COUNTERING INFANTICIDE: NEW PERSPECTIVES ON SEXUAL CONFLICT IN WHITE-FACED CAPUCHIN MONKEYS (*Cebus imitator*)

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ABSTRACT

For over 40 years, the sexual selection hypothesis of infanticide has sparked primatological interest in the evolutionary basis of this presumptively adaptive behavior. Infanticide by males has been largely accepted as a reproductive strategy in that when a new dominant sire kills unweaned infants, lactational amenorrhea ends, and females conceive more rapidly than if their infants had survived to weaning age. Thus, infanticide has been mainly investigated from the male perspective. Sexual conflict theory, which posits that males and females of the same species typically have different reproductive interests that can reduce fitness in the other sex, in general has focused on taxa with shorter life spans. A detailed study of sexual conflict in primates provides the opportunity to advance knowledge in organisms with long lifespans and complex behavior. I investigate several facets of how infanticide affects white-faced capuchins (*Cebus imitator*), a medium-sized platyrrhine with relatively slow life histories that experiences alpha male replacements (AMRs; change in dominant sire of group) accompanied by infanticide in the Sector Santa Rosa, Área de Conservación Guanacaste, Costa Rica.

In my investigation, I found that AMR type does not predict infant survival but that infant age does, with younger infants having a greater risk of mortality. I also found that infants likely have the physiological ability to survive earlier weaning, but they do not appear to be able to wean early enough to decrease the risk of infanticide. My comparative analyses indicated that white-faced capuchins have longer lactation periods than expected based on body size. Allonursing also has the potential to function as a female counterstrategy to infanticide by enabling a faster resumption of cycling to decrease the risk of infanticide and/or decreasing the energy input that each mother makes into her young infants thereby decreasing the costs of infanticide. Finally, I found that AMRs increase reproductive synchrony and shift birth seasonality but that this shift in seasonality does not affect infant survival. Combined, my findings indicate that infanticide has a broader range of effects in white-faced capuchins than previously known and contributes to a greater understanding of sexual conflict theory.

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CHAPTER 1: INTRODUCTION

Infanticide in nonhuman primates has been of interest to primatologists since the sexual selection hypothesis of infanticide (Hrdy, 1974) was first developed over 40 years ago. As a form of sexual conflict, infanticide by males functions as a reproductive strategy, and although a fair amount of research has been conducted on infanticide from the male perspective, less attention has been paid to the effects of infanticide. Sexual conflict theory in general has focused on taxa with shorter lifespans and less complex behavior. Thus, a detailed study of sexual conflict in primates provides the opportunity to advance knowledge in organisms with long lifespans and complex behavior. Infanticide accompanies alpha male replacements (AMRs; the change in the dominant sire in a group) in white-faced capuchins (*Cebus imitator*), a medium-sized platyrrhine with relatively slow life histories including late age at weaning. I investigate several facets of how infanticide affects the white-faced capuchins in the Sector Santa Rosa, Área de Conservación Guanacaste, Costa Rica. Specifically, I ask how AMRs affect infant mortality, I investigate the late weaning age of capuchins to try to unravel its relationship with infanticide and allonursing, and I investigate whether AMRs alter birth seasonality or synchrony.

SEXUAL CONFLICT

Males and females of a species often differ in their optimal reproductive strategies, and if these strategies are at odds with one another sexual conflict can develop

(Parker, 1979). Differences in optimal reproductive strategies between the sexes ultimately stem from differences in the male and female gametes, or anisogamy (Daly & Wilson, 1983). The number of large, energetically expensive ova that a female can produce is drastically lower than the number of small, mobile, energetically inexpensive sperm produced by a male (Bateman, 1948). This difference in gametes sets up the ovum to be the limiting resource and creates different optimal reproductive strategies between the sexes, namely that males enhance their reproductive fitness when they mate with greater numbers of females, and females benefit reproductively when they choose the fittest partner to inseminate their eggs. Descriptions of choosy females and indiscriminate males have been reported throughout the primate order (Mulder & Rauch, 2009). However, many of these descriptions are problematic as they continue support for the stereotype of active males and passive or responsive females, and thus great care should be used in order to make sure that the use of overly gendered terms are limited (see Ahnesjo et al., 2020).

The difference in optimal mating strategies between the sexes is further exacerbated in mammals, as parental investment by the sexes differs drastically (Trivers, 1972). The energetic commitment of gestation and lactation provided by females for their offspring not only limits the total lifetime offspring that females can produce, but also selects for females to be even more discerning in their choice of mate. The increased difference in reproductive strategies between males and females has major consequences for the way males and females of a species interact with each other, leading to sexually antagonistic coevolution of traits, or a sexual arms race (Mulder & Rauch, 2009; Stumpf et al., 2011). Thus, we see adaptations and counteradaptations move through species over time as each sex struggles to gain the upper hand in control over reproduction.

The majority of sexual conflict research has focused on *Drosophila* and other insects because of their ability to rapidly reproduce and researcher ability to alter relevant traits and environmental conditions (Stumpf et al., 2011). However, according to Stumpf and colleagues (2011), this focus on invertebrates has created models of intersexual conflict that do not lend themselves well to primates for four main reasons. First, the models are based on the relatively fixed reproductive behaviors typical of insects, which can make it difficult to apply some of these models to primates as they often exhibit flexibility in their mating behaviors and strategies. Second, in primates mating often serves other functions aside from fertilization as many copulations occur during nonconceptive periods (i.e. during pregnancy or lactation periods when ovulation is suspended). This is an important distinction as many of the insect-based models work on the assumption that males and females also differ in their optimal mating rates. For primates, conflict over mating often concerns the ability of a female to choose her mate rather than the frequency of mating (Parker, 1979; Muller et al., 2011). Third, due to the relatively short lifespan of insects, short-term behaviors and their consequences are necessarily the focus of insect studies. The relatively long lifespan of highly social and intelligent primates allows for behaviors that take place over longer periods of time to also be of importance. Thus, an analysis of long-term behaviors applicable to primates is lacking in models developed from insect studies. The fourth and final area that is severely lacking in the insect-derived models is conflict concerning parental investment. The amount of effort required to raise a primate offspring to become a relatively independent juvenile is enormous and thus is expected to be a major source of conflict between males and females, an idea that traces its roots back forty years (Trivers, 1972).

Manifestations of Sexual Conflict

Sexual conflict is manifested in primates via anatomical, physiological, behavioral, and genetic adaptations (Stumpf et al., 2011). For example, males may exhibit anatomical and physiological adaptations that increase the chance that their sperm inseminates an egg after copulation has occurred. Sperm competition has traditionally been considered a form of intrasexual competition (i.e., male mating competition), however it can also be an expression of sexual conflict because it decreases a female's ability to choose the sire of her offspring. Examples of this type of sexual conflict are increased numbers or rate of sperm production, increased length and speed of sperm, and increased testes size (Hosken et al., 2001). Additionally, the seminal fluid of some primates contains chemicals that induces ovulation in females, causes the females to contract uterine muscles to aid the movement of sperm towards the egg, and decreases the sexual receptivity of the female (Burch & Gallup, 2006; Poiani, 2006). The penile spines found in some primates such as marmosets (*Callithrix jaccus*; Dixson, 1991), is another example of a morphological manifestation of sexual conflict as the spines make conception more likely while damaging the genital tract of the female, exposing her to sexually transmitted infections and making her less likely to mate with other males. Counteradaptations to such male traits include concealed ovulation and periovulatory signals that appear before and remain after ovulation occurs (Stumpf et al., 2011). There is also evidence of post-copulatory female choice in some animals, as orgasms can affect the survival of sperm via vaginal secretions (Baker & Bellis, 1993) and they can cause uterine contractions that help move sperm closer to the egg (Birkhead & Kappeler, 2004). Females may decrease the likelihood of successful reproduction via an acidic vaginal environment and spontaneous abortion (discussed in more detail below) (Roberts et al., 2012; Stumpf et al., 2011).

Genomic imprinting is an example of a genetic manifestation of sexual conflict that exists because offspring have two sets of genes, one from each parent (Moore, 2001; Stumpf et al., 2011; Zeh and Zeh, 2000). The alleles from each parent may code for different rates of growth and development, and the alleles from the father may code for the offspring to develop at a faster rate than is ideal for the mother as the mother needs to balance her energetic investment between current and future offspring (Moore, 2001). Because mammalian mothers devote intense amount of energy into each offspring, an increase in the energy she commits to current offspring will decrease her ability to successfully rear future offspring (Moore, 2001). Thus in genomic imprinting, the paternal allele causes mothers to expend the maximum amount of energy on her current offspring, which typically increase survival rates. However, this intense energy investment in current offspring decreases the female's lifetime reproduction as her energy reserves are depleted and she is less capable of investing in future young (Zeh & Zeh, 2000).

Behavioral manifestations of sexual conflict have been studied in greater detail in primates than anatomical, physiological, and genetic manifestations. Sexual coercion is the main form of behavioral sexual conflict in primates. Sexual coercion is defined as (Smuts & Smuts, 1993, p. 2-3):

> use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease

> the chances that she will mate with other males, at some cost to the female. The functional consequences of male sexual coercion distinguish it from other instances of male aggression against females (e.g., in the context of feeding competition) that do not appear to involve manipulation of sexual opportunities.

Sexual coercion can take many forms, including intimidation, harassment, infanticide (discussed in the next section), and forced copulations (Smuts & Smuts, 1993; Knott, 2009; Stumpf et al., 2011). Through these behaviors, males increase the number of successful copulations with females, whereas females lose their control over mate choice, and may incur injuries in addition to experiencing higher levels of stress and increased rates of spontaneous abortion. The forced copulations found in orangutans are perhaps one of the best-known examples of this behavior. All researchers of wild orangutans have reported observing forced copulations, but the frequency of this behavior varies by location (Mitani, 1985; Knott ,2009; Knott et al., 2010). Two morphs of male orangutan exist, and in at some sites, flanged males (larger, more vocally prolific males with higher testosterone levels) engage mainly in consensual copulations, whereas unflanged males (smaller, quieter males with low testosterone levels) typically engage in forced copulations. However, at other sites, half of all copulations were forced, regardless of whether the male was flanged or not (Knott, 2009). Despite the often high frequency of forced copulations, females rarely sustain injuries. Forced copulations by male orangutans is an example of direct sexual coercion, in which the main goal is to control a female’s immediate reproductive behavior and override her ability to exert mate choice preferences (Knott, 2009; Knott et al., 2010). When forced copulations occur in chimpanzees and humans, on the other hand, excessive aggression typically accompanies it, and this functions as a form of indirect sexual coercion (in addition to direct sexual coercion) as it seeks to also control the future reproductive behavior of a female (Emery

Thompson, 2009; Muller et al., 2011). These differing behavioral strategies manifest by chimpanzees and humans in comparison to orangutans are a result of the behavioral ecology of each species. Chimpanzees and humans live in multimale, multifemale communities, so being able to control a female’s current and future reproductive behavior provides a great reproductive benefit to a male as it reduces the access of competitors in his group. Orangutans, on the other hand, are solitary primates, and thus although these males benefit by controlling a female’s current reproductive behavior, they do not benefit by controlling her future reproductive behavior (Knott, 2009).

Another well-known example of sexual coercion is found in chacma baboons (*Papio ursinus*; Kitchen et al., 2009). High-ranking males of this species frequently engage in aggressive attacks against periovulatory females, and leading females to mate with the males to avoid further aggression. This behavior is also thought to function as both direct and indirect sexual coercion of females (to control her current and future reproductive behavior) as well as to impress rival males, as males may assess the relative strength of other males by the quality of their “wahoo” calls that accompany these aggressive displays.

Infanticide as a form of sexual conflict

Infanticide by males falls under the category of sexual coercion as it directly impacts female reproductive choices. Evidence of infanticide has been documented in 54 species of wild nonhuman primates, including species from nine distinct families (Palombit, 2015). The sexual selection hypothesis of infanticide argues that infanticide serves as a reproductive strategy for males if it meets three conditions (Hrdy, 1974). First, a new male supersedes the dominant sire of a group and attacks infants that are unlikely to be his own offspring. Second, following infanticide the mother of a deceased infant resumes cycling sooner than had the infant survived. Third, the attacking male mates with the newly cycling female. Killing unweaned infants is thought to benefit the infanticidal male by instigating a more rapid resumption of cycling in females due to the earlier cessation of lactational amenorrhea (Hrdy, 1974).

While most evidence to date suggests that infanticide is a form of sexual coercion that is best explained by the sexual selection hypothesis of infanticide (van Schaik, 2000; Palombit, 2015), several alternative explanations of infanticide have been put forth over time, including the ideas that infanticide provides a food source for the killer (unique to cases of cannibalism following infanticide), that it is a consequence of overcrowding, that it is a strategy for eliminating resource competition for one's own offspring, and that it is a by-product of aggression towards females (Hrdy, 1979). These alternative explanations remain poorly supported in the primate literature (Palombit, 2015). For example, the social pathology hypothesis, which argues that infanticide is caused by the aberrant behavior of some individuals in overcrowded populations resulting from human disturbance (e.g., provisioning or habitat destruction), has very limited support outside of captive populations (Palombit, 2015). None of these competing theories has withstood critical analysis based on collected and analyzed data, as males rarely consume the killed infants, infanticide is not correlated with the density of the population, males (and not females that are more likely to work to reduce the threat of competition for their offspring) commit infanticide, and infants (not their mothers) appear to be the clear targets of attack (Hrdy, 1979; Palombit, 2015). Thus, the best current explanation for infanticide that currently exists is one based in Sexual Conflict Theory.

Female counterstrategies to infanticide

Female primates are not just passive recipients of sexual conflict in general and infanticide in particular and as such, they have developed a variety of counteradaptations that function to either reduce its occurrence (selective promiscuity, concealed ovulation, nonconceptive matings, early weaning) or to reduce the costs associated with infanticide (spontaneous abortion). Selective promiscuity is the most prevalent and least energetically taxing counterstrategy (Clarke et al., 2009). Male primates are more protective of the offspring of females with whom they have mated, and, therefore, a female can increase the number of protective males surrounding her infant by mating with multiple males (e.g., Clarke et al., 2009). Male protection of females may result from the development of a consortship between a male and female, in which a long-lasting relationship develops as the male and female preferentially groom each other, as seen in olive baboons (*Papio anubis*; Silk et al., 2020). This may explain the potential function of mating with males that are new to the group, a behavior commonly observed in species that experience AMRs (e.g., Zinner & Deschner, 2000).

Other suggested counteradaptations to infanticide include concealed ovulation and periovulatory signals that appear before, and remain after, ovulation occurs (Hrdy, 1979; Hrdy, 1981). These adaptations decrease the ability of males to detect ovulation thereby reducing male ability to control access to females during their most fertile times. This lack of reproductive control on the part of the male leads to paternity confusion (Hestermann et al., 2001), which may encourage greater investment in/tolerance of infants by males and render infanticide a less successful strategy. Other strategies for avoiding infanticide include differential treatment of the sperm of preferred sires, and social strategies such as female alliances, avoiding nonpreferred males, and encouraging multimale groups (reviewed by Fedigan & Jack, 2013).

INFANTICIDE IN WHITE-FACED CAPUCHIN MONKEYS

Despite being relatively small (around 3 kg), these primates have extremely slow life histories. In white-faced capuchins, interbirth intervals are relatively long (mean IBI = 1.89 years) (Fedigan et al., 2008) and infant survival to 1 year is the strongest predictor of interbirth interval length (mean IBI is 2.25 years when the prior infant lives; 1.05 when prior infant dies; range: 0.67 – 5.58 years) (Fedigan, 2003; Fedigan et al., 2008). Thus female reproductive success is greatly affected by intersexual conflict over reproductive control in this species (Fedigan et al., 2008). Infants also wean at a relatively late age (14-23 months) and they engage in allonursing in order to gain additional milk (Sargeant et al., 2015; see Chapters 3 and 4).

Females give birth to their first offspring at 6-7 years (Hogan et al., 2019), whereas males average 10 years of age before they sire offspring (Jack & Fedigan, 2004b). Males also attain adult body size at 10 years (Jack et al., 2014); however males only develop the complete suite of secondary sex characteristics, including full body size potential, after achieving alpha status (Schoof et al., 2011; Jack et al., 2014). Groups typically consist of similar numbers of adult males and adult females, with an average group size of fifteen (Fedigan & Jack, 2013). Females remain in their natal group for life, but males disperse from the group as juveniles and join new groups every few years as adults (Jack & Fedigan, 2004a,b).

The mating system characteristic of this species is polygynandrous, with members of each sex mating with multiple partners (Jack & Fedigan, 2006). Nonconceptive matings are common in white-faced capuchins (Jack, 2007; Manson et al., 1997), as shown by the higher frequency of copulatory events by pregnant white-faced capuchin females than females who are not pregnant (Carnegie et al., 2005). Pregnant females also mate with subordinate males more often than they mate with the alpha male throughout pregnancy. The higher rate of proceptive behavior observed in pregnant females is thought to help form a sociosexual bond between the female and subordinate male as a way to maintain the multimale social structure, which leads to greater group stability and a decreased the risk of infanticide. Mating with subordinate males is also likely important for securing investment in offspring in the face of a change in the group dominance structure (i.e., if a subordinate male later becomes alpha in the same group). Despite this social mating system, the alpha male within a group sires 80% - 100% of the offspring born during his tenure, as determined by genetic paternity testing (Jack & Fedigan, 2006; Muniz et al., 2010; Wikberg et al., 2017). The mechanism leading to this extreme reproductive skew despite polygynandrous matings and no visible signs of mate guarding by the alpha male is still poorly understood. Because the tenure of an alpha male averages four years (Jack & Fedigan, 2004b), being able to sire offspring without waiting for an infant to be weaned (via infanticide) is thought to greatly benefit an alpha male's reproductive output.

Male white-face capuchins (*Cebus imitator*) engage in infanticide, which imparts severe costs to the lifetime reproduction of females. The mortality rate of infants varies greatly and is significantly correlated with AMRs, which can involve coresident or extragroup males, and they can be peaceful or aggressive (Teichroeb & Jack, 2017). All types of AMRs are associated with increased infant mortality (51%) as compared to times of stable male tenure (26%; Chapter 2, Brasington et al., 2017). Younger infants are at the greatest risk of infanticide, with infants under 8.3 months old experiencing the greatest risk of infanticide (Brasington et al., 2017).

This dissertation examines the effects of infanticide on the Sector Santa Rosa population of white-faced capuchins with regard to infant mortality, female counterstrategies, and birth seasonality. First, in chapter two, I examine how infant age and the type of AMR (coresident or extragroup, aggressive or peaceful) affect infant mortality. In chapter three, I investigate the questions of why white-faced capuchins don’t wean their infants earlier as a potential mechanism for lowering the risk of infanticide, and, if they could wean earlier, how this would impact infanticide risk. In chapter four, I ask whether capuchins have longer lactation periods than expected, and if so, why. In this chapter I also investigate the possibility that allonursing in this, and other primate taxa, is a counterstrategy to infanticide. Finally, in the fifth chapter, I investigate whether AMRs and the accompanying infanticide impact birth seasonality or synchrony in white-faced capuchins. I examine these questions throughout this dissertation with the goal of understanding the effects of infanticide on white-faced capuchins.

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CHAPTER 2: INFANT MORTALITY IN WHITE-FACED CAPUCHINS: THE IMPACT OF ALPHA MALE REPLACEMENTS

ABSTRACT

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 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 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 of infanticide are best considered as different levels of analysis rather than competing hypotheses.

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 ursinus* [Palombit, 2009]; African wild dogs, *Lycaon pictus*, [Creel & Creel, 2002]). For primates that live in 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*: Crocket & 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 imitator*: 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 et al., 2012; chacma baboons: Henzi et al., 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): (1) the infant is unlikely to be his own offspring; (2) the infant's death triggers a more rapid resumption of cycling in the mother than if the infant had survived, and (3) the attacking male mates with the mother of the newly deceased infant.

Although most evidence to date supports the sexual selection hypothesis of infanticide (van Schaik, 2000; Palombit, 2015), 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 et al., 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 et al., 2015), a finding that is often linked to the higher levels of circulating testosterone in males (Soma 2006; Sobolewski et al., 2013; de Almeida et al., 2015). 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 (Sapolsky, 1993; Marshall & Hohmann, 2005).

Here we used 29 years of demographic and behavioral data to describe the types of alpha male replacements that occur in wild white-faced capuchin monkeys (*Cebus 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 based on our past observations of this species.

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 et al., 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 et al., 2008) and a relatively late age at weaning (14-23 months) compared to other primate species of similar size (Sargeant et al., 2015). All group males experience some degree of mating success and, although overt male-male mating competition is rare (Schoof et al., 2014a), non-conceptive copulations are common especially between subordinate males and pregnant females (Carnegie et al., 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 (Jack & Fedigan, 2006; Muniz et al., 2006; Muniz et al., 2010; Godoy et al., 2016b; 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 et al., 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 et al., 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 et al., 2014b).

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 generalized aggression hypotheses:

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 et al., 1999; Japanese macaques, *Macaca fuscata*: Soltis et al., 2000; white-faced capuchins, *Cebus imitator*: Schoof et al., 2014b). 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 et al., 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.

METHODS

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 km^2 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 towards him by group immatures), and morphological cues such as increased body mass (Jack et al., 2014; see Fragaszy et al., 2016 for reports of similar weight gain in the closely related *Sapajus*). 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 vs. 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 2.1).

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.

Inclusion of Infant Subjects

We considered white-faced capuchins as infants from birth to one 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 years 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.

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 (Marshall et al., 1998; Kalinowski et al., 2007) as described in Wikberg et al., 2017. Estimated relatedness (*R*) values for males were computed in the software MLRelate (Kalinowski et al., 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).

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 ID 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 et al., 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 et al., 2015) in R and set the significance level to $p < 0.05$.

RESULTS

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 2.1). 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, $p = 0.042$), and between waltz-ins and takeovers (Fisher's exact test, $p = 0.002$), whereas this was not the case for succession and waltz-ins (Fisher's exact test, $p = 0.456$). 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).

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 2.2). 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 2.2). 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 2.2). 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**), 7 infants were sired by the old alpha male (3 rank reversals, 3 successions, 1 fission), and the remaining 3 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, $\chi^2(0) = 6.313$, $p < 0.001$).

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 generalized aggression hypotheses (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 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 one-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 et al., 2012), and white-thighed colobus infants attacked in the context of AMRs are 6 months 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 et al., 2017]; brown capuchins: 12-18 months [Fragaszy et al., 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*), Racabarren et al. (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 (rage = 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 months 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 6 observed infanticides) or disappear at an average of 98 days post-AMR (including all infant deaths and disappearances (Jack & Fedigan, in review; see Beehner & Bergman, 2008 for similar findings in geladas). 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 review).

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 two 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 (Schoof et al., 2014b; Sargeant et al., 2016), 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 2.1) 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 et al., 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, 1971; Rosenberg et al., 1974), 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 et al. (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.

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 et al., 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 (Schoof & Jack, 2013; Schaebs et al., 2017) 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.

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Table 2.1. Summary of AMRs from 1986 – 2015, including details on wounds.

AMR Date[1]	AMR Type[2]	Wounds recorded	Contest for Alpha[3] (Y/N)	Notes[4]
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 AMD 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 infanticides 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; 1 young ADM and SADM begin transitioning into the group that same day (over a two 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

[1] AMR Date includes group (CP, EX, LV, GN, and SE) experiencing the AMR and year of AMR

[2] AMR Type: SU = succession, FI = fission, RR = rank reversal, TO = takeover, WI = waltz-in

[3] Contest = 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.

[4] Abbreviations found in notes: ADM = Adult male; SADM = Subadult male; IGE=intergroup encounter.

Table 2.2 Table of infant births, survivals through first year, deaths before one year based on group stability or type of AMR. (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.

		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

CHAPTER 3: FEMALE COUNTERSTRATEGIES TO INFANTICIDE: EARLY WEANING AND THE BRUCE EFFECT IN WHITE-FACED CAPUCHINS

ABSTRACT

Infanticide occurs at high rates and imposes high costs to female white-faced capuchins (*Cebus imitator*), and it is expected that there has been strong selection for traits that enable females to decrease the risk of infanticide and/or decrease the costs associated with infanticide. Promiscuity, nonconceptive mating, and concealed ovulation are commonly cited as counteradaptations to infanticide in this species, however we investigated the potential for additional counterstrategies to also occur. Nursing infants are at risk of infanticide because the act of suckling induces lactational amenorrhea in the mother, and thus earlier weaning is a potential counterstrategy to infanticide. We found that white-faced capuchins do not appear have reduced lactation periods but instead nurse for many months after they are likely physiologically capable of weaning. Additionally, we found that although earlier weaning appears possible, this species is unlikely to be able to wean early enough to decrease the risk of infanticide. We also investigated whether female white-faced capuchins are able to decrease the costs associated with infanticide via the Bruce effect (i.e., spontaneous abortion), however we found no evidence that the Bruce effect occurs within this species.

INTRODUCTION

Infanticide as a Male Reproductive Strategy

Infanticide by males is generally accepted as a form of sexual conflict that has a direct and negative impact on female reproductive success (Stumpf et al., 2011). This male reproductive strategy, which involves the killing of unweaned young to end lactational amenorrhea and subsequently mate with the newly cycling mother, is in direct conflict with that of the female (survival of her infant) negating the time and energy she has already invested into the infant via gestation and lactation. Evidence of infanticide has been documented in 54 species of wild nonhuman primates, including species from nine distinct families and in nearly all social systems (Palombit, 2015). Infanticide is especially prevalent in species with alpha male replacements (AMRs; Teichroeb & Jack, 2107), a phenomenon in which a new adult male becomes alpha, and in species with high reproductive skew (one male monopolizes reproduction) (Brasington et al., 2017; Fedigan, 2003). The most widely supported explanation for male infanticide (infanticide herein), is the sexual selection hypothesis, which posits that infanticide by male mammals functions as a reproductive strategy when three main criteria are met (Hrdy, 1974). First, a new male supersedes the dominant sire of a group and attacks infants that are unlikely to be his own offspring. Second, following infanticide the mother of a deceased infant resumes cycling sooner than she would had the infant survived. Third, the attacking male mates with the newly cycling female. Killing unweaned infants is thought to benefit the infanticidal male by instigating a more rapid resumption of cycling in females (Hrdy, 1974). Infanticide dramatically decreases interbirth intervals in species such as white-faced capuchins (*Cebus imitator*) for which infant survival to 1 year is the strongest predictor of interbirth interval length (mean IBI is 2.25 years when the prior infant lives; 1.05 when prior infant dies; range: 0.67 – 5.58 years; Fedigan, 2003; Fedigan et al., 2008).

Female Counteradaptations to Infanticide:

Given the prevalence and wide distribution of infanticide in primates, a variety of female counteradaptations that function to either reduce its occurrence (selective promiscuity, concealed ovulation, nonconceptive matings, early weaning) or to reduce the costs associated with infanticide (spontaneous abortion). The most prevalent and least energetically taxing of these is selective promiscuity (Clarke et al., 2009). Male primates are more protective of the offspring of females with whom they have mated, and, therefore, a female can increase the number of protective males surrounding her infant by mating with multiple males (e.g., Clarke et al., 2009). Male protection of females may result from the development of a consortship between a male and female, in which a long-lasting relationship develops as the male and female preferentially groom each other, as seen in olive baboons (*Papio anubis*) (Smuts, 1985; Bercovitch, 1991; Silk et al., 2020). This may explain the potential function of mating with males that are new to the group, a behavior commonly observed in species that experience AMRs (e.g., Manson et al., 1997; Zinner & Deschner, 2000).

Other suggested counteradaptations to infanticide include concealed ovulation and periovulatory signals that appear before, and remain after, ovulation occurs (Hrdy, 1979; Hrdy, 1981). These adaptations decrease the ability of males to know when a female is ovulating thereby reducing male ability to control access to females during their most fertile times. This lack of reproductive control on the part of the male leads to paternity confusion (Hestermann et al., 2001), which may encourage greater investment in/tolerance of infants by males and render infanticide a less successful strategy. Other strategies for avoiding infanticide include differential treatment of the sperm of preferred sires, and social strategies such as female alliances, avoiding nonpreferred males, and encouraging multimale groups (reviewed by Fedigan & Jack, 2013).

In many mammalian taxa, the presence of a nursing infant causes temporary physiological infertility in the mother (Recabarren et al., 2000). This temporary infertility consists of two parts, *lactational amenorrhea*, during which ovulation and menstruation do not occur, and *residual infertility*, during which ovulation occurs with an inadequate luteal phase making conception unlikely (McNeilly, 2001). This temporary infertility is thought to be caused by the infant suckling the mother, which increases the amount of prolactin, the hormone responsible for milk production and the suppression of reproductive cycling and ovulation (Majumdar & Mangal, 2013). Given the link between extended lactation periods and increased infanticide risk (Palombit, 2015; van Schaik, 2000), early weaning could also function as a counteradaptation to infanticide. If females are able to decrease the length of the lactation period, they could effectively end their lactational amenorrhea and resume cycling earlier when the threat of infanticide is present. Such an adaptation has been observed in white-headed leaf monkeys (*Trachypithecus leucocephalus*), where abrupt weaning occurred during the course of a takeover resulting in the weaning of infants 2.6 months (12.8%) earlier than during stable periods (Zhao et al., 2011).

Despite the widespread distribution of these counteradaptations to reduce the occurrence of infanticide, infanticide still occurs in many species, and often at high rates. In addition to the reproductive costs of infanticide (loss of an infant), the energetic costs of gestation and lactation for an infant that does not survive to reproductive age are enormous (see below). Thus in species where infanticide occurs with some frequency, the more important adaptations may be those that reduce the energetic costs that infanticide imposes on females. While these types of adaptations can be very difficult to study and have received less attention by researchers, long term data sets on well-studied populations are beginning to shed light on these mechanisms and lay the groundwork for future, targeted, studies (Stumpf et al., 2011; e.g., Kalbitzer et al., 2017; Manguette et al., 2019).

One such mechanism to reduce the energetic costs of infanticide on females is a physiological response known as the *Bruce effect*, which involves the spontaneous termination of pregnancies in response to the presence of novel males (Bruce 1959). The Bruce effect has been observed in a variety of mammalian species including mice (*Mus musculus*; Bruce, 1965), prairie voles (*Microtus ochrogaster*; Fraser-Smith, 1975), domestic horses (*Equus caballus*; Berger, 1983), geladas (*Theropithecus gelada*; Roberts et al., 2012), and hamadryas baboons (*Papio hamadryas*; Amann et al., 2017). The best supported hypothesis for the existence of the Bruce effect as a counteradaptation to infanticide is that spontaneous abortion is less energetically costly for females than continuing to invest in that offspring when the threat of infanticide is high (Hrdy, 1979; Roberts et al., 2012).

Here we investigated some of these potential female counteradaptations to infanticide using white-faced capuchins *(Cebus imitator)* as a model. The Santa Rosa population of white-faced capuchins (*Cebus imitator*), located in the Sector Santa Rosa (SSR) of the Área de Conservación Guanacaste, Costa Rica, has been the focus of continuous study since 1983 (Fedigan & Jack, 2012). As such, the project has accumulated over 35 years of demographic data on the population, thus providing a unique opportunity to study the long-term impacts of infanticide on female capuchins. The SSR capuchins reside in multimale, multifemale groups that range in size from 5-35 individuals (Fedigan & Jack, 2012). White-faced capuchins exhibit high degrees of relatedness among female group members due to a combination of female philopatry, high rates of female survival, and high reproductive skew of the alpha male (Perry et al., 2008). Although male white-faced capuchins rarely direct aggression towards females, they do engage in infanticide, which imparts severe costs to the lifetime reproduction of females (Fedigan et al., in prep; Kalbitzer et al., 2017). In this population, the infant mortality rates vary considerably and are significantly correlated with the occurrence of AMRs; 51% mortality in association with AMRs compared to 26% for infants born during times of group stability (Brasington et al., 2017; Chapter 2). The costs of these infant deaths are further compounded by relatively long interbirth intervals (mean IBI = 2.25 years when the prior infant lives; Fedigan et al., 2008).

Given the enormous toll male infanticide has on female reproductive success, it is not surprising that female capuchins engage in a number of different strategies to reduce the occurrence of infanticide. These include, mating with multiple group males, though alpha males do sire the majority of infants born during their tenures (Jack & Fedigan, 2006; Muniz et al., 2010; Wikberg et al., 2017), nonconceptive matings, especially by pregnant females (Manson et al., 1997) who selectively mate with subordinate males (Carnegie et al., 2005), and concealed ovulation (Fedigan & Jack, 2013). Here we investigated other potential counteradaptations of capuchin females to either reduce the occurrence of infanticide, namely early weaning of offspring following an AMR, and the Bruce effect as a mechanism for reducing the energetic costs of infanticide following an AMR.

REDUCING THE OCCURRENCE OF INFANTICIDE

Reproductive costs of infanticide for female capuchins:

The costs of infanticide to the lifetime reproduction of females was recently quantified for the Santa Rosa population (Fedigan et al., in prep). Infanticide has been shown to negatively affect the lifetime reproductive success of white-faced capuchin females in three major ways (Fedigan et al., 2008; Fedigan et al., in prep). First, females that experience a high rate of AMRs during their reproductive years lose about half of their infants, compared to only ⅕ of infants lost to females experiencing lower levels of AMRs. Additionally, the mean age of death from infanticide in this population is 77 days, which Fedigan et al. (in prep) calculated imposes a total loss of 77,500 kJ when the mother's energetic costs through gestation and lactation are included (adult females are estimated to require 1000 kJ/day and 1500 kJ/day when cycling and lactating, respectively). This represents a 32% increase in the energy that the mother expends over this 77-day period compared to that of an adult female that is not pregnant or lactating. Finally, infanticide represents a significant time loss for a female as it lowers the number of infants that she will be able to produce during her reproductive lifespan. When this loss of time, and therefore total number of offspring produced, is quantified, it indicates that each AMR contributes to a “reproductive opportunity cost” of 0.6 infants per female for each infant born in association with an AMR. This number is large considering that the average female in this population only produces 5.7 infants that survive to 1 year of age, and that females likely experience 3.36 AMRs during their reproductive tenure. Thus, a typical female stands to have her lifetime reproductive output decreased by 35% due to time loss caused by infanticides linked with AMRs [(0.6 infants lost per AMR* 3.36 AMRS)/5.7 total lifetime infants = 0.3537].

Early weaning in response to AMRs:

Because nursing infants are the targets of infanticide by new alpha males, weaning infants in response to AMRs might be mechanism for avoiding infanticide. For white-faced capuchins, the high infant mortality rate in association with AMRs, especially for young infants (mean age at death = 77 days, range of greatest risk = birth to 8.3 months; Brasington et al., 2017; Chapter 2), would be expected to exert a strong selective pressure on females to reduce the period of temporary infertility and the resultant interbirth intervals (IBIs). Yet female white-faced capuchins nurse their infants for 14-23 months (Sargeant et al., 2015), causing an extended period of lactational amenorrhea, residual infertility, and relatively long IBIs between surviving infants (2.25 years when the prior infant lives; Fedigan, 2003; Fedigan et al., 2008). This finding begs the question of why don’t female white-faced capuchins wean their infants earlier as a means of reducing their IBI and the risks of infanticide? To address this question, we must first determine if it is a) physiologically possible for capuchins to wean earlier and, if so, b) what impact would earlier weaning have on vulnerability to infanticide.

a) Can capuchins wean their offspring earlier? With the exception of prosimians and the callitrichids, which have 4-5 month and 3-month-long lactation periods respectively, the earliest primate weaning appears to occur at 6 months in several macaque species (*Macaca thibetana*: 6 months [Jablonski et al., 2000]; *Macaca mulatta*: 6 -12 months [Jablonski et al., 2000]. This number may function as a minimum viable weaning threshold for anthropoid primates. However, for capuchins the weaning threshold may be closer to 8 months, as infants in one captive group of tufted capuchins (*Sapajus apella*) survived after forced weaning at 8.7 months following the removal of their mothers (260 days, Recabarren et al., 2000). Likewise, captive *C. albifrons* were separated from their mothers at birth, hand reared by human caretakers, and successfully weaned onto solids between 7-9 months of age (Wilen & Naftolin, 1978). This artificial weaning age induced by researchers is far younger than weaning age for infants left with the mother in captivity. For example, in another captive group of *S. apella*, weaning was estimated to be fully complete at 20.5 months after which there were no subsequent observations of nursing (range: 13 and 34 months; Weaver & de Waal, 2003). The suggested lower threshold for weaning age of captive tufted capuchins (*S. apella*, 8.7 months) is also far earlier than weaning age observed in the wild (12 – 18 months; Di Bitetti & Janson, 2001).

Given these data on closely related taxa in captivity, it does seem physiologically possible for female white-faced capuchins to wean their infants earlier, perhaps as early as 8 months of age. While weaning time in white-faced capuchins is highly variable, the earliest weaning age our group has documented to date is 14 months (Sargeant et al., 2015), though targeted long-term data are needed to realize the full range of weaning ages.

b) What impact would an earlier weaning age have on vulnerability to infanticide? Infanticide in white-faced capuchins is focused heavily on younger infants (mean age at death of 77 days; Fedigan et al., in prep) and age of greatest vulnerability is for infants under 8.3 months (Brasington et al., 2017), although older infants (but not juveniles) have also been killed during AMRs (range: 0 to 332 days; Brasington et al., 2017). Similarly, Janson et al. (2012) reported that all infant *S. nigritus* 8 months and younger are killed after an AMR. Given that this age of peak vulnerability to infanticide following AMRs for both *C. imitator* and *S. apella* coincides with the likely min threshold of weaning (as demonstrated by captive studies: Recabarren et al., 2000; Verderane & Izar, 2019), it seems that weaning infants earlier, as early as 8 months, would not do much to reduce the occurrence of infanticide and would likely put the infants at an increased risk of death from other causes (e.g., predation, starvation). To date we have no evidence of females spontaneously weaning infants in the context of an AMR, as was reported for leaf monkeys (Zhao et al., 2011), though again targeted observations are needed to quantitatively assess this possibility.

As a proxy for behavioral data on weaning in response to AMRs, we examined the interbirth intervals (IBI) for females whose infants survived an AMR with the IBI for females who give birth during periods of group stability as IBIs are directly impacted by the cessation of nursing (via weaning or infant death). For example, in a study of captive *S. apella*, females that were not allowed to nurse their infants experienced an interbirth interval of 1 year (350 days). Because gestation is 155 days, this IBI indicates that they experience a 195-day postponement of conception following the birth of their infant: 42 days for cycling to resume [determined via vaginal cytology; Recabarren et al., 2000] followed by 153 days of residual infertility). When females were allowed to nurse for 260 days, the interbirth interval increased to 613 days via a combination of lactational amenorrhea (159 days), residual infertility (301 days), and gestation (155 days; means from Recabarren et al., 2000; see Figure 3.1). Our examination of the IBIs in the SSR capuchins found that females who have infants that survive an AMR do not experience significantly shorter interbirth intervals (mean = 24.6 months days, n = 29 infants) compared to interbirth intervals during times of group stability (mean = 26.5 months days, n = 122 infants, Hogan, unpublished data; t-test: p = 0.13; Figure 3.2). Though not significant, it does show a 2-month decrease in IBIs for infants who survive an AMR, which is in line with the 2.6-month decrease in weaning age after AMRs reported) in white-headed leaf monkeys (Zhao et al., 2011) possibly indicating that female capuchins do attempt to decrease their lactation period in response to AMRs. Like capuchins, these leaf monkeys have nearly 2 year-long lactation periods (mean during periods of group stability = 20.3 months; mean during AMR = 17.7 months; Zhao et al., 2011), and the 2.6-month decrease shortens the weaning period by 12.8 percent. If the 2-month shortened IBI found in the capuchins reflects a similarly shortened lactation period, the weaning age would be decreased by 8.3% - 13.6% (known weaning age range is 14 to 23 months; Sargeant et al., 2015). Decreasing the weaning age by roughly 10% may indicate an effort by female capuchins to avoid infanticide, though more data are needed.

Even if female white-faced capuchins can wean their infants early by roughly 10% in response to AMRs, this decrease in weaning age would be unlikely to affect infanticide risk due to a lengthy postpartum infertility phase, which, as evidenced by the Recabarren et al. (2000) study, occurs in capuchins even if females do not nurse. Following weaning at around 9 months of age, a female tufted (or white-faced) capuchin experiences a 5 to 6 month-period of further infertility before she is able to conceive her next offspring, followed by a 5-month gestation period, resulting in the 20.4 month IBI. If an infant is weaned at 14 months, the minimum age observed in white-faced capuchins to date, the IBI would be ~ 24 months. Thus the death of an infant over 8 or 9 months of age will have very little impact on female IBI due to residual infertility, which may be why these older infants are not targeted by new alpha males. At this age, infants are relying less heavily on their mother's milk, increasing their consumption of solid foods, and moving around more freely on their own (MacKinnon, 2006) (see Chapter 4 for additional details on nursing stages in white-faced capuchins).

MECHANISMS TO DECREASE THE COST OF INFANTICIDE

The Bruce effect:

Because early weaning does not appear to be a mechanism that would enable capuchins to avoid infanticide or the frequency with which infanticide occurs in this species, it is likely that other mechanisms exist to reduce the costs of infanticide. The Bruce effect (Bruce, 1959), or spontaneous abortion, is one potential mechanism as it would enable females to halt their investment in infants that would be highly susceptible to infanticide due to AMRs. The Bruce effect has been documented to occur in response to the presence of novel males (e.g., in rodents; Bruce, 1959) or periods of high stress (e.g., women living in areas at high risk of deadly rocket strikes; Wainstock et al., 2013). For primates, AMRs involve both of these factors; a new (novel) male rising to alpha status, and this social instability is associated with high levels of stress for group females (e.g., Sapolsky, 2005; Beehner et al., 2005; Wittig et al., 2015).

Demographic data can be used to infer evidence of a Bruce effect such that spontaneous abortion in response to a new alpha male would result in a decrease in the number of births in the period immediately following an AMR. For example, in gelada reproductive units fewer infants are born in the 6 months following an AMR, a finding that was further corroborated by hormonal data indicating pregnancy loss (Roberts et al., 2012). We analyzed 90 infants born near AMRs, and found no evidence of the Bruce effect as there were not fewer infants born in the 6 months immediately following an AMR compared to other 6 month time periods (see Table 3.1; $\chi^2 = 2.648$; $p=0.618$). Note the increased number of infants born in the 7-12 and 13-18 month periods following an AMR reflect increased female fertility following AMRs, many of which are due to the cessation of weaning due to infanticide. Additionally, in an analysis of infant mortality in response to an extreme two-year drought, Campos et al. (2020) found that the Santa Rosa capuchins continued to reproduce during these adverse conditions, experiencing nearly 100% infant mortality, while the Santa Rosa spider monkeys (*Ateles geoffroyi*) ceased reproducing. The authors concluded that capuchin females do not appear to able to shut down reproduction in response to adverse environmental conditions and/or poor maternal health. Collectively, these findings indicate that the Bruce effect is not a likely mechanism employed by white-faced capuchins to decrease the cost of infanticide

CONCLUSIONS

Infanticide imparts severe costs to the lifetime reproduction of white-faced capuchin females, including a measurable decrease in lifetime reproductive fitness and “wasted” time and energy (Fedigan et al., 2008; Fedigan et al., in prep). Considering that lactation alone increases female energetic demands by nearly 1/3 and that the average female has fewer than 6 offspring survive the first year of life, the costs of infanticide are quite high (Fedigan et al., in prep). This high level of waste is exemplified by the fact that females experiencing high levels of AMRs lose roughly 50% of their offspring (Fedigan et al., in prep).

Given these high costs, infanticide by males is expected to exert a strong selective pressure on females to develop strategies to reduce the occurrence of this male reproductive strategy that is so clearly at odds to their own reproductive success. Numerous adaptations against infanticide are commonly cited, such as promiscuous mating, nonconceptive mating, and concealed ovulation, (Carnegie et al., 2005; Jack & Fedigan, 2006; Manson et al., 1997; Muniz et al., 2010; Wikberg et al., 2017). Despite these counteradaptations, infanticide still happens at extremely high rates: infant mortality is 51% following AMRs compared to 26% for stable alpha male tenure (Brasington et al., 2017; Chapter 2). Because infanticide occurs at such high rates and imposes such high costs in this species, we investigated why early weaning, another potential counteradaptation to reduce the occurrence of infanticide, does not also occur in this species. We found that it appears physiologically possible for capuchins to wean earlier, as the observed weaning age (range: 14 – 23 months; Sargeant et al., 2015) far exceeds the probable minimum weaning age (8 months; Recabarren et al., 2000). However, because the minimum weaning age occurs just as the period of greatest vulnerability to infanticide ends (8.3 months; Brasington et al., 2017), it does not appear that white-faced capuchins could wean early enough to reduce their vulnerability to infanticide.

Because female white-faced capuchins seem to have few options for reducing the *occurrence* of infanticide, we looked at one potential mechanism to reduce the *costs* associated with infanticide risk, i.e., the Bruce effect. The ability to spontaneously terminate a pregnancy in response to a new alpha male in the group, a situation that is extremely stressful, does not appear to be possible for female capuchins. Given the widespread occurrence of AMRs and infanticide in this species, there must be other, yet unexplored mechanisms in place to reduce these costs. In the next chapter, we investigate the practice of allonursing as a potential adaptation that capuchin females engage in to reduce the costs, or decrease the risk, of infanticide.

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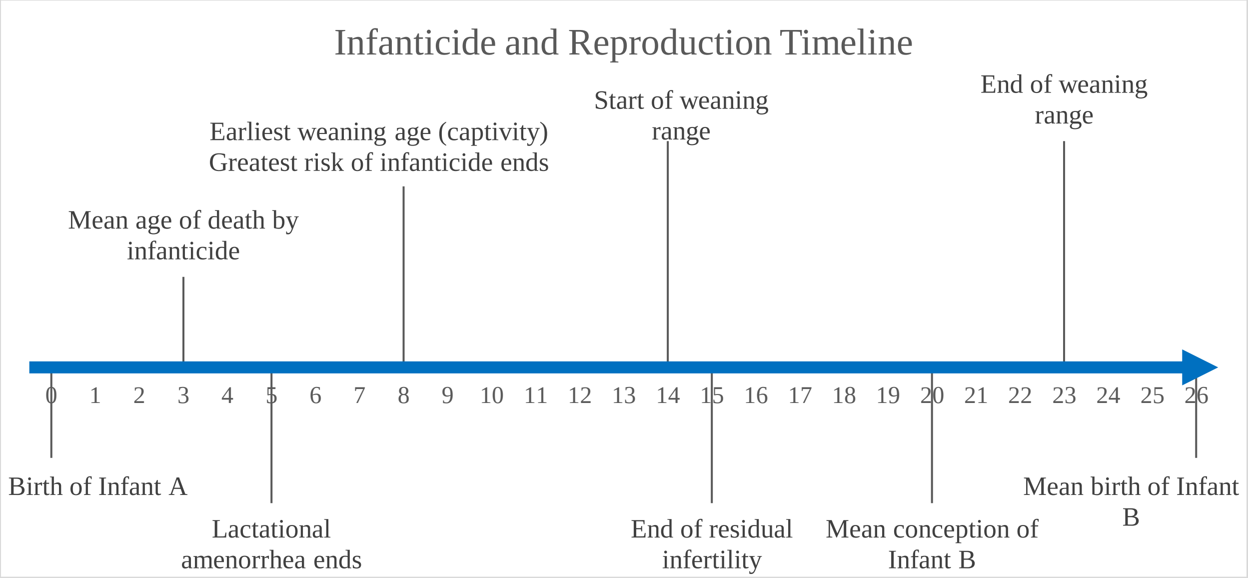

Figure 3.1. Timeline of various reproductive events (lactational amenorrhea, residual infertility, weaning age, conception), and infanticide risk during interbirth interval when the first infant survives. Number along X axis represents number of months since Infant A was born.

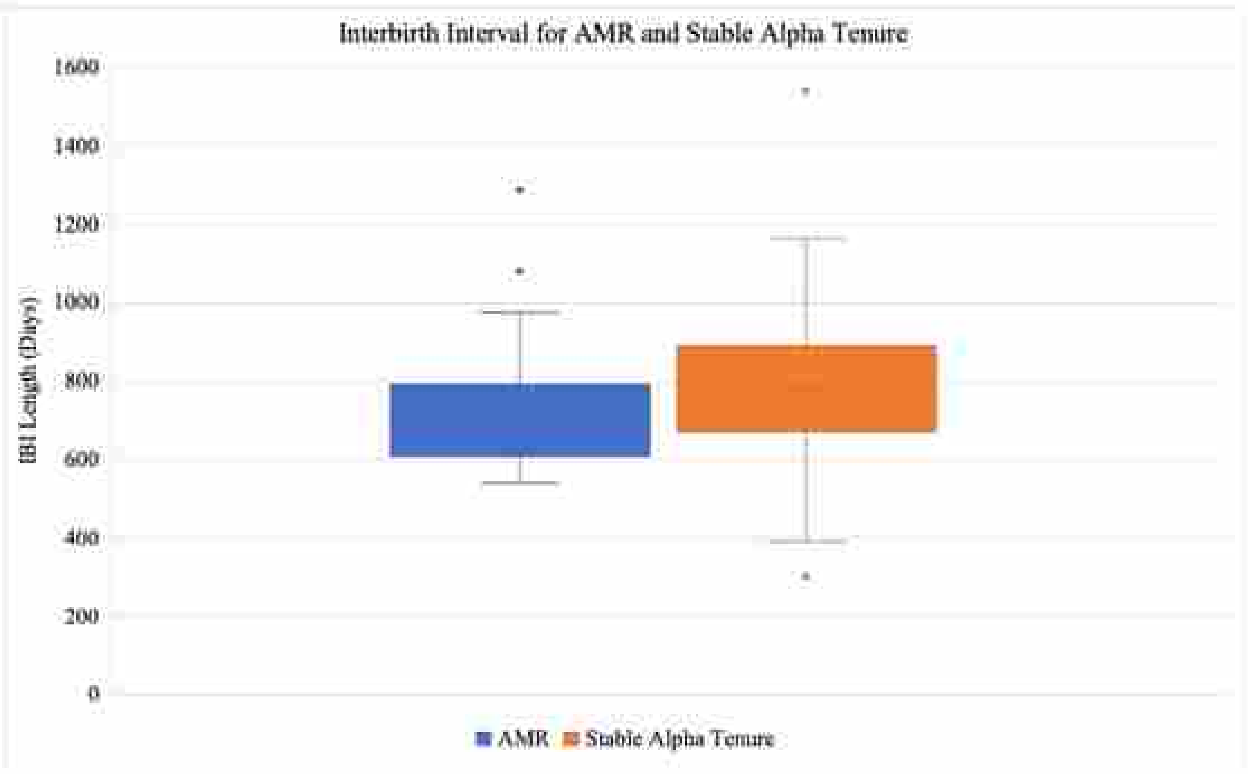

Figure 3.2. Interbirth interval when first infant experiences an AMR (blue) or time of stable alpha male tenure (orange) and survives to one year of age. Dots above and below the box plots and whiskers are outlier data points.

Table 3.1. Number of infants born during various time periods surrounding AMRs.

	Number of Infants Born
6 Months Before AMR	20
6 Months After AMR	19
7 – 12 Months After AMR	27
13 – 18 Months After AMR	24
19 – 24 Months After AMR	18

Timing of 90 infant births relative to AMRs from 1989 – 2013. Infants were excluded if their births could be included in multiple categories due to AMRs being close together.

CHAPTER 4: THE PARADOX OF LATE WEANING AGE IN WHITE-FACED CAPUCHINS: ALLONURSING AS A POTENTIAL COUNTERSTRATEGY TO INFANTICIDE

ABSTRACT

Infanticide by males is expected to exert a strong selective pressure on females to develop strategies to reduce the occurrence and/or costs of this male reproductive strategy that is so clearly at odds to female reproductive success. Male infanticide functions as a reproductive strategy when a new male becomes the dominant sire of a group, attacks unweaned infants likely sired by other males, causing mothers of the deceased infants to cease lactating and resume cycling, and then mating with the newly cycling mothers (sexual selection hypothesis). Thus, lactational amenorrhea, the temporary infertility in mothers caused by the suckling of an infant, plays a major role in enhancing infanticide risk. Despite the risk of infanticide associated with lactation, white-faced capuchins (*Cebus imitator*) nurse for longer than expected based on body size (14-23 months). Although they likely could wean many months earlier, our analysis in the previous chapter showed that it would not decrease the risk of infanticide. Energetically, lactation is the most expensive part of reproduction, so the loss of an infant represents a measurable loss of energy to the female. Here, we examine how the lactation periods of capuchins compare with those of other primates and why weaning occurs so late in white-faced capuchins relative to other species. We then explore the possibility that the long

nursing period in this species may have developed as a strategy to reduce the costs, or decrease the risk, of infanticide.

Allonursing (nursing by nonmothers) is a rare practice in mammals, however it occurs commonly in white-faced capuchins and we propose that it may work in conjunction with an extended lactation period as an adaptation to infanticide. Specifically, we suggest 1) that allonursing functions to decrease the energetic investment that each female makes in her infant when both lactation costs and infanticide risk are high, thus decreasing the energetic costs of losing an infant to infanticide, and 2) that allonursing decreases the risk of infanticide by enabling the mothers of younger infants to resume cycling earlier, thus reducing the risk of infanticide. In both scenarios, mothers whose infants are older and no longer require milk for survival, yet still lactate due to nursing young, may be crucial for supplementing younger infants at high risk of infanticide.

INTRODUCTION: LACTATION IN CAPUCHINS

Do white-faced capuchins have a longer lactation period than other primates?

The length of the lactation period has been shown to be a critical factor in infanticide; mammals with lactation periods longer than their gestation are at the greatest risk for infanticide (Palombit, 2015; van Schaik, 2000). White-faced capuchins have lactation periods (14-23 months [Sargeant et al., 2015]) that far exceed their 5.5-month gestation length (Carnegie et al., 2011). While this gestation period is in accordance with other similarly sized primates, their lactation period far exceeds that of similarly sized species (Table 4.1). To compare whether weaning ages of wild capuchins (*S. apella; C.*

imitator; C. olivaceous; S. nigritus) occur significantly later in their life-history than those of similarly sized primates, we performed a student's t-test of weaning ages among similarly-sized primates and assuming equal variances. Primate species were defined as similarly sized and included in the analysis if the average body mass of the adult females of each species fell within the average minimum and maximum body mass of the adult females in the capuchin group (min=2300g, max=3190g; i.e., *Eulemur fulvus*, *Lemur catta*, and *Varecia variegata*). We confirmed variances were equal between groups using an F-Test for Equality of Two Variances ($F_{3,2}$=1.42, p=0.879).

We found the capuchin group to have significantly longer lactation periods than the group of other similarly sized primates (t(5) = 10.47, p = 0.00013). The result of this comparison is not, however, overly surprising given the much faster paced life histories of the stepsirrhine primates to which the capuchins were compared. Indeed, the long lactation period is in accordance with the overall slow life histories of capuchins despite their small size (around 3 kg). For example, female capuchins do not give birth to their first infant until they are 6-7 years of age (Hogan et al., 2019), while males do not reach sexual maturity until ~7 years of age and do not attain adult body size until around 10 years of age (Jack et al., 2014). A three-way ANOVA was performed to assess whether the weaning ages of 27 primate species can be explained by adult female mass, mass at birth, gestation length, presence of infanticide, and all dyadic interactions of these explanatory variables. We found that only the interaction of adult female mass and birth mass significantly predicted weaning age ($F_{df=1}$ = 6.72, p = 0.02, Figure 4.1). When the interaction of adult female mass and birth mass is plotted against the weaning age of the primates used in the analysis, the capuchin clade (black shapes) stands out compared to the other primates for having much later weaning ages than expected based on body size (Figure 4.1).

Why do white-faced capuchins nurse for so long?

Clearly the capuchin clade stands out among the non-hominoid primates as nursing much longer than expected based up on birth mass and female mass. Here we investigate a variety of interspecific factors proposed to influence the timing of weaning, including: the attainment of a particular body mass, the timing of dental eruption, and/or weaning age may be determined by the relative brain size of a particular species. Note that these factors need not be mutually exclusive.

Weaning once a certain mass is reached. In a study of primates, ungulates, and pinnipeds, Lee and colleagues (1991) found that species in these monotocous taxa consistently weaned once the infant's mass reached four times the birth mass (range 3.2 to 4.9 times neonatal mass). This relationship holds even when controlling for maternal mass, and may help us to understand differences in the age at weaning. Lee et al. (1999) also compared the mass and age of weaning of five primate species (Japanese macaques [*Macaca fuscata*], yellow baboon [*Papio cynocephalus*], olive baboons [*Papio anubis*], chimpanzees [*Pan troglodytes*] and humans [*Homo sapiens*]) under two varying conditions: food abundant (captive) and food restricted (wild). All five species weaned at different ages, but intraspecific comparisons found that wild representatives weaned at ages 1.5 to 3 times older than captive individuals. However, there were no intraspecific differences in terms of infant mass at weaning when comparing captive and wild representations. This supports the idea that a minimum infant size must be attained before weaning to increase chances of survival. However, capuchins do not follow this trend and continue to nurse well after the suggested minimum size (3.2 – 4.9 times birth mass) has been achieved. For instance, *Sapajus apella* weigh 0.210 kg at birth (Fragaszy & Bard, 1997), and by Lee et al.'s (1991) findings, would be expected to wean at 0.840 kg (range = 0.672 and 1.03 kg). However, their mass at weaning is 1.272 kg (Fragaszy & Bard, 1997), which is far heavier (51% heavier) than the expected size. Unfortunately, we lack data for white-faced capuchin mass at weaning age, but we would expect them to follow a pattern similar to *S. apella*. We would expect weaning age for *Cebus albifrons*, which are more similar in size and more closely related to *C. imitator*, to more closely approximate weaning in white-faced capuchins. However, the data we have for *C. albifrons* are less informative as they are based on captive studies in which infants are removed from their mothers at birth and hand-reared. However, even based on these studies, weaning age appears to occur later than expected, or at the very high end of the range, based on achieved body size. When infants were switched over to solid foods by caretakers at 270 days, they achieved a mass more than 4 times than that of their birth mass: females (0.2277 kg at birth) were weaned at 1.1 kg but were expected to wean at 0.91 kg (range = 0.73 – 1.12 kg); males (0.2375 kg at birth) were weaned at 1.3 kg, which is far heavier than the expected 0.95 kg (range = 0.76 – 1.16 kg; Elias 1977; Fleagle & Sammond, 1975). Perhaps part of this deviation from Lee et al.'s (1991) pattern is that capuchins are much smaller than the vast majority of other mammals included in the study. However, Lee et al. (1991) did include three primate species that were smaller than capuchins and all exhibited the opposite trend in that they weaned at smaller mass than expected (*Aotus trivirgatus* weaned at 65% of the expected size, *Saimiri sciureu*s weaned at 82% of the expected size, and *Miopithecus talapoin* weaned at 58% of the expected size). Lee and colleagues suggest that the minimum size required for weaning in primates may be related to the dexterity and power required to successfully forage, especially for foods that require a higher level of skill or processing to access, something that is particularly important in capuchins (Melin et al., 2014).

Other studies suggest that weaning age is more closely related to adult mass. In fact, a very large proportion (66-96%) of the variation observed in life history characters is related to adult mass, typically allometrically (Ross, 1991). For instance, Harvey and Clutton Brock (1985) found that weaning age in primates shares the following relationship with female mass:

$\log(\text{weaning age in days}) = \log(2.71) + 0.56 * \log(\text{adult female body mass (g)})$

This calculation suggests that capuchins, with an adult female body mass of 2900 g, should wean at approximately 235 days or 7.8 months. This is, of course, far earlier than the observed weaning age of 14-23 months, but corresponds almost exactly with the minimum weaning threshold found in captive studies (see Chapter 3; Recabarren et al., 2000). A simpler relationship between weaning and adult mass suggests that offspring are weaned once they have attained 33% of their full mass at maturity (Charnov & Berrigan, 1993). But capuchins again do not fit this pattern, weaning instead at a much higher proportion of the adult mass. For example, weaning occurs in captive *S. apella* once infants reach 53% of an adult female’s mass (Fragaszy & Bard, 1997). By any of the mass-related measures above, capuchins wean far later than expected.

Weaning and dental eruption. Weaning also appears to be heavily correlated with other life history factors, such as the eruption of the first permanent tooth. The timing of dental eruption, when a tooth crown becomes visible above the gum line, is thought to be a stable feature in mammalian development that typically is not influenced by environmental factors such as food scarcity (Smith, 1989). The mandibular first molar is the first permanent tooth to erupt in mammals in general, including primates, and often coincides with the end of weaning (Smith, 1989; Dirks & Bowman, 2007; but see Nee et al., 2005 for concerns regarding life history factors). Captive *C. albifrons* develop their first permanent tooth (1st molars) at 13.5 - 14 months (Fleagle & Schaffler, 1982), which coincides with the earliest age of weaning for *C. imitator* (Sargeant et al., 2015). The timing of dental eruption in primates generally occurs earlier in smaller primates and later in larger ones, however dental eruption in captive *C. albifrons* occurs at a similar time as the larger *Lagothrix lagotricha* and *Cercopithecus aethiops*. As predicted based on body size, the eruption of the first molar occurs earlier for the capuchins than for the larger rhesus macaques (*Macaca mulatta*), chimpanzees (*P. troglodytes*), and humans (*H. sapiens*; Fleagle & Schaffler, 1982).

Weaning and brain size: Brain tissue is energetically expensive compared to other tissue types (Mink et al., 1981). After accounting for body size, mammals with larger brains typically have higher basal metabolic rates (BMR; Isler & van Schaik, 2006). This association is most pronounced in the primate order, where 20% of the brain size variation is related to BMR (Isler & van Schaik, 2006). The high energetic costs associated with relatively large brain size are correlated with smaller litter sizes in altricial mammals and a lower birth rate, slower development, and increased age of sexual maturity in precocial mammals (Isler & van Schaik, 2009). Although most primates are born closer to the precocial end of the spectrum, capuchins are considered behaviorally more altricial at birth than all other primates except the apes (Fragaszy, 1990). In capuchins, both length of gestation and neonatal brain size are average for platyrrhines of their size (Fragaszy, 1990), it is likely that the lengthy duration of the capuchin lactation period is related to the very large size of the capuchin brain since neural tissue is energetically expensive to create (Mink et al., 1981), a factor that has long perplexed primatologists (Janson et al., 2012):

> If the current notion is correct that these slow life histories are a direct result of the relatively large brain size of capuchins … then the cost of large brain size is extreme – the theoretical intrinsic rate of population growth (a rough measure of maximum fitness) in our population … is 0.1/year, a full order of magnitude less than the rmax [intrinsic rate of population increase] of about 1 expected of mammals of equivalent body mass … It is difficult to imagine what benefits of larger brains might repay such a tenfold fitness cost!

We used the encephalization quotient, defined as the ratio between observed brain size to expected brain size based on body size (Jerison, 1973) to compare relative brain sizes among different species. Other measures that focus on specific parts of the brain, such as the neocortex, can be misleading as they “scale hyper-allometrically with brain size” (DeCasien et al., 2017). We use body and brain mass to calculate the EQ of 33 primate species. Of these, capuchins (*Cebus* spp. and *Sapajus*) have the highest EQ among the nonhuman primates (See Table 4.2).

As Table 4.2 indicates, the brains of capuchins, including white-faced capuchins, are very large relative to body size. Capuchins are not born with large brains (which is likely restricted by maternal body size), but instead the major increase in brain size occurs after birth, and the capuchin brain experiences a greater relative increase in size compared to other monkeys (Fragaszy et al., 2004). Thus the long lactation period of this taxonomic group may be required for growing such a large brain post birth. Additionally, physical proximity to the mother may also enhance their learning of complex skills during this time (Verderane & Izar, 2019). Extended nursing may also provide the infants greater protection against infanticide, as the greater proximity to adult females may provide physical protection from males (but see Kalbitzer et al., 2017). This suggestion is supported by the observation that groups of hanuman langurs (*Presbytis entellus*) that have more females are better able to protect infants from infanticide than those with fewer females (Treves, 2000).

PATTERNS OF ALLONURSING OCCURRENCE

Allomaternal care, infant care by individuals other than the mother, is associated with increased speed of infant development, including earlier weaning, in primates (Tecot et al., 2012; van Schaik, 2000). In wild chimpanzees, for example, it has been demonstrated that allomaternal care by older offspring (or other maternal kin) enables mothers to nurse their infants less often, which in turn leads to faster weaning and this decreased energetic load is thought to enable shorter interbirth intervals and ultimately higher reproductive success (Badescu et al., 2016). Allonursing, the act of nursing non-offspring young, is a very energetically expensive form of allomaternal care due to the high energetic costs of lactation (Packer et al., 1992). Allonursing occurs in several capuchin species (*S. apella*: Fragaszy, 2004; *C. imitator*: Sargeant et al., 2015; *C. nigritus*: Baldovino & Di Bitetti, 2008; *C. olivaceous*: O’Brien & Robinson, 1991), and appears to occur more frequently in this clade in comparison to others. Only talapoins [*Miopithecus talapoin*] and bonnet macaques [*Macaca radiata*] have rates of allonursing (>10%) comparable to capuchins [Sargeant, 2014])

Stages of nursing and their relation to allonursing:

Despite the high energetic costs, capuchins engage in allonursing at very high rates, with 12.4% of infant nursing bouts over a 9-month study period coming from non-mothers (Sargeant et al., 2015). In order for allonursing to evolve, females would need to be able to balance their owns costs and benefits to engaging in (or being a recipient of) the behavior, and the costs/benefits to their own offspring. While teasing apart all these costs and potential benefits is difficult, attaining this balance is likely related to the energetic demands of nursing that change throughout the lactation period. We recognize three distinct stages of nursing from birth to complete weaning, differentiated by energetic quality of milk and relative contribution of allonursing to the infant's energy intake.

<u>Birth to 8 weeks - intense energetic demands on the mother</u>: The first 8 weeks of life coincide with high rates of energy consumption for the mother (McCabe & Fedigan, 2007), likely due to the higher-quality milk the mother is producing at this stage (higher in percent total gross energy from crude protein; *S. apella*; Milligan et al., 2010). During this time, allonursing is uncommon, nursing rates are at their highest, and milk consumption is nearly double that of older infants (Sargeant et al., 2015). Although white-faced capuchins can give birth at any time of year, the mean birth peak occurs 8 weeks before the peak fruit abundance in Santa Rosa, matching the peak energetic

demands of the mother and functioning to maximize maternal survival (Carnegie et al., 2011). As relaxed income breeders, capuchins are not expected to be able to store fat (i.e., energetic reserves) in preparation for lactation, and thus are reliant on food sources during lactation to provide all of the necessary energy to make milk (Brockman & van Schaik, 2005). Starting at 8 weeks, the energetic stress on the mother begins to decrease as the infant starts to move off of the mother and begins to allonurse and contact non-milk sources of food (Fragaszy, 1990; Sargeant et al., 2015).

Months 2 to 8 - infants heavily supplemented by allonurses: During this period, capuchin infants begin to climb off the mother and move independently (Fragaszy, 1990) though they still heavily rely on milk as weaning does not occur before this time (Recabarren et al., 2000; Sargeant et al., 2015). This is a period of intense physical development as infants learn to control their bodies and by 6 – 7 months they develop similar patterns of positional behavior as adults (*C. imitator*; Bezanson, 2009; *S. apella*; Fragaszy, 1990). Likewise, infants during this period begin to forage on their own for food, a task enabled by the development of the precision grip at 13-15 weeks (Fragaszy, 1990). By 6 months of age, infant have become efficient in their foraging skills and they spend similar amounts of time foraging and ingesting foods as adults (Bezanson, 2009). In *C. olivaceus*, allomaternal help peaks at months 4-6, enabling mothers to decrease their energy investment in infants without a corresponding drop in the quality of care (O’Brien & Robinson, 1991). Allomaternal care is arguably essential for infant survival as it enables the maintenance of high levels of energetically expensive infant care during the first six months (O’Brien & Robinson, 1991). Similarly, infants aged 4 – 6 months allonurse more frequently than infants a few months older or younger (*S. nigritus*;

Baldovino & Di Bitetti, 2008). In general, mothers benefit energetically when reproductive costs are shared by multiple individuals (Isler & van Schaik, 2012).

Age 8 months to weaned - mothers able to provide milk to non-offspring at low cost: Although mothers are largely responsible for maintaining close proximity to their young infants, after 8 months it is the infants that pursue this nearness, and it is at this stage that the process of weaning begins (*Sapajus* spp.; Verderane & Izar, 2019). At this age, infants are readily able to survive without milk, and the energetic demand on the nursing mother is expected to decrease as infants increase their consumption of solid foods during the weaning process (MacKinnon, 2006). Such a phenomenon is found in human infants and young toddlers. As human infants grow, they have greater total caloric demands, but a smaller percentage of calories comes from milk as they increase the amount of non-milk foods that they eat (Brown et al., 1998). Human infants aged 6-11 months consume 375-500 kcal/d from breast milk, and this caloric amount decreases to 300-350 kcal/d by age 12-24 months (Brown et al., 1998). A similar process likely occurs in capuchins as capuchin mothers consume progressively less energy after a peak energy intake at 8 weeks after birth (McCabe & Fedigan, 2007). Additionally, nursing rates decrease as infants age from birth to 16 months (rates above this age are not reported although nursing continues for many infants; Sargeant et al., 2015). Thus the change in the capuchin mother's energy intake is likely due to her infant's reduced reliance on her for nutrition as it grows more independent. Additionally, the quality of the milk made at the later stages of lactation is also likely to be less energetically expensive, as seen with the milk of *S. apella* for infants over 8 weeks (Milligan et al., 2010). This would make allonursing less of an energetic strain for the mother of older infants and young juveniles.

Another factor that suggests that older infants (aged 8+ months) have lower lactation demands is the fact that white-faced capuchins continue to nurse for 6 - 15 months after reaching this potential minimum weaning age (until age 14-23 months; Sargeant et al., 2015). This lower demand may enable mothers of older infants to provide more milk to non-offspring than mothers of younger infants. Thus, it is perhaps possible that each female's milk supply functions to make her a receiver when her infant is young, and a giver once her infant becomes older. Although ages of infants for allonurses has not been reported, there are a couple of case studies that provide some support for this idea. Following the death of her infant at 2 days of age, the white-faced capuchin mother experienced a significant increase in the rate of allonursing (Sargeant, 2014). In another case, following the death of her 7-month old infant, the mother went from 4 allonusing bouts recorded spread out across 4 months to 15 allonursing bouts in one month (Sargeant, 2014).

Allonursing and infanticide:

Although other primates engage in allonursing (see Table 4.2), it appears more frequently in capuchins than in other taxa (though it is possible that allonursing is underreported in other taxa). Most strikingly, allonursing appears to occur mainly in primates that also experience infanticide. Of the 33 primate species for which information is reported on both allonursing and infanticide, or for which an exhaustive literature search could be completed to determine that the behaviors have not previously been reported, we found that the majority (22/26; 85%) of species that engage in allonursing also experience infanticide (see Table 4.3). This could be an artifact from allonursing being reported less frequently than infanticide and the fact that absences of a behavior are rarely reported. Additionally, the phylogenetic distribution of allonursing necessarily restricts the behavior on multiple closely related species (e.g., multiple capuchin species). We suggest here that there is a relationship between the allonursing and infanticide risk.

This link between allonursing and infanticide has been voiced by others (Pusey & Packer, 1987; Hayes, 2000). For example, in lions (*Panthera leo*), after hiding their cubs for the first 6 weeks of life females form crèches in which they keep cubs together in a communal space with other cubs and lactating females. Lion cubs are at great risk of infanticide by invading males (27% of cub mortality) and these crèches enable the female lions to better protect their cubs against infanticide as multiple females together can actively ward off an infanticidal male (Pusey & Packer, 1987). Pusey and Parker (1994) argued that that allonursing in lions was not intentional, but simply a by-product of sharing communal space that is unlikely to provide important nutrition to the cubs. Likewise, allonursing in rodents has been attributed to the need for females to communally nest to protect against infanticide via active defense by multiple females (Hayes, 2000).

What do the primate species that exhibit both infanticide and allonursing all have in common? Perhaps it is some combination of high rates of infanticide and female philopatry. For example, in species like chimpanzees (female dispersal) and gorillas (bisexual dispersal), infanticide does occur, but allonursing is absent possibly due to the lack of inclusive fitness benefits. Additionally, in chimpanzees infanticide occurs in three contexts: between communities by males, intracommunity by males, and intracommunity by females (Murray et al., 2007). Although infanticide rates are low over all, females are responsible for up to 7.9% and 19% infant mortality rate in Kasekela and Mitumba (two communities within Gombe), respectively (Murray et al., 2007). These relatively low rates of infanticide are likely to have strong effects on the species given the low reproductive rate. Chimpanzees are fully weaned by 4 - 4.5 years, based on fecal stable nitrogen isotopes (Badescu et al., 2016), and postpartum amenorrhea lasts for 3.86 years (Wallis, 1997). Given the risk of female infanticide within communities, it should not be a surprise that allonursing does not appear to occur among chimpanzees in the wild (Badescu et al., 2016), although one occurrence in a captive setting has been documented (Savage et al., 1973).

Weaning for mountain gorillas (*Gorilla beringei beringei*) occurs around 40 months, however this age varies with infanticide risk, as infants living in unimale groups have a 2-3 times higher risk of infanticide and are significantly more likely to be weaned earlier than infants born into unimale groups (Eckhardt et al., 2016). The overall rate of infanticide is 5.5 % for mountain gorillas (Robbins et al., 2013). Given this low rate and the fact that females typically disperse from their natal group, allonursing would not be expected to occur. However, mountain gorillas have been documented allonursing in the wild (Fossey, 1979). Interestingly, one study found that 40% of adult female western gorillas (*Gorilla gorilla*) reside with at least one other genetically related adult female, despite natal and secondary dispersal by females (Bradley et al., 2007). There are currently no reports of adult female mountain gorillas residing with adult female kin, however if female mountain gorillas are found to reside with female kin as well, then kin selection could explain the occurrence of allonursing.

INFANTICIDE, ALLONURSING AND WEANING AGE IN OTHER CAPUCHIN SPECIES

Many of the features of white-faced capuchins highlighted above (e.g., EQ, infanticide rate, allonursing rate, weaning age) are similar to that of other capuchin species. For instance, infanticide occurs in several species of capuchins, including *C. imiator*, *C. olivaceous*, *S. nigritus* (Ramirez Llorenz et al., 2008). In *S. nigritus*, infant mortality is 62.5% in the context of AMRs, 22.5% during stable years (Ramirez-Llorenz et al. 2008), which is similar to the pattern observed in *C. imitator* (infant mortality is 51% near AMR, 26% during stable alpha male tenure; Brasington et al., 2017). Additionally, all three of these species exhibit high rates of allonursing, above 10% for each species (i.e., allonursing accounts for >10% of all nursing [mother-offspring, and mother-nonoffspring] bouts combined; e.g., C. *imitator*: 12.4% [Sargeant et al., 2015], *C. olivaceous*: 11.4% [O’Brien & Robinson, 1991], *S. nigritus*: 13% [Baldovino & Di Bitetti, 2008]). Likewise, weaning age for these three species has a large range that approaches 2 years (*C. imiator*, 14-23 months, Sargeant et al., 2015; *C. olivaceous*, 18 months, (O’Brien & Robinson, 1991); *S. nigritus*, 9-23 months, Baldovino & Di Bitetti, 2008). Weaning is described as a slow, gradual process for capuchins, that ends by the time they are two-years-old (Fragaszy et al., 2016). The late age of weaning for capuchins is likely due to the need to grow large brains and become efficient at extractive foraging (Fragaszy et al., 2016). Evidence for this is limited, as young juveniles spend similar amounts of time foraging for embedded invertebrates as older juveniles and adults (MacKinnon, 2006). However, the actual amount of embedded invertebrates consumed is unknown, and it is likely that the rates of eating are lower for young juveniles as they develop the skills necessary to be efficient (MacKinnon, 2006).

Proposed explanations of allonursing in capuchins

The similarities among the above-mentioned capuchin species (*C. imiator*, *C. olivaceous*, *S. nigritus*) indicate that white-faced capuchins are not alone in their high rates of infanticide and allonursing and late weaning age. Although the late weaning age may be related to the time it takes to develop proficiency with the complex skills necessary for extractive foraging, it doesn't explain why allonursing occurs at such high rates. Thus it is possible that the proposed function of allonursing in this species, i.e., reducing the cost of infanticide to the mother, is also at work in these other species. Previous investigations into allonursing have suggested that, at the proximate level, allonursing functions to soothe the infant (*S. nigritus*; Baldovino & Di Bitetti, 2008), and provide increased milk acquisition (*C. imitator*; Sargeant et al. 2015), while the ultimate explanations suggested argue that altruism plays a role in maintaining high levels of allonursing in capuchins (Baldovino & Di Bitetti, 2008), as a result of kin selection (*C. imitator*; Sargeant et al., 2015) and /or reciprocity (*C. olivaceus*; O'Brien & Robinson, 1991).

In white-faced capuchins, the mechanism that keeps allonursing in place may be a combination of kin selection and reciprocity. Sargeant and colleagues (2015) determined that all three of the players in an allonursing triad (e.g., mother, allonurse, and infant) benefit because females allonurse maternal kin more than unrelated infants. This means that the allonurse benefits via kin selection, the mother benefits from high quality allomaternal help, and the infant receives more milk. Relatedness is very high among female group members, as most live with many maternal, or even full, kin (Perry et al., 2008). However, female capuchins do not exclusively allonurse maternal kin, indicating that kin selection is not the only factor at work. Thus, the reciprocal benefits of allonursing also appear to be at work as nearly all lactating females in a group participate (Sargeant et al., 2015). Because female capuchins very rarely reject allonursing attempts, it is does not appear that individuals attempt to cheat the system in this species.

These proposed explanations do not exclude the possibility that allonursing also functions to decrease the cost, or reduce the risk, of infanticide in the other capuchin species. Baldovino and Di Bitetti (2008) argue that the original function of allonursing may have been milk transfer, but that it now plays a more social role.

Because allonursing has been described as a clade-wide phenomenon (Fragaszy et al., 2004), there was perhaps an original function of allonursing shared by capuchin species, such as a counterstrategy to infanticide. We suggest that allonursing may enable females to resume cycling earlier, which may function to reduce the risks of infanticide for unweaned infants. Increased allomaternal care in general and allonursing in particular is observed for infants ages 4-6 months for *C. olivaceus* (O'Brien & Robinson, 1991) and *S. nigritus* (Baldovino & Di Bitetti, 2008), respectively, suggesting that there may have been selection on capuchins in general to provide extra infant care at these ages; perhaps, and we have suggested, to decrease the costs associated with infanticide.

Allonursing as a counterstrategy to infanticide

We have suggested that allonursing functions as a counterstrategy to infanticide in two ways: 1) decreasing the cost associated with the death of an infant by reducing the energetic investment into the infant and 2) decreasing the risk of infanticide by enabling the mother to resume ovarian cycling more quickly. Both of these suggestions posit that allonursing energetically benefits mothers of infants aged 2 – 8 months old in particular. In addition to being an energetically costly period of development, this period (birth to 8.3 months) experiences the greatest infanticide risk (Brasington et al., 2017; Chapter 2). Thus there is a great risk that the energy that the mother is investing in her offspring will be “wasted.” Allonursing may function to decrease the amount of energy a mother invests in her offspring during this time period, thus decreasing the amount of energy “wasted” if she loses her infant to infanticide. It is likely that an even greater benefit of the supplemental milk supply from allonurses is the faster resumption of ovarian cycling. Female *S. apella* end lactational amenorrhea during this time period despite continuing to nurse (resumption of estrus cycle occurs at 5.3 months [3 months before weaning in captivity]; Recabarren et al., 2000). This resumption of cycling may also reduce the risks of infanticide, as the sexual selection hypothesis of infanticide indicates killing unweaned infants functions to end lactational amenorrhea, thus enabling the new male to conceive more quickly (assuming he is able to mate with the mother of the deceased infant; Hrdy, 1974). Ovarian cycling may be the proximate cue for males to not kill offspring. Prior studies of *C. imitator* have shown that all group males experience increases in testosterone when group females are cycling, despite the lack of observable indicators of ovulation (Schoof et al., 2014).

A final thought to consider is that, rather than functioning as a counteradaptation to infanticide, allonursing could instead simply function to enhance maternal and infant survival which may be stressed due to the long lactation period required for the development of extractive foraging behaviors. For example, one infant survived from age

6 months until age 2.5 after his mother died, a feat only possible due to allonursing (Baldovino & Di Bitetti, 2008). However, when the energetic cost of infanticide is considered, it makes sense to consider the ways that females may be able to lessen or avoid the energetic blow of infanticide. Sharing the energetic load during lactation, so that each lost infant received a slightly lower energetic investment from its own mother, is one way in which such an energetic loss could be lessened.

CONCLUSION

Although rare in mammals, allonursing is common in capuchins and may function as a possible mechanism for reducing the costs or risks of losing an infant to infanticide or avoiding infanticide all together. White-faced capuchins have very long lactation periods compared to other primates of similar size. The high energetic cost of lactation, which can last up to two years, is expected to be very taxing, especially when the chance of the infant dying is high. To compensate, intense levels of allonursing may have been selected for in female white-faced capuchins. The energetic cost of losing an infant may be lessened for the mother when other females have contributed energetically to that infant. Perhaps more importantly, allonursing may enable females to resume cycling earlier, which can decrease the risk of infanticide because males can detect ovulation in females (Schoof et al., 2014). These possibilities are worth noting because many of the studies of sexual conflict have ignored long-term behaviors only present in species with longer lifespans (Stumpf et al., 2011). Thus, we suggest allonursing may be a counterstrategy to infanticide. By retaining the ability to lactate beyond the minimum needs of their young, nursing infants 6 to 15 extra months in white-faced capuchins, females can retain their ability to lactate and nurse the younger infants in the group (particularly of close kin; Sargeant et al., 2015) and provide a great deal of energetic support to those females. This energetic support is likely to be incredibly important to the mothers in the second stage of nursing, as it may enable them to resume ovarian cycling (lessening the risk of infanticide) and it may have the additional benefit of decreasing the energy investment each mother makes into her young infant (decreasing the cost of infanticide).

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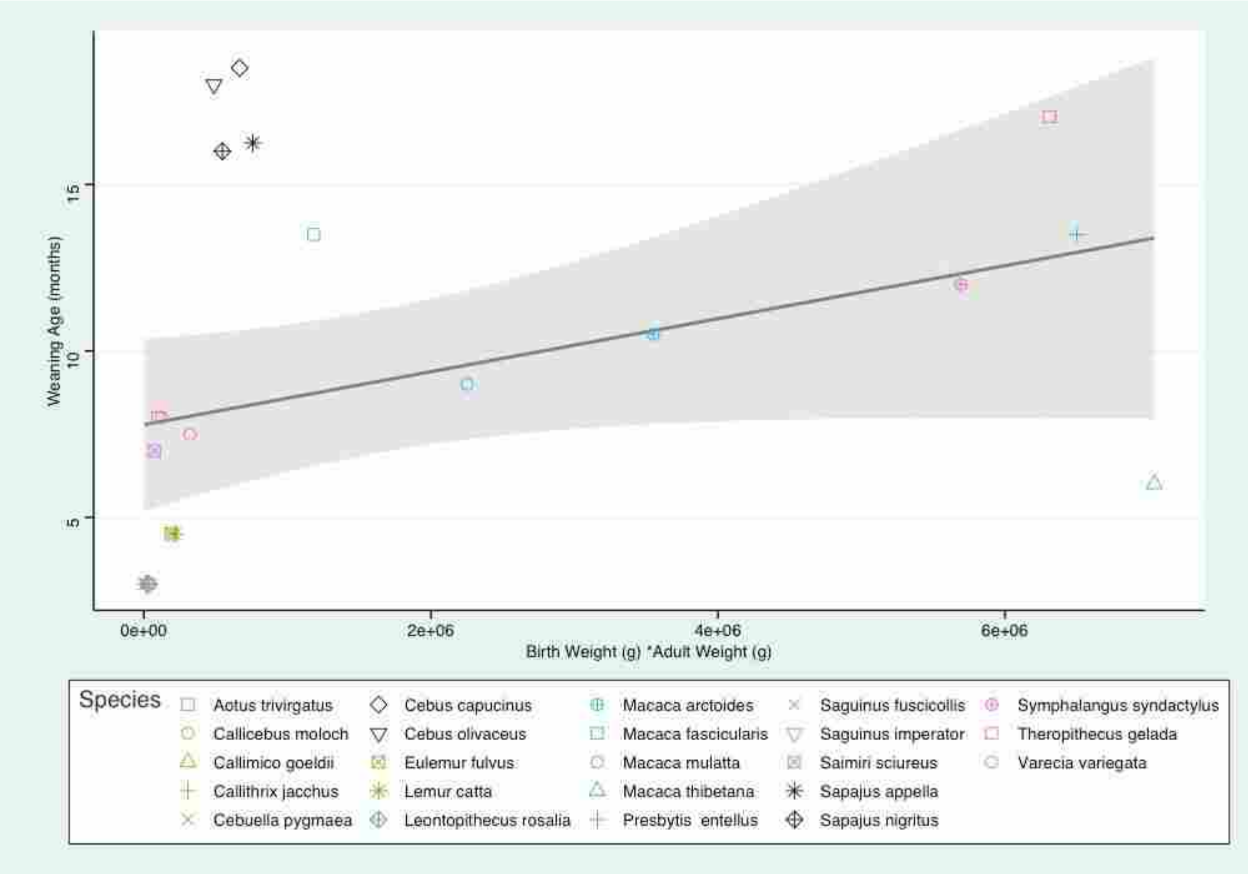

Figure 4.1. Weaning age in months relative to the interaction of birth mass and adult female mass for 23 species of primates. Due to extreme differences in body size between the great ape clade and other primates, the great apes and humans were removed from the figure. The shaded area indicates the 95% confidence interval of the regression.

Table 4.1. Adult female mass, neonatal mass, gestation length, and age at weaning across primates.

Species	**adult female mass (g)**	**birth mass (g)**	**gestation days**	**weaning months**	**Infanticide**
Aotus trivirgatus	1,000	97	133	8	no
Callicebus moloch	1,241	100	160	8	no
Callimico goeldii	621	50	155	3	no
Callithrix jacchus	352	30	148	3	yes
Cebuella pygmaea	156	14	137	3	no
Sapajus nigritus	2300	238	156	9 to 23	yes
Sapajus appella	3190	238	155	12 to 18, 20.5	yes
Cebus imitator	2900	230	155	14 to 23	yes
Cebus olivaceus	2395[R]	204[s]	149 - 158[t]	18	yes
Eulemur fulvus	2333	81.4	118	4.5	yes
Gorilla beringei	97700	2110	256	40	yes
Homo sapiens	48260	3250	259	6 to 36	yes
Lemur catta	2460	88.2	135	4 to 5	yes
Leontopithecus rosalia	659	50	129	3	no
Macaca arctoides	7100	500	176	6 to 15	no
Macaca fascicularis	3410	347	167	9 to 18	yes
Macaca mulatta	4743	475	167	6 to 12	yes
Macaca thibetana	12800	550	_	6	no
Pan troglodytes	32150	1756	228	48 to 54	yes
Pongo pygmaeus	37143	1750	244	36 - 48	no
Presbytis entellus	13000	500	22	12 to 15	yes
Saguinus fuscicollis	419	39	150	3	no
Saguinus imperator	525	47	150	3	no
Saimiri sciureus	668	109	155	6 to 8	yes
Symphalangus syndactylus	10600	537	230-235	>12	no
Theropithecus gelada	13600	464	170	1.42 years	yes
Varecia variegata	3000	107.5	102	7 to 8	yes

Adult female mass, birth mass, and gestation length gathered from Garber and Leigh (1997), Hartwig (1996), Harvey and Clutton-Brock (1985) and Jablonski et al. (2000). Weaning data from Jablonski et al. (2000), DeCasien et al. (2017), and Sauther (1998). Other sources labeled as follows: s = O’Brien and Robinson (1991); t = Robinson and Janson (1987); r = Ford and Davis (1992).

Table 4.2. Body mass, brain mass, encephalization quotient, reported allonursing and infanticide in a variety of nonhuman primate females.

Taxon	**Female Body Mass (kg)**	**Brain Mass (g)**	**EQ**	**Allonurse**	**Infanticide**	**Philopatry**	**Seasonality**
Homo sapiens	40.10	1250.00	8.78	yes	yes	--	aseasonal
Cebus_olivaceus	2.20	70.85	3.48	yes	yes	female	highly seasonal
Cebus_capucinus	2.44	72.77	3.34	yes	yes	female	moderately seasonal
Pan_troglodytes	32.15	376.13	3.06	no	yes	male	aseasonal
Sapajus_apella	2.49	67.53	3.05	yes	yes	female	highly seasonal
Miopithecus talapoin	1.10	37.70	2.95	yes	no	female	highly seasonal
Erythrocebus patas	5.60	106.60	2.80	yes	yes	female	highly seasonal
Pan_paniscus	33.20	346.24	2.76	no	no	male	aseasonal
Pongo_pygmaeus	36.95	350.55	2.60	no	no	bisexual dispersal	aseasonal
Ateles geoffroyi	6.75	110.90	2.57	yes	yes	male	bimodal?
Saimiri_sciureus	0.77	24.52	2.45	no	yes	female	highly seasonal
Macaca_radiata	3.86	71.88	2.43	yes	yes	female	highly seasonal
Papio_cynocephalus	13.13	161.87	2.40	yes	yes	female	aseasonal
Rhinopithecus roxellana	9.00	121.70	2.33	yes	yes	female	highly seasonal
Macaca_mulatta	5.67	86.43	2.25	yes	yes	female	highly seasonal
Presbytis entellus	11.40	135.20	2.21	yes	yes	female	moderately seasonal
Cercopithecus aethiops	3.56	59.80	2.13	yes	yes	female	highly seasonal
Macaca fuscata	9.10	109.10	2.07	yes	yes	female	highly seasonal
Gorilla_gorilla	74.84	442.37	2.05	no	yes	bisexual dispersal	aseasonal

Cercopithecus_mitis	4.63	68.18	2.04	no	yes	female	moderately seasonal
Theropithecus gelada	13.60	131.90	1.91	no	yes	female	moderately seasonal
Gorilla_beringei	97.70	460.00	1.78	yes	yes	bisexual dispersal	aseasonal
Alouatta_caraya	4.24	49.52	1.57	yes	yes	bisexual dispersal	aseasonal
Callithrix jacchus	0.29	7.90	1.51	yes	yes	bisexual dispersal	aseasonal
Saguinus_mystax	0.54	11.38	1.44	yes	no	bisexual dispersal	
Alouatta_palliata	5.70	55.10	1.43	yes	yes	bisexual dispersal	aseasonal
Presbytis johnii	12.00	84.60	1.33	yes	yes	female	
Varecia_variegata	3.00	32.64	1.30	yes	yes	female	highly seasonal
Lemur_catta	2.46	20.20	0.92	yes	yes	female	highly seasonal
Microcebus murinus	0.08	1.80	0.79	yes	no	female	highly seasonal
Colobus vellerosus	6.90			yes	yes	female	aseasonal
Samiri boliviensis	0.70			yes	no	female	seasonal
Varecia rubra	3.548			yes	yes	female	seasonal

Data on female body and brain mass copied from DeCasien et al., 2017. Encephalization Quotient (EQ) was calculated using an adaptation of Jerison's (1973) formula that only included data from the females of each species:
EQ_{female}= brain $mass_{female}$/ [0.12 * (body $mass_{female})^{0.67}$]

Table 4.3. Summary of the number of nonhuman primate species for which data on both allonursing and infanticide is known. Specifics on species are provided in Table 4.2.

	Allonursing Present	Allonursing Absent
Infanticide Present	22	5
Infanticide Absent	4	2

CHAPTER 5: THE IMPACT OF ALPHA MALE REPLACEMENTS ON REPRODUCTIVE SEASONALITY AND SYNCHRONY IN WHITE-FACED CAPUCHINS (*CEBUS IMITATOR*).

ABSTRACT

The change in the dominant sire within a group (i.e., alpha male replacement, AMR) occurs seasonally and is associated with high rates of infant mortality in white-faced capuchins (*Cebus imitator*). Thus, AMRs may influence birth seasonality and synchrony in this species if the deaths of young, unweaned infants enable the mothers that lost infants to resume cycling and conceive seasonally and/or synchronously. We found that AMRs appear to shift the conception and birth peaks by a few months; however, this shift away from the presumptive food peak does not appear to affect infant survival as it did not differ based on the timing of birth. We suggest that this lack of a difference in survival was due to the varied diet of the capuchin so that different foods are available throughout the year. We also found evidence that the ecological birth peak of white-faced capuchins aligns with peak caterpillar abundance instead of peak fruit abundance. Additionally, AMRs do have an impact on birth synchrony in this species, as a higher percentage of infants are born within three-month (55%) and six-month (87%) time periods following AMRs compared to times of stable alpha male tenure (38% and 66%, respectively).

INTRODUCTION

Various degrees of reproductive seasonality are observed among primate populations (Di Bitetti & Janson, 2000; Janson & Verdolin, 2005), running the gamut from species with no evidence of seasonality (some populations of *Pan troglodytes*; Wallis, 1997) to highly seasonal breeders (*Lemur catta*; Cavigelli & Pereira, 2000). Reproduction often coincides with specific ecological factors, such as photo period, temperature, and rainfall (Bronson & Heideman, 1994), which influence the local plant community and phenology, and thus affect the type and timing of potential food items (van Schaik & Brockman, 2005). Highly and moderately seasonal breeders (species that have >2/3 or between 1/3 and 2/3 of offspring born within a three-month period, respectively) may time births or weaning to seasons that provide the greatest food abundance to maximize survival of mother and infant (van Schaik et al., 1999). Maternal survival may be prioritized in species living in unpredictable environments because females may only achieve a physiological condition that is able to conceive, sustain a pregnancy, and lactate during a time of peak food abundance (Capital breeders; Janson & Verdolin, 2005). For species living in environments in which peak food abundance is predictable, infant survival can be maximized by having weaning occur during the period of peak food abundance (Income-I breeders) or maternal survival can be maximized by having the period of greatest lactational demand occur during the period of peak food abundance (Income-II breeders; Janson & Verdolin, 2005).

Reproductive synchrony occurs when conceptions and births within a group occur within the same time period. This may be driven by high birth seasonality, synchronous infant deaths (e.g., infant predation or infanticide), and social factors, such as alpha male replacements (AMRs; i.e., when a new male becomes the dominant sire within a group) (Janson & Verdolin, 2005; Packer & Pusey, 1983). Thus, reproductive seasonality may lead to reproductive synchrony. However, the reverse case – that synchrony may cause seasonality – is not assumed to occur since factors affecting birth synchrony, such as infant predation or infanticide, typically do not occur seasonally (Janson & Verdolin, 2005). For instance, although lions (*Panthera leo*) are not seasonal breeders, the timing of male takeovers and the subsequent infanticide and resumption of cycling in the mother leads to reproductive synchrony within prides (Packer & Pusey, 1983). However, more recent evidence suggests that seasonal and synchronous infant death can occur if infanticide follows a seasonal pattern. For instance, male takeovers occur seasonally in geladas (*Theropithecus gelada*) and are associated with high levels of infanticide as the new alpha male kills roughly half of unweaned infants (Beehner & Bergman, 2008). In the year following a takeover, reproductive units exhibit a "social birth" peak in which 54.4% of infants are born over a three-month period (December – February). This birth peak is more synchronous than the ecological birth peak seen in groups not experiencing a takeover, with 37.4% of infants born August – October, coinciding with peak food availability (Beehner & Bergman, 2008). Thus, the timing of takeovers affects both reproductive seasonality and synchrony in geladas.

Like the geladas, white-faced capuchins (*Cebus imitator*) have alpha male replacements (AMRs) that are both seasonal, with most occurring January through April (Fedigan, 2003), and strongly associated with high infant mortality (Brasington et al., 2017, Chapter 2). Thus, these seasonal AMRs and associated infant deaths have the potential to influence reproductive synchrony. The effects of AMRs on the timing of capuchin reproduction are of interest because previous studies indicate that the birth peak of white-faced capuchins coincides with peak fruit abundance (Carnegie et al., 2011). If AMRs do shift the timing of the birth peak, as seen in the geladas, how might this impact infant survival? Here, we investigate the impact of AMRs on reproductive seasonality and synchrony in white-faced capuchins using a long-term data set focused on multiple groups residing in the Sector Santa Rosa (SSR), Área de Conservación Guanacaste Costa Rica. Due to the seasonal nature of AMRs and the moderate seasonality displayed by white-faced capuchins, we expect that AMRs will produce a birth peak separate from the ecological birth peak. Because the ecological birth peak has been shown to occur during the time of peak fruit abundance, a shift away from this timing has the potential to decrease female reproductive success via increased infant mortality. Such a result would indicate that AMRs have a stronger negative effect on female lifetime reproductive success than previously thought. AMRs are currently known to be associated with high infant mortality in this species (Brasington et al., 2017, Chapter 2), so if the subsequent infant was less likely to survive due to the timing of its birth, it would be a larger blow to female reproduction than previously known.

The Sector Santa Rosa (SSR) population of white-faced capuchins (*Cebus imitator*) are considered moderately seasonal breeders as 44% of their births occur during a three-month period in the wet season from May to July (Carnegie et al., 2011). It has been suggested that this seasonality is largely driven by seasonal fruit abundance. Peak fruit abundance in Santa Rosa occurs eight weeks following the birth peak, and the eighth week of lactation is thought to be the most energetically expensive for the females (McCabe & Fedigan, 2007; Chapter 4). This birth seasonality follows the pattern observed in Income II breeders, functioning to enhance maternal survival (Janson & Verdolin, 2005; Carnegie et al., 2011). The long lifespan of capuchins also suggests that female reproductive success (and thus, maternal survival) is prioritized over infant survival (Carnegie et al., 2011). Despite the clear role of ecological factors in birth seasonality in this population, social factors (i.e., Alpha Male Replacements [AMR]) also appear to influence the timing of births (Fedigan, 2003). The vast majority of AMRs occur during the dry season between January and April (Fedigan, 2003). Conception rates increase 3-6 months following AMRs, causing 71% of post-AMR conceptions to occur in the wet season (Fedigan, 2003). In turn, these conceptions would cause births to occur earlier in the dry season than the aforementioned May – July birth peak. The delay in conceptions following AMRs is likely influenced by two factors: delays in infanticide following the AMR and residual infertility following the end of lactational amenorrhea. Confirmed cases of infanticide have been observed up to three months (mean = 46 days) post-AMR in this population, and suspected cases of infanticide have a wider range of the timing of death after AMRs (mean = 98 days, range: 0 – 254 days [8.5 months] post-AMR; Jack & Fedigan, 2018).

An additional cause of the delay in conceptions following AMRs is the residual infertility following the end of lactational amenorrhea (*Sapajus apella*, Recabarren et al., 2000). This infertility is thought to be caused in part by suckling-induced increases in prolactin (the hormone that induces milk production but also interferes with ovarian cycling), as it begins when the infant is still nursing; however, this infertility also appears to continue past the end of weaning (Majumdar & Mangal, 2013, Recabarren et al., 2000). Thus, even if a female has lost or weaned her infant, she still may not be ready to conceive for months afterward (see Chapter 3 for a more detailed discussion of residual infertility). However, the length of residual infertility observed in *S. apella* is far longer than what we observe in *C. imitator* when an infant dies before age one. We can approximate the timing of when female white-faced capuchins regain their fertility *following the death of an infant* by looking at the interbirth intervals when the first infant dies before age one. For females that lose their infants before age one, the mean age at death is 132 days (based on data from Brasington et al., 2017) and the IBI is 1.05 years (Fedigan, 2003). Thus, resumption of cycling can be approximated to occur 93 days after losing an infant (IBI of 1.05 years – 158 days gestation – 132 mean age at death = 93 days). This three-month window of residual infertility following the death of an infant is far shorter than the ~7-month period of residual infertility that is observed in *S. apella* following the end of weaning (Recabarren et al., 2000). Thus, the delay in post-AMR infant mortality (mean = 98 days) and residual infertility (mean = 93 days based on IBI) together make it unlikely that females may be able to conceive immediately after losing an infant to infanticide.

METHODS

The study population of white-faced capuchins in Sector Santa Rosa (SSR) has been the focus of continuous study since 1983, making it the second-longest continuous field study of New World monkeys (Fedigan & Jack, 2012). This tropical dry forest was originally dominated by semi-evergreen trees, but sustained 400 years of anthropogenic changes to creates open cattle pastures. Since 1971, the forest has been in a state of regeneration as the removal of cattle ranches within the park has allowed the pastures to return gradually to forests during the intervening years, creating a patchwork landscape composed of various seral stages (Fedigan & Jack, 2012). The climate has predictable weather patterns, with a long wet season from mid-May to mid-November (heaviest rains are typically in October, >400 mm monthly total rainfall), followed by a long dry season (mid-November to mid-May) during which little to no rainfall occurs during the driest months. Some years also have a short dry season from late July through August. The difference in rainfall between the wet and dry seasons is more extreme than the vast majority (98.9%) of terrestrial locations and makes it a global seasonality hotspot with regard to rainfall (Campos, 2018). Whereas rainfall varies to an extreme extent between seasons, mean monthly temperature varies by less than 5 °C between the coldest and warmest months, making the seasonal variation smaller than 95% of terrestrial habitats. The hottest temperatures occur in April or early May (mean monthly temperature ~30 °C), and October and November are the coldest months (mean monthly temperature ~26 °C; Campos, 2018).

We analyzed demographic and ecological data (ripe fruit biomass and rainfall) from seven groups of SSR capuchins over a 30+ year timespan (SE: 1986 – 1993; CP: 1986 – 2012; LV: 1990 – 2019; EX: 2007 – 2016; GN: 2007 – 2019; CPRM: 2013 – 2019; CPAD 2013 – 2019). Infanticide has been observed within this population, especially in the context of AMRs, and has a strong effect on infant mortality: mortality occurs in 26% of infants born during times of group stability (i.e., the infant does not experience an AMR from conception to twelve months of age), but occurs in 51% of infants when in the context of AMRs (Brasington et al., 2017; Chapter 2). The mean timing of infant death following an AMR is 46 days for known infanticide events and 98 days for suspected infanticide events (Brasington et al., 2017; Chapter 2). Additionally, there are multiple cases of infants dying that were conceived just before an AMR and born five months after the AMR (Jack & Fedigan, 2018). Infants were considered to be at risk of infanticide if an AMR occurred any time between conception and twelve months of age.

We modeled our methods following those described in Tinsley Johnson et al. (2018) in regard to analyzing the seasonality of conceptions and births, as well as the costs to birth timing. Additionally, postpartum return to cycling was not included in this analysis as we lack hormonal data on the majority of females required to determine this (as white-faced capuchins do not display distinct physical or behavioral changes to indicate its occurrence). However, data on interbirth intervals from previous studies can be used to approximate return to cycling, which can inform us of when to expect females to conceive after infanticide. The interbirth interval for females is relatively long (mean IBI = 1.89 years) and infant survival to one year is the strongest predictor of interbirth interval length (mean IBI is 2.25 years when the prior infant lives; 1.05 when a prior infant dies; range: 0.67 – 5.58 years; Fedigan, 2003; Fedigan et al., 2008).

Data preparation

AMRs and births in this population were recorded during monthly censuses, and conception dates were estimated using the known gestation for this species (158 days; Carnegie et al., 2011). We determined whether each conception or birth occurred 3-6 months or 9-12 months following an AMR, respectively (yes/no). The time period for conception was based on a previous study indicating that conceptions rise 3-6 months following AMRs (Fedigan, 2003), a finding that is likely related to the fact that infanticide occurs, on average, three months after an AMR (mean = 98 days; Jack & Fedigan, 2018).

Climatological data in Santa Rosa, including daily total rainfall, has been recorded since the 1970s. For all infants included in this study (N = 274), the total rainfall in the previous 30 days was calculated as a proxy for food abundance. Total rainfall has previously been used as a proxy for resource availability in the SSR, with the expectation that both fruit and insects increase in abundance as rainfall increases (Fedigan et al., 2008). Additionally, monthly fruit biomass has been calculated in Santa Rosa starting in 2008. To calculate fruit biomass, values for tree size and proportion of ripe fruit on each tree are combined for each species, and values for all species are combined each month and divided by the sampling area in order to give the monthly grams of fruit/hectare (Carnegie et al., 2011). Although rainfall serves as a proxy for food biomass, monthly measures of fruit biomass are expected to paint a more accurate picture of fruit availability than rainfall data. However, data on rainfall is available for 22 years longer than fruit biomass, thus allowing us to expand our data set and substantially increase our statistical power. Thus, we were interested in looking at both measures: rainfall for its longevity and fruit biomass for its better accuracy in indicating fruit availability.

We used the birth data to search for a seasonal birth peak. We used our findings on the birth peak to investigate the costs of being born at different times of the year by determining whether each infant born before 2018 survived until two years of age (n =243). Following the rationale of Tinsley Johnson et al. (2018), we selected this age as it represents the end of weaning for capuchins (range 14 – 23 months; Sargeant et al., 2015).

Data analysis

For our analysis, we ran models for three outcome variables: conceptions, births, and infant deaths. We used the *Mu-MIn* package (version 1.43.17: Barton, 2016) in R (R Core Team, 2018: Version 3.5.1) to average all models for each outcome variable based on Akaike's Information Criterion corrected for small sample sizes (AICc).

Determining Conception Peak

In order to determine whether ecological and social conception peaks were present, we followed van Schaik et al.'s (1999) categorizations of seasonality and determined the number of infants conceived each month. We separated conceptions into two groups: those that occurred 3 – 6 months following an AMR (social conceptions), and those that did not (ecological conceptions).

Outcome variable: Conception

For each month from June 1986 to August 2019 (n = 404 months), we determined the proportion of females under observation that conceived 3 – 6 months following an AMR and the proportion that conceived without following an AMR (# of conceptions in the group/ total # of females in the group). We used this information as the dependent variable in a gaussian linear mixed-effects model (LMM) ran using the *lme4* package in R (Version 1.1-21: Bates et al., 2015). We created models that predicted monthly conceptions that included two predictor variables and their interactions: total monthly rainfall, and whether or not an AMR occurred 3 – 6 months prior. This time frame for rainfall was used as a proxy for monthly fruit biomass; peak fruit abundance occurs roughly one month following the onset of the wet season in tropical dry forests with long dry seasons (i.e., at least six months; van Schaik & Pfannes, 2005), such as SSR (Campos, 2018). Accordingly, peak fruit abundance has previously been shown to occur one month following the onset of the rainy season (June 17 compared to mid-May; Carnegie et al., 2011). Month and year (month-year) were included as a random effect in all models since each month is included twice as an observation in the data (for each month, the proportion of adult females that conceived following an AMR were calculated as well as the proportion of adult females that conceived without exposure to an AMR). To identify significant predictors and their interactions, we performed chi-square tests using the drop1 function in the *stats* R package (Version 3.5.1: R Core Team, 2018) to eliminate each predictor or predictor interaction through model selection in order to identify which resulted in the best fit model.

Since we also have data on monthly fruit biomass from 2008 through 2018, we ran a separate set of gaussian LMMs that included monthly fruit biomass data instead of rainfall as a predictor variable. These models included a smaller number of conceptions (n = 174) and months (n = 221 months) than the rainfall models. All other parameters for the model were the same as for the rainfall model.

Determining Birth Peak

In order to determine whether ecological and social birth peaks were present, we followed van Schaik et al.'s (1999) categorizations of seasonality and we determined the number of infants born in each month. We separated infant births into two groups: those that occurred 9 – 12 months following an AMR (social births), and those that did not (ecological births).

Outcome variable: Birth

As with conceptions, we determined the proportion of females under observation that gave birth 9 - 12 months following an AMR and the proportion that gave birth outside of this time frame between June 1986 and December 2019 (404 months). We used this information as the dependent variable in a gaussian linear mixed-effects model (LMM). We created models that predicted monthly births that included two predictors and their interactions: total monthly rainfall and whether or not an AMR occurred 9 – 12 months prior (yes/no). Month and year (month-year) were included as random effects since each month is included twice in the data (for each month, the proportion of adult females that gave birth following an AMR were calculated as well as the proportion of adult females that gave birth without exposure to an AMR). As with the conception models, we performed chi-square tests to identify significant predictors.

As with the conception models, we also ran models that swapped out the total monthly rainfall predictor and replaced it with monthly fruit biomass. Again, these models covered a shorter time frame (2008 through 2018; n = 221 months) with fewer births (n = 178) but were otherwise identical to the other birth models that used rainfall as a proxy for fruit biomass.

Outcome variable: Costs to birth timing

After determining a birth peak, we determined whether survivorship to two years differed between infants born within the birth peak and those born outside of it. We used three binomial general linear mixed-models (GLMMs), run using the *lme4* package in R (Version 1.1-21: Bates et al., 2015) to determine whether infant survival to age two could be predicted by being born within the birth peak. For all three models, the predictor was whether or not an infant was born within the birth peak or outside of the peak, and birth year and mother identity were included as random effects. The first model looked at survival to age two years for all infants born during the study. The next model included only infant deaths <u>not</u> suspected to be caused by infanticide in order to look at ecological costs of being born outside of the birth peak. The final model looked for costs associated with being born outside of the birth peak that were not caused by AMRs, so only infants born outside the context of AMRs (and deaths that were not infanticide) were included. We performed a chi-square test using the drop1 function in the *stats* R package to eliminate each predictor or predictor interaction in order to identify which were significant in the best fit model.

RESULTS

AMR seasonality Of the 34 AMRs included in this analysis, 74% of them occurred between January and May, and 21% (7/34) occurred in May alone. The majority (86%; 6/7) of the May AMRs have occurred since 2006.

Outcome variable: Conception

The interaction of AMR and total monthly rainfall, and AMR individually, were significant predictor variables (interaction: LRT = 6.54, p($X^2_{df=1}$) = 0.01057; AMR only: LRT = 6.56, p($X^2_{df=1}$) = 0.01043) of the proportions of females in the population that had conceived in a given month. This model was a better fit for the data than the one that used monthly fruit biomass (AICc = -352.77 for rainfall model vs. AICc = -217.56 for fruit biomass model).

Conceptions exhibit a moderately seasonal peak, with 38% of all conceptions occurring in October, November, and December (Figure 5.1). Ecological conceptions occurred in November, December, and January (39%), which corresponds to the end of the wet season in mid-November and the beginning of the dry season (Campos 2018). The social (i.e., AMR-driven) conception peak occurs several months earlier, with nearly half (49%) of conceptions occurring in August, September, and October, which is the wet season (Campos 2018).

The AMRs included in this study were also seasonal, with most (25/34; 74%) occurring in the dry season between January through May, and 21% (7/34) of all AMRs occurred in May alone (May = mode).

Outcome variable: Birth

As with conceptions, the model that included rainfall was a better fit for the data than the model including fruit biomass (AICc = -345.41 for rainfall vs. -191.79 for fruit biomass). As with conceptions, AMR alone and the interaction of AMR and total monthly rainfall were significant predictors of the proportions of females in the population that had given birth in a month (interaction: LRT = 4.46, $p(X^2_{df=1}) = 0.0347$; AMR only: LRT = 12.22, $p(X^2_{df=1}) = 0.0004736$).

Birth Peak

Two overlapping birth peaks were evident (Figure 5.2). In years when AMRs occurred in a group, 55% of infants were born in three months (March, April, May; i.e., social birth peak), and 87% of infants were born over six months (December – May). In years without AMRs, 38% of infants were born in three months (May, June, July; i.e., ecological birth peak), and 66% of infants are born within a six-month period (February – July; same results for March – August). The birth peak for all infants (AMR and non-AMR combined) does not differ from the social birth peak: 38% of birth in March, April, May.

Outcome variable: Costs to birth timing

We found no evidence that the timing of infant births affected survival to age two as infants born within the three-month ecological birth peak (i.e., May, June, July) were not more likely to survive than those born outside of this peak (LRT = 1.06, $p(X^2_{df=1}) = 0.3037$; n = 243). Additionally, when we excluded infants that died/disappeared in association with an AMR (to identify infant deaths due to ecological reasons), there was still no difference in survival for infants born within the birth peak and those born outside of the birth peak (LRT = 1.27, $p(X^2_{df=1}) = 0.2597$; n = 197). When we excluded infants born 9 – 12 months following an AMR, we likewise did not find any survival costs to infants born outside of the ecological peak during times of group stability (LRT = 1.06,

$p(X^2_{df=1}) = 0.3032$; n = 212).

DISCUSSSION

AMR Seasonality

Fedigan (2003) had previously reported that the vast majority of AMRs occur during the dry season between January and April. Our data set, which included 34 AMRs (vs 15 in the 2003 report), has expanded the time period for AMRs by one month, with 74% of AMRs occur between January and May, and 21% (7/34) of the AMRs occur in May alone. Interestingly, most of the recorded May AMRs have occurred since Fedigan published her 2003 paper: 86% (6/7) of the May AMRs have occurred since 2006. This may indicate the effects of long-term climate change, as Campos (2018) found a temperature increase of 0.77 °C since 1970. Alternatively, it may simply represent interannual variation, as Campos did not find evidence of long-term change in total annual rainfall since 1970, but he did find a variable start date for the wet season (April 22 to June 1).

Conception Peak

When a group experiences an AMR in the dry season between January and May, it appears to move the conception peak three months earlier: from the end of the rainy season/early dry season (November through January) to the wet season (August through October, see Figure 5.1). This explains our results of conceptions being predicted by total monthly rainfall alone and the interaction of rainfall and whether an AMR occurred: AMRs move the conception peak from the dry season to the wet season. These results align with a previous study that found that conception occurred 3-6 months following AMRs, causing the majority of post-AMR conceptions to occur in the wet season (Fedigan, 2003).

As previously mentioned, the 3 – 6 month delay in conception described by Fedigan (2003) is likely driven by residual infertility (estimated to be 93 days when deriving from the interbirth interval) and the post-AMR delay in infanticide (mean time between AMR and infant death = 98 days; Jack & Fedigan, 2018). Two factors likely influence the delay in infant mortality following AMRs: delay in group acceptance following AMRs, and the lag time for increased testosterone in coresident AMRs. When a new male achieves alpha status, females may avoid the new alpha for weeks (Fedigan & Jack, 2013; Jack & Fedigan, 2018). This avoidance is a strategy thought to decrease the risk of infanticide (Fedigan & Jack, 2013; Jack & Fedigan, 2018), but it likely also decreases the conception rate immediately following an AMR. The delay in infanticide is likely related to the delay in group acceptance, as it is more difficult to kill infants when females and their young are actively avoiding the new alpha male. This physical distance from the alpha male is likely to afford infants some protection as the infants of lower-ranking females (who spend more time on the periphery of the group) have lower rates of infant mortality following AMRs than infants of higher-ranking, more centrally-located females (Kalbitzer et al., 2017). The delay in infanticide may also be the result of the jostling between males for the alpha position following collaborative group takeovers (Fedigan & Jack, 2013). In the case of AMRs that involve a coresident male taking up the vacant alpha position, there is a period of several months before the new alpha's testosterone reaches alpha levels (Schoof et al., 2012). Given these factors, a 3 – 6 month delay in conceptions post-AMR seems relatively quick.

Birth Peak

Two overlapping birth peaks were found. An ecological birth peak was found in which 38% of births not following an AMR occurred in May, June, and July, which corresponds to the start of the rainy season (Campos, 2018). After groups experience AMRs, the birth peak is shifted two months earlier than the ecological birth peak and results in 55% of births occurring in March, April, and May (the end of the dry season). Thus, the significant interaction of AMRs and rainfall is explained as births move from the wet season to the dry season following an AMR.

AMRs also appear to drive a higher degree of synchrony in the timing of infant births (55% vs. 38% of births in a three-month period; 87% vs. 66% of infants born in a six-month period). This increased cohesion suggests that AMRs, in addition to ecological food demands, may be driving the overall seasonality of births.

The finding that 38% of all births (AMR and non-AMR) occur over a three-month period supports the finding by Carnegie et al. (2011) that the Santa Rosa white-faced capuchins are moderately seasonal breeders. However, the birth peak found by Carnegie et al. (44% of births in May, June, July, 1986 – 2010) matched the ecological birth peak found in this study, but occurs two months later than the overall birth peak we identified (38% of births March, April, May). Two factors likely contributed to this discrepancy in the timing of overall birth peak between this study and Carnegie et al.’s: 1) infants born early in the observation of a new group (n = 56) were omitted from this study because we could not know if they were born following an AMR, and 2) a slightly higher proportion of infant births occurred after AMRs in the years following Carnegie et al.’s study (1986 – 2010: 12.4% of births after AMR; 2011 – 2019: 15.3% of births after AMR).

Carnegie et al. (2011) explained the timing of the (ecological) birth peak in relation to fruit abundance: the birth peak occurs eight weeks before peak fruit abundance. Because the eighth week of lactation is the time of greatest reproductive stress for female capuchins due to maximum lactational demands, this birth timing is thought to enhance maternal survival and categorizes them as Income II (relaxed income) breeders (Carnegie et al., 2011; McCabe & Fedigan, 2007). Although this designation of white-faced capuchins as Income II breeders has recently been supported by another study (Campos et al., 2020), we were unable to show that monthly fruit biomass was a predictor of infant births: our model that included fruit biomass instead of rainfall (a proxy for food biomass) lacked a significant predictor variable or interaction, and the model fit was worse than with rainfall (AICc = -194.56 for fruit biomass vs. -348.18 for rainfall). Thus, we propose that fruit biomass is not what is actually driving these observed patterns during the rainy season. Instead, we suggest that another seasonal food item, namely caterpillars (*Lepidoptera* larvae), drive the ecological birth peak.

The 3140 species of caterpillars in SSR show a distinct seasonal pattern of density (Janzen, 1988). These caterpillars in general, and leaf-eating caterpillars in particular, show a pattern of very low density in the dry season, followed by a sharp increase in density during the first two months of the wet season (late May to mid-July; Janzen, 1988), corresponding to the ecological birth peak of May, June, July that we identified in this study. Melin et al. (2014) found that caterpillar foraging bouts peaked in July, and that high levels of caterpillar foraging were found from June to August, and less intense caterpillar foraging occurred throughout the rest of the wet season (September – November).

The significance of the timing of the ecological birth peak in relation to the caterpillar density is apparent in the investigation of the capuchin diet. Insects comprise roughly 40% of the diet of all white-faced capuchin females, and lactating females consume more energy per hour than pregnant or cycling females due to higher ingestion rates of foods, not longer time spent foraging (McCabe & Fedigan, 2007). Lactating females do not appear to alter their diets, but instead, consume more protein per hour than other females as they consume insects at a faster rate (McCabe & Fedigan, 2007). Caterpillars, in particular, may be easy insects to consume quickly as they are simply plucked off of leaves and require little processing (Melin et al., 2014). Caterpillars are the primary animal food consumed in the wet season: of the time that capuchins spent consuming animals, 22-34% of it was spent eating caterpillars (McKinnon, 2006). Thus, the abundance of caterpillars during the early weeks of nursing, which are the most energetically expensive weeks of reproduction, may provide females with an ideal food source: high-protein, easily obtained, and quickly consumed.

Costs to birth timing

We found no evidence that the timing of infant births (inside of the ecological birth peak or outside of the peak) affected survival to age two, even when the effects of AMRs (altered birth peak and infanticide) are removed. This finding mirrors that of Carnegie et al. (2011), which found that the timing of infant births did not affect survival to one year of age. These results are not unexpected as capuchins have a broad diet, and several foods are available for many months of the year (Carnegie et al., 2011; Fragaszy et al., 2004). For instance, although fruit abundance peaks in June, it is plentiful from April through September (Carnegie et al., 2011). Likewise, caterpillar abundance peaks in July, but they are consumed throughout the entire wet season (Melin et al., 2014). Additionally, other families of insects show peaks at different times of the year, and insects, in general, are abundant throughout the entire year (Melin et al., 2014). Thus, even when the timing of a food item (e.g., insects) occurs too early in the birth season to be of greatest use to the majority of “on-peak” lactating females, females that give birth early, especially those following an AMR, may benefit from the abundance of other insects in the late dry season.

Interestingly, peak caterpillar consumption overlaps with the timing of peak fruit abundance during the wet season, and capuchins rely heavily on both caterpillars and soft fruits during this time (McKinnon, 2006; Melin et al., 2014). Thus, most of the conclusions drawn by Carnegie et al. (2011), which attributed the timing of the birth peak to fruit abundance, are also supported by our results even though we suggest that caterpillars, rather than fruit, drive the ecological birth peak. For instance, like Carnegie et al., we similarly conclude that white-faced capuchins are Income II breeders that prioritize the survival of the mother (Janson & Verdolin, 2005).

Conclusions

AMRs appear to shift the conception and birth peaks by a few months; however, this shift away from the presumptive food peak does not appear to affect infant survival as it did not differ based on the timing of birth. We suggest that this lack of a difference in survival was due to the varied diet of the capuchin so that different foods are available throughout the year. Additionally, monthly fruit biomass did not predict the timing of conception or births. We suggest that caterpillars, instead of fruit, are the food item driving the ecological birth peak.

AMRs appear to increase reproductive synchrony in that a higher percentage of infants are born within three-month (55% vs. 38%) and 6-month (87% vs. 66%) time periods following AMRs. However, the significance of this synchrony with regard to intersexual conflict is doubtful. Thus, AMRs appear to shift both reproductive seasonality and synchrony in white-faced capuchins, however, the ultimate effect of these shifts remains unclear.

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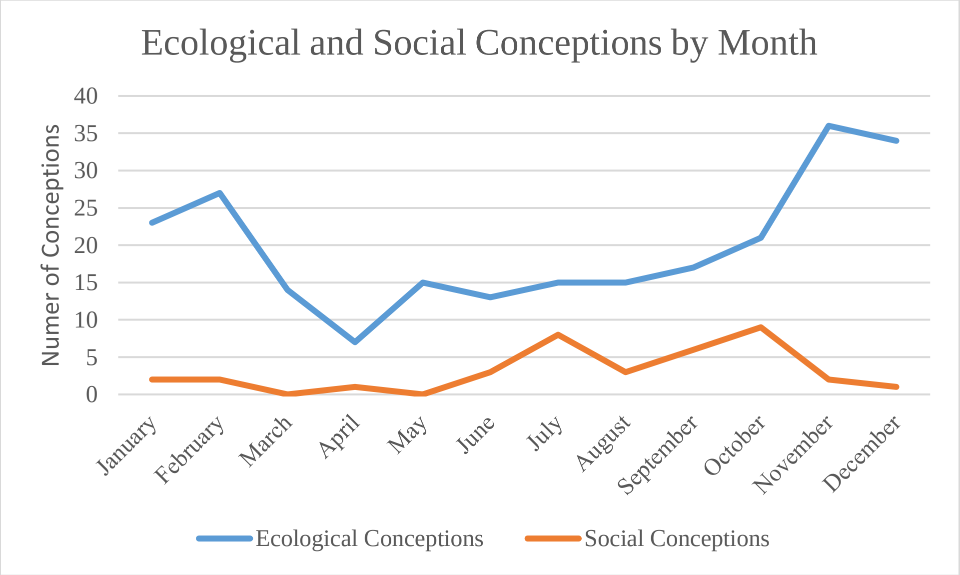

Figure 5.1. Total number of monthly conceptions for infants conceived 3 – 6 months following an AMR (social conceptions) and infants conceived outside of this time period (ecological conceptions).

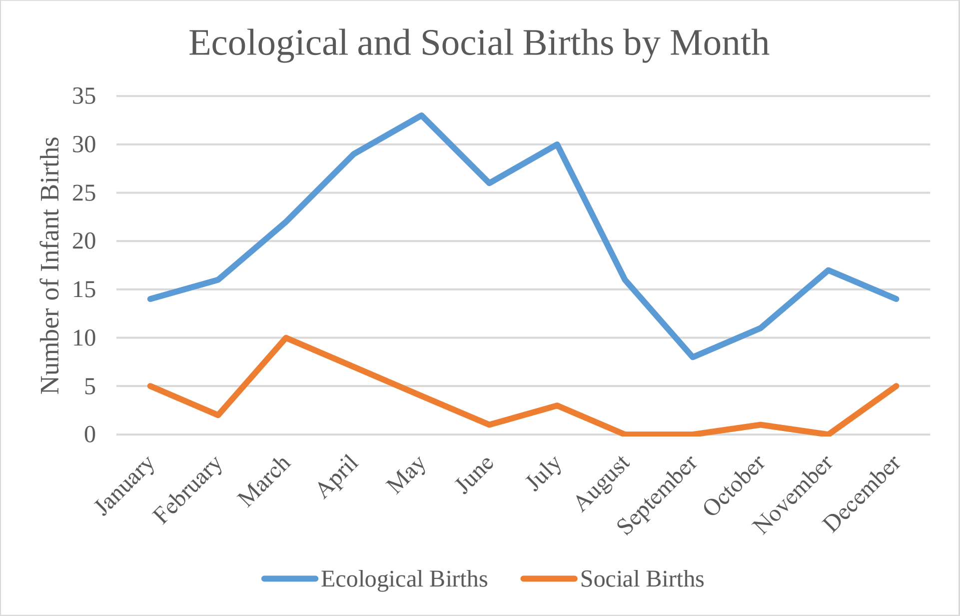

Figure 5.2. Total number of monthly infant births for infants born 9-12 months following an AMR (social births) and infants born outside of this time period (ecological births).

CHAPTER 6: CONCLUSIONS

Throughout this dissertation, I investigated the effects of infanticide on the population of white-faced capuchins (*Cebus imitator*) in the Sector Santa Rosa, Área de Conservación Guanacaste, Costa Rica. I began by looking at how alpha male replacements (AMRs) affect infant mortality and then asked why white-faced capuchins don't wean infants earlier to avoid the risk of infanticide. I continued investigating the nursing behavior 1) to verify that capuchins do nurse longer than expected based on their body size, 2) to understand why capuchins nurse for so long, and 3) to investigate whether allonursing possibly functions as a counterstrategy to infanticide. I then returned to the question of how AMRs affect this population of capuchins by looking the relationship between AMRs and birth seasonality and synchrony. Below I highlight the major findings from each chapter.

In my study of the impact of the different types of AMRs on infant mortality (Chapter 2), I found that infant age predicts the likelihood of survival following an AMR, with the probability of infant survival increasing by 0.4% for each additional day older an infant is at the time of the AMR and thus the greatest risk of infanticide occurs from birth until 8.3 months of age. I also found that the type of AMR (coresident or extragroup male; aggressive or peaceful) did not affect infant mortality rates. Additionally, I updated the mortality rates of infants during times of group stability (26%) and after AMRs (51%)

from earlier research on this population, with an expanded sample size (from N= 97 infants and 18 years of study to N= 221 infants and 30 years of study).

Because infanticide occurs at such high rates and imposes such high costs in this species, I investigated why early weaning, a potential counteradaptation to reduce the occurrence of infanticide, does not also occur in this species. I found that it appears physiologically possible for capuchins to wean earlier, as the observed weaning age (range: 14 – 23 months; Sargeant et al., 2015) far exceeds the probable minimum weaning age (8 months; Recabarren et al., 2000). However, because the minimum weaning age occurs just as the period of greatest vulnerability to infanticide ends (8.3 months; Brasington et al., 2017), it does not appear that white-faced capuchins could wean early enough to reduce their vulnerability to infanticide.

Next, I determined that white-faced capuchins have very long lactation periods compared to other primates of similar size, likely due to the energetic needs of growing a large brain. The high energetic cost of lactation, which can last up to two years, is expected to be very taxing, especially when the chance of the infant dying is high. To compensate, intense levels of allonursing may have been selected for in female white-faced capuchins. Although rare in mammals, allonursing is common in capuchins and may function as a possible mechanism for reducing the costs or risks of losing an infant to infanticide or avoiding infanticide all together. The energetic cost of losing an infant may be lessened for the mother when other females have contributed energetically to that infant. Perhaps more importantly, allonursing may enable females to resume cycling earlier, which can decrease the risk of infanticide because males can detect ovulation in females (Schoof et al., 2014). By retaining the ability to lactate beyond the minimum needs of their young, nursing infants 6 to 15 extra months in white-faced capuchins, females can retain their ability to lactate and nurse the younger infants in the group (particularly of close kin; Sargeant et al., 2015) and provide a great deal of energetic support to those females which in turn can enable them to resume cycling and reduce the risks of infanticide.

Finally, in the last data chapter, I returned to investigate the effects of AMRs on this population of white-faced capuchins by determining whether AMRs alter birth seasonality or synchrony. AMRs appear to shift the conception and birth peaks by a few months; however, this shift away from the presumptive food peak does not appear to affect infant survival as it did not differ based on the timing of birth. I suggest that this lack of a difference in survival was due to the varied diet of the capuchin so that different foods are available throughout the year. I also found evidence that the ecological birth peak of white-faced capuchins aligns with peak caterpillar abundance instead of peak fruit abundance. AMRs do have an impact on birth synchrony in this species, as a higher percentage of infants are born within three-month (55%) and six-month (87%) time periods following AMRs compared to times of stable alpha male tenure (38% and 66%, respectively).

Significance

Sexual conflict theory remains a field of study that has been under-explored in nonhuman primates, mainly due to the long life histories and complex behavior that characterize this Order. The Santa Rosa Capuchin Project is one of only a handful of long-term primate studies that spans several generations (Fedigan & Jack, 2012). Because the project now has nearly 40 years of data, and because infanticide is a known behavior in the species, this population of capuchins has provided an excellent opportunity to explore the effects of infanticide, especially with regard to females, in more detail.

One novel idea that I have added to sexual conflict theory is the possibility allonursing is a potential counterstrategy to infanticide. Previously suggested counterstrategies for female capuchin were largely limited to promiscuity, nonconceptive mating and concealed ovulation. I have also identified two mechanisms by which allonursing may serve as a counterstrategy: 1) faster resumption of ovarian cycling, which is known to be detectable by males (Schoof et al., 2012), thus lessening the risk of infanticide and 2) decreasing the energy investment each mother invests in her infant (decreasing the cost of infanticide). This function of allonursing is a novel suggestion, as previous studies linking allonursing and infanticide in other mammals suggested the allonursing was a by-product of other counterstrategies (e.g., communal nesting).

Additionally, I identified infant age as a major predictor of infanticide. Although this was an expected result, few other populations have been studied long enough for this to be calculated, and thus my findings will likely provide useful information for other populations and species.

Future Research

The findings of this dissertation pave the way for future studies, especially with regard to allonursing. My suggestion that allonursing enables females to resume cycling earlier can be verified via fecal hormones. Values of progesterone and estradiol can be extracted from fecal matter in order to determine when a female resumes cycling after birth, and if all lactating group females were sampled over the course of multiple months, it may be possible to determine when females typically resume cycling. Although impossible to plan, if an AMR did occur during the data collection period, it could be determined whether the mother of any infant killed had resumed cycling yet. Additionally, collecting hormonal data from other cycling females could also identify whether a Bruce effect does occur but is obscured in the demographic data.

In addition to the hormonal data, I suggest that behavioral data on nursing also be collected. More behavioral data regarding which infants are currently nursing could identify with greater precision the mean age at weaning (currently there is a known range of weaning ages, but not a mean age). Once a mean weaning age is determined, it would be possible to detect whether females potentially wean infants earlier during periods of male membership instability. More behavioral data on nursing could also enable us to determine whether any patterns emerge regarding which females or infants engage in allonursing more frequently, potentially shedding light on my suggestion that younger infants receive supplemental milk. These suggestions for future data collection will enable testing of some of the ideas proposed in Chapter Four. These proposed avenues of data collection will also contribute to the wealth of data contained in the Santa Rosa Capuchin Project. This project continues to collect demographic, behavioral, and physiological data that will enable us to address these questions.

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BIOGRAPHY

Lauren Frisoli Brasington was raised in Winchester, Massachusetts by two amazing parents and enjoyed growing up with three great siblings. She attended Colby College in Waterville, Maine, where she earned a BA in Biology. Following college, Lauren was employed for four years as a zookeeper, working mainly with mandrills and gorillas. She then moved to South Carolina to study under Dr. Janice Chism at Winthrop University, where she earned a MS in Biology and became fascinated by sexual conflict theory. For her master's thesis, Lauren studied habitat use of monk sakis in the Peruvian Amazon Rainforest. Lauren continued to pursue her interest in studying New World monkeys by joining Dr. Kathy Jack's lab at Tulane University and receiving her MA in Anthropology. Lauren's favorite thing to do is spend time with her family, which consists of her two young children, her husband, a dog, and a cat. Whenever time (and absence of pandemics) allows, she loves to fly to Boston with her family and get together with her parents, siblings, three nieces, and two nephews.