

Behavioral Biology of Squirrel Monkeys

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Introduction

Squirrel monkeys (*Saimiri* spp.) are one of the top three most commonly involved Neotropical primates in biomedical research (Abee 2000; Tardif et al. 2012). Their physical characteristics, including small size and ease of handling, contribute to their desirability as research subjects. Squirrel monkeys easily adapt to laboratory housing and can be maintained in smaller spaces and less expensive cages compared to larger primates, such as macaques and baboons. This characteristic is especially important in facilities with space limitations.

Animals maintained in laboratory environments often live in restrictive and limiting conditions compared with their natural habitats. Although such environments meet the physical needs of the animals, they are usually not sufficient to allow the animals to express the full range of their species-typical behavior. The environments of most laboratory animals are extremely complex, involving unpredictable elements, as well as routine, predictable tasks, such as feeding and cleaning. Many laboratory

environments lack some or all of the stimuli that will promote desirable natural behavior. Therefore, knowledge of the natural behavior of squirrel monkeys is critical for anyone who plans to work with these animals in a laboratory environment. Understanding the natural history of a species, as well as how members of the species react to stressors, helps researchers to adjust their animals to a captive environment, providing a better model for research. Animals stressed by inadequate housing or inappropriate environmental enhancement may exhibit a host of physiological and psychological manifestations that will influence the way they react to experimental stimuli.

Typical Research Participation

Although there are 8 species of squirrel monkeys currently recognized (Chiou et al. 2011; Lynch Alfaro et al. 2015), the most common species involved in laboratory research are *Saimiri sciureus* and *S. boliviensis*, both South American species.

Squirrel monkeys offer several advantages over Old World monkeys for laboratory research (Abee 2000). Physically they are smaller and easier to handle. Doses of experimental compounds that need to be administered by body weight can be lower. There are no known viral transmission issues with squirrel monkeys. They also adapt to laboratory conditions very well and most procedures can be carried out on unsedated animals relatively easily.

The squirrel monkey is an important animal model for malaria vaccine development studies (Anderson et al. 2017; de Souza et al. 2017; Gunalan et al. 2019; Peterson et al. 2019). Because *Plasmodium* spp., the parasite that causes malaria, are host-specific, animal models used to study human malaria must be susceptible to the same strains that cause the disease in humans. The Bolivian squirrel monkey (*Saimiri boliviensis*) has been shown to be a superior model for studies of the pathogenesis of *P. falciparum* Indochina I (Whiteley et al. 1987), developing lesions and clinical signs similar to those reported in human disease. Squirrel monkeys are used to screen *P. falciparum* vaccine candidates for humans (Alves et al. 2015; Cunha et al. 2017; Tougan et al. 2018; Yagi et al. 2014). Squirrel monkeys (in particular *S. boliviensis* and *S. sciureus*) are susceptible to infection with different strains of *P. vivax*, but each squirrel monkey species/subspecies responds differently depending on the strain of the parasite used (Anderson et al. 2015; Anderson et al. 2017; Gunalan et al. 2019; Peterson et al. 2019). Obaldia et al. (2018) reported positive findings using *S. boliviensis* as a model for *P. vivax* vaccine testing. Differences in susceptibility and response to experimental malaria infections underscore the importance of species identification when using squirrel monkeys. Collins et al. (2009) reported that *S. boliviensis* is a suitable model for testing sporozoite and liver stage vaccines against the Salvador I strain of *P. vivax*. Malaria remains one of the top three diseases causing human mortality worldwide.

Squirrel monkeys are also involved extensively in neuroscience, vision, and hearing research. The squirrel monkey model offers advantages over rodent models in that cortical organization of the squirrel monkey brain more closely resembles that of humans (Gao et al. 2016; Schilling et al. 2018). Studies involving squirrel monkeys have also contributed to our understanding of injury-induced reorganization of the sensory cortex and somatotopic reorganization of the brain stem and thalamus (Cheung et al. 2017; Mowery et al. 2015; Yang et al. 2014). The field of behavioral pharmacology, particularly drug addiction research, has involved squirrel monkeys for many years (Achat-Mendes et al. 2012; Rowlett, et al. 2005; Valdez et al. 2007). Squirrel monkeys have made contributions to studies on drug addiction and its behavioral and physiological sequelae (Desai et al. 2016a; Kangas et al. 2016; Kangas and Bergman 2014).

Contributions to vision research include gene therapy in color vision (Mancuso et al. 2009; Neitz and Neitz, 2014; Shapley et al. 2009), adaptation of the vestibulo-ocular reflex (Migliaccio et al. 2010), and topography of cones, rods, and optic nerve axons. Auditory research has included auditory frequency discrimination (Malone et al. 2015, 2017; Marsh et al. 2015) and mapping of the auditory cortex and projections throughout the brain (Cheung et al. 2017).

Recent research has asked the question of whether squirrel monkeys could be considered an important sylvatic reservoir of the Zika virus in South America. Vanchiere et al. (2018) confirmed that *S. boliviensis* were susceptible to the Zika virus, documenting seroconversion in five out of six animals. There is now a validated fecal assay for Zika virus to be used in South America for rapid assessment of hosts in the forest (Milich et al. 2018).

Behavioral Biology

General Ecology

Squirrel monkeys are distributed widely in the Amazon basin, with disjunct populations occurring in Central America. Eight species are currently recognized: *S. oerstedii* in Central America, and seven South American forms: *S. boliviensis*, *S. sciureus*, *S. collinsi*, *S. ustus*, *S. vanzolinii*, *S. cassiquiarensis*, and *S. macrorodon* (Chiou et al. 2011; Lynch Alfaro et al. 2015). Long-term studies in the wild have been conducted on *S. oerstedii* in Costa Rica (Boinski 1986), *S. boliviensis* in Peru (Mitchell 1990), *S. sciureus* in Suriname (Boinski et al. 2002), and more recently on *S. collinsi* in Brazil (Stone 2007a, b) and *S. vanzolinii* in Brazil (Paim et al. 2017). Until recently, *S. collinsi* was grouped with *S. sciureus* as one species (Merces et al. 2015).

Squirrel monkeys live in various habitats, including primary or secondary rain forests, riverine areas, flooded forests, and mosaic habitats with anthropogenic disturbances (Boinski 1989; Carretero-Pinzón et al. 2017; Lima and Ferrari 2003; Paim et al. 2013; Peres 1994; Pontes 1997; Terborgh 1983). They also do well in areas of secondary growth, perhaps due to their high consumption of insects (Stone 2007a). Compared to other Neotropical primates, lower strata of the forest are often preferred (Fleagle and Mittermeier 1980; Mittermeier and van Roosmalen 1981). Squirrel monkeys also show terrestrial behavior, coming to the forest floor, primarily when foraging for larger insects in the leaf litter, fallen ripe fruit, and flowers (*S. collinsi*: Stone 2007a; *S. cassiquiarensis*: M. Araujo, pers. communication). Squirrel monkey home ranges are large, varying from 150 to 250 ha (Carretero-Pinzón et al. 2017; Mitchell 1990; Stone 2007a), but these are not defended, and there can be overlap in the ranges of neighboring troops (Stone 2007a). In addition, these primates can travel 2–5 km in a day (Mitchell 1990).

Where they are sympatric, *Saimiri* and capuchin monkeys (genus *Sapajus*) can form mixed-species associations, traveling and foraging together. The most common association occurs between *Saimiri* and *Sapajus apella* (Levi et al. 2013; Pinheiro, et al. 2011; Podolsky 1990; Terborgh 1983), although squirrel monkeys can also form polyspecific associations with *Sapajus olivaceous* (Pontes 1997) and cuxiús (genus *Chiropotes*; Pinheiro, et al. 2011). These associations may occur due to enhanced access to fruit resources (Podolsky 1990) or antipredator benefits for both species involved (Levi et al. 2013; Terborgh 1983).

Because of their small size, squirrel monkeys are at high predation risk, particularly infants traveling on their mother's back (Boinski 1986). In fact, it has been argued that the high birth

synchrony within wild squirrel monkey groups is an antipredator adaptation (Boinski 1987; Stone and Ruivo, 2020). The main predators of squirrel monkeys are raptors (Boinski 1987; Stone 2004) and constricting snakes (Ribeiro-Junior et al. 2016). Fear of snakes appears to be learned, as laboratory-raised squirrel monkeys do not react when presented with live snakes (Murray and King 1973). In the wild, seasonality has a strong effect on predator-sensitive foraging in squirrel monkeys. Experimental evidence shows that during the wet season (high fruit availability), squirrel monkeys avoid taking risks when foraging, with juveniles not foraging in open areas (Stone 2007b). Frechette et al. (2014) showed that *S. sciureus* in Suriname use both environmental and social information to assess predation risk, and are more reactive to potential predators at lower heights. Furthermore, field data on *S. oerstedii*, *S. boliviensis*, and *S. sciureus* living in distinct forest types indicates that avian attacks on squirrel monkeys primarily target individuals unprotected by understory vegetation (Boinski et al. 2003).

Social Organization and Social Behaviors

Squirrel monkey groups are generally large, ranging from 25 to 75 individuals (Boinski, 1999). However, unlike patterns of basic ecology, such as diet and habitat use, the social organization in the genus *Saimiri* is extremely diverse. For example, in some species, males are dominant over females (e.g., *S. sciureus*), while others are female-dominant (e.g., *S. boliviensis*), and yet in others, females and males are codominant (*S. oerstedii* and possibly *S. collinsi*; Boinski 1999; Pinheiro and Lopes 2018; Zimpler-DeLorenzo and Stone 2011). Such interspecific differences in social structure have been documented both in wild and captive settings, and extend to characteristics, such as group size, intersexual dominance, within-sex dominance hierarchies, and dispersal patterns (Table 25.1). However, it should be noted that, due to the difficulty of recognizing individual monkeys in the wild, much remains unknown about social structure and interactions in the genus.

Costa Rican squirrel monkeys (*S. oerstedii*), in addition to showing egalitarian interactions between sexes, also show weak female bonds and hierarchies (Boinski 1999); both males and females disperse from the group, though males disperse over longer distances (Blair and Melnick 2012).

Squirrel monkey groups studied in Peru (*S. boliviensis*) showed dominance hierarchies within each sex, along with strong female-bonding and female philopatry (Mitchell et al. 1991). In contrast, *S. sciureus* are characterized by high levels of intragroup aggression; male dominance over females; rigid, linear dominance hierarchies within each sex; weak female social bonds; and both sexes may disperse from their natal group (Boinski et al. 2005). Boinski et al. (2002) propose that fruit patch size and density in each species' habitat determine within-group competition regimes, which in turn shapes social structure (the socioecological model; Wrangham 1980). Another species, *S. macrodon* (studied in Ecuador) is characterized by a high level of kinship among females in a group, with individual females maintaining spatial proximity to closer kin. Like *S. boliviensis*, males disperse and females are philopatric (Montague et al. 2014).

Male–male interaction patterns are also variable among species. Costa Rican monkeys rarely display male–male within-group aggression, even during mating season, and males cooperate in aggressive interactions with neighboring groups and in the defense of infants from predators (Boinski 1994). Conversely, in *S. sciureus*, *S. boliviensis*, and *S. collinsi*, male agonism is high, particularly over access to females (Boinski et al. 2002; Mitchell 1990; Stone 2014). Male *S. boliviensis* and *S. sciureus* often form bachelor groups with conspecifics (Carretero-Pinzón et al. 2016; Mitchell 1990), although *S. collinsi* do not (Stone 2004). However, both *S. boliviensis* and *S. collinsi* show marked sexual segregation within groups, with males remaining at the periphery of the troop, especially during birthing season (Leger et al. 1981; Mendoza et al. 1978; Ruivo et al. 2017; Stone 2014).

Most social interactions occur within age-sex classes, such as play among infants and juveniles, and agonism among adult males (Zimpler-DeLorenzo and Stone 2011). Squirrel monkeys rarely engage in social grooming, and social bonds appear to be reinforced mostly by spatial proximity (Montague et al. 2014; Stone, pers. observation) and vocalizations (Biben and Suomi 1993; Biben and Symmes 1991; Boinski and Mitchell 1997). Play behavior in infants and juveniles is strongly tied to seasonality and resource availability, with less play occurring during the dry season or low food conditions (Stone 2008; Baldwin and Baldwin 1976).

TABLE 25.1

Comparison of Socioecological Parameters across Four Squirrel Monkey Species (*Saimiri* sp).

Trait	<i>S. oerstedii</i>	<i>S. boliviensis</i>	<i>S. sciureus</i>	<i>S. collinsi</i>	References
Group size	35–65	45–75	15–25	35–50	Boinski (1999)
Fruit patches fed on	Small, low density	Large, moderate density	Small, extremely dense	Medium, extremely dense	Boinski et al. (2002), Stone (2007a,b)
Dominance pattern	Egalitarian	Female dominant	Males dominant	Female dominant or co-dominant	Boinski et al. (2002), Stone (2004)
Female bonding	Weak	Strong	Weak	Unknown	Boinski (1999), Boinski et al. (2002)
Male–male aggression	Rare	Common during mating season	Common during mating season	Common during mating season	Baldwin (1969), Boinski and Mitchell (1994), Stone (2014)
Dispersal pattern	Both sexes disperse	Males disperse	Both sexes disperse	Unknown	Blair and Melnick (2012), Boinski et al. (2002), Boinski and Mitchell (1994)

Life History and Reproduction

Squirrel monkeys are characterized by a suite of reproductive and life history traits that distinguish them from other similarly sized New World primates (Garber and Leigh 1997; Hartwig 1996). For example, the genus is characterized by extremely high pre- and postnatal maternal investment, even though singletons are produced. Squirrel monkeys rank highest among Neotropical primates under 2 kg in infant care costs, including the cost of transporting heavy infants over long day ranges (Tardif 1994). The gestation period is long in squirrel monkeys (5 months; Stone 2004), similar to that of the larger capuchins (Hartwig 1996). Even when compared to the twin-producing callitrichines, estimated prenatal growth rates are high (Leighty et al. 2004; Ross 1991).

Not surprisingly, neonates are large, weighing 16%–20% of the mother's body weight (Elias 1977; Kaack et al. 1979; Milligan et al. 2008; Stone, unpublished trapping data; Williams et al. 1994) and have 60% of adult brain mass at birth (Elias 1977). In the laboratory squirrel monkeys produce twins at a rate of approximately 1 in 150 pregnancies (Williams, personal observation). When this occurs, one neonate is usually smaller than the other and does not survive. The first 3 months of life are characterized by rapid somatic and brain growth (Kaplan 1979; Leigh et al. 2004; Manocha 1979). Somatic growth rates are reduced at approximately 6 months of age, which corresponds to weaning in wild *S. collinsi* (Stone 2006). Interestingly, weaning age is highly variable among squirrel monkey species, ranging from 4 months in wild *S. oerstedii* (Boinski and Fragaszy 1989) to up to 18 months in *S. boliviensis* (Mitchell 1990). Interbirth intervals vary from 1 to 2 years, depending on the species (Zimble-DeLorenzo and Stone 2011). Despite having expensive infants, females generally receive little extra-maternal support. In some species, other adult females and juveniles can provide some degree of allocare. For example, in *S. collinsi* and *S. boliviensis*, juvenile females often carry infants for short periods (< 5 min), although never during rapid group travel (Baldwin 1969; Mitchell 1990;

Rosenblum 1972; Stone 2004). Mothers often “exchange” infants for short periods and females who lose their infants may carry the infants of other mothers (Ruivo et al. 2017). Allonursing has not been reported for wild populations, but has been observed in captivity for *S. collinsi* (Pinheiro 2015) and *S. boliviensis* (Williams et al. 1994). In contrast to rapid development during infancy, the juvenile stage (approximately 6 months to 3–5 years) is characterized by an extended period of relatively slow growth (Scollay 1980; Stone 2004). Females become sexually mature between 2.5 and 3.5 years of age, and males breed later, at 4.5–6 years (with variability among species; Zimble-DeLorenzo and Stone 2011).

Squirrel monkeys show a polygamous mating system (Boinski 1987; Mitchell 1990, Stone 2014), and show the most pronounced pattern of seasonal breeding of any Neotropical primate (Di Bitetti and Janson 2000; Table 25.2). The pronounced birth seasonality seen in the wild may or may not persist under captive conditions (P. Castro, personal communication; Trevino 2007; Williams et al. 1986; Williams and Abe 1986; Williams et al., 2010). Within-group birth synchronicity is also common in wild populations. In Costa Rica, females in a group give birth within a 1-week period (Boinski 1987), and in Eastern Amazonia, 80% of the females in a group can give birth in 1–2 nights (Stone 2004). Squirrel monkey males are approximately 30% larger than females (Boinski 1999; Mitchell 1990; Stone, unpublished trapping data), though sexual dimorphism increases in the mating season. This occurs because males gain water weight and adipose tissue on the shoulders, arms, and torso, acquiring a “fatted appearance” (Du Mond and Hutchinson 1967; Mendoza et al. 1978). Male fattening is associated with seasonal changes in hormone levels, rather than with increased food consumption, and may have evolved via sexual selection (Boinski 1992a; Stone 2014). An interesting phenomenon consistently observed during the mating season of *S. collinsi* is infant aggression toward adult males that approach the infant's mother. Infants often chase adult males that are attempting to mate, and males show a submissive response (Ruivo and Stone 2014).

TABLE 25.2

Comparison of Life History and Reproductive Traits across Four Squirrel Monkey Species (*Saimiri* sp).

Trait	<i>S. oerstedii</i>	<i>S. boliviensis</i>	<i>S. sciureus</i>	<i>S. collinsi</i>	References
Gestation length (months)	5	5	5	5	Mitchell (1990), Stone (2004)
Weaning age (months)	4	18	12–18	8	Boinski and Fragaszy (1989), L. Kauffman (pers. comm.), Mitchell (1990), Stone (2006)
Age at first reproduction for female (in years)	2.5	3.5	3.5	3.5	Boinski (1987), Boinski et al. (2005), Mitchell (1990), Stone (2004)
Age at first reproduction for males (in years)	4	6	4.5	4.5	Boinski (1987), Boinski et al. (2005), Mitchell (1990), Stone (2004)
Interbirth interval (yrs)	1	2	1	1–2	Boinski (1987), Boinski et al. (2005), Mitchell (1990), Stone (2004)
Duration of mating season (weeks)	8	8	10	9	Boinski (1987), Boinski et al. (2005), Mitchell (1990), Stone (2014)
Duration of birth season (weeks)	2	8	8	8	Boinski (1987), L. Kauffman (pers. comm.), Mitchell (1990), Stone (2004)
Infant care patterns	Allocare uncommon	Allocare and allonursing	Allocare and allonursing	Allocare common	Boinski (1986), L. Kauffman (pers. comm.), Mitchell (1990), Pinheiro (2015), Stone (2004)

Feeding Behavior

Squirrel monkeys are very active and spend most of their day foraging (Mitchell 1990; Paim et al. 2017; Pinheiro et al. 2013; Stone 2007a). They consume fruits and insects, and show opportunistic consumption of items, such as bird eggs and lizards (Janson and Boinski 1992). Squirrel monkeys are the most insectivorous of Neotropical primates, with up to 75% of foraging/feeding time spent on arthropods (Zimble-DeLorenzo and Stone 2011). Diet varies seasonally, with prey consumption increasing during periods of low fruit availability (Boinski 1986; Lima and Ferrari 2003; Paim et al. 2017; Stone 2007a). Foraging substrates used while searching for insects include live foliage, dead foliage, and leaf litter on the ground (Stone 2007a, Terborgh 1983). Direct intragroup feeding competition is generally low in *Saimiri*, perhaps due to the high proportion of insect prey in their diet, a resource that is difficult to monopolize. However, even when foraging on clumped fruit resources, such as *Scheelea* or *Attalea* palm fruits, individuals are generally tolerant of each other, eating in close proximity or plucking a fruit and leaving the infructescence to eat on a nearby tree branch (Baldwin and Baldwin 1972; Stone 2007b).

Sex differences in diet and foraging behavior have been observed in squirrel monkeys, with females spending more time feeding and foraging, and less time resting, compared to males (Boinski 1988; Montague et al. 2014). In addition, *S. collinsi* females consume more protein in the form of insects than do males (Ruivo et al. 2017), as well as a greater variety of fruit species (Stone 2018). Acquisition of foraging skills, including for large insects, occurs rapidly; in one field study, 1-year old juveniles were as efficient as adults at capturing prey (Stone 2006).

Communication

Few field studies have been conducted on communication (vocal or olfactory) in squirrel monkeys. As pointed out by Zimble-DeLorenzo and Stone (2011), studying communication in *Saimiri* is more feasible in captivity because of the large social groups in the wild. Five main groups of calls have been identified: peeps; twitters; chuck calls; cackles; and noisy calls (Zimble-DeLorenzo and Stone 2011). Studies of wild populations have shown that back-and-forth peeps and chuck calls are used in affiliative contexts, particularly by adult females that are not in close proximity (Boinski 1991; Boinski and Mitchell 1992). Chuck calls also may contain information on the caller's identity (Boinski and Mitchell 1997). In particular, these calls increase auditory contact in densely forested areas where visual contact is difficult, and such vocalizations also affect group cohesion and coordination of group movement (Boinski 1991; Boinski and Mitchell 1992). A specialized maternal vocalization of *S. boliviensis* is the "caregiver call", a call from adult females directed to their infants that is used to coordinate nursing bouts until infants are fully weaned (Boinski and Mitchell 1995). Alarm calls have also been described for wild squirrel monkeys (Stone 2004). One type of high-pitched alarm call is elicited when aerial predators approach the group. A second call is

the "nasal-honk" call, which is given in response to terrestrial predators, such as large constricting snakes, and even humans (Stone 2004).

Olfactory communication accounts for less than 1% of daily behavior time in field populations of *S. oerstedii* (Boinski 1992b). In *S. oerstedii* and *S. collinsi*, males use olfaction when evaluating the estrous condition of females, either by genital sniffing or by sniffing substrates recently used by females (Boinski 1992a; Stone 2014; Williams personal observation). Squirrel monkeys can discriminate urine odors of conspecifics (Laska and Hudson 1995), which has led to the suggestion that urine washing behavior (urinating on palms and rubbing the urine on the soles) functions as a mechanism of social communication, particularly sexual communication (Miller et al. 2008). However, recent field-work on *S. collinsi* by Jasper et al. (2020) has shown that urine washing is predominantly performed by juveniles, and may serve as an anxiety displacement mechanism (Miller et al. 2008; Schino et al. 2011).

Common Captive Behavior

Normal Behavior

Squirrel monkeys continue to show species-typical behavior in most captive settings and can adapt to many social settings; pair housing, as well as small and large social groups (Tardif et al. 2012; Williams et al. 2010). The patterns of male–female and female–female interactions described above can clearly be seen in captive colonies.

Behaviors Affected by Captivity

While squirrel monkeys are not prone to the abnormal behaviors seen in Old World monkeys, there are several behavioral and reproductive traits that need to be considered. The large neonatal sizes mentioned elsewhere in the chapter may necessitate c-sections and nursery rearing of the infants. Although nursery-reared infants can function in a breeding colony, producing and caring for infants at rates similar to dam-reared individuals (Williams, personal observation), they are behaviorally different, particularly when interacting with care staff. In a study that compared Primate Neonatal Neurobehavioral Assessment scores, Mulholland et al. (2020) reported that nursery-reared infants differed from dam-reared infants in motor maturity and control states. Nursery-reared infants had worse balance, slower responses, and were generally quieter than were dam-reared infants.

Squirrel monkeys in captivity live to their mid- to upper-twenties (Akkoç and Williams 2005), much longer than their wild counterparts. Older female squirrel monkeys, particularly those with many pregnancies over the course of their life, can develop an alopecia that resembles hair loss seen as a function of dominance and stressful interactions in other primate species. However, we have demonstrated that this alopecia is due to a chronic telogen effluvium, related to high levels of estrogen hormones, not to physical hair plucking (Horenstein et al. 2005).

Ways to Maintain Behavioral Health

Environment

Several factors related to Neotropical primate sociality and natural living conditions play a role in determining functionally appropriate captive environments (FACES, see Schapiro, this volume) and related management procedures. The social structure of squirrel monkeys, while superficially similar, is significantly different from the typical social structures of Old World monkeys, and housing conditions need to reflect this. Decisions related to enclosure size need to reflect the fact that squirrel monkeys are primarily arboreal animals and the enclosure should include vertical space for climbing, quadrupedal running, and jumping. The *Guide for the Care and Use of Laboratory Animals* (National Research Council 2011) classifies squirrel monkeys as type 2 primates, requiring 3 ft² (0.28 m²) for each animal. Figure 25.1 illustrates squirrel monkey housing with multiple layers of travel paths and perches. All squirrel monkeys should be housed with a temperature range of approximately 75°F–82°F (24°C–27°C), with relative humidity between 40% and 60%. Lower temperatures or humidity levels can lead to upper respiratory problems (Abee 1985).

Since squirrel monkeys are arboreal, the provision of three-dimensional space and differing perch arrangements can vary the cage environment and increase the activity of the animals.

Runs or large pens can be used to allow the squirrel monkeys to move over longer distances. Pens measuring 4' wide by 6' tall by 14' deep can house up to 15 animals. Periodically rearranging the perches and providing new materials is an easy way to provide novelty.

Social Groupings

Saimiri should be housed in species-typical social groups in captivity whenever possible. In the wild, squirrel monkeys live in large social groups containing 20–50 animals (Baldwin and Baldwin 1971; Boinski, 1999), with multiple males and females of different ages. Our experience in captivity is that it is difficult for more than one male to live in a social group when space is limited. *S. boliviensis* females typically stay within the natal social group and males emigrate after they reach 1.5–2 years of age. *S. sciureus* females are more flexible and may emigrate after their first breeding season (Boinski et al. 2002). Removing the males from their natal group when they reach approximately 1.5–2 years old can help reduce intragroup aggression and prevent inbreeding, as the males continue to mature sexually. At this age, the males will usually form an all-male group without any aggression.

Adult females generally maintain social stability in squirrel monkey groups. Saltzman et al. (1989) reported that all age-sex classes in *S. sciureus* spend more time in proximity to adult



FIGURE 25.1 Squirrel monkey (*Saimiri sciureus*) housing with multiple layers of perches and resting points that give them different travel paths. Off the back, there are feeding enrichment devices; a black grooming mat (just below the mid-point) and a feeding trough (just above the upper perch). There is also a piece of destructible enrichment on the ceiling; a paper bag that was filled with food enrichment.

females than any other age-sex class. During the nonbreeding season, South American squirrel monkey social groups will segregate by sex, with males remaining near the periphery of the social group (Baldwin and Baldwin 1972; Hopf 1978; Lyons et al 1992; Stone 2014; Vaitl 1977). Seasonal sexual segregation in captivity is generally expressed in vertical separation of the males and females; with females occupying the upper levels of the housing, relegating the males to perches and structures closer to the ground.

S. sciureus and *S. boliviensis* will fight unfamiliar conspecifics (Williams and Abee 1988), suggesting that frequent movements of animals between social groups should be avoided. Squirrel monkeys that must live separately from their social group for experimental or clinical purposes should be pair housed. If pair housing is not possible, animals should be provided with visual and/or auditory access to conspecifics (Schuler and Abee 2005). Forming new pairs or small groups of females is rarely a problem with squirrel monkeys. Introducing all the females to one another simultaneously will lessen the probability of an individual animal becoming the target of aggression. Male pairs or triplets can be housed together if care is taken when introducing the animals. Juvenile males will bond together quickly, and adult males will tolerate others, if there are no females housed in visual contact. When introducing new animals to an established social group, it is important to give members of the social group contact with the new animal in small subgroup situations, prior to introducing the entire group. Placing the new animal in a neutral cage with a small subset of the social group, and swapping out social group members periodically, will give the new animal an opportunity to establish relationships, prior to living in the whole group. This process will work for females during the entire year and for males during the breeding season only. Males can be difficult to introduce to a new group of females during the nonbreeding season, when they are normally segregated from the female social core. Increased levels of aggression should be expected at the beginning and end of the breeding season, when hormonal changes lead to increases in social interactions between males and females. The squirrel monkey breeding season occurs during short days; in the northern hemisphere, it typically runs from January through April for outdoor-housed colonies, and into May and June in indoor colonies (Schiml et al. 1996; Trevino 2007; Williams et al. 2010).

Enrichment and Feeding Strategies

Squirrel monkeys are omnivores in the wild and may spend up to 75% of their time eating as they move through the forest. Squirrel monkeys' captive diets can be supplemented with many fruits and vegetables, depending on seasonal availability. Additional items such as Gatorade®, multivitamins, and food pellet rewards may be added for experimental or clinical reasons.

Squirrel monkeys are naturally active and readily manipulate objects in their enclosure. Destructible enrichment and devices that require time to open or manipulate can be provided to occupy the animals' time. Small objects, such as plastic golf balls and polyvinyl chloride (PVC) plumbing joints, can be employed, with or without food enrichment, to increase



FIGURE 25.2 *Saimiri boliviensis* juvenile manipulating food enrichment from a device made from an old syringe cover. The device has holes cut into the side just bigger than the food item to be retrieved.

activity rates. Feeding or foraging boards can also be used, as the presence of artificial turf forage boards has been shown to increase activity (Fekete et al. 2000). Because squirrel monkeys are naturally inquisitive and active, the provision of multiple perches, swings, and other hanging devices will increase activity levels. Figure 25.2 shows a squirrel monkey puzzling over a mealworm feeder. In all caging conditions, food items and perch arrangements can be used to vary the environment of the animals and, consequently, increase activity levels and sensory stimulation. Perches and manipulanda should be rotated and replaced routinely to prevent habituation.

Communication

Communication between animals within a given social group includes olfactory, visual, and vocal signals. Olfaction is most important during the breeding and birthing seasons. Vocal signals are very important for squirrel monkeys, with infants possessing a wide repertoire of sounds, including grumbles, tucks, purrs, chucks, and peeps (Biben and Symmes 1986) to communicate their wellbeing to the mother. In adults, several calls are used to signal alarm, display general disturbance or excitement, or establish contact when group members are visually separated. Visual cues are of primary importance in a number of displays intended to assert dominance or reduce tension between individuals. Visual cues involving facial expressions

can be associated with fear or aggression. In a captive enclosure, visual barriers that a submissive monkey can use to break the stare of a more aggressive monkey should be provided. These “hide-boxes” can be made from a piece of a large diameter PVC pipe or another opaque material. However, remember that caregivers and researchers must be able to see the animals for health checks and other observations. Males use scent to determine the receptivity of females, and females use scent to identify individual infants. When cleaning squirrel monkey enclosures, it is preferable to avoid heavily scented products.

Training

Squirrel monkeys have a long history in cognitive research (Gazes et al. 2018; Thomas and Frost 1983; Woodburne and Rieke 1966) and can readily be trained using positive reinforcement training techniques (Gillis et al. 2012; Rogge et al. 2013). Squirrel monkeys can be trained to voluntarily participate in many aspects of their care, including the presentation of body parts, sitting on a scale, or moving from one cage to another on command. Rogge et al. (2013) found that it only took a few sessions to train the animals to present their hands for inspection on command, even when they were trained in their social group. They can also be trained to participate in more complex tasks, such as using a joystick and computer screen (Judge et al. 2005; Washburn et al. 1989), or engaging in token exchange procedures (Hopper et al. 2013; Talbot et al. 2011.). When training squirrel monkeys, it is important to remember to use very small portions of food as reinforcers, because the animals can quickly become satiated and stop working if given too much food.

Special Situations

Investigators not accustomed to using small nonhuman primates in their research should also be aware of squirrel monkey characteristics that may require alteration of experimental procedures. Squirrel monkeys are predisposed to hypoglycemia (Abee 1985; Brady 1990, Brady et al. 1991). The normal blood glucose concentration for adult squirrel monkeys is 80 ± 28 mg/dL (Loeb and Quimby 1989). Prolonged research procedures, fasting, or debilitating conditions that result in anorexia may place animals at risk for a hypoglycemic crisis. Their small size, low body fat reserves, and long extremities all contribute to rapid heat loss when they are anaesthetized or debilitated. The body temperature of at-risk animals should be monitored for body temperature on a regular basis. Awake, restrained squirrel monkeys normally have a body temperature of 38°C – 39.5°C , while healthy, active, struggling animals may rapidly increase their body temperatures to as high as 41°C .

Although social housing of squirrel monkeys is desirable, fight-related injuries do occur in such housing, especially when social groups are first established. Close attention to group compatibility, careful supervision of newly established groups, and provision of hiding places in animal enclosures can help reduce such injuries or prevent them altogether (Williams and Abee 1988). When wounds do occur, they can usually be divided into crushing-type injuries (more commonly inflicted by female squirrel monkeys) or lacerations (commonly inflicted by males) (Ruiz et al. 2005).

Conclusions and Recommendations

Squirrel monkeys have many qualities that make them an important biomedical research model. Their small size, ease of handling, and lack of viruses that are pathogenic in humans are particularly desirable for studies requiring frequent handling without sedation. Our aim in this chapter is to provide a background through which you can better appreciate the behavior and biology of squirrel monkeys. Each species has a unique set of environmental and social needs that must be met for the animals to thrive in captivity. Even within a single taxonomic order, such as primates, there are major differences among genera in requirements for functionally appropriate captive environments. When designing appropriate housing for squirrel monkeys it is imperative to consider their ecology, social structure, and social organization. Squirrel monkeys are small arboreal insectivores, that are constantly in motion, and that have complex social needs. By designing their homes to match their biological needs, you will have a healthier, less stressed research animal.

REFERENCES

- Abee, C. R. 1985. “Medical care and management of the squirrel monkey.” In *Handbook of Squirrel Monkey Research*, edited by L. Roseblum and C. Coe, 447–488. New York: Plenum Press.
- Abee, C. R. 2000. “Squirrel monkey (*Saimiri* spp.) research and resources.” *ILAR Journal* 41 (1):2–9. doi:10.1093/ilar.41.1.2.
- Achat-Mendes, C., Platt, D.M. and Spealman, R.D. 2012. “Antagonism of metabotropic glutamate 1 receptors attenuates behavioral effects of cocaine and methamphetamine in squirrel monkeys. *Journal of Pharmacology and Experimental Therapeutics*, 343 (1):214–224.
- Akkoç, C. C., and L. E. Williams. 2005. “Population modeling for a captive squirrel monkey colony.” *American Journal of Primatology* 65 (3):239–254.
- Alves, F. A., M. Pelajo-Machado, P. R. Totino, M. T. Souza, E. C. Goncalves, M. P. Schneider, J. A. Muniz, M. A. Krieger, M. C. Andrade, C. T. Daniel-Ribeiro, and L. J. Carvalho. 2015. “Splenic architecture disruption and parasite-induced splenocyte activation and energy in *Plasmodium falciparum*-infected *Saimiri sciureus* monkeys.” *Malar Journal* 14:128. doi:10.1186/s12936-015-0641-3.
- Anderson, D. C., S. A. Lapp, S. Akinyi, E. V. Meyer, J. W. Barnwell, C. Korir-Morrison, and M. R. Galinski. 2015. “*Plasmodium vivax* trophozoite-stage proteomes.” *Journal of Proteomics* 115:157–76. doi:10.1016/j.jprot.2014.12.010.
- Anderson, D. C., S. A. Lapp, J. W. Barnwell, and M. R. Galinski. 2017. “A large scale *Plasmodium vivax*-*Saimiri boliviensis* trophozoite-schizont transition proteome.” *PLoS One* 12 (8):e0182561. doi:10.1371/journal.pone.0182561.
- Baldwin, J. D. 1969. “The ontogeny of social behavior of squirrel monkeys (*Saimiri sciureus*) in a seminatural environment.” *Folia Primatologica* 11:35–79.
- Baldwin, J. D., and J. Baldwin. 1972. “The ecology and behavior of squirrel monkeys (*Saimiri oerstedii*) in a natural forest in western Panama.” *Folia Primatologica* 18 (3):161–184. doi:10.1159/000155478.

- Baldwin, J. D., and J. I. Baldwin. 1976. "Effects of food ecology on social play: A laboratory simulation." *Z Tierpsychologie* 40 (1):1–14. doi:10.1111/j.1439-0310.1976.tb00922.x.
- Baldwin, J. D., and J. I. Baldwin. 1971. "Squirrel monkeys (*Saimiri*) in natural habitats in Panama, Colombia, Brazil, and Peru." *Primates* 12 (1):45–61.
- Biben, M., and S. J. Suomi. 1993. "Lessons from primate play." In *Parent-Child Play: Descriptions and Implications*, edited by K. MacDonald, 185–196. New York: SUNY Press.
- Biben, M., and D. Symmes. 1986. "Play vocalizations of squirrel monkeys (*Saimiri sciureus*)." *Folia Primatologica* 46 (3):173–182. doi:10.1159/000156250.
- Biben, M., and D. Symmes. 1991. "Playback studies of affiliative vocalizing in captive squirrel-monkeys - familiarity as a cue to response." *Behaviour* 117 (1/2):1–19. doi:10.1163/156853991x00094.
- Blair, M. E., and D. J. Melnick. 2012. "Genetic evidence for dispersal by both sexes in the Central American Squirrel Monkey, *Saimiri oerstedii citrinellus*." *American Journal of Primatology* 74 (1):37–47. doi:10.1002/ajp.21007.
- Boinski, S. 1987. "Birth synchrony in squirrel-monkeys (*Saimiri-Oerstedii*) - a strategy to reduce neonatal predation." *Behavioral Ecology and Sociobiology* 21 (6):393–400. doi:10.1007/Bf00299934.
- Boinski, S. 1988. "Sex-differences in the foraging behavior of squirrel-monkeys in a seasonal habitat." *Behavioral Ecology and Sociobiology* 23 (3):177–186. doi:10.1007/Bf00300352.
- Boinski, S. 1989. "The effects of body size, morphological specializations, and food distribution on foraging behavior in the cebinae." *American Journal of Physical Anthropology* 78 (2):195–195.
- Boinski, S. 1991. "The coordination of spatial position - a field-study of the vocal behavior of adult female squirrel-monkeys." *Animal Behaviour* 41:89–102. doi:10.1016/S0003-3472(05)80505-6.
- Boinski, S. 1992a. "Monkeys with inflated sex appeal." *Natural History* 101(7):42–49.
- Boinski, S. 1992b. "Olfactory communication among costa-rican squirrel-monkeys - a field-study." *Folia Primatologica* 59 (3):127–136. doi:10.1159/000156650.
- Boinski, S. 1994. "Affiliation patterns among male costa-rican squirrel-monkeys." *Behaviour* 130:191–209. doi:10.1163/156853994x00523.
- Boinski, S. 1999. "The social organizations of squirrel monkeys: Implications for ecological models of social evolution." *Evolutionary Anthropology* 8 (3):101–112. doi:10.1002/(Sici)1520-6505(1999)8:3<101::Aid-Evan5>3.0.Co;2-O.
- Boinski, S., E. Ehmke, L. Kauffman, S. Schet, and A. Vreedzaam. 2005. "Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii*, *S-boliviensis* and *S-sciureus*): II. Within-species and local variation." *Behaviour* 142:633–677. doi:10.1163/1568539054352860.
- Boinski, S., and D. M. Fragaszy. 1989. "The ontogeny of foraging in squirrel-monkeys, *saimiri-oerstedii*." *Animal Behaviour* 37:415–428. doi:10.1016/0003-3472(89)90089-4.
- Boinski, S. H. 1986. "The ecology of squirrel monkeys in Costa Rica." *Dissertation Abstracts International* B47 (5):1893.
- Boinski, S., and C. L. Mitchell. 1992. "Ecological and social-factors affecting the vocal behavior of adult female squirrel-monkeys." *Ethology* 92 (4):316–330. doi:10.1111/j.1439-0310.1992.tb00969.x.
- Boinski, S., and C. L. Mitchell. 1994. "Male residence and association patterns in Costa Rican squirrel monkeys (*Saimiri oerstedii*)." *American Journal of Primatology* 34 (2):157–169. doi:10.1002/ajp.1350340207.
- Boinski, S., and C. L. Mitchell. 1995. "Wild squirrel monkey (*Saimiri sciureus*) "caregiver" calls: Contexts and acoustic structure." *American Journal of Primatology* 35 (2):129–137. doi:10.1002/ajp.1350350205.
- Boinski, S., and C. L. Mitchell. 1997. "Chuck vocalizations of wild female squirrel monkeys (*Saimiri sciureus*) contain information on caller identity and foraging activity." *International Journal of Primatology* 18 (6):975–993. doi:10.1023/A:1026300314739.
- Boinski, S., K. Sughrue, L. Selvaggi, R. Quatrone, M. Henry, and S. Cropp. 2002. "An expanded test of the ecological model of primate social evolution: Competitive regimes and female bonding in three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*)." *Behaviour* 139:227–261. doi:10.1163/156853902760102663.
- Brady, A. G., G. E. Hutto, L. E. Williams, and C. R. Abee. 1991. "Comparison of two tests for identifying squirrel monkey infants at risk for hypoglycemia." *AALAS Bulletin* 30(4):28–29.
- Brady, A. G., L. E. Williams, and C. R. Abee. 1990. "Hypoglycemia of squirrel monkey neonates: implications for infant survival." *Laboratory Animal Science* 40 (3):262–5.
- Carretero-Pinzón, X., T. R. Defler, and M. Ruiz-Garcia. 2016. "How does the Colombian squirrel monkey cope with habitat fragmentation? Strategies to survive in small fragments." In: *Phylogeny, Molecular Population Genetics, Evolutionary Biology and Conservation of the Neotropical Primates*, edited by M. Ruiz-Garcia and J.M. Shostell, 2–16. Nova Science Publisher: New York.
- Carretero-Pinzón, X., T.R. Defler, C.A. McAlpine, and J.R. Rhodes. 2017. "The influence of landscape relative to site and patch variables on primate distributions in the Colombian Llanos." *Landscape Ecology* 32 (4):883–896. doi:10.1007/s10980-017-0493-z.
- Cheung, S. W., C. A. Atencio, E. R. J. Levy, R. C. Froemke, and C. E. Schreiner. 2017. "Anisomorphic cortical reorganization in asymmetric sensorineural hearing loss." *Journal of Neurophysiology* 118 (2):932–948. doi:10.1152/jn.00119.2017.
- Chiou, K. L., L. Pozzi, J. W. Lynch Alfaro, and A. Di Fiore. 2011. "Pleistocene diversification of living squirrel monkeys (*Saimiri* spp.) inferred from complete mitochondrial genome sequences." *Molecular Phylogenetics and Evolution* 59 (3):736–745. doi:10.1016/j.ympev.2011.03.025.
- Collins, W. E., J. S. Sullivan, E. Strobert, G. G. Galland, A. Williams, D. Nace, T. Williams, and J. W. Barnwell. 2009. "Studies on the Salvador I strain of *Plasmodium vivax* in non-human primates and anopheline mosquitoes." *American Journal of Tropical Medicine Hygiene* 80 (2):228–235.
- Cunha, J. A., L. J. M. Carvalho, C. Bianco-Junior, M. C. R. Andrade, L. R. Pratt-Riccio, E. K. P. Riccio, M. Pelajo-Machado, I. J. da Silva, P. Druilhe, and C. T. Daniel-Ribeiro. 2017. "Increased plasmodium falciparum parasitemia in non-splenectomized *saimiri sciureus* monkeys treated with clodronate liposomes." *Front Cell Infect Microbiol* 7:408. doi:10.3389/fcimb.2017.00408.

- de Souza, H., E. H. Costa-Correa, C. Bianco-Junior, M. C. R. Andrade, J. D. C. Lima-Junior, L. R. Pratt-Riccio, C. T. Daniel-Ribeiro, and P. R. R. Totino. 2017. "Detection of signal regulatory protein alpha in *Saimiri sciureus* (squirrel monkey) by anti-human monoclonal antibody." *Frontiers in Immunology* 8:1814. doi:10.3389/fimmu.2017.01814.
- Desai, R. I., M. R. Doyle, S. L. Withey, and J. Bergman. 2016a. "Nicotinic effects of tobacco smoke constituents in nonhuman primates." *Psychopharmacology* 233 (10):1779–1789. doi:10.1007/s00213-016-4238-5.
- Desai, R. I., K. A. Sullivan, S. J. Kohut, and J. Bergman. 2016b. "Influence of experimental history on nicotine self-administration in squirrel monkeys." *Psychopharmacology* 233 (12):2253–2263. doi:10.1007/s00213-016-4274-1.
- Di Bitetti, M. S., and C. H. Janson. 2000. "When will the stork arrive? Patterns of birth seasonality in neotropical primates." *American Journal of Primatology* 50 (2): 109–130. doi:10.1002/(sici)1098-2345(200002)50:2<109::Aid-ajp2>3.0.Co;2-w.
- Du Mond, F. V., and T. C. Hutchinson. 1967. "Squirrel monkey reproduction: The "fatted" male phenomenon and seasonal spermatogenesis." *Science* 158:1067–1070 doi:10.1126/science.158.3804.1067.
- Elias, M. F. 1977. "Relative maturity of cebus and squirrel monkeys at birth and during infancy." *Developmental Psychobiology* 10 (6):519–528. doi:10.1002/dev.420100605.
- Fekete, J. M., J. L. Norcross, and J. D. Newman. 2000. "Artificial turf foraging boards as environmental enrichment for pair-housed female squirrel monkeys." *Contemporary Topics in Laboratory Animal Science* 39 (2):22–26.
- Fleagle, J. G., and R. A. Mittermeier. 1980. "Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys." *American Journal of Physical Anthropology* 52 (3):301–314. doi:10.1002/ajpa.1330520302.
- Frechette, J. L., K. E. Sieving, and S. Boinski. 2014. "Social and personal information use by squirrel monkeys in assessing predation risk." *American Journal of Primatology* 76 (10):956–66. doi:10.1002/ajp.22283.
- Gao, Y., P. Parvathaneni, K. G. Schilling, F. Wang, I. Stepniewska, Z. Xu, A. S. Choe, Z. Ding, J. C. Gore, L. M. Chen, B. A. Landman, and A. W. Anderson. 2016. "A 3D high resolution ex vivo white matter atlas of the common squirrel monkey (*Saimiri sciureus*) based on diffusion tensor imaging." *Proceedings SPIE – The International Society for Optical Engineering* 9784. doi:10.1117/12.2217325.
- Garber, P. A., and S. R. Leigh. 1997. "Ontogenetic variation in small-bodied New World primates: Implications for patterns of reproduction and infant care." *Folia Primatologica* 68 (1):1–22. doi:10.1159/000157226.
- Gazes, R. P., A. R. Billas, and V. Schmitt. 2018. "Impact of stimulus format and reward value on quantity discrimination in capuchin and squirrel monkeys." *Learning and Behavior* 46 (1):89–100. doi:10.3758/s13420-017-0295-9.
- Gillis, T. E., A. C. Janes, and M. J. Kaufman. 2012. "Positive reinforcement training in squirrel monkeys using clicker training." *American Journal of Primatology* 74 (8):712–720. doi:10.1002/ajp.22015.
- Gunalan, K., J. M. Sa, R. R. Moraes Barros, S. L. Anzick, R. L. Caleon, J. P. Mershon, K. Kanakabandi, M. Paneru, K. Virtaneva, C. Martens, J. W. Barnwell, J. M. Ribeiro, and L. H. Miller. 2019. "Transcriptome profiling of Plasmodium vivax in Saimiri monkeys identifies potential ligands for invasion." *Proceedings of the National Academy of Sciences of the United States of America* 116 (14):7053–7061. doi:10.1073/pnas.1818485116.
- Hartwig, W. C. 1996. "Perinatal life history traits in New World monkeys." *American Journal of Primatology* 40 (2):99–130. doi:10.1002/(Sici)1098-2345(1996)40:2<99::Aid-Ajp1>3.0.Co;2-V.
- Hopf, S. 1978. "Huddling subgroups in captive squirrel monkeys and their changes in relation to ontogeny." *Biology of Behavior* 3:147–162.
- Hopper, L., A. Holmes, L. Williams, and S. Brosnan. 2013. "Dissecting the mechanisms of squirrel monkey (*Saimiri boliviensis*) social learning." *PeerJ* 1:e13. doi:10.7717/peerj.13.
- Horenstein, V.D., L. E. Williams, A.R. Brady, C.R. Abee, and M.G. Horenstein. 2005. "Age-related diffuse chronic telogen effluvium-type alopecia in female squirrel monkeys (*Saimiri boliviensis boliviensis*)." *Comparative Medicine* 55 (2):169–174.
- Janson, C. H., and S. Boinski. 1992. "Morphological and behavioral adaptations for foraging in generalist primates: The case of the cebines." *American Journal of Physical Anthropology* 88 (4):483–498. doi:10.1002/ajpa.1330880405.
- Jasper, J.M, Delacath, N.A., Aghababian, S.C., Brown, C.E. and Stone, A.I. 2020. Why do squirrel monkeys urine wash? A field study of Saimiri collinsi in Eastern Amazonia, Brazil. *American Journal of Primatology* 82 (S1): 58.
- Judge, P. G., T. A. Evans, and D. K. Vyas. 2005. "Ordinal representation of numeric quantities by brown capuchin monkeys (*Cebus apella*)." *Journal of Experimental Psychology: Animal Behavior Process* 31 (1):79–94. doi:10.1037/0097-7403.31.1.79.
- Kaack, B., L. Walker, K. R. Brizzee, and R. H. Wolf. 1979. "Comparative normal levels of serum triiodothyronine and throxine in nonhuman primates." *Laboratory Animal Science* 29:191–194.
- Kangas, B. D., and J. Bergman. 2014. "Operant nociception in nonhuman primates." *Pain* 155 (9):1821–1828. doi:10.1016/j.pain.2014.06.010.
- Kangas, B. D., M. Z. Leonard, V. G. Shukla, S. O. Alapafuja, S. P. Nikas, A. Makriyannis, and J. Bergman. 2016. "Comparisons of Delta9-tetrahydrocannabinol and anandamide on a battery of cognition-related behavior in nonhuman primates." *Journal of Pharmacology Experimental Therapeutics* 357 (1):125–33. doi:10.1124/jpet.115.228189.
- Kaplan, J. N. 1979. "Growth and development of infant squirrel monkeys during the first six months of life." In *Nursery Care of Nonhuman Primates*, edited by G.C. Ruppenthal and D.J. Reese, 153–164. Springer US: Boston, MA.
- Laska, M., and R. Hudson. 1995. "Ability of female squirrel-monkeys (*saimiri-sciureus*) to discriminate between conspecific urine odors." *Ethology* 99 (1):39–52.
- Leger, D. W., W. A. Mason, and D. M. Fragaszy. 1981. "Sexual segregation, cliques, and social power in squirrel-monkey (*Saimiri*) groups." *Behaviour* 76 (3–4):163–181. doi:10.1163/156853981x00068.
- Leighty, K. A., G. Byrne, D. M. Fragaszy, E. Visalberghi, C. Welker, and I. Lussier. 2004. "Twinning in tufted capuchins (*Cebus apella*): Rate, survivorship, and weight gain." *Folia Primatologica* 75 (1):14–8. doi:10.1159/000073425.

- Levi, T., K. M. Silvius, L. F. B. Oliveira, A. R. Cummings, and J. M. V. Fragoso. 2013. "Competition and facilitation in the capuchin-squirrel monkey relationship." *Biotropica* 45 (5):636–643. doi:10.1111/btp.12046.
- Lima, E. M., and S. F. Ferrari. 2003. "Diet of a free-ranging group of squirrel monkeys (*Saimiri sciureus*) in eastern brazilian amazonia." *Folia Primatologica* 74 (3):150–158. doi:10.1159/000070648.
- Loeb, W. F., and F. W. Quimby, eds. 1989. *The Clinical Chemistry of Laboratory Animals*. Pergamon Press: New York.
- Lynch Alfaro, J. W., J. P. Boubli, F. P. Paim, C. C. Ribas, M. N. Silva, M. R. Messias, F. Rohe, M. P. Mercês, J. S. Silva Junior, C. R. Silva, G. M. Pinho, G. Koshkarian, M. T. Nguyen, M. L. Harada, R. M. Rabelo, H. L. Queiroz, M. E. Alfaro, and I. P. Farias. 2015. "Biogeography of squirrel monkeys (genus *Saimiri*): South-central Amazon origin and rapid pan-Amazonian diversification of a lowland primate." *Molecular Phylogenetics and Evolution* 82 Pt B:436–454. doi:10.1016/j.ympev.2014.09.004.
- Lyons, D. M., S. P. Mendoza, and W. A. Mason. 1992. "Sexual segregation in squirrel monkeys (*Saimiri sciureus*): A transactional analysis of adult social dynamics." *Journal of Comparative Psychology* 106 (4):323–30. doi:10.1037/0735-7036.106.4.323.
- Malone, B. J., R. E. Beitel, M. Vollmer, M. A. Heiser, and C. E. Schreiner. 2015. "Modulation-frequency-specific adaptation in awake auditory cortex." *Journal of Neuroscience* 35 (15):5904–5916. doi:10.1523/JNEUROSCI.4833-14.2015.
- Malone, B. J., M. A. Heiser, R. E. Beitel, and C. E. Schreiner. 2017. "Background noise exerts diverse effects on the cortical encoding of foreground sounds." *Journal of Neurophysiology* 118 (2):1034–1054. doi:10.1152/jn.00152.2017.
- Mancuso, K., W. W. Hauswirth, Q. Li, T. B. Connor, J. A. Kuchenbecker, M. C. Mauck, J. Neitz, and M. Neitz. 2009. "Gene therapy for red-green colour blindness in adult primates." *Nature* 461 (7265):784–787. doi:10.1038/nature08401.
- Manocha, S. L. 1979. "Physical growth and brain development of captive-bred male and female squirrel monkeys, *Saimiri sciureus*." *Experientia* 35 (1):96–98. doi:10.1007/BF01917901.
- Marsh, H. L., A. Q. Vining, E. K. Levandoski, and P. G. Judge. 2015. "Inference by exclusion in lion-tailed macaques (*Macaca silenus*), a hamadryas baboon (*Papio hamadryas*), capuchins (*Sapajus apella*), and squirrel monkeys (*Saimiri sciureus*)." *Journal of Comparative Psychology* 129 (3):256–267. doi:10.1037/a0039316.
- Mendoza, S. P., E. L. Lowe, J. M. Davidson, and S. Levine. 1978. "Annual cyclicality in the squirrel-monkey (*Saimiri sciureus*) - relationship between testosterone, fattening, and sexual-behavior." *Hormones and Behavior* 11 (3):295–303. doi:10.1016/0018-506x(78)90033-8.
- Mercês, M. P., J. W. Lynch Alfaro, W. A. Ferreira, M. L. Harada, and J. S. Silva Junior. 2015. "Morphology and mitochondrial phylogenetics reveal that the Amazon River separates two eastern squirrel monkey species: *Saimiri sciureus* and *S. collinsi*." *Molecular Phylogenetics and Evolution* 82 (Pt B):426–435. doi:10.1016/j.ympev.2014.09.020.
- Migliaccio, A. A., L. B. Minor, and C. C. Della Santina. 2010. "Adaptation of the vestibulo-ocular reflex for forward-eyed foveate vision." *Journal of Physiology* 588 (Pt 20):3855–3867. doi:10.1113/jphysiol.2010.196287.
- Milich, K. M., B. J. Koestler, J. H. Simmons, P. N. Nehete, A. Di Fiore, L. E. Williams, J. P. Dudley, J. Vanchiere, and S. M. Payne. 2018. "Methods for detecting Zika virus in feces: A case study in captive squirrel monkeys (*Saimiri boliviensis boliviensis*)." *PLoS One* 13 (12):e0209391. doi:10.1371/journal.pone.0209391.
- Miller, K.R., K. Laszlo, and S.J. Suomi. 2008. "Why do captive tufted capuchins (*Cebus apella*) urine wash?" *American Journal of Primatology* 70 (2):119–126. doi:10.1002/ajp.20462.
- Milligan, L. A., S. V. Gibson, L. E. Williams, and M. L. Power. 2008. "The composition of milk from Bolivian squirrel monkeys (*Saimiri boliviensis boliviensis*)." *American Journal of Primatology* 70 (1):35–43. doi:10.1002/ajp.20453.
- Mitchell, C. L. 1990. "The ecological basis for female social dominance: A behavioral study of the squirrel monkey (*Saimiri sciureus*) in the wild." *Dissertation Abstracts International* B51(4):1614.
- Mitchell, C.L., S. Boinski, and C. P. van Schaik. 1991. "Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedii* and *S. sciureus*)." *Behavioral Ecology and Sociobiology* 28:55–60.
- Mittermeier, R. A., and M. G. van Roosmalen. 1981. "Preliminary observations on habitat utilization and diet in eight Surinam Monkeys." *Folia Primatologica* 36 (1–2):1–39. doi:10.1159/000156007.
- Montague, M.J., T.R. Disotell, and A. Di Fiore. 2014. "Population genetics, dispersal, and kinship among wild squirrel monkeys (*Saimiri sciureus macrodon*): Preferential association between closely related females and its implications for insect prey capture success." *International Journal of Primatology* 35 (1):169–187. doi:10.1007/s10764-013-9723-7.
- Mowery, T. M., R. M. Sarin, P. V. Kostylev, and P. E. Garraghty. 2015. "Differences in AMPA and GABAA/B receptor subunit expression between the chronically reorganized cortex and brainstem of adult squirrel monkeys." *Brain Research* 1611:44–55. doi:10.1016/j.brainres.2015.03.010.
- Mulholland, M.M., L. E. Williams, and C. R. Abee. 2020. "Rearing condition may alter neonatal development of captive Bolivian squirrel monkeys (*Saimiri boliviensis boliviensis*)." *Developmental Psychobiology*. doi:10.1002/dev.21960.
- Murray, S. G., and J. E. King. 1973. "Snake avoidance in feral and laboratory reared squirrel-monkeys." *Behaviour* 47 (3–4):281. doi:10.1163/156853973x00120.
- National Research Council. 2011. *Guide for the Care and Use of Laboratory Animals*. 8th ed. National Academy Press: Washington, DC.
- Neitz, M., and J. Neitz. 2014. "Curing color blindness--mice and nonhuman primates." *Cold Spring Harbor Perspectives in Medicine* 4 (11):a017418. doi:10.1101/cshperspect.a017418.
- Obaldia, N., E. Meibalan, J. M. Sa, S. Ma, M. A. Clark, P. Mejia, R. R. Moraes Barros, W. Otero, M. U. Ferreira, J. R. Mitchell, D. A. Milner, C. Huttenhower, D. F. Wirth, M. T. Duraisingh, T. E. Wellems, and M. Marti. 2018. "Bone marrow is a major parasite reservoir in plasmodium vivax infection." *mBio* 9 (3):e00625-18. doi:10.1128/mBio.00625-18.
- Paim, F. P., J. D. E. Silva, J. Valsecchi, M. L. Harada, and H. L. de Queiroz. 2013. "Diversity, geographic distribution and conservation of squirrel monkeys, saimiri (primates, cebidae),

- in the floodplain forests of central amazon." *International Journal of Primatology* 34 (5):1055–1076. doi:10.1007/s10764-013-9714-8.
- Paim, F. P., C. A. Chapman, H. L. de Queiroz, and A. P. Paglia. 2017. "Does resource availability affect the diet and behavior of the vulnerable squirrel monkey, *Saimiri vanzolinii*?" *International Journal of Primatology* 38 (3):572–587. doi:10.1007/s10764-017-9968-7.
- Peres, C. A. 1994. "Primate responses to phenological changes in an amazonian terra-firme forest." *Biotropica* 26 (1):98–112. doi:10.2307/2389114.
- Peterson, M. S., C. J. Joyner, R. J. Cordy, J. L. Salinas, D. Machiah, S. A. Lapp, H. C. Ma, E. V. S. Meyer, S. Gumber, and M. R. Galinski. 2019. "*Plasmodium vivax* parasite load is associated with histopathology in *Saimiri boliviensis* with findings comparable to *P. vivax* pathogenesis in humans." *Open Forum Infectious Diseases* 6 (3):ofz021. doi:10.1093/ofid/ofz021.
- Pinheiro, T., S. F. Ferrari, and M. A. Lopes. 2011. "Polyspecific associations between squirrel monkeys (*Saimiri sciureus*) and other primates in eastern Amazonia." *American Journal of Primatology* 73 (11):1145–1151. doi:10.1002/ajp.20981.
- Pinheiro, T., S. F. Ferrari, and M. A. Lopes. 2013. "Activity budget, diet, and use of space by two groups of squirrel monkeys (*Saimiri sciureus*) in eastern Amazonia." *Primates* 54 (3):301–308. doi:10.1007/s10329-013-0351-9.
- Pinheiro, T., and M. A. Lopes. 2018. "Hierarchical structure and the influence of individual attributes in the captive squirrel monkey (*Saimiri collinsi*)." *Primates* 59 (5):475–482. doi:10.1007/s10329-018-0668-5.
- Pinheiro, T.M. 2015. "Sistema social do macaco-de-cheiro (*Saimiri collinsi*) em cativeiro." Ph.D. thesis, Universidade Federal do Pará, Belem, Brazil.
- Podolsky, R. D. 1990. "Effects of mixed-species association on resource use by *Saimiri sciureus* and *Cebus apella*." *American Journal of Primatology* 21 (2):147–158. doi:10.1002/ajp.1350210207.
- Pontes, A. R. M. 1997. "Habitat partitioning among primates in Maraca island, Roraima, northern Brazilian Amazonia." *International Journal of Primatology* 18 (2):131–157. doi:10.1023/A:1026364417523.
- Ribeiro-Junior, M. A., S. F. Ferrari, J. R. Lima, C. R. da Silva, and J. D. Lima. 2016. "Predation of a squirrel monkey (*Saimiri sciureus*) by an Amazon tree boa (*Corallus hortulanus*): even small boids may be a potential threat to small-bodied platyrrhines." *Primates* 57 (3):317–322. doi:10.1007/s10329-016-0545-z.
- Rogge, J., K. Sherenco, R. Mallng, E. Thiele, S. Lambeth, S. Schapiro, and L. Williams. 2013. "A comparison of positive reinforcement training techniques in owl and squirrel monkeys: time required to train to reliability." *Journal of Applied Animal Welfare Science* 16 (3): 211–220. doi:10.1080/10888705.2013.798223.
- Rosenblum, L. A. 1972. "Sex and age differences in response to infant squirrel monkeys." *Brain and Behavior Evolution* 5 (1):30–40. doi:10.1159/000123735.
- Ross, C. 1991. "Life-history patterns of new-world monkeys." *International Journal of Primatology* 12 (5): 481–502. doi:10.1007/Bf02547635.
- Rowlett, J.K., Platt, D.M., Lelas, S., Atack, J.R. and Dawson, G.R. 2005. "Different GABAA receptor subtypes mediate the anxiolytic, abuse-related, and motor effects of benzodiazepine-like drugs in primates." *Proceedings of the National Academy of Sciences* 102 (3):915–920.
- Ruivo, L. V. P., A. I. Stone, and M. Fienup. 2017. "Reproductive status affects the feeding ecology and social association patterns of female squirrel monkeys (*Saimiri collinsi*) in an Amazonian rainforest." *American Journal of Primatology* 79 (6):e22657. doi:10.1002/ajp.22657.
- Ruivo, L. V. P., and A.I. Stone. 2014. "Jealous of mom? Interactions between infants and adult males during the mating season in wild squirrel monkeys." *Neotropical Primates* 21:165–170.
- Ruiz, J. C., A. G. Brady, S. L. Gibson, L. E. Williams, and C. R. Abee. 2005. "Morbidity and mortality of adult female Bolivian squirrel monkeys in a 10-year-period." *Contemporary Topics in Laboratory Animal Science* 44(4):74.
- Saltzman, W., S. P. Mendoza, and W. A. Mason. 1989. "Social dynamics of sequential group formation among female squirrel monkeys." *American Journal of Primatology* 18(2):164.
- Schilling, K. G., V. Janve, Y. Gao, I. Stepniewska, B. A. Landman, and A. W. Anderson. 2018. "Histological validation of diffusion MRI fiber orientation distributions and dispersion." *Neuroimage* 165:200–221. doi:10.1016/j.neuroimage.2017.10.046.
- Schimpl, P. A., S. P. Mendoza, W. Saltzman, D. M. Lyons, and W. A. Mason. 1996. "Seasonality in squirrel monkeys (*Saimiri sciureus*): Social facilitation by females." *Physiology and Behavior* 60 (4):1105–13. doi:10.1016/0031-9384(96)00134-5.
- Schino, G., M. Palumbo, and E. Visalberghi. 2011. "Factors affecting urine washing behavior in tufted capuchins (*Cebus apella*)." *International Journal of Primatology* 32 (4):801–810. doi:10.1007/s10764-011-9502-2.
- Schuler, A. M., and C. R. Abee. 2005. "Squirrel monkeys (*Saimiri*)." In *Enrichment of Nonhuman Primates*, 73–88. NIH Office of Laboratory Animal Welfare: Bethesda.
- Scollay, P. A. 1980. "Cross-sectional morphometric data on a population of semifree-ranging squirrel-monkeys, *saimiri-sciureus* (iquitos)." *American Journal of Physical Anthropology* 53 (2):309–316. doi:10.1002/ajpa.1330530216.
- Shapley, R. 2009. "Vision: Gene therapy in colour." *Nature* 461 (7265):737–739. doi:10.1038/461737a.
- Stone, A.I. 2004. "Juvenile feeding ecology and life history in a neotropical primate, the squirrel monkey (*Saimiri sciureus*)." Ph.D. Dissertation, Program in Ecology and Evolutionary Biology, University of Illinois at Urbana-Champaign.
- Stone, A. I. 2006. "Foraging ontogeny is not linked to delayed maturation in squirrel monkeys (*Saimiri sciureus*)." *Ethology* 112 (2):105–115. doi:10.1111/j.1439-0310.2005.01121.x.
- Stone, A. I. 2007a "Responses of squirrel monkeys to seasonal changes in food availability in an eastern Amazonian forest." *American Journal of Primatology* 69 (2):142–57. doi:10.1002/ajp.20335.
- Stone, A. I. 2007b. "Ecological risk aversion and foraging behaviors of juvenile squirrel monkeys (*Saimiri sciureus*)." *Ethology* 113 (8):782–792. doi:10.1111/j.1439-0310.2007.01377.x.

- Stone, A. I. 2008. "Seasonal effects on play behavior in immature *Saimiri sciureus* in Eastern Amazonia." *International Journal of Primatology* 29:195–205.
- Stone, A. I. 2014. "Is fatter sexier? Reproductive strategies of male squirrel monkeys (*Saimiri sciureus*)." *International Journal of Primatology* 35 (3–4):628–642. doi:10.1007/s10764-014-9755-7.
- Stone, A.I. 2018. "The foraging ecology of male and female squirrel monkeys (*Saimiri collinsi*) in Eastern Amazonia, Brazil." In *La primatología en Latinoamérica 2*, edited by B. Urbani, M. Kowalewski, R.G.T. Cunha, S. de la Torre and L. Cortés-Ortiz, 229–237. Instituto Venezolano de Investigaciones Científicas: Caracas, Venezuela.
- Stone, A.I. and L.V.P. Ruivo. 2020. "Synchronization of weaning time with peak fruit availability in squirrel monkeys (*Saimiri collinsi*) living in Amazonian Brazil." *American Journal of Primatology* 82 (7): e23139. doi:10.1002/ajp.23139.
- Talbot, C. F., H. D. Freeman, L. E. Williams, and S. F. Brosnan. 2011. "Squirrel monkeys' response to inequitable outcomes indicates a behavioural convergence within the primates." *Biology Letters* 7 (5):680–682. doi:10.1098/rsbl.2011.0211.
- Tardif, S. D. 1994. "Relative energetic cost of infant care in small-bodied neotropical primates and its relation to infant-care patterns." *American Journal of Primatology* 34 (2):133–143. doi:10.1002/ajp.1350340205.
- Tardif, S., A. Carville, D. Elmore, L.E. Williams, and K. Rice. 2012. "Reproduction and breeding of nonhuman primates." *Nonhuman Primates in Biomedical Research* 2012: 197
- Terborgh, J. 1983. *Five New World primates*. Princeton University Press: Princeton, NJ.
- Thomas, R. K., and T. Frost. 1983. "Oddity and dimension-abstracted oddity (Dao) in squirrel-monkeys." *American Journal of Psychology* 96 (1):51–64. doi:10.2307/1422208.
- Tougan, T., N. Arisue, S. Itagaki, Y. Katakai, Y. Yasutomi, and T. Horii. 2018. "Adaptation of the *Plasmodium falciparum* FCB strain for in vitro and in vivo analysis in squirrel monkeys (*Saimiri sciureus*)." *Parasitology International* 67 (5):601–604. doi:10.1016/j.parint.2018.05.012.
- Trevino, H. S. 2007. "Seasonality of reproduction in captive squirrel monkeys (*Saimiri Sciureus*)." *American Journal of Primatology* 69 (9):1001–1012. doi:10.1002/ajp.20409.
- Vaitl, E. A. 1977. "Social context as a structuring mechanism in captive groups of squirrel monkeys (*Saimiri sciureus*)." *Primates* 18:861–874.
- Valdez, G.R., Platt, D.M., Rowlett, J.K., Rüedi-Bettschen, D. and Spelman, R.D. 2007. "κ Agonist-induced reinstatement of cocaine seeking in squirrel monkeys: a role for opioid and stress-related mechanisms." *Journal of Pharmacology and Experimental Therapeutics* 323 (2):525–533.
- Vanchiere, J. A., J. C. Ruiz, A. G. Brady, T. J. Kuehl, L. E. Williams, W. B. Baze, G. K. Wilkerson, P. N. Nehete, G. B. McClure, D. L. Rogers, S. L. Rossi, S. R. Azar, C. M. Roundy, S. C. Weaver, N. Vasilakis, J. H. Simmons, and C. R. Abec. 2018. "Experimental zika virus infection of neotropical primates." *American Journal of Tropical Medicine and Hygiene* 98 (1):173–177. doi:10.4269/ajtmh.17-0322.
- Washburn, D. A., W. D. Hopkins, and D. M. Rumbaugh. 1989. "Automation of learning-set testing: the video-task paradigm." *Behavior Research Methods Instruments and Computers* 21 (2):281–284. doi:10.3758/bf03205596.
- Whiteley, H. E., J. I. Everitt, I. Kakoma, M. A. James, and M. Ristic. 1987. "Pathologic changes associated with fatal *Plasmodium falciparum* infection in the Bolivian squirrel monkey (*Saimiri sciureus boliviensis*)." *American Journal of Tropical Medicine and Hygiene* 37 (1):1–8. doi:10.4269/ajtmh.1987.37.1.
- Williams, L.E., A.G. Brady, and C.R. Abec. 2010. "Squirrel monkeys." In *The UFAW Handbook on the Care and Management of Laboratory and Other Research Animals*, Eighth Edition, edited by R. Hubrecht and J. Kirkwood, 564–578. Wiley-Blackwell: Oxford, UK.
- Williams, L., Vitulli, W., McElhinney, T., Wiebe, R.H. and Abec, C.R. 1986. "Male behavior through the breeding season in *Saimiri boliviensis boliviensis*." *American journal of primatology* 11 (1):27–35.
- Williams, L. E., and C. R. Abec. 1988. "Aggression with mixed age-sex groups of bolivian squirrel-monkeys following single animal introductions and new group formations." *Zoo Biology* 7 (2):139–145. doi:10.1002/zoo.1430070207.
- Williams, L., S. Gibson, M. McDaniel, J. Bazzel, S. Barnes, and C. Abec. 1994. "Allomaternal interactions in the Bolivian squirrel monkey (*Saimiri boliviensis boliviensis*)." *American Journal of Primatology* 34 (2):145–156. doi:10.1002/ajp.1350340206.
- Williams, L., W. Vitulli, T. Mcelhinney, R. H. Wiebe, and C. R. Abec. 1986. "Male-behavior through the breeding-season in *Saimiri boliviensis boliviensis*." *American Journal of Primatology* 11 (1):27–35. doi:10.1002/ajp.1350110104.
- Woodburne, L.S., and G.K. Rieke. 1966. "Response to symbols by squirrel monkeys." *Psychonomic Science* 5 (11):429–430.
- Wrangham, R. W. 1980. "An ecological model of female-bonded primate groups." *Behaviour* 75 (3/4):262–300. doi:10.1163/156853980x00447.
- Yagi, M., G. Bang, T. Tougan, N. M. Palacpac, N. Arisue, T. Aoshi, Y. Matsumoto, K. J. Ishii, T. G. Egwang, P. Druilhe, and T. Horii. 2014. "Protective epitopes of the *Plasmodium falciparum* SERA5 malaria vaccine reside in intrinsically unstructured N-terminal repetitive sequences." *PLoS One* 9 (6):e98460. doi:10.1371/journal.pone.0098460.
- Yang, P. F., H. X. Qi, J. H. Kaas, and L. M. Chen. 2014. "Parallel functional reorganizations of somatosensory areas 3b and 1, and S2 following spinal cord injury in squirrel monkeys." *Journal of Neuroscience* 34 (28):9351–9363. doi:10.1523/JNEUROSCI.0537-14.2014.
- Zimble-Delorenzo, H. S., and A. I. Stone. 2011. "Integration of field and captive studies for understanding the behavioral ecology of the squirrel monkey (*Saimiri* sp.)." *American Journal of Primatology* 73 (7):607–622. doi:10.1002/ajp.20946.