ZOO ECOLOGY OF A PRIMATE SPECIES:

SQUIRREL MONKEY (*SAIMIRI* SP.)

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ZOO ECOLOGY OF A PRIMATE SPECIES:

SQUIRREL MONKEY (*SAIMIRI* SP.)

Heather Susanne Zimbler-DeLorenzo

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DISSERTATION ABSTRACT

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SQUIRREL MONKEY (*SAIMIRI* SP.)

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Understanding how captivity affects the behavioral and development traits of a species is important for management and conservation in zoos. The ecology of squirrel monkeys (*Saimiri* sp.) may be different in captivity than in their natural environment. I investigated five common ecological aspects: reproduction, vigilant behaviors, life history traits, and generational changes in seasonality. Reproduction in squirrel monkeys is naturally seasonal with speculation as to the environmental factor with the greatest influence. In captivity, different types of habitats used to house squirrel monkeys may affect seasonality of reproduction. Those individuals housed in outdoor enclosures maintained a seasonal peak of births while those monkeys kept in indoor enclosures reproduced throughout the year. These habitat-based differences in reproduction allowed for analysis of environmental variables, and temperature had a large impact on births.

Captivity also provides the opportunity to determine whether differences exist in vigilant responses of individuals to playbacks of alarm calls, in regards to whether anti-predator responses are innately predisposed or require experience. Captive squirrel monkeys presented with alarm, predator, and control sounds elicited a greater amount of vigilant behaviors to alarm calls compared to other sounds. However these behaviors were not maintained for a minute after the playback. Interestingly, a “group personality” seemed to be exhibited; responses were not related to group size or type of enclosure. Captive squirrel monkeys were naïve yet still able to correctly respond to alarm calls by displaying vigilant behaviors.

Differences due to captive environments may affect life history traits of squirrel monkey populations. Variation in life history traits occurs between sexes, zoos, and generations of squirrel monkeys maintained in captivity. Prospective analyses predict that juvenile and adult survivals have the greatest impacts on population growth. Fertility, however, is the demographic trait that contributes the most to changes in population size based on a retrospective analysis. The seasonality of reproduction has previously been shown to vary depending on type of habitat. With several generations of squirrel monkeys established in captivity, change in reproduction timing allowed for testing of whether this change is due to plasticity or selection. Using pedigree data, differences between when mothers and daughters have their offspring reflects environmental influences, rather than heritability. Seasonal reproduction is significantly different between the wild and captive generations, however not between the two captive generations.

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INTRODUCTION

Preserving the behavioral and developmental diversity of animals maintained in captivity allows for zoos to achieve their full potential in conservation. Captive propogation efforts and reintroduction programs are dependent on captive animals exhibiting normal reproductive and behavioral repertoires. To thrive in captivity, a species must adapt their behaviors to the altered environmental conditions [Carlstead 1996].

Behavioral and population ecology takes an evolutionary and ecological view toward understanding the behaviors of animals and how they enable them to adapt to their local environment [Krebs and Davies 1993]. However, behavioral ecology may be quite different in the wild versus the zoo environment. This difference is important for zoo biologists and conservationists to understand. Also, zoo behavioral ecology reflects complications of genotype and phenotype.

An understanding of the ways in which animals sense and react to their environment is of crucial importance to the preservation of viable populations in altered or captive habitats. Studies on the behavioral ecology of animals can provide significant contributions to their conservation. In collaboration with the zoos and breeding facilities around North America, I have chosen to examine some well-studied traits by behavioral ecologists: alarm calling, life history patterns, and reproductive patterns. These easily measured traits are examples of how we can study individual and population behaviors as a model for studies of zoo ecology.

CHAPTER ONE: INTEGRATION OF FIELD AND CAPTIVE STUDIES FOR UNDERSTANDING THE BEHAVIORAL ECOLOGY OF *SAIMIRI*

Understanding the ways in which animals sense and respond to their environment can provide crucial contexts for the preservation of viable populations in altered or captive habitats. Studies of behavioral ecology can provide significant contributions to conservation through evolutionary and ecological perspectives of how animals adapt to their environment [Krebs and Davies 1993]. Captive studies can aid in understanding aspects of species-specific behavior, especially when behaviors are difficult to observe in the wild. Successful breeding in captivity is also dependent on an understanding of social and reproductive patterns in natural populations. Zoos provide advantages to researchers by allowing for longitudinal studies of behavior and reproduction, as well as opportunities for gathering data on all aspects of life history [Hardy 1996]. Studies of field populations can provide contextual information regarding the adaptive nature of behaviors that are studied in captivity.

Squirrel monkeys (genus *Saimiri*) are small, Neotropical primates (700-1000 grams) [Mitchell 1990; Smith and Jungers 1997] distributed in Central America and the Amazon basin [Baldwin and Baldwin 1985]. They are the second-most commonly used primate in laboratory studies [Kinzey 1997] for over 40 years, providing much information on *Saimiri* nutrition, physiology, reproduction, and life history variables is available [Rosenblum and Cooper 1968; Rosenblum and Coe 1985]. In addition, these laboratory studies have led to an increase in research in natural habitats (reviews provided by Rosenblum and Cooper [1968] and Rosenblum and Coe [1985]). Squirrel monkeys are interesting study subjects because they do not fit the usual models of life history and behavior. That is, they have long juvenile periods, intra- and inter-specific differences in group composition and structure, and an unusual reproductive physiology associated with male fattening, as detailed below in the “life history” section. By studying squirrel monkeys in both wild and captive situations, we were able to gain a more complete understanding of their behavioral ecology, how their behaviors function in current environments, and how these behaviors may have evolved in the first place. In this review, we will describe the important characteristics of the behavioral ecology of *Saimiri*: ecology, life history, behavior, reproduction, communication, and conservation since Rosenblum and Coe’s review [1985]. We hope that the approach of integrating captive and wild studies presented here can serve as a model for better understanding of other species.

ECOLOGY

According to Rylands *et al.* [2000] and Rylands and Mittermeier [*in press*], four South American species of squirrel monkeys are recognized currently: *Saimiri boliviensis* (western Amazonia), *S. sciureus* (eastern Amazonia), *S. ustus* (southern Amazonia), and *S. vanzolinii* (range restricted to extreme western Amazonia). The fifth species, *S.*

oerstedii, occurs Central America. The ecology of *S. sciureus* and *S. boliviensis* has been well-documented and reviewed by Rosenblum and Coe [1985]. Very little is known about the ecology of *S. ustus* and *S. vanzolinii* [Ingberman et al. 2008]. Since 1985, four long-term field studies on squirrel monkey ecology have been conducted: *S. oerstedii* [Boinski 1986], *S. boliviensis* [Mitchell 1990], *S. sciureus* in Brazil [Stone 2004], and *S. sciureus* in Suriname [Boinski 1999]. Shorter-term studies were also performed on *S. sciureus* [Lima and Ferrari 2003] and on *S. boliviensis* [Peres 1994].

Squirrel monkeys are omnivorous, feeding mostly on fruit and insects [Janson and Boinski 1992], although the composition of their diet varies seasonally. In all *Saimiri* field populations studied to date, a higher degree of insectivory occurs in the dry season [Boinski 1987; Mitchell 1990; Lima and Ferrari 2003; Stone 2007a]. They also exhibit predation on Neotropical fruit-eating bats. *S. oerstedii* has been observed attacking the leaf tents made by these bats and stalking the inhabitants. Adult males are generally more successful. Those bats not captured by the squirrel monkeys are most likely caught by double-toothed kites that follow the monkeys when feeding [Boinski and Timm 1985].

Squirrel monkeys are arboreal, spending most of their time in trees actively foraging [Ausman et al. 1985; Baldwin and Baldwin 1985]. Compared to other Neotropical primates, they forage in the understory, which provides the most protection from aerial predators [Boinski et al. 2003; Stone 2007b]. Home range can vary with food availability (increasing as food resources decrease) although with almost no territorial behavior [Baldwin and Baldwin 1985; Boinski 1986; Mitchell 1990; Peres 1994], although a lack of territoriality is not always exhibited [Stone 2007a]. Compared to other species found in the same habitats (*Cebus* and *Callicebus* groups), squirrel monkeys maintain a wider home range [Fragaszy 1985; Peres 1994]. Population density of *Saimiri* may be dependent on habitat (ranging from 8 to 528 monkeys per km^2) [Kinzey 1997]. The Central American squirrel monkey, *Saimiri oerstedii,* prefers to inhabit secondary forest, although it will utilize primary and late successional forest when food availability declines [Boinski 1987]. This has also been documented for *S. sciureus* in Brazil [Stone 2007a]. Seasonal variations in habitats used occur among all squirrel monkey populations and are mostly due to the differences in distribution and quality of food [Stone 2007a]. For example, *S. oerstedii* has been documented adjusting foraging strategies according to seasonal variations, i.e. changing foraging habitat, increase range size, and/or increase both the hourly rate of troop movement and time spent foraging [Boinski 1987]. Similarly, *S. boliviensis* studied in western Brazil greatly increases its home range to include flooded forest [Peres 1994]. *S. sciureus*, on the other hand, foraged as time minimizers, reducing time spent obtaining resources, rather than expanding their range [Stone 2007c].

For squirrel monkeys (*Saimiri sciureus*) maintained in captivity, enclosure size and substrate quantity and type are important influences of the habitat on the behavior of the social group. Locomotion is seen to increase significantly with an increase in space (consistent with other primate studies). However, aggression and play did not seem affected by spatial density. Aggression remains low in captivity, which is characteristic of the species in field populations.

Seasonality in food abundance appears to affect perceived predation risk. Age and seasonal fruit availability influence predator sensitive foraging of *S. sciureus*. Specifically, juveniles may be more sensitive to environmental fluctuations, possibly making them more susceptible to predators [Stone 2007a].

Appleton and Boinski's [1991] parasitological analysis of wild *Saimiri oerstedii* agrees with Dunn's [1968] listing of documented parasites found in captive squirrel monkeys. Studies have been conducted to determine the prevalence of natural infections by trypanosome species in *S. sciureus* and *S. ustus* [Ziccardi and Lourenco-de-Oliveira 1997] and coccidia [Duszynski et al. 1999].

LIFE HISTORY

As with most Neotropical primates, available life history data on *Saimiri* derive mostly from captive studies focusing on morphometric measurements and on reproduction [e.g. Long and Cooper 1968; Scollay 1980]. Squirrel monkeys exhibited an unusual combination of life history, demographic, and ecological features not found in other similarly sized Neotropical primates (Table 1). In their analysis of life histories of primates, Garber and Leigh [1997: 15] note that squirrel monkeys "present a distinct set of reproductive, social and life-history attributes when compared to other small-bodied New World primates". Likewise, after examining the life histories of 16 platyrrhine (New World primate) genera, Hartwig [1996: 99] concluded that squirrel monkeys have "the most unusual package of perinatal life history traits".

Gestation length in wild populations of *Saimiri sp.* [5 months, Mitchell 1990; Stone 2004] is nearly a month longer than those of the similarly-sized *Aotus* and similar to those of the larger *Callicebus* and *Cebus* [Hartwig 1996]. Estimated prenatal growth rates are also high, even when compared to the twin-producing callitrichines [Ross 1991; Hartwig 1996; Garber and Leigh 1997]. Neonates, a single offspring each birth season depending on the species, are well-developed representing 16-20% of maternal weight, the largest percentage reported for any anthropoid primate [Long and Cooper 1968; Elias 1977; Kaack et al. 1979]. For instance, although *Saimiri* and *Callicebus* show similar gestation lengths, although *Callicebus* infants are only 8% of their adult weight at birth [Garber and Leigh 1997]. The large neonates of squirrel monkeys have 60% of adult brain mass at birth [Elias 1977; Garber and Leigh 1997].

Rapid somatic and brain growth continues during the first three months of life [Kaplan 1979; Manocha 1979]. Using captive data from Manocha [1979], Hartwig [1995] and Garber and Leigh [1997] showed that 90-96% of adult brain size is attained by the first two months. By 6 months, squirrel monkey infants weigh approximately 50%-69% of maternal body weight [Kaplan 1979; Scollay 1980]. Analyses by Tardif [1994] show that *Saimiri* rank highest among Neotropical primates under 2 kg in infant care costs, particularly because of the cost of transporting a heavy infant over long day-ranges [up to 2-5 km, Mitchell 1990]. Somatic growth rates are reduced around 6 months of age [Garber and Leigh 1997], which corresponds to the natural onset of weaning in *S. sciureus* [Stone 2006]. However, weaning age is highly variable among *Saimiri* species.

S. oerstedii are weaned at 4 months [Boinski and Fragaszy 1989], while *S. boliviensis* infants continue to nurse for 18 months [Mitchell 1990].

Despite rapid development as infants, the juvenile period of squirrel monkeys is characterized by an extended period of relatively slow growth for several years [Scollay 1980; Ross 1991]. Captive *Saimiri sciureus* males and females show continually decelerating growth in the first 2-3 years of life [Russo et al. 1980]. Age at first reproduction in all *Saimiri* species is also reached relatively late, despite their small body mass [Stone 2004]. Reproducing the earliest, wild female *S. oerstedii* first breed at 2.5 years [Boinski 1986] and males at 4 years of age [Robinson and Janson 1987; Boinski 1992a]. Wild male *S. sciureus* first breed at 4.5 years [Robinson and Janson 1987; Boinski 1992a] while female *S. sciureus* breed a little earlier in captivity, between 3.5-4 years [Taub 1980]. Displaying the latest ages, wild female *S. boliviensis* age at first reproduction occurs slightly later at 3.5 years [Mitchell 1990] and males (semi-free and wild individuals) breed at 5-6 years of age [Baldwin 1969; Scollay 1980; Mitchell 1990]. Interbirth intervals in wild *S. boliviensis* are 2 years [Mitchell 1990]. *S. sciureus* females may breed every year, though not all do so [Stone 2004]

SOCIAL BEHAVIOR

The social behavior of squirrel monkeys from field studies in Central and South America, as well as semi-natural captive environments was reviewed by Baldwin [1985]. Most social interactions occurred within age-sex classes. Adult females were usually the only individuals involved in between age-group interactions, although this is strongly affected by the annual reproductive cycle. Adult males usually travel on the periphery of the group but became attracted to adult females during the mating season [Mitchell 1990; Izar et al. *in press*]. After the eighth week of post-partum development, infants began interacting with other females in the group and engage in peer play. Social grooming was not a common interaction in *Saimiri*.

Interspecific differences in group structure in wild squirrel monkeys have provided tests of ecological models of social evolution that were suggested by van Schaik [1989]. The comparison of female bonding in *Saimiri boliviensis* and *S. oerstedii* by Mitchell *et al.* [1991] support the ecological model for female social relationships. Boinski *et al.* [2002] also found that female within-group direct competition was related to the distribution of fruit patches in the habitat of three species of squirrel monkeys (*Saimiri boliviensis, S. oerstedii, and S. sciureus)*, thus also supporting the ecological model of primate social evolution.

Male affiliation patterns have also received attention in two long-term field studies of *Saimiri boliviensis* and *S. oerstedii* [Boinski 1994]. Previous research investigated the social structure of these species in captive semi-free ranging habitats [Coe and Rosenblum 1974; Rosenblum and Coe 1985]; however, these studies did not account for the extensive differences in behavior between species. The pattern of male affiliation in *S. oerstedii* is dramatically different from both wild and captive populations of South American *Saimiri*. Unlike *S. boliviensis*, male *S. oerstedii* are philopatric and do not display male-male within-troop aggression. Males cooperate in the sexual investigations of females, as well as the aggressive interactions with neighboring males and deference of infants and sub-adults from predators. Unlike their associated females, males do not have much of a dominance hierarchy [Boinski 1994].

Primates are known for forming mixed-species groups and associating with other animals in their habitats. Waser [1987] identified an interspecific association between *Cebus* and *Saimiri* in South America. Squirrel monkeys have been documented forming mixed groups with capuchins (*Cebus apella* and *C. albifrons*) and could be receiving a benefit from alarm calls given by the other. This association was nearly exclusively initiated and maintained by the squirrel monkey with few benefits for the capuchin [Podolsky 1990]. Squirrel monkeys gained enhanced protection using the additional vigilance and benefited seasonally by capuchins' knowledge of fruit locations. This research was expanded by Boinski [1989] to include *S. oerstedii* and marked differences were found. Unlike their South American counterparts, very little association with *Cebus* occurred, with no evidence of *Saimiri* initiating or maintaining these interactions. This may be because of little dietary overlap between the two species. *Saimiri* troops are usually accompanied by at least one species of bird; most common is the double-toothed kite (*Harpagus bidentatus*) [Boinski 1986; Stone 2004]. In Costa Rica, *S. oerstedii* can also be followed by gray-headed tanagers (*Eucometis penicillata*) and tawny-winged woodcreepers (*Dendrocincla anabatina*).   This is a commensal relationship in which the prey that are caught by the birds had already been flushed out by the monkeys and were caught during flight [Boinski and Scott 1988].

Expanding upon Baldwin and Baldwin's [1974] research on play in field and semi-captive settings, Stone [2008] investigated whether seasonal differences in the wild (more specifically, food abundance) affected play in *Saimiri sciureus*. Play is strongly tied to seasonality, as the percentage of time dedicated to play was reduced during the dry season when food is relatively scarce.

REPRODUCTION

Squirrel monkeys are characterized by a polygamous mating system [Boinski 1987; Mitchell 1990; Izar et al. *in press*] and highly seasonal breeding [Di Bitetti and Janson 2000; Stone 2004]. *Saimiri* is the only genus in the family *Cebidae* for which seasonal reproduction has been documented [Hayssen et al. 1993], both in the wild [Boinski 1987; Mitchell 1990; Stone 2004] and in captivity [DuMond and Hutchinson 1967; Baldwin and Baldwin 1985; Rosenblum and Coe 1985; Trevino 2007]. In a wild population of *S. sciureus*, the dry season corresponded to mating (approximately 8 weeks) and gestation (5 months), and the wet season corresponded to birth (approximately 8 weeks) and lactation (approximately 6 months). Both Costa Rican (*S. oerstedii*) and Peruvian squirrel monkeys (*S. boliviensis*) mate over a period of 2 months, corresponding to the dry season [Boinski 1987; Mitchell 1990].

Baldwin and Baldwin [1985] reviewed birth seasons of captive and wild populations of squirrel monkeys. The largest captive breeding colony of Brazilian squirrel monkeys in North America was shown to exhibit a similar single birth season. This pattern of birth tends to occur during the summer in the Northern hemisphere, which is six months later than wild populations in South America. However, seasonality of reproduction in squirrel monkeys raised in captivity was dependent on whether the enclosure in which they were housed was exposed to environmental elements (outdoor) or kept at optimal conditions (indoor) [Trevino 2007]. The role of environmental variables on reproductive seasonality is debated; rainfall, photoperiod, latitude, temperature have all been suggested as factors [Baldwin and Baldwin 1985; Rosenblum and Coe 1985; Trevino 2007].

All squirrel monkey species are sexually dimorphic, with males 30-35% larger than females [Mitchell 1990; Smith and Jungers 1997; Boinski 1999]. DuMond and Hutchinson [1967] first described the seasonal weight gain that occurs in males during the brief mating period. Fat deposition and water retention produces a "fatted" appearance in the upper torso, arms and shoulders [Mendoza et al. 1978; Mitchell 1990; Boinski 1992a; Stone 2004]. This is controlled by hormonal changes and is not related to additional food consumption by males during this period [Nadler and Rosenblum 1972; Stone 2004].

Although this seasonal enlargement may be associated with sexual selection, female choice has not been reported in all species. In the wild, *Saimiri sciureus* females have not been observed presenting sexually to males, following males, or calling to males [Izar et al. *in press*]. Males competed aggressively for access to females, and fatting may have served the purposes of intrasexual selection [Blumstein et al. 2000]. Similarly, female choice has not been observed in *S. boliviensis* studied in Peru, where females are dominant to males but males compete aggressively for access to females [Mitchell 1990, 1994]. The largest male (established visually) was responsible for 90% of long consortships (> 6 hrs) observed [Mitchell 1990]. In both *S. boliviensis* and *S. sciureus*, fatting appeared to protect males from wounds caused by the high levels of intrasexual aggression. In contrast to South American squirrel monkeys, female *S. oerstedii* in Costa Rica solicit copulations, and preferentially solicit from the most fatted males in the troop (established visually). Boinski [1987; 1992a] reported that during one breeding season, the most fatted male obtained 70% of copulations, while smaller males mated only when larger males rejected female solicitations.

In the wild, births are distributed within a 2-8 week period [Terborgh 1983; Boinski 1986; Stone 2004], usually corresponding to the peak period of food availability [Di Bitetti and Janson 2000]. In addition, within-group birth synchronicity is common. Females may give birth within a one week period [Boinski 1987]. In one population of *S. sciureus*, 12 of 15 gestating females gave birth in one night [Stone 2004]. One potential adaptive explanation for this synchronicity is predator avoidance [Boinski 1987]. Infanticidal behavior has never been reported and the seasonality of births makes infanticide an unlikely male strategy [van Schaik 2000]. Interbirth intervals in wild *S. boliviensis* are 2 years [Mitchell 1990]. *S. sciureus* females may breed every year, though not all do so [Stone 2004].

Although infants require a high allocation of maternal resources through lactation and transport, females receive little extramaternal assistance. Paternal care has not been reported in the genus, though in some populations other females and juveniles can provide some degree of allocare. Stone [2004] found that *S. sciureus* juveniles often helped during short periods (< 5 minutes) with infant carrying, primarily during rest phases, or remained in close proximity to the infant, “embracing it” while the mother was away. Juveniles never carried infants during group travel, although mothers often "exchanged" infants for short periods. Juvenile female *S. boliviensis*, helped in similar ways, such as by carrying and associating with infants for short periods. Allonursing has not been reported in other wild populations, although captive *S. boliviensis* females may nurse infants other than their own if they experience reproductive failure [Williams et al. 1994]. In Costa Rica, juveniles rarely approached infants and virtually no extramaternal care was observed [Boinski 1986].

COMMUNICATION

For the last 30 years, communication has been a main focus of research on squirrel monkeys [last review by Newman 1985]. The vocal repertoire of the squirrel monkey was first described by Winter *et al*. [1966], with only a few vocalizations added since [Winter 1969a, b; Newman et al. 1983; Newman 1985]. Most of the previous vocal communication research has focused on the structural characteristics and classifications of the calls, as well as their ontogeny.

There is a strong innate quality to most of the vocalizations, shown through a series of experimental studies using infants and muted mothers [Newman 1985]. This genetic component, however, is also aided by learning. Although infants can produce calls shortly after birth, the appropriate reactions to hearing calls, production of adult-like calls (chuck calls particularly), and individual recognition of the caller develop over time [McCowan and Newman 2000]. With the development of new technology and information from research since Winter *et al.*'s [1973] study of squirrel monkey vocalizations, Hammerschmidt *et al.* [2001] further investigated the innateness of *Saimiri* vocal production. The results support the original findings; squirrel monkey infants, even without the opportunity to hear adults, develop all call types of the species-specific vocal repertoire.

Most of the communication research in *Saimiri* since Newman's [1985] review has focused on vocal behavior using playback studies in captive environments [Biben et al. 1986; Biben and Symmes 1991; McCowan et al. 2001; Fichtel and Hammerschmidt 2003]. More recently, studies have begun utilizing wild populations, most of which were affiliative vocalizations emitted by adult females, specifically, chuck calls and peeps [Boinski and Newman 1988; Boinski and Mitchell 1992, 1997]. Captive playback experiments have shown that adult females are more likely to respond to conspecific chucks [Soltis et al. 2002] and that this exchange creates a distinct 'question' and 'answer' response [Biben et al. 1986; Biben 1993] within a defined reply time period [Masataka and Biben 1987]. These laboratory studies only emphasize proximate explanations of vocal behaviors. Chuck calls are not associated with behavioral contexts and, instead, function to maintain affiliative social relationships among females [Biben and Symmes 1991; Biben 1993] or as signals reflecting emotional state [Jürgens 1988].

Field studies can indicated the ultimate function of vocal behaviors to be understood. Chuck calls increase auditory contact among adult females in densely forested areas where visual contact is obscured. Rather than just forming a signal based on acoustic structure for individual identity, the chuck call also affects group cohesion and foraging activity [Boinski and Mitchell 1997]. None of the studies conducted on natural populations of *Saimiri* have shown evidence that affiliative or affective states affect the caller [Boinski and Newman 1988; Boinski 1991]. These calls provide mostly coordination of troop movement and maintenance of troop cohesion [Boinski and Mitchell 1992].

Only a few studies examined calls other than chucks, i.e. alarm peeps, mobbing calls, and caregiver calls. Alarm calls are innate but the appropriate response to these calls develop during life. The calls contain substantial information, such as urgency of threat and caller identification; enough for an individual squirrel monkey to make a suitable behavioral response [McCowan et al. 2001]. By communicating the severity of the threat and affective state of the caller, callers may produce for an increase in chance of survival in their group by just modifying the frequency and amplitude of the call [Fichtel and Hammerschmidt 2003]. Another call that has received much less attention is the caregiver call, a call from adult females directed to infants and used to coordinate nursing bouts. This specialized maternal vocalization is only found in *Saimiri boliviensis* [Boinski and Mitchell 1995]; no evidence of it has been found in the other species. The advantageous nature of the caregiver call for *S. boliviensis* may be due to a combination of ecological and life history factors, because infants are not weaned until approximately 18 months old (compared to 4 months of age for *S. oerstedii* and 4-6 months of age for *S. sciureus*) [Mitchell 1990].

Boinski and Newman [1988] conducted the first vocalization study of *S. oerstedii* in their natural habitat. There are population differences in call structure within the species that are related to taxonomic divisions. The twitter is a specialized call that initiates travel in a troop by providing information about the location of the caller. *S. oerstedii* emit a structurally different twitter (produced at a loud intensity and heavily modulated) and chuck calls not previously documented. These differences in calls between field and captive studies may be attributed to the restricted laboratory environments in which some of the studies were conducted [Boinski 1996].

Studying vocalizations in the natural habitat of *Saimiri* can be difficult because the large social groups are dispersed in the forest. Soltis *et al.* [2002] showed that an auditory stimulus alone can elicit a chuck response, so the monkeys do not need to see the caller. Much of primate vocalization is related to quiet affiliation contexts, which were not readily tested in playback experiments. Biben and Symmes [1991] were able to show that playbacks of close range calls on squirrel monkeys can be successful in eliciting responsive vocalizations in a relaxed, affiliative contact.

Only a few systematic studies had researched olfactory communication in the squirrel monkey by the time that Newman [1985] summarized communication, over 20 years ago. None of the reviewed studies at that time were performed in field populations. Boinski [1992b] compared of quantitative and qualitative results on olfaction from a wild population of *Saimiri oerstedii* to test hypotheses generated from these previous laboratory studies. Of daily behaviors, olfaction only accounted for less than 1% of mean sample time. However, field observations support conclusions of captive studies that males still use olfaction when evaluating estrous condition of females; and that females using it to identify individuals, specifically their infants. Urine hand-washing seems to aid in communication of reproductive status, rather than for territory marking as hypothesized for other species. Scent marking trails also does not seem to be involved in the maintenance of group cohesion. Understanding the natural ecology of a species is important when making conclusions from laboratory findings, as shown by Boinski [1992b].

Laska and colleagues [Laska and Hudson 1993a, b; Laska et al. 1995; Laska and Hudson 1995; Laska et al. 1996; Laska et al. 2000] have thoroughly investigated olfaction in captive *Saimiri*. By developing a new testing paradigm, Laska and Hudson [1993a] were able to use psychophysical methods to simulate foraging behaviors guided by olfaction showing that squirrel monkeys have a well-developed and increased olfactory sensitivity to monomolecular odorants [Laska et al. 2000]. They can discriminate between odors [Laska and Freyer 1997], as well as artificial odor mixtures [Laska and Hudson 1993b] and urine odors of conspecifics [Laska and Hudson 1995]. Furthermore, *Saimiri* is capable of learning different odors rapidly [Laska and Hudson 1993a] and can retain that information as long-term memory [Laska et al. 1996].

Very little research has been conducted on the visual communication of squirrel monkeys since Newman's [1985] review. Due to the densely forested canopy environment in which *Saimiri* inhabits, it is not surprising that visual behaviors would be expected to play a small role in communication. Investigations into color vision in laboratory studies constitute almost of all the research. Jacobs and Neitz [1987] found that inheritance of color vision in *Saimiri* is discretely different from Old World monkeys and humans, although they share color vision polymorphism. One unusual feature found is an unequal variation of color vision in the sexes; all males are dichromatic, while females have dichromatic or trichomatic color vision by inheriting the cone pigment allele on an X chromosome. To further complement these laboratory findings, field studies would be able to provide an ecological and evolutionary importance of visual communication in *Saimiri*.

CONSERVATION

Saimiri is abundant in South America; however, only small populations occur in Central America, primarily in Costa Rica. Previously, of all the species of squirrel monkeys, only the newest species, *S. vanzolinii*, was listed as vulnerable by the IUCN Red List (since 1994). However, in 2008, *S. oerstedii* also received attention and was upgraded from endangered to vulnerable [IUCN 2008]. Almost nothing is known about captive and wild ecology of *S. ustus*. Despite this gap in knowledge, *S. ustus* is not listed as vulnerable. Further information on the species' ecology might change its status. Cropp and Boinski [2000] showed that *S. oerstedii* was becoming extremely threatened due to habitat loss and use in the pet trade in Central America (already extinct in Panama and only found in two national parks in Costa Rica). Development of a conservation plan has been difficult because *S. oerstedii* is not an "umbrella" species and prefers habitats, primarily second growth forest, different from other endangered species in the regions where it is found. Boinski *et al.* [1998] suggest focusing conservation efforts on protecting a single site or a tight cluster of sites that provide necessary corridors for troop movement. Even though the populations are at low numbers and in a small region, Boinski *et al.* [1998] believed there was no need for reintroduction or translocation of *S. oerstedii* individuals.

The behavioral ecology of a species may be quite different in their natural environment and in captivity. This contrast is important for zoo biologists and conservationists to understand if the preservation of a species in a wild state is the main purpose, i.e. for reintroductions. To preserve behavioral diversity among animals maintained in zoos, it is important for captive animals to develop normal behavioral repertoires [Carlstead 1996].

Table 1. Comparison of life history, demographical, and ecological parameters across three squirrel monkey species

Trait	*S. oerstedii*	*S. boliviensis*	*S. sciureus*	References
Group size	40-65	45-75	15-50	Boinski et al. (2002), Mitchell (1990), Boinski (1999)
Number of breeding females	14	23	15	Boinski (1986), Mitchell (1990), Stone (2004)
Duration of birth season (weeks)	2	8	8	Boinski (1986), Mitchell (1990), Stone (2006)
Duration of mating season (weeks)	8	8	9	Boinski (1987c), Mitchell (1990), Stone (2006)
Diet (% foraging time allocated to insects)	90%	75%	79%	Boinski et al. (2002); Mitchell (1990), Baldwin and Baldwin (1981)
Neonate/mother ratio	?	0.181	0.163	Elias (1977), Garber and Leigh (1997)
Neonate brain weight/neonate body weight	?	?	0.60	Elias (1977), Manocha (1979)
Seasonal male enlargement	Yes	Yes	Yes	Boinski (1992), Mitchell (1990), Mendoza (1978)
Infant mortality (first 12 months)	50%	?	? (at least 20%)	Boinski (1986), Stone (2004)
Weaning age (months)	4	12-18	6-8	Boinski and Fragaszy (1989), Mitchell (1990), Stone (2006)
Age at first reproduction (females)	2.5	3.5	3.5	Boinski (1986), Mitchell (1990), Taub (1980)
Age at first reproduction (males)	4	6	4.5	Boinski (1992), Mitchell (1990), Robinson and Janson (1987)
Rate of direct competition for food (event/hour/individual)	0.0001	0.005	0.022	Boinski et al (2002)

CHAPTER TWO: SEASONALITY OF REPRODUCTION IN CAPTIVE SQUIRREL MONKEYS (*SAIMIRI SCIUREUS*)

Abstract. Seasonality of reproduction is believed to be influenced by environmental factors such as humidity, temperature, and photoperiod. In primates, there has been much speculation about which environmental factors have the greatest influence on reproductive seasonality. To determine whether environmental factors affect seasonality of reproduction of squirrel monkeys in captivity, I used path analysis to compare number of births and matings per month with monkeys kept in indoor enclosures (maintained at optimal temperatures) and those kept in outdoor enclosures (exposed to the elements). Since a different pattern of seasonality was found to occur, I was able to test whether temperature, rainfall, or photoperiod could explain the temporal variation in reproduction. Squirrel monkeys raised in captivity displayed different patterns of seasonality of reproduction, depending on the conditions in which they are housed ($\chi_3^2 = 25.12$, $P < 0.001$; G = 28.10, $P < 0.001$). Temperature seemed to have a large impact on number of births and matings per month (matings: path coefficient = 0.799; births: path coefficient = -1.315). Understanding what factors regulate reproduction for animals and how these factors affect reproduction differently in wild versus captive populations are important to conservation and management of species.

INTRODUCTION

Seasonal variation in reproduction is well documented among primates in the wild, as well as those raised in, or transferred to, captivity [DuMond 1968; Kleiman et al. 1988; Hodgen 1986; Lindburg 1987; Taub et al. 1978]. By maintaining a birth season (a discrete period of time in which births occur), free-living animals are able to use optimal periods of the year for reproduction [Lindburg 1987]. The largest captive breeding colony of Brazilian squirrel monkeys (*Saimiri sciureus cassiquiarensis*) in North America was shown by Taub et al. [1978] to maintain a single birth season. *Saimiri* is the only genus in the family Cebidae for whom seasonal reproduction has been documented [Hayssen et al. 1993]. However, this temporal pattern of reproduction is documented among other primates such as *Callithrix jacchus* (marmosets) [Hodgen 1986] and *Leontopithecus rosalia* (golden lion tamarin) [Kleiman et al. 1988].

Squirrel monkeys are small, Neotropical primates. Speculation abounds as to which factors affect their reproductive seasonality [Di Betti and Janson 2000; DuMond 1968; Lindburg 1987]. In the wild and in captivity, female squirrel monkeys can give birth every year with definite seasons of mating and births prominent in the wild. Females have very short estrous cycles, lasting 7-8 days, which occur only during the mating season, between December and February [Rosenblum 1968]. Pregnant females undergo a length of gestation of 148 to 172 days, about 5.5 months during the dry season, from July to October [Logdberg 1993]. Newborn infants are seen with their mothers during the height of the rainy season, from January to March [Lindburg 1987; Wolf et al. 1975]. Five to six months following birth, infants are completely weaned [Rosenblum 1968]. This pattern of birth, however, in captivity tends to occur during summer in the

Northern hemisphere, which is six months later than what has been reported for wild populations of squirrel monkeys in South America [DuMond 1968].

The role of environmental factors, such as rainfall, temperature and photoperiod, on reproductive seasonality are not fully understood [DuMond 1968; Harrison and Dukelow 1973]. Because infant squirrel monkeys weigh about 17% of the mass of their mothers, mothers need additional nutrients, such as fruits, during pregnancy and lactation that are plentiful during the rainy season [ISIS/CMS Specimen Reference 2009; Stone 2007c]. Dumond [1968] found a positive correlation between amount of rainfall and reproductive season of *Saimiri sciureus* both in the wild (Amazon) and in captivity (southern Florida). However, captive situations provide the ability to experimentally manipulate food resources; good-quality food is available for the entire year and is not regulated by the amount of rainfall, therefore it would be expected that births would be evenly distributed throughout the year. Neotropical primates in the wild also exhibit an increase in seasonality of reproduction (a decrease in the duration of reproduction) with latitude because availability of resources is unpredictable [Di Bitetti and Janson 2000]. Extremely high temperatures are especially detrimental to reproduction in relatively small species (average of 600 g), such as the squirrel monkey, which has a thermoneutral zone that ranges from 25 to 35° C [Stitt and Hardy 1971]. Temperatures below thermoneutrality also have an inhibitory effect on reproduction but can be offset with an increase in food intake [Bronson 1989].

Squirrel monkeys (*Saimiri sciuerus*) maintained in captive environments across North America provide a good opportunity to investigate the role that environmental factors may play on seasonality of reproduction. Unlike in natural environments, captivity allows the ability to control and manipulate specifics in the habitats. In this paper, I investigate the temporal pattern of reproduction using an extensive dataset on squirrel monkeys maintained in zoos in North America. I first looked at whether indoor housed *Saimiri* exhibit less breeding seasonality than outdoor housed *Saimiri*. Because indoor monkeys are maintained at constant conditions year-round, I would expect that animals kept indoors may reproduce (births and mating) throughout the year therefore exhibiting less seasonality than those squirrel monkeys housed in outdoor enclosures. Environmental factors including rainfall, temperature, and photoperiod have been suggested as proximate factors influencing timing of mating and reproduction [Lindburg 1987]. Although these factors probably are not mutually exclusive, the role of environmental factors on reproductive seasonality in *Saimiri* is not fully understood. Another goal of this study is to find evidence of the roles that these three environmental variables may play in the temporal variation in reproduction in order to enhance breeding and maintenance programs.

MATERIALS AND METHODS

Data Collection

Historical records of captive living animals and their predecessors are available for *Saimiri sciureus* through the North American Regional Studbook, which was provided by the American Zoo and Aquarium Association. The studbook provides accurate information available for genetic and demographic analyses of a specific species. It contains all known biographical information for each squirrel monkey housed at an accredited zoo in North America, which has been entered in SPARKS (Single

Population Analysis and Record Keeping System software maintained by keepers). Each individual is assigned a unique numerical identifier (studbook number) that allows the construction of a pedigree (for genetic analyses) and age-specific schedules of birth and death (for demographic analyses). Supplementary information may also be recorded, as appropriate for that species, to help studbook keepers track an individual [ISIS/CMS Specimen Reference, 2009].

The type of enclosures in which the squirrel monkeys were housed at each zoo was categorized as indoor or outdoor. If one of the environmental variables being investigated was regulated (such as temperature, etc.) or the animals did not have access to the outdoor part of the enclosure during the entire day, the enclosure was classified as ‘indoor.’ Squirrel monkeys were considered to be housed in an outdoor enclosure if during the day they were exposed to outdoor temperatures, rainfall, and natural photoperiod. Even though “outdoor” squirrel monkeys may have indoor sleeping quarters, most do not have additional lighting, although they may contain heaters.

Birth dates for each individual squirrel monkey were obtained from the studbook, as well as whether the individual was born in captivity or obtained from a wild population. A total of 132 individual squirrel monkeys from 35 zoos were included in the dataset (Appendix I). To test effects of environmental variables on seasonality of reproduction, only individuals born in captivity in the United States and those maintained in outdoor exhibits were used, so that an overall temporal pattern of reproduction could be determined for captive-only populations (64 individuals from 15 zoos). Date of breeding was calculated by subtracting length of gestation (160 days) from the date of birth of the offspring, (160 days is an average of all previously published lengths of gestations [Logdberg 1993]). Actual date of breeding was not available in the studbooks because it was difficult to determine pregnancy and because squirrel monkeys may copulate multiple times before fertilization occurs.

Meteorological data regarding rainfall and temperature were obtained online from the National Oceanic and Atmospheric Administration (NOAA) of the US Department of Commerce. Datasets for average monthly rainfall and temperature were on the National Climatic Data Center of NOAA and were recorded for all breeding and birth dates for each animal. Daily photoperiod was obtained from the US Naval Observatory Astronomical Applications Department online through tables of sunrise and sunset times for a specific day at a specific location. The environmental data may be limited because microclimate information was not available.

Breeding and birth dates were categorized according to months for statistical comparisons. With input from each zoo, data were divided into two categories: squirrel monkeys housed in indoor enclosures and exposed to regulated environmental variables, and those monkeys housed in outdoor enclosures year-round.

Data Analysis

All analyses were performed using SAS statistical software version 9.1 for Windows [SAS Institute 2002, Cary, NC]. Normality tests were performed on each environmental factor with the Shapiro-Wilk test (PROC UNIVARIATE). Variables that were non-normal were transformed using the most appropriate transformation. Rainfall was transformed using a square-root transformation, temperature required a reflect square-root transformation due to a negative skew, and photoperiod was log transformed.

Tests for co-linearity of environmental variables were also performed (PROC REG). All statistical tests were two-tailed, and the level of significance was $\alpha = 0.05$.

To determine whether there was an effect of environmental variables on seasonality of reproduction, a comparison of the pattern of births between indoor and outdoor enclosures was performed using Likelihood Ratio statistical significance test (G-test) (PROC FREQ). Months of births were pooled into seasons because of small samples for certain months. Seasons were assigned according to the solstices: winter (21 December to 21 March), spring (21 March to 21 June), summer (21 June to 21 September), and autumn (21 September to 21 December).

A standardized partial regression (path analysis) was used to determine the direct effect of temperature, rainfall, and photoperiod on number of births and number of matings per month for monkeys housed in outdoor enclosures (PROC REG with STB option). Data were standardized because variables were measured on different scales. A path coefficient is a standardized partial-regression coefficient that shows the direct effect of an independent variable on the dependent variable. Because there were more than two possible casual variables, coefficients were partial-regression coefficients, which measure the effect of one variable on another while controlling for the remaining variables [Wright 1921; 1934].

RESULTS

Some squirrel monkeys were maintained in captive environments within outdoor enclosures, and were, therefore, exposed to all environmental factors being tested. These monkeys displayed a mating season from January to April (Figure 1a) and a birth season of June to October (Figure 1b). Other squirrel monkeys were housed in indoor enclosures and continued to mate and reproduce throughout the year. Differences between seasonality of matings of squirrel monkeys housed in indoor and outdoor enclosures were significant (G = 18.79, $P = 0.003$). The majority of the matings resulting in pregnancy occurred during winter for both enclosures, however monkeys maintained in outdoor exhibits mated 68.75% during the winter while indoor monkeys only mated 39.71% during winter. Matings for monkeys housed in indoor enclosures were more evenly spread throughout the year. There was also a significant difference in the birth season between the two types of enclosures (G = 28.10, $P < 0.001$). Although births occurred most frequently during summer for both types of enclosures, they happened at different rates (outdoor: 67.19%; indoor: 33.82%). Indoor monkeys again showed a more evenly distributed pattern of births during the year.

Multiple regression revealed that about 40% of the variation in number of matings among months was potentially explained by environmental variables ($r^2 = 0.416$, F = 1.90, $P = 0.208$). However, about 96% of the variation in the number of births in different months was potentially explained by temperature, rainfall, and photoperiod ($r^2 = 0.963$, F = 69.13, $P < 0.001$).

For squirrel monkeys housed in outdoor enclosures, number of matings per month increased during months of cooler temperatures. Path analysis revealed a strong association of number of matings and mean monthly temperature (p = 0.799; $P = 0.145$; t = 1.62; Figure 2a). Temperature had a significant effect on number of births, with more occurring during times of warmer temperatures (p = -1.315; $P < 0.001$; t = -10.54). Since a reflect square-root transformation was used for temperature, the highest temperature values, became the lowest transformed values. Overall, temperature had a greater influence on number of matings and births per month than rainfall and photoperiod when effects of environmental variables were independently tested (Figure 2a & 2b).

Matings were most common during shorter photoperiod months for squirrel monkeys housed in indoor enclosures (p = 0.330; $P = 0.535$; t = 0.65). Photoperiod had a significant influence on number of births per month (p = -0.425; $P = 0.011$; t = -3.31), with more occurring during months of longer photoperiod. Photoperiod was of secondary importance in both seasonality of matings and births. Effect of rainfall, by comparison, was a trivial influence on both number of matings (p = -0.229; $P = 0.590$; t = -0.56) and births per month (p = -0.024, $P = 0.758$; t = 6.71).

Of the environmental variables used in analysis of number of matings and births, only temperature and photoperiod were significantly correlated ($r = -0.842$, $P < 0.001$). Therefore, multi-collinearity between environmental variables does not seem to be an issue. The low variance-inflation factors (VIF ≤ 3.55) for the environmental variables indicate that standard errors for estimates for each variable were not increased much due to multi-collinearity. Petraitis et al. [1996] recommend a variance inflation factor ≤ 10; otherwise effects of collinearity may affect the conclusion.

Only two environmental variables analyzed in the path analyses had a high degree of collinearity, which would have an effect on the partial-regression coefficients. As collinearity increases among predictor variables, ability to detect a statistically non-zero path coefficient (significant effect) is reduced. This decreases the chances of rejecting the null hypothesis due to large standard errors or underestimated coefficients, rather than unimportance of effect. A high condition index (CI ≥ 30) indicates that there is possible underestimation for those variables that are correlated [Belsley et al. 1980]. This was evident in my path analysis for temperature and photoperiod (CI = 49.814). Therefore, the path coefficient for photoperiod may have a stronger effect on number of matings and number of births per month than indicated. Temperature had a coefficient > -1.0, which is caused by a high condition index and a correlation with photoperiod. Therefore, the value for temperature was over-estimated. However, because temperature seemed to have the greatest impact on seasonality of both matings and births, this over-estimation does not affect the importance of temperature. Also due to the high condition index, both photoperiod and rainfall may have been somewhat under-estimated. In particular, photoperiod may play a larger role in seasonality of reproduction. Rainfall, however, did not seem to impact timing, even with this under-estimation.

DISCUSSION

Squirrel monkeys raised in captivity displayed different patterns of seasonality of reproduction depending on whether the enclosure in which they were housed was exposed to environmental elements (outdoor) or kept at optimal conditions (indoor). Indoor monkeys exhibited less of a seasonality pattern by continuing to mate and reproduce throughout the year, while outdoor monkeys had definite seasons of matings and births restricted to a range of months. With a birth season of five months from June to October, outdoor squirrel monkeys in captivity gave birth during summer months and mated during winter. Although the timing was different, this is similar to the pattern shown in the wild and unlike those monkeys that are kept indoors. Variation in environmental elements for monkeys housed in indoor enclosures may aid in the exhibit of a seasonal reproductive pattern. The temporal pattern of outdoor births coincides with previously published season of birth from Monkey Jungle (a captive breeding colony in South Florida), which is a six-month shift from the seasonality of wild squirrel monkeys in South America [DuMond 1968].

Because there was a significant difference between temporal patterns of reproduction of squirrel monkeys housed in indoor and outdoor enclosures, I was able to further analyze the effects of certain environmental factors such as temperature, photoperiod, and rainfall on reproductive timing of squirrel monkeys. These factors may not be mutually exclusive on their effects of reproductive timing for *Saimiri sciureus*. It appears that both temperature and photoperiod were important factors for temporal timing of reproduction; although, demonstrated by the high correlation between these two factors, there may actually be an interaction of these variables on seasonality of matings and births. Kriegsfeld et al. [2000] showed that gonadal development of adult male prairie voles (*Microtus ochrograster)* was enhanced by the interaction of temperature and photoperiod. Fecundity of tropical fishes has also been shown to be determined by both temperature and photoperiod [Holt and Riley 2001]. Also, there may exist other interactions of environmental factors not tested in this study.

The regression for seasonality of births was significant, with most of the variation in number of births per month being explained by these specific environmental variables tested. Although the path analysis for seasonality of mating was not significant, it did show the opposite pattern of path coefficients in the path analysis for seasonality of births, as expected. Therefore, a temporal pattern of reproduction and mating existed for squirrel monkeys in captivity maintained in outdoor enclosures.

The role of environmental variables on reproductive seasonality of *Saimiri* is still not fully understood. Of the variables tested, temperature seemed to have the greatest impact on reproduction of captive squirrel monkeys. As temperature increased, number of matings per month decreased and number of births per month increased. Due to the type of transformation required for the temperature measures (reflect square-root), the highest temperature became the lowest transformed value. Therefore, a negative path coefficient for temperature would indicate a relationship of number of births and matings per month with higher temperatures. Matings happened during the opposite time of the year, when temperatures were cooler. This is the pattern that was expected and also is in agreement with Dumond's [1968] observation of matings during winter months and births during summer.

Photoperiod could be a secondary indicator for the temporal pattern of both matings and births. Matings occurred during months of shorter photoperiods (less sunlight and more darkness), while births occurred during months of longer photoperiods (more sunlight). The impact of photoperiod was statistically significant only on number of births per month. However, importance of photoperiod on number of matings per month was underestimated because of its correlation with temperature.

Rainfall did not seem to be an important indicator for matings or births of outdoor squirrel monkeys in captivity. In the wild, squirrel monkeys are mainly insectivorous but consume fruit during the rainy season when it is plentiful [Stone 2007c]. Boinski and Fowler [1989] also found a dramatic increase in the amount of new leaves at the beginning of the wet season, which are an additional food source for *Saimiri*. Infants are born during this time when availability of fruit is at its highest (January to March)

[DiBitetti and Janson 1999; Stone 2007c], but this pattern is not maintained in captivity. Field studies have shown that the yearly pattern of reproduction is related to rainfall and food availability [Boinski and Fowler 1989], so that the birth season occurs during the time of the year when fruit production is the greatest [Boinski 1987]. To ensure adequate nutrition for infants, the optimal period would be to coincide time of weaning with fruit and insect availability. Perhaps, the constant food supply has lessened the importance of rainfall on reproductive timing for captive animals by reducing the relationship between rainfall and food availability found in their natural environment. Rasmussen [1985] also showed that lemurs maintained in captivity had different timing of reproduction due to change in latitude. In the wild on the island of Madagascar, breeding would naturally coincide with the beginning of the wet season causing an over-abundance of resources. Similar findings have been found in captive lion tamarin populations in Brazil, whose peak birth periods occur in September and October, the same time of increasing rainfall. However, constant provisioning of food resources did not affect the number of litters per year, as expected [French et al. 1996].

Other environmental variables not tested in this paper may be involved in regulation of seasonality of reproduction in squirrel monkeys. Any variables that are highly regulated with temperature and/or photoperiod may be driving the seasonality exhibited. This study could only investigate the association of environmental factors with reproduction. An experimental study that can regulate temperature and photoperiod while altering the other environmental variable will be able to tease them apart and determine causation of by specific variables. Social influences, such as group size and numbers of males and females, may have an impact on the temporal variation of matings and births. Social facilitation by other females was the main hypothesis invoked by Schiml et al. [1996] to explain seasonal reproduction in squirrel monkeys. This has been shown in other seasonally breeding mammals, such as rhesus macaques (*Macaca mulatta* [Vandenbergh and Drickamer 1974]) and domestic sheep (*Ovis aires* [Wayne et al. 1989]).

Understanding what regulates reproduction, especially whether there are differences between those animals kept in captivity and those that live in the wild, for animals is important for conservation of a species. This study had limitations due to the scope of the question. The date of breeding was back-calculated from date of birth for each individual because squirrel monkeys do not show any outward signs of pregnancy. Length of gestation has been estimated to be 148 to 172 days [Logdberg 1993]. I used an average of all reported lengths of gestation for my calculations, which may have affected overall tightness of seasonality of matings. Average length of gestation used in the calculation may not have been the actual gestation time for each individual. Therefore, the actual pattern of mating seasonality may differ slightly from that shown here.

Further studies can now investigate whether there are any differences in life history or survival for squirrel monkeys that reproduce seasonally and those that reproduce year round. Perhaps importance of reproducing seasonally is socially based in the wild, allowing for babies in a group to be better protected by the group if born around the same time. Boinski [1999] has suggested that predation pressure is a factor for species exhibiting synchronous breeding. In *S. sciureus,* all pregnant females give birth within a week of each other. However, in captivity, predators are no longer a threat and food is plentiful all year long, providing the ability for squirrel monkeys to be released from predation pressures and make the most of their habitat. Additional research also can look into whether this is purely an adaptation to a local environment (plasticity of life history traits) or whether evolution is taking place by comparing generations of squirrel monkeys born in captivity. Would squirrel monkeys that have lived in captivity for generations be able to be reintroduced back into the wild and begin reproducing seasonally?

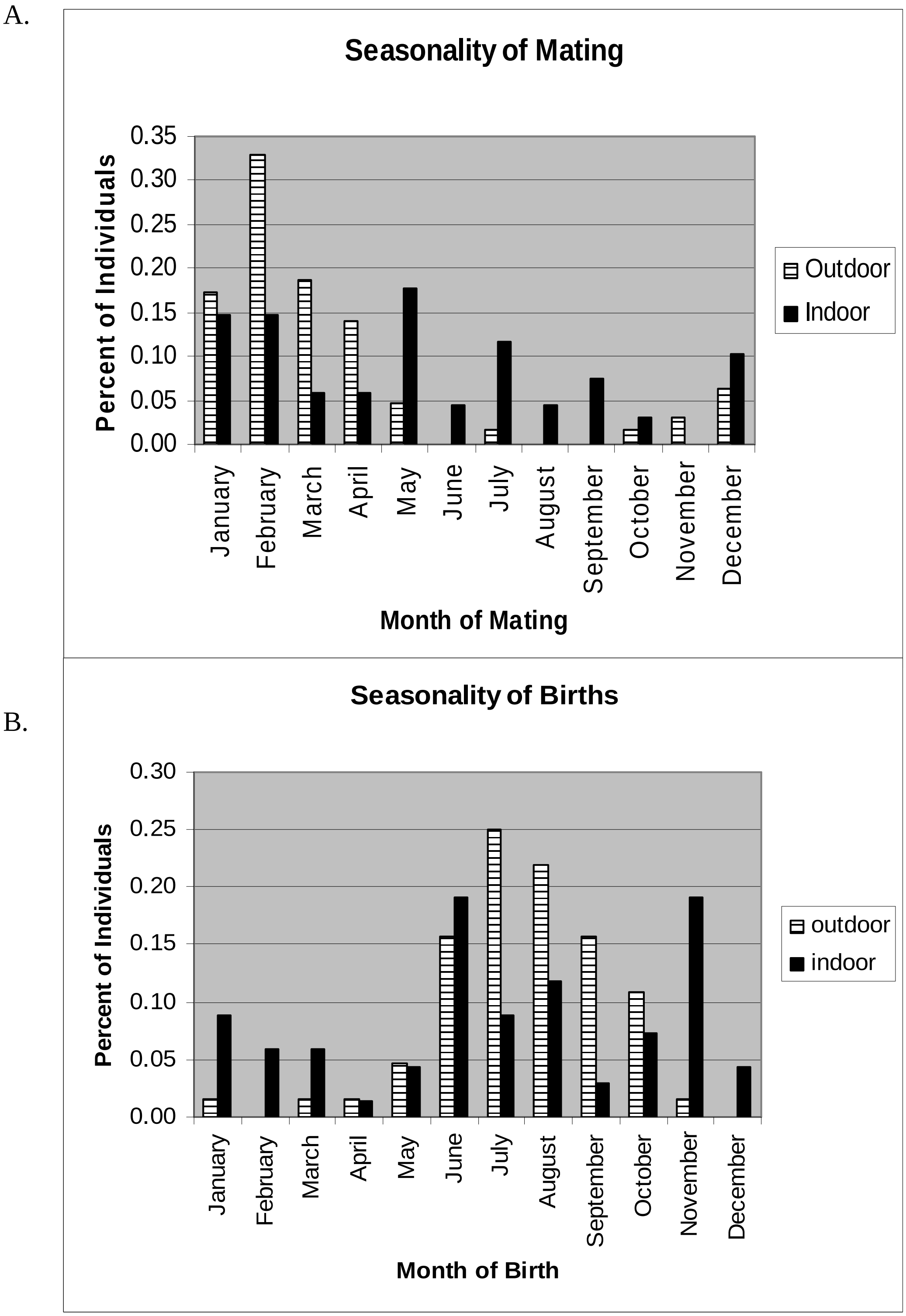

Figure 1: Comparison of seasonality of squirrel monkeys maintained in indoor and outdoor enclosures for A) mating (calculated from birth dates) and B) births.

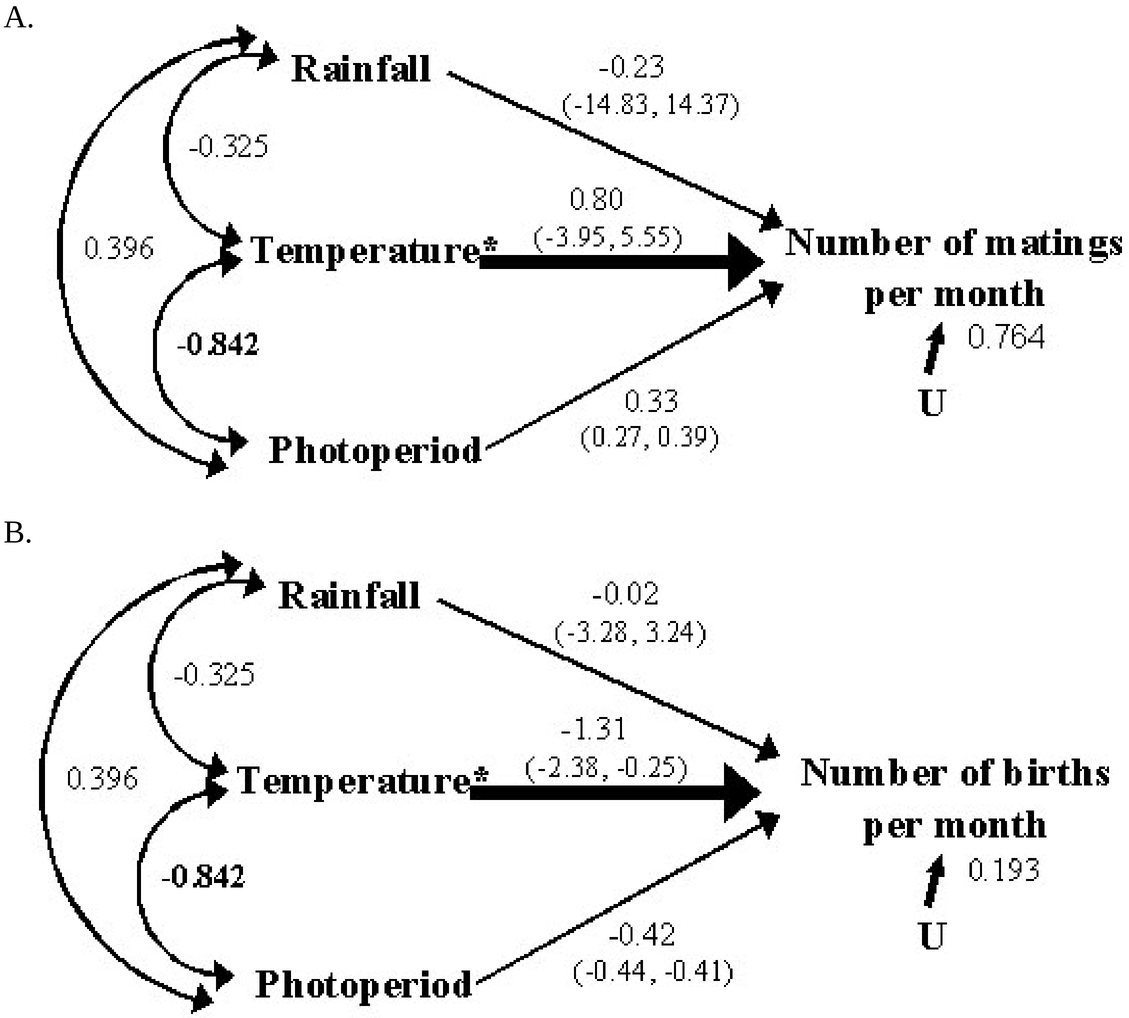

Figure 2: Path model of the influence on squirrel monkeys maintained in outdoor enclosures of environmental variables, rainfall, temperature, and photoperiod, on number per month of: A) matings and B) births. Correlations between environmental variables appear on the left of the diagram between independent variables. Path coefficients were found only for interactions between environmental variables and dependent variable (number of births per month). Lower and upper 95% confidence limits on the path coefficients and on the proportion of unexplained variance of terms are shown in parentheses. Path coefficients are located above respective confidence limits. U indicates the path coefficient for unexplained variation found by the $\surd(1 - r^2)$ [Li, 1977]. *****Temperature values were normalized using a reflect-square-root transformation; therefore causing the lowest temperature values to become the highest values.

Appendix I – Zoos that house or have housed squirrel monkeys in North America.

Facility	Location	Enclosure	Latitude	Births	Year of births
Amigata Grande Ranch	Houston, TX	Indoor	29° 59' N	1	1980
Baylor University Strecker Museum	Waco, TX	Indoor	31° 37' N	2	1980
Chicago Zoological Park	Brookfield, IL	Indoor	41° 53' N	5	1979, 1983, 1988, 1989
Cleveland Metroparks Zoological Park	Cleveland, OH	Indoor	41° 24' N	3	1980, 1981, 1990
University of California – Davis, Raptor Center	Davis, CA	Indoor	38° 31' N	2	1989, 1991
Denver Zoological Gardens	Denver, CO	Indoor	39° 45' N	7	1997, 1998, 2000
Ft Wayne Children’s Zoological Garden	Ft. Wayne, IN	Indoor	41° 0' N	3	1988, 1990, 1993
Utah’s Hogle Zoo	Salt Lake City, UT	Indoor	40° 46' N	1	2000
Oakland Zoo in Knowland Park	Oakland, CA	Indoor	37° 49' N	4	1994, 1997, 1998, 2000
Henry Vilas Zoo	Madison, WI	Indoor	43° 8' N	1	1984
Memphis Zoological Garden & Aquarium	Memphis, TN	Indoor	35° 3' N	2	1982, 1984
Louisiana Purchase Gardens & Zoo	Monroe, LA	Indoor	32° 31' N	1	2000
New York Bronx Zoo	Bronx, NY	Indoor	40° 47' N	13	1980, 1988, 1999, 2000, 2001
Omaha’s Henry Doorly Zoo	Omaha, NE	Indoor	41° 18' N	4	1977, 1985, 1990, 1995
Philadelphia Zoological Gardens	Philadelphia, PA	Indoor	39° 53' N	2	1999, 2000
Santa Barbara Zoological Gardens	Santa Barbara, CA	Indoor	34° 26' N	9	1985, 1986, 1988, 1989, 1990, 1995, 1999
Woodland Park Zoological Gardens	Seattle, WA	Indoor	47° 39' N	2	1977, 1980
Sedgwick County Zoo	Wichita, KS	Indoor	37° 39' N	3	1980, 2000
Tulsa Zoo and Living Museum	Tulsa, OK	Indoor	36° 12' N	2	1978, 1992
Brevard Zoo	Melbourne, FL	Outdoor	27° 58' N	1	1995
Busch Gardens	Tampa, FL	Outdoor	27° 58' N	5	1992, 1995, 1997, 1999
Caldwell Zoo	Tyler, TX	Outdoor	32° 21' N	16	1992, 1993, 1994, 1995, 1996, 1997, 1999
Lincoln Park Zoo	Chicago, IL	Outdoor	41° 53' N	5	1979, 1980, 1983, 1984
Florida Cypress Gardens	Winter Haven, FL	Outdoor	28° 33' N	5	1983, 1986, 1987, 1988
Dreher Park Zoo	W Palm Beach, FL	Outdoor	26° 41' N	2	1984
Greenville Zoo	Greenville, SC	Outdoor	33° 4' N	1	1991

Montgomery Zoo	Montgomery, AL	Outdoor	32° 23' N	1	1995
Virginia Zoological Park	Norfolk, VA	Outdoor	36° 54' N	1	1980
San Antonio Zoological Garden & Aquarium	San Antonio, TX	Outdoor	29° 32' N	11	1974, 1981, 1982, 1983, 1987, 1990, 1991
San Francisco Zoological Garden	San Francisco, CA	Outdoor	37° 46' N	1	1992
Turtle Back Zoo	West Orange, NJ	Outdoor	40° 42' N	1	1978
Lion Country Safari	W Palm Beach, FL	Outdoor	26° 41' N	13	1982, 1987, 1988, 1989, 1991, 1994, 1995, 1997, 1998, 1999, 2000
Cameron Park Zoo	Waco, TX	Outdoor	31° 37' N	1	2000
Bramble Park Zoo	Watertown, SD	Outdoor	44° 55' N	1	1997

CHAPTER THREE: VIGILANCE AND RESPONSES TO ALARM YAPS IN CAPTIVE SQUIRREL MONKEYS (*SAIMIRI SCIUREUS*)

Abstract. The availability of squirrel monkey groups maintained in captivity (i.e. research facilities and zoos) provides an opportunity to investigate whether behavioral differences exist in the responses of captive populations to alarm call playbacks. Previous studies have shown that reactions to alarm calls are innately predisposed; however appropriate anti-predator behaviors require experience, and animals raised in captive situations lack exposure to predators. The behavioral responses of all ages of squirrel monkeys were recorded after the presentation of two alarm calls, two predator sounds, and two control sounds. Sounds of both alarm calls (own alarm call and other *Saimiri* alarm call) elicited significantly more vigilant behaviors than both predator and control sounds. Group members did not maintain vigilant behaviors. Unlike previous studies, the mean response of vigilant behaviors did not vary by sex or age. The behavioral responses of the squirrel monkeys seemed to be influenced by facility but not by group size or type of enclosure. We found that naïve captive squirrel monkeys were still able to distinguish between control sounds and alarm calls by displaying vigilant behaviors, displaying behaviors more like their own group than other groups.

INTRODUCTION

Vocal signals are important because they can modify the behaviors of individuals other than the caller. Such signals can be documented with recording and by observing the behavioral reactions of the receiver [Marler 1965; Seyfarth and Cheney 2003]. Both monkeys and apes utilize composite signals that include more than one physical quality of vocal communication such as specifics about the sender and/or receiver, modality, context, or information about internal state [Marler 1965; McCowan et al. 2001]. Such calls often signal an alarm due to the presence of a predator by the type and/or urgency of the predatory threat [Winter et al. 1966; Newman 1985].

The genus *Saimiri* consists of several squirrel monkey species found in Central and South America [Kinzey 1997]. The audible frequency range for vocal communication in these species is very large (0.1 kHz to at least 32 kHz) allowing for full communication of the caller's perception of predators and other animals [Green 1975; Newman 1985]. Winter et al. [1966] first described the vocal repertoire of the squirrel monkey, which now consists of six main call groups based on structural features of the sound: peeps (containing the alarm peep), twitters, chucks (containing the alarm yap), cackles, pulsed calls, and noisy calls [Newman 1985].

Squirrel monkeys give acoustically different alarm calls (peep and yap) associated with the contexts of potential danger [Boinski and Mitchell 1992]. Alarm calls are produced appropriately for the type of predator (aerial versus terrestrial), and different calls may elicit different behavioral responses [Newman 1985]. It has also been suggested, however, that these calls refer to the urgency of the predatory threat rather than the class of predator [Jürgens 1982; McCowan et al. 2001]. The alarm peep specifically refers to “aerial” predators [Newman 1985; Emmons 1987] or rapidly moving objects and terrestrial animals [Herzog and Hopf 1984; McCowan et al. 2001]. When heard, the surrounding animals will become vigilant by finding shelter and stopping all activity. It is a stereotypical call that can last for several hundred milliseconds with a peak frequency of 14-16 kHz. Responses to the alarm peep can be elicited with a playback stimulus even without a visual motivation [Winter 1968; Newman 1985]. Most research on alarm calls and vigilance of squirrel monkeys has focused on the responses to the peep vocalization in laboratory [Winter et al. 1966; Winter et al. 1973; Hammerschmidt et al. 2001; McCowan et al. 2001] and field studies [Boinski et al. 2003].

Alarm yaps are equivalent to a ‘mobbing’ call, which notifies a terrestrial predator that it has been noticed and may cause members of the troop to surround the stimuli while continuing to vocalize [Herzog and Hopf 1984]. The function of the yap seems to be in situations of fright and aggression [Jürgens 1982] and can be elicited by snakes and other terrestrial predators [Winter 1968; Newman 1985; McCowan et al. 2001], as demonstrated by field studies of ocelots [Emmons 1987]. The structure of the yap call is complex, variable, and produced about once per second [Newman 1985]. Unlike with the peep, the mobbing response to an alarm yap might be based on past history or ecology of the species. Boinski *et al.* [1999] showed that terrestrial predator alarms in a closely related species, brown capuchins (*Cebus apella*) in captivity, are emitted despite the absence of any predatory threat.

Herzog and Hopf’s [1984] laboratory experiments found mixed reactions to both types of alarm calls (alarm peep and yap) in infant squirrel monkeys raising questions about whether there is an innate predisposition. When reared in isolation, infants ran to their surrogate mother when they heard an alarm peep, which is the appropriate species-response, while the responses were quite variable with the playbacks of yaps. When a visual model was combined with the yap vocalization, squirrel monkey infants avoided the presentation and increased contact with the surrogate mother. These differences in behavioral reactions to alarm call playbacks suggests that appropriate predatory responses to the yap vocalization requires social learning. Innate fear of predators has not been shown in other primate species such as rhesus macaques [Mineka et al. 1981; Mineka et al. 1984] and cotton-top tamarins [Hayes and Snowdon 2007].

Rearing environment may be related to the differences in responses to alarm calls, as seen in other mammalian species. Captive-reared Belding's ground squirrels were more likely to respond to any stimulus during playbacks than field-reared juveniles [Mateo and Holmes 1999a]. Differences with innate fear of snake-like objects in wild and captive rearing environments have been exhibited in several species of primates. Rhesus macaques raised in captivity exhibit a strong fear of snakes [Joslin et al. 1964] and could learn to fear arbitrary objects by observation [Stephenson 1967]. Lab-reared squirrel monkeys exhibit no latency period when reaching for food in a fearful situation, as compared to wild-reared [Murray and King 1973]. Captive indoor-housed cotton-top tamarins do not have a fear of natural predators, as shown by the lack of alarm calling and mobbing behavior to the presentation of a live snake [Friant et al. 2008]. The ontogeny of behavioral responses to alarm calls may be dependent on the early rearing environment of the individual [Mateo and Holmes 1999a], even where there is an innate predisposition. However, innate and learned components of species-specific reactions to alarm calls may interact with each other [Seyfarth and Cheney 1990].

The availability of squirrel monkey groups maintained in captivity (i.e. research facilities and zoos) provides an opportunity to study whether behavioral differences exist in the responses of captive populations to alarm call playback experiments. The purpose of the present study was to investigate the behavioral responses of captive squirrel monkeys to the yap vocalization. We were able to include a large sample size (271 individuals from 14 facilities) and presented a variety of sounds for comparison (two alarm calls [yaps], two predator sounds [aerial and ground], and two controls [bird song and white noise]). Although previous studies have shown that a response to an alarm peep call is innately predisposed [Winter 1968; Herzog and Hopf 1984; Hauser 1988; Boinski et al. 1999; Hammerschmidt et al. 2001], fully appropriate anti-predator responses to alarm peeps have been shown to require experience [Hauser 1988; Seyfarth and Cheney 1990; Oda and Masataka 1996; Mateo and Holmes 1999b]. Since captive individuals have had little to no prior experience, we would predict from the "experience" hypothesis that adult squirrel monkeys would not exhibit reactions to alarm call playbacks. The safety of captivity is expected to produce naïve adult monkeys. If, alternatively, responses to alarm calls were innately determined, then we would predict vigilant behaviors that reflect the potential presence of a predator. Thus, according to this hypothesis, we expect squirrel monkeys to become vigilant and possibly exhibit the mobbing behavior produced in the wild by the alarm yap, as well as exhibit differences between age groups. It is probable, however, that responses to alarm calls are a mixture of instinct and experience as shown in other studies [Seyfarth and Cheney 1990; Mateo and Holmes 1999a], and intermediate results would support partial roles of both innate and learned mechanisms for the context-dependent response to calls and the sounds of threats.

METHODS

Study subjects

Squirrel monkeys (*Saimiri sciureus*) from fourteen captive facilities (based on AZA *Saimiri sciureus* studbook; Table 1) around North America were subjects of this study. Individuals were assigned random identifier numbers and categorized based on age groups (infant, juvenile, sub-adult, adult) and sex based on physical appearances and birthdate, when possible. Some facilities' monkeys were marked with hair shavings or neckbands to allow for reliable recognition. The group size at each location and type of housing enclosure were also noted.

Vocalization recordings and playbacks

A wireless speaker (Sony Wireless RF Speakers SRS-RF930RK, frequency response 913.5 - 914.5 MHz) was located outside each enclosure (unless the type of enclosure required the speaker be inside, although the observer remained outside) at least 24 hours before any playbacks to allow habituation. Alarm call vocalizations (yap) of each squirrel monkey group were elicited using a stuffed toy snake. A few groups would not vocalize at the stuffed toy snake, so the keepers attempted to elicit the call by bringing a predator into view of the monkeys (live snake, owl or dog). Vocalizations were recorded using a Marantz recorder (Marantz PMD660 Portable Solid State

Recorder; Marantz America, Inc., Mahwah, NJ) and used as part of the playback experiment. All sounds utilized in the playback experiments were modified to 15 seconds in length using spectrograms from Raven 1.2 (Cornell Lab of Ornithology, Ithaca, NY) and presented at peak amplitudes approximating natural intensities (20 dB at ~5 m from the sound origin) [McCowan et al. 2001].

During each playback, the group was observed using instantaneous scan sampling in 1-min intervals [Altmann 1974]. For locations with a larger population of squirrel monkeys, more than one observer recorded behaviors with an inter-observer index of reliability > 88.5% [Martin and Bateson 1986]. Individuals were observed for 10 minutes before a sound was presented to ensure that the observer had no impact on the behavior of the animals and to obtain a baseline for pre- and post-stimuli comparisons. All behaviors immediately as the sound was played and for 10 minutes after the sound were recorded. The behavior of each individual monkey was recorded according to an ethogram where behaviors were categorized into two main classes: vigilant (calling, looking up/down/toward speaker, fleeing) and non-vigilant behaviors (locomoting, feeding, social interactions, inactivity). We defined vigilant behaviors the same as McCowan *et al.* [2001]; stopping previous activities and beginning vigilant gazing (looking toward the source of the sound, or scanning the surroundings), freezing, or sudden flight in response to the sound played.

The sounds presented to the squirrel monkeys included (i) an alarm call (yap) recorded from the focal group, (ii) squirrel monkey alarm call (yap) from a different group, (iii) growls of ocelot (*Leopardus pardalis*; 0-4 kHz), (iv) bird song (2-7.5 kHz), (v) Harpy Eagle sound (*Harpia harpyja*; 2-11 kHz), and (iv) white noise (0-11 kHz).

The order in which the sounds were presented each day was randomized. Using the recorder and wireless speaker, sounds were played at the same amplitude and frequency as normally would be produced by the monkeys. A session of all 6 sounds was played once per day to avoid degradation of responses, for a total of 3 days. Each session lasted 6 hours (allowing for an hour between each presentation of a sound). A different sample of each sound was played each day to avoid habituation to the particular sound. One of the squirrel monkey alarm calls, bird song, harpy eagle sound and ocelot sound were purchased from the British Library Sound Archive, London, UK.

Data analyses

Data were gathered for ten minutes before and after playback of each sound. To make a comparison for each individual, we needed to determine whether the behaviors exhibited differed by minute using a chi-square. There was no significant difference in the frequency of non-vigilant behaviors exhibited in the ten pre-stimulus minutes for all sounds presented ($\chi_9^2 = 4.551$, $P = 0.872$). Therefore, only the minute before the playback was used for comparison since it was representative of all other pre-playback minutes. This was also the same for the ten post-stimulus minutes ($\chi_8^2 = 2.711$, $P = 0.951$). Comparisons for behavioral responses were therefore made with the minute before, the minute during and the minute after the playback.

Using a mixed model regression (Proc Mixed), data were analyzed using the following variables: sound (own alarm call, other *Saimiri* alarm call, harpy eagle, ocelot, white noise, bird song), sex, age class (infant, juvenile, sub-adult, adult), day of sound (1, 2, or 3), interaction between day and sound, group size, and type of enclosure (outdoor,

outdoor with open top, indoor). The effect of animals being housed as groups (hereafter referred to as ‘facility’) and individual identifiers were included as random effects. Facility might have an effect ($z = 1.93$, $P = 0.027$) on the other variables; therefore it was also analyzed as part of the model (Proc Mixed). Facilities in which individual identification was not possible were removed from detailed analyses of sex and age (172 individuals from 3 facilities; Table 1). All analyses were performed using SAS statistical software version 9.1 for Windows [SAS Institute 2002, Cary, NC].

RESULTS

Vigilant responses to presentation of sounds

Using a mixed model regression, the mean response of vigilant behaviors of all individuals observed was significantly different depending on the type of sound broadcasted ($n = 271$, $F_{5,1717} = 91.14$, $P < 0.001$). The variables sex ($n = 99$, $F_{1,1059} = 0$, $P = 0.9908$) and age ($F_{1,1059} = 1.75$, $P = 0.1559$) were not significant for the 99 individually identifiable subjects from 11 facilities tested, and therefore were removed from the model presented below. Overall, captive squirrel monkeys increased their vigilant behaviors to the different sounds presented in this study.

Both alarm calls (own alarm call and other *Saimiri* alarm call) elicited greater responses of vigilant behaviors than both predator and control sounds (Figure 1). The alarm call exemplars presented did not elicit significant differences in vigilant behaviors ($\chi^2 = 56.105$, $P < 0.0001$; Table 2) as more than half of the monkeys observed became vigilant when an alarm call was played (other *Saimiri* alarm call 55.88%, own alarm call 67.55%; Table 2). These responses were significantly different from the behaviors exhibited with the presentation of control and predator sounds ($\chi^2 = 56.105$, $P < 0.0001$). We predicted that the four other sounds presented (predator and control sounds) would not elicit vigilant behaviors. However, both sounds of two main predators of squirrel monkeys in the wild resulted in some vigilant behaviors (harpy eagle 19.34%, ocelot 20.34%; Table 2), as did the two control sounds (bird song 14.04%, white noise 10.40%; Table 2). Even though both predator and control sounds elicited some vigilant behaviors upon presentation, these were not significantly different ($\chi^2 = 1.247$, $P < 0.446$; Table 2).

Maintenance of vigilant behaviors

Overall, vigilant behaviors exhibited in response to sounds presented to all of the captive squirrel monkeys were not maintained for more than a minute after the sound was played (Figure 1). Only a few instances of maintenance occurred for both the control and predator sounds (bird song 2.42%; harpy eagle 4.37%). Only slightly more vigilant behaviors were exhibited for more than 1 minute after an alarm call was presented (other *Saimiri* alarm call 8.65%, own alarm call 7.84%). Most squirrel monkeys that became vigilant after the broadcast of one of the playbacks did not maintain that response for more than one minute. However, vigilant responses were more likely to be maintained depending on the type of sound presented. A squirrel monkey’s alarm call elicits the longest, although not statistically significant, response compared to control sounds ($\chi^2 = 3.463$, $P = 0.0627$).

Habituation to sound presentation

Exemplars of all sounds were presented each day for three days. Responses to the broadcasts (n = 99, $F_{2,1059} = 13.26$, $P < 0.0001$) by captive squirrel monkeys were significantly different according to the day presented. Vigilant behaviors were more abundant on the first day of a sound being broadcasted; as the experiment progressed the monkeys seemed to habituate to the sounds by reducing their likelihood of becoming vigilant (Figure 2). However, whether the monkeys remained vigilant after the presentation of a sound was not affected by how many days a type of sound was played for the three days of the experiment (n = 99, $F_{2,1059} = 0.31$, $P = 0.734$).

Facility effects

Captive squirrel monkeys not only respond as unique individuals but individuals within a group at each facility responded more similarly to each other than to individuals at other facilities (n = 271, $F_{11,1717} = 10.36$, $P < 0.001$). The effect of the facility may be due to group size. However, group size was not significant factor in the model (n = 271, $F_{1,1717} = 0.52$, $P < 0.472$) and neither was the type of enclosure in which the groups were maintained (n = 271, $F_{2,1717} = 0.28$, $P < 0.756$). Therefore, by statistically controlling for these factors, each group's behaviors were significantly different from squirrel monkeys at a different facility.

DISCUSSION

There is a wealth of information about the development of signals to alarming situations and the appropriate responses to those calls. A wide range of species, including vervet monkeys [Seyfarth et al. 1980; Seyfarth and Cheney 1990; Smith and Harper 2003], ring-tailed lemurs [Pereira and Macedonia 1991], prairie dogs [Slobodchikoff et al. 1991], and chickadees [Ficken 1990] show greater vigilant behavioral responses to alarm calls than other sounds presented. This universal response to augment behavior appropriate to a situation in an alarming context suggests that there is a definite innate component to responses to alarm calls. However, these initial reactions are usually not fully developed and modified over time with experience to become species-appropriate responses [McCowan et al. 2001; Smith and Harper 2003].

Our playback experiment tested the behavioral responses of captive squirrel monkeys to a variety of sounds (control sounds, predator sounds, and alarm calls) using monkeys in zoos and research facilities across North America. McCowan *et al.* [2001] showed that captive squirrel monkeys responded differentially to alarm peeps than to sham and chuck playback calls. We found a similar pattern when using alarm yap vocalizations; more vigilant behaviors were exhibited after the playback of an alarm call compared to predator and control sounds. Therefore, captive squirrel monkeys seem to be able to distinguish between sounds presented and react appropriately by displaying vigilant behaviors to alarm calls (both alarm peeps and yaps), even with little to no previous experience. Although raising primates in captivity has been shown to alter reproductive patterns [D'Hooghe et al. 1996; Trevino 2007] and increase the production of repetitive behaviors [Marriner and Drickamer 1994], naïve primates seem to be able to display species-typical behavioral responses to predatory situations.

The captive squirrel monkeys studied in this playback experiment did not show a dramatic difference in their increase of vigilant behaviors for predator sounds versus control sounds. This is not an unusual finding; Blumstein et al. [2000] suggests that the sounds of predators do not influence responsiveness, unlike visual cues. This may be because predators are unlikely to vocalize while hunting; however, the sound should represent the presence of a predator. Diana monkeys in the wild do show an increase in their number of long-distance calls after playbacks of leopard and eagle vocalizations [Zuberbuhler et al. 1997]. Although vigilant behaviors are not being observed, these monkeys are still reacting to a change in their environment. Squirrel monkeys maintained in zoos and research facilities are naïve animals, unlike their wild counterparts, with very little experience to the sight and sounds of predators. Additionally, the sounds that they may be exposed to in a zoo from captive predators are not associated with predatory attacks, thus the monkeys may actually learn that the sounds are neutral, effectively background noise.

Vigilant responses in captive squirrel monkeys were not maintained after the broadcast of any of the sound exemplars, although a squirrel monkeys' alarm call impacts the behavioral reactions for most. We expected these behaviors to persist for an unnaturally long length of time given the naiveté of the monkeys. Mateo and Holmes [1999b] reared young Belding's ground squirrels in captivity and found that they will emit an exaggerated response to playback stimuli, remaining alert longer. They concluded that this unusual response was due to experience prior to the pups emerging from their natal burrow. Vigilant responses in captive squirrel monkeys were not displayed for more than a minute after playback for all but one sound. Unfortunately, there are no data from the literature for wild populations of squirrel monkeys that documents the length of vigilant responses to allow for a comparison.

During our analyses, the specific “facility” was included as a random variable to control for differences in environment among the different groups of monkeys. However, we found that each group was different, and therefore this variable became a covariate for our model of predicting vigilant behavior. Individuals acted more like their group-mates than individuals in other groups. Most previous playback studies only tested one group of captive animals and tested them while in group settings. We have shown that an animal’s vigilant responses can be widely varied depending on their housing environment or grouping and that conclusions on just one population may not be representative of a species as a whole. Additionally, when removing individuals from a group to test their response, the extremely important influence that group-mates’ responses have on the individual are disregarded. In an effort to discover a source of the differences in behavior between facilities, we looked for an effect of group size or type of enclosure. Vigilance can be affected by group size [Elgar 1989; Roberts 1996], and we also surmised that the type of enclosure (indoor, outdoor, exposed outdoor) may influence the monkeys’ perception of their safety. However, neither group size nor type of enclosure (at least as we categorized them) seemed to influence the behavioral responses of the captive squirrel monkeys.

Why were some groups easily provoked to alarm, while others seemed unfazed by any object presented? The reactions of the individual monkeys within each zoo seemed to be similar to group-mates and consistent over time. The fearfulness an individual exhibits when it encounters novel stimuli can be influenced by many factors, both genetic and environmental. Although many of the groups consisted of related individuals, individuals are moved from zoo to zoo to avoid inbreeding, so not all group-mates are related. Thus, genetics probably only played a minor roll. We believe that a possible explanation for these differences between groups is that each zoo/research center group displayed a "group personality". This was evident when we attempted to elicit alarm calls from each group that would be used in the playbacks. Some groups immediately emitted alarm calls and exhibited mobbing behavior when a stuffed toy snake was shown. Others were almost completely unresponsive, hardly even looking at the toy. For these unalarmed groups, we attempted to make the toy snake appear to be a greater threat, putting the toy snake inside the enclosure. This was still not perceived as a threat by some groups, and the zoo keepers became resourceful to elicit alarm calls, bringing live snakes, owls, and dogs into view of the monkeys. Seeing these live predators often elicited calls, but for a few groups, even these visual cues elicited nothing but curious stares. Similarly, the groups that were difficult to elicit alarm calls from were also less responsive to the playbacks.

Environmental factors may have also influenced the behavioral reactions of the monkeys to the calls presented that were not tested in our model. Some of these variables may be related to their housing such as the size and type of enclosure (although the classification used for the type of enclosure did not show an effect), husbandry techniques used, amount and variety of enrichment given, activities and animals within view (noise levels, numbers of visitors, predators within site). Social group dynamics may affect group a member depending on the length of time the group has been living together and the social interactions within the group.

Although there is a growing field of animal personality research, we could not find studies that examined the personality of an overall group. Our findings raise many questions about group and individual personalities: What are the main factors affecting the group personality [Mateo and Holmes 1999b]? Are dominant individuals within each group setting the tone for how the others should act? Or is the physical habitat the main influence on the personality of the individual (anecdotally, the groups most difficult to alarm were one located in a building intended for children's learning and playing, and one in a zoo that used very loud fireworks to discourage vultures from landing)? If an individual is moved to another group will its behavior change to match the new group? These questions could be of interest in many social species, both in captivity and in the wild.

Table 1. Population information for squirrel monkey groups used in the playback experiments. *Notated zoos were not included in all analyses because individual identifications were not possible.

Facility	**Group size**	**# Adults**	**# Subadults**	**# Juveniles**	**# Infants**
Alexandria Zoological Park	2	1	1	0	0
Kansas City Zoo	4	4	0	0	0
Lion Country Safari	10	9	0	0	1
Louisiana Purchase Gardens and Zoo	3	1	1	1	0
Monkey Jungle/ DuMond Conservancy*	150	?	?	?	?
Montgomery Zoo	9	3	5	0	1
Oakland Zoo	8	7	0	0	1
Philadelphia Zoo*	12	10	0	1	1
Phoenix Zoo	16	8	0	5	3
Riverview Park and Zoo*	10	7	1	1	1
Sante Fe Teaching College	2	2	0	0	0
Sedgwick County Zoo	4	4	0	0	0
University of South Alabama	38	17	3	18	0
Utah’s Hogle Zoo	3	3	0	0	0
TOTALS	**271**	**76**	**11**	**26**	**8**

Table 2. The individual values and means for the proportion of vigilant responses to sounds presented during the 3-day playback experiment (*d.f.* = 1717). Chi-square values are presented with each sound compared to a control sound. * Denotes significance at the ∝ = 0.05.

Sound	**Category**	**Day 1**	**Day 2**	**Day 3**	**Mean**	**SE**	χ^2	***P***
Birdsong	Control	0.140	0.098	0.143	0.140	0.015	0.42	0.514
White noise	Control	0.221	0.028	0.125	0.104	0.056	0.42	0.514
Ocelot	Predator	0.294	0.132	0.137	0.203	0.053	0.87	0.446
Harpy Eagle	Predator	0.261	0.130	0.189	0.193	0.038	1.25	0.446
Own alarm call	Alarm Call	0.835	0.717	0.443	0.676	0.116	56.11	<0.01*
Other *Saimiri* alarm call	Alarm Call	0.717	0.440	0.557	0.559	0.082	36.95	<0.01*

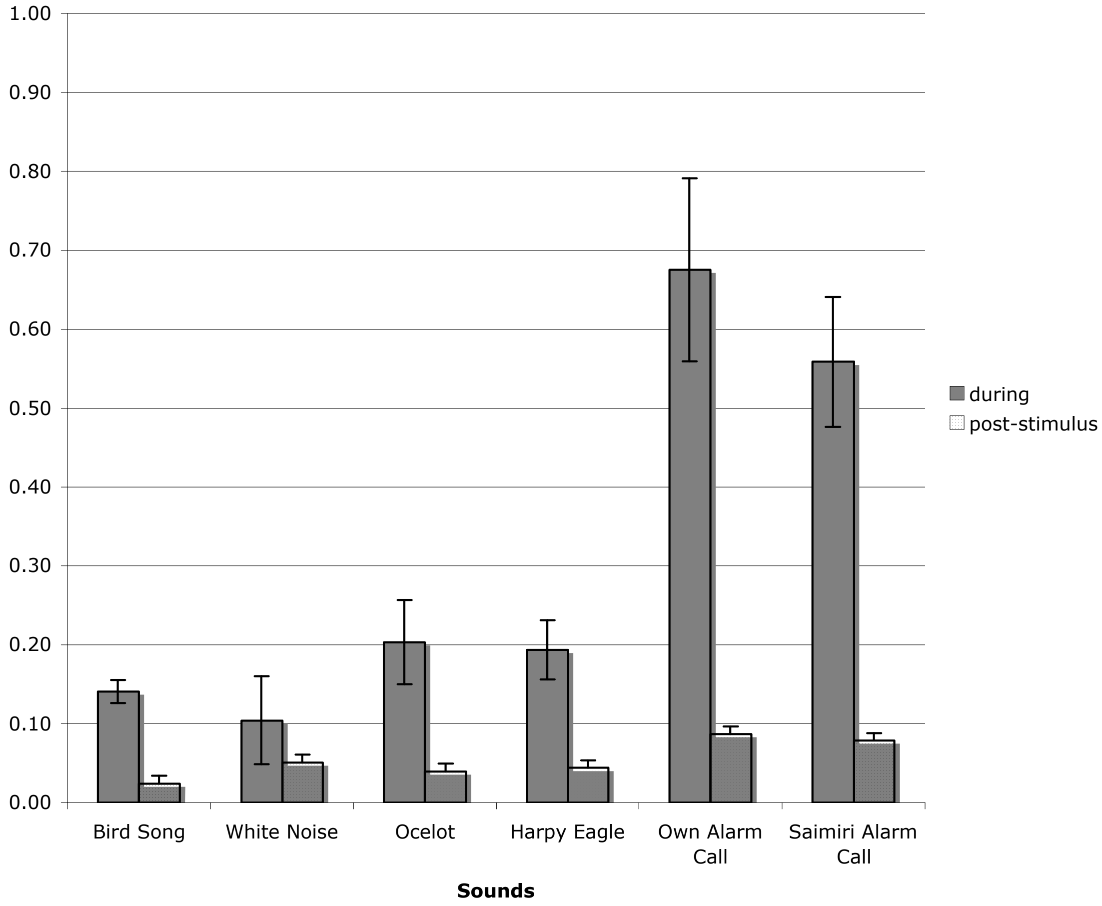

Figure 1: The mean proportion of vigilant behaviors exhibited after playback sound presented to a squirrel monkey group over a 3-day experiment. Presentation of the vigilant behaviors exhibited the minute a playback sound is presented and the following minute show that these behaviors are not maintained.

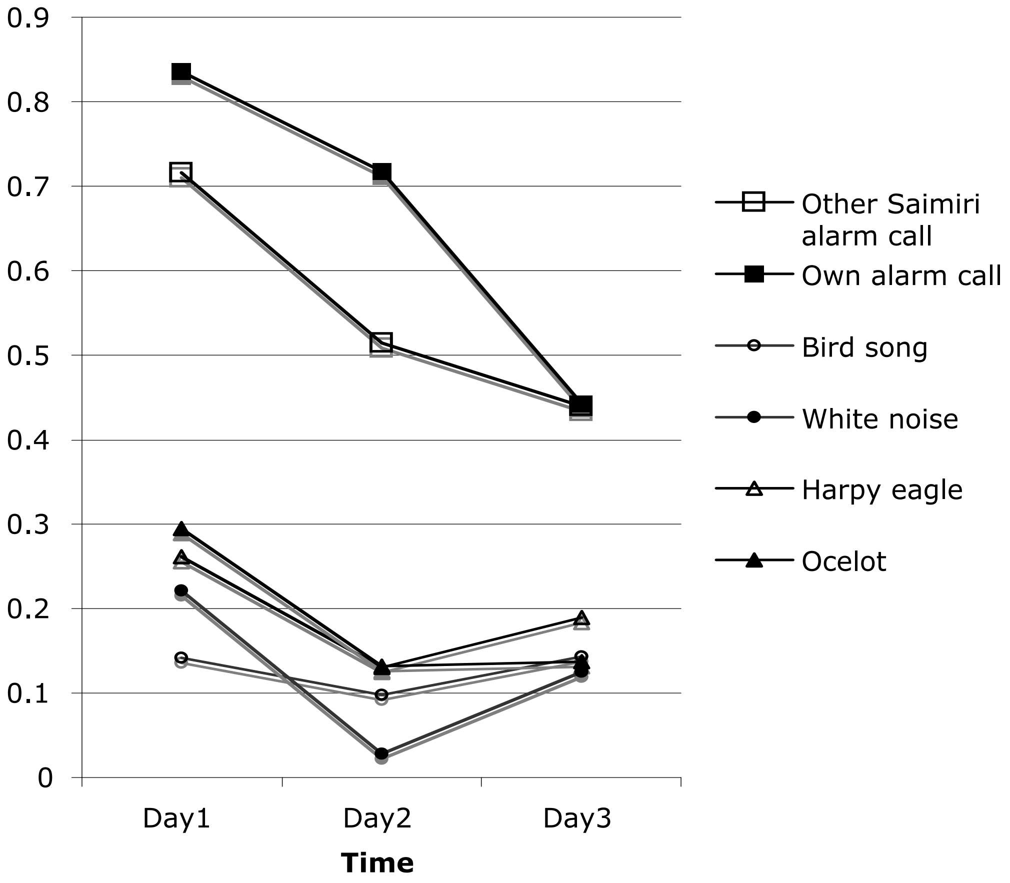

Figure 2 – Evidence of habituation in proportion of vigilant behavior exhibited by the captive squirrel monkeys for each sound over the three experiment days. Alarm calls elicited the greatest proportion of vigilant behaviors, although the monkeys exhibited habituation to the alarm call playbacks by decreasing their vigilant responses.

CHAPTER FOUR: DEMOGRAPHY OF SQUIRREL MONKEYS IN CAPTIVE ENVIRONMENTS AND ITS EFFECT ON POPULATION GROWTH

Abstract. Understanding which life history variables have the greatest influence on population growth rate has great conservation importance. This study uses population models and life-table response experiment analyses to explore the demographic mechanisms responsible for differences in population growth among sexes, zoological facilities, and generations of captive squirrel monkey populations. Variation in life history traits occurs within each group analyzed. Those traits that vary the most are age at maturity, age at last reproduction, and fertility. Using prospective analyses, juvenile and adult survivals were predicted to be the demographic traits that affect population growth. Fertility is the life history characteristic trait that contributes the most to changes in population size of all tested variables, although it is not predicted to do so based on elasticity analyses.

INTRODUCTION

Understanding which life history variables have the greatest influence on population growth rate [Stearns 1992; Caswell 2001; Oli and Dobson 2003] and the pattern of environmental influence on such variables has conservation importance [Heppell 1998; Foster and Vincent 2004; Young et al. 2006]. In the case of captive animals and endangered/threatened species, knowing which life-history variables have the strongest impact on population growth rate enables managers to target those parameters [Fisher et al. 2000; Gerber and Heppell 2004]. Those life history characteristics with the greatest influence on changes in population size are also expected to experience strong selection pressure [Stearns 1992; Caswell 2001]. Demographic variables that define the life history of a population (*i.e.* fertility, survival) have been shown to be correlated with changes in behavioral and social traits, as well as affected by environmental parameters [Ross 1998; Kappeler et al. 2003].

Applying various models of population regulation and demographic mechanisms can aid management and conservation of wild and captive populations. Perturbation analysis (how population statistics respond to changes in vital rates) can be applied in two ways: prospective analyses (sensitivity and elasticity) and retrospective analyses (life-table response experiment and variance decomposition) [Caswell 2000]. Prospective analyses calculate changes in population growth rate and have proven useful for evaluating management programs for endangered and invasive species [Crouse et al. 1987; McEvoy and Coombs 1999; Parker 2000]. Elasticity analyses, more specifically, allow for the proportional estimates and comparison of effects of changes in survival and reproduction of particular life stages and its impacts on population growth. Unlike sensitivity analyses, elasticities, as partial derivatives, can be interpreted as the relative contribution of the matrix elements on λ rather than absolute changes [de Kroon et al. 2000; Caswell 2001]. Being prospective analyses, sensitivities and elasticities do not indicate factors that may have limited a population's past success. These analyses are best suited to identify species that would benefit from management programs but sometimes these projections may not be realized. Not all demographic traits can easily be changed because of environmental limits [Caswell 2000]. Dobson and Oli [2001] termed the changes exhibited by a demographic variable under environmental constraints, the environmental "scope" of a trait. Life-table response (LTRE) analysis, on the other hand, presents the observed variation in population growth in terms of the relative importance of each demographic trait. Using LTRE analyses, changes in population growth rate between two populations can be separated into the contribution of each demographic trait [Caswell 2001].

The purpose of this study is to examine the life history of a species in a captive environment and contribution of demographic traits to population growth rate. Zoos provide current and historical data of species ever maintained at their facility. Using squirrel monkeys (*Saimiri* sp.), I will examine the demographic traits of all zoological populations using a variety of perturbation analyses. Although captive populations are provided with optimal access to resources allowing for developmental and reproductive rates to occur near maximum levels [Lee and Kappeler 2003], differences in management of the populations (*i.e.* densities of the groups, housing environments, foraging opportunities, management of reproductive rates) would be expected to create variation in demographic traits and population growth rates among zoos. Using the historical and current data on captive squirrel monkeys, I documented the life history characteristics of the population. Comparisons of demography of squirrel monkey populations are made between sexes, among zoological facilities, and over generations of monkeys in captivity. Unlike other studies of species in the wild where paternity is usually unknown, I was able to compare males and females. By conducting LTRE analyses of populations with differing growth rates, I examined whether the demographic mechanisms underlying changes in population size are consistent across zoological facilities. By comparison of sensitivity, elasticity and LTRE analyses, I identified the demographic processes that are most likely to produce changes in population size and the traits that actually do influence population changes.

METHODS

Study Subjects

Squirrel monkeys (genus *Saimiri*) are small, Neotropical primates naturally distributed in Central America and the Amazon basin (males: 740 g; females: 635 g) [Sussman 2003]. They are omnivorous, feeding mostly on fruit and insects [Janson and Boinski 1992], although the composition of their diet varies seasonally. Maturity is reached relatively late for a species with such small body mass, females first breed at 3.5 years and males at 4.5 years [Taub 1980]. Groups usually consist of 15 to 50 individuals with an average of 15 breeding females [Boinski 1999]. *Saimiri* was first seen in North American zoos in 1876 but captive births did not occur until the 1960s.

Data for captive populations of *Saimiri* were obtained from the Common Squirrel Monkey studbook, which contained historical records of captive living animals and their predecessors, as provided by the Association of Zoos and Aquariums. It contains all known biographical information for each squirrel monkey housed at an accredited zoo in North America, which has been entered in SPARKS (Single Population Analysis and Record Keeping System software maintained by keepers). Each individual is assigned a unique numerical identifier (studbook number) that allows the construction of a pedigree (for genetic analyses) and age-specific schedules of birth and death (for demographic analyses) [ISIS 2009].

Demographic Methods

A pedigree was created for the entire captive squirrel monkey population using Pedigree Viewer, a shareware program, version 5.5 [Kinghorn and Kinghorn 2003]. Relationships were traced back to founders of the population, revealing four generations of offspring produced in captivity.

Age-structured life tables were created for specific zoos to analyze variation among zoos. As the population of squirrel monkeys reproduces seasonally (depending on the type of housing), a birth-pulse model was utilized. A postbreeding census was conducted on the population [Alberts and Altmann 2003]. The life history characteristics evaluated the demographic status of a population by summarizing the information on age distribution, fertility, mortality, and survivorship. Survival (P_x) was the probability of surviving from age class (x) to the next age class ($x+1$). Survivorship (l_{x}), the probability of surviving from birth to each age class (x) was also calculated. Juvenile survival (P_j) was the survival from birth until age at maturity and adult survival (P_{a}) was from age of maturity (α) to age at last reproduction (ω). Age-specific birth rate (m_x) was the average number of offspring produced by a female in that age class divided by the number of females that produced offspring plus the number of females that did not but survived to the next age class. For post-breeding censuses, fertility was calculated by multiplying survival with age-specific birth rate ($F = m_x * P_x$) [Caswell 2006]. Because some individuals included in the post-breeding census were still alive and reproducing, age at last reproduction (ω) was estimated using the formula from Gaillard *et al.* [2005]:

$$\omega = \alpha + \left(\frac{s}{\lambda - s} \right)$$

Using life table data, matrix models were created for each population using PopTools 3.0.6 [Hood 2008]. The population growth rate (λ) is the dominant eigenvalue of the population projection matrix and defined as the rate of growth per time unit (one year) [Stearns 1992; Caswell 2001]. Sensitivity analyses reveal potential influences on changes in demographic traits on population growth. They can be calculated directly from the eigenvalues of the projection matrix. The sensitivity of λ to a change in each trait is measured while all the others are held mathematically invariant [Caswell 2001]:

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}}$$

Elasticity analyses allow for the estimation and comparison of the effects of changes in survival, growth, and reproduction of specific age-classes, as the proportional contribution of different aspects of the life cycle to population growth rate. Sensitivities reflect the influence on λ of a unit (absolute) change in a demographic variable, while elasticies reveals the influence of a proportional (relative) change in the variable. The elasticity of a each specific trait in the matrix can be calculated [Caswell 2001]:

$$e_{ij} = \frac{\partial \ln \lambda}{\partial \ln a_{ij}}$$

However, age at maturity (**α**) and age at last reproduction (**ω**) are not included in the demographic data of Leslie matrix models (a discrete age-structure model of population growth) [Caswell 2001], therefore sensitivities and elasticities of all demographic traits were calculated using the characteristic equation in a partial life-cycle model [Oli and Zinner 2001].

$$1 = FP_j^{\alpha-1}\lambda^{-\alpha} - FP_j^{\alpha-1}P_a\lambda^{-\alpha-1} + FP_j^{\alpha}\lambda^{-\alpha-1} - FP_j^{\alpha}P_a^{\omega-\alpha}\lambda^{-\omega-1} + P_a\lambda^{-1}$$

A fixed-design life table response experiment (LTRE) analysis was conducted on three sets of two-sample comparisons of populations with increasing and decreasing population growth rates. These analyses should reveal the contributions of each demographic trait to the differences in population growth. A change in each demographic parameter (*p*) was calculated as $\Delta p = p^{\text{population 1}} - p^{\text{population 2}}$. Sensitivities were calculated at the mean of demographic traits for the two populations being compared. The total difference in population growth (λ) was calculated as $\Delta\lambda = \lambda^{\text{population 1}} - \lambda^{\text{population 2}}$. The Δλ is composed of the contributions of the difference in each model parameter *p* for each population [Caswell 2001]:

$$\Delta\lambda \approx \sum_{ij} \Delta p \frac{\partial \lambda}{\partial p}$$

RESULTS

The historical and current captive population of squirrel monkeys consists of 718 individuals maintained at 52 zoological parks of the Association of Zoos and Aquariums

(AZA; Figure 1). Observed maximum life span (until death) in captivity is 35 years for both males and females, although the average is 16 years. Males and females become reproductively mature between 3 and 5 years. Females continue to breed until 28 years old, and males breed until 29 years old. Breeding of squirrel monkeys naturally has increased over time with 151 individual mothers and 68 fathers. Translocations among zoos began in 1972 and occur at an average yearly rate of 3.3% (ranging from 0% to 10.3%). The sex-ratio of the breeding population in zoos is female-biased (3 males: 5 females). Infant mortality is moderate, averaging 10% per year.

Variation among zoos

Although the squirrel monkey groups are managed as one entire population by the AZA, variation may still exist in life history traits among zoological facilities. Because of the smaller group sizes that squirrel monkeys are normally kept, only four zoos have maintained at least 29 squirrel monkeys, including current and historical individuals (Brookfield Zoo, n = 38; Caldwell Zoo, n = 32; Lion Country Safari, n = 37; San Antonio Zoological Park and Aquarium, n = 29).

Demographic variables were analyzed for each zoo. Age at maturity (α) varied throughout the population for both sexes (Table 1). Caldwell Zoo males reproduce, on average, the earliest at 4.60 years of age while males at the Brookfield Zoo mature at double this age at about 9.25 years. Females show a similar pattern, although with a different effect of zoological facility. Age at maturity for females occurs around 4.00 years of age at the San Antonio Zoo while females at Lion Country Safari reproduce for the first time when more than twice as old (9.38 years). Individuals of both sexes continue to reproduce throughout most of their lifespan. The age at last reproduction (ω) can vary as much as 6 years for either sex (females: 12.35 - 18.88 years; males: 12.00 – 16.88 years). Overall, males and females at Brookfield Zoo display greater survival and reproduce later for the first time than other facilities.

Juvenile survival (P_j) is not that variable among zoo populations (Table 1). It is almost equivalent between sexes, although females at the Caldwell Zoo experience less survival in comparison. Adult survival (P_a) is slightly more variable than juvenile survival, although not by much (Table 1). Female survivorship is greater in almost all populations compared to males, although differences in lifespan between zoos can vary as much as 9 years. This a large amount of time for a species with an average life span of 16 years. Depending on the sex of an individual, survivorship is affected by the facility in which the group of squirrel monkeys is housed ($F = 9.14$, $p < 0.001$; Table 1). Adult male survivorship is greater for Caldwell Zoo compared to males at the other three zoological facilities, unlike juvenile survival that is extremely high and consistent among zoos. Females also have varying survivorship depending on their zoological facility; juvenile survival was high for all but Caldwell Zoo. Adult survival, on the other hand, was extremely high and consistent among zoos, except for San Antonio Zoological Park. Overall, females have a greater adult survivorship compared to males ($F = 12.01$, $p < 0.001$).

Females are limited to one birth per event (only three cases of twins reported in captivity). This trend is exaggerated in captivity with females breeding less frequently than in the wild where females breed every year (between 1.22 to 5.50 years; Table 1) [Stone 2004]. Fertility is particularly variable among zoo populations (Table 1). Male fertility varies by as much as four-fold and female fertility by three-fold. Female squirrel monkeys at Caldwell Zoo display higher fertility compared to females housed at other zoos. Males, compared to females, can sire more than one offspring each year and all fertilities are greater than 0.10. Males at Caldwell Zoo and San Antonio Zoo have much greater fertilities compared to other zoos. Most males maintain an interbirth interval of one year, although Caldwell Zoo males produce more than one offspring each year (Table 1).

Population growth rate (λ) is also variable among zoos (Table 1). Female population growth rates are close to 1.0 for all populations. Male population growths, on the other hand, vary much more around 1.0 compared to females. Most zoological facilities have population growth rates above 1.0 for both males and females. The Brookfield Zoo, however, is the only zoo with both sexes having declining population growth rates ($\lambda < 1.0$). Patterns of elasticity differ between zoological facility and between sexes within each zoo. For all populations, juvenile and adult survivals have the highest elasticities of all the traits (Table 2), suggesting that these demographic variables are potentially the most influential life history traits (Figure 2). Age at maturity, age at last reproduction, and fertility had very low elasticities in all populations and sexes.

The main difference between sensitivity and elasticity analyses is the scale that the data is presented. Elasticities present proportional sensitivities. Therefore, fertility, which has the highest sensitivity values of all demographic traits analyzed, has low elasticities. The relative contribution of fertility on λ is less than other life history characteristics.

Variation over time

Three generations of squirrel monkeys are established (although the third generation only consists of two individuals as of 2008) in captivity, not including the original founders from wild populations. As squirrel monkeys have lived in captivity, life history characteristics have been modified (Table 3). Males and females are maturing at about two years earlier (5.50 to 6.13 years) than the wild generation (8.14 years). Even with earlier maturation, current age at first reproduction in captivity is still later than for populations in nature (3.75 years) [Stone 2004]. Unlike age at maturity and last reproduction, juvenile and adult survival does not vary as much among generations. Juvenile survival has been uniformly while adult survival has increased slightly. Over generations, fertility has greatly decreased in the captive squirrel monkey population (Table 3). Currently, population growth has been decreasing over time. The wild and first generation of squirrel monkeys display an increasing population ($\lambda > 1$).

Juvenile and adult survivals exhibit the highest elasticities among the generations (Table 2), as seen with the comparison of zoological facilities. The elasticity of fertility appeared to decrease in captivity (Table 3). Age at maturity and age at last both display low elasticities for all generations. Age at last reproduction seems to be increasing slightly during time in captivity.

Life-table response experiments (LTRE)

Three LTREs were analyzed to compare two populations of differing population growths rates. The first two comparisons evaluated two zoological facilities with increasing and decreasing population growths. The difference in λ between the two populations ($\Delta\lambda$) was 0.121 (females: Lion Country Safari v. San Antonio Zoo) and 0.301 (males: San Antonio Zoo v. Brookfield Zoo). The total LTRE contributions were 0.110 and 0.341, respectively, slightly lower and higher than the observed differences in population growth. The LTRE contributions of the demographic variables were similar between comparisons of an increasing/decreasing population (Table 4). For both population comparisons, fertility made the largest contribution to the observed increase in population growth rate. Estimates of fertility incorporate interbirth interval. A high influence of F indicates that individuals are decreasing their interbirth intervals. All other demographic traits (α, ω, P_j, P_a) made minor influences.

The third comparison was of the wild and first generation of squirrel monkeys. Since being in captivity, population growth rates have declined, with $\Delta\lambda = 0.221$. The total LTRE contribution is 0.248, slightly more than that of the actual changes in population growth rates. As with the previous individual zoo comparisons, fertility also made the largest contribution to differences in population growth rate between generations.

DISCUSSION

This study uses population models and life-table response experiment analyses to explore the demographic mechanisms responsible for differences in population growth among zoological facilities and generations of captive squirrel monkey populations. Variation in life history traits occurs between sexes, zoos, and generations of squirrel monkeys maintained in captivity. Those traits that display variation include age at maturity, age at last reproduction, and fertility. Fertility is the demographic trait that contributes the most to population growth of all tested variables, although it is not predicted to do so based on elasticity analyses.

What is the demography of the captive squirrel monkey population and does it vary amongst zoological facilities and generations in captivity? It is important to identify demographic mechanisms that underlie changes in population growth rates, especially when changes in growth rates reflect regulation of population size [Dobson and Oli 2001]. Variation in life history characteristics occurs among zoos with age at maturity, age at last reproduction, and fertility exhibiting the greatest ranges. Juvenile and adult survivals are mostly consistent among zoo populations. Zoos with increasing population growth rates maintain earlier ages of maturity, later ages of last reproduction, high rates of juvenile and adult survival, most importantly, greater fertility, and therefore shorter interbirth intervals. The number of offspring is invariant (as only one young is born at a time) therefore reproductive rates would be expected to be important towards influencing population growth rates. Actually, it is the frequency of reproduction that causes reproductive variation. The impact of reproductive frequency has been shown to constrain and enhance population size [Schaaf et al. 1993; Pleguezuelos et al. 2007].

Life-cycle data are normally presented and analyzed based on female demographic data. Captivity, on the other hand, provides the opportunity to gather accurate data on both sexes. This is a major advantage to be able to compare life-cycles for males and females. How do males and females differ and why? On average, males become reproductively mature (7.33 years of age) only slightly later than females (6.97 years of age), although both sexes continue to mate and reproduce until about the same age (males: 14.19; females: 15.43). Females display greater juvenile survival compared to males, although this trait is pretty consistent. Unlike the other demographic traits, which only somewhat vary between sexes, fertility is drastically different. Males have a much greater rate of fertility compared to females. This finding is not surprising, as females can only produce one offspring per season while males can sire more than one offspring in a population. Although according to the LTRE analysis, female fertility contributed a greater overall proportion to changes in λ. Other demographic traits (*i.e.* age at maturity and last reproduction) contributed greater proportions to λ in males than females.

Variation in life history characteristics also occurs among generations. The generation of wild squirrel monkeys introduced into captivity display a later age of maturity, a younger age of last reproduction, and high fertility compared to later captive generations. Adult survival is high, although not as high as future offspring generations. Juvenile survival is 1.0 because to be considered part of the wild generation each individual reproduced at least once, meaning that all survived to be at least juveniles. Future generations (first and second captive generations) displayed an earlier age of maturity, later age of reproduction, greater rates of adult survival, and lower fertility. Those traits that vary the most among zoological facilities were the same traits that are vary among generations. This suggests that the observed differences in traits across zoos is likely due to local environmental variations rather than to genetic effects, which are expected to be more stable from one generation to the other [Noel et al. 2007]. An important finding that may aid management of captive populations in zoos is that fertility has decreased over generations. This may be attributed to individual group structures of each zoo and whether there is more than one reproductive male. But the overall population of captive squirrel monkeys will not continue to grow as they did in the past.

Now that the life-history characteristics of squirrel monkeys in captivity among zoos and generations are identified, what are the demographic mechanisms responsible for population regulation? Using LTRE analyses, I examined the contribution of each demographic trait towards population growth. It is important to be able to identify demographic traits of a population and determine whether these characteristics affect changes in population growth rate [Oli et al. 2001; Oli and Zinner 2001; Oli and Dobson 2003; Oli and Armitage 2004]. The change in age at maturity should be negative when comparing populations of increasing and decreasing population growth rates (earlier maturity increases population growth), while the remaining demographic variables should be positive. Age at maturity followed the predicted pattern in the comparison of zoological facilities, but not among generations, in which later generations produced offspring earlier. As has been suggested, age at maturity is an influential life-history variable with substantial impacts on population sizes [Rochet 2000; Dobson and Oli 2001; Mills and Lindberg 2002]; in captivity, however, was not a major influence toward the change in population size of squirrel monkeys. Age at last reproduction, although highly variable among zoos, contribute little to changes in λ, which is similar to its impact in other mammalian species [Oli et al. 2001]. Overall, the differences in population growth rate between zoological facilities and generations are almost entirely due to the contributions of fertility.

A high influence of fertility on population growth is expected for small mammals that are categorized as “fast” on the fast-slow continuum. Primates have unusual life histories and, in general, fall somewhere along the slow end of the life history continuum (long gestation, small litters, low mortality rates, long life spans, large brains) [Ross 1998; Dobson and Oli 2007, 2008]. Within primates, there also exists a fast-slow continuum. Prosimians and New World monkeys (*viz*. squirrel monkeys) would be classified as a "fast" primate compared to Old World monkeys and great apes [Kappeler et al. 2003]. Fertility was shown to be an influential trait on changes in population growth of captive squirrel monkeys.

This difference between what demographic traits are expected to cause changes in population growth rate and what traits actually contribute to λ is important for management and conservation. Adult and juvenile survival elasticity is expected to be high for long-lived species. High elasticity values for fertility should be high for shorter lived species such as many fish and invertebrates [Heppell et al. 2000; Gerber and Heppell 2004]. In captive squirrel monkeys, the sensitivity and elasticity of juvenile and adult survival are among the highest of the demographic traits, as expected. This would predict that P_j and P_a should have the greatest effects on changes in population size. Although population growth rate was potentially most sensitive to changes in survival, the LTRE analyses revealed that P_j and P_a did not change and barely contributed to changes in λ. On the other hand, fertility and age at maturity are the least elastic and, therefore, would be expected to contribute the smallest amount to changes in population size. Demographic traits and their sensitivities to population growth may be different in nature. Survival rates, which are high in captive environments, display little environmental scope. However, in field populations, survival rates are not as high and may be more important to changes in population size.

In captive environments such as zoological facilities, fertility is the most important demographic trait, even with low elasticities. Survival, both juvenile and adult, is extremely high and constant due to zoo conditions that do not allow survival much influence over population growth rate. Therefore, fertility (due primarily to the frequency of births) is extremely variable allowing it to affect changes in population size. Perturbation analyses may not always match. Elasticity and life-table responses experiments have previously given inconsistent conclusions as the demographic traits that effect population growth rate [Caswell 2000]. Münzbergová [2007] suggest that the difference between prospective and retrospective analyses in their study on a perennial herb could be explained by high variation in generative reproduction between populations and years. The demographic trait that contributes most to the variability in λ is not necessarily the one to which population growth rate is most sensitive [Horvitz et al. 1997; Pfister 1998]. These prospective analyses may not be applicable to wild populations when based on captive demographic data.

The results of this study show that demographic traits of a population that are predicted to affect population growth rate (elasticity analysis) may not be the same traits that led to differences in growth rates among populations. Using captive reared animals to estimate biological limits of wild populations assumes several factors: disease treated in captivity would not affect survival as it would normally in the wild, ability to find and gather food is independent of age, predation pressure in the wild is negligible (because not present in captivity), and husbandry methods of captive populations are not restricting [Lubben et al. 2008]. Overall, population modeling aids in the understanding of factors that affect changes in population dynamics in any environment [Dobson and Oli 2001].

Table 1. Mean values of demographic traits of the largest populations of squirrel monkeys in zoos used to analyze among-zoo variation.

Population Location	**Age at maturity (α)**		**Age at last reproduction (ω)**		**Juvenile survival (P_j)**		**Adult survival (P_a)**		**Fertility (F)**		**Interbirth Interval**		**Population growth (λ)**	
	M	*F*	*M*	*F*	*M*	*F*	*M*	*F*	*M*	*F*	*M*	*F*	*M*	*F*
Brookfield Zoo (n = 32)	9.25	8.26	16.88	12.35	.998	1.00	.974	.998	.103	.070	1.10	1.65	.969	.958
Caldwell Zoo (N = 38)	4.60	6.25	12.00	14.28	.998	.949	.999	.998	.456	.146	.688	1.22	1.26	1.05
Lion Country Safari (n = 37)	8.50	9.38	13.50	18.88	.988	1.00	.970	.994	.139	.109	1.00	2.48	1.08	1.07
San Antonio Zoo (n = 29)	7.60	4.00	14.41	16.21	1.00	1.00	.967	.976	.391	.043	1.00	5.50	1.27	.949

Table 2. Sensitivities and elasticies of **λ** to changes in demographic traits in captive squirrel monkeys.

Population/ sex	Sensitivities					Elasticities				
	α	ω	P_j	P_a	F	α	ω	P_j	P_a	F
Brookfield Zoo (female)	-.008	.002	.353	.480	1.74	-.026	.186	.372	.500	.128
Brookfield Zoo (male)	-.009	.012	.719	.179	.781	-.085	.182	.737	.182	.182
Caldwell Zoo (female)	-.024	.010	.419	.508	.942	-.069	.128	.378	.491	.131
Caldwell Zoo (male)	-.061	.015	.645	.341	.537	-.145	.104	.534	.272	.194
Lion Country Safari (female)	-.015	.005	.138	.784	1.41	-.014	.075	.129	.728	.143
Lion Country Safari (male)	-.022	.006	.163	.756	1.33	-.021	.074	.149	.679	.172
San Antonio Zoo (female)	-.001	.007	.261	.608	2.09	-.004	.132	.279	.626	.095
San Antonio Zoo (male)	-.037	.004	.573	.424	.586	-.086	.042	.498	.322	.180
Wild Generation	-.118	.002	.279	.700	1.04	-.087	.015	.206	.511	.283
First Generation	-.021	.003	.179	.762	1.22	-.017	.039	.166	.636	.198
Second Generation	-.019	.022	.293	.512	1.78	-.038	.224	.299	.544	.157

Table 3. Values of demographic traits of generations of squirrel monkeys in zoos used to analyze variation over time in captivity.

Population Location	**Age at maturity (α)**	**Age at last reproduction (ω)**	**Juvenile survival (P_j)**	**Adult survival (P_a)**	**Fertility (F)**	**Interbirth Interval**	**Population growth (λ)**
Wild generation (N = 103)	8.14	10.21	1.00[a]	.875	.368	1.31	1.35
First generation (N = 89)	6.13	11.32	1.00	.998	.194	1.26	1.14
Second generation (N = 26)	5.50	11.04 [b]	.988	.999	.085 [b]	---- [c]	.969[b]

[a] All individuals in the first generation were wild-caught and brought into the zoos near the end of their juvenile period. Only those who reproduced are included as generation one, therefore all individuals survived as juveniles ($P_j = 1.00$).

[b] All individuals in the third generation are still alive and reproducing, therefore an age at last reproduction and interbirth interval cannot be accurately calculated (so far individual squirrel monkeys have only had one offspring)

Table 4. Analysis of life-table response experiments (LTRE) for populations of captive squirrel monkeys, comparing populations under different conditions of population regulation

Treatment comparison/ demographic parameter (p)	**Change in parameter (Δ)**	**Sensitivity**	**LTRE contribution**
Lion Country Safari vs. San Antonio Zoo (females):			
α	-2.01	.001	-.002
ω	1.93	.008	.002
P_j	-.051	.082	-.004
P_a	.000	.761	.000
F	.076	1.35	.102
San Antonio Zoo vs. Brookfield Zoo (males):			
α	-1.65	-.016	.023
ω	3.86	.021	.081
P_j	.002	.398	.001
P_a	-.007	.287	-.002
F	.288	.815	.234
First Generation vs. Wild generation			
α	-2.01	-.020	.040
ω	1.11	.001	.001
P_j	.000	.233	.000
P_a	.123	.735	.009
F	-.174	1.14	-.198

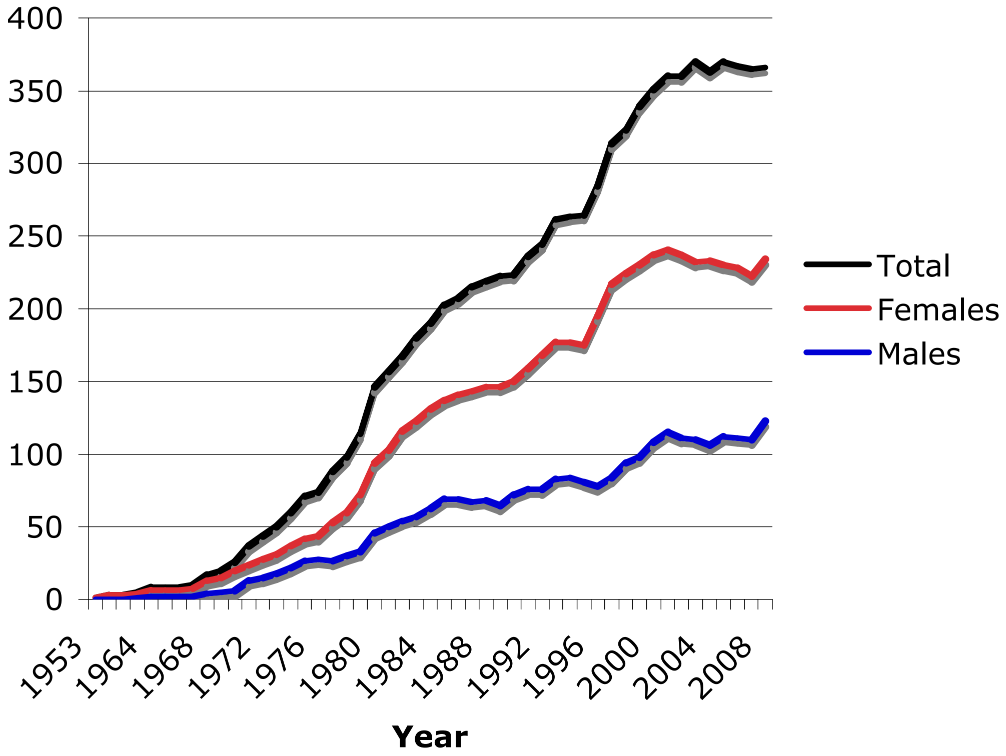

Figure 1. Census of *Saimiri* in the AZA population

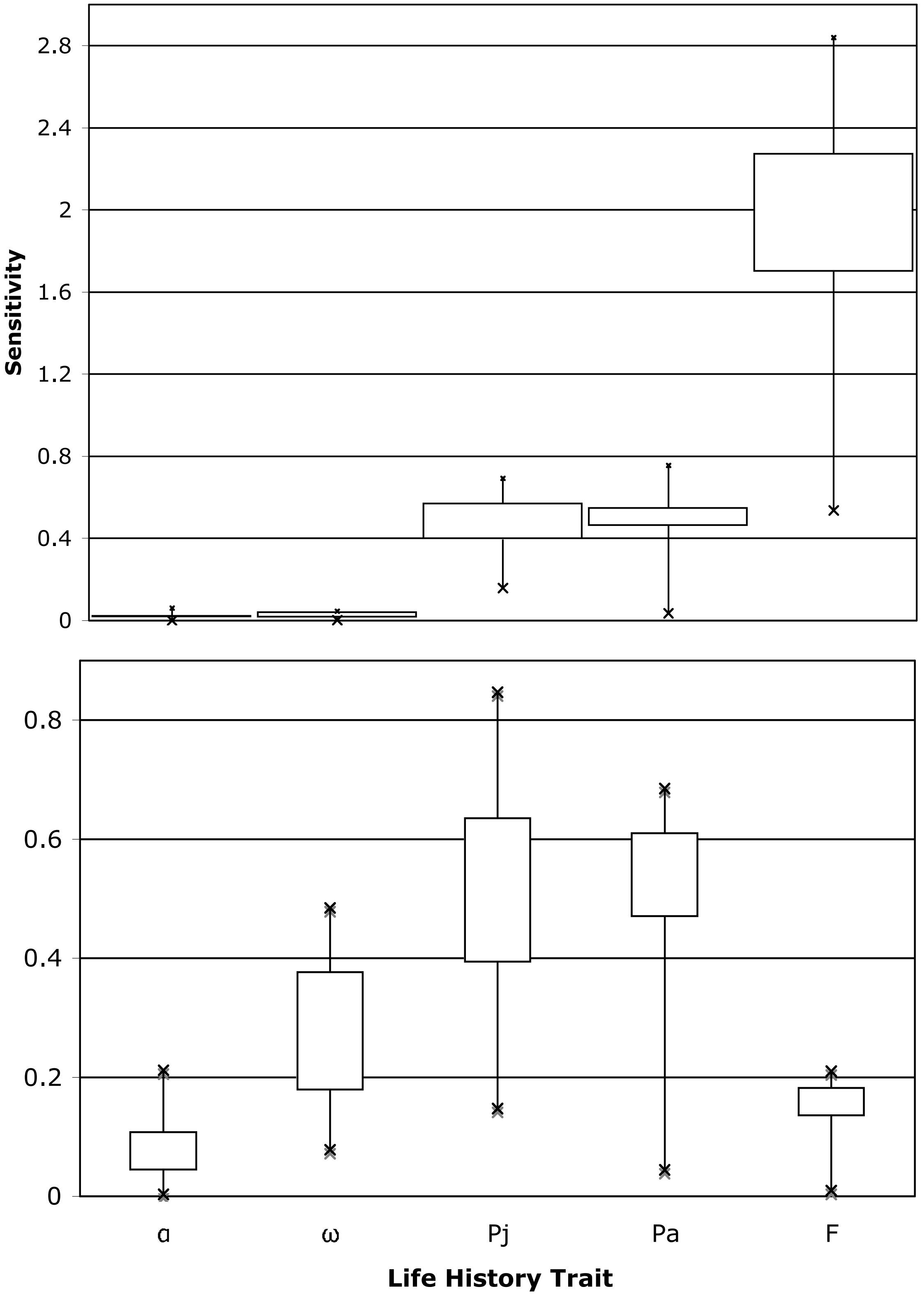
Sensitivity
2.8
2.4
2
1.6
1.2
0.8
0.4
0
0.8
0.6
0.4
0.2
0
α
ω
Pj
Pa
F
Life History Trait

Figure 2. For four populations of captive squirrel monkeys, sensitivities (*A*) and elasticities (*B*) of population growth rate (λ) to life history traits are shown: age at maturity ($\boldsymbol{\alpha}$), juvenile survival (P_j), adult survival (P_a), fertility (F), and last age of reproduction (ω).

CHAPTER FIVE: GENERATIONAL VARIATION IN SEASONALITY OF REPRODUCTION OF CAPTIVE SQUIRREL MONKEYS

Abstract. Zoo environments provide a place to understand how variation changes occur when populations are brought from nature to captivity. The timing of births is an already shown trait to be extremely plastic in captivity, allowing individuals to shift their seasonality or become aseasonal depending on the housing environment. This change in reproduction timing could be because of plasticity in reproductive patterns or generational differences between mothers and their daughters through selection. Data for historical and current captive populations of *Saimiri*, as well as a wild population, were used to create a pedigree. Differences between when mothers and daughters have their offspring reflects developmental constraints, rather than heritable traits. Therefore, selection on the date of birth is not occurring because individuals seem to be changing their patterns of seasonal births. There is a significant difference in the seasonality of births among generations of captive squirrel monkeys due to the comparison between the wild and two captive generations. The retention of the seasonal peak exhibited in the captive generations of squirrel monkeys is a reflection of the environment and plasticity, rather than a genetic pre-disposition.

INTRODUCTION

Captive primates often differ from natural populations in their seasonality of reproduction [Hayssen et al. 1993b; Trevino 2007]. When individuals are transferred from the Southern to Northern hemisphere, a well-documented six-month shift in births occurs [DuMond 1968; Bielert and Vandenbergh 1981]. This shift, as well as differences in the degree of seasonality, has been observed in captive squirrel monkeys (*Saimiri sciureus*) (Chapter 2). Timing of matings and births is dependent on type of housing conditions. In indoor zoo enclosures, squirrel monkeys become aseasonal and produce offspring throughout the year [Trevino 2007]. In wild populations, squirrel monkeys display a highly seasonal, synchronous reproduction with females coming into estrus within several days of each other. Breeding occurs during a four to eight week period at the start of the wet season during when there is plentiful food abundance (January and February) [Rosenblum and Cooper 1968; Stone 2006].

Captive environments, such as a zoological facility, may affect the behavior, ecology, and life history of a species causing differences to occur between wild and captive populations [Kleiman et al. 1996]. The behavior of any wild species is the product of many generations of natural selection and adaptation to specific environmental conditions. Reproduction produces genetic changes in a captive population and since a species' behavior derives from its genetic endowment, generations in captivity may act on gene frequencies in populations [Kleiman 1980; Carlstead 1996]. Now that a few generations of squirrel monkeys have been established in zoos from wild founders, some demographic traits have been documented to change over generations as individuals adapted to new environments (Chapter 4). For specific life history characteristics, these adjusted traits are passed down from mother to offspring suggesting a genetic component (*i.e.* seasonality of reproduction).

The purpose of this study is to examine effects that captivity have on reproductive seasonality, using current and historical data of squirrel monkeys (*Saimiri* sp.) in zoos. In captive populations, variation in life history traits occurs among zoos and generations of squirrel monkeys (Chapter 4). The timing of births is a trait that is extremely plastic in captivity (Chapter 2). Individuals shift their seasonality or become aseasonal depending on the housing environment [Trevino 2007]. Over generations in captivity, I expect reproduction of squirrel monkeys to show a trend towards less seasonality and more births year round. This would be especially true for individuals kept in indoor housing under consistent environmental conditions. This change could be because individuals' change in their reproductive patterns due to plasticity or because generational changes occurred (viz., daughters differ greatly from mothers). I will test this idea by specifically examining the similarity of mother-daughter pairs. The results from this study will shed some light on which mechanism is contributing the most to changes in seasonality of reproduction in captive squirrel monkeys, and the relative influence of the two mechanisms.

METHODS

Study Subjects

Squirrel monkeys (genus *Saimiri*) are small, Neotropical primates distributed in Central America and the Amazon basin. The wet season, from January to June, corresponds to births and most of the lactation period. The dry season occurs from July through December, during which mating and most of gestation occurs. Fruit availability is highest during the wet season. Births in *Saimiri sciureus* occur over an 8-week period in January/February of each year [Stone 2006]. The reproduction of captive populations of squirrel monkeys varies depending on the housing environment. Those animals in outdoor enclosures display a seasonality in reproduction (June to October), while indoor monkeys continued to reproduce throughout the year [Trevino 2007].

Data for captive populations of *Saimiri* were obtained from the Common Squirrel Monkey studbook, which contained historical records of captive living animals and their predecessors, as provided by the Association of Zoos and Aquariums. It contains all known biographical information for each squirrel monkey housed at an accredited zoo in North America, which has been entered in SPARKS (Single Population Analysis and Record Keeping System software maintained by keepers). Each individual is assigned a unique numerical identifier (studbook number) that allows the construction of a pedigree [ISIS 2009]. Three generations of squirrel monkeys occurred (although the third generation only consists of two individuals as of 2008) in captivity, not including the original founders from wild populations. Analyses do not include the third captive generation.

Data for the wild population were gathered by Stone [2006] from March 2002 to March 2003 in the village of Ananim, 150 km east of Belém, Brazil. The population consisted of two groups of squirrel monkeys (troop A had 44 individuals and troop B had 50 individuals).

Pedigree Analysis

A pedigree was created for the entire captive squirrel monkey population using Pedigree Viewer, a shareware program, version 5.5 [Kinghorn and Kinghorn 2003]. Relationships were traced back to founders of the population, revealing four generations of offspring produced in captivity.

Data Analyses

Homogeneity of variances on the seasonality of reproduction among generations of captive squirrel monkeys was analyzed using Levene's Test for homogeneity. A Welch's analysis of variance (ANOVA) test was used for comparison of seasonality among generations (PROC GLM) followed by Scheffé's Test to analyze differences among the treatments. Post-hoc analysis (Tukey's test) was used in conjunction with the ANOVA to determine which means were significantly different from one another. Analyses of mother-daughter pairs (Proc GLM) allow for the comparison of variation in birth dates between and among mothers. Estimates of mother-daughter similarity were derived from a one-way ANOVA with mother identification as a factor and calculated as twice the intra-class correlation coefficient (because the coefficient of relatedness is 0.5) [Falconer and Mackay 1996]. Additional analyses of the repeatability of birthdates of mother-offspring pairs were performed based on type of enclosure, categorized as indoor or outdoor, using the Hartley F_{max} test. All analyses were performed using SAS statistical software for Windows [SAS, 2002]. Significance level for all tests was $\alpha = 0.05$.

RESULTS

Squirrel monkeys in their natural habitats reproduce during the rainy season, between January and February. Births, on the other hand, have occurred in zoos mostly year-round for both generations born in captivity. First generation birth dates happened all year long (from January to December), although a seasonal peak occurred between May and September (mean: July; median: August; Figure 1). Second generation births ranged from the middle of April through December (mean and median: July; Figure 1) without a distinctive seasonal peak, as seen with the first generation. There was a significant change in the seasonality of births among generations of captive squirrel monkeys ($F = 307.46$, $p < 0.0001$; Table 1). Post-hoc comparison of the generations showed significant differences only occurring between the wild generation and each captive generation ($p < 0.05$, Tukey test).

The variances of birth dates across generations were not equal ($F = 3.77$, $p = 0.029$, Levene's test) because of the difference between the wild and both captive generations. Date of births between the wild generation and each captive generation was significantly different ($p < 0.05$, Scheffe's Test). The variance was about 75 times greater in the offspring generations compared to the wild generations [σ^2: 77.09 (wild generation); 6738.77 (first generation); 5560.68 (second generation)]. However, the two captive generations have maintained a similar variance in the seasonality of birth dates.

Variation among mother-daughter pairs was significant among captive squirrel monkeys ($F_{49,90} = 2.09$, $p = 0.001$, $R^2 = 0.532$). Therefore mothers and daughters differ in when their offspring are born. The crude and preliminary heritability estimate for seasonality of reproduction between mother and offspring in the wild generation and first captive generation was high ($h^2 = 0.706$). Mean birth dates did not vary between those individuals who produced offspring that survived to be a year old ($n = 75$, $\mu = 196$) and those who did not ($n = 19$, $\mu = 199$) ($t = 0.88$, $p > 0.10$).

The repeatability of birthdates between mother-offspring pairs for outdoor enclosures was moderate ($R^2 = 0.554$). Mothers and offspring are more likely to have similar seasonality of reproduction in indoor enclosures ($R^2 = 0.823$). The variances of birthdates for captive squirrel monkeys in the two types of enclosures are significantly different (F ratio = 3.92, $p < 0.05$).

DISCUSSION

Reproductive seasonality is a very important aspect in the life history of a individual, as one must be able to adjust to, and even anticipate, the changes taking place in its environment if individuals are to be successful [Follet 1984; Zhang et al. 2000]. In wild populations, squirrel monkeys maintain a tight reproductive synchrony. The breeding season is six weeks long (January and February) with most births occurring within 10 days of each other [Stone 2007a, c]. After being introduced to zoological facilities, I found that captive born *Saimiri sciureus* no longer give birth within the same mean or range of dates as in natural populations. This suggests that the relatively narrow birth period in these animals is an extremely plastic trait that facilitates reproductive success in new environments. In captivity, however, the variation in seasonality of reproduction is different compared to wild populations and also dependent on the type of enclosure in which the monkeys are maintained. Mothers and daughters are more similar in when they have offspring in indoor enclosures than outdoor habitats. Genetic heritability of dates of births is high, therefore suggesting that the change in seasonal reproduction over generation of captive squirrel monkeys is a heritable trait passed down generations. In the absence of environmental factors, social factors associated with kinship become more important to reproduction. In the wild, social factors are likely secondary but important, and masked by the influence of environmental factors.

Based on three generations (the original wild population and two captive offspring generations), captive births are becoming slightly less seasonal. Both captive generations displayed a different seasonal reproduction than that of the founding population with a disparity by as much as 60-fold. Births no longer occurred within a short period, and instead squirrel monkeys reproduced throughout the year. This pattern of a trait losing its seasonality in captivity has been exhibited by other species. Wapiti stags in captivity rut all year round while in natural populations they have a specific rutting season [Heape 1990]. Although the second generation showed less of a seasonal peak than the first generation, both captive generations were similar in their patterns of birth. Possibly with a few more generations, this seasonality would no longer be present. Loss of seasonality has mainly been seen in domesticated animals, such as pigs and cattle [Rowlands and Weir 1984]. Sheep and goats, on the other hand, have retained their seasonal reproduction despite domestication [Bronson 1991].

Heritability (in the narrow sense) refers to the proportion of phenotypic variation of a trait that is due to additive genetic effects. Analyses of heritability are important because they determine the evolutionary responsiveness of a trait to natural selection by estimating components of variance (and, hence, heritability) from ANOVA [Falconer and Mackay 1996]. Several studies have shown that life-history traits, which are closely related to reproductive fitness, have lower heritabilities than morphological and physiological traits, presumed to be less related to fitness [Weigensberg and Roff 1996; Merila and Sheldon 1999; Roff 2002]. There is high heritability among captive squirrel monkeys in the seasonality of reproduction as displayed by similar dates of births between the first and second generations. There is commonality in environmental influences, therefore the differences between when mothers and daughters have their offspring depending on the type of housing enclosure reflects a heritable trait rather than developmental constraints. Individuals seem to be extremely similar in their patterns of seasonality even when exposed to environmental factors, supporting heritability of seasonal patterns of reproduction. Substantial heritable components have been shown to occur in the interval timing of seasonal reproductive rhythms of mammals [Prendergast et al. 2004; Prendergast 2005]

Not only does variation exist in the seasonality of reproduction in captive squirrel monkeys, but also differences occur in births (and therefore matings) based on environmental variation of the enclosures. Individuals maintained in indoor enclosures at zoos reproduced throughout the year without a clearly defined seasonal peak, as seen with generational reproduction. Outdoor housed squirrel monkeys also reproduced throughout the year but had the remnants of a seasonal peak from June to October (Chapter 2) [Trevino 2007]. The differences in reproduction in the first and second captive generations of squirrel monkeys is an expression of a genetic pre-disposition, rather than a reflection of the environment. With species influenced by the changing seasons, such as squirrel monkeys, marmosets, and tamarins, the artificial conditions occurring in indoor enclosure can alter reproduction [Brand 1980; Trevino 2007]. Those squirrel monkeys in outdoor enclosures seem to still be able to queue on environmental parameters that are responsible for reproductive seasonality. Offspring in indoor enclosures, however, are more like their mothers in their birthdates. The underlying association between kin is now present, which would not be evident in the wild because of the influences of environmental variables. There is a social aspect that governs reproduction.

More research is needed to understand the effect that climatological factors, such as temperature, humidity and photoperiod, have on breeding in zoos. Temperature has been shown to be an influential environmental factor on reproduction timing for squirrel monkeys housed in enclosures exposed to the natural elements [Trevino 2007]. Modifying habitats and breeding programs of squirrel monkeys can mitigate these influences. Zoological facilities maintain populations of animals as representatives of those species for education of the public, breeding programs, and conservation. It is important that these populations maintain those natural behaviors of the species it is representing. These characteristic traits can be influenced by time in captivity, housing, environmental conditions, and management procedures.

Table 1. Mean and standard deviations of birth dates among generations of captive squirrel monkeys.

Generation	**N**	**Mean**	**SD**
Wild	16	3.46	9.55
First	89	202.84	82.09
Second	26	191.38	74.57

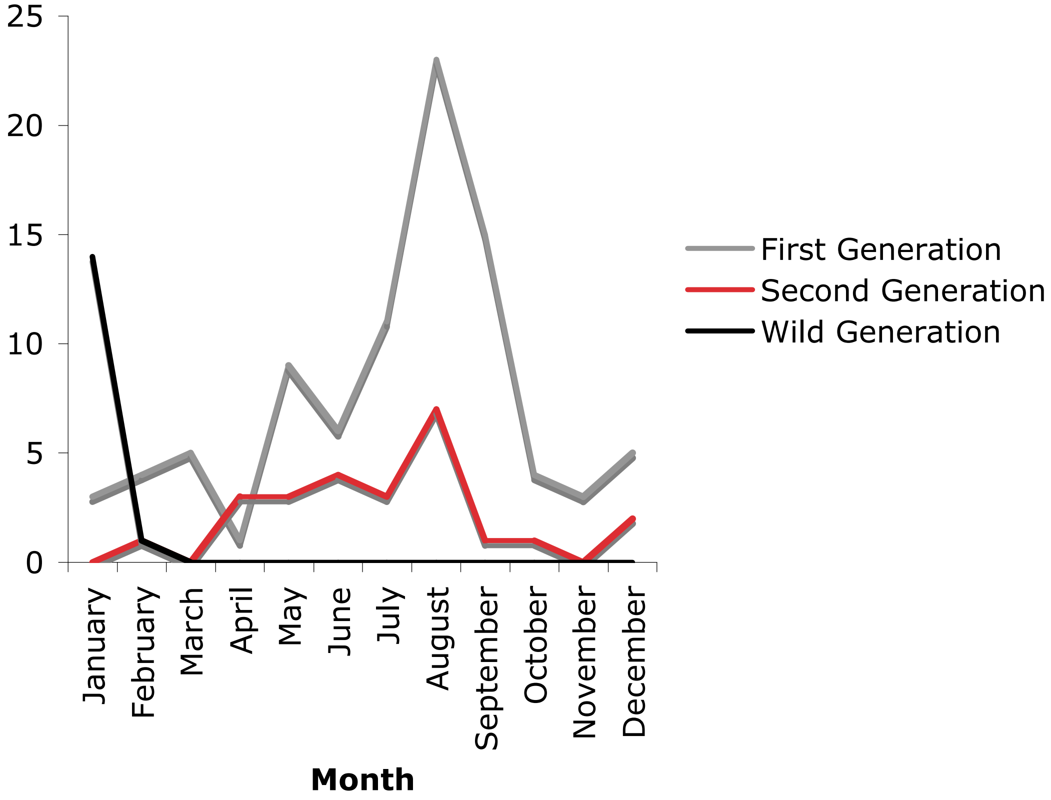

Figure 1. Seasonality of births among generations of captive squirrel monkeys. The founding generation (from wild populations) was born in January and February. The captive populations display a six-month shift in reproduction, with births mostly occurring from August to October.

CONCLUSIONS

Zoos are typically underrated as research resources, although the amount of research conducted at zoos has increased over the past twenty years [BIAZA 2002; Stoinski *et al.* 1998]. They provide a key role in the conservation of species, specifically primates, and have become focal points for research by academic and zoological scientists. Conservation programs began with an *ex situ* emphasis, breeding and reintroduction of endangered species. Recently, zoos have included *in situ* conservation programs, aiming to protect the species and their habitats [Wallis 1997].

Successful captive breeding and conservation programs require a detailed knowledge of all aspects of species biology and natural history. Researchers are able to study animals closely in zoological facilities as well as have control over environmental and social variables [Hosey 1997; Stoinski *et al.* 1998]. Improvements on animal management, including breeding, handling, transporting, and caring for animals, are developed usually in zoos before being applied in natural habitats. Studies, such as this one, serves to demonstrate the importance of research in zoos and other captive situations both for understanding the fundamental biology of a species and for interpreting and evaluating data from the wild.

The Association of Zoos and Aquariums (AZA) has invested extensively in encouraging zoological institutions to engage in scientific research. The Conservation and Science (C&S) Network of the AZA have five main components that involve all 180-member institutions: studbooks, species survival plans (SSPs), taxon advisory groups (TAGs), fauna interest groups (FIGs), and scientific advisory groups (SAGs). All of these outlets allow for maintenance and exchange of information on specific species. Currently, AZA maintains studbooks on 53 species of primates, including the Common Squirrel Monkey (*Saimiri sciureus*). Using studbook information and current status of the species in the wild, TAGs prioritize species for cooperative conservation efforts by AZA institutions and develop regional collection plans. They work closely with the Primate Specialist Group of the IUCN/The World Conservation Union Species Survival Commission [Wiese and Hutchins 1997].

Much of the information acquired through zoo research is of great relevance to conservation generally and to the conservation of species and habitats in particular. Understanding how a species behaves in wild is important for the maintenance of natural behaviors and life history characteristics of those kept in captivity. These studies in field habitats also provide appropriate contexts in which the behaviors would naturally occur. It is vital to gather the same behavioral and demographic data from species in their captive environments. These altered habitats allow for opportunities to investigate behaviors that are difficult to observe in the wild.

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