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Costs of male infanticide for female capuchins: When does an adaptive male reproductive strategy become costly for females and detrimental to population viability?

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Abstract

Objectives: Infanticide in white-faced capuchins (*Cebus capucinus imitator*) typically occurs in association with alpha male replacements (AMRs). Although infanticide is likely adaptive for males, it imposes costs on females that are difficult to quantify without long-term demographic data. Here we investigate effects of AMRs and infanticide on female reproductive success and how these costs affect capuchin groups. We investigate (1) effects of AMR frequency on the production of surviving infants; (2) energetic and (3) temporal “opportunity costs” of infant loss; and (4) how AMR frequency impacts capuchin group sizes.

Materials and methods: We censused six groups (7–33 years/group, 74 adult females). We modeled surviving infant production in relation to AMR. We estimated a female's energy requirements for lost infants and the temporal cost relative to the median reproductive window. We simulated how varying AMR rates would affect future capuchin group sizes.

Results: Females exposed to more frequent AMR tended to produce fewer surviving offspring. We estimate the average lost infant requires approximately 33% additional energy intake for its mother and represents 10% of the average reproductive opportunity window available to females. Simulated populations remain viable at the observed rate of AMR occurrence but decrease in size at even slightly higher rates.

Discussion: While infanticide is adaptive for males, for females it affects lifetime reproductive success and imposes energetic and opportunity costs. Although capuchin populations have evolved with AMRs and infanticide, small increases in AMR frequency may lead to population decline/extinction. Infanticide likely plays a large role in population maintenance for capuchins.

KEYWORDS
alpha male replacement, *Cebus capucinus imitator*, long-term data, population viability analysis, survival analysis

1 | INTRODUCTION

The killing of conspecific infants by adult males is widespread in the animal kingdom (Agrell et al., 1998; Lukas & Huchard, 2014; van Schaik & Janson, 2000) and has been reported for many primate species (Palombit, 2015). Some early explanations for male infanticide in primates proposed that these behaviors were by-products of generalized male aggression, maladaptive responses to artificial crowding, or were due to other anthropogenic causes (Sommer, 2000). However, the sexual selection hypothesis has come to be the most widely accepted ultimate explanation for infanticide (Palombit, 2012; Rees, 2009). The sexual selection hypothesis posits that a male can increase his reproductive success by killing an unrelated infant if doing so accelerates the mother's return to ovulatory cycling and receptivity, which in turn facilitates the infanticidal male's opportunity to mate with the mother and sire his own offspring (Hrdy, 1974; Hrdy, 1999). There is strong support for these premises of the sexual selection explanation for male infanticide in a number of species (Palombit, 2015; van Schaik & Janson, 2000). Infanticide is particularly common in socially-living species with high reproductive skew, in which the highest ranking (alpha) male typically sires the majority of the offspring in the group during his tenure but is periodically replaced, often aggressively, and usually by unrelated males (alpha male replacements, or AMRs; Beehner & Bergman, 2008; Brasington et al., 2017; Teichroeb & Jack, 2017).

Infanticide by males is one conspicuous facet of conflict between male and female reproductive strategies that is hypothesized to result from fundamental disparities in reproductive investments. This conflict begins with anisogamy (differential egg vs. sperm investment) and culminates for mammals in the greater parental investment by females than males in offspring due to the costs of gestation and lactation (Gowaty, 2018; Stumpf et al., 2011; Trivers, 1972). Under these circumstances, sexual selection theory posits that a male's reproductive success is limited by the number of fertile females he can inseminate, whereas a female's reproductive success is limited by the number of offspring she can successfully rear to maturity. Thus, sexual conflict arises as the result of selection on males to increase the number of offspring that they sire, with potential costs to females; versus counter strategies by females to enhance their successful rearing of offspring in spite of costs imposed by male strategies. Examples of female counterstrategies to male infanticide and mating coercion identified to date include: polyandrous and post-conceptive mating, concealed and unpredictable ovulation, synchronous breeding, cryptic female choice, voluntary dispersal between groups, alliances with female kin, and forming friendships with resident males (Agrell et al., 1998; Fedigan & Jack, 2012; Manguette et al., 2019; Packer & Pusey, 1983; Palombit, 2012; Scott et al., 2019; Xiang et al., 2020).

Infanticide results in an obvious cost to the infant and an inferred cost to the mother. Although some studies have mentioned or qualitatively described female costs (e.g., Agrell et al., 1998; Palombit, 2015; van Schaik & Janson, 2000), efforts to quantify the costs of male infanticide to female reproductive success are limited (but see Kalbitzer et al., 2017; Manguette et al., 2019; Robbins et al., 2013; Steyaert et al., 2013; Swedell et al., 2014). This may be in part because it is challenging to measure lifetime reproductive success in long-lived wild animals in general and because it is even more difficult to measure the costs of female counterstrategies to infanticide. However, long-term observations of a primate population where male infanticide occurs with regularity offer an opportunity to quantify some of the short and long-term costs of infanticide to a female's reproductive success. For example, we can calculate the proportion of a female's infants that are lost to infanticide, estimate the lost energetic costs of gestating and lactating allocated to an infant that was later killed, and estimate the lost opportunities to produce surviving infants over the female's limited reproductive lifetime.

Beyond the costs of male infanticide to the reproductive success of individual females, since population growth is strongly affected by infant recruitment success, it is worthwhile investigating how and whether AMR events influence population growth. Population viability analysis (PVA) is a tool commonly used by demographers and conservation planners to predict a species' (or population's) future state by simulating change over time using empirical parameters, including initial population size, and birth, death and fecundity rates (Beissinger & McCullough, 2002; Morris & Doak, 2002). In many PVAs, a "catastrophe" parameter is included to mimic the effects of rare events that generate markedly different vital rates, such as a hurricane resulting in elevated mortality. Such catastrophes, while rare, often dramatically alter a population's growth trajectory (Crain et al., 2019). Given the outsized effect of AMRs on infant mortality (with an AMR event often leading to numerous infant deaths in the subsequent months; Brasington et al., 2017), they can be considered catastrophes that affect only infants for the purposes of PVA simulation, and by varying the rate of AMR occurrence across simulations, we can estimate how population maintenance is affected by infanticide.

The white-faced capuchins (*Cebus capucinus imitator*) in the Santa Rosa Sector of Área de Conservación Guanacaste, Costa Rica, are a suitable study population for addressing the costs of infanticide to female reproductive success and to population growth because the death or killing of infants is common following the replacement of an alpha male in our study animals (Brasington et al., 2017) and alpha males sire the majority of infants (80%–100%; Wikberg et al., 2017). We have tracked the life histories, demographic patterns, and socioecology of these primates for more than three decades (Melin et al., 2020), and researchers have previously described the substantial effect of repeated AMRs on infant mortality in our study species (Brasington et al., 2017; Campos et al., 2020; Fedigan, 2003; Fedigan & Jack, 2004; Gros-Louis et al., 2003; Kalbitzer et al., 2017; Manson et al., 2004; Perry, 2012). However, we have not yet assessed how spates of infant deaths in the context of AMRs affect female fitness or population growth. In this study, we address the following questions:

1. What are the costs of male infanticide to adult female capuchins? We measure these costs in three ways:

   a. What is the cost of AMR-related infanticide risk to a female's production of surviving infants?
   b. What are the energetic costs of infanticide to females in terms of lost energy that was allocated to gestating and lactating for infants that are killed?
   c. What are the temporal costs of infanticide to females in terms of reduced future reproductive opportunities, given the small number of opportunities that slow-reproducing females are likely to have during their remaining lifetimes?
2. How do repeated AMR events, and associated infant deaths, potentially affect population viability?

2 | MATERIALS AND METHODS

2.1 | Study site and species

We collected data for this study over 34 years between May 1986 and July 2019 in the Santa Rosa Sector of the Área de Conservación Guanacaste in Costa Rica. The Santa Rosa Sector consists of 108 km^2 of tropical dry forest and experiences a dry season from approximately December to May. All research conducted for and reported in this paper was authorized by the Costa Rican Ministry of the Environment, Energy and Technology (MINAET), and complied with protocols approved by the Life and Environmental Sciences Animal Care Committee (LESACC) of the University of Calgary (AC20-0148). White-faced capuchins live in year-round groups of kin-related adult females and their offspring associated with multiple adult and subadult males. While capuchins living in Santa Rosa's study populations behave similarly to capuchin groups elsewhere and share similar demographic trends, there are important differences (see Perry, 2012; Perry et al., 2012 for detailed comparisons of our study groups with the nearby, well-studied populations of Lomas Barbudal). Therefore, all descriptions hereafter are of Santa Rosa capuchins only. Group sizes in our study population average 15 members, ranging from 4 to 35 individuals (Table 1). Santa Rosa capuchin males disperse from their natal group at approximately 4.5 years (Jack & Fedigan, 2004a) and continue to disperse to other social groups approximately every 4 years throughout their lives, although there is much variation (Jack & Fedigan, 2004b). Females, with few exceptions, remain in their natal groups, first give birth between 6 and 7 years of age, and continue to produce infants approximately every 2 years thereafter (Jack & Fedigan, 2009). In our study population, there is a birth peak between April and July; however, these animals are not strongly seasonal breeders (Campos et al., 2017; Carnegie et al., 2011). AMRs most often occur when new males enter established groups, usually in coalitions with other immigrant males who cooperate to drive out resident males. A lower ranking resident male may also become alpha if the prior alpha disappears from the group or by overthrowing the prior alpha. Large groups may also fission, to form two sister groups, one of which will gain a new alpha male (usually a resident male who was subordinate in the parent group). Finally, males sometimes happen upon a group without resident adult males, and they can take up residency with little resistance.

During and subsequent to all types of AMRs, resident males and females may be wounded and infants often perish (Brasington et al., 2017; Fedigan, 2003; Fedigan & Jack, 2004). Although an infanticidal attack occurs so rapidly that it is difficult and rare to observe it clearly, we have directly observed recently immigrated males attacking and fatally wounding infants. In other instances, we can strongly infer infanticide when we recover the body of a dead infant with canine punctures of the type we have seen adult male capuchins inflict (Figure 1). The youngest confirmed dispersal event documented in our study population is 20 months (Jack & Fedigan, 2004a), and all infants (< 1 year) are highly dependent upon their mothers for milk, warmth, transportation, and so forth. Thus, all infants who disappear without their mothers are assumed to be deaths (though not all are assumed to be the result of male infanticide).

2.2 | Study groups and data collection

Since 1983, we have intensively tracked the demographic and life history events in six social groups of Santa Rosa's capuchin population (Table 1). Some of these groups have been followed from the beginning of our intensive research program in Sector Santa Rosa in 1986; others were followed until their extinction or only for limited periods during independent research projects. One study group (CP) fissioned in 2014 and both splinter groups (CP/AD and CP/RM) remain under observation.

TABLE 1 Study groups included in this study

Group	Years studied	Years observed	Alpha male replacements (AMRs)	Min. Group size	Max. Group size
CP/AD	2013–2019	7	3	14	21
CP/RM	1986–2019	33	5	6	35
EX	2007–2016	10	3	8	13
GN	2007–2019	13	3	23	33
LV	1990–2019	30	11	12	25
SE	1986–1993	7	3	4	13

Note: Group size includes individuals of all ages and sex. One study group (CP) fissioned in 2014 and both splinter groups (CP/AD and CP/RM) remain under observation.

FIGURE 1 Body of infant capuchin recovered following an infanticidal attack in 2019. Note canine puncture wounds below the arm. Photo courtesy of Saul Cheves

During the years in which they were studied, each group was observed frequently (see below) to collect data on births, deaths, dispersal, and social and foraging behavior. When a group was first habituated, or when a new individual (usually a male) entered the group from outside our study population, we estimated the individual's age based on their size and morphology in comparison to individuals of known ages. For most months of each year, we monitored each study group for at least 2 days per week, and during less intensive periods of data collection we monitored study groups at least twice per month. Between 1991 and 2010, there were eight gaps in data collection for some of the groups lasting 3–8 months. For the most recent years of this study (2000–2019), there were four gaps of less than 5 months, and none since 2010. It is possible that during these periods, takeover attempts were launched; however, we know that no successful AMRs occurred during these gaps because in all cases the alpha males remained in place when the groups were next censused. The total data set includes 100 group-years of observation, and up to five generations of females have been observed in our long-term study groups. During this time, we observed 29 AMR risk periods (see below), and stable periods between the end of one AMR period and the start of another lasted for an average of 3.5 years (median 2.1 years, range 93 days to 14 years).

We define two separate risk categories for infants: (1) those at high risk of infanticide because of an AMR, and (2) those at lower risk (stable periods). Any infant who is born before an AMR but exposed to an AMR event at any point during their first year of life, or is born in the 5.5 months following an AMR, is considered to be at high risk of infanticide, whereas infants who do not meet these exposure criteria are considered to be at low risk of infanticide. We include the 5.5 months following an AMR because that is the gestation length for our study species (158 +/− 8 days; Carnegie et al., 2011); therefore, infants born prior to this threshold are likely the offspring of the previous alpha male. In some instances, males competed for the alpha male position over the course of several months before the group membership stabilized. In such cases, we extend the high-risk period to be the duration of the unsettled period plus the 5.5 months following stabilization.

The reproductive data analyzed in this study come from 74 adult females tracked either until their death/disappearance or until July 2019 (the end of observation for this study), and include 296 infant births and 102 infant deaths (i.e., the monkey survived <12 months). The birth dates of infants born during data gaps were estimated based on their size when we first encountered them and on our experience with infants of known age ($N = 21$). Dates of death for infants that disappeared during the periods when groups were not monitored were estimated as the midpoint of the period. For this study, infants were considered to have survived if they were still alive after 1 year, which is the approximate length of dependency and start of weaning age for capuchins (Fragaszy et al., 2004; Sargeant et al., 2015).

2.3 | Data availability

The data that support the findings of this study are openly available in PRISM Dataverse: University of Calgary's Data Repository at https://doi.org/10.5683/SP2/KJJCXO.

2.4 | Data analysis–cost of male infanticide to adult female capuchins

To investigate the effect of male infanticide on female reproductive success, we took three independent approaches: (1) calculating the effect of AMRs on an adult female's total output of surviving infants; (2) estimating the energetic cost of infant loss by comparing the energetic requirements of an adult female who loses an offspring to an adult female with a surviving offspring; and (3) calculating the temporal cost of infanticide loss to a female's limited reproductive opportunities. All statistical analyses were completed using R (v3.6.3; R Core Team, 2018).

(1) To calculate the effect of AMRs on an adult female's total output of surviving infants, we examined whether females who experienced a higher rate of AMRs during their reproductive window had a lower rate of surviving infant production. We fit a negative binomial generalized linear mixed model using the Bayesian R package rstanarm (Goodrich et al., 2018), with the number of surviving offspring produced by an individual female as the outcome variable, the number of AMRs a female was exposed to while reproductively active as a predictor variable, and group affiliation as a grouping variable. To control for reproductive differences due simply to longer-lived individuals producing more offspring, the length of time (in years) a female was reproductively active was included in the model as an offset. Hence, the outcome variable can be interpreted as the rate of surviving infant production. For this analysis, a female's reproductive window length was defined as starting with the birth of her first infant (for which we know the AMR context of that birth) until 1 year

following the birth of her final infant within the study period. Only females with more than one infant born were included in this analysis. To prevent bias in our sample towards short-lived infants at the end of our study period, infants born less than a year from the end of our study period or the death/disappearance of their mother were not included. As a result of these measures, a total of 56 adult females and 246 infants were included in this analysis.

(2) To estimate the energetic costs that females pay as a result of infanticide (i.e., "wasted" energy allocated to reproduction and parental care), we used previously published estimates on the energetic requirements of gestation and lactation (Bergstrom et al., 2019) and reproductive data from our study population. In brief, Bergstrom et al. (2019) took the minimum required daily energy intake for body maintenance of captive male *Cebus albifrons* obtained under experimental conditions (Ausman et al., 1986; Ausman & Hegsted, 1980) and adjusted these values to account for (1) the mean weight of captive adult female *Cebus capucinus imitator* and (2) the estimated extra energy requirements of gestation (1.25×) and lactation (1.5×) for non-human primates (Key & Ross, 1999). The gestation length for an infant is 158 days (+/− 8 days; Carnegie et al., 2011) and weaning age is variable but starts approximately at 1 year of age (Sargeant et al., 2015). The loss of an infant to infanticide requires that the mother gestated and nursed that infant until it was killed. Therefore, the energetic costs of infanticide can be estimated as the sum of the gestation costs for the lost infant plus the lactation costs for the duration of its life, as compared to an adult female who was not pregnant or lactating for the same time period. For this analysis, we calculated the time cost of each infant lost to suspected infanticide (age at death plus gestation length) and the estimated excess energy cost invested in this infant before it is death. Using these individual estimates, we calculate the median energy cost of an infant lost to infanticide.

(3) To estimate the reproductive time lost for female capuchins due to infanticide, we first calculated interbirth intervals (IBI) for all infants with an older sibling in cases where birth dates were known for both. We defined interbirth interval to be the total length of time in days between the birth of infants 1 and 2. We categorized IBIs into two types: "surviving" IBIs occurred when the first sibling survived for at least 1 year; "early death" IBIs occurred when the first sibling died during their first year. From these data, we report the median for IBIs following infant loss versus successfully raising an infant to weaning.

Using our estimated gestation length, weaning age, and median IBI lengths, we estimated the difference in time between two scenarios that result in the same outcome of one surviving infant: (1) an adult female who successfully rears an infant to approximate weaning age, and (2) an adult female who loses an infant to infanticide, but successfully rears the subsequent infant. Next, we calculated the median reproductive lifespan using Kaplan–Meier estimation to account for the fact that many of the adult females in our data set are still alive and reproductively active (and thus right-censored). Only a small minority of the females in our study sample who died experienced periods of fertility completion before death that were longer than our median IBI, and in a separate analysis, Alberts et al. (2013) concluded that general senescence outpaced reproductive senescence (i.e., death preceded reproductive cessation) in Santa Rosa females. Therefore, we defined a female's potential reproductive window to be the period between the youngest known age at first birth for our study population (5.8 years; unpublished data) and either their death or the termination of the study. In total 72 adult females are included in our survivorship estimates: 39 died before the end of the study, and 33 were still alive. Kaplan–Meier estimation was conducted using the "survival" package (v. 2.44–1.1; Therneau, 2019) in R. From these data, we can estimate the median length of an adult female's reproductive window, and, using IBI data for "surviving" intervals and "lost infant" intervals, estimate how many reproductive opportunities an average female capuchin has, and how many opportunities to produce surviving infants are lost to infanticide.

2.5 | Data analysis–effect of alpha male replacement risk on capuchin populations

To understand how repeated AMR events affect capuchin populations, we conducted a demographic population viability analysis (PVA) using a custom-written simulation program, and vital rates obtained from our study groups. The source code for our program is open source and available (Hogan, 2021), and detailed methodology is provided in Appendix S1. Female group composition of three Santa Rosa capuchin groups of different sizes were used as starting populations in the population viability analysis (Table 2). In brief, we used monthly survival, fecundity, and AMR rates determined from our capuchin study groups to simulate population changes of a single capuchin group while varying the rate at which AMR events occurred. For this analysis, we conduct 50 years of monthly simulations 10,000 times for each AMR rate on each of the 3 starting capuchin population sizes. The frequent dispersal of males, even as juveniles, can lead to large stochastic shifts in group sizes. Therefore, we estimate vital rates for the juvenile and adult life stages for female capuchins only, whereas infant mortality rates include both males and females. Male infants are tracked while they are still of nursing age (i.e., < 12 months) because this affects their mother's reproductive status, but they are not included in population estimates. We calculated monthly age-specific mortality for non-infants (> 12 months) using the Siler model mortality parameters estimated for our study population (Colchero et al., 2021). For infant mortality, we subset the monthly mortality rate between months of group stability and months in which an AMR occurred and therefore infants were at higher risk of infanticide (Appendix S1). During PVA design, we determined that adult female capuchins did not experience elevated risk of death in association with AMR periods. We used a time-varying Cox proportional hazards model to test whether cumulative months of AMR exposure predicted the risk of death for adult females. We found that it did not (log-hazard $= -0.00402$, hazard ratio $= 0.996$, $p = 0.836$, $n = 6263$ female-months, number of deaths $= 45$). Therefore age-specific mortality risk did not vary based on whether the group was experiencing an AMR. Fecundity rates were estimated by calculating the percentage of capuchin females who conceived (back calculated

TABLE 2 Female group composition of the three Santa Rosa capuchin groups used as starting populations in population viability analysis

Total females	Adult females	Juvenile females	Infant females	Infant males
7	5	1	1	1
13	10	2	1	1
18	10	5	3	3

from infant birth dates) in each month following the birth of an infant, from the total number of females who had not yet conceived in a previous month. Females whose infant was killed prior to weaning conceived a second infant sooner on average than those who successfully reared the first infant to weaning age, thus, we calculated two conception probabilities which varied depending on the survival of the previous infant.

Using these parameters for our PVA, we recorded the ending group size for each group for each trial and determined the proportion of simulated trials that resulted in group stability, growth, decline, or extinction. For each group, stability was considered to be any ending population that was $+/-$ 25% of the initial group size. Two important assumptions made in this analysis are (1) while mortality is age-dependent, we do not impose a fixed limit to female lifespan (Lande, 1988), and, (2) we do not include any measures of density-dependence because visual inspection of the data did not reveal any relationship between group size and rate of change (Morris & Doak, 2002). Both assumptions are conservative, in that any error introduced by their omission will result in a lower estimate of extinction risk for our simulated populations.

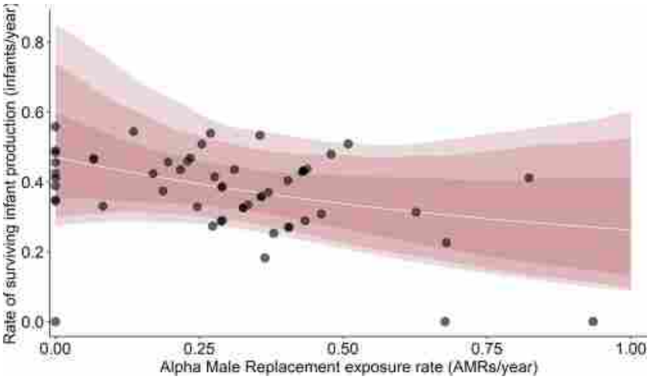

FIGURE 2 Female reproductive costs, depicted as the effect size of alpha male replacement (AMR) rate experienced by an adult female's offspring on the rate of surviving offspring she produces. A higher rate of infants exposed to AMR events tends to reduce the rate of surviving offspring production although the uncertainty associated with this effect was large. Points are individual adult females from our study ($N = 56$), shaded areas represent the 80% (darkest), 95% and 99% (lightest) credible intervals from a negative binomial model. Group affiliation was also included in the model but does not appear to affect surviving offspring

3 | RESULTS

3.1 | Female reproductive success

Infant mortality rates for infants exposed to AMR-associated risk were much higher than those that were not: infant mortality was 55% (49/89) for infants with AMR-risk exposure, whereas only 24% (40/167) of infants not exposed to AMR-risk died in their first year of life. For females that had at least 10 years of reproductive opportunity ($N = 23$), 51% (28/55) of infants exposed to AMR-related infanticide risk died, whereas only 18% (19/106) infants born to these same females during low-risk periods died at less than 1 year of age. Thus, the average female loses approximately half of her infants exposed to high infanticide risk, and about one in five of her infants born during low-risk time periods. According to the negative binomial model, females who experienced more AMRs during their reproductive lifespan tended to produce fewer surviving infants per year, although the uncertainty associated with this effect was large (estimate for the slope: -0.6, standard error: 0.6, 80% credible interval: -1.2–0.1; Figure 2).

3.2 | Female energetic costs

The median age at death for infants who died in association with AMR exposure was 77 days (range: 0–332 days, standard deviation: 102 days). While nursing, an adult female capuchin is estimated to require 500 kJ/day of energy to compensate for lactation costs in excess of the energy required by a non-lactating, non-pregnant adult female capuchin (estimated to be 1000 kJ/day; all nutritional intake estimates from Bergstrom et al., 2019). The median excess energy cost to mothers for infants killed in suspected infanticide attacks was estimated to be 78,000 kJ (range: 40,000–200,000 kJ, standard deviation: 51,000 kJ). This represents a 33% increase in energy expenditure relative to an adult female who remained non-pregnant and non-lactating over this same timeframe (Figure 3).

3.3 | Female reproductive time costs

For all adult females over the course of our study, the median interbirth interval (IBI) was 773 days between the birth of the first and the second infant in the interval if the first infant survived. However, when an adult female loses the first infant in the interval, the median IBI is reduced to 380 days, about half the length of the "surviving" interval. Following infant loss, 95% of adult females conceive a second infant within 12 months of the loss of their previous infant; only 6% of females who have a living infant conceive a second prior to this mark. The estimated median length of an adult female's reproductive window based on survivorship estimates was 11.99 years (95% credible interval: 8.74 to 17.63 years, $N = 72$). Given the rate of male

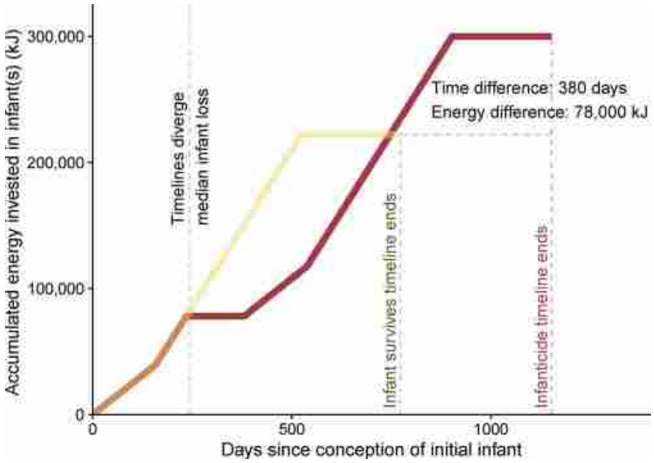

FIGURE 3 Female energetic costs depicted as the difference in time and energy costs for an adult female capuchin to produce a single surviving infant if (a) they first lose an infant to infanticide (red line) and successfully rear the second, or (b) the first infant survives (beige line)

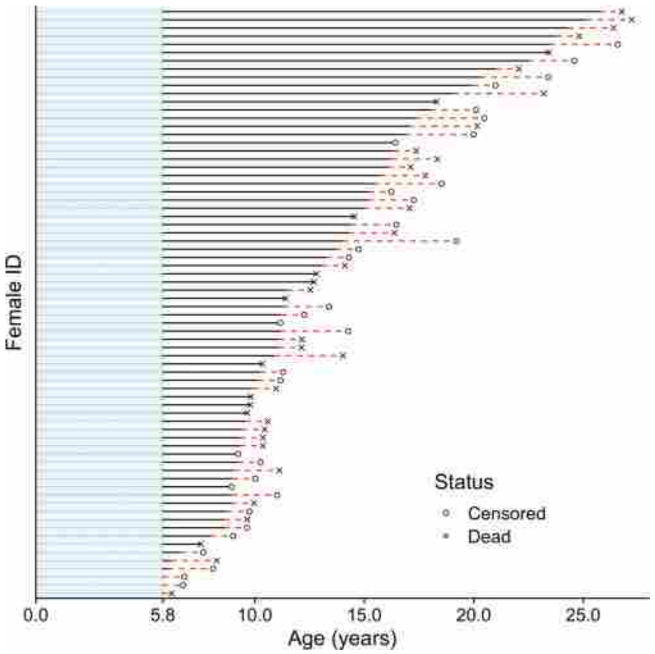

FIGURE 4 Estimated female reproductive time costs, measured via the "effective" reproductive window length (solid black lines starting at adulthood, 5.8 years) and the amount of reproductive time "lost" due to infant mortality (dotted red lines). Each horizontal line represents the life of one of the 72 adult females included in the survival analysis. The first 5.8 years of life, shaded blue, are not part of the reproductive window. Females that are still alive at the end of our study period are "censored" as their reproductive window has not yet been completed

takeovers in our study populations (3% of census months), the average female can expect to experience approximately 4.3 risk periods over her reproductive lifetime. Using the median value for reproductive window length and a median IBI following a surviving offspring (773 days), we estimate that an average female would have the opportunity to produce 5.7 infants during her lifetime if all her infants survive. Since every infant lost to infanticide results in a median time cost of 380 days, each such loss results in an approximately 0.5 infant "reproductive opportunity cost" to the female (Figure 4).

3.4 | Effects of varying rates of AMR on simulated capuchin populations

PVA simulations predicted that after 50 years, capuchin groups experiencing the 3% monthly AMR rate observed for Santa Rosa's capuchins were likely to be the same size or larger than their starting population (66%–85% of trials; Figure 5). These values reflect the trajectories of our study groups of comparable sizes over the past 30 years, validating our PVA model parameters and design. Every 1% increase in the AMR rate increased the likelihood of group decline or extinction, and regardless of starting size, groups declined or went extinct in the majority of trials at AMR rates above 6%.

4 | DISCUSSION

Infant capuchins in our study groups are at high risk of being fatally wounded by newly immigrant males, and similar to previous reports on this population (Brasington et al., 2017; Kalbitzer et al., 2017), we found that infant mortality rates more than double for infants exposed to the heightened infanticide risk associated with AMRs. From the perspective of the reproducing capuchin female, we found that she can expect to lose half of the infants she produces during these high-risk periods, as compared to a loss of only one in five infants during periods when the position of alpha male (i.e., the probable sire of her infants; Wikberg et al., 2017) is stable in the group and infanticide risk is low. Thus, infanticide can have a substantial impact on female reproductive success. Furthermore, the cost to the mother of infant death goes beyond the loss of that particular infant in at least two other respects.

First, at a basic physiological level, we estimate that a female capuchin expends 33% more energy in order to gestate and nurse an infant that is later lost in comparison to a female that does not conceive or lactate over the same timeframe. These additional energetic costs imposed on pregnant/lactating females are not negligible in a mammalian population, such as our study animals, that lives in a tropical dry forest environment where food shortage and energetic deficits occur seasonally (Bergstrom et al., 2018; Bergstrom et al., 2019). Trade-offs between reproduction and lifespan are known to occur amongst other primates (McLean et al., 2019), and investigation into how infant loss affects a female capuchin's lifespan may prove illuminating, although accumulation of a larger sample of female capuchins tracked for their entire adult life will be required.

Second, female capuchins exhibit a slow pace of reproduction, giving birth to approximately one infant every 2 years if the first infant survives, or one every 1.05 years if the first infant in the interval dies.

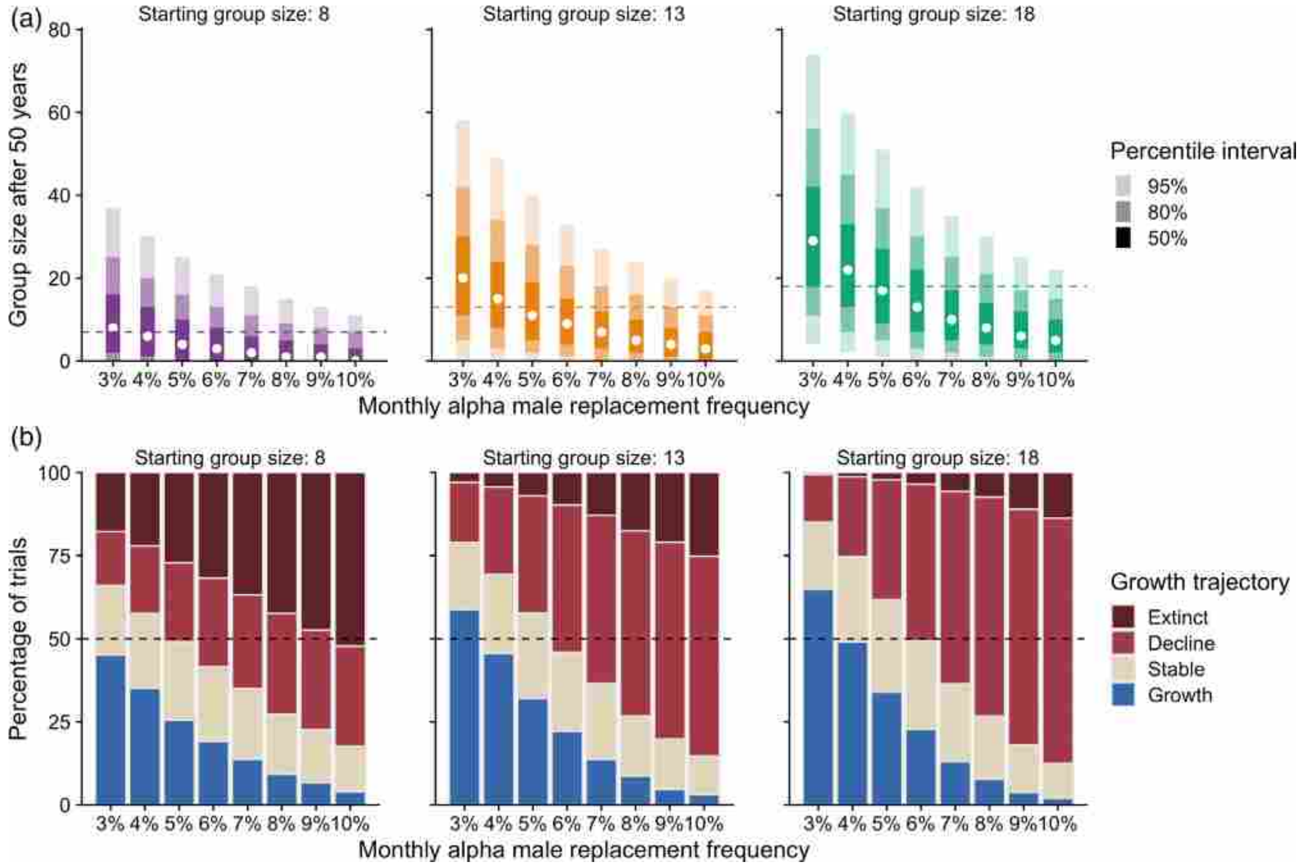

FIGURE 5 Population effects of varying rates of alpha male replacement (AMR) on three simulated capuchin groups. Each group/AMR combination was simulated for 50-year intervals 10,000 times. The observed rate of AMR frequency for Santa Rosa's capuchin population is 3%. (a) The median ending population per group per AMR rate, with 50%, 80%, and 95% quantile intervals around each median. The dashed horizontal line reflects the starting population of each group. (b) The proportion of trials per AMR rate and study group that resulted in group extinction (dark red), decline (light red), stability (beige) or growth (blue). Population size only represents the females of a group

Our long-term life history dataset indicates that the median female is reproductively active over a 12 year period, which would give her the opportunity to produce only 5.7 infants during her lifetime if all her infants survive (the optimum scenario). When an infant dies before 1 year of age, the mother's subsequent IBI is shortened, but if her future survival and reproductive success remain fixed, she will have fewer remaining opportunities in her lifetime to produce surviving infants. Under these conditions, there is a "reproductive opportunity loss" associated with each infant death. And, given that the average female experiences multiple AMR events during her reproductive years (approximately one every 3 years in our study population), she may suffer a substantial reduction in her lifetime opportunities to produce infants that survive beyond weaning.

Although our data indicate that adult female capuchins are not at increased risk of mortality themselves during AMR events, injury and mortality risk may not be consistent across all females. For example, only adult females with vulnerable infants may face AMR-related dangers as they put themselves in harm's way defending their infant. Similarly, Kalbitzer et al. (2017) determined that higher-ranking, more central females were at higher risk of infanticide loss; it is plausible that such females are also at higher risk themselves. Similar rank-effects of pregnancy loss have been observed in other primate species, such as olive baboons (Bailey et al., 2021). We often find females with significant wounding during periods of unstable group membership and such sub-lethal injuries may have significant, detrimental effects on those females that are undetected by our analysis.

We also addressed the question of whether these extensive costs to female reproductive success translate into negative effects on population maintenance. Using PVA simulations, we asked at what rate of AMRs would capuchin groups of different sizes remain stable, decline, or become extinct. We found that AMRs occur in our study population at a rate of 3% of census group months (approximately once every 3 years), which is just below a level that, according to our simulations, would result in population decline. These simulations suggest that more frequent AMR occurrence would lead to high likelihood of group decline or extinction. In our 34 years of tracking these animals, we have observed one group to reach extinction (SE). In this case, the group was reduced to a lone adult female (who later disappeared) after the group experienced three AMRs over a five-year period, with multiple resultant deaths. Two current study groups (AD, which fissioned from CP in 2013, and BC, which fissioned from GN in 2019) and one formerly studied group (EX) recently experienced similarly high AMR rates and all substantially declined in size. The PVA simulations (plus our observed extinction of study group SE and the declines of AD, BC, and EX) suggest that the current rate of AMR events is not far below a level at which their associated effects on infant mortality and female reproductive success would have a negative effect on population maintenance.

In Santa Rosa, AMR events frequently occur in the late dry season, a time of improved visibility in the forest due to leaf abscission and reduced group ranging due to a severe reduction in water availability (Campos et al., 2014; Campos & Fedigan, 2009). It is likely that these conditions result in more frequent intergroup encounters and more opportunities for males to assess their chances at succeeding in a group takeover. Although Santa Rosa forests are well protected and regenerating, habitat loss is a pressing concern for capuchins elsewhere in Central and South America (DeGama-Blanchet & Fedigan, 2006; Johnson & Brown, 2018), which could lead to similar levels of intergroup encounters and subsequent male takeovers, ultimately adding an additional stressor onto the population viability of capuchins in unprotected habitats. Such effects may similarly play out even in the protected forests of Santa Rosa, as climate change leads to more frequent and more severe drought events (Campos, 2018; Campos et al., 2015).

Even though male reproductive strategies such as infanticide benefit the male perpetrators who are not sires of their victims, these behaviors impose important costs on females (Palombit, 2015; van Schaik & Janson, 2000) and can lead to a reduction in lifetime reproductive success. It is not surprising, then, that female capuchins have evolved numerous counter-strategies for infanticide avoidance, including promiscuous and non-conceptive mating (particularly targeting lower ranking males while already pregnant) and concealed ovulation (Jack & Fedigan, 2006; Manson et al., 1997; Muniz et al., 2010; Wikberg et al., 2017). Although these measures may be effective at reducing infanticide effects, such events continue to occur at high rates in our study population, with females losing many of the infants who are exposed to AMR-related risk. Why have more extreme counter-strategies, such as spontaneous abortion (the “Bruce Effect”) or accelerated weaning, not evolved? Brasington (2020) concludes that accelerated weaning is likely not an effective strategy due to the capuchin female's long period of postpartum infertility (estimated to be 5–6 months in tufted capuchins; Recabarren et al., 2000). And while capuchins do appear to be likely candidates for evolving the Bruce effect (Zipple, 2019), a demographic inference approach to our study population undertaken by Brasington (2020) did not find evidence of reduced birth rates in the months following AMR, which would be an indicator of spontaneous abortions. Similarly, during a recent period of extreme drought (2015–2016), capuchin females continued to produce offspring, nearly all (8/9) of which did not survive, whereas the sympatric spider monkey population did not produce a single infant during the same timespan (Campos et al., 2020). Given these results, it is plausible that capuchin females are not able to respond to extreme stressors with spontaneous termination of pregnancy. However, we can not definitively rule out the possibility of such effects without more targeted investigation, such as collecting and analyzing hormone samples to track a female's reproductive status directly.

5 | CONCLUSION

There are significant and multiple forms of costs to females beyond the immediate loss of a particular offspring due to infanticide. Female capuchins who experience higher rates of AMR during their reproductive lifetime showed a tendency to produce surviving offspring at lower rates, but our ability to detect such effects may have been limited by environmental influences on female fertility and infant survival that were not included in our models (e.g., food abundance, drought, density dependence). Furthermore, population viability analysis simulations suggest that AMR risk is a limiting factor on population growth, and that the rate at which we have observed AMRs to occur is just under the predicted rate at which population stagnation or extinction would be expected to occur more often than not. Our findings demonstrate that the costs of infanticide for the Santa Rosa capuchins are of negative consequence for the reproductive success of females, and that even a small increase in the rate of AMRs could be detrimental to the viability of the population. Altogether, it is evident that infanticide is costly to females and may be a major driver of capuchin population dynamics.

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CONFLICT OF INTEREST

All authors declare there are no conflicts of interest.

AUTHOR CONTRIBUTIONS

Linda Fedigan: Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources;

supervision; writing-original draft; writing-review & editing. **Jeremy Hogan:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; validation; visualization; writing-original draft; writing-review & editing. **Fernando Campos:** Conceptualization; data curation; formal analysis; investigation; methodology; software; validation; visualization; writing-original draft; writing-review & editing. **Urs Kalbitzer:** Conceptualization; data curation; formal analysis; methodology; software; validation; visualization; writing-original draft; writing-review & editing. **Katharine Jack:** Conceptualization; data curation; funding acquisition; investigation; project administration; resources; supervision; writing-original draft; writing-review & editing.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in PRISM Dataverse: University of Calgary's Data Repository at https://doi.org/10.5683/SP2/KJJCXO.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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