Animal Behaviour 117 (2016) 145–153

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Age and reproductive status influence dominance in wild female Phayre's leaf monkeys

Amy Lu [a, b, *], Carola Borries [a, b], Morgan L. Gustison [c], Eileen Larney [a], Andreas Koenig [a, b]

[a] Department of Anthropology, Stony Brook University, Stony Brook, NY, U.S.A.
[b] Interdepartmental Doctoral Program in Anthropological Sciences, Stony Brook University, Stony Brook, NY, U.S.A.
[c] Department of Psychology, University of Michigan, Ann Arbor, MI, U.S.A.

ARTICLE INFO

Article history:
Received 2 November 2015
Initial acceptance 8 January 2016
Final acceptance 2 March 2016
Available online 6 June 2016
MS. number: A15-00937

Keywords:
female–female competition
hierarchy
individualistic hierarchies
rank
resource-holding potential

In group-living mammals, social dominance can be achieved and maintained via kin support, winner–loser effects and individual differences in resource-holding potential (RHP). When dominance is based on RHP, the likelihood of winning is also influenced by the incentive to compete. For females, this equation can be quite complex, as both age and reproductive state can alter the relative value of resources and the risks associated with fighting. For example, females that are young, pregnant or lactating may have high nutritional demands, while lactating females also face risks associated with offspring survival. To date, however, there have been few studies investigating how such factors influence female agonistic relationships. Here, we use 2 years of data to evaluate how age and reproductive state influence the probability of winning, focusing on two groups (5–9 and 10–12 females) of wild Phayre's leaf monkeys, *Trachypithecus phayrei crepusculus*, at Phu Khieo Wildlife Sanctuary, Thailand. Consistent with previous studies, we found that young females and pregnant females were more likely to win dyadic interactions in the smaller group, PA. By contrast, the likelihood of winning was unrelated to age in the larger group, PB. Moreover, differences between reproductive states were less pronounced in PB, with females that were pregnant or in early lactation being more likely to win compared to females that were cycling. The deviating results for PB were likely associated with a greater number of competitors and small age differences intensifying intrasexual competition. These results highlight the importance of individual as well as demographic factors in female dominance relationships. In this population, females with high nutritional demands are more likely to win agonistic encounters, suggesting that female–female competition occurs primarily over access to resources.

In gregarious animals, social dominance often determines priority of access to resources (e.g. food, mates), resulting in reproductive advantages for dominant as opposed to subordinate individuals (Ellis, 1995; Stockley & Bro-Jørgensen, 2011). In nonhuman primates, for instance, long-term field studies have shown that dominant females often mature earlier, reproduce faster and have improved offspring survivorship (reviewed in Pusey, 2012; but see Fedigan, Carnegie, & Jack, 2008; Gouzoules, Gouzoules, & Fedigan, 1982).

Unsurprisingly, much research has focused on the processes by which individuals achieve and maintain dominance over others. These processes can vary substantially across species, as best exemplified by the diverse dominance systems found in female mammals. In the matrilineal systems described for many cercopithecine primates (e.g. *Papio* spp., *Macaca* spp.: Chapais, 1992) and spotted hyaenas, *Crocuta crocuta* (Holekamp & Smale, 1991), for instance, the likelihood of winning is largely determined by coalitionary support from kin (i.e. ‘maternal rank inheritance’: Kawai, 1958; Kawamura, 1958), resulting in dominance relationships that remain stable through time (Bramblett, Bramblett, & Bishop, 1982; Hausfater, Altmann, & Altmann, 1982). By contrast, in the majority of mammals, including African elephants, *Loxodonta africana* (Archie, Morrison, Foley, Moss, & Alberts, 2006), several ungulate species (mountain goats, *Oreamnos americanus*: Côte, 2000; bighorn sheep, *Ovis canadensis*: Favre, Martin, & Festa-Bianchet, 2008) and some primates, particularly those characterized by female dispersal (mantled howler monkeys, *Alouatta palliata*: Jones, 1980; eastern gorillas, *Gorilla beringei*: Robbins, Stoinski, Fawcett, & Robbins, 2005; chimpanzees, *Pan troglodytes*: Wittig & Boesch, 2003; Phayre's leaf monkeys, *Trachypithecus phayrei*: Koenig,

---

* Correspondence: A. Lu, Department of Anthropology, S529-SBS Building, Circle Road, Stony Brook University, Stony Brook, NY 11794-4364, U.S.A.
E-mail address: amy.lu@stonybrook.edu (A. Lu).

http://dx.doi.org/10.1016/j.anbehav.2016.04.020
0003-3472/

Larney, Lu, & Borries, 2004; but also see grey langurs, *Semnopithecus entellus*: Borries, Sommer, & Srivastava, 1991, for female philopatric species), the outcome of dyadic encounters is often influenced by experience (i.e. winner–loser effects) and/or individual factors related to resource-holding potential (RHP; i.e. absolute fighting ability: Parker, 1974) such as body size or aggressiveness (Stockley & Bro-Jørgensen, 2011). When the likelihood of winning is based on experience, dominance relationships remain fairly stable (Côte, 2000; Robbins, Robbins, Gerald-Steklis, & Steklis, 2005). By contrast, when dominance is primarily achieved and maintained through individual differences in RHP, the probability of winning is expected to change in parallel with fluctuations in body condition (Lu, Borries, Caselli, & Koenig, 2013). In addition, individuals may be more likely to win when the incentive to compete increases (Broom, Koenig, & Borries, 2009). Females are expected to escalate contests only when the value of resources is high relative to the costs of aggression and potential defeat (Hammerstein, 1981; Parker, 1974). Indeed, even in more stable hierarchies, temporary changes in dominance are theoretically possible when resources become more critical for reproduction and/or survival. Thus, changes in resource value, nutritional demands or fighting ability might all lead to corresponding changes in social dominance.

Age may also influence the probability of winning; however, age effects may be more directly explained by age-related differences in experience or RHP. Positive associations between age and dominance (Archie et al., 2006; Côte, 2000; Šárová et al., 2013; Wittig & Boesch, 2003) generally reflect the importance of experience and winner–loser effects, while inversed U-shaped (Packer, 1979; Robbins et al., 2005), or negative relationships (Borries et al., 1991; Hirsch, 2007; Jones, 1980; Koenig et al., 2004; Lu et al., 2013), reflect the importance of RHP (i.e. prime-aged individuals are in the best condition). In some cases where age and dominance are negatively related, the youngest and most dominant individuals are the smallest and least experienced, and therefore seem to have low RHP (Hirsch, 2007; Lu et al., 2013). One explanation for this pattern is that the high energetic costs of reproduction coupled with growth increases the incentive to compete for adolescent females (Broom et al., 2009; Lu et al., 2013). Alternatively or in addition, when females are closely related, older females may gain inclusive benefits by ‘deferring’ to younger females with higher reproductive value (Combes & Altmann, 2001; Hirsch, 2007; Hrdy & Hrdy, 1976). For instance, this argument may apply to grey langurs (Hrdy & Hrdy, 1976), a species where dominance is individualistic, despite females being philopatric. Thus, the incentive to compete can change with nutritional demands or the potential payoffs associated with age. In addition, recent studies on baboons have found that older females may suffer higher costs associated with aggressive competition. Older female baboons are more likely to get injured, and when injured, heal more slowly (Archie, Altmann, & Alberts, 2014), potentially favouring deferment in competitive encounters.

Female reproductive state may also alter the costs and benefits of contests. As mammalian females transition from one reproductive state to another, their nutritional demands change, peaking during lactation (Speakman, 2008). However, in capital breeders (i.e. animals using stored energy for reproduction; Jönsson, 1997), females may cover some of the costs of lactation with energy stored while cycling or pregnant. Indeed, in capital breeders, successful conception is contingent upon achieving positive energy balance, a system that ensures reproductive investment only when the probability of success is high (Negus & Berger, 1987). Thus, based purely on current nutritional demands, capital-breeding females may be more likely to compete while cycling and pregnant, particularly if such interactions result in access to resources as well as reproductive suppression of opponents, as has been suggested for baboons (Huchard & Cowlishaw, 2011; Wasser & Starling, 1988). By contrast, for lactating females, the increased nutritional demands favouring competition may be offset by hampered fighting ability and the potential cost of injury (to the mother or infant) while caring for a dependent (Huchard & Cowlishaw, 2011; Lu et al., 2013; Seyfarth, 1976). While similar risks (e.g. miscarriage) may pertain to pregnant females, pregnant females do not face the costs of having to monitor an additional individual while engaging in competitive encounters. Recent data on spotted hyaenas also suggest that lactating females face resource allocation costs (East et al., 2015), with energy devoted towards milk production constraining a female's ability to invest in the immune system, and thus heal from injury. Taken together, this suggests that unlike cycling and pregnant females, lactating females should generally refrain from competitive encounters.

Female agonistic tactics can therefore be quite complex and contingent on a variety of fluctuating costs (e.g. potential infant death, resource allocation trade-offs) and benefits that males simply do not face. Despite this complexity, most studies on intrasexual competition have focused on males (Andersson, 1994), with little attention paid to females until recently (Clutton-Brock & Huchard, 2013). Importantly, individualistic systems of dominance offer a window of opportunity for studying the competitive strategies of females. Because agonistic interactions often do not involve third-party support, the outcome of competitive encounters is entirely dependent on individual fighting ability and changes in the incentive to compete. In a previous study, we found that female dominance in one group of grey langurs decreased with age and fluctuated with reproductive state such that females rose in dominance 6 months prior to conception, reached peak competitive ability at parturition and decreased in dominance thereafter (Lu et al., 2013). Here, we aim to investigate whether age and reproductive state bear similar importance in the competitive strategies of Phayre's leaf monkeys, *Trachypithecus phayrei crepusculus*.

Phayre's leaf monkeys are colobine primates that live in permanent bisexual groups consisting of 1–5 adult males, 3–12 females, and associated offspring (Koenig & Borries, 2012). Dispersal is female biased. Births can occur throughout the year, but are concentrated during the months of November to April. Correspondingly, conceptions peak 7 months earlier, during April to October, and are timed to improvements in female body condition (Lu et al., 2011). These patterns suggest that Phayre's leaf monkeys are capital breeders (Jönsson, 1997; Negus & Berger, 1987).

A previous report based on a small data set (Koenig et al., 2004) found that like grey langurs (Borries et al., 1991; Hrdy & Hrdy, 1976; Lu et al., 2013), dominance relationships in female Phayre's leaf monkeys are individualistic and inversely related to age. Here we expand this analysis with a much larger data set, investigating how age and/or reproductive state influence social dominance, defined as the probability of winning dyadic interactions.

We predicted that younger females and females that were cycling or pregnant would be more likely to win agonistic encounters. By contrast, older females and females with dependent offspring were expected to face greater costs associated with competitive interactions. We therefore predicted that these females would be more likely to defer to others, resulting in a reduced likelihood of winning.