test (or Breslow test in SPSS) to test for statistical differences in tenure length between OMUs with and without followers. The Wilcoxon test puts more emphasis at the beginning of the survival curve, i.e., shorter tenures, thus giving more weight to the more common, shorter tenures rather than the less common, longer tenures (Kleinbaum and Klein, 2012).

Number of females acquired

We compared the number of females acquired by leader males with and without followers as a measure of their reproductive potential. We calculated each leader male's average number of females acquired by taking the mean of the monthly number of females present in his OMU for the duration of his tenure. We also took into account the variation over time in the number of females within OMUs and examined both the total number of females ever acquired by a leader male during his entire tenure, as well as the maximum number of females present at a given time. Because the total number of females acquired by leader males were not all present in the OMU at the same time, the total number of females ever acquired by a leader male was greater than his maximum number of females present simultaneously. The mean of the monthly number of females gives a snapshot of the number of females a leader male actually has access to at any point in time (each month), whereas the total number of females acquired gives an estimate of the total reproductive potential of a leader male over his reproductive lifespan, which should also vary depending on the birth rate and tenure length of each female.

To examine the relationship between the number of females acquired and the average follower-male score, for each leader male we calculated the annual mean number of females acquired from the monthly numbers of females for the years 2005 and 2007–2011 (because we do not have follower male data from 2006 we excluded female number data as well for this year for this analysis). We then calculated a mean female number score for every leader male by taking the average of the annual means and then examined the relationship between this score and each male's average follower-male score.

Female tenure

We calculated the tenure length for each female as the number of days from the date she was acquired by a leader to the date that he lost her (as per Swedell et al., 2011). A male loses a female when she dies, disappears, or transfers from one OMU to another. For each leader male, we calculated the average of the tenure lengths of all females that resided in his OMU during the study period. Because many tenures were censored in the study population, we also calculated female tenures using the actual acquisition dates of females who were acquired before March 1, 2005 and compared the mean real female tenure with the mean censored female tenure to get a better estimate of how long females really resided with each leader male.

In addition to the average amount of time a leader male had females in his OMU, we also examined the total amount of time a leader had all of his females. We calculated the total number of female-days for each leader male by summing all the tenure lengths (calculated in numbers of days) of all females that resided in each leader male's OMU. We then examined the relationship between this number and the leader male's average follower-male score.

Time-to-peak since OMU formation

For leader males who acquired more than one female, we examined whether the presence of followers affected the time it took to acquire the maximum number of females present at the same time in the OMU. We refer to this as the time-to-peak since OMU formation, and define it as the duration of time from a leader's first female acquisition to the time when he had the maximum number of females present simultaneously in the OMU. We calculated time-to-peak as a proportion of tenure length to control for differences in tenure lengths among leaders.

Peak duration of leader males

We calculated peak durations for leader males who acquired at least two females during their tenure, defined as the duration of time during which they had the maximum number of females present at the same time in their OMUs. The maximum number of females present simultaneously in the OMU was usually less than the total number of females acquired throughout a leader's career. The peak duration is the length of time that a leader was able to retain his maximum number of females. We examined whether follower males were present in the OMU for at least part of the time during these peak durations and looked at the differences in peak durations between OMUs that had follower males and those that did not have a follower at all during the leader's peak. We excluded leader males whose tenures or peak durations occurred for the most part in 2006 because we did not have follower male data from 2006.

Birth rates

To estimate the maximum potential reproductive success of hamadryas males, we analyzed data on the births of infants born to all the females belonging to a leader male during his tenure. We calculated conception dates for females as 180 days prior to the dates of their infants' births (Swedell, 2011) and assigned probable paternity to leader males in whose OMUs the females conceived. If a female gave birth within 6 months of being taken over, we assigned paternity to the prior leader male if the conception date fell within the female's tenure in the previous leader male's OMU. Based on observations of copulations, we assumed the leader male to be the most likely father even if follower males were present in the OMU because copulations with non-leader males are rare (Kummer, 1968; Swedell, 2006). At Filoha, only about 5% of copulations by adult females involve potentially reproductive sub-adult or adult non-leader males, with only about half of these by follower males (Swedell, unpublished data).

For our analyses of births, we excluded 2 males whose tenures were very short — <4 months, and, therefore, much shorter than the gestation period (180 days) of females. We may have missed a few births during our longest gap in data collection, from June 2010 to the end of the year, if infants born during this period also died during this period. However, given the relatively low mortality of hamadryas infants in this population (12.9%, Swedell et al., 2014) it is unlikely that the number of missed births would be substantial enough to affect the outcomes of our analyses.

We estimated rates of offspring production in OMUs with and without followers by dividing the total number of offspring produced in OMUs with and without followers by the total number of leader male-years (LM-years) represented by OMUs with and without follower males, respectively. We estimated birth rates from the female perspective for each OMU by dividing the total number of infants produced by all the females in an OMU by the total tenure length of all females in that OMU.

To further assess the potential net benefit to leaders of having followers, we compared the difference in total number of infants produced by leaders with and without followers. To assess this difference while controlling for the number of females, we divided the total number of infants born in each OMU by the average number of females in that OMU.

Ethical note

This research complied with protocols approved by the Institutional Animal Care and Use Committee of Queens College of the City University of New York (Protocol #93). This research was conducted with the permission of and following the guidelines of the Ethiopian Wildlife Conservation Authority and adhered to the legal requirements of Ethiopia.

RESULTS

Leader male tenure

Mean tenure lengths were significantly shorter for leader males that never had a follower male in their OMU ($28.7 \pm$ SE 2.9 months; range = 3.7–56.2, $N = 29$ males) compared to leader males that had one or more follower males in their OMU at some point during their tenure ($49.0 \pm$ SE 3.2 months; range = 3.9–83.2, $N = 36$ males; t test: $t = -4.559$, $P < 0.001$; Table 1). These tenure lengths are underestimates, however, as there were both left- and right-censored tenures in the sample, i.e., many tenures had started before March 1, 2005 and many males were still leaders at the end of the study period. Because the population has been studied continuously since 2002, we knew or estimated quite closely the start dates of some of the leader tenures that started

TABLE 1. Summary of demographic parameters for leader males with followers compared to leaders without followers (mean ± SE)

	No followers	Followers
Leader male tenure (months)	28.7 ± 2.9	49.0 ± 3.2
Mean monthly number of females	1.7 ± 0.13	3 ± 0.22
Total number of females (median)	2	5
Female tenure (months)	19.9 ± 1.9	29.8 ± 1.5
Time to peak since OMU formation (months)	14.9 ± 2.9	29.2 ± 2.8
Peak duration of leader males (months)	10.7 ± 1.7	16.8 ± 2.2
Birth rate: infants per leader male year	0.35	1.14
Birth rate: infants per female year	0.19	0.38
Total birth rate: infants/female	0.42	1.56

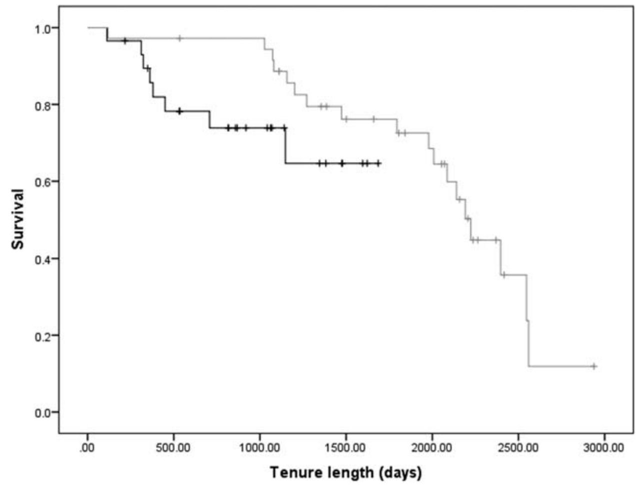

Fig. 1. Survivorship curves for leader males with followers (grey line, $N = 36$) compared to those without followers (black line, $N = 29$). Both curves include right-censored data, marked by crosses.

before March 1, 2005. Using these known or closely estimated start dates, we calculated the real tenure lengths. The actual tenures of leader males with followers in their OMUs were much longer, with a mean of 58.7 ± SE 3.5 months (range = 3.9–97.9), as 14 of the 36 leader tenures in this sample had started before March 1, 2005. However, the mean tenure of leaders without followers did not change using the actual start dates (mean = 28.9 months) as there was only one leader whose tenure had started before March 1, 2005.

We performed a Kaplan–Meier survival analysis to compare the tenure lengths of leader males with and without followers. The survival distribution of the tenure lengths of leader males with follower males was significantly different from that of leaders without followers (Wilcoxon $\chi^2(1) = 4.071$, $P = 0.044$; Fig. 1). From the Kaplan–Meier analysis, the estimated mean tenure length of leaders without followers was 43.3 months and the estimated mean tenure length of leaders with followers was 69.4 months. The longest tenure of leaders with followers was about twice as long as the longest tenure of leaders without followers.

We examined the total number of followers in each leader male's OMU throughout his tenure as leader to determine whether this number affected his tenure length. The followers representing the total number during a leader's entire tenure were not often present in his OMU all at the same time. We found that even leader males with only one follower ever in their OMUs had significantly longer tenures than leader males with no followers at all (mean = 45.1 ± SE 4.2 months, range = 3.9–73.0, $N = 19$ males; t test: $t = -3.315$, $P = 0.002$; uncensored tenure: 54.8 ± SE 4.8 months). Leader males with a minimum of two followers ever (and a maximum total of five followers) had the longest tenures overall, with a mean of 53.4 ± SE 4.9 months (range = 21.8–83.2, $N = 17$ males; uncensored tenure: 63 ± SE 4.9 months). Again, this was significantly longer than the mean tenure length of leader males with no followers (t test: $t = -4.6$, $P < 0.001$). There was no significant difference in tenure lengths of leader males with only one follower versus leaders with two or more followers (t test: $t = -1.302$, $P = 0.202$). There was a significant effect of the total number of followers (0–5) a leader male had during his entire tenure on his tenure length (ANOVA: $F(5, 59) = 4.604$, $P = 0.001$): the more followers that joined an OMU throughout the tenure of a leader male, the longer the tenure length of the leader male.

Males with more than one follower sometimes had multiple followers present simultaneously in their OMUs. Most leaders usually had only one follower at a time (22 out of 36 OMUs with followers); for these males, the mean tenure length was 45.4 months (uncensored tenures: 55.9 months). Twelve leader males had 2 followers at the same time; for these males, the mean tenure length was 52.3 months (uncensored: 58.3). Only 2 OMUs had three follower males present simultaneously for at least some length of time and these leader males had tenure lengths of 83 and 56 months (uncensored: 98 and 85). The actual tenure length of the male who has been a leader for 98 months is in fact longer than this because he was still a leader at the end of the study period.

Number of females acquired by leader males

The total number of females acquired by leader males during their entire tenure ranged from one to 14. 35% (23 out of 65) of leader males only acquired one and two females during their entire tenure. Only 22% (5 of 23) of these leader males also had follower males. If we include leader males who acquired 3 females, constituting 49% of all leader males in Band 1, then only 31% (10 of 32) of these leaders (with one to three females) had follower males. In contrast, leader males who acquired 4 or more females constituted 51% (33 out of 65) of the population, and 79% (26) of these leaders had a follower male at some point.

The mean number of females (based on monthly numbers of females) acquired by leaders with followers (3 ± SE 0.22; range = 1–7.2, $N = 36$) was significantly greater than the mean number of females acquired by leaders without followers (1.7 ± SE 0.13; range = 1–3.8, $N = 29$; Mann–Whitney $U = 191$, $P < 0.001$; Table 1). The mean monthly number of females acquired by leader males was significantly positively correlated with the average follower-male score (Spearman's $\rho = 0.498$, $P < 0.001$, $N = 65$). The mean monthly number of females of leader males was also significantly positively correlated with leader male's tenure length (Spearman's $\rho = 0.494$, $P < 0.001$, $N = 65$; Fig. 2).

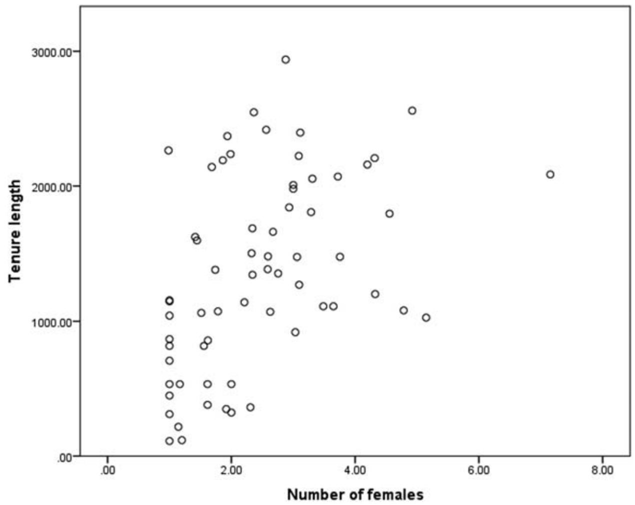

Fig. 2. Relationship between number of females acquired by a leader male and that male's tenure length.

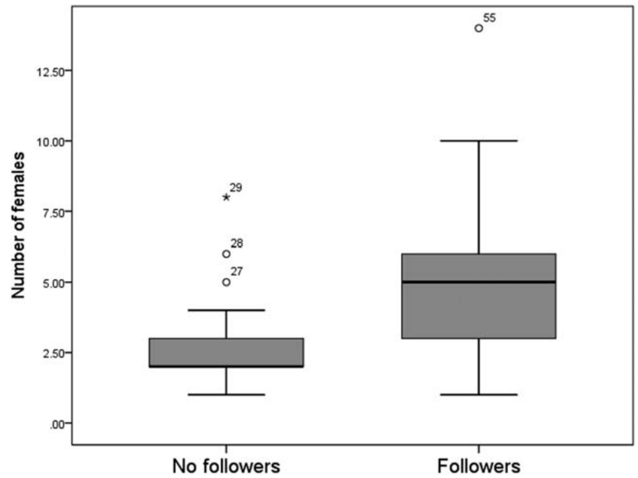

Fig. 3. Total number of females acquired by leader males without followers ($N = 29$) compared to leaders with followers ($N = 36$).

An examination of the total number of females ever acquired by leader males during their entire tenure reveals that leader males with followers in their OMUs acquired more than twice as many females over their tenure as leaders, with a median of five females acquired overall (range = 1–14, interquartile range (IQR) = 3–6, $N = 36$ leader males), compared to leader males in OMUs without followers, who acquired a median of two females during their tenure as leader (range = 1–8, IQR = 1.5–3.5, $N = 29$ leader males; Mann–Whitney $U = 203$, $P < 0.001$; Fig. 3; Table 1).

To further elucidate the relationship between follower males and number of females acquired by leader males, we compared the total number of females acquired by leader males with various combinations of numbers of followers over time. Leader males who never had followers acquired a mean total number of 2.6 females ($N = 29$); with one follower 4.2 females ($N = 19$ leader males); and with two or more followers 6.1 females ($N = 17$).

A comparison of males with only one versus multiple followers simultaneously revealed that leader males with only one follower male at a time acquired a mean of 4.7 females ($N = 22$ leader males), with two simultaneous followers 5.8 females ($N = 12$), and with three simultaneous followers 5 females ($N = 2$). (Using uncensored tenures, leaders with one follower acquired five females, with two followers had six females and with three followers had six females.) There was a significant difference in the number of females acquired by leader males between OMUs containing different numbers of simultaneously present follower males (Kruskal–Wallis H test: $\chi^2(3) = 21.019$, $P < 0.001$).

Female tenure

We compared the mean female tenure length in OMUs with and without follower males. Leaders with followers had a mean female tenure length of 29.8 ± SE 1.5 months (range = 2.1–49.3, $N = 36$; uncensored tenures: 35.5 months), whereas leaders without followers had significantly shorter female tenures with a mean female tenure length of 19.9 ± SE 1.9 months (range = 3.7–40.4, $N = 29$; uncensored tenures: 20.1; t test: $t = -4.072$, $P < 0.001$; Table 1). We found the mean female tenure per leader male to be significantly positively correlated with the leader male's follower-male score (Pearson correlation $r = 0.276$, $P = 0.026$, $N = 65$). We also found individual female tenures in OMUs to be significantly positively correlated with the total number of followers (0–5) that ever lived in an OMU (Spearman's $\rho = 0.157$, $P = 0.011$, $N = 258$).

We also compared female tenure lengths between small and large OMUs. As previously mentioned, although small OMUs containing one to two females (i.e., leader males acquired only one or two females during their tenures) were common in our study population, very few of these OMUs actually contained follower males. Using individual female tenures (rather than the average female tenure for each leader male or OMU) we found that females in one- and two-female OMUs had significantly shorter tenures with a mean of 18.3 ± SE 2.3 months (range = 8 days to 57.8 months, $N = 37$ tenures), compared to females in OMUs containing more than two females who had a mean tenure length of 28.1 ± SE 1.2 months (range = 4 days to 82.7 months, $N = 221$ tenures; Mann–Whitney $U = 2843$, $P = 0.003$).

The mean tenure length of all females was 26.7 ± SE 1.14 months (range = 4 days to 82.7 months, $N = 258$ tenures). We took a closer look at the tenures of females with relatively long tenures, i.e., all tenure lengths that were above the mean. Of the total 258 tenures included in the analyses, 123 female tenures were longer than the mean tenure of 26.7 months. Of these 123 tenures, 80% were in OMUs that had followers and 20% were in units without followers.

Finally, we examined the total number of female days or months that characterized leader males with and without followers. The mean number of female-months represented by leader males who never had a follower was 53.3 ± SE 8.2 months (range = 3.7–183.6, $N = 29$) and the mean number of female-months represented by leader males who had followers in their OMU at some point in time was 148.4 ± SE 12.4 months (range = 4.2–314.6, $N = 36$). We found the number of female-days per leader male to be significantly positively related to follower-male score (Spearman's $\rho = 0.511$, $P < 0.001$, $N = 65$).

Time-to-peak since OMU formation

Because hamadryas OMUs generally start with one female and increase gradually over time as males take over individual females (Pines et al., 2015), the time it takes for a leader to reach maximum OMU size is a potential determinant of his eventual reproductive success. For OMUs with more than one female, we examined leader males' time-to-peak since OMU formation in relation to follower membership of OMUs. Leader males who had never had a follower male in their OMUs reached their peak on average 14.9 ± SE 2.9 months (range = 0–42.3, $N = 21$; Table 1) after formation of their OMUs or 43.4% of the time into their tenure. By contrast, leaders with followers in their OMUs at some point during their tenure reached their peak much later into their tenure, on average 29.2 ± SE 2.8 months (range = 0–53.7, $N = 28$; Table 1) after forming their units or 54.9% of the time into their tenure. The difference in peaking time between leaders with and without followers was significant (t test: $t = -3.545$, $P = 0.001$).

Peak duration of leader males

Leader males with one or more follower males present during the time they had their peak number of females had a mean peak duration of 16.8 ± SE 2.2 months (range = 8 days to 37.5 months, $N = 22$ leaders), whereas leaders without any followers present during their peak had a significantly shorter mean peak duration of 10.7 ± SE 1.7 months (range = 1–34.8, $N = 24$ leaders; Mann–Whitney $U = 166$, $P = 0.031$; Table 1). Some of the peak durations calculated here are shorter than the actual peak durations due to right-censoring. Sixteen peak durations are under-estimated because they were ongoing at the end of the study period: 12 of these did not have a follower during the peak, at least until the end of the study period, and 4 had followers.

Birth rates

Our comparison of inferred birth rates for leader males with and without followers, on the assumption that leader males sired all of the infants conceived in their OMUs, revealed a rate of production of surviving offspring in OMUs without followers of 0.35 infants per LM-year (24 infants born in 68.1 male-years) and a rate in OMUs with followers of 1.14 infants per LM-year (165 infants born in 144.8 male-years; Table 1). If we assume that leader males with followers lost 3% of their paternity to their followers (based on the observed copulation rate of 2.5–3% for followers), then OMUs with followers would still achieve a birth rate of 1.11 infants per LM-year, which is three times higher than the rate of offspring production in OMUs without followers.

Examining the data from the female perspective, females in OMUs without followers gave birth to a total of 24 surviving infants in 126.8 female-years, yielding a rate of 0.19 infants per female-year (Table 1). By comparison, females in OMUs with followers gave birth to 165 infants in 438.8 female-years, or 0.38 infants per female-year (Table 1). Females in OMUs with followers thus produced twice as many surviving offspring per female-year than females in OMUs without followers.

An examination of total birth rates of leader males revealed that leaders without followers achieved a birth rate of 0.42 infants/female (range = 0–1.7, $N = 28$) during their tenures and leaders with followers had a birth rate of 1.56 infants/female (range = 0–3.22, $N = 35$) during their tenures (Table 1). Thus leaders with followers benefitted from 1 extra surviving offspring/female compared to leaders without followers.

DISCUSSION

The results of these analyses suggest that follower males serve an important role in hamadryas society in enhancing the fitness of leader males. In this study, leader males with followers benefited from tenure lengths that were twice as long and acquired twice as many females compared to leader males without followers. Moreover, females in OMUs with followers had tenures themselves that were at least 50% longer, ultimately yielding a far higher reproductive output for OMUs with followers compared to those without followers (Table 1).

Although the nature of relationships between males is competitive in many mammals, a number of species are characterized by male–male tolerance and cooperation, including feral horses (*Equus caballus*, Feh, 1999), striped hyenas (*Hyaena hyaena*, Wagner et al., 2008), dolphins (*Tursiops sp.*, Randic et al., 2012), lions (*Panthera leo*, Packer et al., 1991), and some primates (van Hooff and van Schaik, 1994). Typically such tolerance manifests in the formation of coalitionary alliances among males to increase access to females or to defend females from rivals. The benefits obtained from such an alliance may be mutual, or more one-sided such that the resident, for example, gains more than the secondary male. As a reproductive strategy, therefore, it may be advantageous for a resident male to tolerate the presence of secondary males as he may fare better than he would otherwise or at least he may have nothing to lose, whereas engaging in risky aggressive behavior to exclude secondary males may be more costly. From a theoretical perspective, therefore, the tolerance by hamadryas leader males of their followers is presumably due to net reproductive or other benefits obtained by the leaders as a result of the presence of followers.

Although paternity certainty often declines with the number of females and males in a group (Dunbar, 1988; Brotherton and Komers, 2003), in hamadryas this is unlikely to be the case as leader males form "permanent consortships" (Bergman, 2006) with their females and non-leader males copulate rarely (Kummer, 1968; Sigg et al., 1982; Nitsch et al., 2011), with followers obtaining only 2.5–3% of all copulations (Swedell, unpublished data). Rather than diminishing a leader's share of the offspring, the presence of followers may instead help prevent leaders from losing conceptions to non-OMU males, as is known to happen in other primates with single-male groups such as snub-nosed monkeys (Guo et al., 2010) in which leader males of different OMUs appear to form coalitions to increase paternity certainty within their respective OMUs (Xiang et al., 2014). Moreover, followers rarely challenge their leaders and therefore leaders do not have to actively defend females from their followers. Based on a previous study on our study population, only 1 (possibly 2) follower out of 16 formed an OMU by directly challenging and taking over his leader's females (Pines et al., 2011). A potentially higher cost to hamadryas leaders than paternity loss would be risk of injury or death if leaders actively engaged in aggression to keep followers out (cf. MacCormick et al., 2012). Given that the overall reproductive success of hamadryas leaders in multi-male OMUs was much higher than that of leaders of single-male OMUs in our study, leaders with followers would still benefit even if a small portion of paternity was lost to followers.

Results similar to our findings have been obtained for other species with similar social systems. In the closely related gelada in which OMUs typically contain a single male, leader males of multi-male units have longer tenures, more females and more surviving offspring than leaders of OMUs without followers (Dunbar, 1984; Snyder-Mackler et al., 2012). Gelada followers actively help the leader in defense against bachelor males, who tend to chase males from single-male units more than from multi-male units (Snyder-Mackler et al., 2012). Similarly, hamadryas leader males residing alone in an OMU may be more vulnerable to attacks by other males, and their tenures may get terminated before they are able to acquire more than one or two females.

Secondary males may enable resident males to retain their females in the face of outside threats even if they do not actively help the resident acquire more females. Given that hamadryas OMUs within a band/clan maintain relatively close proximity and the threat to leaders from non-OMU males is constant, the presence of followers may be crucial to retention of females during takeovers. We do not yet know to what extent hamadryas followers actively participate in unit defense, but simply the presence of followers in an OMU may help retain females while their leaders are engaged in aggressive competition with challengers or retrieving abducted females (cf., Pines and Swedell, 2015). Gelada followers, for example, often remain with OMU females while the leader fights with male challengers (Dunbar and Dunbar, 1975; Mori, 1979), and this may help prevent loss of those females. By helping to prevent takeovers, followers also indirectly help boost infant survival because post-takeover infant mortality in hamadryas is very high (67%, Swedell et al., 2014).

The tolerance shown by hamadryas leaders to followers may be explained by a fundamental qualitative difference in the relationships between resident and secondary males in hamadryas baboons compared to other species with similar social systems. Hamadryas are characterized by male philopatry and thus males within a band are closely related (Swedell et al., 2011, Städele et al., 2015a). Inclusive fitness benefits are known to be an important factor in the development of support and tolerance among male relatives (van Hooff and van Schaik, 1994). Beyond kinship, it is also likely that past social interactions between two males influence which OMU, i.e., which leader male, a follower male ends up joining (Abegglen, 1984). As juveniles and adults, hamadryas males, including leaders and followers, maintain close affiliative social relationships (Kummer, 1968; Abegglen, 1984; Swedell, 2006). These relationships may underlie the preponderance of multi-male units in hamadryas society compared to other polygynous groups that have both one-male and multi-male groups: 55% of hamadryas OMUs over a 6.5-year period, as opposed to 33% of gelada units (Snyder-Mackler et al., 2012) and 40% of mountain gorilla groups (Bradley et al., 2005) are multi-male.

In this study, leaders without followers generally acquired very few females, usually just one or two. They reached their peak size very quickly, after which they did not acquire any more females and their tenure ended soon after. By contrast, OMUs with followers took a longer absolute time to reach their peak size (although the difference is small if we control for tenure length). During this time, however, leaders acquired more than twice as many females and each female they had already acquired gave birth in the OMU. Once they had acquired their maximum number of simultaneously present females, leaders with followers were able to hold on to this number of females for longer compared to leaders without followers. Ultimately, multi-male hamadryas OMUs produced many more (almost four times as many) infants per female as single-male OMUs, even accounting for the possibility of some paternity loss to followers. The median tenure of dominant males in mammals is known to accurately estimate breeding lifespan because males do not sire many offspring outside of their dominance period (Soulsbury, 2010; Lukas and Clutton-Brock, 2014). This is likely the case for hamadryas males as well, and leader tenures should largely determine lifetime reproductive success. Our data show that reproductive exclusivity in single-male units does not necessarily translate to higher reproductive success and, therefore, for hamadryas males it is not in their best interests to be in smaller, single-male units.

Ultimately there may be characteristics of leader males that enable them to attract both a large number of females and follower males. It is possible that as a leader male acquires more females, the growing size of the OMU attracts followers for varying lengths of time. At a threshold size of four females or more, followers are likely attracted to these OMUs not only for the adult females present but also for the offspring of those females, whom these followers could potentially take over in the future (Swedell, 2006). Leader male tolerance may be traded for cooperation and support from followers, who may then reap inclusive fitness benefits due to kinship with the leader. The followers may be learning to become leaders during this time and whether by active defense or inadvertently influencing female choice they likely enable the leader to acquire more females and retain them for longer. By maintaining social relationships with females, followers may indirectly encourage female choice for their leaders and therefore prolong female tenures, as hamadryas females may have preferences for specific males that influence outcomes of takeovers (Bachmann and Kummer, 1980; Swedell, 2000; Pines and Swedell, 2011). Followers are also very interested in infants and may help protect infants from potential infanticidal attacks.

For young males in hamadryas society, there are three possible options: (i) acquire females and become a leader; or, until he can acquire females, remain a bachelor as either (ii) a follower male or (iii) a solitary male. As a long-term strategy it is likely more profitable for bachelor males to join OMUs as followers, rather than remaining solitary, as they may gain from inclusive fitness benefits if they are related to the leader, achieve surreptitious copulations, and/or inherit some of the females in the future (Pines et al., 2011). They may also inherit the daughters of these OMU females, as suggested by Swedell (2006), who found a correlation between the number of followers and the number of pregnant females as well as the number of immature females in an OMU. Based on a previous analysis from our study population, three out of 16 followers established their OMUs by inheriting females from their leaders (Pines et al., 2011). An additional seven followers formed initial units with prereproductive females (Pines et al., 2011), many of whom may have derived from the followers' previous OMUs in which they undoubtedly maintained social relationships with the females and their offspring. For a follower male who is unable to acquire his own females, it may be more costly to leave than to remain with an OMU. Hamadryas males do not form all-male groups and therefore the alternative for a follower who cannot become a leader is to become solitary. As a solitary male, he would be completely deprived of sexual as well as social access to females.

In conclusion, these results demonstrate that hamadryas leaders derive benefits from the presence of followers in their OMUs. Similar to other baboons and geladas in which (presumably) unrelated males form coalitions to keep other males away, it appears that in the hamadryas multi-level social system with male philopatry, (presumably) related males may use cooperation to mitigate male competition over access to females. Within this cooperative and competitive landscape, males who have not formed reproductive units may benefit from joining an OMU rather than remaining solitary. The relationship between leaders and followers thus appears to be a mutually beneficial one in which the two males show mutual tolerance and possibly collaborate either directly against extra-OMU males or more indirectly to increase longevity of OMUs. Followers likely provide crucial services to unit members and therefore "buy their right to stay" (cf., van Hooff, 2000) in the OMU. Such a relationship falls along the continuum for coalitionary behavior among mammals (Olson and Blumstein, 2009).

The results of this study contribute to our understanding of the range of possible competitive and cooperative relationships that may exist among males in a multi-level society. The evolution of a multi-level polygynous society such as that of the hamadryas likely occurred as a result of sub-structuring of larger groups into smaller sub-units as a result of ecological pressures (Jolly, 1963, 1993; Kummer, 1968; Dunbar, 1983, 1988). Males would have then found it advantageous to remain with small groups of females to increase paternity certainty, and social pressures such as sexual coercion and infanticide threat (cf., Swedell et al., 2014) would have favored cross-sex bonding by females for protection against coercive and infanticidal males (Henzi and Barrett, 2003; Swedell and Saunders, 2006; Grueter et al., 2012; Swedell and Plummer, 2012). While these cross-sex bonds are crucial to the stability and longevity of OMUs, it is the bonds among males deriving from male philopatry that keep hamadryas bands intact (Kummer, 1984). This study enhances our understanding of the evolution of this system as it demonstrates how the hamadryas leader-follower relationship may be a crucial link in the interconnected hamadryas society.

These results carry implications for human evolution if one postulates the development of a multi-level social organization, such as that found in hamadryas baboons, as a fundamental step during the evolution of human sociality. As outlined by Swedell and Plummer (2012), a multi-level society allows the simultaneous presence of kin bonds among males (Kummer, 1968; Abegglen, 1984; Städele et al., 2015a), kin bonds among females (Swedell, 2002; Städele et al., 2015b), and pair-bonding between the sexes (Kummer, 1968; Swedell, 2006), all of which serve functions at different levels of social structure. Crucial to this model is the possibility of kin-based, cooperative bonds among males, thought to have been important in early hominins, which have generally been assumed to be present in hamadryas society but never explicitly demonstrated. The demonstration of a beneficial relationship between follower and leader males in hamadryas society lends credibility to the idea that kin-based cooperative relationships among males can co-exist with both intersexual pair bonds and bonds among females (Swedell and Plummer, 2012), thereby highlighting the utility of hamadryas baboon society for modeling human social evolution.

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