

- Niemitz, C. (1984). *Biology of Tarsiers*. Gustav Fischer, Stuttgart.
- Niemitz, C., Nietsch, A., Warter, S., and Rimpler, Y. (1991). *Tarsius diana*: a new primate species from central Sulawesi (Indonesia). *Folia Primatol.* 56:105–116.
- Nietsch, A. (1999). Duet vocalizations among different populations of Sulawesi tarsiers. *Int. J. Primatol.* 20:567–583.
- Nietsch, A., and Kopp, M. (1998). The role of vocalization in species differentiation of Sulawesi tarsiers. *Folia Primatol.* 69:371–378.
- Nietsch, A., and Niemitz, C. (1992). Indication for facultative polygamy in free-ranging *Tarsius spectrum*, supported by morphometric data. In: *International Primatological Society Abstracts*. International Primatological Society, Strasbourg. p. 318.
- Pallas, P. S. (1778). *Novae Species quad e Glirium Ordinae cum Illustrationibus Variis Complurium ex hoc Ordinae Animalium*, W. Walther, Erlangen.
- Petiver, J. (1705). *Gazophylacii Naturae et Artis*, London.
- Pocock, R. I. (1918). On the external characteristics of the lemurs and of *Tarsius*. *Proc. Zool. Soc. Lond.* 1918:19–53.
- Poorman, P., Cartmill, M., and MacPhee, R. (1985). The G banded karyotype of *Tarsius bancanus* and its implications for primate phylogeny. *Am. J. Phys. Anthropol.* 66:215.
- Roberts, M. (1994). Growth, development and parental care patterns in western tarsiers, *Tarsius bancanus* in captivity: evidence for a slow life history and non-monogamous mating system. *Int. J. Primatol.* 15:1–28.
- Roberts, M., and Kohn, F. (1993). Habitat use, foraging behavior and activity patterns in reproducing western tarsiers, *Tarsius bancanus*, in captivity: a management synthesis. *Zoo Biol.* 12:217–232.
- Rosenberger, A., and Szalay, F. (1980). On the tarsiiiform origins of the Anthropoidea. In: Ciochon, R., and Chiarelli, A. (eds.), *Evolutionary Biology of the New World Monkeys and Continental Drift*. Plenum Press, New York. pp. 139–157.
- Ross, C. (1994). The craniofacial evidence for anthropoid and tarsier relationships. In: Fleagle, J., and Kay, R. (eds.), *Anthropoid Origins*. Plenum Press, New York. pp. 469–547.
- Schultz, A. (1948). The number of young at a birth and the number of nipples in primates. *Am. J. Phys. Anthropol.* 6:1–23.
- Shekelle, M. (2003). *Taxonomy and biogeography of eastern Tarsiers* [PhD thesis]. Washington University, St. Louis.
- Shekelle, M., Leksono, S., Ischwan, L., and Masala, Y. (1997). The natural history of the tarsiers of north and central Sulawesi. *Sulawesi Prim. News.* 4:4–11.
- Sherman, P., Braude, S., and Jarvis, J. (1999). Litter sizes and mammary numbers of naked mole-rats: breaking the one-half rule. *J. Mammal.* 80:720–733.
- Simons, E., and Bown, T. (1985). *Afrotarsius chatrathi*, the first tarsiiiform primate (Tarsiidae) from Africa. *Nature* 313:475–477.
- Simpson, G. G. (1945). The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* 85:1–350.
- Storr, G. (1780). *Prodromus methodi mammalium*. Tubingen.
- Tremble, M., Muskita, Y., and Supriatna, J. (1993). Field observations of *Tarsius diana* at Lore Lindu National Park, central Sulawesi, Indonesia. *Trop. Biodivers.* 1:67–76.
- Trent, B., Tucker, M., and Lockard, J. (1977). Activity changes with illumination in slow loris *Nycticebus coucang*. *Appl. Anim. Ethnol.* 3:281–286.
- Ulmer, F. A. (1963). Observations on the tarsier in captivity. *Zool. Garten* 27:106–121.
- Waser, P. (1976). *Cercocebus albigena*: site attachment, avoidance and intergroup spacing. *Am. Nat.* 110:911–917.
- Wolfe, J., and Summerlin, C. (1989). The influence of lunar light on nocturnal activity of the old field mouse. *Anim. Behav.* 37:410–414.
- Wolin, L., and Massouput, L. (1970). Morphology of the primate retina. In: Noback, C. R., and Montagna, W. (eds.), *The Primate Brain*. Appleton-Century-Crofts, New York. pp. 1–27.
- Wright, P. C. (1990). Patterns of paternal care in primates. *Int. J. Primatol.* 11:89–102.
- Wright, P. C., Toyama, L., and Simons, E. (1988). Courtship and copulation in *Tarsius bancanus*. *Folia Primatol.* 46:142–148.

## 6

## Callitrichines

## The Role of Competition in Cooperatively Breeding Species

Leslie J. Digby, Stephen F. Ferrari, and Wendy Saltzman

## INTRODUCTION

The callitrichines are best known for their suite of reproductive and behavioral characteristics that are unusual or unique among the primates. Social suppression of repro-

duction, postpartum ovulation, twinning, cooperative care of young, and flexible mating systems make this a useful group of animals for testing hypotheses about the evolution of reproductive strategies and social systems. In addition, these species are characterized by claw-like nails on all digits but

the hallux, two molars instead of the three typical of platyrrhines (2.1.3.2 dental formula, except in *Callimico*), small body size (from 120 g in *Cebuella* to 650 g in *Leontopithecus*), and dramatic variation in coloration, ear tufts, and even “mustaches” (detailed physical descriptions in Eisenberg and Redford 1999). When reviewed by Goldizen (1987a), information on these species in the wild was limited to five long-term studies, most of which focused on the genus *Saguinus* (e.g., Dawson 1978, Neyman 1978, Terborgh and Goldizen 1985). The past two decades have witnessed a surge of work on the subfamily Callitrichinae, including field studies of several species for which little or no data were available 15 years ago (e.g., *Callimico goeldii*, Porter et al. 2001, *Callithrix geoffroyi*, Passamani and Rylands 2000, *Leontopithecus* spp., Kleiman and Rylands 2002, *Saguinus tripartitus*, Kostrub 2003). Nevertheless, intensive long-term ecological and behavioral studies are still restricted to just over a dozen species (e.g., Rylands 1993a, Kleiman and Rylands 2002), and the majority of taxa, including the 10 newly described species and subspecies (Rylands et al. 2000), are known primarily from general surveys or initial species descriptions.

Field studies of callitrichines have investigated topics as diverse as cognitive mapping (Bicca-Marques and Garber 2001), the influence of color vision polymorphism on foraging behavior (Caine et al. 2003, Smith et al. 2003), reproductive endocrinology (Savage et al. 1997, French et al. 2003), foraging biomechanics (Hourani et al. 2003, Vinyard et al. 2003), nutritional content of food (Heymann and Smith 1999, Smith 2000), and genetics (Nievergelt et al. 2000, Faulkes et al. 2003). Field data have been complemented by laboratory studies on energetics (Genoud et al. 1997, Power et al. 2003), nutrition and digestion (Power et al. 1997, Ullrey et al. 2000), phylogenetics (Barroso et al. 1997, Seuánez et al. 2002), neuroendocrine and behavioral control of reproduction (Abbott et al. 1998, Saltzman 2003), and ovulation and pregnancy using ultrasonography (Jaquish et al. 1995, Oerke et al. 2002), as well as many biomedically oriented studies of reproduction, immune response, and disease (reviewed in Mansfield 2003).

Our goal here is to summarize the most recent information available on the behavior, ecology, and reproduction of callitrichine primates, with an emphasis on comparisons among genera. We then examine the extent to which competition plays a role in social interactions and reproductive success in these cooperatively breeding primates.

## TAXONOMY AND DISTRIBUTION

### Taxonomy

The systematics of the Platyrrhini has undergone extensive revision at all levels since the classic review of Hershkovitz (1977), and the callitrichines have been among the most controversial taxa. Because it combines morphological, genetic, and ecological perspectives, the recent revision by

Rylands et al. (2000, see also Groves 2001) is perhaps most representative of the current consensus and is followed here (see Appendix 6.1). According to these authors, the subfamily Callitrichinae is a monophyletic group containing six genera [*Callimico* (Goeldi's monkey), *Callithrix* (Atlantic marmosets), *Cebuella* (pygmy marmoset), *Leontopithecus* (lion tamarins), *Mico* (Amazonian marmosets), and *Saguinus* (tamarins)], with a total of 60 species and subspecies. We will also include the newly proposed genus name *Callibella* for the dwarf marmoset (van Roosmalen and van Roosmalen 2003).

*Callimico goeldii* has posed the major problem for callitrichine taxonomists. Its small body size and claw-like nails are characteristic of callitrichines, but its third molar and singleton births are typical of the larger-bodied platyrrhines. This led to the monospecific genus being placed at various times within the Callitrichidae (Hill 1957, Napier and Napier 1967), the Cebidae (Cabrera 1958, Simons 1972), or even its own family, the Callimiconidae (Hershkovitz 1977). The current, widely held consensus is that *Callimico* is a true, albeit atypical, callitrichine. This is strongly supported by a number of recent molecular studies (Schneider and Rosenberger 1996, Tagliaro et al. 1997, Canavez et al. 1999, von Dornum and Ruvolo 1999) that clearly place *Callimico* as a sister group of the marmosets (*Callithrix*, *Mico*, *Callibella*, and *Cebuella*).

The marmosets have also been the subject of recent taxonomic revisions. Rosenberger (1981) proposed that *Cebuella* should be included within the genus *Callithrix*. This view has been supported by many genetic studies (e.g., Canavez et al. 1999, Tagliaro et al. 2000) but never widely accepted. Schneider and Rosenberger (1996) and Rylands et al. (2000) not only excluded this proposition but instead reinstated the genus *Mico*, which is equivalent to Hershkovitz's (1977) Amazonian *Callithrix argentata* group. The inclusion of *Mico* avoids paraphyly and is consistent with differences in the dental morphology of *Callithrix* and *Mico* as well as with their allopatric distribution. Recent studies of Amazonian marmosets (Corrêa et al. 2002, Gonçalves et al. 2003) have adopted the new arrangement.

The newest genus to be added to the callitrichine subfamily is *Callibella* (van Roosmalen and van Roosmalen 2003). Although it was originally included in *Mico*, detailed genetic and morphological studies of the recently described black-crowned dwarf marmoset (intermediate in size between *Cebuella* and *Mico*) (van Roosmalen et al. 1998) support the creation of the new genus (Aguilar and Lacher 2003, van Roosmalen and van Roosmalen 2003).

### Distribution

Current knowledge of the zoogeography of the callitrichine genera is little changed from that reviewed by Hershkovitz (1977). Perhaps the most significant alteration has been the extension of the southern limit of the range of *Leontopithecus*, following the discovery of *Leontopithecus*

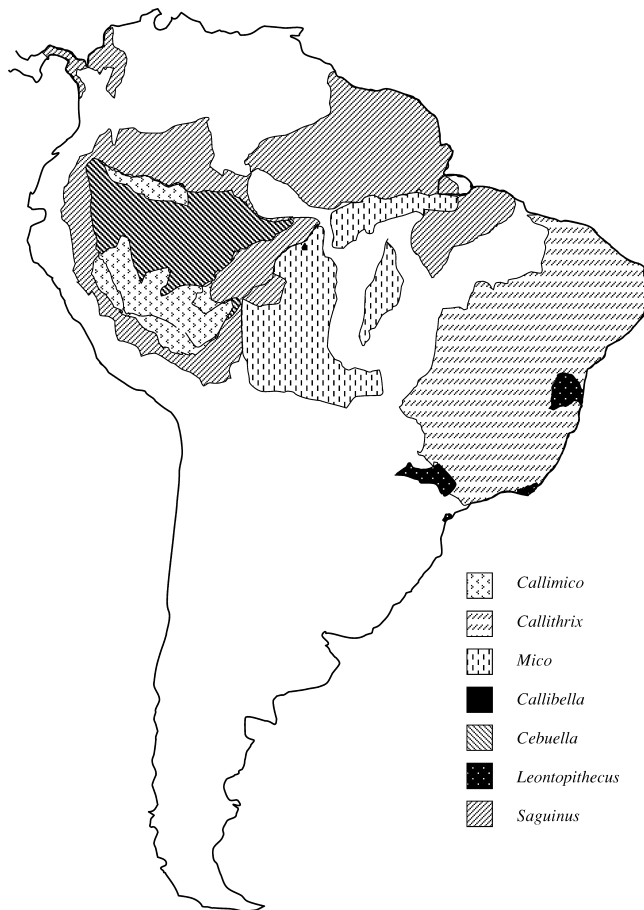


Figure 6.1 Distribution map of the Callitrichinae (based on Rylands et al. 1993, Eisenberg and Redford 1999, van Roosmalen and van Roosmalen 2003, Infonatura 2004).

*caissara* in the southern Brazilian state of Paraná (Lorini and Persson 1990). *Leontopithecus* species are now found in four distinct areas, corresponding to the geographic ranges of the four known species (Fig. 6.1).

Two genera, *Callimico* and *Cebuella*, have roughly equivalent geographic ranges in western Amazonia. Recent studies (van Roosmalen and van Roosmalen 1997, Ferrari et al. 1999) have confirmed that both genera range as far east as the left bank of the Madeira, where they are potentially parapatric with *Mico*.

*Saguinus* is sympatric with *Callimico* and *Cebuella* throughout their distributions but also ranges much farther north and east. There is now confirmation of sympatric zones between *Saguinus* and *Mico* on the upper Madeira River (Schneider et al. 1987) as well as the lower Toncantins–Xingu interfluvium (Ferrari and Lopes Ferrari 1990).

Marmosets of the genus *Mico* are found in the southern Amazon Basin between the Madeira and the Tocantins Rivers and as far south as northeastern Paraguay (Hershkovitz 1977). The newly described *Callibella* also inhabits the area west of the Rio Aripuanã and overlaps with at least one *Mico* species. *Callithrix* ranges farther south and east than *Mico*. This includes sympatry with *Leontopithecus chrysomelas*

and *L. rosalia* in some regions (Rylands 1989), though preferences for high or low elevation may limit range overlap.

## ECOLOGY

### Habitat

As might be expected from their wide geographic distribution, callitrichines inhabit a wide variety of neotropical habitats, with correspondingly variable patterns of occupation. There are some general ecological differences among the genera, with *Callithrix* and *Mico* tending to form larger groups, to occupy smaller home ranges, and consequently, to have higher population densities than *Saguinus* and *Callimico*. However, home range size and population density vary by up to two orders of magnitude not only within the Callitrichinae but also within some genera (Table 6.1). Consequently, it is difficult to identify genus-specific or even species-specific patterns, especially where data are based on observations of a single group or population.

The key factor determining differences between marmosets and tamarins appears to be the marmosets' morphological specializations for the dietary exploitation of plant exudates (e.g., gums and saps) (Ferrari 1993). The ability to exploit exudates systematically as a substitute for fruit throughout the year allows marmosets to inhabit resource-poor or highly seasonal habitats in which tamarins may be unable to survive. Such habitats include not only the wooded ecosystems of the Cerrado, Caatinga, and Chaco biomes and Amazonian savannas but also forests that have suffered intense anthropogenic disturbance. Distributed throughout tropical Brazil south of the Amazon, marmosets—in particular *Callithrix jacchus* and *C. penicillata*—can thrive in such unlikely habitats as city parks, backyards, and even coconut plantations (Rylands and de Faria 1993, L. J. D. and S. F. F., personal observation). *Callibella* takes this ability to make use of disturbed habitats to an extreme and may be dependent on human occupation of a habitat (e.g., the presence of orchards and gardens) (van Roosmalen and van Roosmalen 2003).

*Cebuella*, in contrast to *Callithrix* and *Mico*, appears to be a habitat specialist. It may reach extremely high ecological densities in riparian forest but is usually absent from neighboring areas of *terra firma* forest (Soini 1988). This unusual distribution pattern appears to be related to *Cebuella*'s specialization for exudativory (groups may inhabit a single gum tree for long periods) and the avoidance of competition with sympatric callitrichines. In this context, the apparent specialization of *Cebuella* can be interpreted as an accentuated preference for a marginal habitat type, which may be relatively unsuitable for other callitrichines.

### Ranging Patterns

With regard to both home range size and population density, the major division between *Callithrix* and *Mico* appears to

**Table 6.1** Habitat, Home Range, and Daily Path Length

SPECIES AND LOCATION	HABITAT <sup>1</sup>	HOME RANGE (HA)	DAILY PATH LENGTH (M/DAY)	HOME RANGE OVERLAP (%)	REFERENCES
<i>Callimico goeldii</i>					
Pando, Bolivia	SC	30–150	Approx. 2,000		Pook and Pook 1981, Porter 2001a Christen 1999
Virazon, Bolivia	RV	45–50			
<i>Callithrix jacchus</i>					
João Pessoa, Brazil	AF (2)	2–5	1,300	46–86 23–99	Maier et al. 1982, Alonso and Langguth 1989 Digby and Barreto 1996, Castro 2000 Mendes Pontes and Monteiro da Cruz 1995
Nisia Floresta, Brazil	AF (2)	0.7–5.2	912–1,243		
Dois Irmãos, Brazil	AF (2)	4.11			
<i>C. penicillata</i>					
Brasília, Brazil	G	3.5			de Faria 1986
<i>C. aurita</i>					
Cunha, Brazil	AF (2)	35.3	958.8	15	Ferrari et al. 1996
Fazenda Lagoa, Brazil	SC	16.5	986		Martins 1998
<i>C. flaveiceps</i>					
Caratinga, Brazil	AF (2)	33.86–35.5	883.8–1,222.5	80	Ferrari 1988, Ferrari et al. 1996, Corrêa et al. 2000, Guimarães 1998
<i>C. kuhlii</i>					
Lemos Maia, Brazil	WS	10	830–1,120	50	Rylands 1989
<i>Cebuella pygmaea</i>					
Peru	V	0.1–0.5	280–300	0	Soini 1982, 1988; Heymann and Soini 1999
Ecuador	TF	0.4–1.09			de la Torre et al. 2000
<i>Mico intermedius</i>					
Mato Grosso, Brazil	ED	22.1	772–2,115	22	Rylands 1986a
<i>M. argentatus</i>					
Tapajós, Brazil	WS	4–24			Albernaz and Magnusson 1999
Caxiuanã, Brazil	AM	35			Veracini 2000
<i>Saguinus fuscicollis</i>					
Manu, Peru	AM (L)	30–100 <sup>2</sup>	1,220	23 76	Terborgh 1983, Goldizen 1987a Garber 1988 Peres 2000
Rio Blanco, Peru	AM (L)	40	1,849		
Rio Uruçu, Brazil	TF	149	1,150–2,700		
<i>S. f. weddeilli</i>					
Cachoeira Samuel, Brazil	TF	44+	1,312		Lopes and Ferrari 1994
<i>S. imperator</i>					
Manu, Peru	AM (L)	30–100 <sup>2</sup>	1,420		Terborgh 1983, Goldizen 1987a
<i>S. mystax</i>					
Rio Blanco, Peru	AM (L)	40 <sup>2</sup>	1,946	23	Garber 1988
Quebrada Blanco, Peru	AM	41–45	1,500–1,720		Heymann 2000, 2001
<i>S. niger</i>					
Caxiuanã, Brazil	AM	35			Veracini 2000
<i>S. midas midas</i>					
French Guiana	AM (H)	31.1–42.5			Day and Elwood 1999
<i>S. tripartitus</i>					
Tiputini, Ecuador	AM	16–21	500–2,300		Kostrub 2003
<i>Leontopithecus rosalia</i>					
Poço das Antas, Brazil	AF (2)	21.3–73	955–2,405	61	Dietz et al. 1997, Peres 2000 Kierulff et al. 2002
Fazenda União, Brazil	AF	65–229	1,873–1,745		
<i>L. caissara</i>					
Superagüi, Brazil	AF	125.5–300	1,082–3,398		Prado 1999a,b as cited in Kierulff et al. 2002
<i>L. chrysomelas</i>					
Lemos Maia, Brazil	WS	36	1,410–2,175	7	Rylands 1989
Una, Brazil	AF	66–130.4	1,684–2,044	Approx 10–14	Dietz et al. 1994b, Keirulff et al. 2002, Raboy and Dietz 2004
<i>L. chrysopygus</i>					
Morro do Diabo, Brazil	AF (1)	113–199	1,362–2,088		Valledares-Padua 1993, Valledares-Padua and Cullen 1994 as cited in Kierulff et al. 2002
Caetetus, Brazil	SC	276.5–394	1,164–3,103		Passos 1997 as cited in Kierulff 2002, Passos 1998

<sup>1</sup> AF, Atlantic Forest; AF (2), secondary Atlantic Forest; AF (1), interior Atlantic Forest; SC, sandy clay forest; RV, riverine forest; G, gallery/Cerrado forest; TF, terra firma forest; V, Varzea; ED, evergreen dryland forest; AM, Amazonian forest; AM (L), Amazonian lowland forest; AM (H), Amazonian highland forest; WS, white-sand forest.

<sup>2</sup> Home range of mixed groups (two species) of tamarins.

lie not between the two genera but between patterns characteristic of *C. jacchus* and *C. penicillata* and the remaining species. Typically, *C. jacchus* and *C. penicillata* occupy home ranges of less than 10 ha, with correspondingly high population densities. Other marmosets (Table 6.1) tend to occupy much larger home ranges (up to 35 ha) with correspondingly lower population densities. However, the data available for *Mico argentatus* indicate that this species may be more similar to *C. jacchus* and *C. penicillata*, at least under equivalent ecological conditions (i.e., forest patches in savanna ecosystems and anthropogenic fragments) (Albernaz and Magnusson 1999, Corrêa et al. 2002, Gonçalves et al. 2003). With additional data on the ecology of these species, we may find that observed differences are more closely related to habitat characteristics than to taxon-specific variables.

These findings implicate habitat quality as a primary determinant of home range size and, consequently, population density. For marmosets, the key factors are likely to be the availability of exudate sources and arthropod abundance. Because many gum-producing plants (e.g., Leguminosae, Vochysiaceae) are abundant in the habitats favored by marmosets, arthropod abundance is probably the limiting factor. This may account for the relatively large home ranges recorded for *C. aurita* and *C. flaviceps*, which occur in comparatively seasonal ecosystems in which arthropods may be relatively scarce.

Home range sizes of *Saguinus* and *Leontopithecus* are highly variable, with some species and populations showing small home ranges similar to those of the marmosets and others extending to over 100 ha (Table 6.1). The larger home ranges and correspondingly lower population densities are consistent with the tamarins' relatively high degree of frugivory (Tables 6.1 and 6.2). *Callimico* shows a similar pattern of large home range and relatively small group size (Tables 6.1 and 6.3), in spite of its ability to utilize fungus during periods of fruit scarcity (Porter 2001b).

Population densities of both *Callithrix* and *Leontopithecus* decrease farther south, where climate and, presumably, resource abundance are far more seasonal. Once again, differences are disproportionate relative to differences in body size, with home ranges reported for *L. caissara* and *L. chrysopygus* being the largest for any callitrichine (Passos 1998, Prado 1999b as cited in Kierulff et al. 2002). It is interesting to note, however, that *L. rosalia* may be relatively abundant in anthropogenic forest patches, with home range sizes similar to those recorded for *C. aurita* and *C. flaviceps* (Table 6.1).

### Territoriality

Callitrichines typically respond to intergroup exchanges with vocalizations, chases, and occasionally physical aggression (Hubrecht 1985; Garber 1988, 1993a; Peres 1989, Lazaro-Perea 2001; but see also van Roosmalen and van Roosmalen 2003). While such intergroup aggression can be interpreted as territoriality (e.g., Peres 1989, Lazaro-Perea

2001), the high degree of overlap between home ranges in some species (e.g., up to 80%–90% in *C. jacchus*; Mendes Pontes and Monteiro da Cruz 1995, Digby and Barreto 1996) (Table 6.1) may indicate that these behaviors are being used primarily for mate defense or defense of a specific set of currently fruiting trees or exudate sources (e.g., Garber 1988, 1993a; Peres 2000). Intergroup interactions may also serve a second function in allowing individuals to monitor the composition and status of neighboring groups and to assess possible mating opportunities (Digby 1992, Ferrari and Diego 1992, Goldizen et al. 1996, Schaffner and French 1997, Lazaro-Perea 2001, Kostrub 2003; see below).

### Mixed-Species Troops

The presence of *mixed-species troops* (two or more species associating in a nonrandom fashion, often coordinating activities; e.g., Pook and Pook 1982) plays an important role in the ecology of several callitrichine species. To date, all mixed-species troops include *Saguinus fuscicollis* interacting with either *S. mystax*, *S. imperator*, *S. labiatus*, or *Mico emiliae* (reviewed in Heymann and Buchanan-Smith 2000). At some sites, two of the *Saguinus* species also associate with *Callimico* (e.g., Porter 2001b). Though expected to generate costs due to niche overlap, mixed-species troops appear to limit competition via differential use of forest strata and foraging techniques (Terborgh 1983, Heymann and Buchanan-Smith 2000). Potential benefits include increased protection from predators, increased foraging efficiency (including increased insect capture rates), and resource defense (reviewed in Heymann and Buchanan-Smith 2000).

### Foraging Behavior

#### Exudates

In the wild, callitrichines are known to exploit a wide variety of food types, avoiding only non-reproductive plant parts such as leaves and bark (Garber 1993a,b, Rylands and de Faria 1993, Digby and Barreto 1998, Heymann and Buchanan-Smith 2000, Smith 2000, Porter 2001b, Kierulff et al. 2002) (Table 6.2). The principal feature of callitrichine diets is their variety, and the only clear taxon-specific pattern is the marmosets' use of plant exudates (primarily gums, with some sap) as a dietary staple. All callitrichines eat some exudates, but *Callithrix*, *Mico*, and *Cebuella* are morphologically specialized for the systematic harvesting and digestion of gum and are thus able to sustain high levels of exudativory throughout the year (Ferrari 1993).

The marmosets' specializations for exudativory include elongated, chisel-like lower incisors and a wide jaw gape that permit them to gouge through the bark of gum-producing plants, thus provoking exudate flow (Hershkovitz 1977; Vinyard et al. 2001, 2003). Gums contain complex polysaccharides, a potentially high-energy source but one which cannot be broken down enzymatically by other mammals (reviewed in Power and Oftedal 1996, Heymann and Smith

**Table 6.2 Diet**

SPECIES AND LOCATION	% TIME FORAGING AND FEEDING	% TIME FEEDING ON				REFERENCES
		REPRODUCTIVE PLANT PARTS <sup>1</sup>	EXUDATES	ANIMAL PREY	OTHER	
<i>Callimico goeldii</i> Pando, Bolivia	15	29	1	33	29 (fungus), 27 (unknown)	Porter 2001b, 2004
<i>Callithrix jacchus</i> Joao Pessoa, Brazil	27	18.1	76.4	5.4	12.9 (fungus)	Alonso and Langguth 1989
Nisia Floresta, Brazil	43	23	68	9		Digby (unpublished data)
<i>C. aurita</i> Cunha, Brazil	17	40.5	30	29.5	2 (fungus)	Corrêa et al. 2000
Fazenda Lagoa, Brazil	6	11	50.5	38.5		Martins and Setz 2000
<i>C. flaviceps</i> Caratinga, Brazil (1)		14.4	65.7	19.9		Ferrari et al. 1996
Caratinga, Brazil (2)	11.8	2.0	83.2	14.7		Corrêa et al. 2000
<i>C. kuhlii</i> Lemos Maia, Brazil	23	58.2	28.3	13.5		Rylands 1989, Corrêa et al. 2000
<i>C. geoffroyii</i> Espírito Santo, Brazil	21	15	68.6	15.4		Passamani 1998, Passamani and Rylands 2000
<i>Cebuella pygmaea</i> Rio Nanay, Peru	48 <sup>2</sup>	Minor	67	33		Ramirez et al. 1977
<i>Mico intermedius</i> Mato Grosso, Brazil		74.9	15.5	9.6		Rylands 1982 as cited in Corrêa et al. 2000
<i>M. argentatus</i> Caxiuana, Brazil		36	59	5		Veracini 1997 as cited in Corrêa et al. 2000
<i>Saguinus fuscicollis</i> Quebrada Bl., Peru		64.2	30.3	5.8		Knogge and Heymann 2003
Rio Blanco, Peru	12.9	39.2	7.6	53.1		Garber 1988
Pando, Bolivia		63	12	26	6 (unknown)	Porter 2001b
<i>S. f. weddeilli</i> Cachoeira Samuel, Brazil	9.8	69.6	15.8	7.3		Lopes and Ferrari 1994
<i>S. labiatus</i> Pando, Bolivia		73	8	11	8 (unknown)	Porter 2001b
<i>S. mystax</i> Quebrada Blanco Peru		77.6	19.8	2.7		Knogge and Heymann 2003
Rio Blanco, Peru	13.1	50.6	1.5	47.8		Garber 1988
<i>S. niger</i> Fazenda Vitória, Brazil		87.5	3.1	9.4		Oliveira and Ferrari 2000
Caxiuana, Brazil	17.6	71.1	23.81	4.5		Veracini 2000
<i>S. tripartitus</i> Tiputini, Ecuador		62	12	21	5 (unknown)	Kostrub 2003
<i>Leontopithecus rosalia</i> Poço das Antas, Brazil	18.5	83.5	1.4	14.9		Dietz et al. 1997
União, Brazil	10.4	84.6	0	15.4		Kierulff 2000 as cited in Kierulff et al. 2002
<i>L. caissara</i> Superagüi, Brazil	29.4 <sup>2</sup>	75.5	1.3	10.3	12.9 (fungus)	Prado 1999b as cited in Kierulff et al. 2002
<i>L. chrysomelas</i> Lemos Maia, Brazil	27	74–89, <sup>3</sup> 11 flowers	3–11 <sup>3</sup>	13–15		Rylands 1989
<i>L. chrysopygus</i> Morro do Diabo, Brazil	6–10	78.5	7.8	13.5		Valladares-Padua 1993 as cited in Kierulff et al. 2002
Caetetus, Brazil	29.9	74.7	15.2	10.1		Passos 1999 as cited in Kierulff et al. 2002

<sup>1</sup> Includes fruit, seeds, flowers, and nectar.

<sup>2</sup> Includes foraging.

<sup>3</sup> Percent of plant records only; flowers made up 0%–20% of monthly diet (percent overall diet not reported).

**Table 6.3** Group Size, Composition, and Mating Patterns

SPECIES	GROUP SIZE	ADULT MALES	ADULT FEMALES	MATING PATTERNS <sup>1</sup>	REFERENCES
<i>Callimico goeldii</i>	4–12	1–3	1–3	M/PG/PA	Reviewed in Porter 2001a
<i>Callibella humilis</i>	6–8			M?/PG	van Roosmalen and van Roosmalen 2003
<i>Callithrix jacchus</i>	3–16	2–7	2–6	M/PG/PGA	Barreto 1996, Digby and Barreto 1996, Lazaro-Perea et al. 2000, Faulkes et al. 2003
<i>C. penicillata</i>	3–13	3	2		Reviewed in de Faria 1986
<i>C. aurita</i>	4–11	1–2	2–3	M/PG	Ferrari et al. 1996, Martins and Setz 2000
<i>C. flaviceps</i>	5–20	3–5	1–6	M/PG	Ferrari and Diego 1992, Coutinho and Corrêa 1995, Guimarães 1998
<i>C. geoffoyi</i>	2–8	2	1		Passamani 1998, Chiarello and de Melo 2001, Price et al. 2002
<i>C. kuhlii</i>	5	2	1		Rylands 1989
<i>Cebuella pygmaea</i>	2–9	1–2	1–2	M/PG? <sup>2</sup>	Soini 1982, 1988; Heymann and Soini 1999; de la Torre et al. 2000
<i>Mico intermedius</i>	9–15	2–3	2–5	M/PA	Rylands 1986b
<i>M. argentatus</i>	6–10	1–3	1–2		Albernaz and Magnusson 1999, Tavares and Ferrari 2002
<i>Saguinus fuscicollis</i>	2–10	1–4	1–2	M/PA/ PG/PGA	Goldizen 1987a,b 2003; Garber 1988; Porter 2001a; Heymann 2001
<i>S. f. weddelli</i>	4–11	1–2	1–2	M/PG	Garber and Leigh 2001, Buchanan-Smith et al. 2000, Lopes and Ferrari 1994
<i>S. mystax</i>	3–11	1–4	1–2	M/PG <sup>3</sup>	Garber 1988, Heymann 2000, Smith et al. 2001
<i>S. niger</i>	5–7	3–4	1		Oliveira and Ferrari 2000
<i>S. labiatus labiatus</i>	2–13	2	1		Buchanan-Smith et al. 2000, Garber and Leigh 2001
<i>S. oedipus</i>	2–10			M/PG <sup>3</sup>	Savage et al. 1996a
<i>S. tripartitus</i>	2–9	1–4	1–2	PA	Heymann et al. 2002, Kostrub 2003
<i>Leontopithecus rosalia</i>	2–11	0–5	0–4	M/PA/PG	Baker et al. 1993, Dietz and Baker 1993
<i>L. caissara</i>	4–7				Prado 1999a
<i>L. chrysomelas</i>	3–10	1–3	1–3	M/PG	Dietz et al. 1994b, Baker et al. 2002, Raboy and Dietz 2004
<i>L. chrysopygus</i>	2–7	≤2	≤2		Passos 1994, reviewed in Kierulff et al. 2002

<sup>1</sup> Designations are based on reports from the field (direct observation of copulations and/or birth unless otherwise noted). M, monogamy; PG, polygyny; PA, polyandry; PGA, polygynandry.

<sup>2</sup> PG based on short interbirth interval.

<sup>3</sup> PG based on presence of pregnant females.

1999). Marmosets are able to digest gums more efficiently than other callitrichines because their intestines have a comparatively enlarged and complex cecum (e.g., Ferrari and Martins 1992, Ferrari et al. 1993), allowing for relatively slow gut passage rates and microbial fermentation (Power and Oftedal 1996). Once digested, plant gums provide not only carbohydrates but also minerals (particularly calcium) and proteins (Garber 1984, Smith 2000).

*Saguinus*, *Leontopithecus*, and *Callimico* are opportunistic gummivores. Though exudates may provide as much as half of the diet during some periods (Porter 2001b), this is invariably a temporary phenomenon and exudates are never a dietary staple. *Saguinus* has been observed parasitizing gouge holes made by *Cebuella* (Soini 1988), but most exudate sources are either rare (broken branches) or seasonal (e.g., insect bore holes, *Parkia pendula* fruit pods; Garber 1993a). In addition, the digestive tracts of *Saguinus* and *Leontopithecus* are not specialized for gum consumption, decreasing their digestive efficiency (Ferrari and Martins 1992, Power and Oftedal 1996). One compensatory strategy

may be to concentrate gum feeding in the late afternoon, which allows longer retention time (overnight) and, presumably, better absorption of nutrients (Heymann and Smith 1999).

#### *Fruits, Nectar, and Fungus*

Fruit is the primary food item for many callitrichine species, especially among *Saguinus* and *Callimico*. Callitrichines typically exploit relatively small fruit patches, characteristic of the lower forest strata, and prefer disturbed and edge habitats (thus reducing competition with larger-bodied primates). Fruit can be a highly seasonal resource, especially in habitats of low diversity. Because *Saguinus* and *Leontopithecus* are unable to compensate systematically for fruit scarcity by gouging exudate sources, they are especially vulnerable to such seasonality. Small body size limits the potential for the exploitation of nonreproductive plant parts, as indicated by the lack of reports of folivory (Table 6.2). As a last resort under extreme seasonal fruit scarcity, *Saguinus* may turn to resources such as nectar

(Terborgh and Goldizen 1985). Although relatively nutritious, nectar is normally available in quantities too small to be harvested adequately by vertebrates as large as *Saguinus*.

Another potential alternative resource is fungus, which may contribute significantly to the diet of some species (*Callimico*, Porter 2001b; *C. aurita*, Corrêa et al. 2000) during certain parts of the year. It is interesting to note that, while fungi (including types of jelly and bamboo fungus) are a dietary staple of *Callimico* in some months, they are not exploited by sympatric tamarins (*S. fuscicollis* and *S. labiatus*), reinforcing the role of divergent diets in reducing competition in these species (Porter 2001b).

Availability of fruit tends to correlate with arthropod abundance, with both resources relatively scarce during the dry season. While seasonal fluctuations in resource abundance are faced by all primates, their effects may be relatively severe for callitrichines because of their small body size and high metabolic rate. Goldizen et al. (1988), for example, found that resource scarcity in the dry season resulted in potentially deleterious weight loss in *S. fuscicollis*. Thus, specialization for gum feeding among the marmoset genera may be the decisive factor permitting them to reproduce at 5- to 6-month intervals (Ferrari 1993, Ah-King and Tullberg 2000), in contrast with other callitrichines, which normally produce only one litter per year (but see Smith 2000).

### Prey

Animal material, predominantly arthropods, is the third major component of callitrichine diets. Typical arthropod prey species are large-bodied and mobile and generally depend on camouflage as a predator-avoidance strategy. The characteristic callitrichine foraging behavior is the stealthy "scan and pounce" technique (Soini 1988, Ferrari 1993, Rylands and de Faria 1993, Porter 2001b). In addition, callitrichines will often pursue disturbed prey that has fallen to the forest floor (Rylands and de Faria 1993).

Extractive foraging is an important strategy for both *S. fuscicollis* and *Leontopithecus* species. In both cases, the animals spend a relatively large proportion of foraging time investigating concealed hiding places manually, rather than visually. For *S. fuscicollis*, the manipulative investigation of substrates, such as bark crevices, on vertical supports in the lower strata of the forest appears to be a key factor in niche separation with sympatric tamarin species (Terborgh 1983, Heymann and Buchanan-Smith 2000). Extractive foraging is also thought to contribute to more complex cognitive abilities (e.g., Gibson 1986, Day et al. 2003).

In addition to arthropods, vertebrates (e.g., nestlings, small lizards, and frogs) are included in callitrichine diets (Ferrari 1988, Digby and Barreto 1998, Smith 2000, Porter 2001b, Kierulff et al. 2002) (Table 6.2). All large prey, but especially vertebrates, are highly valued food items; and their capture almost invariably provokes solicitation from younger group members, resulting in a variety of social interactions ranging from passive food transfer to agonistic behavior (Digby and Barreto 1998).

## REPRODUCTION

### Reproductive Potential

Callitrichines are characterized by a collection of traits that results in a high reproductive potential for some females while at the same time restricting breeding opportunities for others. All species studied, with the exception of *Callimico goeldii* and possibly *Callibella humilis*, typically ovulate multiple ova and produce litters of two or more infants. In captivity, 50%–80% of litters comprise dizygotic twins, with the remainder comprising singletons, triplets, or, less frequently, quadruplets (Ziegler et al. 1990a, Baker and Woods 1992, Tardif et al. 2003, De Vleeschouwer et al. 2003). Only rarely, however, do more than two infants survive from a single litter. Ovulation number correlates with maternal body mass and thus may vary in response to maternal nutritional status (e.g., *C. jacchus*, Tardif et al. 2003).

Callitrichines typically ovulate and may conceive within 2–4 weeks after giving birth (Heistermann and Hodges 1995, French et al. 2002, Tardif et al. 2003). Unlike other primates, ovulation in these species is not inhibited by lactation, although postpartum ovulation may be delayed slightly in females nursing more than one infant (Ziegler et al. 1990b, Baker and Woods 1992) (Table 6.4). Combined with gestation lengths ranging from 125 days in *Leontopithecus* spp. to 184 days in *Saguinus oedipus* (Ziegler et al. 1987a, French et al. 2002) (Table 6.4), this pattern allows breeding females to produce litters at approximately 5- to 6-month intervals. Most species frequently produce two litters per year in captivity, and most genera (*Callithrix*, *Mico*, *Cebuella*, and *Callimico*) also do so in the wild (Stevenson and Rylands 1988, Soini 1993, Digby and Ferrari 1994, Porter 2001a). *Leontopithecus* and *Saguinus*, in contrast, typically breed only once per year in the wild, with most births clustered during the first half of the rainy season, corresponding with the period of maximal fruit availability (Snowdon and Soini 1988, Ferrari and Lopes Ferrari 1989) (Table 6.4).

The reproductive potential of callitrichines is further enhanced by rapid maturation in both males and females. Females are typically capable of ovulation and conception by 12–17 months of age (Table 6.4), while males produce sperm by 13–18 months and can sire infants by 15–25 months (Abbott and Hearn 1978, Epple and Katz 1980, Ginther et al. 2002). However, the onset of sexual maturity, especially in females, is often obscured by social suppression of reproductive function (see below). Ovarian cycles last from approximately 19 days in *L. rosalia* to 28 days in *C. jacchus* (Harlow et al. 1983, French and Sibley 1985) (Table 6.4). Like other platyrrhines, callitrichines do not menstruate and exhibit no conspicuous external signs of ovulation. Sexual behavior can occur throughout the ovarian cycle and pregnancy but is most common during the periovulatory period (Kendrick and Dixson 1983, Converse et al. 1995, Digby 1999, De Vleeschouwer et al. 2000a).



**Table 6.4 Reproductive Parameters (Based on Captive Animals, Unless Otherwise Noted; Average  $\pm$  Standard Error)**

SPECIES	GESTATION LENGTH (DAYS)	INTERBIRTH INTERVAL (DAYS)	AGE AT FEMALE MATURITY (MONTHS) <sup>1</sup>	CYCLE LENGTH (DAYS)	PEAK BIRTH PERIOD	POSTPARTUM OVULATION <sup>2</sup>	REFERENCES
<i>Callimico goeldii</i>	151–152		Approx. 13	23.9 $\pm$ 0.4	Sept–Nov (Bolivia)	22–23	Dettling 2002, Dettling and Pryce 1999, Pook and Pook 1981
<i>Callithrix jacchus</i>	143–144	162	Approx. 13	28.6 $\pm$ 1.0	Weakly bi-modal, most Oct–Feb	10–20	Abbott and Hearn 1978, Digby and Barreto 1993, Harlow et al. 1983, Lazaro-Perea et al. 2000, Tardif et al. 2003, Torii et al. 1987
<i>C. kuhlii</i>	143.1 $\pm$ 1.6	156.3 $\pm$ 2.9	Approx. 12–15	24.9 $\pm$ 0.6		13.6 $\pm$ 1.2	French et al. 1996, Smith et al. 1997
<i>Cebuella pygmaea</i>	141.9	212.7 $\pm$ 122.3	15–17	28.6 $\pm$ 4.1	May–Jun, Oct–Jan (NE Peru)	15.6 $\pm$ 4.1	Ziegler et al. 1990a, Carlson et al. 1997, Spurlock 2002
<i>Saguinus fuscicollis</i>	149.8 $\pm$ 2.4	185	13	25.7 $\pm$ 1.0	Nov–Feb (SE Peru)	17 $\pm$ 3.4	Epple and Katz 1980, Tardif et al. 1984, Goldizen et al. 1988, Heistermann and Hodges 1995, Kuederling and Heistermann 1997
<i>S. oedipus</i>	183.7 $\pm$ 1.1	240–267 <sup>3</sup> 332.9 $\pm$ 53.6 (field)	15–17	23.6 $\pm$ 1.2	Mar–Jun (Colombia)	16.5 $\pm$ 1.6 to 30.8 $\pm$ 5.2 <sup>3</sup>	French et al. 1983; Ziegler et al. 1987a,b, 1990b; Baker and Woods 1992; Savage et al. 1997
<i>Leontopithecus rosalia</i>	125.0	182–215 <sup>3</sup> 311 $\pm$ 11.2 (field)	12–17	18.5 $\pm$ 0.3	Sept–Nov (SE Brazil)	Non-conceptive	French and Stribley 1985; French et al. 1989, 2002; Baker and Woods 1992; Dietz et al. 1994a; Monfort et al. 1996
<i>L. chrysomelas</i>	125.3 $\pm$ 3.0	160.6–257.8 <sup>3</sup>	17	21.5 $\pm$ 2.5	Oct–Apr (E Brazil)	17.3 $\pm$ 3.5, non-conceptive	De Vleeschouwer et al. 2000a,b, 2003; Bach et al. 2001; French et al. 2002
<i>L. chrysopygus</i>		242		23.0 $\pm$ 2.0		Non-conceptive	Wormell and Price 2001, French et al. 2002

<sup>1</sup> Age at which females first undergo ovulatory cycles or reproductive hormone elevations, especially when housed in the absence of a dominant female.

<sup>2</sup> Days from parturition.

<sup>3</sup> Depending on lactation, litter size, and/or origin of dam (see text).

Reproduction can continue into old age; however, ovulatory cycles may become irregular or cease, and reproductive output may decline in the oldest females (Tardif and Ziegler 1992, Tardif et al. 2002). Thus, while callitrichines have the highest annual reproductive potential of any anthropoid primate, actual lifetime reproductive output is limited by their relatively short reproductive tenure, relatively high infant mortality rates, and suppression of reproduction in socially subordinate individuals (Tardif et al. 2003).

### Mechanisms of Reproductive Suppression

One of the most striking features of callitrichine reproduction is the monopolization of breeding by a single, behaviorally dominant female in most social groups. Although similar breeding patterns are found throughout the callitrichine subfamily (French 1997), the underlying mechanisms, particularly the relative contributions of physiological suppression and behavioral inhibition, appear to differ across genera. In captive *Leontopithecus* and *Callimico*, for example, eldest daughters living with their natal families typically undergo ovulatory cycles indistinguishable from those of breeding females (Dettling and Pryce 1999, French et al.

2002), suggesting that inhibition of sexual behavior is the primary cause of reproductive failure. Among captive *Saguinus*, in contrast, adult daughters routinely fail to ovulate while living with their natal families (Epple and Katz 1984, Ziegler et al. 1987b, Kuederling et al. 1995). Captive *Callithrix* females appear to be intermediate, with up to 50% or more of eldest daughters ovulating while living with their natal families (Saltzman et al. 1997, Smith et al. 1997). Endocrine studies of free-living callitrichines, however, have not consistently supported findings from captivity. For example, data on wild *L. rosalia* indicate that periods of ovarian insufficiency occur in adult daughters living with their natal families (French et al. 2003), whereas both ovulatory cyclicity and pregnancy have been detected in wild *S. oedipus* daughters (Savage et al. 1997).

The physiological, sensory, and behavioral determinants of ovulation suppression have been investigated in several species. Circulating or excreted concentrations of cortisol, a stress-responsive hormone from the adrenal cortex, are similar in dominant and subordinate females or, in some cases, lower in subordinates (Saltzman et al. 1994, 1998; Ziegler et al. 1995; Smith and French 1997), suggesting that ovulation suppression cannot be attributed to generalized

stress (Abbott et al. 1997). Instead, anovulation appears to result from a specialized neuroendocrine mechanism activated by specific social cues (Abbott et al. 1997). In *C. jacchus*, anovulation in subordinate females is mediated by suppression of luteinizing hormone (LH) secretion from the anterior pituitary, which is associated with enhanced negative feedback and diminished positive feedback effects of estrogen. Hypothalamic secretion of gonadotropin-releasing hormone (GnRH) does not appear to be altered by social subordination, suggesting that pituitary responsiveness to GnRH may be dampened (Abbott et al. 1997). Olfactory cues from dominant females have been implicated in the initiation and maintenance of ovulation suppression in several species but may play a redundant role with other cues (Epple and Katz 1984; Savage et al. 1988; Barrett et al. 1990; Abbott et al. 1993, 1998).

Reproductive failure in subordinate females can occur in response to either intrasexual (i.e., rank-related suppression) or intersexual (i.e., inbreeding avoidance) influences. The specific roles of these two factors differ among species. Captive *S. oedipus* females require cohabitation with an unrelated male in order to commence ovulatory cyclicity, even after removal from the natal family (Widowski et al. 1990, 1992). Among captive *C. jacchus* females, in contrast, ovulation suppression is determined by intrasexual dominance relationships: daughters living with their families frequently ovulate even in the absence of unrelated males but only if they are not behaviorally subordinate to another female (Saltzman et al. 2004; Alencar et al. unpublished observations). Nonetheless, *C. jacchus* daughters do not normally engage in sexual behavior unless they have access to an unrelated male (Saltzman 2003, Saltzman et al. 2004).

Male callitrichines, like females, engage in little or no intersexual copulatory behavior while living with their natal families. This appears to reflect inbreeding avoidance rather than intrasexual, rank-related suppression and is not generally associated with suppression of testosterone or LH concentrations (French et al. 1989, Baker et al. 1999, Ginther et al. 2001).

## SOCIAL ORGANIZATION

### Group Composition

Group composition in callitrichines varies from two to 20 individuals, with *Mico* and *Callithrix* species tending to have larger groups than *Saguinus*, *Callimico*, or *Leontopithecus* (Table 6.3). *Cebuella* tends to have the smallest groups, with most containing a single breeding pair and young (Soini 1982, 1988; de la Torre et al. 2000) (Table 6.3). Solitary animals have been noted in several populations, and male–female pairs appear to be rare and not always successful at raising young (Terborgh and Goldizen 1985, Goldizen 2003; see also Porter 2001a for *Callimico*). Differences in group size across species are likely tied to increased recruitment rates through biannual

births in marmosets and to the diet and habitat preferences of the different genera (Koenig 1995, Heymann 2000, Goldizen 2003; see Ecology above). Intriguing preliminary data on *Callibella* note that, while group size falls within the typical callitrichine range (six to eight individuals), aggregations of up to 30 individuals sometimes form (van Roosmalen and van Roosmalen 2003).

Although some early reports indicated that group membership could be dynamic, with individuals frequently moving in and out of groups (e.g., Dawson 1978, Neyman 1978, Scanlon et al. 1988), more recent studies based on direct follows of animals indicate more stable, extended family groups (Ferrari and Digby 1996, Goldizen et al. 1996, Nievergelt et al. 2000, Baker et al. 2002; but see also Garber et al. 1993). Typical of family groups, both sexes may emigrate as individuals mature and as groups grow in size (e.g., Goldizen et al. 1996, Porter et al. 2001, Baker et al. 2002). In *L. rosalia*, some 60% of individuals born into a group will have dispersed by 3 years of age and 90% by 4 years of age (Baker et al. 2002). Of those individuals that remain with their natal group, most become breeders by the time they are 4 years old (Baker et al. 2002). Similar patterns have been described for *S. fuscicollis* (Goldizen et al. 1996). Although both sexes may disperse, males have a higher probability than females of entering an established group (Ferrari and Diego 1992; Baker et al. 1993, 2002; Goldizen et al. 1996). Females may “float” as solitary individuals waiting for a breeding vacancy in an already established group, or they may form a new group with other recent emigrants (Lazaro-Perea et al. 2000, Baker et al. 2002). Breeding takeovers by individuals within their natal group are more likely to occur when unrelated mates are available (Ferrari and Diego 1992, Goldizen et al. 1996, Saltzman et al. 2004). The general pattern of extended family groups with occasional immigration (typically, but not always, into a breeding position) has been supported by studies of genetic relatedness within *C. jacchus* groups (Nievergelt et al. 2000), but periods of instability can result in groups of mixed parentage (Faulkes et al. 2003).

### Social Relationships

Groups are typically cohesive, and individuals often rest in physical contact with one another and allogroom (Ferrari 1988, Alonso and Langguth 1989, Digby 1995b, Heymann 1996). Allogrooming has been described as asymmetrical in at least some wild groups, with females typically receiving more grooming than they perform and breeding individuals of both sexes being favored grooming partners (Goldizen 1989, Digby 1995b, Heymann 1996, Kostrub 2003, Lazaro-Perea et al. 2004). Breeding females may be performing a “service” that entices nonbreeding females to remain in the group (Lazaro-Perea et al. 2004). There is no evidence that breeding females preferentially groom one potential sexual partner over another (Heymann 1996, Kostrub 2003).

Aggressive behavior in callitrichines is relatively rare (e.g., fewer than 0.1 acts/hr in *S. mystax*; Heymann 1996, Garber

1997) and mild, typically consisting of cuffs, “arch walks,” piloerection, chases, avoidance, and submissive vocalizations; it occurs most often in feeding contexts (Goldizen 1989, Baker et al. 1993, Digby 1995b, Garber 1997, Kostrub 2003). Rates of aggression can increase following changes in group composition, for example, the loss of a breeding female (Lazaro-Perea et al. 2000). Experimental exposure to unfamiliar “intruders” or changes in membership of captive groups can also elicit physical attacks (reviewed in Anzenberger 1993, Caine 1993). The pattern of aggression suggests that it is used to limit access to mates and to control group membership (Anzenberger 1993, Lazaro-Perea et al. 2000, Baker et al. 2002). Where intersexual dominance has been described, either there is no clear pattern of male or female dominance (e.g., Digby 1995b, Kostrub 2003) or males are able to displace females at feeding sites (Baker and Dietz 1996). Intrasexual dominance can have profound implications for reproductive success in these species (Baker et al. 1993, Digby 1995a,b; Lazaro-Perea et al. 2000) and will be discussed in detail below.

#### Mating Systems

Callitrichine mating systems have been described as monogamous, polyandrous, polygynous, and polygynandrous, with variation occurring both within and between groups and populations (reviewed in Garber 1997, Baker et al. 2002, Goldizen 2003, Saltzman 2003) (Table 6.3) (note: we use these terms to describe patterns of copulation only). Such flexible mating strategies are linked to changes in both group composition and social relationships, and specific patterns appear to be more typical of some genera than others.

The presence of more than one reproductively active male (polyandry and polygynandry) has been described for a number of species but appears to be most prevalent in *Saguinus* and *Leontopithecus* (Table 6.3). In *L. rosalia*, “potentially polyandrous” groups (based on the presence of two or more potentially reproductive males) were noted in 46% of monthly censuses, but direct observations of the timing of copulatory behavior together with information on probable fertile periods indicated that most groups were “genetically” monogamous, including six of seven potentially polyandrous groups (Baker et al. 1993). Other species exhibit little or no competition over access to breeding females (e.g., Kostrub 2003, Schaffner and French 2004). Only a handful of polyandrous groups have been noted among *Mico* (*M. humeralifer*, Rylands 1986b) and *Callithrix* (*C. jacchus*, two males copulating with two females in a newly formed group, Lazaro-Perea et al. 2000, see also Schaffner and French 2004 for captive *C. kuhlii*). The limited data available for *Cebuella* (Soini 1988) and *Callimico* suggest that groups typically contain a single breeding male. Possible reasons for differences across genera may involve differential costs of infant care: species using larger home ranges and having smaller overall group sizes may benefit more from infant care shared by two “potential” fathers (Heymann 2000, Goldizen 2003).

Female reproductive strategies also vary across marmoset and tamarin species. Although breeding is typically restricted to a single female, the presence of multiple breeding females in some groups demonstrates that reproductive suppression is not absolute. It is notable that even when suppression is relaxed, breeding appears to be restricted to no more than two females, even in groups containing additional females of breeding age. Polygyny has been documented in multiple wild groups of *Callithrix*, *Callibella*, *Saguinus*, and *Leontopithecus* and inferred (based on a short interval between births) in *Cebuella* (Table 6.3). Additional groups have been documented to contain two pregnant/lactating females, although tenure in the group was unknown (i.e., a female may have immigrated into a group while pregnant) or one of the females failed to raise young (*S. mystax*, Garber et al. 1993, *S. oedipus*, Savage et al. 1996a; *Callimico goeldii*, Porter 2001a; plus additional groups of *S. fuscicollis*, Goldizen et al. 1996, and *L. rosalia*, Baker et al. 2002). Only in *Mico* have multiple breeding females not been reported. The presence of two breeding females and their resulting young would presumably increase average costs of infant care in terms of time spent carrying and food sharing (see below). Some species or populations may be better able to accommodate these costs because of larger group sizes, more steady food supply (e.g., exudates), and smaller home ranges that allow caretakers to reduce travel while maintaining contact with their group (Digby and Barreto 1996, Goldizen 2003).

A further complication in describing the mating system of callitrichines is the occurrence of extragroup copulations in some species. In *C. jacchus*, for example, both reproductive and nonreproductive males and females have been observed participating in extragroup copulations, often during or just after aggressive intergroup interactions (Digby 1999, Lazaro-Perea et al. 2000). Thus, even some groups described as “monogamous” based on within-group copulation patterns may show more complex patterns of potential and actual paternity.

#### Infant Care

The high cost of infant care (due to twinning, high infant/maternal weight ratios, and frequent overlap of lactation and pregnancy in some species) is thought to be a key determinant of many aspects of callitrichine behavior, most notably the high level of cooperative care of young (reviewed in Tardif et al. 1993, 2002). Captive studies have provided detailed information on the proximate mechanisms and energetics of infant carrying (e.g., Tardif et al. 1993, Tardif 1997, Nievergelt and Martin 1999) and have demonstrated several species differences in patterns of infant care, including latency to onset of alloparental behavior, degree of maternal involvement, and overall time spent carrying (Tardif et al. 1993).

In both *L. rosalia* and *Callimico*, mothers are typically the sole caretakers for up to the first 3 weeks of an infant’s life (Schradin and Anzenberger 2001, Tardif et al. 2002, see also de Oliveira et al. 1999 for an exception in *L. chrysomelas*);

but *Saguinus*, *Callithrix*, *Mico*, and *Cebuella* adult males and other group members may begin carrying the infant as early as the day of birth (reviewed in Tardif et al. 2002). The mother's social status can also influence the onset of allo-maternal care, with subordinate breeding females avoiding potential helpers for the first 10 days postpartum (Digby 1995a). In some tamarin species, males may actually care for infants more than the mother (e.g., *S. oedipus*, Savage et al. 1996b; *S. fuscicollis*, Goldizen 1987a,b), whereas mothers act either as primary caretakers or as equal partners in *Callithrix*, *Mico*, and *Callimico* (*C. jacchus*, Digby 1995a, Yamamoto and Box 1997; *M. humeralifer*, Rylands 1986b; *Callimico*, Schradin and Anzenberger 2001). The extent of maternal care can also be influenced by group size and composition, litter size, and maternal weight (reviewed in Tardif et al. 1993, Bales et al. 2002). Both captive and field data confirm the general pattern that marmosets (e.g., *C. jacchus* and *M. argentata*) carry less frequently and for a shorter period of time than do tamarins (e.g., *S. fuscicollis* and *S. oedipus*), with *L. rosalia* being intermediate (Tardif et al. 1993, 2002; Savage et al. 1996b). Differences in carrying patterns are once again likely to be linked to daily path length, home range size, and ultimately differences in diet and habitat use (Tardif et al. 1993, Goldizen 2003, see above).

Several hypotheses have been proposed to explain why group members other than the parents (alloparents) participate in infant care in the callitrichines: (1) enhancing direct fitness by gaining experience in caretaking behaviors, (2) increasing inclusive fitness, (3) maintaining group membership while waiting for a breeding spot to become vacant, and (4) caretaking as a courtship strategy for breeding males (reviewed in Tardif 1997, Bales et al. 2000). While there is some evidence that caretaking experience and overall number of helpers increase infant survival, evidence for a connection between helping behavior and future reproductive opportunities (either inheritance of breeding position or as a courting strategy) is currently lacking (Tardif 1997, Bales et al. 2000).

## CONSERVATION STATUS

The Callitrichinae include not only some of the world's most critically endangered species but also species such as *C. jacchus* that thrive under disturbed conditions and are unlikely to be threatened with extinction. A characteristic shared by all endangered callitrichine species is a relatively small geographic range combined with critical levels of anthropogenic habitat alteration. As a group, *Leontopithecus* faces the most serious threat, with two species listed as critically endangered (*L. caissara* and *L. chrysopygus*) and two listed as endangered (*L. rosalia* and *L. chrysomelas*, Rylands and Chiarello 2003). Only four other species are allocated endangered status by the World Conservation Union (*S. oedipus*, *S. bicolor*, *C. flaviceps*, and *C. aurita*;

IUCN Species Survival Commission 2003), but numerous species are classified as data deficient, including several of the newly described species of *Mico*. While the more endangered species of callitrichines receive official protection and are the subjects of conservation-oriented research projects (e.g., the Golden Lion Tamarin Project), their survival still depends on careful metapopulation management (e.g., chapters in Kleiman and Rylands 2002).

## COMPETITION IN COOPERATIVELY BREEDING SPECIES

Cooperatively breeding species are characterized, in part, by their unusual propensity to share in the rearing of offspring. In this system, parents, older siblings, members of the extended family, and in some cases unrelated individuals participate in resource and territory defense, infant carrying, food sharing, babysitting, and even allonursing (chapters in Solomon and French 1997). Such behaviors, along with low rates of physical aggression, are typical of the callitrichines (Garber 1997, Schaffner and Caine 2000). The cooperative nature of some aspects of callitrichine behavior, however, belies the fact that typically only two (or sometimes three) individuals receive the majority of the benefits from such a "cooperative" system. Unlike communal breeding (Price and Evans 1991), in which there is shared parentage of the young, most callitrichines invest time and energy into rearing the offspring of other group members. Though helpers may gain indirect benefits in the form of inclusive fitness or caretaking experience (reviewed in Tardif 1997), direct benefits accrue primarily to those individuals that are able to breed. This reproductive skew is expected to give rise to intense, if sometimes subtle, reproductive competition.

Control or manipulation of breeding opportunities can occur prior to conception as well as after birth. Competition can be manifest in acquisition and maintenance of social status, physiological suppression of ovulation, interference in the feeding and care of young, and, in extreme cases, infanticide. Below, we outline some of the means by which callitrichines compete for reproductive opportunities and examine potential causes for variation in these mechanisms across genera.

### Social Status and Reproduction

Within groups, social status can play a profound role in determining the reproductive opportunities and reproductive success of both males and females. Breeding individuals (both males and females) are typically those that are socially dominant over all others within the group (Baker et al. 1993, Dietz and Baker 1993, Digby 1995a,b, Goldizen et al. 1996).

The mechanisms by which females' social status results in differential reproductive success include both inhibition of sexual behavior and suppression of ovulation (see

Mechanisms of Reproductive Suppression, above). There has been some debate on whether subordinate females' failure to reproduce results from direct manipulation by the dominant female (e.g., dominant control model; Snowdon 1996) or whether it is more appropriately interpreted as a type of self-inhibition on the part of the subordinate female in an attempt to reduce wasted reproductive effort (e.g., conceiving or giving birth to infants that are unlikely to survive—self-restraint model; Snowdon 1996; see also Wasser and Barash 1983). In either scenario, socially dominant females are able to maintain reproductive sovereignty in most cases and thus also gain the benefits of a relatively higher reproductive success. Even in groups where subordinate females are able to conceive, the dominant female will typically produce more infants and have higher infant survival rates (Digby 1995a, Goldizen et al. 1996). In *L. rosalia*, for example, dominant females had twice the reproductive success of subordinate breeding females (Dietz and Baker 1993); and in *C. jacchus*, dominant breeding females gave birth to twice as many infants and had nearly twice the overall survival rate (Digby 1995a).

For males in potentially polyandrous groups, dominance may determine the likelihood of paternity. As noted above, dominance plays little or no role in access to females during the periovulatory period in some species (*S. mystax*, Garber et al. 1993, *S. tripartitus*, Kostrub 2003, *S. fuscicollis*, Goldizen 1989, but note that some consort behavior has been reported). In contrast, Baker et al. (1993) were able to demonstrate that the more dominant of the two sexually active males in *L. rosalia* groups was responsible for 94% of sexual behavior during periods when the female was most likely to conceive. In one of these groups, direct aggression was used by a dominant male to prevent the subordinate male's access to the breeding female. Mate guarding by dominant males has also been observed in *C. jacchus* (Digby 1999) and *Cebuella* (Soini 1987).

In summary, both subordinate males and females may be subject to interference or inhibition of sexual behavior, and subordinate females may also undergo physiological suppression of reproduction. With both polyandrous and polygynous groups occurring in several genera, however, it is clear that these mechanisms are not always successful in maintaining reproductive sovereignty for the dominant male–female pair. When subordinates do breed, postpartum reproductive competition may play a role in determining which infants survive.

### Infanticide

Perhaps the most extreme form of reproductive competition in callitrichines is the killing of infants by females other than the mother. Infanticide in primates is typically associated with the killing of infants by unrelated males that have recently joined or taken over a group (e.g., langurs, *Presbytis entellus*, Hrdy 1979; gorillas, *Gorilla gorilla beringei*,

Watts 1989). However, the sexual selection hypothesis (Hrdy 1979) put forth to explain these cases of infanticide is not applicable to most callitrichine incidents because the killing of dependent young will not necessarily bring females back into estrus more quickly (due to the limited influence of lactation on ovulation in these species). Instead, competition for access to alloparents or other resources in polygynous groups could lead to enforced neglect and/or killing of infants (Digby 1995a, 2000). Infanticide by females has now been reported in several free-ranging groups and populations of *C. jacchus* (Digby 1995a, Yamamoto et al. 1996, Roda and Mendes Pontes 1998, Lazaro-Perea et al. 2000), several captive groups of *C. jacchus* (reviewed by Saltzman 2003), and at least one captive group of *L. chrysomelas* (De Vleeschouwer et al. 2001). In five of the six cases where social status was known, the dominant female was observed or strongly suspected of killing the offspring born to the socially subordinate female (in the sixth case, the perpetrator became dominant following the infanticide) (Roda and Mendes Pontes 1998). In at least three cases, the perpetrator gave birth within days or weeks after the infanticide (Digby 1995a, Roda and Mendes Pontes 1998, Lazaro-Perea et al. 2000). In some cases, subordinate females that had lost their infants (either to infanticide or to unknown causes) subsequently carried and occasionally nursed infants born to the dominant female (Digby 1995a, Roda and Mendes Pontes 1998).

The harassment of subordinate females with young, the protective rearing strategies used by subordinate mothers (e.g., the extended period before alloparental care is tolerated), and the increased chance of infant loss when the births of dominant and subordinate females are closely spaced support the hypothesis that infanticide by females is a response to resource competition (Digby 1995a, Saltzman 2003). The intensity of competition between females is likely to vary across callitrichine genera due in part to such factors as typical group size (the smaller groups of *Saguinus* and *Cebuella* would result in less severe reproductive skew within the population), population density (higher densities will likely result in fewer reproductive vacancies within the population), and diet (with less seasonally influenced foods such as gum allowing for smaller home range sizes and, thus, lower infant care costs). Specifically, the marmosets' ability to maintain large groups in high-density areas may allow for a higher proportion of polygynous groups in these species. Once reproductive suppression is relaxed, however, infanticide by females may provide an alternative strategy by which dominant females may maintain their reproductive sovereignty (Digby 2000, Hager and Johnstone 2004).

Infanticide by females other than the mother is unusual among primate species but has been well documented in several other cooperatively breeding species (e.g., wild dogs, *Lycaon pictus*, Frame et al. 1979, black-tailed prairie dogs, *Cynomys ludovicianus*, Hoogland 1985, meerkats,

*Suricata suricatta*, Clutton-Brock et al. 1998). In addition to the reproductive state of the perpetrator (either in the late stages of pregnancy or lactating), the other striking pattern among these species is that the perpetrator is likely to be closely related to the victim. Given the potential loss of inclusive fitness in these cases, we can only assume that the benefits to the infanticidal female must be greater than the costs, suggesting particularly intense reproductive competition. This hypothesis remains to be tested.

## CONCLUSION

Although social tolerance and cooperation are important aspects of callitrichine social organization, it is important to consider the reproductive skew that often results from this type of social system. Only a portion of the population directly benefits from the behavior of helpers, who may delay their own reproduction for many years or forfeit it altogether (e.g., Goldizen et al. 1996). As a result, intense competition over the limited number of reproductive positions may occur. This competition may be subtle (suppression of ovulation and inhibition of sexual behavior) or overt (infanticide), but it nonetheless has a profound impact on the reproductive success of these animals. Ultimately, our understanding of callitrichine social organization and reproductive strategies will need to balance the cooperative aspects of their social interactions with the inevitable reproductive competition inherent in all social systems.

## REFERENCES

- Abbott, D. H., Barrett, J., and George, L. M. (1993). Comparative aspects of the social suppression of reproduction in female marmosets and tamarins. In: Rylands, A. B. (ed.), *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*. Oxford University Press, Oxford. pp. 152–163.
- Abbott, D. H., and Hearn, J. P. (1978). Physical, hormonal and behavioural aspects of sexual development in the marmoset monkey, *Callithrix jacchus*. *J. Reprod. Fertil.* 53:155–166.
- Abbott, D. H., Saltzman, W., Schultz-Darken, N. J., and Smith, T. E. (1997). Specific neuroendocrine mechanisms not involving generalized stress mediate social regulation of female reproduction in cooperatively breeding marmoset monkeys. *Ann. N.Y. Acad. Sci.* 807:219–238.
- Abbott, D. H., Saltzman, W., Schultz-Darken, N. J., and Tannenbaum, P. L. (1998). Adaptations to subordinate status in female marmoset monkeys. *Comp. Biochem. Physiol.* 119:261–274.
- Aguilar, J. M., and Lacher, T. E., Jr. (2003). On the morphological distinctiveness of *Callithrix humilis* van Roosmalen et al., 1998. *Neotrop. Primates* 11:11–17.
- Ah-King, M., and Tullberg, B. S. (2000). Phylogenetic analysis of twinning in Callitrichinae. *Am. J. Primatol.* 51:135–146.
- Albernaz, A. L., and Magnusson, W. E. (1999). Home-range size of the bare-ear marmoset (*Callithrix argentata*) at Alter do Chão, Central Amazonia, Brazil. *Int. J. Primatol.* 20:665–677.
- Alonso, C., and Langguth, A. (1989). Ecologia e comportamento de *Callithrix jacchus* (Primates: Callitrichidae) numa ilha de floresta Atlântica. *Rev. Nordestina Biol.* 6:107–137.
- Anzenberger, A. (1993). Social conflict in two monogamous New World primates: pairs and rivals. In: Mason, W. A., and Mendoza, S. P. (eds.), *Primate Social Conflict*. State University of New York Press, New York. pp. 291–329.
- Bach, A., Raboy, B., and Dietz, J. (2001). Birth seasonality in wild golden-headed lion tamarins (*Leontopithecus chrysomelas*) in Una Reserve, Bahia state, Brazil. *Am. J. Primatol.* 54:69.
- Baker, A. J., Bales, K., and Dietz, J. M. (2002). Mating system and group dynamics in lion tamarins. In: Kleiman, D. G., and Rylands, A. B. (eds.), *Lion Tamarins: Biology and Conservation*. Smithsonian Institution Press, Washington DC. pp. 188–212.
- Baker, A. J., and Dietz, J. M. (1996). Immigration in wild groups of golden lion tamarins (*Leontopithecus rosalia*). *Am. J. Primatol.* 38:47–56.
- Baker, A. J., Dietz, J. M., and Kleiman, D. G. (1993). Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. *Anim. Behav.* 46:1091–1103.
- Baker, A. J., and Woods, F. (1992). Reproduction of the emperor tamarin (*Saguinus imperator*) in captivity, with comparisons to cotton-top and golden lion tamarins. *Am. J. Primatol.* 26:1–10.
- Baker, J. V., Abbott, D. H., and Saltzman, W. (1999). Social determinants of reproductive failure in male common marmosets housed with their natal family. *Anim. Behav.* 58:501–513.
- Bales, K., French, J. A., and Dietz, J. M. (2002). Explaining variation in maternal care in a cooperatively breeding mammal. *Anim. Behav.* 63:453–461.
- Bales, K. L., Dietz, J. M., Baker, A. J., Miller, K., and Tardif, S. D. (2000). Effects of allocare-givers on fitness of infants and parents in callitrichid primates. *Folia Primatol.* 71:27–38.
- Barreto, C. E. (1996). Comportamento de fêmeas reprodutivas em grupos poligínicos de *callithrix jacchus* (Primates: Callitrichidae) no ambiente natural: perfil das interações afiliativas, agonísticas e da marcação de cheiro [masters thesis]. Universidade Federal do Rio Grande do Norte.
- Barrett, J., Abbott, D. H., and George, L. M. (1990). Extension of reproductive suppression by pheromonal cues in subordinate female marmoset monkeys, *Callithrix jacchus*. *J. Reprod. Fertil.* 90:411–418.
- Barroso, C. M. L., Schneider, H., Schneider, M. P. C., Sampaio, I., Garada, M. L., Czelusniak, J., and Goodman, M. (1997). Update of the phylogenetic systematics of New World monkeys: further DNA evidence for placing the pygmy marmoset (*Cebuella*) within the genus *Callithrix*. *Int. J. Primatol.* 18:651–674.
- Bicca-Marques, J. C., and Garber P. A. (2001). Cognitive ecology and within-patch foraging decisions in tamarins. *Am. J. Primatol.* 32(suppl.):40.
- Buchanan-Smith, H. M., Hardie, S. M., Caceres, C., and Prescott, M. J. (2000). Distribution and forest utilization of *Saguinus* and other primates of the Pando department, northern Bolivia. *Int. J. Primatol.* 21:353–379.
- Cabrera, A. (1958). Catálogo de los mamíferos de America del Sur. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 26:1–307.
- Caine, N. G. (1993). Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: the role of predation pressures. In: Rylands, A. B. (ed.), *Marmosets and*

- Tamarins: Systematics, Behaviour, and Ecology*. Oxford University Press, Oxford. pp. 200–219.
- Caine, N. G., SurrIDGE, A. K., and Mundy, N. I. (2003). Dichromatic and trichromatic *Callithrix geoffroyi* differ in relative foraging ability for red–green color camouflaged and non-camouflaged food. *Int. J. Primatol.* 24:1163–1174.
- Canavez, F. C., Moreira, M. A. M., Simon, F., Parham, P., and Seuánez, H. N. (1999). Phylogenetic relationships of the Callitrichinae (Platyrrhini, Primates) based on beta2-microglobulin DNA sequences. *Am. J. Primatol.* 48:225–236.
- Carlson, A. A., Ziegler, T. E., and Snowdon, C. T. (1997). Ovarian function of pygmy marmoset daughters (*Cebuella pygmaea*) in intact and motherless families. *Am. J. Primatol.* 43:347–355.
- Castro, C. (2000). Ecology and behavior of the common marmoset, *Callithrix jacchus*. *Neotrop. Primates* 8:50–51.
- Chiarello, A. G., and de Melo, F. R. (2001). Primate population densities and sizes in Atlantic forest remnants of northern Espírito Santo, Brazil. *Int. J. Primatol.* 22:379–396.
- Christen, A. (1999). Survey of Goeldi's monkeys (*Callimico goeldii*) in northern Bolivia. *Folia Primatol.* 70:107–111.
- Clutton-Brock, T. H., Brotherton, N. M., Smith, R., McIlrath, G. M., Kansky, R., Gaynor, D., Oriain, M. J., and Skinner, J. K. (1998). Infanticide and expulsion of females in a cooperative mammal. *Proc. R. Soc. Lond. B Biol. Sci.* 265:2291–2295.
- Converse, L. J., Carlson, A. A., Ziegler, T. E., and Snowdon, C. T. (1995). Communication of ovulatory state to mates by female pygmy marmosets, *Cebuella pygmaea*. *Anim. Behav.* 49:615–621.
- Corrêa, H. K. M., Coutinho, P. E. G., and Ferrari, S. F. (2000). Between-year differences in the feeding ecology of highland marmosets (*Callithrix aurita* and *Callithrix flaviceps*) in south-eastern Brazil. *J. Zool.* 252:421–427.
- Corrêa, H. K. M., Coutinho, P. E. G., and Ferrari, S. F. (2002). Dieta de grupos de *Mico argentatus* em fragmentos naturais de Alter do Chão, Santarém, Pará. *Livro de Resumos do X Congresso Brasileiro de Primatologia*, p. 46.
- Coutinho, P. E. G., and Corrêa, H. K. M. (1995). Polygyny in a free-ranging group of buffy-tufted-ear marmosets, *Callithrix aurita*. *Folia Primatol.* 65:25–29.
- Dawson, G. A. (1978). Composition and stability of social groups of the tamarin, *Saguinus oedipus geoffroyi*, in Panama: ecological and behavioral implications. In: Kleiman, D. G. (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Institution Press, Washington DC. pp. 23–37.
- Day, R. L., Coe, R. L., Kendal, J. R., and Laland, K. N. (2003). Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Anim. Behav.* 65:559–571.
- Day, R. T., and Elwood, R. W. (1999). Sleeping site selection by the golden-handed tamarin *Saguinus midas midas*: the role of predation risk, proximity to feeding sites, and territorial defense. *Ethology* 105:1035–1051.
- de Faria, D. S. (1986). Tamanho, composição de um grupo social e área de vivência (home-range) do sagüi *Callithrix jacchus penicillata* na mata ciliar do córrego capetinga, Brasília, DF. In: Thiago de Mello, M. (ed.), *A Primatologia no Brasil*, vol. 2. pp. 87–105.
- de la Torre, S., Snowdon, C. T., and Bejarana, M. (2000). Effects of human activities on wild pygmy marmosets in Ecuadorian Amazonia. *Biol. Conserv.* 94:153–163.
- Dettling, A., and Pryce, C. R. (1999). Hormonal monitoring of age at sexual maturation in female Goeldi's monkeys (*Callimico goeldii*) in their family groups. *Am. J. Primatol.* 48:77–83.
- Dettling, A. C. (2002). Reproduction and development in Goeldi's monkey (*Callimico goeldii*). *Evol. Anthropol.* 1(suppl.):207–210.
- de Oliveira, M. S., Lopes, F. A., Alonso, C., and Yamamoto, M. E. (1999). The mother's participation in infant carrying in captive groups of *Leontopithecus chrysomelas* and *Callithrix jacchus*. *Folia Primatol.* 70:146–153.
- De Vleeschouwer, K., Heistermann, M., Van Elsacker, L., and Verheyen, R. F. (2000a). Signaling of reproductive status in captive female golden-headed lion tamarins (*Leontopithecus chrysomelas*). *Int. J. Primatol.* 21:445–465.
- De Vleeschouwer, K., Leus, K. K., and Van Elsacker, L. (2003). Characteristics of reproductive biology and proximate factors regulating seasonal breeding in captive golden-headed lion tamarins (*Leontopithecus chrysomelas*). *Am. J. Primatol.* 60:123–137.
- De Vleeschouwer, K., Van Elsacker, L., Heistermann, M., and Leus, K. (2000b). An evaluation of the suitability of contraceptive methods in golden-headed lion tamarins (*Leontopithecus chrysomelas*), with emphasis on melengestrol acetate (MGA) implants: (II) endocrinological and behavioural effects. *Anim. Welf.* 9:385–401.
- De Vleeschouwer, K., Van Elsacker, L., and Leus, K. (2001). Multiple breeding females in captive groups of golden-headed lion tamarins (*Leontopithecus chrysomelas*): causes and consequences. *Folia Primatol.* 72:1–10.
- Dietz, J. M., and Baker, A. J. (1993). Polygyny and female reproductive success in golden lion tamarins, *Leontopithecus rosalia*. *Anim. Behav.* 46:1067–1078.
- Dietz, J. M., Baker, A. J., and Miglioretti, D. (1994a). Seasonal variation in reproduction, juvenile growth, and adult body mass in golden lion tamarins (*Leontopithecus rosalia*). *Am. J. Primatol.* 34:115–132.
- Dietz, J. M., de Sousa, N. F., and da Silva, J. R. (1994b). Population structure and territory size in golden-headed lion tamarins, *Leontopithecus chrysomelas*. *Neotrop. Primates* 2(suppl.):21–23.
- Dietz, J. M., Pere, C. A., and Pinder, L. (1997). Foraging ecology and use of space in wild golden lion tamarins (*Leontopithecus rosalia*). *Am. J. Primatol.* 41:289–305.
- Digby, L. (1992). Intruders in the wild: intergroup encounters in a natural population of *Callithrix jacchus*. Abstracts of the XIVth Congress of the International Primatological Society Strasbourg, France, p. 293.
- Digby, L. J. (1995a). Infant care, infanticide, and female reproductive strategies in polygynous groups of common marmosets (*Callithrix jacchus*). *Behav. Ecol. Sociobiol.* 37:51–61.
- Digby, L. J. (1995b). Social organization in a wild population of *Callithrix jacchus*. Part II: Intragroup social behavior. *Primates* 36:361–375.
- Digby, L. J. (1999). Sexual behavior and extra-group copulations in a wild population of common marmosets (*Callithrix jacchus*). *Folia Primatol.* 70:136–145.
- Digby, L. J. (2000). Infanticide by female mammals: implications for the evolution of social systems. In: van Schaik, C. P., and Janson, C. H. (eds.), *Infanticide by Males and Its Implications*. Cambridge University Press, Cambridge. pp. 423–446.

- Digby, L. J., and Barreto, C. E. (1993). Social organization in a wild population of *Callithrix jacchus*. Part I: Group composition and dynamics. *Folia Primatol.* 61:123–134.
- Digby, L. J., and Barreto, C. E. (1996). Activity and ranging patterns in common marmosets (*Callithrix jacchus*): implications for reproductive strategies. In: Norconk, M., Rosenberger, A., and Garber, P. A. (eds.), *Adaptive Radiations of Neotropical Primates*. Plenum Press, New York, pp. 173–185.
- Digby, L. J., and Barreto, C. E. (1998). Vertebrate predation in common marmosets. *Neotrop. Primates* 6:124–126.
- Digby, L. J., and Ferrari, S. F. (1994). Multiple breeding females in free-ranging groups of *Callithrix jacchus*. *Int. J. Primatol.* 15:389–397.
- Eisenberg, J. F., and Redford, K. H. (1999). *Mammals of the Neotropics: The Central Neotropics. Ecuador, Peru, Bolivia, Brazil*, vol. 3. University of Chicago Press, Chicago.
- Epple, G., and Katz, Y. (1980). Social influences on first reproductive success and related behaviors in the saddle-back tamarin (*Saguinus fuscicollis*, Callitrichidae). *Int. J. Primatol.* 1:171–183.
- Epple, G., and Katz, Y. (1984). Social influences on estrogen excretion and ovarian cyclicity in saddle back tamarins (*Saguinus fuscicollis*). *Am. J. Primatol.* 6:215–227.
- Faulkes, C. G., Arruda, M. F., and Da Cruz, A. O. M. (2003). Matrilineal genetic structure within and among populations of the cooperatively breeding common marmoset, *Callithrix jacchus*. *Mol. Ecol.* 12:1101–1108.
- Ferrari, S. F. (1988). The behaviour and ecology of the buffy-headed marmoset, *Callithrix flaviceps* (O. Thomas, 1903) [PhD thesis]. University College, London.
- Ferrari, S. F. (1993). Ecological differentiation in the Callitrichidae. In: Rylands, A. B. (ed.), *Marmosets and Tamarins: Systematics, Ecology and Behaviour*. Oxford University Press, Oxford, pp. 314–328.
- Ferrari, S. F., Corrêa, H. K. M., and Coutinho, P. E. G. (1996). Ecology of the “southern” marmosets (*Callithrix aurita* and *Callithrix flaviceps*). In: Norconk, M. A., Rserberger, A. L., and Garber, P. A. (eds.), *Adaptive Radiations of Neotropical Primates*. Plenum Press, New York, pp. 157–171.
- Ferrari, S. F., and Diego, V. H. (1992). Long-term changes in a wild marmoset group. *Folia Primatol.* 58:215–218.
- Ferrari, S. F., and Digby, L. J. (1996). Wild *Callithrix* groups: stable extended families? *Am. J. Primatol.* 38:19–27.
- Ferrari, S. F., Iwanaga, S., Ramos, E. M., Messias, M. R., Ramos, P. C. S., and Cruz Neto, E. H. (1999). Expansion of the known distribution of Goeldi’s monkey (*Callimico goeldii*) in south-western Brazilian Amazonia. *Folia Primatol.* 70:112–116.
- Ferrari, S. F., Lopes, M. A., and Krause, E. A. K. (1993). Gut morphology of *Callithrix nigriceps* and *Saguinus labiatus* from western Brazilian Amazonia. *Am. J. Phys. Anthropol.* 90:487–493.
- Ferrari, S. F., and Lopes Ferrari, M. A. (1989). A re-evaluation of the social organization of the Callitrichidae, with references to the ecological differences between genera. *Folia Primatol.* 52:132–147.
- Ferrari, S. F., and Lopes Ferrari, M. A. (1990). A survey of primates in central Pará. *Bol. Mus. Para. Emílio Goeldi Série Zool.* 6:169–179.
- Ferrari, S. F., and Martins, E. S. (1992). Gummivory and gut morphology in two sympatric callitrichids (*Callithrix emiliae* and *Saguinus fuscicollis weddelli*) from western Brazilian Amazonia. *Am. J. Phys. Anthropol.* 88:97–103.
- Frame, L. H., Malcohm, J. R., Frame, G. W., and van Lawick, H. (1979). Social organization of African wild dogs (*Lycan pictus*) on the Serengeti Plains, Tanzania 1967–78. *Z. Tierpsychol.* 50:225–249.
- French, J. A. (1997). Proximate regulation of singular breeding in Callitrichid primates. In: Solomon, N. G., and French, J. A. (eds.), *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge, pp. 34–75.
- French, J. A., and Stribley, J. A. (1985). Patterns of urinary oestrogen excretion in female golden lion tamarins (*Leontopithecus rosalia*). *J. Reprod. Fertil.* 75:537–546.
- French, J. A., Abbott, D. H., Scheffler, G., Robinson, J. A., and Goy, R. W. (1983). Cyclic excretion of urinary oestrogens in female tamarins (*Saguinus oedipus*). *J. Reprod. Fertil.* 68:177–184.
- French, J. A., Bales, K. L., Baker, A. J., and Dietz, J. M. (2003). Endocrine monitoring of wild dominant and subordinate female *Leontopithecus rosalia*. *Int. J. Primatol.* 24:1281–1300.
- French, J. A., Brewer, K. J., Schaffner, C. M., Schalley, J., Hightower-Merritt, D. L., Smith, T. E., and Bell, S. M. (1996). Urinary steroid and gonadotropin excretion across the reproductive cycle in female Wied’s black tufted-ear marmosets (*Callithrix kuhli*). *Am. J. Primatol.* 40:231–245.
- French, J. A., De Vleeschouwer, K., Bales, K., and Heistermann, M. (2002). Lion tamarin reproductive biology. In: Kleiman, D. G., and Rylands, A. B. (eds.), *Lion Tamarins: Biology and Conservation*. Smithsonian Institution Press, Washington DC, pp. 133–156.
- French, J. A., Inglett, B. J., and Dethlefs, T. M. (1989). The reproductive status of nonbreeding group members in captive golden lion tamarin social groups. *Am. J. Primatol.* 18:73–86.
- Garber, P. A. (1984). Proposed nutritional importance of plant exudates in the diet of the Panamanian tamarin, *Saguinus Oedipus geoffroyi*. *Int. J. Primatol.* 5:1–15.
- Garber, P. A. (1988). Diet, foraging patterns, and resource defense in a mixed species troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. *Behaviour* 105:18–34.
- Garber, P. A. (1993a). Feeding ecology and behaviour of the genus *Saguinus*. In: Rylands, A. B. (ed.), *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*. Oxford University Press, Oxford, pp. 273–295.
- Garber, P. A. (1993b). Seasonal patterns of diet and ranging in two species of tamarin monkeys: stability versus variability. *Int. J. Primatol.* 14:145–166.
- Garber, P. A. (1997). One for all and breeding for one: cooperation and competition as a tamarin reproductive strategy. *Evol. Anthropol.* 5:187–222.
- Garber, P. A., Encarnacion, F., Moya, L., and Pruetz, J. D. (1993). Demographic and reproductive patterns in moustached tamarin monkeys (*Saguinus mystax*): implications for reconstructing platyrrhine mating systems. *Am. J. Primatol.* 29:235–254.
- Garber, P. A., and Leigh, S. R. (2001). Patterns of positional behavior in mixed species groups of *Callimico goeldii*, *Saguinus labiatus*, and *Saguinus fuscicollis* in northwestern Brazil. *Am. J. Primatol.* 55:17–31.
- Genoud, M., Martin, R. D., and Glaser, D. (1997). Rate of metabolism in the smallest simian primate, the pygmy marmoset (*Cebuella pygmaea*). *Am. J. Primatol.* 41:229–245.



- Gibson, K. R. (1986). Cognition, brain size, and the extraction of embedded food resources. In: Else, J. G., and Lee, P. C. (eds.), *Primate Ontogeny, Cognition, and Social Behavior*. Cambridge University Press, Cambridge. pp. 93–103.
- Ginther, A. J., Carlson, A. A., Ziegler, T. E., and Snowdon, C. T. (2002). Neonatal and pubertal development in males of a cooperatively breeding primate, the cotton-top tamarin (*Saguinus oedipus oedipus*). *Biol. Reprod.* 66:282–290.
- Ginther, A. J., Ziegler, T. E., and Snowdon, C. T. (2001). Reproductive biology of captive male cottontop tamarin monkeys as a function of social environment. *Anim. Behav.* 61:65–78.
- Goldizen, A. W. (1987a). Tamarins and marmosets: communal care of offspring. In: Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*. University of Chicago Press, Chicago. pp. 34–43.
- Goldizen, A. W. (1987b). Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behav. Ecol. Sociobiol.* 20:99–109.
- Goldizen, A. W. (1989). Social relationships in a cooperatively polyandrous group of tamarins (*Saguinus fuscicollis*). *Behav. Ecol. Sociobiol.* 24:79–89.
- Goldizen, A. W. (2003). Social monogamy and its variations in callitrichids: do these relate to the costs of infant care? In: Reichard, U. H., and Boesch, C. (eds.), *Monogamy: Mating Strategies and Partnerships in Birds, Humans, and Other Mammals*. Cambridge University Press, Cambridge. pp. 232–247.
- Goldizen, A. W., Mendelson, J., van Vlaardingen, M., and Terborgh, J. (1996). Saddle-back tamarin (*Saguinus fuscicollis*) reproductive strategies: evidence from a thirteen-year study of a marked population. *Am. J. Primatol.* 38:57–84.
- Goldizen, A. W., Terborgh, J., Cornejo, F., Porras, D. T., and Evans, R. (1988). Seasonal food shortage, weight-loss and the timing of births in saddle-back tamarins (*Saguinus fuscicollis*). *J. Anim. Ecol.* 57:893–901.
- Gonçalves, E. C., Ferrari, S. F., Silva, A., Coutinho, P. E. G., Menezes, E. V., and Schneider, M. P. C. (2003). Effects of habitat fragmentation on the genetic variability of silvery marmosets, *Mico argentatus*. In: Marsh, L. K. (ed.), *Primates in Fragments*. Kluwer Academic, New York. pp. 17–28.
- Groves, C. P. (2001). *Primate Taxonomy*. Smithsonian Institution Press, Washington DC.
- Guimarães, A. (1998). Ecology and social behavior of buffy-headed marmosets, *Callithrix flaviceps*. *Neotrop. Primates* 6:51–52.
- Hager, R., and Johnstone, R. A. (2004). Infanticide and control of reproduction in cooperative and communal breeders. *Anim. Behav.* 67:941–949.
- Harlow, C. R., Gems, S., Hodges, J. K., and Hearn, J. P. (1983). The relationship between plasma progesterone and the timing of ovulation and early embryonic development in the marmoset monkey (*Callitrichidae*). *J. Zool.* 201:273–282.
- Heistermann, M., and Hodges, J. K. (1995). Endocrine monitoring of the ovarian cycle and pregnancy in the saddle-back tamarin (*Saguinus fuscicollis*) by measurement of steroid conjugates in urine. *Am. J. Primatol.* 35:117–127.
- Hershkovitz, P. (1977). *Living New World Monkeys (Platyrrhini), with an Introduction to Primates*. vol. 1. Chicago University Press, Chicago.
- Heymann, E. W. (1996). Social behavior of wild moustached tamarins, *Saguinus mystax*, at the Estación Biológica Quebrada Blacno, Peruvian Amazonia. *Am. J. Primatol.* 38:101–113.
- Heymann, E. W. (2000). The number of adult males in callitrichine groups and its implications for callitrichine social evolution. In: Kappeler, P. M. (ed.), *Primate Males: Causes and Consequences of Variation in Group Composition*. Cambridge University Press, Cambridge. pp. 64–71.
- Heymann, E. W. (2001). Interspecific variation of scent-marking behaviour in wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis*. *Folia Primatol.* 72:253–267.
- Heymann, E. W., and Buchanan-Smith, H. (2000). The behavioral ecology of mixed-species troops of callitrichine primates. *Biol. Rev.* 75:169–190.
- Heymann, E. W., Encarnación, F., and Canaquin, J. E. (2002). Primates of the Río Curaray, northern Peruvian Amazon. *Int. J. Primatol.* 23:191–201.
- Heymann, E. W., and Smith, A. C. (1999). When to feed on gums: temporal patterns of gummivory in wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Callitrichinae). *Zoo Biol.* 18:459–471.
- Heymann, E. W., and Soini, P. (1999). Offspring number in pygmy marmosets, *Cebuella pygmaea*, in relation to group size and number of adult males. *Behav. Ecol. Sociobiol.* 46:400–404.
- Hill, W. C. O. (1957). *Primates, Comparative Anatomy and Taxonomy. Hapalidae*, vol. III. University of Edinburgh Press, Edinburgh.
- Hoogland, J. L. (1985). Infanticide in prairie-dogs: lactating females kill offspring of close kin. *Science* 230:1037–1040.
- Hourani, P. E., Vinyard, C. J., and Lemelin, P. (2003). Forelimb forces during gouging and other behaviors on vertical substrates in common marmosets. *Am. J. Phys. Anthropol.* 36(suppl.):118.
- Hrdy, S. B. (1979). Infanticide among animals—review, classification, and examination of the implications for the reproductive strategies of females. *Ethol. Sociobiol.* 1:13–40.
- Hubrecht, R. C. (1985). Home range size and use and territorial behavior in the common marmoset, *Callithrix jacchus jacchus*, at the Tapacura Field Station, Brazil. *Int. J. Primatol.* 6:533–550.
- InfoNatura (2004). *Birds, Mammals, and Amphibians of Latin America*, version 3.2. Arlington, Virginia, NatureServe, <http://www.natureserve.org/infonatura> (accessed July 1, 2004).
- IUCN Species Survival Commission (2003). *IUCN Red List*. IUCN, Gland, Switzerland, <http://www.redlist.org/>.
- Jaquish, C. E., Toal, R. L., Tardif, S. D., and Carson, R. L. (1995). Use of ultrasound to monitor prenatal growth and development in the common marmoset (*Callithrix jacchus*). *Am. J. Primatol.* 36:259–275.
- Kendrick, K. M., and Dixson, A. F. (1983). The effect of the ovarian cycle on the sexual behaviour of the common marmoset (*Callithrix jacchus*). *Physiol. Behav.* 30:735–742.
- Kierulff, M. C. M. (2000). Ecology and behaviour of translocated groups of golden lion tamarins (*Leontopithecus rosalia*) [PhD diss.]. University of Cambridge, Cambridge.
- Kierulff, M. C. M., Raboy, B. E., Procópio de Oliveira, P., Miller, K., Passos, F. C., and Prado, F. (2002). Behavioral ecology of lion tamarins. In: Kleiman, D. G., and Rylands, A. B. (eds.), *Lion Tamarins: Biology and Conservation*. Smithsonian Institution Press, Washington DC. pp. 157–187.
- Kleiman, D. G., and Rylands, A. B. (2002). *Lion Tamarins: Biology and Conservation*. Smithsonian Institution Press, Washington DC.

- Knogge, C., and Heymann, E. W. (2003). Seed dispersal by sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis*: diversity and characteristics of plant species. *Folia Primatol.* 74:33–47.
- Koenig, A. (1995). Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *Am. J. Primatol.* 35:311–317.
- Kostrub, C. E. (2003). The social organization and behavior of golden-mantled tamarins, *Saguinus tripartitus*, in eastern Ecuador [PhD diss.]. University of California, Davis.
- Kuederling, I., Evans, C. S., Abbott, D. H., Pryce, C. R., and Epple, G. (1995). Differential excretion of urinary oestrogen by breeding females and daughters in the red-bellied tamarin (*Saguinus labiatus*). *Folia Primatol.* 64:140–145.
- Kuederling, I., and Heistermann, M. (1997). Ultrasonographic and hormonal monitoring of pregnancy in the saddle back tamarin, *Saguinus fuscicollis*. *J. Med. Primatol.* 26:299–306.
- Lazaro-Perea, C. (2001). Intergroup interactions in wild common marmosets, *Callithrix jacchus*: territorial defense and assessment of neighbors. *Anim. Behav.* 62:11–21.
- Lazaro-Perea, C., Arruda, M. F., and Snowdon, C. T. (2004). Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Anim. Behav.* 67:627–636.
- Lazaro-Perea, C., Castro, C. S. S., Harrison, R., Araujo, A., Arruda, M. F., and Snowdon, C. T. (2000). Behavioral and demographic changes following the loss of the breeding female in cooperatively breeding marmosets. *Behav. Ecol. Sociobiol.* 48:137–146.
- Lopes, M. A., and Ferrari, S. F. (1994). Foraging behaviour of a tamarin group (*Saguinus fuscicollis weddelli*), and interactions with marmosets (*Callithrix emiliae*). *Int. J. Primatol.* 15:373–387.
- Lorini, V. G., and Persson, M. L. (1990). Uma nova espécie de *Leontopithecus* Lesson, 1840, do sul do Brasil (Primates, Callitrichidae). *Bol. Mus. Nac. Rio Janeiro Zool.* 338:1–14.
- Maier, W., Alonso, C., and Langguth, A. (1982). Field observations on *Callithrix jacchus jacchus*. *Z. Saugetierk.* 47:334–346.
- Mansfield, K. (2003). Marmoset models commonly used in biomedical research. *Comp. Med.* 53:383–392.
- Martins, M. M. (1998). Feeding ecology of *Callithrix aurita* in a forest fragment of Minas Gerais. *Neotrop. Primates* 6:126–127.
- Martins, M. M., and Setz, E. Z. F. (2000). Diet of buffy tufted-eared marmosets (*Callithrix aurita*) in a forest fragment in southeastern Brazil. *Int. J. Primatol.* 21:467–476.
- Mendes Pontes, A. R., and Monteiro da Cruz, M. A. O. (1995). Home-range, intergroup transfers, and reproductive status of common marmosets, *Callithrix jacchus*, in a forest fragments in northeastern Brazil. *Primates* 36:335–347.
- Monfort, S. L., Bush, M., and Wildt, D. E. (1996). Natural and induced ovarian synchrony in golden lion tamarins (*Leontopithecus rosalia*). *Biol. Reprod.* 55:875–882.
- Napier, J. R., and Napier, P. H. (1967). *A Handbook of Living Primates*. Academic Press, New York.
- Neyman, P. F. (1978). Aspects of the ecology and social organization of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In: Kleiman, D. G. (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Institution Press, Washington DC. pp. 39–71.
- Nievergelt, C. M., Digby, L. J., Ramakrishnan, U., and Woodruff, D. S. (2000). Genetic analysis of group composition and breeding system in a wild common marmoset (*Callithrix jacchus*) population. *Int. J. Primatol.* 21:1–20.
- Nievergelt, C. M., and Martin, R. D. (1999). Energy intake during reproduction in captive common marmosets (*Callithrix jacchus*). *Physiol. Behav.* 65:849–854.
- Oerke, A. K., Heistermann, M., Kuderling, I., Martin, R. D., and Hodges, J. K. (2002). Monitoring reproduction in Callitrichidae by means of ultrasonography. *Evol. Anthropol.* 11(suppl. 1):183.
- Oliveira, A. C. M., and Ferrari, S. F. (2000). Seed dispersal by black-handed tamarins, *Saguinus midas niger* (Callitrichinae, Primates): implications for the regeneration of degraded forest habitats in eastern Amazonia. *J. Trop. Ecol.* 16:709–716.
- Passamani, M. (1998). Activity budget of Geoffroy's marmoset (*Callithrix geoffroyi*) in an Atlantic forest in southeastern Brazil. *Am. J. Primatol.* 46:333–340.
- Passamani, M., and Rylands A. B. (2000). Feeding behavior of Geoffroy's marmoset (*Callithrix geoffroyi*) in an Atlantic Forest fragment of south-eastern Brazil. *Primates* 41:27–38.
- Passos, F. C. (1994). Behavior of the black lion tamarin, *Leontopithecus chrysopygus*, in different forest levels in the Caetetus Ecological Station, São Paulo, Brazil. *Neotrop. Primates* 2(suppl.):40–41.
- Passos, F. C. (1997). Padrão de atividades, dieta e uso do espaço em um grupo de mico-leão-preto (*Leontopithecus chrysopygus*) na Estação Ecológica do Caetetus, SP [PhD thesis]. Universidade Federal de São Carlos, São Carlos.
- Passos, F. C. (1998). Ecology of the black lion tamarin. *Neotrop. Primates* 6:128–129.
- Passos, F. C. (1999). Dieta de um grupo de mico-leão-preto, *Leontopithecus chrysopygus* (Mikan) (Mammalia, Callitrichidae), na Estação Ecológica do Caetetus, São Paulo. *Rev. Brasil. Zool.* 16(suppl. 2):269–278.
- Peres, C. A. (1989). Costs and benefits of territorial defense in wild golden lion tamarins, *Leontopithecus rosalia*. *Behav. Ecol. Sociobiol.* 25:227–233.
- Peres, C. A. (2000). Territorial defense and the ecology of group movements in small-bodied neotropical primates. In: Boinski, S., and Garber, P. A. (eds.), *On the Move: How and Why Animals Travel in Groups*. University of Chicago Press, Chicago. pp. 100–123.
- Pook, A. G., and Pook, G. (1981). A field study of the status and socioecology of Goeldi's monkey (*Callimico goeldii*) in northern Bolivia. *Folia Primatol.* 35:288–312.
- Pook, A. G., and Pook, G. (1982). Polyspecific association between *Saguinus fuscicollis*, *Saguinus labiatus*, *Callimico goeldii* and other primates in north-western Bolivia. *Folia Primatol.* 38:196–216.
- Porter, L. M. (2001a). Social organization, reproduction and rearing strategies of *Callimico goeldii*: new clues from the wild. *Folia Primatol.* 72:69–79.
- Porter, L. M. (2001b). Dietary differences among sympatric Callitrichinae in northern Bolivia: *Callimico goeldii*, *Saguinus fuscicollis* and *S. labiatus*. *Int. J. Primatol.* 22:961–992.
- Porter, L. M. (2004). Forest use and activity patterns of *Callimico goeldii* in comparison to two sympatric tamarins, *Saguinus fuscicollis* and *Saguinus labiatus*. *Am. J. Phys. Anthropol.* 124:139–153.

- Porter, L. M., Hanson, A. M., and Becerra, E. N. (2001). Group demographics and dispersal in a wild group of Goeldi's monkeys (*Callimico goeldii*). *Folia Primatol.* 72:108–110.
- Power, M. L., and Oftedal, O. T. (1996). Differences among captive callitrichids in the digestive responses to dietary gum. *Am. J. Primatol.* 40:131–144.
- Power, M. L., Oftedal, O. T., Savage, A., Blumer, E. S., Soto, L. H., Chen, T. C., and Holick, M. F. (1997). Assessing vitamin D status of callitrichids: baseline data from wild cotton-top tamarins (*Saguinus oedipus*) in Colombia. *Zoo Biol.* 16:39–46.
- Power, M. L., Tardif, S. D., Power, R. A., and Layne, D. G. (2003). Resting energy metabolism of Goeldi's monkey (*Callimico goeldii*) is similar to that of other callitrichids. *Am. J. Primatol.* 60:57–67.
- Prado, F. (1999a). Ecology and behavior of black-faced lion tamarins. *Neotrop. Primates* 7:137.
- Prado, F. (1999b). Ecologia, comportamento e conservação do mico-leão-de-cara-preta (*Leontopithecus caissara*) no Parque Nacional de Superagüi, Guaraqueçaba Paraná [Master's thesis]. Universidade Estadual Paulista, Botucatu.
- Price, E. C., and Evans, S. (1991). Terminology in the study of callitrichid reproductive strategies. *Anim. Behav.* 34:31–41.
- Price, E. C., Piedade, H. M., and Wormell, D. (2002). Population densities of primates in a Brazilian Atlantic forest. *Folia Primatol.* 73:54–56.
- Raboy, B. E., and Dietz, J. M. (2004). Diet, foraging, and use of space in wild golden-headed lion tamarins. *Am. J. Primatol.* 63:1–15.
- Ramirez, M. F., Freese, C. H., and Revilla, J. C. (1977). Feeding ecology of the pygmy marmoset, *Cebuella pygmaea*, in northeastern Peru. In: Kleiman, D. G. (ed.), *The Biology and Conservation of the Callitrichidae*. Smithsonian Institution Press, Washington DC, pp. 91–104.
- Roda, S. A., and Mendes Pontes, A. R. (1998). Polygyny and infanticide in common marmosets in a fragment of Atlantic Forest of Brazil. *Folia Primatol.* 69:372–376.
- Rosenberger, A. L. (1981). Systematics of the higher taxa. In: Coimbra-Filho, A. F., and Mittermeier, R. A. (eds.), *Ecology and Behavior of Neotropical Primates*, vol. 1. Academia Brasileira de Ciências, Rio de Janeiro, pp. 9–27.
- Rylands, A. B. (1982). Behaviour and ecology of three species of marmosets and tamarins (Callitrichidae, Primates) in Brazil [PhD thesis]. University of Cambridge, Cambridge.
- Rylands, A. B. (1986a). Ranging behaviour and habitat preference of a wild marmoset group, *Callithrix humeralifer* (Callitrichidae, Primates). *J. Zool. Lond. (A)* 210:489–514.
- Rylands, A. B. (1986b). Infant-carrying in a wild marmoset group, *Callithrix humeralifer*: evidence for a polyandrous mating system. In: Thiago de Mello, M. (ed.), *A Primatologia No Brasil*, vol. 2. Sociedade Brasileira de Primatologia, Brasília, pp. 131–144.
- Rylands, A. B. (1989). Sympatric Brazilian callitrichids—the black-tufted-ear marmoset, *Callithrix kuhli*, and the golden-headed lion tamarin, *Leontopithecus chrysomelas*. *J. Hum. Evol.* 18:679–695.
- Rylands, A. B. (1993a). *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*. Oxford University Press, Oxford.
- Rylands, A. B. (1993b). The ecology of the lion tamarins, *Leontopithecus*: some intrageneric differences and comparisons with other callitrichids. In: Rylands, A. B. (ed.), *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*. Oxford University Press, Oxford, pp. 296–313.
- Rylands, A. B., and Chiarello, A. G. (2003). Official list of Brazilian fauna threatened with extinction—2003. *Neotrop. Primates* 11:43–49, <http://www.mma.gov.br/port/sbf/fauna/index.cfm>.
- Rylands, A. B., and de Faria, D. S. (1993). Habitats, feeding ecology, and home range size in the genus *Callithrix*. In: Rylands, A. B. (ed.), *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*. Oxford University Press, Oxford, pp. 262–272.
- Rylands, A. B., Schneider, H., Langguth, A., Mittermeier, R. A., Groves, C. P., and Rodríguez-Luna, E. (2000). An assessment of the diversity of New World primates. *Neotrop. Primates* 8:61–93.
- Saltzman, W. (2003). Reproductive competition among female common marmosets (*Callithrix jacchus*): proximate and ultimate causes. In: Jones, C. (ed.), *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*. American Society of Primatologists, Norman, OK, pp. 197–229.
- Saltzman, W., Pick, R. R., Salper, O. J., Liedl, K. J., and Abbott, D. H. (2004). Onset of plural cooperative breeding in common marmoset families following replacement of the breeding male. *Anim. Behav.* 68:59–73.
- Saltzman, W., Schultz-Darken, N. J., and Abbott, D. H. (1997). Familial influences on ovulatory function in common marmosets (*Callithrix jacchus*). *Am. J. Primatol.* 41:159–177.
- Saltzman, W., Schultz-Darken, N. J., Scheffler, G., Wegner, F. H., and Abbott, D. H. (1994). Social and reproductive influences on plasma cortisol in female marmoset monkeys. *Physiol. Behav.* 56:801–810.
- Saltzman, W., Schultz-Darken, N. J., Wegner, F. H., Wittwer, D. J., and Abbott, D. H. (1998). Suppression of cortisol levels in subordinate female marmosets: reproductive and social contributions. *Horm. Behav.* 33:58–74.
- Savage, A., Giraldo, L. H., Soto, L. H., and Snowdon, C. T. (1996a). Demography, group composition, and dispersal in wild cotton-top tamarins (*Saguinus oedipus*) groups. *Am. J. Primatol.* 38:85–100.
- Savage, A., Shideler, S. E., Soto, L. H., Causado, J., Giraldo, L. H., Lasley, B. L., and Snowdon, C. T. (1997). Reproductive events of wild cotton-top tamarins (*Saguinus oedipus*) in Colombia. *Am. J. Primatol.* 43:329–337.
- Savage, A., Snowdon, C. T., Giraldo, L. H., and Soto, L. H. (1996b). Parental care patterns and vigilance in wild cotton-top tamarins (*Saguinus oedipus*). In: Norconk, M. A., Rosenberger, A. L., and Garber, P. A. (eds.), *Adaptive Radiations of Neotropical Primates*. Plenum Press, New York, pp. 187–199.
- Savage, A., Ziegler, T. E., and Snowdon, C. T. (1988). Sociosexual development, pair bond formation, and mechanisms of fertility suppression in female cotton-top tamarins (*Saguinus oedipus*). *Am. J. Primatol.* 14:345–359.
- Scanlon, C. E., Chalmers, N. R., and Monteiro da Cruz, M. A. O. (1988). Changes in the size, composition and reproductive condition of wild marmoset groups (*Callithrix jacchus jacchus*) in north east Brazil. *Primates* 29:295–305.
- Schaffner, C. M., and Caine, N. G. (2000). The peacefulness of cooperatively breeding primates. In: Aureli, F., and de Waal, F. B. M. (eds.), *Natural Conflict Resolution*. University of California Press, Berkeley, pp. 155–169.
- Schaffner, C. M., and French, J. A. (1997). Group size and aggression: “recruitment incentives” in a cooperatively breeding primate. *Anim. Behav.* 54:171–180.

- Schaffner, C. M., and French, J. A. (2004). Behavioral and endocrine responses in male marmosets to the establishment of multimale breeding groups: evidence for non-monopolizing facultative polyandry. *Int. J. Primatol.* 25:709–732.
- Schneider, H., Martins, E. S., and Leão, V. (1987). Syntopy and troops association between *Callithrix* and *Saguinus* from Rondônia. *Int. J. Primatol.* 8:527.
- Schneider, H., and Rosenberger, A. L. (1996). Molecules, morphology and platyrrhine systematics. In: Norconk, M. A., Rosenberger, A. L., and Garber, P. A. (eds.), *Adaptive Radiations of Neotropical Primates*. Plenum Press, New York. pp. 3–19.
- Schradin, C., and Anzenberger, G. (2001). Infant carrying in family groups of Goeldi's monkeys (*Callimico goeldii*). *Am. J. Primatol.* 53:57–67.
- Seuánez, H. N., Di Fiore, A., Moreira, Â. M., da Silva Almeida, C. A., and Canavez, F. C. (2002). Genetics and evolution of lion tamarins. In: Kleiman, D. G., and Rylands, A. B. (eds.), *Lion Tamarins: Biology and Conservation*. Smithsonian Institution Press, Washington DC. pp. 117–132.
- Simons, E. L. (1972). *Primate Evolution: An Introduction to Man's Place in Nature*. MacMillan, New York.
- Smith, A. C. (2000). Composition and proposed nutritional importance of exudates eaten by saddleback (*Saguinus fuscicollis*) and mustached (*Saguinus mystax*) tamarins. *Int. J. Primatol.* 21:69–83.
- Smith, A. C., Buchanan-Smith, H. M., Surrige, A. K., and Mundy, N. I. (2003). Leaders of progressions in wild mixed-species troops of saddleback (*Saguinus fuscicollis*) and mustached tamarins (*S. mystax*), with emphasis on color vision and sex. *Am. J. Primatol.* 61:145–157.
- Smith, A. C., Tirado Herrera, E. R., and Buchanan-Smith, H. M. (2001). Multiple breeding females and allo-nursing in a wild group of mustached tamarins (*Saguinus mystax*). *Neotrop. Primates* 9:67–69.
- Smith, T. E., and French, J. A. (1997). Social and reproductive conditions modulate urinary cortisol excretion in black tufted-ear marmosets (*Callithrix kuhli*). *Am. J. Primatol.* 42:253–267.
- Smith, T. E., Schaffner, C. M., and French, J. A. (1997). Social and developmental influences on reproductive function in female Wied's black tufted-ear marmosets (*Callithrix kuhli*). *Horm. Behav.* 31:159–168.
- Snowdon, C. T. (1996). Infant care in cooperatively breeding species. *Adv. Study Behav.* 25:648–689.
- Snowdon, C. T., and Soini, P. (1988). The tamarins, genus *Saguinus*. In: Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F., and da Fonseca, G. A. B. (eds.), *Ecology and Behavior of Neotropical Primates*, vol. 2. World Wildlife Fund, Washington DC. pp. 223–298.
- Soini, P. (1982). Ecology and population dynamics of the pygmy marmoset, *Cebuella pygmaea*. *Folia Primatol.* 39:1–21.
- Soini, P. (1987). Sociosexual behavior of a free-ranging *Cebuella pygmaea* Callitrichidae, Platyrrhini troop during post-partum estrus of its reproductive female. *Am. J. Primatol.* 13:223–230.
- Soini, P. (1988). The pygmy marmoset, genus *Cebuella*. In: Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F., and da Fonseca, G. A. B. (eds.), *Ecology and Behavior of Neotropical Primates*, vol. 2. World Wildlife Fund, Washington DC. pp. 79–129.
- Soini, P. (1993). The ecology of the pygmy marmoset, *Cebuella pygmaea*: some comparisons with two sympatric tamarins. In: Rylands, A. B. (ed.), *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*. Oxford University Press, Oxford. pp. 257–261.
- Solomon, N. G., and French, J. A. (1997). *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge.
- Spurlock, L. B. (2002). Reproductive suppression in the pygmy marmoset *Cebuella pygmaea*. *Diss. Abst. Int.* B62:3872.
- Stevenson, M. F., and Rylands, A. B. (1988). The marmosets, genus *Callithrix*. In: Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F., and da Fonseca, G. A. B. (eds.), *Ecology and Behavior of Neotropical Primates*, vol. 2. World Wildlife Fund, Washington DC. pp. 131–222.
- Tagliaro, C. H., Schneider, M. P. C., Schneider H., Sampaio, I. C., and Stanhope, M. J. (1997). Marmoset phylogenetics, conservation perspectives, and evolution of the mtDNA control region. *Mol. Biol. Evol.* 14:674–684.
- Tagliaro, C. H., Schneider, M. P. C., Schneider, H., Sampaio, I., and Stanhope, M. J. (2000). Molecular studies of *Callithrix pygmaea* (Primates, Platyrrhini) based on transferrin intronic and ND1 regions: implications for taxonomy and conservation. *Genet. Mol. Biol.* 23:729–737.
- Tardif, S. D. (1997). The bioenergetics of parental behavior and the evolution of alloparental care in marmosets. In: Solomon, N. G., and French, J. A. (eds.), *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge. pp. 11–33.
- Tardif, S. D., Harrison, M. L., and Simek, M. A. (1993). Communal infant care in marmosets and tamarins: relation to energetics, ecology, and social organization. In: Rylands, A. B. (ed.), *Marmosets and Tamarins: Systematics, Behaviour, and Ecology*. Oxford University Press, Oxford. pp. 220–234.
- Tardif, S. D., Richter, C. B., and Carson, C. L. (1984). Reproductive performance of three species of Callitrichidae. *Lab. Anim. Sci.* 34:272–275.
- Tardif, S. D., Santos, C. V., Baker, A. J., van Elsacker, L., Ruiz-Miranda, C. R., Moura, A. C. A., Passos, F. C., Price, E. C., Rapaport, L. G., and De Vleeschouwer, K. (2002). Infant care in lion tamarins. In: Kleiman, D. G., and Rylands, A. B. (eds.), *Lion Tamarins: Biology and Conservation*. Smithsonian Institution Press, Washington DC. pp. 213–232.
- Tardif, S. D., Smucny, D. A., Abbott, D. H., Mansfield, K., Schultz-Darken, N., and Yamamoto, M. E. (2003). Reproduction in captive common marmosets (*Callithrix jacchus*). *Comp. Med.* 53:364–368.
- Tardif, S. D., and Ziegler, T. E. (1992). Features of female reproductive senescence in tamarins (*Saguinus* spp.), a New World primate. *J. Reprod. Fertil.* 94:411–421.
- Tavares, L. I., and Ferrari, S. F. (2002). Diet of the silvery marmoset (*Callithrix argentata*) at CFPn: seasonal and longitudinal variation. In: Lisboa, P. L. B. (ed.), *Caxiuanã, Populações Tradicionais, Meio Físico e Diversidade Biológica*. Belém. pp. 707–719.
- Terborgh, J. (1983). *Five New World Primates: A Study in Comparative Ecology*. Princeton University Press, Princeton, NJ.
- Terborgh, J., and Goldizen, A. W. (1985). On the mating system of the cooperatively breeding saddle-backed tamarin (*Saguinus fuscicollis*). *Behav. Ecol. Sociobiol.* 16:293–299.
- Torii, R., Koizumi, H., Tanioka, Y., Inaba, T., and Mori, J. (1987). Serum LH, progesterone and estradiol-17 $\beta$  levels throughout the ovarian cycle, during the early stage of pregnancy and after the parturition and the abortion in the common marmoset, *Callithrix jacchus*. *Primates* 28:229–238.

- Ullrey, D. E., Bernard, J. B., Peter, G. K., Lu, Z., Chen, T. C., Sikarski, J. G., and Holick, M. F. (2000). Vitamin D intakes by cotton-top tamarins (*Saguinus oedipus*) and associated serum 25-hydroxyvitamin D concentrations. *Zoo Biol.* 18:473–480.
- Valladares-Padua, C. (1993). The ecology, behavior and conservation of the black lion tamarin (*Leontopithecus chrysopygus*, Mikan, 1823) [PhD thesis]. University of Florida, Gainesville.
- Valladares-Padua, C., and Cullen, L., Jr. (1994). Distribution, abundance and minimum viable metapopulation of the black lion tamarin (*Leontopithecus chrysopygus*). *Dodo J. Wildl. Preserv. Trusts* 30:80–88.
- van Roosmalen, M. G. M., and van Roosmalen, T. (1997). An eastern extension of the geographical range of the pygmy marmoset, *Cebuella pygmaea*. *Neotrop. Primates* 5:3–6.
- van Roosmalen, M. G. M., and van Roosmalen, T. (2003). The description of a new marmoset genus, *Callibella* (Callitrichinae, Primates), including its molecular phylogenetic status. *Neotrop. Primates* 11:1–10.
- van Roosmalen, M. G. M., van Roosmalen, T., Mittermeier, R. A., and Rylands, A. B. (1998). A new and distinctive species of marmoset (Callitrichidae, Primates) from the lower Rio Aripuanã, state of Amazonas, central Brazilian Amazonia. *Goeldiana Zool.* 22:1–27.
- Veracini, C. (1997). O comportamento alimentar de *Callithrix argentata* (Linnaeus 1771) (Primata Callitrichinae). In: Lisboa, P. L. B. (ed.) *Caxiuanã MCT/CNPq*, Belem. pp. 437–446.
- Veracini, C. (2000). Dado preliminaries sobre a ecologia de *Saguinus niger* na Estação Científica Ferreira Penna, Caxiuanã, Brasil. *Neotrop. Primates* 8:108–113.
- Vinyard, C. J., Wall, C. E., Williams, S. H., and Hylander, W. L. (2003). Comparative function of skull morphology of tree-gouging primates. *Am. J. Phys. Anthropol.* 120:153–170.
- Vinyard, C. J., Wall, C. E., Williams, S. H., Schmitt, D., and Hylander, W. L. (2001). A preliminary report on the jaw mechanics during tree gouging in common marmosets (*Callithrix jacchus*). In: Brook, A. (ed.), *Dental Morphology: 12<sup>th</sup> International Symposium on Dental Morphology*. Sheffield Academic Press, Sheffield. pp. 283–297.
- von Dornum, M., and Ruvolo, M. (1999). Phylogenetic relationships of the New World monkeys (Primates, Platyrrhini) based on nuclear G6PD DNA sequences. *Mol. Phylogenet. Evol.* 11:459–476.
- Wasser, S. K., and Barash, D. P. (1983). Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. *Q. Rev. Biol.* 58:513–538.
- Watts, D. P. (1989). Infanticide in mountain gorilla—new cases and a reconsideration of the evidence. *Ethology* 81:1–18.
- Widowski, T. M., Porter, T. A., Ziegler, T. E., and Snowdon, C. T. (1992). The stimulatory effect of males on the initiation but not the maintenance of ovarian cycling in cotton-top tamarins (*Saguinus oedipus*). *Am. J. Primatol.* 26:97–108.
- Widowski, T. M., Ziegler, T. E., Elowson, A. M., and Snowdon, C. T. (1990). The role of males in the stimulation of reproductive function in female cotton-top tamarins, *Saguinus o. oedipus*. *Anim. Behav.* 40:731–741.
- Wormell, D., and Price, E. (2001). Reproduction and management of black lion tamarin, *Leontopithecus chrysopygus* at Jersey Zoo. *Dodo J. Wildl. Preserv. Trusts* 37:34–40.
- Yamamoto, M. E., and Box, H. O. (1997). The role of non-reproductive helpers in infant carrying in captive *Callithrix jacchus*. *Ethology* 103:760–771.
- Yamamoto, M. E., Box, H. O., Albuquerque, F. S., and Arruda, M. F. (1996). Carrying behavior in captive and wild marmosets (*Callithrix jacchus*): a comparison between two colonies and a field site. *Primates* 37:297–304.
- Ziegler, T. E., Bridson, W. E., Snowdon, C. T., and Eman, S. (1987a). Urinary gonadotropin and estrogen excretion during the postpartum estrus, conception, and pregnancy in the cotton-top tamarin (*Saguinus oedipus oedipus*). *Am. J. Primatol.* 12:127–140.
- Ziegler, T. E., Savage, A., Scheffler, G., and Snowdon, C. T. (1987b). The endocrinology of puberty and reproductive functioning in female cotton-top tamarins (*Saguinus oedipus*) under varying social conditions. *Biol. Reprod.* 37:618–627.
- Ziegler, T. E., Scheffler, G., and Snowdon, C. T. (1995). The relationship of cortisol levels to social environment and reproductive functioning in female cotton-top tamarins, *Saguinus oedipus*. *Horm. Behav.* 29:407–424.
- Ziegler, T. E., Snowdon, C. T., and Bridson, W. E. (1990a). Reproductive performance and excretion of urinary estrogens and gonadotropins in the female pygmy marmoset (*Cebuella pygmaea*). *Am. J. Primatol.* 22:191–203.
- Ziegler, T. E., Widowski, T. M., Larson, M. L., and Snowdon, C. T. (1990b). Nursing does affect the duration of the post-partum to ovulation interval in cotton-top tamarins (*Saguinus oedipus*). *J. Reprod. Fertil.* 90:563–570.

**Appendix 6.1 Species and Subspecies Names for the Callitrichines**

SPECIES AND SUBSPECIES	COMMON NAME
<i>Callimico goeldii</i>	Goeldi's monkey
<i>Callithrix aurita</i>	Buffy-tufted-ear marmoset
<i>Callithrix flaviceps</i>	Buffy-headed marmoset
<i>Callithrix geoffroyi</i>	Geoffroy's tufted-ear marmoset
<i>Callithrix jacchus</i>	Common or white-tufted-ear marmoset
<i>Callithrix kuhlii</i>	Wied's black-tufted-ear marmoset
<i>Callithrix penicillata</i>	Black-tufted-ear or black-pencilled marmoset
<i>Cebuella pygmaea pygmaea</i>	Pygmy marmoset
<i>Cebuella pygmaea niveiventris</i>	White-bellied pygmy marmoset
<i>Callibella humilis</i>	Black-crowned dwarf marmoset
<i>Mico acariensis</i>	Rio Acari marmoset
<i>Mico argentatus</i>	Silvery marmoset
<i>Mico chrysoleucus</i>	Golden-white tassel-ear marmoset
<i>Mico emiliae</i>	Sneathlage's marmoset
<i>Mico humeralifer</i>	Black and white tassel-ear marmoset
<i>Mico intermedius</i>	Aripuanã marmoset
<i>Mico leucippe</i>	Golden-white bare-ear marmoset
<i>Mico manicorensis</i>	Manicoré marmoset
<i>Mico marcai</i>	Marca's marmoset
<i>Mico mauesi</i>	Maués marmoset
<i>Mico melanurus</i>	Black-tailed marmoset
<i>Mico nigricaps</i>	Black-headed marmoset
<i>Mico saterei</i>	Sateré marmoset
<i>Saguinus bicolor</i>	Pied bare-face tamarin
<i>Saguinus fuscicollis avilapiresi</i>	Ávila Pires' saddle-back tamarin
<i>Saguinus fuscicollis crandalli</i>	Crandall's saddle-back tamarin
<i>Saguinus fuscicollis cruzlimai</i>	Cruz Lima's saddle-back tamarin
<i>Saguinus fuscicollis fuscicollis</i>	Spix's saddle-back tamarin
<i>Saguinus fuscicollis fuscus</i>	Lesson's saddle-back tamarin
<i>Saguinus fuscicollis illigeri</i>	Illiger's saddle-back tamarin
<i>Saguinus fuscicollis lagonotus</i>	Red-mantle saddle-back tamarin
<i>Saguinus fuscicollis leucogenys</i>	Andean saddle-back tamarin
<i>Saguinus fuscicollis melanoleucus</i>	White saddle-back tamarin
<i>Saguinus fuscicollis nigrifrons</i>	Geoffroy's saddle-back tamarin
<i>Saguinus fuscicollis primitivus</i>	Saddle-back tamarin
<i>Saguinus fuscicollis weddelli</i>	Weddell's saddle-back tamarin
<i>Saguinus geoffroyi</i>	Geoffroy's tamarin
<i>Saguinus graellsii</i>	Graell's black-mantle tamarin
<i>Saguinus imperator imperator</i>	Black-chinned emperor tamarin
<i>Saguinus imperator subgriseus</i>	Bearded emperor tamarin
<i>Saguinus inustus</i>	Mottled-face tamarin
<i>Saguinus labiatus labiatus</i>	Red-bellied tamarin
<i>Saguinus labiatus rufiventris</i>	Red-bellied tamarin
<i>Saguinus labiatus thomasi</i>	Thomas' mustached tamarin
<i>Saguinus leucopus</i>	Silvery-brown bare-face tamarin
<i>Saguinus martinsi martinsi</i>	Martin's bare-face tamarin
<i>Saguinus martinsi ochraceus</i>	Ochraceous bare-face tamarin
<i>Saguinus midas</i>	Golden-handed or Midas tamarin
<i>Saguinus mystax mystax</i>	Spix's mustached tamarin
<i>Saguinus mystax pileatus</i>	Red-cap mustached tamarin
<i>Saguinus mystax Pluto</i>	White-rump mustached tamarin
<i>Saguinus niger</i>	Black-handed tamarin
<i>Saguinus nigricollis hernandezi</i>	Hernández-Camacho's black-mantle tamarin
<i>Saguinus nigricollis nigricollis</i>	Spix's black-mantle tamarin
<i>Saguinus oedipus</i>	Cotton-top tamarin
<i>Saguinus tripartitus</i>	Golden-mantle saddle-back tamarin
<i>Leontopithecus caissara</i>	Black-faced lion tamarin
<i>Leontopithecus chrysomelas</i>	Golden-headed lion tamarin
<i>Leontopithecus chrysopygus</i>	Black or golden-rumped lion tamarin
<i>Leontopithecus rosalia</i>	Golden lion tamarin

Source: Adapted from Rylands et al. (2000), van Roosmalen and van Roosmalen (2003).