

Infant mortality in white-faced capuchins: The impact of alpha male replacements

Lauren F. Brasington¹ | Eva C. Wikberg² | Shoji Kawamura² |
Linda M. Fedigan³ | Katharine M. Jack¹

¹Department of Anthropology, Tulane University, New Orleans, Louisiana

²Department of Integrated Biosciences, University of Tokyo, Kashiwa, Chiba, Japan

³Department of Anthropology, University of Calgary, Calgary, Alberta, Canada

Correspondence

Lauren Brasington, Department of Anthropology, Tulane University, 6823 St. Charles Ave, New Orleans 70118, LA.
Email: lbrasing@tulane.edu

Funding information

Leaky Foundation; Louisiana Board of Regents, Grant number: LEQSF-RD-A-09; Natural Sciences and Engineering Research Council of Canada; National Geographic Society; Japan Society for the Promotion of Science; Nacey Maggioncalda Foundation; School of Liberal Arts Lurcy Fund Newcomb Institute Stone Center for Latin American Studies; Canada Foundation for Innovation Canada Research Chair Program

Infanticide is common in the context of alpha male replacements (AMR), particularly in groups where alpha males experience high reproductive skew and the infants are unlikely to be related to a new alpha male. We examined the relationship between the rate of infant mortality, infant age, and the occurrence and type of AMR in white-faced capuchin monkeys (*Cebus capucinus imitator*) of the Santa Rosa population in Sector Santa Rosa, Área de Conservación Guanacaste. Specifically, we investigated how the source of the new alpha male (coresident or extragroup) and relative aggression level during AMRs influenced infant mortality in this species. Between 1986 and 2015, we recorded 221 births in five study groups. Infants present at the time of an AMR, or born within 5.5 months following an AMR (i.e., conceived prior to AMR), experienced significantly higher mortality than those born during periods of group stability. Infant age was a significant predictor of infant survival, with the probability of surviving increasing by 0.4% for each additional day older an infant was at the time of the AMR. Infant mortality rates did not differ between AMRs by coresident males and extragroup males, possibly because the degree of relatedness between infants and new alphas did not significantly differ between coresident and extragroup AMRs. Infant mortality rates did not differ significantly between aggressive AMRs and more peaceful AMRs. Our results are consistent with predictions derived from the sexual selection hypothesis (SSH) of infanticide and suggest that future studies examine the role of testosterone as an underlying proximate mechanism for the aggression leading to this behavior. We argue that the sexual selection and generalized aggression hypotheses (GAH) of infanticide are best considered as different levels of analysis rather than competing hypotheses.

KEYWORDS

alpha male replacements, capuchin, coresident males, infanticide, male aggression

1 | INTRODUCTION

Infanticide has been documented in 54 species of nonhuman primates from nine distinct families (Palombit, 2015). In many social mammals, infanticide is common in the context of alpha male replacements (AMRs from herein), particularly in groups where

reproductive skew favors the alpha male and infants are unlikely to be related to the new alpha male (e.g., lions, *Panthera leo*, Packer & Pusey, 1983; Packer, 2001; chacma baboons, *Papio hamadryas ursinus* Palombit, 2009; African wild dogs, *Lycaon pictus*, Creel & Creel, 2002). For primates that live in multimale, multifemale groups characterized by male dispersal, AMRs can occur in a variety

of ways (Teichroeb & Jack, 2017). An AMR is termed a *takeover* when an extragroup male aggressively challenges the resident alpha male, sometimes with the aid of coalition partners, and takes over the role of alpha male (e.g., red howlers, *Alouatta seniculus*: Crockett & Pope, 1993; Pope, 2000). AMRs also occur via *rank reversals* whereby a subordinate coresident male rises to alpha status via aggressive challenge to the current alpha male (e.g., chacma baboons: Palombit, 2009). When a group's alpha male dies or disappears because of extrinsic factors (i.e., not caused by aggressive challenge by another male), the subsequent alpha male may come from within the group and need not fight for the position of alpha, a process referred to as *succession* or *queuing* (succession in this paper) (e.g., rhesus macaques, *Macaca mulatta*: Vessey & Meikle, 1987). In cases where a group's alpha dies or disappears and there are no males residing in the group to fill the position, an extragroup male can take up the alpha male vacancy. In such situations, known as *waltz-ins*, the extragroup male (or males) joins an all-female group (e.g., mantled howlers, *Alouatta palliata*: Glander, 1992; white-faced capuchins, *Cebus capucinus*: Fedigan & Jack, 2004). Lastly, an AMR may occur via group *fission*, when a group splits and a subordinate coresident male assumes the alpha position in one of the resultant groups (e.g., geladas, *Theropithecus gelada*: Dunbar, 1986; Snyder-Mackler, Beehner, & Bergman, 2012; chacma baboons: Henzi, Lycett, Weingrill, & Piper, 2000; Japanese macaques, *Macaca fuscata*: Fukuda, 1989).

Increased infant mortality in association with AMRs has been reported for many primate species and has provided general support of the sexual selection hypothesis (SSH) of infanticide (Palombit, 2015). This hypothesis suggests that males who commit infanticide experience increased reproductive success if the following three conditions are met (Hrdy, 1974): (i) the infant is unlikely to be his own offspring; (ii) the infant's death triggers a more rapid resumption of cycling in the mother than if the infant had survived; and (iii) the attacking male mates with the mother of the newly deceased infant.

Although most evidence to date supports the SSH of infanticide (Palombit, 2015; van Schaik, 2000), some researchers argue that infanticide is not an evolved reproductive strategy and rather is simply a byproduct of male aggression that occurs during the chaos of male reproductive competition (Bartlett, Sussman, & Cheverud, 1993). This explanation of infanticide, known as the generalized aggression hypothesis (GAH), is based upon the observation that males in many species exhibit higher rates of conspecific aggression than do females (de Almeida, Cabral, & Narvaes, 2015), a finding that is often linked to the higher levels of circulating testosterone in males (de Almeida et al., 2015; Sobolewski, Brown, & Mitani, 2013; Soma, 2006). In many primates male testosterone increases during times when male-male competition is high, such as during the mating season or during periods of social instability (Marshall & Hohmann, 2005; Sapolsky, 1993).

Here we used 29 years of demographic and behavioral data to describe the types of AMR that occur in wild white-faced capuchin monkeys (*Cebus capucinus imitator*) in the Santa Rosa Sector of the Área de Conservación Guanacaste, Costa Rica. We then used these data to examine the impact of AMRs on infant mortality and

examine a suite of predictions generated from the sexual selection and generalized aggression hypotheses (GAH) based on our past observations of this species.

1.1 | Study species

White-faced capuchin groups typically consist of 15 members with nearly equal numbers of adult males and females (Fedigan & Jack, 2013). Females are philopatric, and males disperse from their natal group at approximately 4 years of age. Males continue to transfer between groups throughout their lives at approximately 4-year intervals. Most males disperse in the company of other males or join a group that contains former group mates, some of which are relatives (Jack & Fedigan, 2004a, 2004b; Perry, 2012; Wikberg et al., 2014). This pattern of parallel dispersal remains strong throughout all life history stages (Jack & Fedigan, 2004b; Perry, 2012) and although closely related males often disperse together (mean R of dispersing partners = 0.28), the overall relatedness among all coresident males is low (Wikberg et al., 2014) (i.e., as a whole, group males are not closely related to each other despite the presence of closely related male pairs).

White-faced capuchins are considered moderately seasonal breeders (Carnegie, Fedigan, & Melin, 2011) with long interbirth intervals (mean = 1.89 years for all intervals; mean = 2.25 years when the prior infant lives; mean = 1.05 when prior infant dies; range: 0.67–5.58) (Fedigan, 2003; Fedigan, Carnegie, & Jack, 2008) and a relatively late age at weaning (14–23 months) compared to other primate species of similar size (Sargeant, Wikberg, Kawamura, & Fedigan, 2015). All group males experience some degree of mating success and, although overt male-male mating competition is rare (Schoof, Jack, & Ziegler, 2014), non-conceptive copulations are common especially between subordinate males and pregnant females (Carnegie, Fedigan, & Ziegler, 2006). Despite this multimale mating pattern, paternity data indicate that an alpha male sires the majority of group infants, although subordinate males father some infants, particularly when alpha males have long tenures (Godoy, Vigilant, & Perry, 2016a; Jack & Fedigan, 2006; Muniz et al., 2010, 2006; Wikberg et al., 2017).

Alpha male tenure lengths are highly variable in white-faced capuchins, lasting from a period of days up to 18 years (Perry, Godoy, & Lammers, 2012). Although intragroup male-male aggression is rare during times of group stability (i.e., when male group membership and dominance hierarchies are not in flux) (Fedigan, 1993; Jack, 2003), it escalates during periods of group instability (Fedigan, 2003). Under such circumstances, male-male aggression can result in lethal wounds to adult males (Gros-Louis, Perry, & Manson, 2003) and infant deaths or disappearances are common (Fedigan, 2003; Kalbitzer et al., 2017). Infanticide has also been observed, although more rarely, during times of group stability (Schoof, Wikberg, et al., 2014).

In this study, we examined the frequency and manner in which AMRs occur in this species. We then compared infant mortality rates during periods of group stability with times when groups experienced AMRs. For AMR periods only, we examined the predictive value of the

following variables on infant survival to 1 year of age: infant age at time of AMR, the source of the new alpha male (coresident or extragroup), aggression level associated with the AMR, relatedness between infant and new alpha male, and relatedness between incoming and outgoing alpha males. Collectively, these data enabled us to examine the following predictions derived from the sexual selection and GAH:

P1: Infant age, infant mortality, and AMRs.

In accordance with the SSH, we predicted that younger infants would be more likely to die in the context of AMRs. Younger infants (including those conceived prior to, but born after, the AMR) should be at greater risk of infanticide because the reproductive benefit to a male is higher as females experience shorter interbirth intervals after losing a young, heavily nursing, infant as compared to losing an older infant (Hrdy, 1979; van Schaik, 2000). Juveniles are very rarely injured in the context of AMRs in this population (observed in just 1 of 15 AMRs in a previous study Fedigan, 2003), perhaps because their death will have little impact on female interbirth intervals.

In contrast, the GAH argues that infants are not specifically targeted by aggressive males (Bartlett et al., 1993). Therefore, infant age should not be a significant predictor of mortality risk from male aggression (GAH).

P2: Source of the new alpha male (extragroup or coresident) and infant mortality.

The SSH predicts that males will not kill their own offspring, and previous studies of infanticidal attacks in multiple primate species have shown that attacks on infants were not carried out by their genetic sires (Nepal gray langurs, *Semnopithecus schistaceus*: Borries, Laundhard, Epplen, Epplen, & Winkler, 1999; Japanese macaques: Soltis, Thomsen, Matusabayshi, & Takenaka, 2000; white-faced capuchins: Schoof, Wikberg, et al., 2014). All coresident male white-faced capuchins mate with group females (Fedigan & Jack, 2013), and subordinate males do sire some offspring (Wikberg et al., 2017). Extragroup copulations, in contrast, are very rare (Godoy, Vigilant, & Perry, 2016a), and extragroup paternity has not been found in our study population (Wikberg et al., 2017). In the only documented case from the nearby Lomas Barbudal population of this same species, the sire was a familiar former coresident from the female's natal group (Godoy et al., 2016b). Collectively, these findings indicate that although coresident subordinate males who become alphas may have sired group infants, this is unlikely to be the case for new alpha males coming from outside of the group. Males may also be related to group infants if their male kin, with whom they often reside because of parallel dispersal (Wikberg et al., 2014), sire offspring.

In accordance with the SSH we predicted (P2) that infant mortality rates would be lower when infants have the potential to be related to the new alpha male. In the absence of paternity data for most infants during their first year of life, we used the source of the new male as a proxy for male-infant relatedness as coresident males who become alphas have a higher probability of having sired group infants than do

extragroup males who become alphas. Therefore, we expect that (P2a) infant mortality should be lower for coresident male AMRs than extragroup males AMRs. In addition, we expect that (P2b) infant mortality rates to be lower when the new and old alpha males are related to each other.

No difference in the rates of infant mortality is expected by the GAH, either according to male source or relatedness between the new male and the former alpha male or infant.

P3: Aggression level associated with AMRs and infant mortality.

We examined the relationship between infant mortality and the relative aggression level (peaceful or aggressive) associated with the various types of AMRs observed during our study. The SSH does not make any predictions regarding an association between an infant's likelihood of dying and overall aggression levels during AMRs. Based on the role of aggression in the GAH, we predicted that higher rates of infant mortality would be associated with more aggressive AMRs than in association with more peaceful AMRs.

2 | METHODS

2.1 | Study site

Five groups of white-faced capuchins were studied for variable periods between 1986 and 2015 in the Santa Rosa Sector, Área de Conservación Guanacaste, Costa Rica. Santa Rosa consists of 108 km² of protected tropical dry forest in northwest Costa Rica that includes remnants of original evergreen forests in addition to riparian, oak, and mangrove forests, as well as former cattle pastures regenerating in various seral stages (Fedigan & Jack, 2012). Study groups are censused by members of our research team, at minimum, twice per month and for most study years they were the focus of intensive behavioral, and ecological studies by various graduate students and PIs. Our long-term data collection protocol involves the continuous recording of all demographic events (e.g., infant births, deaths, immigrations, and emigrations) as well as behavioral data on group dominance hierarchies based on the direction of aggressive and submissive signals.

The alpha male of a group is discernable based on his behavior (e.g., piloerection, high rates of vigilance), the behavior of other group members (e.g., specialized gargle vocalizations are directed toward him by group immatures), and morphological cues such as increased body mass (see Fragaszy et al., 2016 for reports of similar weight gain in the closely related *Sapajus*; Jack, Schoof, Sheller, Rich, & Klingelhofer, 2014). Given the rarity of aggression among coresident males during stable periods, we were unable to discern ranks of non-alpha males and we distinguish alpha versus subordinate males only (Schoof & Jack, 2013). We carefully recorded the process of AMRs in our study groups, noting the presence and absence of wounding, deaths, or disappearances of group members, and the movement of males between groups (Table 1).

TABLE 1 Summary of AMRs from 1986 to 2015, including details on wounds.

AMR Date ^a	AMR Type ^b	Wounds recorded	Contest for Alpha ^c (Y/N)	Notes ^d
CP2007	SU	No	No	All resident ADM (N = 2) and SADM (N = 1) disappear from group
EX2007	SU	No	No	Alpha male disappears following intergroup encounter (IGE); sole remaining male in group becomes alpha
EX2013	SU	No	No	SADM becomes alpha when former alpha and younger SADM disappear following IGE; the younger SADM returns weeks later with healing wounds thought to be from TO attempt of other group with former alpha
LV2006-1	SU	Yes—minor (see details)	No	Alpha, 1 ADM, and 1 SADM leave group; sole remaining ADM becomes alpha; 1 SADM peacefully joins group 1 month later and 1 young ADM joins peacefully 3 months later; the males seem familiar with one another; 1 minor wound noted on juvenile's mouth (source unknown)
LV2006-2	SU	No	No	Alpha disappears; sole ADM becomes alpha (only 1 SADM in group with him)
GN2011	SU	Yes	Yes	Alpha and Beta male (brothers) disappear following an IGE; 3 ADM remain in group, two of which jostle for alpha over a 1 month period and both sustain minor wounds
CP2012	FI	No	No	Occurred gradually over several months, with group first splitting during the day and eventually occupying different sleep trees; no aggression observed between males or females during the transition
LV1998	RR	Yes	Yes	3 ADM in group; 2 subordinates aggressively overthrow and oust alpha male who is badly injured (as are other males); Beta rises to alpha uncontested by other ADM in group
GN2010	RR	Yes	Yes	Alpha, 1 ADM, 1 Infant disappear following a lot of fighting between alpha and beta male (who were ½ siblings); 2 ADM, and 5 SADM remain in group; 2 ADM fight for alpha status and both are wounded; beta male alpha ascends and former alpha returns as subordinate
CP1990	TO	Yes	Yes	1 extragroup ADM wounds resident alpha; 2 resident SADM in group remain, but former alpha is badly wounded and stays on as subordinate
CP1993	TO	Yes	Yes	3 ADM, 1 SADM extragroup males attack group and kill alpha; many group members die
LV1997	TO	Yes	Yes	2 extragroup ADMs badly wound resident alpha (lone male in group); attacking males are also seriously wounded. Some ADF also sustain more minor wounds
LV2000	TO	Yes	Yes	3 ADM aggressively enter group; alpha male is killed, beta male remains in group as subordinate (also wounded); most group females are wounded; two infants are observed within days of the TO
LV2004	TO	Yes	Yes	3 extragroup ADMs and 2 SADM aggressively challenge and oust 2 resident ADM; all males display heavy wounds (cuts or faces and arms, torn ear, etc. females and several immatures also display wounds frequent fighting between females and the new males occurs
LV2012b	TO	Yes	Yes	2 extragroup ADMs oust resident males (1 ADM and 1 SADM); former alpha badly wounded; 4 ADFs also sustain more minor wounds
EX2012	TO	Yes	Yes	Extragroup ADM and 2 SADM fight and oust resident male (large immature male leaves with former alpha); all males sustain minor wounds as does 1 ADF
SE1989	WI	No	No	Massive male movement in all study groups; All SE males emigrate (many takeover/join neighboring study groups); CP ADM "waltzes into" SE with no contest
CP1989	WI	No	No	Massive male movement in study groups; All CP group males except 1 SADM disappear (2 ADF with juveniles disappear at same time—possible group fission, but there was no prior indication of this and they are not seen again); 1 ADM, 1 SADM, and juvenile male move in, uncontested from neighboring group; no fighting or wounds noted
SE1991	WI	No	No	Former alpha believed to have died (very old); ADM from neighboring group transfers in and becomes alpha; no fighting or wounds observed (no other ADM or SADM males in the group)
LV1993	WI	No	No	4 resident ADM and 2 SADM disappear leaving the group without any resident males; two adult males (one young, one prime age) show up in group with no fighting among them for alpha position, no wounds noted
LV2012a	WI	No	No	Former alpha (sole male in group) disappears following an IGE; one young ADM and SADM begin transitioning into the group that same day (over a 2 week period)
LV2012	WI	No	No	Alpha disappears from group and 3 extragroup ADMs become resident several days later; possible wounds on former alpha (not observed) but no wounds on any of the new group males

ADM, adult male; SADM, subadult male; IGE, intergroup encounter.

^aAMR date includes group (CP, EX, LV, GN, and SE) experiencing the AMR and year of AMR.^bAMR Type: SU, succession; FI, fission; RR, rank reversal; TO, takeover; WI, waltz-in.^cContest = yes means that there were other males vying for the alpha position; Coded as no when there were no other males present in the group to contest the rise of a male to alpha status or no fighting was observed in the transition.

Data collection protocols were approved by both the Tulane University IACUC and the University of Calgary's LESACC, and our research adhered to the legal requirements of Costa Rica and the United States as well as the American Society of Primatologists principles for the ethical treatment of primates.

2.2 | Inclusion of infant subjects

We considered white-faced capuchins as infants from birth to 1 year of age when they become more independent in travel and foraging, although nursing typically continues into the second year of life (Fedigan, 2003; Sargeant et al., 2015). Infants that disappear are presumed dead, as juveniles less than 2-year old have never been observed to disperse successfully (Jack & Fedigan, 2004a). All infants born during the study period ($N = 221$) were included in the analysis of infant survival and group stability. Although our team has directly observed, and indirectly inferred, many instances of infanticide, here we do not distinguish between various causes of infant mortality (i.e., infanticide, natural death, disappearances).

For analyses of infant mortality during AMRs, we included all infants that were deemed as "at risk" during an AMR. Following Kalbitzer et al. (2017), we defined an infant to be at risk if its group experienced an AMR between its conception (inferred at 5.5 months before its birth Carnegie et al., 2011) and reaching 12 months of age.

2.3 | Genetic kinship analysis

We collected fecal samples for subsequent DNA extraction, DNA quantification, amplification of 20 short tandem repeat loci, and capillary electrophoresis (Wikberg et al., 2014, 2017). We were able to determine genotypes for 122 offspring, 40 adult females, and 36 adult males (Wikberg et al., 2014, 2017). Mother-offspring relationships were known from the observation records and confirmed with genetic data (i.e., sharing at least one allele at each locus). Sire-offspring relationships were assigned at the 95% confidence level in the software Cervus (Kalinowski, Taper, & Marshall, 2007; Marshall, Slate, Kruuk, & Pemberton, 1998) as described in Wikberg et al. (2017). Estimated relatedness (R) values for males were computed in the software MLRelate (Kalinowski, Wagner, & Taper, 2006). Male dyads with an R of 0.23 or higher were categorized as close kin, because this threshold corresponds to the lower 99% confidence interval for known half-siblings and grandparent-grandoffspring, which does not overlap with that of known non-kin (Wikberg et al., 2014).

2.4 | Statistical analysis

We used a Fisher exact test to examine whether the proportion of AMRs with and without wounds differed between the types of AMRs with a sufficient sample size (SU, TO, WI). To pinpoint where the difference was, we tested each pair of AMR type using Fisher exact tests and the Holm–Bonferroni method to correct p values for multiple testing.

We tested whether infant survival to age 12 months (yes/no) differed between periods of stability and AMRs using generalized linear mixed models (GLMMs) with binomial distribution and a logit link function. We included group ID and mother ID as random effects because characteristics such as home range quality and mother sociality or dominance rank may affect infant survival (Kalbitzer et al., 2017). We tested whether this model was significantly better than a null model that contained only the random effects using a Likelihood Ratio Test (LRT).

We further used GLMMs with binomial distribution and a logit link function to determine whether infant survival to age 12 months during AMRs (yes/no) was associated with any of three fixed effects: the infant's age at the time of the AMR, the source of the alpha male (extragroup or coresident), and the presence of aggression during the AMR. We included group and male ID as random effects because the propensity to commit infanticide may differ between males. We dropped non-significant fixed effects from the full model (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We tested the optimal model against a null model containing the random effects only using a LRT. We also repeated this analysis with a smaller subset of infants that were present during AMRs involving new and old alphas whose kinship we had determined with genetic data. In addition to the fixed and random effects listed above, we also included the kinship status of the previous alpha to the new alpha as a predictor of infant survival. We conducted the analyses using lme4 (Bates, Maechler, Bolker, & Walker, 2015) in R and set the significance level to $p < 0.05$.

3 | RESULTS

3.1 | Alpha male replacements

We documented 21 AMRs during the study period: 7 takeovers, 2 rank reversals, 6 successions, 5 waltz-ins, and 1 fission. The various types of AMRs differed greatly in terms of observed aggression and wounding patterns between adult males (Table 1). All takeovers and rank reversals were associated with severe wounding of one or more adults and in at least two cases these wounds were lethal to the former alpha male. There were only two incidences of wounding noted in the remaining AMRs (all successions, waltz-ins, and fissions); two males sustained minor wounds as they jostled for the alpha position, and a juvenile sustained a very minor cut near his mouth, the source of which was unknown. There was a significant difference in wounding among the different types of AMR (Fisher's exact test, 2-tailed $p < 0.001$). The proportion of AMRs with wounds was significantly different between successions and takeovers (Fisher's exact test, 2-tailed $p = 0.042$), and between waltz-ins and takeovers (Fisher's exact test, 2-tailed $p = 0.002$), whereas this was not the case for succession and waltz-ins (Fisher's exact test, 2-tailed $p = 0.456$). The small sample sizes for rank reversals and group fissions precluded tests of differences between those types of AMRs and other categories of AMR. Following this pattern of wounding and relative aggression, we collectively labeled takeovers and rank-reversals as *aggressive AMRs* ($n = 9$) and succession, waltz-ins, and fissions as *peaceful AMRs* ($n = 12$).

3.2 | Infant mortality rates

A total of 221 infants were born during the study period. Of these infants, 72 died at ≤ 1 year, resulting in an overall infant mortality rate of 33% (Table 2). Of the 221 infants, 57 were born during periods associated with group instability because of the occurrence of an AMR. Infant mortality was almost twice as high during AMRs (29 of 57 infants died = 51% mortality) than during periods of group stability (43 of 164 infants died = 26% mortality) (Table 2). Only four AMRs were not associated with infant deaths; two of these groups did not contain infants (one succession and one waltz-in), the third group had two infants aged 10 months both of which survived (succession), and the fourth contained a 7-month-old infant that survived (takeover). All types of AMRs were associated with higher infant mortality rates than were recorded during periods of group stability (Table 2). Our GLMM predicting infant survival to 1 year as a function of group stability (yes/no) was significantly different from a null model with only random effects (LRT, $\chi^2(1) = 11.259$, $p < 0.001$, $N = 221$). Group stability predicted infant survival, and the odds ratio indicates that the chance of surviving rather than dying was almost three times higher during group stability than during AMRs (OR = 2.91, reference category = AMR, $p < 0.001$).

In the GLMM predicting survival to 1 year for infants born during AMRs ($N = 57$), infant age at AMR was the only significant predictor (OR = 1.004, $p = 0.048$; P1). As age was measured in days, the odds ratio indicates that for each day older an infant was at the time of an AMR, there was a 0.4% greater chance of survival. Source of the new alpha male (P2a) and relative aggression level of the AMR (P3) did not have significant effects and were not included in the optimal model. The GLMM with infant age as a predictor was significantly better than the null model (LRT, $\chi^2(0) = 4.153$, $p < 0.001$).

In light of these results, we further examined the mortality rate and mean age at death (for infants that do not survive the first year of life) by separating out those present at the time of the AMR and those born within 5.5 months post-AMR (i.e., those conceived prior to the AMR and most likely sired by the previous alpha male). For infants present at the time of an AMR the mortality rate was 45% and mean age at death was 211.7 days (range: 27–332 days; $n = 17$; P1), while the mortality rate for infants born post-AMR is 63% and the mean age at death was

43 days (range: 0–115 days; $n = 12$; P1). The mean age at death for infants born during times of group stability was 125 days ($n = 43$).

We were able to determine paternity for 13 of 28 infants that survived an AMR (other survivors dispersed or perished prior to sampling). While all 13 surviving infants occurred in association with coresident AMRs (P2a), only 3 (23%) were sired by the new alpha male prior to his ascension (3 successions; P2), seven infants were sired by the old alpha male (3 rank reversals, 3 successions, 1 fission), and the remaining three infants were sired by a subordinate male who did not become alpha (1 succession, 2 fissions).

We repeated the analysis of infant survival during periods of AMR in a smaller subset of infants present during AMR involving a new and old alpha male whose kinship could be determined ($N = 42$ infants). Male kinship did not have a significant effect on infant survival (P2b) and was not included in the optimal model (as well as male source and presence of aggression, similar to the previous analysis). The optimal model only included the fixed effect infant age (OR = 1.005, $p = 0.019$; P1), and it was significantly better than the null model (LRT, $\chi^2(0) = 6.313$, $p < 0.001$).

4 | DISCUSSION

Infant mortality in association with AMRs (51%) was nearly double the rate observed during times of group stability (26%). These results closely align with those reported in a sample of 210 infants from the Lomas Barbudal population of this species, where infant mortality was 49% during unstable periods and 18% during times of group stability (Perry et al., 2012). Similar increases in infant mortality in association with AMRs have been reported for a variety of other species, such as geladas and white-thighed colobus monkeys (*Colobus vellerosus*) (Beehner & Bergman, 2008; Teichroeb & Sicotte, 2008). Although these findings alone do not distinguish between the sexual selection (SSH) and the GAH of infanticide, most researchers that find a link between AMRs and infanticide conclude with support for the SSH over the GAH because of specific lines of evidence in their various studies that made the GAH unlikely to be at work. For instance, in their study of infanticide in geladas, Beehner and

TABLE 2 Table of infant births, survivals through first year, deaths before 1 year based on group stability or type of AMR

	Infants born	#Surviving	#Die	Mortality rate	Mean age at death (days)
All years	221	149	72	33%	131.8
Periods of group stability	164	121	43	26%	125.0
Periods of group instability	57	28	29	51%	141.9
Takeover (A/E) ($n = 7$)	15	6	9	60%	139.0
Rank reversal (A/C) ($n = 2$)	7	4	3	43%	44.3
Succession (P/C) ($n = 6$)	20	10	10	50%	143.4
Fission (P/C) ($n = 1$)	5	3	2	40%	111.5
Waltz-in ($n = 5$) (P/E)	10	5	5	50%	214.8

#, number; A, aggressive; P, peaceful; E, extragroup male; C, coresident male. Mean age at death is calculated for infants that do not survive the first year of life.

Bergman (2008) discounted the GAH as most infant deaths related to AMRs "occurred at least a few days after the takeover when levels of aggression were low" (Beehner & Bergman, 2008, p. 1157). In the white-thighed colobus monkeys, the GAH was not supported because aggression was directed at infants and ceased after the infant was killed (Teichroeb & Sicotte, 2008).

Our first prediction (P1), that younger infants would be at greater risk of infanticide than older infants, was supported; indeed infant age at the time of an AMR was the only significant predictor of infant survival in the model. According to our analysis, an infant's chance of surviving to 1 year increases by 0.4% for each subsequent day older it is at the time of the AMR. This means that, for example, an infant aged 1-month at the time of an AMR has a 12% greater chance of surviving to age 1 than an infant born on the day of an AMR. Following this logic, infants aged 250 days (8.3 months) or older should survive an AMR, an upper threshold that is consistent to what has been reported for several other primate species. For example, in geladas most infants attacked in the context of AMRs are under 7 months of age (Beehner & Bergman, 2008), in brown capuchins (*Sapajus [apella] nigritus*) the new alpha male kills nearly all of the infants aged 8 months or younger (Janson, Baldovino, & Di Bitetti, 2012), and white-thighed colobus infants attacked in the context of AMRs are 6-month old or younger (Teichroeb & Sicotte, 2008).

This age threshold should coincide with the age at which the death of an infant will no longer influence female fertility and infants above this threshold, in accordance with the SSH, should be less at risk than those below this threshold. This appears to be the case for the examples provided above where the mean age for infants targeted during AMRs is well below weaning age (geladas wean at ~23 months Lu, Reitsema, Beehner, Bergman, & Snyder-Mackler, 2017; brown capuchins: 12–18 months Frigaszy, Visalberghi, & Galloway, 1997; white-thighed colobus: ~1 year Saj & Sicotte, 2005). It is widely known that nursing impedes the resumption of cycling post-partum, but the length of the infertile period is not well known for many species. In a controlled laboratory study examining the impact of nursing on fertility in female brown capuchins (*Sapajus [Cebus] apella*), Recabarren, Vergara, Martinez, Gordon, and Serón-Ferré (2000) found that females who nursed their young did not resume cycling until 5.3 months post-partum, after which they remained infertile for an additional 10 months (total period of infertility = 15 months). In contrast, those females who did not nurse their infants resumed cycling within 1.5 months, though remained infertile for an additional 5 months, conceiving ~6.5 months post-partum. Based on these data, the death of an infant of 10 or more months of age will have little to no impact the timing of the female's next conception. It is likely, that given their greater range of weaning ages and longer interbirth intervals in comparison to brown capuchins, female white-faced capuchins experience an even longer period of post-partum infertility, which is perhaps why we see infants as old as 322 days (10.7 months) disappearing in association with AMRs.

Although we did have infants older than 8.3 months perish in association with AMRs, the mean age at death was actually much

younger at 4.7 months, a figure closer to the mean age at death for infants born during periods of group stability (4.1 months). Interestingly, when we included only those infants alive at the time of an AMR, the mean age at death increased dramatically to 7 months with an overall mortality rate of 45%. It appears then, that those infants born in the 5.5 months following an AMR (i.e., conceived prior to the AMR), were driving the relationship that we found between infant age and risk of mortality during an AMR. These infants experienced an outstanding 63% mortality rate and the mean age at death was a mere 1.5 months (age = 0–115 days), much younger than the age at death during stable periods. If they survive, these very young infants do, of course, pose the greatest challenge to the future reproductive opportunities of a new alpha male as these new mothers will not successfully conceive again for ~1.8 years (IBI for females with surviving infants is 2.2 years).

It is possible that young infants perish because of their increased vulnerability to injuries in comparison to older individuals. For instance, attacks by adult male Australian sea lions (*Neophoca cinerea*) on pups less than 2-month old have been explained as "misdirected aggression" (Higgins & Tedman, 1990, p. 618) as the pups did not die instantaneously, but instead succumbed to their injuries after suffering from wounds that would likely not kill an older animal. Such evidence has been used to support the GAH in social mammals. However, we have observed infants being killed by new alphas as much as 90 days following an AMR (mean = 45 days for six observed infanticides) or disappear at an average of 98 days post-AMR (including all infant deaths and disappearances (see Beehner & Bergman, 2008 for similar findings in geladas; Jack & Fedigan, in press). Collectively, these data align with predictions derived from the SSH rather than the GAH as many infants die or disappear long after the initial aggression associated with some AMRs has ceased (Jack & Fedigan, in press).

Our second prediction (P2) that infant mortality would be lower in association with AMRs where the new alpha had the potential to be related to group infants was not supported. Although infant mortality rates appeared higher in association with extragroup AMRs (56%) than coresident AMRs (47%) where males would have had the potential to mate with females and sire these infants, male source was not a significant predictor of infant mortality. Further analyses showed that infant survival was also not associated with kinship between the new and old alpha males and that surviving infants were not always sired by the new coresident alpha male prior to his ascension to alpha. Unfortunately, we cannot rule out that coresident males who rise to alpha status are not killing their own infants, as in most cases we do not have genetic samples from these infants prior to their death or disappearance. We do, however, have genetic data from one AMR where an alpha male was observed to kill a 4-day old infant that was born more than 2 months after his ascension to alpha via rank reversal. In this case, we were able to confirm that the former alpha male was the sire of the infant that perished (K. Jack, unpublished data).

Although our results indicate that male source does not predict infant survival, coresident males sired all of the 13 surviving infants

for which we have paternity data. This may potentially provide evidence that female strategies to confuse paternity (i.e., concealed ovulation and mating with all group males) actually work despite high reproductive skew. In observed instances of infanticide in wild nonhuman primates, the genetic sire has killed his own offspring in only 2–6% of cases at the most (van Schaik, 2000). Additionally, there are no reported instances of a genetic sire killing his own offspring in this species and infanticidal males have been described as being “quite tender,” rather than violent, with their infant offspring (Perry, 2012). Although our recent studies found little evidence of paternal kin recognition in this species (Sargeant, Wikberg, Kawamura, Jack, & Fedigan, 2016; Schoof, Wikberg, et al., 2014), this is an area in need of further investigation. However, the fact that coresident males do indeed commit infanticide, and at a rate not significantly less than that of extragroup males, suggests that having mated with a particular female is not enough to deter a male from killing her subsequent infant.

Our final prediction (P3), that relatively more aggressive AMRs (takeovers, rank reversals) are associated with higher rates of infant mortality than are more peaceful AMRs (waltz-ins, successions, fissions), was not supported. Infant mortality rates for both aggressive AMRs (55%) and peaceful AMRs (49%) were close to double the infant mortality rate during times of group stability, indicating that infant mortality in AMRs is not solely a product of increased aggression during these times. This finding may be a function of our sample size, which necessitated us to lump AMRs according to relative aggression levels. It is clear in examining the patterns of aggression associated with each AMR (Table 1) that takeovers, which were the most frequently observed type of AMR ($N = 7$), are indeed the most aggressive. Takeovers were also associated with the highest infant mortality rates (60%) and there were at least two cases in which alpha males died following wounds sustained during these AMRs.

The challenge hypothesis suggests that levels of testosterone increase with aggressive encounters between males (Wingfield, Hegner, Dufty & Ball, 1990). Thus, aggressive AMRs, which are characterized by the presence of aggressive interactions between males, potentially result in higher levels of testosterone in participating males. Rodent studies point to a link between testosterone and infanticide (Rosenberg, 1974; Rosenberg, Denenberg, Zarrow, & Frank, 1971), whereby aggressive male–male encounters and the resulting increase in testosterone levels may provide a mechanism for increasing infanticide rates. However, the lack of overt male–male aggression in peaceful AMRs does not mean that changes in testosterone levels are not occurring. Schoof, Jack, and Carnegie (2011) found a 4-month lag between attainment of alpha status and attainment of alpha levels of testosterone after a peaceful AMR (succession). We suspect that this lag time between the rise to alpha status and testosterone levels occurs only in these more peaceful AMRs as these males are not aggressively challenging and fighting with resident males. This lag time between attaining alpha status and alpha testosterone levels may explain our observation of a mean 98-day lag between AMR and infant deaths as well. Those males who aggressively challenge and evict resident

alpha males, as is the case for takeovers and rank reversal, likely already possess alpha testosterone levels characteristic of alpha male.

4.1 | Support for competing hypotheses or different levels of explanation?

Our findings indicate that infant mortality is significantly higher in the context of AMRs than during periods of group stability, and this finding holds regardless of AMR type. Although our results primarily support the SSH's prediction that younger infants are at greater risk, our descriptive data also provide some support for the GAH. Given that the SSH and GAH are generally presented as competing hypotheses, the results of our analyses are seemingly contradictory. However, these findings can be better understood by placing each hypothesis at the appropriate level of explanation. Indeed, an inaccurate interpretation of the different levels of explanation for biological phenomena is often partly to blame for the debate concerning support of different hypotheses (Grether, Hughes, & Rodd, 2002).

As noted by Beehner and Bergman (2008), the GAH provides a proximate level of explanation with regard to infanticide: high levels of testosterone promote male aggression, which in turn may increase the risk of infanticide. However, this proximate explanation does not explain our finding of high rates of infant mortality in association with peaceful AMRs or our finding that testosterone levels in alpha male white-faced capuchins remain at extremely elevated levels throughout their tenure (Schaebs, Perry, Cohen, Mundry, & Deschner, 2017; Schoof & Jack, 2013) yet they do not continue to attack infants. It is likely that other mechanisms are in place that prohibit the continuation of infant-directed aggression, such as increasing oxytocin levels via grooming received by group members (see Crockford et al., 2013). The SSH, on the other hand, explains how infanticide can be maintained in the species: males that commit infanticide, even if they are peacefully assuming the alpha male position, may be likely to sire more offspring (because of the forced resumption of ovulation caused by the end of lactational amenorrhea). Thus, evidence is likely to exist that supports both hypotheses, if both accurately explain the behavior at different levels. The false dichotomy of these explanations creates an unnecessary distraction in the attempt to understand infanticide more fully.

ACKNOWLEDGMENTS

Our research is supported by: Tulane University's Stone Center for Latin American Studies (KMJ), Newcomb Institute (KMJ), and Lurcy Fund (KMJ) as well as the Louisiana Board of Regents LEQSF-RD-A-09 (KMJ), Leakey Foundation (KMJ), National Geographic Society (KMJ), Nacey Maggioncalda Foundation (KMJ), Natural Sciences and Engineering Research Council of Canada (LMF), Canada Foundation for Innovation, Canada Research Chair Program (LMF), Japan Society for Promotion of Science (ECW, SK). We thank the Costa Rican Park Service and the administration of the Área de Conservación Guanacaste, in particular Roger Blanco Segura, for granting us permission to conduct our research

in Santa Rosa (ACG-PI-023-2012). We would like to thank the many students and research assistants who collected the demographic and genetic data used in this study. This manuscript was greatly improved thanks to Marina Cords and two anonymous reviewers.

REFERENCES

- Bartlett, T. Q., Sussman, R. W., & Cheverud, J. M. (1993). Infant killing in primates: A review of observed cases with specific reference to the sexual selection hypothesis. *American Anthropologist*, 95, 958–990.
- Bates, D., Maechler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <http://lme4.r-forge.r-project.org>. Accessed 1 Jun 2017.
- Beehner, J. C., & Bergman, T. J. (2008). Infant mortality following male takeovers in wild geladas. *American Journal of Primatology*, 70, 1152–1159.
- Borries, C., Laundhard, K., Epplen, C., Epplen, J. T., & Winkler, P. (1999). DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. *Proceedings of the Royal Society of London B*, 266, 901–904.
- Carnegie, S. D., Fedigan, L. M., & Melin, A. D. (2011). Reproductive seasonality in female capuchins (*Cebus capucinus*) in Santa Rosa (Area de conservación guanacaste), Costa Rica. *International Journal of Primatology*, 32, 1076–1090.
- Carnegie S., Fedigan L. M., & Ziegler T., (2006). Post-conceptive mating in white-faced capuchins: Hormonal and sociosexual patterns in cycling, non-cycling and pregnant females. In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. Luecke, (Eds.), *New perspectives in the study of mesoamerican primates: Distribution, ecology, behavior and conservation* (pp. 387–409). New York: Springer.
- Creel S., & Creel N. M. (2002). *The African wild dog: Behavior, ecology and conservation*. Princeton, NJ: Princeton University Press.
- Crockett C. M., & Pope T. R., (1993). Consequences of sex differences in dispersal for juvenile red howler monkeys. In M. E. Pereira, & L. A. Fairbanks, (Eds.), *Juvenile primates: Life history, development, and behavior* (pp. 104–118). New York: Oxford University Press.
- Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbühler, K., & Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society of London B*, 280, 20122765.
- de Almeida, R. M. M., Cabral, J. C. C., & Narvaes, R. (2015). Behavioural, hormonal and neurobiological mechanisms of aggressive behaviour in human and nonhuman primates. *Physiology and Behavior*, 143, 121–135.
- Dunbar R. I. M., (1986). The social ecology of gelada baboons. In D. I. Rubenstein, & R. W. Wrangham, (Eds.), *Ecological aspects of social evolution: Birds and mammals* (pp. 332–351). Princeton, NJ: Princeton University Press.
- Fedigan, L. M. (1993). Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology*, 14, 853–877.
- Fedigan, L. M. (2003). The impact of male take-overs on infant deaths, births and conceptions in *Cebus capucinus* at Santa Rosa, Costa Rica. *International Journal of Primatology*, 24, 723–741.
- Fedigan, L. M., Carnegie, S. D., & Jack, K. (2008). Predictors of reproductive success in female white-faced capuchins. *American Journal of Physical Anthropology*, 137, 82–90.
- 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., (2012). Tracking monkeys in Santa Rosa: Lessons from a regenerating tropical dry forest. In P. M. Kappeler, & D. P. Watts, (Eds.), *Long-term field studies of primates* (pp. 165–184). Heidelberg: Springer Press.
- 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.
- Fragaszy, D. M., Izar, P., Liu, Q., Eshchar, Y., Young, L. A., & Visalberghi, E. (2016). Body mass in wild bearded capuchins, (*Sapajus libidinosus*): Ontogeny and sexual dimorphism. *American Journal of Primatology*, 78, 473–484. <https://doi.org/10.1002/ajp.22509>
- Fragaszy, D., Visalberghi, E., & Galloway, A. (1997). Infant tufted capuchin monkeys' behaviour with novel foods: Opportunism, not selectivity. *Animal Behaviour*, 53, 1337–1343.
- 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, 419–440.
- Glander, K. E. (1992). Dispersal patterns in Costa Rican mantled howling monkeys. *International Journal of Primatology*, 13, 415–436.
- Godoy, I., Vigilant, L., & Perry, S. E. (2016a). Cues to kinship and close relatedness during infancy in white-faced capuchin monkeys, *Cebus capucinus*. *Animal Behaviour*, 116, 139–151.
- Godoy, I., Vigilant, L., & Perry, S. E. (2016b). Inbreeding risk, avoidance and costs in a group-living primate, *Cebus capucinus*. *Behavioral Ecology and Sociobiology*, 70, 1601–1611.
- Grether, G. F., Hughes, K. A., & Rodd, F. H. (2002). Attraction to orange: Sexiness, not gluttony—response. *Science*, 296, 847–848.
- Gros-Louis, J., Perry, S., & Manson, J. H. (2003). Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*). *Primates*, 44, 341–346.
- Henzi, S. P., Lycett, J. E., Weingrill, A., & Piper, S. E. (2000). Social bonds and the coherence of mountain baboon troupes. *Behaviour*, 137, 663–680.
- Higgins, L. V., & Tedman, R. A. (1990). Effect of attacks by male Australian sea lions, *Neophoca cinerea*, on mortality of pups. *Journal of Mammalogy*, 71, 617–619.
- Hrdy, S. B. (1974). Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu. *Rajasthan. Folia Primatologica*, 22, 19–58.
- 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. (2003). Explaining variation in affiliative relationships among male white-faced capuchins (*Cebus capucinus*). *Folia Primatologica*, 74, 1–16.
- Jack, K. M., Schoof, V. A., Sheller, C. R., Rich, C. I., & Klingelhofer, P. P. (2014). The influence of age and rank on fecal testosterone, DHT, and cortisol excretion in male white-faced capuchin monkeys (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. *General and Comparative Endocrinology*, 195, 58–67.
- Jack K. M., & Fedigan L. M. (In Press). Alpha male capuchins (*Cebus capucinus imitator*): Keystone individuals or generics in a keystone role? In U. Kalbitzer, & K. M. Jack, (Eds.), *Primate Life History, Sex Roles, and Adaptability: Essays in honour of Linda M. Fedigan, Developments in Primatology: Progress and Prospects*. New York: Springer.
- Jack K. M., & Fedigan L. M., (2006). Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*). In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. Luecke, (Eds.), *New perspectives in the study of mesoamerican primates: Distribution, ecology, behavior and conservation* (pp. 367–386). New York: Springer.
- Jack, K. M., & Fedigan, L. M. (2004a). Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 2: Patterns and causes of natal emigration. *Animal Behaviour*, 67, 761–769.

- Jack, K. M., & Fedigan, L. M. (2004b). Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 2: Patterns and causes of secondary dispersal. *Animal Behaviour*, 67, 771–782.
- Janson C., Baldovino M. C., & Di Bitetti M., (2012). The group life cycle and demography of brown capuchin monkeys (*Cebus [apella] nigratus*) in Iguazú national park, Argentina. In P. M. Kappeler, & D. P. Watts, (Eds.), *Long-Term field studies of primates* (pp. 185–214). Heidelberg: Springer.
- Kalbitzer, U., Bergstrom, M. L., Carnegie, S. D., Wikberg, E. C., Kawamura, S., Campos, F. A., ... Fedigan, L. M. (2017). Female sociality and sexual conflict shape offspring survival in a Neotropical primate. *Proceedings of the National Academy of Sciences. Early Addition*, 114, 1892–1897. <https://doi.org/10.1073/pnas.1608625114>
- Kalinowski, S. T., Wagner, A. P., & Taper, M. L. (2006). ML-RELATE: A computer program for maximum likelihood estimation of relatedness and relationship. *Molecular Ecology Notes*, 6, 576–579.
- Kalinowski, S. T., Taper, M. L., & Marshall, T. C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, 16, 1099–1106.
- Lu, A., Reitsema, L.J., Beehner, J.C., Bergman, T.J., Snyder-Mackler, N. (2017). Triangulating Weaning in Wild Geladas (*Theropithecus gelada*) using Observational, Isotopic, and Gut microbial Evidence. Paper presented at the 2017 American Association of Physical Anthropologists Annual Meeting.
- Marshall, T. C., Slate, J., Kruuk, L. E. B., & Pemberton, J. M. (1998). Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology*, 7, 639–655.
- Marshall, A. J., & Hohmann, G. (2005). Urinary testosterone levels of wild male bonobos (*Pan paniscus*) in the Lomako Forest, Democratic Republic of Congo. *American Journal of Primatology*, 65, 87–92. <https://doi.org/10.1002/ajp.20099>
- Muniz, L., Perry, S., Manson, J. H., Gilkenson, H., Gros-Louis, J., & Vigilant, L. (2006). Father-daughter inbreeding avoidance in a wild primate population. *Current Biology*, 16, R156–R157.
- 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.
- Packer, C., & Pusey, A. E. (1983). Adaptations of female lions to infanticide by incoming males. *American Naturalist*, 121, 716–728.
- Packer, C. (2001). Infanticide is no fallacy. *American Anthropologist*, 102, 829–831.
- Palombit, R. A. (2015). Infanticide as sexual conflict: Male strategies and female counterstrategies. *Cold Spring Harbor Perspectives in Biology*, 7, a017640. <https://doi.org/10.1101/cshperspect.a017640>
- Palombit R. A., (2009). Friendships with males: A female counterstrategy to infanticide in the Okavango chacma baboons. In M. N. Muller, & R. W. Wrangham, (Eds.), *Male aggression against females in primates* (pp. 377–409). Cambridge, MA: Harvard University Press.
- Perry S., (2012). The behavior of wild white-faced capuchins: Demography, life history, social relationships, and communication. In H. J. Brockmann, M. Naguib, T. J. Roper, J. C. Mitani, & L. W. Simmons, (Eds.), *Advances in the study of behavior* (pp. 135–181). New York: Academic Press, Volume 44.
- Perry S., Godoy I., & Lammers W., (2012). The lomas barbudal monkey project: Two decades of research on *cebus capucinus*. In P. Kappeler, & D. Watts, (Eds.), *Long-Term field studies of primates* (pp. 141–164). Heidelberg: Springer.
- Pope T. R., (2000). The evolution of male philopatry in Neotropical monkeys. In P. M. Kappeler, (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 219–235). Cambridge, UK: Cambridge University Press.
- Recabarren, M. P., Vergara, M., Martinez, M. C., Gordon, K., & Serón-Ferré, M. (2000). Impact of lactation upon fertility in the New World primate capuchin monkey (*Cebus apella*). *Journal of Medical Primatology*, 29, 350–360.
- Rosenberg, K. M., Denenberg, V. H., Zarrow, M. X., & Frank, B. L. (1971). Effects of castration and testosterone on the rat's pup-killing behavior and activity. *Physiology and Behavior*, 7, 363–368.
- Rosenberg, K. M. (1974). Effects of pre- and post-pubertal castration and testosterone on pup-killing behavior in the male rat. *Physiology and Behavior*, 13, 159–161.
- Saj, T. L., & Sicotte, P. (2005). Male takeover in *Colobus vellerosus* at Boabeng-Fiema monkey sanctuary, central Ghana. *Primates*, 46, 211–214.
- Sapolsky, R. M. (1993). Endocrinology alfresco: Psychoendocrine studies of wild baboons. *Recent Progress in Hormone Research*, 48, 437–468. <https://doi.org/10.1016/B978-0-12-571148-7.50020-8>
- Sargeant, E. J., Wikberg, E. C., Kawamura, S., & Fedigan, L. M. (2015). Allonursing in white-faced capuchins (*Cebus capucinus*) provides evidence for cooperative care of infants. *Behavior*, 152, 1841–1869.
- Sargeant, E. J., Wikberg, E. C., Kawamura, S., Jack, K. M., & Fedigan, L. M. (2016). Paternal kin recognition and infant care in white-faced capuchins (*Cebus capucinus*). *American Journal of Primatology*, 78, 659–668.
- Schaebs, F. S., Perry, S. E., Cohen, D., Mundry, R., & Deschner, T. (2017). Social and demographic correlates of male androgen levels in wild white-faced capuchin monkeys (*Cebus capucinus*). *American Journal of Primatology*, 79, e22653.
- Schoof, V. A. M., & Jack, K. M. (2013). The association of intergroup encounters, dominance status, and fecal androgen and glucocorticoid profiles in wild male white-faced capuchins (*Cebus capucinus*). *American Journal of Primatology*, 75, 107–115.
- Schoof, V. A. M., Jack, K. M., & Carnegie, S. D. (2011). Rise to power: A case study of male fecal androgen and cortisol levels before and after a non-aggressive rank change in a group of wild white-faced capuchins (*Cebus capucinus*). *Folia Primatologica*, 82, 299–307.
- Schoof, V.A.M., Jack, K.M., & Ziegler, T.E. (2014). Male response to female ovulation in white-faced capuchins (*Cebus capucinus*): Variation in testosterone, DHT, and glucocorticoid production. Special issue: A.V. Georgiev, M. Emery Thompson (Guest Eds.), The high price of success: Costs of male mating effort in primates. *International Journal of Primatology*, 35, 643–660.
- Schoof, V. A. M., Wikberg, E. C., Jack, K. M., Fedigan, L. M., Ziegler, T. E., & Kawamura, S. (2014). Infanticide during periods of social stability: Kinship, resumption of ovarian cycling, and mating access in white-faced capuchins (*Cebus capucinus*). *Neotropical Primates*, 21, 192–196.
- Snyder-Mackler, N., Beehner, J. C., & Bergman, T. J. (2012). Defining higher levels in the multilevel societies of geladas (*Theropithecus gelada*). *International Journal of Primatology*, 33, 1054–1068.
- Sobolewski, M., Brown, J., & Mitani, J. (2013). Female parity, male aggression, and the Challenge Hypothesis in wild chimpanzees. *Primates*, 54, 81–88.
- Soltis, J., Thomsen, R., Matusabayshi, K., & Takenaka, O. (2000). Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behavioral Ecology and Sociobiology*, 48, 195–202.
- Soma, K. K. (2006). Testosterone and aggression: Berthold, birds and beyond. *Journal of Neuroendocrinology*, 18, 543–551.
- Teichroeb, J. A., & Jack, K. M. (2017). Alpha male replacements in nonhuman primates: Variability in processes, outcomes and terminology. *American Journal of Primatology*, 79, e22674.
- Teichroeb, J. A., & Sicotte, P. (2008). Infanticide in ursine colobus monkeys (*Colobus vellerosus*) in Ghana: New cases and a test of the existing hypotheses. *Behaviour*, 145, 727–755.
- van Schaik C. P., (2000). Infanticide by male primates; the sexual selection hypothesis revisited. In C. P. van Schaik, & C. H. Janson, (Eds.), *Infanticide by males and its implications* (pp. 27–60). Cambridge, UK: Cambridge University Press.
- Vessey, S., & Meikle, D. (1987). Factors affecting social behavior and reproductive success of male rhesus monkeys. *International Journal of Primatology*, 8, 281–292.

- Wikberg, E. C., Jack, K. M., Campos, F. A., Fedigan, L. M., Sato, A., Bergstrom, M. L., . . . Kawamura, S. (2014). The effect of male parallel dispersal on the kin composition of groups in white-faced capuchins (*Cebus capucinus*). *Animal Behaviour*, 96, 1–9.
- Wikberg, E. C., Jack, K. M., Fedigan, L. M., Campos, F. A., Sato, A., Bergstrom, M. L., . . . Kawamura, S. (2017). Inbreeding avoidance and female mate choice shape reproductive skew in capuchin monkeys (*Cebus capucinus*). *Molecular Ecology*, 26, 653–667.
- Wingfield, J. C., Hegner, R. E., Dufty Jr., A. M., & Ball, G. F. (1990). The “challenge hypothesis”: Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist*, 136, 829–846.
- Zuur A. F., Ieno E. N., Walker N. J., Saveliev A. A., & Smith G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. New York: Springer-Verlag.

How to cite this article: Brasington LF, Wikberg EC, Kawamura S, Fedigan LM, Jack KM. Infant mortality in white-faced capuchins: The impact of alpha male replacements. *Am J Primatol*. 2017;e22725.
<https://doi.org/10.1002/ajp.22725>