Chapter 7
Balancing Cooperation and Competition in Callitrichid Primates: Examining the Relative Risk of Infanticide Across Species

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Abstract At least eight cases of infanticide by females other than the mother have been observed in wild groups of common marmosets (*Callithrix jacchus*), with several more cases described for captive groups. Infanticide by females other than the mother has not, however, been documented for wild groups of other callitrichid species. Why might such overt aggression toward infants be more likely in one species than in others? In the common marmoset, a variety of social, reproductive and ecological characteristics – including short inter-birth intervals (and the resulting potential for overlap of pregnancies and births), habitat saturation, small home ranges, and low cost of infant care (including decreased travel costs and short dependency periods compared to other callitrichids) – may contribute to an increased likelihood of two breeding females being present in a group, which in turn may give rise to the potential for competition between breeding females and, ultimately, to infanticide. These conditions are less common in wild groups of most other callitrichid species. All callitrichids balance the need for cooperative care of young with the reproductive competition that results from limited reproductive opportunities; however, ecological and social conditions appear to tip the balance toward infanticide more frequently in common marmosets than in other callitrichid species.

Resumen Al menos ocho casos de infanticidio por hembras distintas a la madre han sido observados en grupos silvestres de marmosetas comunes (*Callithrix jacchus*), con muchos más casos descritos para grupos cautivos. Sin embargo, infanticidio por hembras distintas a la madre no ha sido documentado en grupos silvestres de otras especies de calitrícidos ¿Porqué podría la agresión tan evidente hacia infantes ser más probable en una especie que en otras? En las marmosetas comunes, una variedad de características sociales, reproductivas y ecológicas – incluyendo intervalos cortos entre nacimientos (y el resultado potencial de traslape de

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embarazos y nacimientos), la saturación del hábitat, ámbitos hogareños pequeños y bajo costo de cuidado infantil (incluyendo disminución de costos de viaje y períodos cortos de dependencia comparados con otros calitrícidos) – pueden contribuir al aumento de la posibilidad de que dos hembras reproductoras se presenten en un grupo, lo cual aumenta el potencial para competencia entre la hembras reproductoras y, ultimadamente, a cometer infanticidio. Dichas condiciones son menos comunes en los grupos silvestres de otras especies calitrícidos. Todos los calitrícidos equilibran la necesidad de cuidado cooperativo de los jóvenes con la competencia reproductiva que resulta de oportunidades reproductivas limitadas; no obstante, las condiciones ecológicas y sociales parecen inclinar la balanza hacia el infanticidio con más frecuencia en las marmosetas comunes que en otras especies de calitrícidos.

Resumo Pelo menos oito casos de infanticídio realizados por fêmeas que não as mães foram observados em grupos de sagüi comum selvagens (*Callithrix jacchus*), com vários outros casos sendo descritos para grupos vivendo em cativeiro. Entretanto, infanticídios por fêmeas que não as mães não têm sido bem documentados em grupos selvagens de outras espécies de calitriquídeos. Por que esta agressão em relação aos infantes é mais comum em uma espécie do que em outras? Em sagüi comum, uma variedade de características sociais, reprodutivas e ecológicas – incluindo o intervalo curto entre nascimentos (e o resultante potencial de sobreposição de gestações e nascimentos) saturação de habitat, áreas de uso pequenas e baixo custo do cuidado parental (incluindo diminuição no custo do deslocamento e o período de dependência curto comparado com outros calitriquídeos) – podem contribuir para o aumento da probabilidade de duas fêmeas reprodutoras estarem presentes em um mesmo grupo, que por sua vez favorece o surgimento de competição potencial entre as fêmeas reprodutoras e, eventualmente, o infanticídio. Estas condições são menos comuns em grupos selvagens da maioria das demais espécies de calitriquídeos. Todos os calitriquídeos fazem o balanço entre a necessidade de cuidado cooperativo dos infantes e a competição reprodutiva que resulta das oportunidades limitadas de reprodução; entretanto, as condições ecológicas e sociais parecem inclinar a balança em relação ao infanticídio mais frequentemente em sagüis comuns do que em outras espécies de calitriquídeos.

7.1 Introduction

Female–female competition plays an important role in the reproductive strategies of female primates (e.g., Hrdy 1981; Altmann 1997; Jones 2003) and is likely to play a critical role in the evolution of mammalian social systems (Gowaty 1997; Digby 2000). In recent years an increasing number of studies have documented the roles of social dominance, aggression, and interference by females in controlling and/or limiting the ability of other females to breed and raise young successfully (e.g., Pusey et al. 1997; Gowaty 1997; Saltzman and Abbott 2005). This type of competition is carried to an extreme in cases where one female kills another female's young (e.g., Sherman 1981; Hoogland 1995, reviewed in Digby 2000).

At first glance, the cooperatively breeding callitrichids may not appear to be a likely example of such extreme reproductive competition. This group is better known for shared infant care, flexible mating strategies, and a relatively low rate of aggression (Tardif et al. 1993, 2003; Garber 1997; Digby et al. 2007, Porter and Garber this volume, Chap. 4; Ferrari this volume, Chap. 8). However, cooperatively breeding species are also known for restricting reproduction to a small subgroup of adults within each group (Abbott et al. 1993; French 1997). Such restriction of reproduction will naturally lead to competition over which animals lay claim to reproductive sovereignty (Saltzman 2003; Digby et al. 2007, Yamamoto et al. this volume, Chap. 6). Indeed, it is likely that the delicate balance between the need for cooperation and the conditions that give rise to competition have ultimately shaped many aspects of callitrichid social organization and reproductive tactics.

Callitrichid females may influence the breeding success of other females in a variety of ways, including physiological suppression of ovulation, inhibition of sexual behavior (including interference during copulation), and aggression toward females attempting to join a group (reviewed in Saltzman 2003; note that subordinate females also likely play an active role in restricting their own reproduction, thus avoiding wasted reproductive effort; Wasser and Barash 1983; Saltzman 2003; Abbott et al. 2009; Saltzman et al. 2009 Yamamoto et al. this volume, Chap. 6 2009). Perhaps the most dramatic means by which one callitrichid female can influence the reproductive success of another, however, is via infanticide. Eight cases of infanticide by females other than the mother have been observed among wild callitrichids (all in the common marmoset, *Callithrix jacchus*), with another four observed and several inferred under similar circumstances, in captivity (see Table 7.1; Saltzman 2003; Abbott et al. 2009).

Across mammals, infanticide has been observed under a variety of circumstances, with perpetrators being male or female, related or unrelated to the victim. Of the five hypotheses put forth to explain infanticide (Hrdy 1979), the sexual selection hypothesis is the one most commonly invoked to explain infanticide in primates (van Schaik and Janson 2000). This hypothesis postulates that one individual, typically a male, will gain access to a potential mate more quickly by killing that individual's dependent young. For most callitrichid species, however, the killing of dependent young would have minimal influence on the mother's resumption of fertility, because lactation has little or no inhibitory effect on ovulation (Abbott et al. 1993; French 1997; Digby et al. 2007). Correspondingly, infanticide by males has never, to our knowledge, been reported in wild callitrichid groups (see Table 7.1).

Only one occurrence of maternal infanticide has been reported in wild callitrichids: a saddle-back tamarin (*Saguinus fuscicollis*) infant was cannibalized after falling off

Table 7.1 Reported cases of infanticide in callitrichids

Species	Field/ lab	Observed/ inferred	Perpetrator	Relationship to victim	Comments	References
Callithix jacchus	Field	1 Obs.	Other (subordinate) breeding female, but subsequently became dominant	Unknown	Perpetrator attacked 2-week-old infant on two occasions; gave birth approximately 1 month later	Roda and Mendes Pontes (1998)
C. jacchus	Field	1 Obs.	Probably other (dominant) breeding female	Not closely related based on genetic tests ($R < 0.14$)	Perpetrator gave birth 2 days later	Digby (1995) and Nievergelt et al. (2000)
C. jacchus	Field	3 Obs.	Other (dominant) breeding female	Grandmother in one case; others unknown		Yamamoto et al. (1996) and Arruda et al. (2005)
C. jacchus	Field	1 Obs.	Other (dominant) breeding female	Unknown	Perpetrator gave birth 1 month after infanticide	Lazaro-Perea et al. (2000)
C. jacchus	Field	1 Obs.	Dominant female from neighboring group	Unknown	Involved incursions into a recently vacated home range	Melo et al. (2003)
C. jacchus	Field	1 Obs.	Other (subordinate) breeding female, but subsequently became dominant	Unknown	Perpetrator attacked and cannibalized infant after it had apparently been wounded by birds; gave birth 2 months later	Bezerra et al. (2007)
C. jacchus	Lab	2 Obs.	Eldest daughter of breeding female	Full- or half-sister	Perpetrator subsequently became dominant female	Alonso (1986)
C. jacchus	Lab	1 Obs./1 inf.	Other breeding female/unknown	Grandmother	Perpetrator gave birth 1 week later/ other breeding female gave birth 4 days later	Kirkpatrick-Tanner et al. (1996)
C. jacchus	Lab	1 Obs./ several inferred	Other (transiently subordinate) breeding female	Grandmother	Perpetrator gave birth 1 week later	Saltzman (2003) and Saltzman et al. (2008)
Saguinus fuscicollis	Field	1 Obs.	Mother of infant	Mother	Infant fell repeatedly immediately before infanticide; other adult female gave birth 2.5 months later	Herrera et al., (2000)

its carrier several times (Herrera et al. 2000). Two hypotheses may apply to this case: exploitation (e.g., cannibalism or "conspecific predation"; Hrdy 1979; Ebensperger 1998; note that cannibalism is unlikely to have a major fitness impact on the perpetrator in terms of nutrition, see Digby 2000) and maternal manipulation, in which a mother kills an infant in the hope of improving her future reproductive success (Hrdy 1979). Maternal infanticide is very rare in free-ranging populations of non-human primates (Hrdy 1999), so this case is of great interest in itself. The majority of infanticides in callitrichids, however, involve the killing of infants by breeding females other than the mother. These cases will be the focus of the remainder of this chapter.

Most cases of infanticide by females other than the mother can best be explained by the resource competition hypothesis (Hrdy and Hausfater 1984; Digby 2000). This model predicts that by killing unrelated infants, a female will gain increased access to resources for herself and her young, both immediately and in the future (Hrdy 1979; Sherman 1981; Hoogland 1995). While typically construed in terms of access to food or sleeping sites, the resource competition model can also apply to other limited resources such as breeding opportunities or access to helpers. As such, the model is compatible with the restrictive breeding patterns observed in most callitrichid species. Indeed, in most observed cases (Table 7.1), the socially dominant breeding female has killed infants born to a subordinate female, thereby allowing the dominant to maintain reproductive sovereignty (e.g., Digby 1995; Kirkpatrick-Tanner et al. 1996; Roda and Mendes Pontes 1998; see Fig. 7.1).

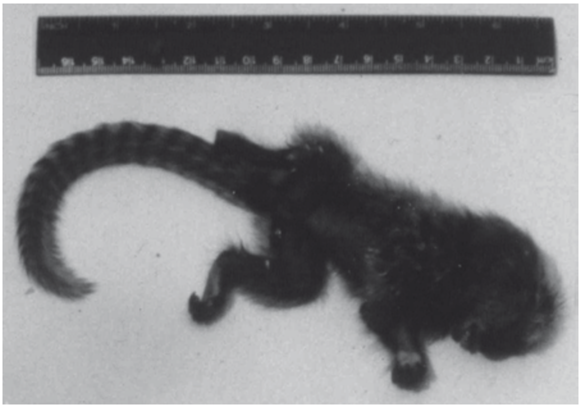

Fig. 7.1 Common marmoset infant killed by fellow group member (most likely the dominant female). The 24-day-old infant exhibits puncture wounds over the body and skull, a broken jaw, and torn skin around the genitalia. The infanticide was directly observed, but identification of the perpetrator could only be narrowed down to three group members: the dominant female (who gave birth 2 days later), the subordinate adult male that had been carrying the infant (and stayed with the infant for close to an hour after the attack, trying to pick it up), and a subadult male who, based on genetic analysis, was likely a maternal half-sibling of the victim. The mother of the victim went on to both carry and occasionally nurse the infants of the dominant female (Digby 1995; Nievergelt et al. 2000; photo by L. Digby)

Resource limitations and competition for breeding opportunities are likely to occur across the callitrichids. In addition, it is clear that breeding is not always restricted to a single female, and that infants born to secondary females in common marmosets, as well as in a handful of other callitrichid species, do sometimes survive. Why, then, do common marmoset infants appear to be more vulnerable to infanticide than infants of other species? To address this question, we will examine the delicate balance between the reproductive strategies of subordinate females (e.g., when do the benefits of breeding as a secondary female outweigh the costs of potential infant loss?) and those of dominant females (e.g., when secondary females do breed, when is the cost of sharing resources high enough to trigger infanticide?). We focus here on the idea that infanticide occurs when the reduced costs that favor plural breeding change just enough to push dominant breeding females over a threshold, such that the once-tolerated plural breeding becomes too costly and intense reproductive competition results. We examine species differences in breeding patterns, group composition, travel costs, infant care, population density, dominance relationships, and reproductive physiology in order to develop a preliminary framework to explain why common marmosets appear to be more susceptible to shifts in this balance between single and plural breeding and, therefore, more vulnerable to infanticide than the other callitrichid species.

7.2 Conditions that may Give Rise to Infanticide in Callitrichids

7.2.1 Multiple Breeding Females

In all but one case of infanticide observed in callitrichids under natural conditions, the groups contained two breeding females (the exception occurred when a female common marmoset from one group attacked an infant from another group: Melo et al. 2003). This is notable in a taxon known for restricting breeding to a single female in each group (reviewed in Abbott et al. 1993; Tardif et al. 2003) and suggests that when the mechanisms that usually restrict breeding fail, females may resort to infanticide to regain reproductive sovereignty. Although non-breeding females could potentially kill infants, such cases are rare among mammals (Digby 2000).

Groups containing multiple breeding females have been documented in 11 species of callitrichids (see Table 7.2; see also French 1997). More cases of plural breeding have been reported for common marmosets (11+ cases; see Table 7.2; up to 50% of surveyed groups ($n=6$); Digby personal observation), golden lion tamarins (*Leontopithecus rosalia*; 10% of group-years: Dietz and Baker 1993), and saddle-back tamarins (12% of group-years: Goldizen et al. 1996) than for the other callitrichids. It should be noted, however, that systematic data on the rates of plural breeding are not available for other species; there are only some case

Table 7.2 Plural breeding and infant outcomes in wild callitrichids

Species	Number of observed cases of multiple breeding females	Number of infants or pregnancies lost/total observed in plural breeding groups	(Survival of infants born to subordinate vs. dominant females); context/comments	References
Callithrix jacchus				
Nisia Floresta – 1	3	11/23 Infants	(33% vs. 62%); subordinate females sole carriers of own infants for at least 10 days; in contrast dominant females allow helpers to carry immediately after birth	Digby and Barreto (1993) and Digby (1995)
Nisia Floresta – 2	7+	26/68 Infants	(0% vs. 76%)[a]	Arruda et al. (2005)
Santo Antonio Ranch	1	8/13 Infants	(66% vs. 75%; latter female became dominant during the study)	Roda and Mendes Pontes (1998)
Callithrix aurita	1	2/7 Infants	(67% vs. 75%) both breeding females carried own infants exclusively for relatively long periods (10 days to 4 weeks)	Coutinho and Corrêa (1995)
Callithrix flaviceps	1	7/9 Infants	(50% vs. 100%); subordinate females sole carriers of own infants for 15 days; dominant female allowed allomaternal care at 2 days	Guimarães (1998)
Cebuella pygmaea	1[b]			de la Torre et al. (2000)
Callimico goeldi	4[c]		Mothers tolerated allomaternal care when infants less than 10 days old	Christen (1999), Porter (2001), Masataka (1981) as cited in Porter (2001), and Rehg (pers. comm.)
Callibella humillis	"Several"		Singleton births?; lack of allomaternal care; parking of infants	van Roosmalen and van Roosmalen (2003)
Saguinus fuscicollis				
Acre	1	0/4 Infants	(100% vs. 100%); all survived for 4+ months	Calegaro-Marques et al. (1995)
Cocha Cashu	5 (10.6% of group-years)	1/5 Pregnancies	Dominance not specified; at least one breeding daughter lost infant immediately after birth (breeder's mother was in last month of pregnancy); surviving infants born at least 3 months apart	Goldizen et al. (1996)

(continued)

Table 7.2 (continued)

Species	Number of observed cases of multiple breeding females	Number of infants or pregnancies lost/total observed in plurally breeding groups	(Survival of infants born to subordinate vs. dominant females); context/comments	References
Quebrada Blanco	1	1/3 Infants	(100% vs. 0%). Infants born to subordinate after maternal infanticide. Survived at least 2 months	Herrera et al. (2000)
Saguinus mystax				
Padre Isla	3[d]	1 female per group had surviving offspring	Dominance status not noted; plural breeding groups were among the largest in population, with an average of 10 individuals	Garber et al. (1993)
Quebrada Blanco	1	1/3 Infants	Infant died on day of birth; other breeding female gave birth next day; dominance status not noted	Smith et al. (2001) and Löttker et al. (2004)
Saguinus oedipus	3[e]	3/4 Infants	New males had immigrated into group; dominance status not noted	Savage et al. (1996, 1997)
Leontopithecus rosalia	11 (in 6 groups)/10% of group samples[f]	6 Infants; 7–8% of group-breeding seasons	(33% vs. 68%) Subordinates/daughters more likely to lose infants; some groups had unrelated males, others did not. Incestuous matings never resulted in successful young	Dietz and Baker (1993) and Baker et al. (2002)
Leontopithecus chrysomelas	1?			Raboy and Dietz (2004)

[a] Based on groups with two breeding females that, however, maintained a monogamous mating system (i.e., using extra-group copulations)

[b] Based on short interbirth interval

[c] Based on presence of two infants

[d] Based on presence of two pregnant females or one pregnant and one lactating female

[e] Based on presence of two pregnant females

[f] Dietz and Baker (1993) assume polygyny as long as the two females that have bred in the past remain in the group, even if only one female continues to breed

studies. Nevertheless, it seems likely that species differ in their propensities toward plural breeding.

Why some groups contain a second breeding female and others do not is not well understood, but several determinants of plural breeding have been proposed, including group composition, infant-care costs, timing of births, reduced opportunities for dispersal, and dominance relationships (see reviews by French 1997; Smith et al. 2001, Yamamoto et al. this volume, Chap. 6). A thorough examination of this issue is beyond the scope of this chapter, but it is clear that a propensity toward plural breeding is an important factor in determining whether or not infanticide is likely to occur in a given species. We cover some of the basic costs of these variables and their possible relationship to the threat of infanticide, below.

7.2.2 Infant Care Costs, Ecology, and the Propensity for Multiple Breeding Females

7.2.2.1 Group Composition

The degree of tolerance for a second breeding female and her infants may be determined by group size and composition. Some studies have indicated that infant survivorship is significantly correlated with the number of adults in a group (e.g., common marmoset: Koenig 1995; pygmy marmoset, *Cebuella*: Heymann and Soini 1999, reviewed in Yamamoto et al. this volume, Chap. 6), and one might assume that in a large group, the large number of potential helpers would enable sharing of infant care costs to a degree that two breeding females could successfully raise young. Nevertheless, an association has not been found between group size and plural breeding (Dietz and Baker 1993; Digby 1995; Goldizen et al. 1996; Table 7.3).

Instead, the actual composition of the group, especially relatedness among group members, may be more important than group size. Infanticide might be predicted to be less likely to occur in groups with closely related breeding females (mother and daughter, sisters) compared to those with unrelated females, because of inclusive fitness costs. The data do not currently support this prediction, however, as infanticide has been observed in groups with both unrelated (e.g., Digby 1995) and related (e.g., Yamamoto et al. 1996) breeding females (Table 7.1). The fact that females have killed related infants may indicate that these females would have incurred very high costs by tolerating the presence of other females' infants in the group (e.g., Hager and Johnstone 2004).

The presence of an unrelated male may also increase both the likelihood of a group breeding plurally (Saltzman et al. 2004, 2008) and the survivorship of young (e.g., no infants survived from father–daughter inbreeding in golden lion tamarins: Dietz and Baker 1993). Notably, in some plurally breeding groups of common marmosets, females may avoid inbreeding by mating with extra-group males (Arruda et al. 2005). Species or populations may differ in females' access to extra-group

Table 7.3 Group size, home range and daily path length in wild callitrichids

Species	Group size (average)	Home range size (ha)	Daily path length (m/day)	References
Callithrix jacchus	3–16 (8.7)	2–5.2	912–1,243	Digby and Barreto (1996), Lazaro-Perea et al. (2000), and Koenig (1995)
Callithrix flaviceps	5–20 (13)	33.9–35.5	884–1,223	Ferrari and Diego (1992), Ferrari and Rylands (1994), and Guimarães (1998)
Callithrix aurita	4–11	16.5–35.3	959–986	Ferrari et al. (1996) and Martins (1998)
Mico intermedius	9–15 (12)	22.1	772–2,115	Rylands (1986a, b) and Ferrari and Rylands (1994)
Mico argentatus	6–10 (7.3)	4–35		Albernaz and Magnusson (1999) and Tavares and Ferrari (2002)
Cebuella pygmaea	2–9 (5.0)	0.1–1.09	280–300	Heymann and Soini (1999) and de la Torre et al. (2000)
Callimico goeldii	4–12 (7.7)	30–150	2,000	Porter (2001)
Callibella humilis	up to 30 (6–8)	–	–	van Roosmalen and van Roosmalen (2003)
Saguinus fuscicollis	2–10 (5.3)	30–149	1,150–2,700	Goldizen (2003) and Heymann (2000, 2001)
Saguinus mystax	3–11 (5.3)	40–45	1,500–1,720	Garber (1988) and Heymann (2000)
Saguinus tripartitus	2–9 (5.1)	16–21	500–2,300	Kostrub (2003)
Leontopithecus rosalia	2–11 (5.4)	21.7–229	955–2,405	Baker et al. (2002), Dietz et al. (1997) and Kierulff et al. 2002
Leontopithecus chrysomelas	3–10 (6.7)	36–130	1,410–2,044	Baker et al. (2002) and Raboy and Dietz (2004)

males due to differences in the degree of overlap in home ranges and the frequency of encounters with neighboring groups. It is unclear, however, whether or not the presence of an unrelated male influences vulnerability to infanticide other than by increasing the likelihood of breeding by a secondary female.

7.2.2.2 Travel Costs

The ability of a group to support two breeding females, and the threshold at which one female will no longer tolerate the presence of another female's young, are likely also tied to costs of infant care. Though direct measures of energy requirements are difficult to obtain under natural conditions, the distance that a parent or helper must carry infants can be a useful indirect measure of costs (e.g., Tardif 1997).

Digby and Barreto (1996) noted that common marmosets that were carrying infants traveled significantly less than the group as a whole traveled when no young infants were present. Qualitative observations indicated that infant carriers often stayed in central areas of the group's relatively small home range (see Table 7.3), while other group members foraged in a larger circuit around them. This reduction in travel may reduce infant-care costs to the point where a second set of twins could be raised without energetically over-taxing helpers (Digby and Barreto 1996). Such a strategy would be difficult for species with much larger home ranges, as fewer active infant carriers would be left behind.

The cost of carrying infants should also vary with the length of time that infants take to achieve locomotor independence, which differs considerably among the callitrichid species. Under captive conditions, for example, in the first 8 weeks after birth, common marmosets are carried less than 20% of the time, while saddle-back tamarins are carried more than 60% and golden lion tamarins about 30% of the time (Tardif et al. 1993, 2003). Shorter infant dependency periods may allow for a greater initial tolerance of two sets of infants, but can also leave the offspring of secondary breeding females vulnerable to infanticide, if other costs, such as competition over access to helpers, become too great.

7.2.2.3 Infant Care and Overlapping Dependency Periods

While both small home range size and shorter dependency periods should reduce the costs of infant care and, therefore, favor plural breeding in common marmosets, they may not be enough to counter the cost of two sets of infants born in close succession, resulting in overlapping dependency periods and more intense competition for limited resources (e.g., helpers). Infants born to subordinate female common marmosets were unlikely to survive if they were born less than a month before or after the infants of the dominant female (Digby 1995; Saltzman et al. 2008). Similarly, for saddle-back tamarins, Goldizen et al. (1996) suggested that a 3-month interval before or after the birth of the infants of the primary breeding female is necessary for the successful rearing of infants by a secondary female. Breeding asynchronously may be more difficult in the *Callithrix* species than in other species, as the *Callithrix* species usually breed twice per year, with births tending to cluster around two birth peaks (reviewed in Digby et al. 2007). Golden lion tamarins have one of the more pronounced birth peaks among the callitrichids, with most births occurring in a 3-month window (French et al. 2002); thus, plurally breeding groups in this species may frequently face periods in which two sets of infants need to be cared for simultaneously. *Saguinus* species, on the other hand, exhibit only weak seasonality and annual births (reviewed in French 1997; Digby et al. 2007), making them less vulnerable to overlapping periods of infant dependency.

7.2.2.4 Population Density/Habitat Saturation

Habitat saturation has also been put forth as a possible correlate of plural breeding in callitrichids. In Poço das Antas, Brazil (golden lion tamarins), Cocha Cashu, Peru (saddle-back tamarins) and Santo Antonio, Brazil (common marmosets), high population densities appear to make it difficult for an adult female to find a breeding position outside of her natal group (Dietz and Baker 1993; Goldizen et al. 1996; Roda and Mendes Pontes 1998). Based on the hypothesis that emigration is risky, Dietz and Baker (1993) modeled the costs and benefits to dominant female golden lion tamarins, of tolerating a breeding daughter, and found that mothers gain an overall benefit by allowing daughters to remain and breed in the natal group. When the costs and benefits to the primary breeding female shift, however – for example, if breeding within the natal group results in inbreeding – then eviction of the daughter from the natal group is predicted (Dietz and Baker 1993; Dietz et al. 2000; Baker et al. 2002). Notably, when female golden lion tamarins do breed with related males, there are much higher mortality rates (Dietz et al. 2000). Such a pattern may indicate that secondary females are willing to risk reproduction within their natal group if the risk associated with emigration is sufficiently high. Infants born to these females would very likely be all the more vulnerable to infanticide.

7.2.3 Dominance Relationships and the Propensity for Infanticide

For infanticide to occur, a perpetrator must gain access to the intended victim. Among primates, which typically carry young infants, this usually means that the perpetrator must have either greater physical strength or greater social power than the infant's caretaker (Hrdy 1976; Maestripieri and Carroll 1998; Treves 2000). Callitrichids typically share the care of young, sometimes even from the first day following birth; however, subordinate breeding female common marmosets appear to be more cautious than dominant females, not allowing others to carry their infants for up to 10 days postpartum (Digby 1995). It is unclear if similar patterns occur in plurally breeding groups of other callitrichid species.

Most cases of infanticide in common marmosets appear to be perpetrated by females that are already behaviorally dominant over the victim's mother or that will become dominant following the infanticide (see Table 7.1; it is to be noted, however, that this is not necessarily the case under captive conditions: Saltzman 2003; Saltzman et al. 2008). In golden lion tamarins, daughters (which are usually, but not always, subordinate to their mothers) typically suffer higher infant mortality than their mothers when two females breed within the same group (Dietz and Baker 1993); however, the contribution of infanticide is unclear. Further research on potential differences in the intensity and/or nature of dominance relationships across the callitrichid species is necessary to elucidate the role they may play in the relative vulnerability of their young.

7.2.4 Reproductive Physiology

7.2.4.1 Suppression of Reproduction

Callitrichid species differ markedly, both in the degree to which reproduction is suppressed in subordinate females and in the mechanisms of suppression. As described above, laboratory studies indicate that mechanisms of reproductive failure range from inhibition of sexual behavior in fully fertile subordinate females (e.g., golden lion tamarins: French et al. 2002) to inhibition of fertility as a consequence of ovulation suppression (e.g., common marmosets: Abbott 1984; cotton-top tamarins, *S. oedipus*: Snowdon et al. 1993). Among species exhibiting suppression of reproductive physiology, the consistency of this suppression varies considerably, at least in captivity, from anovulation and reproductive failure in virtually all subordinate females (e.g., cotton-top tamarins: Snowdon et al. 1993) to the occurrence of ovulatory cyclicity and even conceptions in a sizeable minority of subordinates (e.g., common marmoset: Saltzman et al. 1997, 2004).

Although these patterns have not always been borne out in studies of free-living animals (reviewed in Digby et al. 2007), it is tempting to speculate that interspecific differences in the stringency of reproductive suppression may be associated with differences in the ability of groups to support the infants of more than a single breeding female. For example, the absence of strict suppression in callimico (*Callimico goeldii*; Dettling and Price 1999), in which secondary breeding females are routinely tolerated (Porter 2001), may reflect the low costs of raising singleton infants when compared to the costs of raising twins, typical in the other callitrichid species. The more context-dependent suppression (e.g., varying with age: Baker et al. 2002; group composition: Abbott 1984; Saltzman et al. 1997, 2004) seen in golden lion tamarins and common marmosets may suggest that ecological and/or social conditions change frequently enough to make it cost-effective for females to employ a more flexible strategy, attempting to breed as subordinates under some circumstances, but forgoing breeding attempts under other circumstances (Yamomoto et al. this volume, Chap. 6).

Differences in the extent of suppression may be associated with differences in vulnerability to infanticide. Strict forms of reproductive suppression may have evolved in subordinate breeding females in response to a high risk of reproductive failure; this may enable the females to avoid wasting reproductive effort (Wasser and Barash 1983; Abbott et al. 2009; Saltzman et al. 2009). It also follows that this stricter reproductive suppression is expected to reduce the frequency of plural breeding and, consequently, the likelihood of infanticide. In contrast, more flexible forms of suppression may reflect an increased likelihood that subordinate females might, at least occasionally, breed successfully (depending on timing of births, etc.). By enabling subordinate females to breed, these flexible forms of suppression may increase both the rate of plural breeding and, consequently, the likelihood of infanticide. Further research into species differences in the extent and mechanisms of reproductive suppression might therefore shed light on patterns of infanticide as well.

7.2.4.2 Proximate Mechanisms of Female Aggression Toward Infants

When two females breed concurrently within the same social group, the relative timing of births may be a critical determinant of infanticide. Infanticide was committed by female common marmosets in the late stages (i.e., final 1–2 months) of pregnancy in most known cases from wild populations (in which pregnancy status was reported) and in many captive cases as well (Saltzman 2003). Correspondingly, in a recent study of captive common marmosets, multiparous females exhibited a markedly reduced attraction to, as well as tolerance of, unfamiliar infants during late pregnancy, as compared to early pregnancy and the early post-partum period (Saltzman and Abbott 2005). These findings suggest that the hormonal milieu of late pregnancy may inhibit maternal responsiveness and promote infanticide in this species. Such a pattern would contrast strikingly with that in other mammals, in which hormonal changes in late pregnancy typically enhance maternal responsiveness (Numan and Insel 2003). Assessment of variation in this tendency in other callitrichid species awaits further study.

7.3 Discussion: Balancing Cooperation and Competition in Callitrichids

Callitrichids exhibit numerous behavioral, ecological, and reproductive differences among species that may render the infants of some species more likely to fall victim to infanticide. Strikingly, almost all the reported cases of infanticide in wild callitrichids have occurred in plural breeding groups, with one breeding female killing the offspring of another. Perhaps the most important determinant of the likelihood of infanticide, therefore, is the propensity for groups to contain a second breeding female. With the exception of callimico and, perhaps, dwarf marmosets (*Callibella*), plural breeding in callitrichid groups appears to be the exception rather than the rule (French 1997). In species such as golden lion tamarins and saddle-back tamarins, ecological and social factors such as high population density and/or the presence of unrelated males in the groups may encourage secondary females to attempt breeding in the presence of a primary breeding female. In common marmosets, saturated habitats, the ability to live in small, highly overlapping home ranges, and access by females to unrelated males in either their own or a neighboring group may be key factors giving rise to plural breeding.

Once multiple females breed within a group, these females may still attempt to limit each other's reproductive success. Overlapping periods of infant dependency, births occurring during the final stages of another female's pregnancy, relatedness and relative social status of breeding females may all contribute to the fitness costs associated with tolerating a second set of infants within a group. When the costs exceed a given threshold and become too high, females may resort to infanticide as a means of decreasing resource competition and increasing their own overall reproductive success. The ecology, social organization and reproductive biology of common marmosets appear to put this species at greater risk for infanticide than other callitrichids.

Could infanticide be occurring in other callitrichid species? Importantly, in most of these species, when groups are observed to contain two pregnant females, most secondary females are not successful in raising their young (i.e., one or both of the pregnancies are not carried to term or neonates from one or both females are never found; see Table 7.2). In golden lion tamarins, for example, infant survival rates in polygynous groups were roughly half of those in monogamous groups (47% vs. 83%: Dietz and Baker 1993; Baker et al. 2002), and the infant survival rate for subordinate females was significantly lower than that for dominant females (33% vs. 68%: Dietz and Baker 1993). A similar pattern arises in cotton-top tamarins, with 75% ($n=4$ pregnancies) of plural breeding females being unsuccessful (infants not seen) compared to only 8% loss ($n=13$ pregnancies) in groups with a single breeding females (excluding losses that occurred in a drought year; Savage et al. 1996). Thus, females in several callitrichid species lose infants under conditions that are consistent with the resource competition model. It remains to be determined whether infant losses under these conditions result from infanticide or from other sources of mortality.

Why have no infanticides been reported for these species? Perhaps it is not surprising that infanticide has not been observed, given the probable rarity of the behavior combined with the timing of most births (occurring at night or out of sight of the observer). In fact, in view of these constraints, the fact that infanticide has been observed repeatedly in free-living common marmosets is quite striking. Importantly, the disparity between common marmosets and at least some other callitrichid species is unlikely to be caused by differences in the number of observation hours. Golden lion tamarins and saddle-back tamarins, for example, are both subjects of long-term field studies. Another possibility is that some species employ an earlier form of infant loss, in which unfavorable social or ecological conditions promote fetal reabsorption or spontaneous abortion. Only with additional field studies and more long-term data will we know whether these disappearances are part of a typical pattern of spontaneous mortality (reflecting, for example, differences in infant viability or maternal care between experienced and primiparous breeding females, or inbreeding by subordinate females) or whether they reflect a greater risk of neonatal infanticide in plural breeding groups.

At this point, we can only speculate about the relative importance of the ecological, behavioral, and physiological parameters discussed here, in determining patterns of infanticide. Future studies on species differences in the propensity for infanticide will need to focus observations on females in plural breeding groups, especially during the period immediately following birth. In addition, as more data become available, detailed analyses of the costs and benefits to primary breeding females of tolerating a second breeding female and her young, as performed for golden lion tamarins by Dietz and Baker (1993; Baker et al. 2002),will need to be carried out for more species. Ultimately, we believe that such studies will point to a delicate balance between the need for cooperative care of the young and the inherent competition that results from the restriction of reproduction to a small minority of adults. Thus, perhaps ironically, it is the cooperative nature of callitrichid reproductive strategies that ultimately gives rise to the conditions driving some females to infanticide.

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