INTRODUCTION

Alpha male replacements in nonhuman primates: Variability in processes, outcomes, and terminology

Julie A. Teichroeb[1] (iD) | Katharine M. Jack[2]

[1] Department of Anthropology, University of Toronto Scarborough, Toronto, Ontario, Canada

[2] Department of Anthropology, Tulane University, New Orleans, Louisiana

Correspondence
Julie A. Teichroeb, Department of Anthropology, University of Toronto Scarborough, 1265 Military Trail, M1C 1A4, Toronto, ON, Canada.
Email: jteichroeb@utsc.utoronto.ca

Alpha male replacements occur in all primates displaying a dominance hierarchy but the process can be extremely variable. Here, we review the primate literature to document differences in patterns of alpha male replacements, showing that group composition and dispersal patterns account for a large proportion of this variability. We also examine the consequences of alpha male replacements in terms of sexual selection theory, infanticide, and group compositions. Though alpha male replacements are often called takeovers in the literature, this term masks much of the variation that is present in these processes. We argue for more concise terminology and provide a list of terms that we suggest more accurately define these events. Finally, we introduce the papers in this special issue on alpha male replacements in the *American Journal of Primatology* and discuss areas where data are still lacking.

KEYWORDS
group composition, infanticide risk, sexual selection, social organization, takeover

1 | INTRODUCTION

Males compete for access to receptive females, who are always a limiting resource, thus male competition usually leads to the formation of male dominance hierarchies within groups (Darwin, 1871; Trivers, 1972). In many species, there is a clear association between male dominance rank and reproductive success (e.g., Cowlishaw & Dunbar, 1991) and as such, males are expected to compete, sometimes fiercely, to attain more dominant positions within a group (Lukas & Clutton-Brock, 2014). Even in solitary species, changes in male age, physical condition, and dominance status result in male replacement or changes in access to breeding females (Banes, Galdikas, & Vigilant, 2015). However, the ways that a male becomes alpha can be highly variable depending on the group composition and dispersal patterns of a particular species. Even within a single species there is often variability in the form of alpha male replacements. For example, in ursine colobus monkeys (*Colobus vellerosus*), males may transfer and takeover groups singly or in all-male bands, challenge the alpha male of their current group (i.e., a rank reversal), or join dispersing females to start a new group (Sicotte et al., 2017; Teichroeb, Wikberg, & Sicotte, 2009; Teichroeb, Wikberg, & Sicotte, 2011). The rates at which alpha male replacements occur, the aggressiveness of these events, their durations, and the consequences for different individuals are also inconsistent. After discussing these issues and reviewing the literature focused on determinants of this variation, we decided to initiate a

symposium on alpha male replacements at the 83rd meetings of the American Association of Physical Anthropologists in 2014. The papers given in this symposium as well as the discussions afterward led to the collection of papers within this special issue of the *American Journal of Primatology*. These papers, focused on a range of primate species, demonstrate the difficulties males face in acquiring and maintaining the dominant position within a group and the different tactics they can use. They also show how changes in an alpha male can lead to cascading effects on other individuals in the group, for example eviction of other males (Borries, Perlman, & Koenig, 2017), female dispersal (Sicotte et al., 2017), or infanticide and fetus loss (Amann, Pines, & Swedell, 2017). Below, we: (i) review the primate literature and examine explanations for the extent of variability in the process of alpha male replacements; (ii) examine the consequences of alpha male replacements for different individuals in the group; (iii) lay out each replacement process that has been identified and argue for the need of increased consistency in the terms used for each process; (iv) introduce the papers within this special issue on alpha male replacements; and (v) suggest directions for future research.

1.1 | Determinants of variability in alpha male replacements

Two of the most obvious sources of variation affecting alpha male replacements in nonhuman primates are group compositions (i.e., the

number of resident adult males and adult females) and species typical dispersal patterns. When groups contain a single adult male (uni-male, uni-female or uni-male, multi-female), new alpha males must come from outside the group and males must disperse from the natal group. Age-graded groups, in which the alpha male is replaced by a younger resident male, represent a different set of reproductive challenges and these are discussed below. Despite the presence of a single resident adult male, these two types of group compositions (uni-male, uni-female and uni-male, multi-female) show quite different patterns of alpha male replacements (Table 1). Due to the presence of a pair-bond, uni-male, uni-female species may experience lower rates of alpha male challenges and replacements compared to uni-male, multi-female species in which there exists a surplus of extra group males in the population (Butynski, 1982, 1990; Hrdy, 1979). Lower intra-sexual competition for mates is expected in pair-bonded species because of a more equal adult sex ratio (Kvarnemo & Ahnesjö, 1996; Weir, Grant, & Hutchings, 2011). However, in the uni-male, uni-female Azara's owl monkeys (*Aotus azarai*), Fernandez-Duque & Huck (2013) have shown that replacement of either the resident male or female within a pair bond can occur relatively frequently (27 female and 23 male replacements in 149 group-years) and be intensely aggressive if the density of non-mated intruders is high. They argue that population-wide and group specific sex ratios do not always determine the level of intra-sexual competition if non-mated floaters range widely.

For species forming uni-male, multi-female groups, alpha male replacements are reported to occur at a rate between 0.07 and 2.07 per year (Janson & van Schaik, 2000) because of intense competition between resident males and floater males to reproductively monopolize a group of females (Butynski, 1982, 1990; Henzi & Lawes, 1987; Hrdy, 1979; Kvarnemo & Ahnesjö, 1996; Weir et al., 2011). New alpha males generally need to defeat the former alpha in order to take up the dominant position within the group and thus they tend to be prime-aged and in top physical condition (Borries et al., 2017; Marty, Hodges, Agil, & Engelhardt, 2017; van Noordwijk & van Schaik, 2001). Whether or not females disperse in uni-male, multi-female groups may also alter the process of alpha male replacement. Where females do not transfer, female groups tend to be large and therefore extremely attractive to outside males, intensifying the competition for the alpha male position (e.g., *Cercopithecus mitis*, Henzi & Lawes, 1988; *Presbytis entellus*, Newton, 1988). When females transfer, and have more control over group size and which male they associate with, males may become an alpha by attracting females to them and forming a new group rather than ousting another male from an existing group (also called a "female split-merger" (Sterck & van Hooff, 2000)) (e.g., *P. thomasi*, Sterck, Willems, van Hooff, & Wich, 2005; *Gorilla gorilla gorilla*, Stokes, Parnell, & Olejniczak, 2003; *Rhinopithecus roxellana*, Qi, Li, Garber, Ji, & Watanabe, 2009). Though not technically an alpha male replacement, female split-mergers are an important route to new group formation in several primate species.

When groups typically contain more than one male (i.e., multi-male, multi-female or multi-male, uni-female groups) new alpha males can come from within the group or outside the group, depending on the dispersal pattern (e.g., Borries et al., 2017; Clarke, Pradhan, & van Schaik, 2009; Jack et al., 2014; Leimberger & Lewis, 2017). There is a paucity of data on alpha male replacements in multi-male, uni-female species (Table 1) but a wealth of data from multi-male, multi-female species, which show that dispersal patterns are a strong determinant of the source of new alpha males. When males are philopatric, new alpha males necessarily come from inside the group and males attain high dominance rank over time sometimes with aggressive challenges to the alpha male that lead to rank reversals. High rank for males in these species may rely on coalitions with other males (*Pan troglodytes*, Mitani, 2009; Atelins, Strier, 1994) and relationships with high-ranking females (*P. paniscus*, Furuichi, 2011; Surbeck, Mundry, & Hohmann, 2011) to a greater degree than for males in species where males are not philopatric.

In the case of species that form multi-male, multi-female groups in which females are philopatric or both sexes disperse, new alpha males may come from inside or outside the group. Within-group males that become alpha are generally those that immigrated as subordinates and were able to improve their dominance rank over time (e.g., *Propithecus verreauxi*, Leimberger & Lewis, 2017; *M. fuscata*, Sprague, 1992, 1998; *Macaca fascicularis*, van Noordwijk & van Schaik, 2001). In these cases, males usually immigrate before attaining full body size as they are viewed as less of a threat to resident, higher-ranking males. However, in many species, once males reach full body size their immigration attempts are resisted and adult males must aggressively challenge and evict resident males, a process known as a takeover (e.g., *Cebus capucinus*, Jack & Fedigan, 2004; *Colobus vellerosus*, Teichroeb et al., 2011). Immigration of young males into existing groups, even at lower ranks, is not an option in all species. In this volume, Marty et al. (2017) show that crested macaque (*Macaca nigra*) males face strong resistance when they try to immigrate into new groups, which may force these males to wait to disperse. Once they attain large body size and prime physical condition in their natal group, males may be more successful in challenging for the alpha position in a new group. Delayed dispersal by males to avoid competition with prime males before attaining full body size has also been documented in chacma baboons (*Papio ursinus*, Beehner et al., 2009).

Some species that form multi-male, multi-female groups also show a type of alpha male replacement that has been termed succession (Scarry & Tujague, 2012). In these systems, males enter a group as a subordinate and wait for more dominant positions to open up as males disperse or die, with the beta male usually taking the alpha male's place in these instances. Alpha males may disperse if they can attain greater mating success in another group, such as joining a group with more females (e.g., *C. capucinus*, Jack & Fedigan, 2004) or fewer related females (e.g., *P. cynocephalus*, Alberts & Altmann, 1995), or when there is a female mating preference for recent immigrant males (e.g., *M. mulatta*, Berard, 1999). Succession is opportunistic in some species, occurring in a small percentage of alpha male replacements (e.g., *C. capucinus*, Jack et al., 2014) but it also occurs habitually in others like rhesus (*M. mulatta*) and Japanese macaques (*M. fuscata*), where it has also been referred to as queuing (Berard, 1999; Bercovitch, 1997; Georgiev et al., 2016; Kokko & Johnstone, 1999; Manson, 1998; Sprague, Suzuki, & Tsukahara, 1996). In these species, rank among males usually correlates with tenure in the group rather than fighting ability (Vessey & Meikle, 1987).

TABLE 1 Observed processes of alpha male replacement for primate groups with different group compositions

Group composition	Processes	Primate example[a]	References	Best term for process
Solitary/semi-solitary	1. Alpha defends current territory with long calls	*Pongo pygmaeus wurmbii*	Spillman et al. (2017)	Need more data
	2. Dominance determined during each interaction	*Microcebus murinus*	Eberle and Kappeler (2004)	
Uni-male, uni-female	1. Desertion by resident male (within-group subadult pair-bonds with the female)	*Hylobates lar*	Palombit (1994)	Succession
	2. Death of resident male	*Pithecia aequatorialis*	Di Fiore, Fernandez-Duque, and Hurst (2007)	Waltz-in
	3. Resident male killed by new male(s)	*Aotus azarai*	Fernandez-Duque and Huck (2013)	Takeover
	4. Resident male evicted	*Eulemur rubriventer*	Overdorff and Tecot (2007)	Takeover
	5. Resident male deposed but stays (group temporarily becomes multi-male)	*Hylobates lar*	Sommer and Reichard (2000)	Takeover
Uni-male, multi-female	1. Death of resident male	*Presbytis thomasi*	Steenbeek et al. (2000)	Waltz-in
	2. Death of resident male (within-group subadult inherits alpha position—age-graded group)	*Alouatta seniculus*	Pope (1990)	Succession
	3. Resident male killed by new male(s)	*Colobus vellerosus*	Sicotte et al. (2007)	Takeover
	4. Resident male evicted	*Semnopithecus johnii*	Kavana, Erinjery, and Singh (2014)	Takeover
	5. Resident male deposed but stays (group becomes multi-male)	*Theropithecus gelada*	Snyder-Mackler et al. (2012)	Takeover
	6. Females are herded in a new one-male unit (the former alpha remains in the other unit)	*Papio hamadryas hamadryas*	Amann et al. (2017)	Fission
Multi-male, uni-female	No references found			Need more data
Multi-male, multi-female	1. Desertion by or death of alpha male, new alpha from outside the group	*Callithrix flaviceps*	Ferrari and Diego (1992)	Waltz-in
	2. Desertion by all resident males, new alpha from outside the group	*Cebus capucinus*	Fedigan and Jack (2004)	Waltz-in
	3. Death of alpha, new alpha from inside the group	*Mandrillus sphinx*	Setchell, Wickings, and Knapp (2006b)	Succession
	4. Death or dispersal of alpha, beta takes alpha position	*Macaca mulatta*	Berard (1999)	Succession
	5. Alpha killed and replaced by resident male	*Cebus apella nigritus*	Scarry and Tujague (2012)	Rank reversal
	6. Alpha killed and replaced by extra-group male	*Alouatta palliata*	Dias, Rangel-Negrín, Veà, and Canales-Espinosa (2010)	Takeover
	7. Alpha evicted by resident male	*Cebus capucinus*	Gros-Louis, Perry, and Manson (2003)	Rank reversal
	8. Alpha evicted by extra-group male	*Eulemur fulvus rufus*	Ostner and Kappeler (2004)	Takeover
	9. Alpha deposed by resident male but stays	*Papio cynocephalus*	Palombit (2003)	Rank reversal
	10. Alpha deposed by resident who was supported by newly high-ranked mother	*Pan paniscus*	Furuichi (2011)	Rank reversal
	11. Alpha male deposed by extra-group male but stays (follower strategy)	*Macaca fuscata*	Sprague (1992)	Takeover
	12. One large groups splits into sister groups, such that one or both sister groups has a new alpha male	*Papio ursinus, P. papio*	Kalbitzer, Heistermann, Cheney, Seyfarth, and Fischer (2015)	Fission

[a]Though we provide only one example of each process from the literature, there are usually many other examples available.

Age-graded groups may represent a special type of succession, where the alpha male is tolerant of younger male(s) staying in their natal group (Eisenberg, Muckenhirn, & Rudran, 1972) if their presence aids with defense against predators (van Schaik & Höstermann, 1994) or conspecifics (van Schaik, 1996). In some cases, these males are the offspring of the alpha male and one of them may inherit the alpha position in the group when the alpha dies or disperses (e.g., *Gorilla beringei beringei*, Robbins, 1995; *Presbytis senex senex*, Rudran, 1973; *P. thomasi*, Steenbeek, Sterck, de Vries, & van Hooff, 2000).

New alpha males can also come from within the group but attain the dominant position by challenging the current alpha (i.e., rank reversal or rank turnover, Sprague et al., 1996). In Nepal gray langurs (*Semnopithecus schistaceus*), Borries et al. (2017) were able to contrast the outcome of successful alpha male replacements by recent immigrant males (takeovers) versus those where males achieved the alpha position within their own group. They found that the immigrant tactic was used in three quarters of cases and that some of these males were hyper-aggressive, achieving longer alpha tenures (mean of 398 days) than males that attained alpha status through rank reversals (mean of 19 days); however, the immigrant tactic did not yield a greater number of offspring overall.

It is important to note that many primate species show both uni-male, multi-female, and multi-male, multi-female groups in the same population. The occurrence of these two types of group compositions appears to be related to both female group size and a male's ability to monopolize access to these females (Nunn, 1999; Sterck & van Hooff, 2000). Therefore, within the same species, there may be variability in the processes of alpha male replacement (Table 1). Hamadryas baboons (*Papio hamadryas hamadryas*) are an excellent example of a species with variable group composition and several different routes to the alpha male role (Pines, Saunders, & Swedell, 2011; Amann et al., 2017). Within hamadryas multi-level societies, breeding units can be single male or can contain multiple males, when a "follower" male stays in association with a breeding unit. Follower males can attain alpha status by challenging the current alpha, opportunistically taking the dominant position after the alpha male dies or disappears, or peacefully inheriting the alpha position. Solitary males also are present in these societies, and they may challenge the alpha male of a breeding unit or opportunistically gain alpha status after a former alpha dies or disappears; indicating at least five different routes to becoming an alpha male in this species (Pines et al., 2011). Indeed, such variability in the mode to alpha male is common for many species.

Even for primates that do not form permanent groups (i.e., solitary and semi-solitary species), individual's ranges will overlap and one male may be dominant over all others at a given time (Banes et al., 2015; Bearder, 1987; Singleton & van Schaik, 2001). Dominant males can be deposed or replaced, though there are less available observational data on how these interactions occur compared to what we find in group-living primates. In Sumatran orangutans (*Pongo pygmaeus wurmbii*), Spillman, Willems, van Noordwijk, Mitra Setia, and van Schaik (2017) have shown that flanged males may continually update their information on which male is dominant by long calling and with aggressive encounters near sexually receptive females. While in gray mouse lemurs (*Microcebus murinus*), males assert dominance by

mate guarding females during the mating seasons but may not maintain these dominance relationships over the rest of the year (Eberle & Kappeler, 2004).

The occurrence of male parallel dispersal and the formation of all-male bands also represent important sources of variation in the form of alpha male replacements. While males often immigrate into groups alone, immigrating with other males may give them an advantage in replacing the current alpha male because they have coalition partners (Fedigan & Jack, 2013; Pusey & Packer, 1987). For example, in this issue Leimberger and Lewis (2017) found that Verreaux's sifaka (*Propithecus verreauxi*) males that immigrated with partner(s) were more likely to take over the alpha male position (100% success) than those that immigrated alone (0% success). Alpha male replacements by single immigrant males versus those that result from the entrance of a group of males may be very different in terms of their duration and the amount of social upheaval they cause. For example, in ursine colobus monkeys (*Colobus vellerosus*), alpha male replacements by single immigrant males were often over within a few days because these intruder males appeared to be in peak physical condition, whereas when several males immigrated together, the process of alpha male replacement could take up to several months because these were collections of lower-quality males who fought among themselves and with the resident male(s) for the alpha position (Sicotte et al., 2017; Teichroeb et al., 2011, Teichroeb, Wikberg, Badescu, MacDonald, & Sicotte, 2012).

The amount of aggression that occurs during alpha male replacements is variable. In some species, alpha male replacements have been reported to be so aggressive that the former alpha male or other participants were killed or seriously injured (e.g., *Alouatta palliata*, Dias et al., 2010; *Papio hamadryas hamadryas*, Pines et al., 2011; *Cebus apella nigritus*, Scarry & Tujague, 2012; *C. vellerosus*, Sicotte, Teichroeb, & Saj, 2007; *Rhinopithecus bieti*, Zhu et al., 2016). Former alpha males also will often remain in the group (e.g., *S. schistaceus*, Borries, Launhardt, Epplen, Epplen, & Winkler, 1999; Borries, Perlman, & Koenig, 2017; *Theropithecus gelada*, Snyder-Mackler, Alberts, & Bergman, 2012; *C. vellerosus*, Teichroeb et al., 2011). The ability of females to disperse and join certain males over others may quell the amount of aggression that is useful for males due to the fact that those that are overly aggressive are not chosen by females (e.g., *R. roxellana*, Qi et al., 2009). Succession also limits the amount of aggression observed, as subordinate males may more peacefully move into a vacancy in the alpha position (Berard, 1999; Jack et al., 2014). Indeed, in species like rhesus macaques that show succession habitually, physical attributes that help in direct contest competition, like long canines may not be present and scramble competition among males via sperm competition (e.g., large testis) may be evident (Higham, Heistermann, & Maestripieri, 2011; Higham & Maestripieri, 2014). There are cases where no aggression occurs between males because the former alpha male has died or disappeared and new alphas do not face a challenge in joining the group (Table 1). In white-faced capuchins (*C. capucinus*), there are several cases (N = 3) in which all of the resident adult males abandoned their group in favor of another with greater numbers of females, allowing neighboring males to "waltz-in," and take-up residency in the abandoned group without resistance (Fedigan & Jack, 2004).

Finally, the rate at which alpha male replacements occur is variable, both within and between species. As noted above, the likelihood of challenges to the alpha position has been linked to the density of non group males (Butynski, 1982, 1990; Hrdy, 1979; Port & Johnstone, 2013), which may be greater in species with uni-male, multi-female social units (Janson & van Schaik, 2000). Larger female group sizes also may increase the rates at which alpha male replacements occur because these groups are more attractive to non group males (e.g., Beehner & Bergman, 2008; *A. seniculus*, Crockett & Janson, 2000; *T. gelada*, Dunbar, 1984; *C. capucinus*, Fedigan & Jack, 2004). Female reproductive condition also may influence how attractive a group is at a certain time. For example, influxes of floater males enter red tail monkey (*Cercopithecus ascanius*) groups during periods of synchronized female estrus and the competition among the males may lead to long-term changes in the resident male(s) that are present after the mating season (Cords, 1984). Higher rates of alpha male replacements were once thought to be linked with the degree of human disturbance in an area (Curtin & Dolhinow, 1978), however this hypothesis has garnered little support (Newton, 1986, 1988; Reena & Ram, 1992).

1.2 | Outcomes of alpha male replacements

1.2.1 | Female mate choice and infanticide

While alpha male replacements are a manifestation of male-male competition, they also have important effects on the other two mechanisms of sexual selection, female mate choice and sexual conflict (Darwin, 1871; Muller & Wrangham, 2009). Understanding the processes of female mate choice is vital for interpreting the impact of sexual selection in primates (Manson, 2007). However, for species characterized by female philopatry and male dispersal, female mate choice is largely limited to those males that immigrate into their groups. That is, female mate choice may be primarily determined by male-male competition, which establishes male group composition. While extra-group mating opportunities may occur, resident males may use counter-strategies to constrain the mating of within-group females (e.g., mate-guarding, mate-herding, Smuts & Smuts, 1993). If the winner of male-male competition is able to takeover a group and monopolize the females within it, female mate choice becomes a Hobson's choice (i.e., not a real choice, Fedigan, 1982). In other species, females may be able to exercise some control over which male is alpha in the group (*Cebus capucinus*, Gros-Louis et al., 2003; *Miopithecus talapoin*, Rowell, 1974; *Mandrillus sphinx*, Setchell et al., 2006a; *Procolobus badius temminckii*, Starin, 1981) but for most species there is relatively little evidence that females are able to strongly impact the outcome of male-male competition and other counter-strategies such as encouraging multi-male groups, concealed ovulation, and polyandrous mating may evolve (reviewed in Fedigan & Jack, 2013).

When dispersal is an option, females can play an active role in mate choice by leaving the group after an alpha male replacement. For example, in this volume, Sicotte and colleagues (2017) show that female ursine colobus (*Colobus vellerosus*) were more likely to disperse

following the parallel immigration of several low-quality males that competed for the alpha position over an extended period of time, than when the group was taken over by a single apparently higher-quality male that quickly ousted competitors. Previous work had shown that males in uni-male, multi-female groups give more costly displays, emit longer loud calls, and defeat males in multi-male groups in intergroup encounters indicating superior fighting ability (Teichroeb & Sicotte, 2010; Teichroeb et al., 2012). In this species, infanticide by males was a serious risk for females that stayed in their group however mate choice via dispersal only was seen for females that did not have an infant. Dispersal is rarely an option in female philopatric species and has only been reported to occur with any regularity in capuchins (*Cebus* and *Sapajus* species, reviewed in Jack & Fedigan, 2009). In their study of white-faced capuchins (*Cebus capucinus*), Jack and Fedigan (2009) documented that female dispersal most strongly supports the infanticide avoidance hypothesis as dispersal, while still rare, is more likely to occur in association with alpha male replacements than during times of group stability.

Infanticide by the new male following an alpha male replacement has been observed in a wide range of primate species and is considered to be one of the most extreme and costly manifestations of sexual conflict (reviewed in Palombit, 2015). The rate of alpha male replacement is closely linked with the risk of infanticide by males (Amann et al., 2017; Janson & van Schaik, 2000). Killing dependent infants can be beneficial to the new alpha male under conditions in which when freed of their dependent offspring, females resume cycling more quickly than if their infants had lived, allowing the new males to mate with them and potentially sire their own infant (i.e., the sexual selection hypothesis, Hrdy, 1977). This means that when alpha male tenures are long, the rate of infanticide decreases (Clarke et al., 2009; Wikberg et al., 2017). There is empirical evidence that some alpha males can have disproportionately long tenures, for example up to 18 years in *Cebus capucinus* (Perry, 2012), which makes their groups stable over a longer period, and lowers infanticide risk (*Cebus capucinus*, Muniz et al., 2010; *G. b. beringei*, Robbins et al., 2013; *Presbytis thomasi*, Steenbeek et al., 2000; *Colobus vellerosus*, Teichroeb et al., 2011, 2012; Wikberg et al., 2017). In species where males immigrate into the bottom of the hierarchy, large age, and rank differences between incoming and resident males may mean that infanticide is not profitable for new males because they are unlikely to get mating access to a female after her infant dies (Broom, Borries, & Koenig, 2004).

Female counter-strategies to infanticide by males are numerous and may be behavioral, social, and/or physiological (reviewed in Palombit, 2015). According to Amann et al. (2017), within 2 weeks of an alpha male replacement, female hamadryas baboons (*Papio hamadryas hamadryas*) display swellings, regardless of their reproductive condition, and mate with the new alpha male. Socially, these females reinforce one-male units by maintaining strong social ties with their unit male. These authors also report that hamadryas females used the physiological counter-strategy of pregnancy termination following an alpha male replacement (Amann et al., 2017). Known as the "Bruce Effect," this process was first noted in mice whereby spontaneous abortion by pregnant females occurred following exposure to a strange male (Bruce, 1959). Amann et al. (2017) found that female hamadryas

baboons were more likely to experience pregnancy termination in the context of a takeover (~44% of pregnancies) than during other times (~16% of pregnancies). The authors suggest that this counter-strategy enables females to cease investing in the production of an offspring that may be killed by their new alpha male (see also Colmenares & Gomendio, 1988). Stillbirths in the context of alpha male replacements also have been reported in geladas (80% or 8/10 cases where pregnant females were present during a takeover compared to a baseline rate of 2%) (Roberts, Lu, Bergman, & Beehner, 2012). While female hamadryas baboons, like other female primates, are able to employ a wide-range of counter-strategies to adult male infanticide, most are unsuccessful; infant mortality in the species rises from 12.9% during times of group stability to 67% in association with an alpha male replacement (Swedell, Leedom, Saunders, & Pines, 2014).

1.2.2 | Group composition

The composition of a group may affect its susceptibility to alpha male replacements. For example, in some species, groups containing a single adult male show a greater risk of alpha male replacements than do multi-male groups (e.g., *Cebus capucinus*, Fedigan & Jack, 2011; *Alouatta pigra*, Van Belle & Estrada, 2008). This increased risk of alpha male replacements in uni-male groups is thought to be a strong selective factor in the evolution of multi-male systems (Port, Johnstone, & Kappeler, 2010, 2012; Snyder-Mackler et al., 2012) and multi-level societies (Xiang et al., 2014) as this social structure enables males to join forces to defend females against extra-group males. In a mathematical model examining alpha male replacements and infanticide risk, Pradhan and van Schaik (2008) showed that when males vary greatly in their fighting ability and dominant males are disproportionately powerful relative to their competitors, multi-male groups may actually be more prone to alpha male replacements because only the strongest males are able to retain the alpha position in a uni-male group. This is the pattern that has been identified for ursine colobus monkeys, where only 8.5% of males have been found to be able to maintain a position as the alpha male of a uni-male group and multi-male groups show greater rates of alpha male replacement and infanticide (*Colobus vellerosus*, Sicotte et al., 2017; Teichroeb et al., 2012).

Female group size also has been shown to have a profound effect on a group's susceptibility to alpha male replacements such that strategies to curb female group size have evolved (Chapman & Pavelka, 2005; Steenbeek & van Schaik, 2001; Treves & Chapman, 1996). Presumably to counter infanticide risk, females may attempt to maintain smaller group sizes by dispersing from larger into smaller groups, evicting other females, resisting the immigration of new females, or by group fission (*A. seniculus*, Crockett & Janson, 2000; *C. vellerosus*, Teichroeb et al., 2009). When female dispersal is less common, females also may actively encourage the formation and maintenance of multimale groups as a means of increasing male tenure lengths, group stability, and promoting infant survivorship (Fedigan & Jack, 2011).

As mentioned above, the processes of alpha male replacements are variable both inter- and intra-specifically (Table 1) and the process

by which a replacement occurs (i.e., the source of the new alpha male) may or may not cause alterations in group composition. In some alpha male replacements, the former alpha may stay in the group after the immigration of a new male(s), in what is sometimes called a "follower" strategy (e.g., *Theropithecus gelada*, Snyder-Mackler et al., 2012; *M. fuscata*, Sprague, 1992; *Macaca fascicularis*, Wheatley, 1982). This has been suggested to be an infant protection strategy by former alpha males (Borries et al., 1999). Research in geladas (*T. gelada*) also has shown that these follower males may be successful in siring offspring and may lengthen the tenure of the new alpha by aiding in defense against extra-groups males, which stabilizes the group and leads to higher levels of infant survival, with 0.37 surviving offspring per female year versus 0.28 in single-male groups (Snyder-Mackler et al., 2012). In other cases where new alphas immigrate into a group, there is complete replacement of all resident males, particularly in species where coalitions of males oust resident males (e.g., *Cebus capucinus*, Fedigan & Jack, 2013). When new alphas come from within the group, as in rank-reversals or succession, the former alpha may be ousted or remain in the group as subordinate and group composition may remain virtually unchanged (Borries et al., 2017). Alpha male replacements that result in group fission will have the most profound changes on group composition as entire matrilines may split into sister groups, at least one of which will have a new alpha male (e.g., *T. gelada*, Dunbar, 1984; *M. fuscata*, Fukuda, 1989; *Papio ursinus*, Henzi, Lycett, Weingrill, & Piper, 2000; Snyder-Mackler et al., 2012).

Changes to male group composition during alpha male replacements can have important influences on male mating success and reproductive skew within a group. In this issue, Fernández (2017) shows that male Sanje mangabeys (*Cercocebus sanjei*) form clear dominance hierarchies and exhibit skewed mating when male ranks are stable, with the alpha male gaining 75% of copulations, which supports a priority-of-access model. However, after an alpha male and beta male replacement, male rank was unstable, mating skew broke down, and subordinate males managed to achieve greater mating success than dominant males. The new alpha and beta male only achieved 33% of copulations in total during this unstable period. This shows that the social upheaval that occurs during the process of an alpha male replacement can be beneficial to lower-ranking and less competitive males, allowing them greater mating access to females during this time.

2 | TERMINOLOGY

The most frequently used term for alpha male replacements in the primate literature is "takeover." However, this term is limited in its applicability and is used for various situations in different publications. We suggest that to avoid confusion and facilitate comparisons between all of the different processes of alpha male replacements, some consensus needs to be reached regarding the best term for each type of replacement. With the aid of the participants in this special issue of the *American Journal of Primatology*, we have compiled a list of terms that for historical reasons and reasons of clarity, we judge to be

the best terms to use in future research on alpha male replacements. Definitions for these terms are provided below. These terms are based on the source of the new alpha male (i.e., from within or outside the group), but with no mention of the fate of the former alpha male or whether or not the process is accomplished via coalitions. For simplicity, these terms refer only to the mode by which a new male takes up the alpha position in a group. In Table 1, we indicate which of these terms apply to the various circumstances and outcomes surrounding some observed instances of alpha male replacements.

2.1 | Alpha male replacement

A turnover (change in) the alpha male of a group.

2.2 | Types of alpha male replacement

Takeover

An extragroup male uses aggression to "take over" the alpha male position within a group or unit. Other terms used for this process: outside takeover, bluff immigrant.

Rank reversal

A subordinate co-resident male rises to alpha status via aggressive challenge to the current alpha. Other terms used for this process: inside takeover, rank turnover.

Succession

A subordinate co-resident male rises to the dominant position following the death or disappearance of the group's alpha male. This may occur opportunistically or be a habitual form of alpha male replacement in some species. Other term used for this process: queuing.

Waltz-in

An extragroup male becomes alpha by immigrating into an all-female group following the death/disappearance/dispersal of all resident males, including the alpha.

Fission

A group splits into two or more sister groups resulting in a new alpha male in at least one of these new groups.

3 | FUTURE DIRECTIONS

The observation of alpha male replacements is opportunistic, however, because they are a necessary occurrence in all primate species, most primate researchers at long-term field sites have data on these interactions. We encourage the submission of papers describing alpha male replacements in as many species as possible. Data are especially lacking on how alpha male replacements occur in multi-male, uni-female groups, and more information is needed to understand how males in solitary and semi-solitary species attain and maintain their

dominance status. Relatively little data are available on the degree of female control over which male becomes alpha in their group and further research should focus on both the role of female participation in coalitionary action against an intruder male and female mate choice in stabilizing male residence. Research is just beginning on the outcomes and reproductive success of alterative male tactics in gaining alpha status (e.g., Borries et al., 2017; Snyder-Mackler et al., 2012; Wikberg et al., 2017) and this is an exciting new area of inquiry.

REFERENCES

Alberts, S. C., & Altmann, J. (1995). Balancing costs and opportunities: Dispersal in male baboons. *The American Naturalist*, *145*, 279–306.

Amann, A., Pines, M., & Swedell, L. (2017). Contexts and consequences of takeovers in hamadryas baboons: Female parity, reproductive state and observational evidence of pregnancy loss. *American Journal of Primatology*.

Banes, G. L., Galdikas, B. M., & Vigilant, L. (2015). Male orang-utan bimaturism and reproductive success at camp leakey in tanjung putting national park, Indonesdia. *Behavioral Ecology and Sociobiology*, *69*, 1785–1794.

Bearder, S. K. (1987). Lorises, bushbabies, and tarsiers: Diverse societies in solitary foragers. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 11–23). Chicago: Chicago University Press.

Beehner, J. C., & Bergman, T. J. (2008). Infant mortality following male takeovers in wild geladas. *American Journal of Primatology*, *70*, 1152–1179.

Beehner, J. C., Gesquiere, L., Seyfarth, R. M., Cheney, D. L., Alberts, S. C., & Altmann, J. (2009). Testosterone related to age and life-history stages in male baboons and geladas. *Hormones and Behavior*, *56*, 472–480.

Berard, J. D. (1999). A four-year study of the association between male dominance rank, residency status, and reproductive activity in rhesus macaques (*Macaca mulatta*). *Primates*, *40*, 159–175.

Bercovitch, F. B. (1997). Reproductive strategies of rhesus macaques. *Primates*, *38*, 247–263.

Borries, C., Launhardt, K., Epplen, C., Epplen, J. T., & Winkler, P. (1999). Males as infant protectors in Hanuman langurs (Presbytis entellus) living in multimale groups—defense pattern, paternity and sexual behavior. *Behavioral Ecology and Sociobiology*, *46*, 350–356.

Borries, C., Perlman, R. F., & Koenig, A. (2017). Characteristics of alpha males in Nepal gray langurs. *American Journal of Primatology*.

Broom, M., Borries, C., & Koenig, A. (2004). Infanticide and infant defense by males—Modeling the conditions in primate multi-male groups. *Journal of Theoretical Biology*, *231*, 261–270.

Bruce, H. M. (1959). An exteroceptive block to pregnancy in the mouse. *Nature*, *184*(4680), 105.

Butynski, T. M. (1982). Harem-male replacement and infanticide in the blue monkey (*Cercopithecus mitis stuhlmanni*) in the Kibale Forest, Uganda. *American Journal of Primatology*, *3*, 1–22.

Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high and low density subpopulations. *Ecological Monographs*, *60*, 1–26.

Chapman, C. A., & Pavelka, M. S. M. (2005). Group size in folivorous primates: Ecological constraints and the possible influence of social factors. *Primates*, *46*, 1–9.

Clarke, P., Pradhan, G., & van Schaik, C. P. (2009). Intersexual conflict in primates: Infanticide, paternity allocation, and the role of coercion. In M. N. Muller, & R. W. Wrangham (Eds.), *Sexual coercion in primates and humans* (pp. 42–77). Cambridge, MA: Harvard University Press.

Colmenares, F., & Gomendio, M. (1988). Changes in female reproductive condition following male take-overs in a colony of hamadryas and hybrid baboons. *Folia Primatological*, *50*, 157–174.

Cords, M. (1984). Mating patterns and social structure in redtail monkeys (*Cercopithecus ascanius*). *Zeitschrift Fur Tierpsychologie*, *64*, 313–329.

Cowlishaw, G., & Dunbar, R. I. M. (1991). Dominance rank and mating success in male primates. *Animal Behaviour*, *41*, 1045–1056.

Crockett, C. M., & Janson, C. H. (2000). Infanticide in red howlers: Female group size, group composition, and a possible link to folivory. In C. P. van Schaik, & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 75–89). Cambridge: Cambridge University Press.

Curtin, R., & Dolhinow, P. (1978). Primate social behavior in a changing world. *American Scientist*, *66*, 468–475.

Darwin, C. (1871). *The decent of man, and selection in relation to sex*. London: Murray.

Di Fiore, A., Fernandez-Duque, E., & Hurst, D. (2007). Adult male replacement in socially monogamous equatorial saki monkeys (*Pithecia aequatorialis*). *Folia Primatologica*, *78*, 88–98.

Dias, P. A. D., Rangel-Negrín, A., Veà, J. J., & Canales-Espinosa, D. (2010). Coalitions and male-male behavior in *Alouatta palliata*. *Primates*, *51*, 91–94.

Dunbar, R. I. M. (1984). *Reproductive decisions: An economic analysis of gelada baboon social strategies*. Princeton, NJ: Princeton University Press.

Eberle, M., & Kappeler, P. M. (2004). Sex in the dark: Determinants and consequences of mixed male mating tactics in *Microcebus murinus*, a small solitary nocturnal primate. *Behavioral Ecology and Sociobiology*, *57*, 77–90.

Eisenberg, J. F., Muckenhirn, N. A., & Rudran, R. (1972). The relation between ecology and social structure in primates. *Science*, *176*, 863–874.

Fedigan, L. M. (1982). *Primate paradigms: sex roles and social bonds*. Montreal: Eden Press.

Fedigan, L. M., & Jack, K. M. (2004). The demographic and reproductive context of male replacements in *Cebus capucinus*. *Behaviour*, *141*, 755–775.

Fedigan, L. M., & Jack, K. M. (2011). Two girls for every boy: The effects of group size and composition on the reproductive success of male and female white-faced capuchins. *American Journal of Physical Anthropology*, *144*, 317–326.

Fedigan, L. M., & Jack, K. M. (2013). Sexual conflict in white-faced capuchins: It's not whether you win or lose. In M. L. Fisher, J. R. Garcia, & R. S. Chang (Eds.), *Evolution's empress: Darwinian perspectives on women* (pp. 281–303). New York: Oxford University Press.

Fernández, D. (2017). Consequences of a male takeover on mating skew in wild Sanje mangabeys. *American Journal of Primatology*.

Fernandez-Duque, E., & Huck, M. (2013). Till death (or an intruder) do us part: Intrasexual-competition in a monogamous primate. *PLoS ONE*, *8*, e53724.

Ferrari, S. F., & Diego, V. H. (1992). Long-term changes in a wild marmoset group. *Folia Primatologica*, *58*, 215–218.

Fukuda, F. (1989). Habitual fission-fusion and social organization of the Hakone troop T of Japanese macaques in Kanagawa Prefecture, Japan. *International Journal of Primatology*, *10*, 419–439.

Furuichi, T. (2011). Female contributions to the peaceful nature of bonobo society. *Evolutionary Anthropology*, *20*, 131–142.

Georgiev, A. V., Christie, D., Rosenfield, K. A., Ruiz-Lambides, A. V., Maldonado, E., Emery Thompson, M., & Maestripieri, D. (2016). Breaking the succession rule: The costs and benefits of an alpha-status take-over by an immigrant rhesus macaque on Cayo Santiago. *Behaviour*, *153*, 325–351.

Gros-Louis, J., Perry, S., & Manson, J. H. (2003). Violent coaltionary attacks and intrapecific killing in white-faced capuchin monkeys (*Cebus capucinus*). *Primates*, *44*, 341–346.

Henzi, S. P., & Lawes, M. (1987). Breeding season influxes and the behavior of adult male samango monkeys (*Cercopithecus mitis albogularis*). *Folia Primatologica*, *48*, 125–136.

Henzi, S. P., & Lawes, M. (1988). Strategic responses of male samango monkeys (*Cercopithecus mitis*) to a decline in the number of receptive females. *International Journal of Primatology*, *9*, 479–495.

Henzi, S. P., Lycett, J. E., Weingrill, A., & Piper, S. E. (2000). Social bonds and the coherence of mountain baboon troops. *Behaviour*, *137*, 663–680.

Higham, J. P., & Maestripieri, D. (2014). Revolutionary coalitions in male rhesus macaques. *Behaviour*, *147*, 1889–1904.

Higham, J. P., Heistermann, M., & Maestripieri, D. (2011). The energetics of male-male endurance rivalry in free-ranging rhesus macaques, *Macaca mulatta*. *Animal Behaviour*, *81*, 1001–1007.

Hrdy, S. B. (1977). *The langurs of abu—female and male strategies of reproduction*. Cambridge, MA: Harvard University Press.

Hrdy, S. B. (1979). Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, *1*, 13–40.

Jack, K. M., Brasington, L. F., Ritchotte, K., Wikberg, E. C., Kawamura, S., & Fedigan, L. M. (2014). Bide your time: Method of alpha male replacement, infant deaths, and time to conception in *Cebus capucinus*. *American Journal of Primatology*, *76*(suppl 1), 79.

Jack, K. M., & Fedigan, L. M. (2004). Male dispersal patterns in white-faced capuchins, *Cebus capucinus* part 2: Patterns and causes of secondary dispersal. *Animal Behaviour*, *67*, 771–782.

Jack, K. M., & Fedigan, L. M. (2009). Female dispersal in female philopatric species, *Cebus capucinus*. *Behaviour*, *146*, 471–497.

Janson, C. H., & van Schaik, C. P. (2000). The behavioral ecology of infanticide by males. In C. P. van Schaik, & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 469–494). Cambridge: Cambridge University Press.

Kalbitzer, U., Heistermann, M., Cheney, D., Seyfarth, R., & Fischer, J. (2015). Social behavior, patterns of testosterone and glucocorticoid levels differ between male chacma and *Guinea baboons*. *Hormones and Behavior*, *75*, 100–110.

Kavana, T. S., Erinjery, J. J., & Singh, M. (2014). Male takeover and infanticide in Nilgiri langurs *Semnopithecus johnii* in the Western Ghats, India. *Folia Primatologica*, *85*, 164–177.

Kokko, H., & Johnstone, R. A. (1999). Social queuing in animal societies: A dynamic model of reproductive skew. *Proceedings of the Royal Society of London B*, *266B*, 571–578.

Kvarnemo, C., & Ahnesjö, I. (1996). The dynamics of operational sex ratios and competition for mates. *Trends in Ecology and Evolution*, *11*, 404–408.

Leimberger, K. G., & Lewis, R. J. (2017). Patterns of male dispersal in verreaux's sifaka (*Propithecus verreauxi*) at kirindy mitea national park. *American Journal of Primatology*.

Lukas, D., & Clutton-Brock, T. (2014). Costs of mating competition limit male lifetime breeding success in polygynous mammals. *Proceedings of the Royal Society of London B: Biological Sciences*, *281*, 2014–2018.

Manson, J. H. (1998). Evolved psychology in a novel environment–male macaques and the "seniority rule." *Human Nature*, *9*, 97–117.

Manson, J. H. (2007). Mate choice. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 447–463). New York: Oxford University Press.

Marty, P. R., Hodges, K., Agil, M., & Engelhardt, A. (2017). Alpha male replacements and delayed dispersal in crested macaques (*Macaca nigra*). *American Journal of Primatology*.

Mitani, J. C. (2009). Cooperation and competition in chimpanzees: Current understanding and future challenges. *Evolutionary Anthropology*, *18*, 215–227.

Muller, M., & Wrangham, R. W. (Eds.). (2009). *Sexual coercion in primates and humans*. Cambridge, MA: Harvard University Press.

Muniz, L., Perry, S., Manson, J. H., Gilkenson, H., Gros-Louis, J., & Vigilant, L. (2010). Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. *American Journal of Primatology*, *72*, 1118–1130.

Newton, P. N. (1986). Infanticide in an undisturbed forest population of hanuman langurs, *Presbytis entellus*. *Animal Behaviour*, *34*, 785–789.

Newton, P. N. (1988). The variable social organization of Hanuman langurs (*Presbytis entellus*), infanticide, and the monopolization of females. *International Journal of Primatology*, *9*, 59–77.

Nunn, C. L. (1999). The number of males in primate social groups: A comparative test of the socioecological model. *Behavioral Ecology and Sociobiology*, *46*, 1–13.

Ostner, J., & Kappeler, P. M. (2004). Male life history and the unusual adult sex ratios of redfronted lemur, *Eulemur fulvus rufus*, groups. *Animal Behaviour*, *67*, 249–259.

Overdorff, D. J., & Tecot, S. R. (2007). Social pair-bonding and resource defense in wild red-bellied lemurs (Eulemur rubriventer). In L. Gould, & M. L. Sauther (Eds.), *Lemurs: Ecology and adaptation* (pp. 235–254). New York: Springer.

Palombit, R. A. (1994). Dynamic pair bonds in hylobatids: Implications regarding monogamous social systems. *Behaviour*, *128*, 65–101.

Palombit, R. A. (2003). Male infanticide in wild savanna baboons: Adaptive significance and intraspecific variation. In C. B. Jones (Ed.), *Sexual selection and reproductive competition in primates: New perspectives and directions* (pp. 367–412). Norman, OK: American Society of Primatologists.

Palombit, R. A. (2015). Infanticide as sexual conflict: Coevolution of male strategies and female counterstrategies. *Cold Spring Harbor Perspectives in Biology*, *7*, a017640.

Perry, S. (2012). The behavior of wild white-faced capuchins: Demography, life history, social relationships, and communication. In J. Brockmann, T. J. Roper, M. Naguib, L. Barrett, S. Healy, & M. Zuk (Eds.), *Advances in the study of behavior* (pp. 135–181). Burlington, VT: Academic Press.

Pines, M., Saunders, J., & Swedell, L. (2011). Alternative routes to the leader male role in a multi-level society: Follower versus solitary male strategies and outcomes in Hamadryas baboons. *American Journal of Primatology*, *73*, 679–691.

Pope, T. R. (1990). The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. *Behavioral Ecology and Sociobiology*, *27*, 439–446.

Port, M., & Johnstone, R. A. (2013). Facing the crowd: Intruder pressure, within-group competition, and the resolution of conflicts over group-membership. *Ecology and Evolution*, *3*, 1209–1218.

Port, M., Johnstone, R. A., & Kappeler, P. M. (2010). Costs and benefits of multi-male associations in redfronted lemurs. *Biology Letters*, *6*, 620–622.

Pradhan, G. R., & van Schaik, C. P. (2008). Infanticide-driven intersexual conflict over matings in primates and its effect on social organization. *Behaviour*, *145*, 251–275.

Pusey, A. E., & Packer, C. (1987). Dispersal and philopatry. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 250–266). Chicago: University of Chicago Press.

Qi, X. G., Li, B. G., Garber, P. A., Ji, W., & Watanabe, K. (2009). Social dynamics of golden snub-nosed monkey (*Rhinopithecus roxellana*): Female transfer and one-male unit succession. *American Journal of Primatology*, *71*, 670–679.

Reena, M., & Ram, M. B. (1992). Rates of takeovers in groups of Hanuman langurs (*Presbytis entellus*) at Jaipur. *Folia Primatologica*, *58*, 61–71.

Robbins, A. M., Gray, M., Basabose, A., Uwigeli, P., Mburanumwe, I., Kagoda, E., & Robbins, M. M. (2013). Impact of male infanticide on the social structure of mountain gorillas. *PLoS ONE*, *8*, e78256.

Robbins, M. (1995). A demographic analysis of male life history and social structure of mountain gorillas. *Behaviour*, *132*, 21–47.

Roberts, E., Lu, A., Bergman, T. J., & Beehner, J. C. (2012). A bruce effect in wild geladas. *Science*, *335*, 1222.

Rowell, T. (1974). Contrasting adult male roles in different species of nonhuman primates. *Archives of Sexual Behaviour*, *3*, 143–149.

Rudran, R. (1973). Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. *Folia Primatologica*, *19*, 166–192.

Scarry, C. J., & Tujague, M. P. (2012). Consequences of lethal intragroup aggression and alpha male replacement on intergroup relations and home range use in tufted capuchin monkeys (*Cebus apella nigritus*). *American Journal of Primatology*, *74*, 804–810.

Setchell, J. M., Wickings, E. J., & Knapp, L. A. (2006a). Violent coalitional attack by female mandrills against an injured alpha male. *American Journal of Primatology*, *68*, 411–418.

Setchell, J. M., Wickings, E. J., & Knapp, L. A. (2006b). Life history in male mandrills (*Mandrillus sphinx*): Physical development, dominance rank, and group association. *American Journal of Physical Anthropology*, *131*, 498–510.

Sicotte, P., Teichroeb, J. A., & Saj, T. L. (2007). Aspects of male competition in *Colobus vellerosus*: Preliminary data on male and female loud calling, and infant deaths after a takeover. *International Journal of Primatology*, *28*, 627–636.

Sicotte, P., Teichroeb, J. A., Vayro, J. V., Fox, S. A., Bădescu, I., & Wikberg, E. C. (2017). The influence of male takeovers on female dispersal in *Colobus vellerosus*. *American Journal of Primatology*.

Singleton, I., & van Schaik, C. P. (2001). Orangutan home range size and its determinants in a Sumatran swamp forest. *International Journal of Primatology*, *22*, 877–911.

Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. *Advances in the Study of Behavior*, *22*, 1–63.

Snyder-Mackler, N., Alberts, S. C., & Bergman, T. J. (2012). Concessions of an alpha male? Cooperative defense and shared reproduction in multi-male primate groups. *Proceedings of the Royal Society B*, *279B*, 3788–3795.

Sommer, V., & Reichard, U. (2000). Rethinking monogamy: The gibbon case. In P. M. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 159–168). Cambridge, UK: Cambridge University Press.

Spillman, B., Willems, E. P., van Noordwijk, M. A., Mitra Setia, T., & van Schaik, C. P. (2017). Confrontational assessment in the roving male

promiscuity mating system of the Bornean orangutan. *Behavioral Ecology and Sociobiology*, *71*, 20.

Sprague, D. S., Suzuki, S., & Tsukahara, T. (1996). Variation in social mechanisms by which male attained the alpha rank among Japanese macaques. In J. E. Fa, & D. G. Lindburg (Eds.), *Evolution and ecology of macaque societies* (pp. 444–458). Cambridge: Cambridge University Press.

Sprague, D. S. (1992). Life history and male intertroop mobility among Japanese macaques (*Macaca fuscata*). *International Journal of Primatology*, *13*, 437–453.

Sprague, D. S. (1998). Age, dominance rank, natal status, and tenure among male macaques. *American Journal of Physical Anthropology*, *105*, 511–521.

Sprague, D. S., Suzuki, S., & Tsukahara, T. (1996). Variation in social mechanisms by which male attained the alpha rank among Japanese macaques. In J. E. Fa, & D. G. Lindburg (Eds.), *Evolution and ecology of macaque societies* (pp. 444–458). Cambridge: Cambridge University Press.

Starin, D. (1981). Monkey moves. *Natural History*, *90*, 36–43.

Steenbeek, R., & van Schaik, C. P. (2001). Competition and group size in Thomas's langurs (*Presbytis thomasi*): The folivore paradox revisited. *Behavioural Ecology and Sociobiology*, *49*, 100–110.

Steenbeek, R., Sterck, E. H. M., de Vries, H., & van Hooff, J. A. R. A. M. (2000). Costs and benefits of the one-male, age-graded, and all-male phases in wild Thomas's langur groups. In P. M. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 130–145). Cambridge: Cambridge University Press.

Sterck, E. H. M., & van Hooff, J. A. R. A. M. (2000). The number of males in langur groups: Monopolizability of females or demographic processes? In P. M. Kappeler (Ed.), *Primate males* (pp. 120–129). New York: Cambridge University Press.

Sterck, E. H. M., Willems, E. P., van Hooff, J. A. R. A. M., & Wich, S. A. (2005). Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). *Behaviour*, *142*, 845–868.

Stokes, E. J., Parnell, R. J., & Olejniczak, C. (2003). Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behavioural Ecology and Sociobiology*, *54*, 329–339.

Strier, K. B. (1994). Brotherhoods among Atelins: Kinship, affiliation, and competition. *Behaviour*, *130*, 151–167.

Surbeck, M., Mundry, R., & Hohmann, G. (2011). Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proceedings of the Royal Society B*, *278*, 590–598.

Swedell, L., Leedom, L., Saunders, J., & Pines, M. (2014). Sexual conflict in a polygynous primate: Costs and benefits of a male-imposed mating system. *Behavioral Ecology and Sociobiology*, *68*, 263–273.

Teichroeb, J. A., & Sicotte, P. (2010). The function of male agonistic displays in ursine colobus monkeys (*Colobus vellerosus*): Male competition, female mate choice or sexual coercion? *Ethology*, *116*, 366–380.

Teichroeb, J. A., Wikberg, E. C., Badescǔ, I., MacDonald, L. J., & Sicotte, P. (2012). Infanticide risk and male quality influence optimal group composition for *Colobus vellerosus*. *Behavioral Ecology*, *23*, 1348–1359.

Teichroeb, J. A., Wikberg, E. C., & Sicotte, P. (2009). Female dispersal patterns in six groups of ursine colobus (*Colobus vellerosus*): Infanticide avoidance is important. *Behaviour*, *146*, 551–582.

Teichroeb, J. A., Wikberg, E. C., & Sicotte, P. (2011). Dispersal in male ursine colobus monkeys (*Colobus vellerosus*): Influence of age, rank and contact with other groups on dispersal decisions. *Behaviour*, *148*, 765–793.

Treves, A., & Chapman, C. A. (1996). Conspecific threat, predation avoidance, and resource defense: Implications for grouping in langurs. *Behavioral Ecology and Sociobiology*, *39*, 43–53.

Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136–179). Chicago: Aldine Publishing Co.

Van Belle, S., & Estrada, A. (2008). Group size and composition influence male and female reproductive success in black howler monkeys (*Alouatta pigra*). *American Journal of Primatology*, *70*, 613–619.

van Noordwijk, M. A., & van Schaik, C. P. (2001). Career moves: Transfer and rank challenge decisions by male long-tailed macaques. *Behaviour*, *138*, 359–395.

van Schaik, C. P. (1996). Social evolution in primates: The role of ecological factors and male behaviour. *Proceeding of the British Academy*, *88*, 9–31.

van Schaik, C. P., & Höstermann, M. (1994). Predation risk and the number of adlt males in a primate group: A comparative test. *Behavioral Ecology and Sociobiology*, *35*, 261–272.

Vessey, S. H., & Meikle, D. B. (1987). Factors affecting social-behavior and reproductive success of male rhesus-monkeys. *International Journal of Primatology*, *8*, 281–292.

Weir, L. K., Grant, J. W. A., & Hutchings, J. A. (2011). The influence of operational sex ratio on the intensity of competition for mates. *American Naturalist*, *177*, 167–176.

Wheatley, B. P. (1982). Adult male replacement in macaca fascicularis of east kalimantan, Indonesia. *International Journal of Primatology*, *3*, 203.

Wikberg, E. C., Jack, K. M., Fedigan, L. M., Campos, F. A., Sato, A., Bergstom, M., . . . Kawamura, S. (2017). Inbreeding avoidance and female mate choice shape reproductive skew in capuchin monkeys (*Cebus capucinus*). *Molecular Ecology*, *26*, 653–667.

Xiang, Z. F., Yang, B. H., Yu, Y., Yao, H., Grueter, C. C., Garber, P. A., & Li, M. (2014). Males collectively defend their one-male units against bachelor males in a multi-level primate society. *American Journal of Primatology*, *76*, 609–617.

Zhu, P., Ren, B., Garber, P. A., Xia, F., Grueter, C. C., & Li, M. (2016). Aiming low: A resident male's rank predicts takeover success by challenging males in Yunnan snub-nosed monkeys. *American Journal of Primatology*, *78*, 974–982.