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An assessment of behavior associated with reproduction and infant caretaking in a captive family group of Saguinus midas midas

Melissa Elizabeth Martenson
Portland State University

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Title: An Assessment of Behavior Associated With Reproduction and Infant Caretaking in a Captive Family Group of Saguinus midas midas.

APPROVED BY THE MEMBERS OF THE THESIS COMMITTEE:

[redacted]

Roger D. Jennings, Chair

[redacted]

Thomas Kindermann

[redacted]

Hugo Maynard

[redacted]

Jill D. Mellen

[redacted]

Marc R. Feldesman

The present study gathered both general and specific information about the behavior of a captive family group of Saguinus midas midas [red-handed tamarins] housed at the Washington Park Zoo, Portland, Oregon, USA. Saguinus midas midas is a rarely studied species, and detailed information about the behavior of this species is virtually nonexistent. For this reason, this

study collected information about both activity budgets and social grouping within this family group.

The primary focus of this study was, however, the socialization of captive juvenile tamarins with respect to several behaviors relevant to reproductive success among the Callitrichidae. The behaviors assessed were: scent marking [reproductive suppression]; mounting, thrusting, allogrooming, huddling [pair-bonding]; food transferring, and infant carrying [infant caretaking]. Socialization was defined as the process of social learning that guides young primates in the day to day life of a species and was assumed to occur via two potential processes: active participation and passive observation. It was supposed that juveniles may learn behaviors relevant to pair-bonding and infant caretaking by participating in interactions with other group members. It was also supposed that juveniles may further learn about these behaviors by observing a pair-bonded male and female. Recognizing the potential importance of both socialization processes, this study attempted to answer several questions with respect to the aforementioned behaviors: do juveniles and adults engage in these behaviors, and, if the behavior is a social interaction, with whom?

Behavioral observations occurred during two phases. During Phase 1, the family group consisted of the adult mated pair, 3 subadult triplets, and 2 juvenile twins. During Phase 2, the family group consisted of the adult mated pair, 2 juvenile twins, and 2 infant twins. Throughout each phase, the family group was observed for two 80-min observation sessions, one occurring prior to noon and the other after noon, five times weekly for 6 weeks. Both scan and continuous sampling of behavior were employed.

The data show that adult, subadult, and juvenile members of a rarely studied species participate in a wide variety of behaviors and that the behavior of

this species is similar to that of other callitrichids. The results also indicate that even individuals of a highly social species spend time alone when given the opportunity. Furthermore, the data suggest that the birth of infants may afford the mated pair an opportunity to reinforce the existing pair-bond. With respect to socialization, the results reported here support the contention that the socialization process somehow fosters, among young primates, the development of behaviors crucial to the life of a species. Moreover, the results further suggest that active participation may be the most stable form of socialization within this family group and that interactions with adults play a major role.

AN ASSESSMENT OF BEHAVIOR ASSOCIATED WITH REPRODUCTION AND INFANT CARETAKING IN A CAPTIVE FAMILY GROUP OF *Saguinus midas midas*

by

Melissa Elizabeth Martenson

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TO THE OFFICE OF GRADUATE STUDIES:

The members of the Committee approve the thesis of Melissa Elizabeth Martenson presented April 4, 1991.

[redacted]

Roger D. Jennings, Chair

[redacted]

Thomas Kindermann

[redacted]

Hugo Maynard

[redacted]

Jill D. Mellen

[redacted]

Marc R. Feldesman

APPROVED:

[redacted]

Cord Sengstake, Chair, Department of Psychology

[redacted]

C. William Savery, Interim Vice Provost for Graduate Studies and Research

This paper is dedicated to my parents,
Ernest and Helena Benkich,
because they believed.

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INTRODUCTION

The destruction of tropical South American rain forests is endangering the survival of vast numbers of animal species ranging from insects to primates. At this time, at least one species within the Family Callitrichidae, lion-tamarins, is on the verge of extinction (Mittermeier, 1986). One step in preventing the loss of such species involves the establishment of successful captive breeding programs. This necessitates research which focuses upon parameters relevant to reproductive success among this Family of primates.

TAXONOMY AND DISTRIBUTION OF THE CALLITRICHIDAE

The Family of primates known as the Callitrichidae is comprised of four genera, Callithrix, Cebuella, Saguinus, and Leontopithecus (marmosets, pygmy marmosets, tamarins, and lion-tamarins, respectively) (Napier & Napier, 1985). These small, clawed, neotropical primates inhabit South American forests and are the only anthropoid primates that regularly give birth to twins (approximately every 6 months) (Hershkovitz, 1977).

The most striking distinction between marmosets and tamarins appears to be a result of adaptation to their differing diets (Napier & Napier, 1985). Marmosets eat a diet which is primarily insectivorous but supplemented largely with gums and saps. Tamarins, on the other hand, consume a diet comprised largely of fruits supplemented with insects. The dentition of these respective genera differ considerably in that all marmosets have V-shaped mandibles with incisors that are as long as the canines, while all tamarins possess U-shaped mandibles with canines that are longer than the incisors (the more traditional canine dentition). The pattern of dentition exhibited by the marmosets can clearly be seen to have adaptive value, for such a pattern facilitates the gouging of trees to obtain saps and gums.

In addition to possessing disparate patterns of dentition, marmosets and tamarins appear to inhabit different geographical areas of South America. Members of the genera Callithrix and Saguinus, for example, generally do not coexist in the same geographic region; only two species are known to be sympatric (Callithrix argentata and Saguinus midas), and the only known area of overlap exists at the mouth of the Amazon (Napier & Napier, 1985).

SOCIAL AND MATING SYSTEMS OF THE CALLITRICHIDAE

A General Description

Monogamy is rare among primates and mammals in general; 14% of primates are reported to be monogamous while only 3% of mammals are described as such (Kleiman, 1977; Ruthberg, 1983). Until recently, all members of the Family Callitrichidae have been described as living in monogamous extended family groups consisting of a breeding pair and its offspring (Eisenberg, Mukenhirn, and Rudran, 1972; Epple, 1975a; Kleiman, 1977; Leutenegger, 1980; Redican, 1976; Redican & Taub, 1981). This conclusion regarding the mating system and social structure of marmosets and tamarins has been based upon the following observations garnered from both captive and field studies (Goldizen, 1988; Sussman & Garber, 1987): (a) groups in the wild contain a single breeding female and a single set of comparably aged young (Goldizen, 1987a; Sussman & Kinzey, 1984), (b) captive groups are most successful when kept either as lone male/female pairs or male/female pairs with offspring (Epple, 1978b; Evans & Poole, 1983), (c) males and other group members help care for infants (Goldizen, 1987a), and (d) adult marmosets and tamarins exhibit little sexual dimorphism either physically or behaviorally (Kleiman, 1977).

The generalization that all callitrichids are monogamous and live in extended family groups has been ubiquitous in the primate literature for many years. It is now, however, under revision.

In 1985, Terborgh and Goldizen published the results from a 5-year study of a wild population of Saguinus fuscicollis in Peru. They reported that monogamous as well as polyandrous, and, rarely, polygynous groups of these tamarins exist in the wild. Clearly, the breeding structure of Saguinus fuscicollis appears to be not only more complex than first believed but highly variable as well. These results strongly suggest that the presumption of simple monogamy among all callitrichids must be reassessed.

Although a revision of the blanket statement that all callitrichids are monogamous appears necessary, there are three generalizations which remain, as yet, unchallenged. The first of these generalizations is that marmosets and tamarins are referred to as being "pair-bonded". All captive studies of callitrichids clearly show that males and females are capable of forming strong bonds (see Epple, 1978a, for example). The term "pair-bonded" is used to describe the social relationship between two unrelated individuals of the opposite sex. The correct usage of the term implies that two individuals spend a disproportionately large amount of time together and engage in mutually reinforcing nonsexual behaviors such as grooming and huddling on a daily basis (Eisenberg et al., 1972; Wickler & Seibt, 1983).

While this term is usually associated with a monogamous mating system, Sussman and Garber (1987) have suggested that there is no evidence to indicate that such bonds must be formed or maintained by only a single male and female. Goldizen (1989) addressed this issue. While observing a polyandrous group of wild Saguinus fuscicollis Goldizen noted pair-bonded relationships existing between two males and a single female. She reported that the males appeared to be codominant and shared equally in their access to the female, both socially and sexually. Thus, whether the mating system of a callitrichid group is monogamous or polyandrous, the concept of "pair-bondedness" is clearly important.

The second undisputed generalization is that the future reproductive success of individuals in many species of the Callitrichidae is dependent upon prior infant caretaking experience with younger siblings. Researchers have shown that the offspring of inexperienced adults of three species, Saguinus fuscicollis (Epple, 1975b), Leontopithecus rosalia (Hoage, 1978), and Saguinus oedipus (Kirkwood, Epstein, & Terlecki, 1983; Tardif, Richter, & Carson, 1984), die at a much higher rate, often from abuse or neglect, than those offspring born to experienced individuals.

The third and final generalization is that only one female per group gives birth. In the Callitrichidae this appears to be accomplished via reproductive suppression. The dominant and reproductively active female somehow suppresses reproduction in all subordinate females within a group. In Saguinus oedipus (French, Abbott, & Snowdon, 1984; Heistermann, Kleis, Prove, & Wolters, 1989), Saguinus fuscicollis (Epple & Katz, 1984), and Callithrix jacchus jacchus (Evans & Hodges, 1984), this suppression seems to occur at the endocrine level. Females housed in family groups or in the presence of an adult cycling female exhibit no ovarian cyclicity. The exact mechanism of this suppression is not yet known although scent marking of the dominant female is hypothesized to be important (French et al., 1984; Heistermann et al., 1989; Ziegler, Savage, Scheffler, & Snowdon, 1987).

Relevance to Reproductive Success

Pair-bonding, infant caretaking experience, and reproductive suppression, although different behaviorally, share a common attribute. Each can be thought of as contributing to the future reproductive success of individual marmosets and tamarins. The crucial importance of pair-bond formation, with respect to successful reproduction among these primates, was demonstrated by Epple and Katz (1980). Their study reported that juvenile male and female Saguinus fuscicollis, removed from their natal groups at 6 months of age, sired/conceived at a much slower rate when paired with oppositely sexed individuals of the same age as compared with oppositely sexed, sexually experienced adults. Furthermore, all young females paired with adult males reproduced while two of eight young females paired with young males had shown no signs of pregnancy 3 years after pairing. Behaviorally, juvenile pairs exhibited more play and less social behavior characteristic of pair-bonded individuals than the juvenile/adult pairs. Interestingly, the frequency of copulations did not differ among the two groups.

From the aforementioned results, one might question whether the delayed reproduction exhibited by juvenile pairs is related to their deficient performance of behaviors associated with pair-bond formation. One might also question whether this failure to adequately pair-bond resulted from being removed from the natal group at such an early age. It is conceivable that the socialization process which occurs as young monkeys develop in their natal groups is important in somehow teaching young individuals how to engage appropriately in behaviors pertinent to pair-bond formation. Taking this a step further, it is also conceivable that the adequate formation of a pair-bond is somehow related to a female's ability to conceive and successfully rear offspring.

The importance of prior infant caretaking experience and its relation to future reproductive success has been discussed previously. How does reproductive suppression impact the future reproductive success of young and/or subordinate animals? Time may be the critical element. Remaining in the natal group as a nonreproductive individual through the birth and rearing of at least one set of offspring affords an individual time to practice infant caretaking behaviors and gain experience in parental skills. This period, as suggested earlier, may also give an individual time to be actively involved in a socialization process and acquire the social skills needed to form an adequate pair-bond, ultimately leading to successful reproduction. Thus, the time that young marmosets and tamarins spend in their natal groups as nonreproductive individuals may be not only beneficial but necessary with respect to ensuring their own future reproductive success.

RESEARCH AND THE ZOO

In a world where species are becoming extinct at an alarming rate, zoos have become increasingly important centers for the propagation of endangered species (Hutchins, 1987). A goal of many modern zoos is the creation of environments which both elicit and support behaviors necessary for successful reproduction. Knowledge of ecology, diet, social systems, and behavior is crucial to the development of such environments. Hutchins (1987) states that while improvements in exhibit design, veterinary medicine, reproductive technology, and nutrition have enhanced the success of captive breeding programs, some of the most significant improvements have been the result of an increased knowledge of animal behavior.

Research which seeks to identify and define behaviors important to a species' reproductive success may greatly enhance the success of captive breeding programs. Furthermore, such research also allows zoos to quantify and share information pertaining to reproductive success. With this in mind, the author chose to examine several specific social behaviors among the members of a family group of Saguinus midas midas (red-handed tamarins) housed at the Washington Park Zoo, Portland, Oregon, USA. Saguinus midas midas is in no immediate threat of extinction at this time. It is the author's hope, however, that observations of this rarely studied species will contribute to increasing the reproductive success of all species of the Callitrichidae.

BRIEF DESCRIPTION OF THE STUDY SPECIES

Saguinus midas midas (red-handed tamarins) is one of only two subspecies of Saguinus midas which is, in turn, 1 of 11 species of tamarins (Napier & Napier, 1985). Saguinus midas is common in Surinam, French Guyana, and Brazil but is considered to be vulnerable in Guyana and possibly parts of eastern Brazil. Saguinus midas, like all other members of the Callitrichidae, is a forest dweller, and this species is known to occupy a wide variety of forest habitats including high and low rain forest, savanna forest, and swamp forest among others. This species is also reported to survive well in edge habitats and secondary vegetation (Wolfheim, 1983).

At this time, relatively little is known about the mating system and behavior of this species. No detailed behavioral studies have, to the author's knowledge, been published on this species/subspecies. These tamarins, like all other callitrichids, are, however, assumed to be monogamous until proven otherwise. The mean group size for Saguinus midas in the wild is reported to be five individuals (Ferrari & Lopes-Ferrari, 1989), and this species is believed to live in extended family groups (Hershkovitz, 1977; Napier & Napier, 1985). As in all species of callitrichids, the adult female generally gives birth to twins, and the adult male, as well as other family members, is active in infant care (Christen, 1974; Hershkovitz, 1977; Napier & Napier, 1985).

THE QUESTION

This study endeavored to gain general information about this species. Saguinus midas midas is a rarely studied species, and information about the behavior of this species is virtually nonexistent. For this reason, this study sought to obtain information about activity budgets and social grouping within this captive group.

The primary focus of this study, however, was the socialization of captive juvenile Saguinus midas midas with respect to several behaviors relevant to reproductive success among the Callitrichidae. Socialization, here, refers to the process of social learning that guides young primates in the development of behaviors important in the day to day life of a species (Fedigan, 1982). Such socialization is believed to occur both through participation and the observation of others (McKenna, 1979). Thus, juveniles may learn behaviors relevant to pair-bonding and infant caretaking by participating in interactions with other group members. In addition, juveniles may further learn about these behaviors by observing a pair-bonded male and female; the adult male and female, in other words, may serve as role models for the juveniles.

Recognizing the importance of both socialization processes, this study attempted to answer several questions. The following behaviors, known to be important in successful reproduction among the Callitrichidae, were assessed: scent marking (reproductive suppression); mounting, thrusting, allogrooming, huddling (pair-bonding); food transferring, and infant carrying (infant caretaking) (Epple, 1975a; Evans & Hodges, 1984; Evans & Poole, 1983, 1984; Feistner & Price, 1990; Kirkwood, Epstein, & Terlecki, 1983; Tardif, Carson, & Clapp, 1986). The questions addressed in the present study were: do juveniles and adults engage in these behaviors, and, if the behavior is a social interaction, with whom? The following hypotheses were tested:

1. Because of the importance of these behaviors in callitrichid society (Cebul & Epple, 1984; Epple & Katz, 1980; Tardif et al., 1984; Ziegler et al., 1987), it was hypothesized that both juveniles and adults would engage in these behaviors.

2. It was also hypothesized, because the adults were assumed to be pair-bonded and, thus, proficient in these behaviors, that the juveniles would engage in mounting, thrusting, allogrooming, and huddling more with the adults than animals of any other age-class.

3. Because the adults were assumed to be pair-bonded, it was further hypothesized that they would engage in mounting, thrusting, allogrooming, and huddling more so with each other than any other animals in the group.

4. Finally, since scent marking is believed to play a vital role in the adult female's ability to maintain her breeding status, it was hypothesized that the adult female would exhibit the highest rate of scent marking within this family group.

METHOD

SUBJECTS

The subjects of this study were members of a captive family group of Saguinus midas midas (red-handed tamarins) housed at the Washington Park Zoo, Portland, Oregon, USA. During the first 6 weeks of the study (Phase 1) the family group consisted of an adult mated pair (paired approximately 4 years prior to the onset of this study) and 5 offspring, of which 3 were subadult triplets and 2 were juvenile twins (see Table I for sex and ages of all individuals). The adult female was pregnant throughout Phase 1.

During the interim week between the completion of Phase 1 and the beginning of Phase 2, two changes with respect to group composition occurred. On October 24, 1990, the 3 subadults were separated from the remainder of the group and sent to other zoos. In addition, on October 29, 1990, the adult female gave birth to triplets.

As a result of the aforementioned events, the group composition at the beginning of Phase 2 was as follows: the adult mated pair, 2 juvenile twins, and 3 infant triplets. One of the infant triplets was found dead in the enclosure exactly 1 week after its birth. Thus, for the remaining 5 weeks of Phase 2 the group consisted of the adult mated pair, 2 juvenile twins and 2 infant twins. All animals included in this study were captive born.

All animals were housed in a zoo enclosure which allowed them access to two on-exhibit areas measuring approximately 9 x 7 x 11 ft (2.7 x 2.1 x 3.4 m) each. The on-exhibit enclosures were connected by a wire-mesh tunnel located

TABLE I

AGE AND SEX CLASSIFICATIONS FOR MEMBERS OF THE FAMILY GROUP OF *Saguinus midas midas* AT THE WASHINGTON PARK ZOO

Age-class	Sex	Age at begin. of Phase 1	Age at end of Phase 1	Age at end of Phase 2
Adult [A♂]	M	6 yr 9 mo	6 yr 10.5 mo	7 yr 0 mo
Adult [A♀]	F	6 yr 8 mo	6 yr 9.5 mo	6 yr 11 mo
Subadult [Sc]	M	1 yr 9 mo	1 yr 10.5 mo	----[b]
Subadult [S♂]	M	1 yr 9 mo	1 yr 10.5 mo	----[b]
Subadult [S♀]	F	1 yr 9 mo	1 yr 10.5 mo	----[b]
Juvenile [J1]	M	4 mo	5.5 mo	7 mo
Juvenile [J2]	F	4 mo	5.5 mo	7 mo
Infant	?[a]	----	----	6 wk
Infant	?[a]	----	----	6 wk
Infant	?[a]	----	----	deceased[c]

[a] Sex is not evident at this age.

[b] Subadults were not present during Phase 2.

[c] This infant died when 1 week old.

in the off-exhibit area. The animals also had access to an off-exhibit wire-mesh enclosure measuring approximately 4 x 4 x 8 ft (1.2 x 1.2 x 2.4 m). Each enclosure contained tree limbs, and straw was spread liberally on the floor of the two on-exhibit areas. The temperature within the enclosures was maintained at 75° F (23.9° C), and the average humidity was 55-60%. All three enclosures were visually isolated, although acoustic and olfactory contact between the enclosures was possible. The animals were fed twice daily and maintained on a diet consisting of Zu/Preem Marmoset Diet®, fresh fruits (grapes, oranges, and bananas), yogurt, and hard-boiled eggs (M. Marshall, personal communication, August 10, 1990).

ANIMAL IDENTIFICATION

During Phase 1 of the study, individual identification of all animals within age-classes was quite difficult with the exception of the adults. To ensure reliability, continuous and scan samples of behavior in Phase 1 were recorded on an age-graded basis for both subadults and juveniles and an individual basis for adults. Reliable identification of individuals was, however, possible during scans of social grouping, and data were recorded on an individual basis. The ability to identify individuals during scans of social grouping was due, in large part, to the fact that the observer could visually compare the occupants of each of the on-exhibit enclosures.

The reliable identification of individuals was much easier during Phase 2 of the study both because there were fewer individuals and the observer had become more familiar with each individual. All behaviors and social groupings were, therefore, scored on an individual basis during Phase 2 of the study.

BEHAVIORAL OBSERVATIONS

Behavior Codes

Many of the behaviors scored in this study were modeled after those described by Stevenson and Poole (1976) and Epple and Katz (1980). Tables II and III present the definitions for all behaviors scored during continuous and scan sampling, respectively.

Behavior Sampling Procedures

Phase 1. The family group of *Saguinus midas midas* was observed for two 80-min observation sessions, one occurring prior to noon and the other after noon, five times weekly for 6 weeks. Observations began the week of September 9, 1990 and ended the week of October 14, 1990. During all sessions the observer stood in the visitor viewing area and was separated from the subjects by only the Plexiglas front of the enclosure and a planter box measuring approximately 2 ft (0.61 m) in width. All observations took place during regular zoo hours.

Continuous sampling as well as scan sampling of behavior were utilized (Crockett, in press). Continuous sampling is a behavior-based sampling method in which all occurrences of specified behaviors and interactions are recorded. Scan sampling, on the other hand, is a time-based sampling method in which the observer records the behavior occurring at the instant that a predetermined time interval ends. A timing device set at 1-min intervals was used to mark time, and data were recorded on a modified checksheet. During each 80-min observation session each on-exhibit enclosure served as the focal enclosure for a total of 30 min of continuous sampling; the remaining 20 min was time allotted for animal identification and scan sampling. An outline of a typical observation session is

TABLE II

ETHOGRAM FOR CONTINUOUS SAMPLING OF BEHAVIOR FOR CAPTIVE *Saguinus midas midas*

Behavior	Definition
mounting	one animal mounts another but no pelvic thrusting is observed
thrusting	one animal mounts another and pelvic thrusting is observed
scent marking	an animal rubs its anogenital, suprapubic, or sternal region against an underlying surface
huddling	a single bout of huddling includes any period of resting in close physical contact which is not altered by a participant in the interaction moving away or the addition of a new individual; animals must remain in such contact for at least 1 minute in order to be recorded as a huddle
allogrooming	a single bout of allogrooming includes all contacts, which are not separated by more than 5 seconds, where an animal uses its hands and/or tongue to search another animal's fur
food transferring	the transfer of a food object from one animal to another; straw and twigs are not considered to be food objects

TABLE III

ETHOGRAM FOR SCAN SAMPLING OF BEHAVIOR FOR CAPTIVE <u>Saguinus midas midas</u>

Behavior	Definition
mounting	an animal mounts or is mounted by another animal but no pelvic thrusting is observed
thrusting	an animal mounts or is mounted by another animal and pelvic thrusting is observed
scent marking	an animal rubs its anogenital, suprapubic, or sternal region against an underlying surface
sniffing	an animal places its nasal area within 3 cm of another animal's anogenital region or other surface [e.g., climbing branch]
huddling	an animal rests in close physical contact with another individual
allogrooming	an animal uses its hands and/or tongue to search another animal's fur or an animal is the recipient of such grooming
autogrooming	an animal uses its hands and/or tongue to search its own fur
playing	an animal is involved in tumbling, wrestling, play-biting, or play-chasing with another animal; these behaviors are unaccompanied by vocalizations and/or tongue flicking
gnawing	an animal chews upon any of the climbing branches in the enclosure
eating/drinking	an animal consumes food or water

TABLE III

ETHOGRAM FOR SCAN SAMPLING OF BEHAVIOR FOR CAPTIVE Saguinus midas midas

[continued]

Behavior	Definition
food transferring	an animal is involved in the transfer of a food object between itself and another individual; straw and twigs are not considered to be food objects
foraging	an animal uses its hands to search through straw on the floor of the enclosure
infant transferring	an animal is involved in the active transfer of an infant between itself and another individual
infant carrying	an animal is in possession of an infant by either holding it or by the infant's clinging to the carrier
stationary	an animal is alert, immobile, not engaged in any active behavior, and has no physical contact with another individual
locomoting	an animal is actively moving from one location to another by walking, jumping, etc.
pacing	an animal locomotes back and forth across the same surface
other	an animal engages in any behavior not listed above
not visible	an animal is not in view

presented in Figure 1. The order of observation of the enclosures was determined randomly prior to each observation session by the flipping of a coin.

During continuous sampling all occurrences of the following behaviors were recorded (consult Table II for definitions of behaviors): mounting, thrusting, scent marking, huddling, allogrooming, and food transferring. All participants in the behavior as well as the direction of the interaction were recorded for each occurrence of mounting, thrusting, allogrooming, and food transferring. With respect to huddling, a huddle was scored and its composition recorded each time an initial huddle was formed or a change in the composition of an existing huddle, by the addition or loss of an individual, occurred. If the initiator of a huddle was discernible, this was also recorded.

Scan sampling was used to gain information regarding both social grouping and the amount of time spent in various behaviors. Social grouping, in this study, referred only to the common use of an enclosure and implied nothing about social interactions. When scan sampling for social grouping, at the tone, the observer recorded the occupants of the focal enclosure, moved to the second on-exhibit enclosure and recorded its occupants, and then recorded the occupants of the off-exhibit enclosure by process of elimination.

When scan sampling for behavior, at the tone, the observer scanned the focal enclosure from left to right and recorded the behavior of each animal in the enclosure as one or more of the following (see Table III for definitions of behaviors): mounting, thrusting, scent marking, sniffing, huddling, allogrooming, autogrooming, playing, gnawing, eating/drinking, food transferring, foraging, infant transferring, infant carrying, stationary, locomoting, pacing, other, or not visible. If the focal enclosure was empty, the observer counted to 5, moved to the second on-exhibit enclosure and scanned that enclosure from left to right

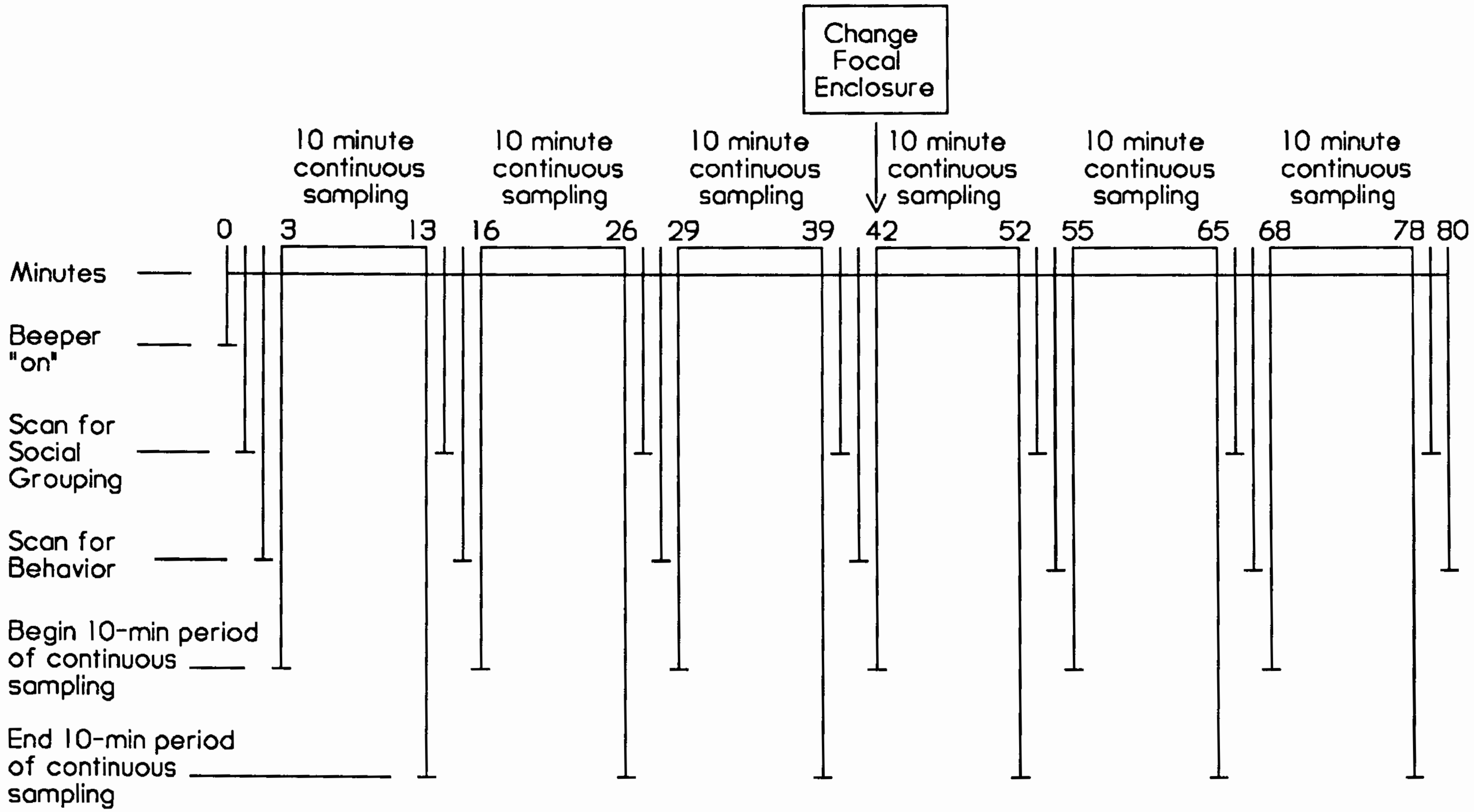


Figure 1. Timeline of a typical 80-minute observation session.

recording the behavior of each animal therein.

Phase 2. As in Phase 1, the family group of Saguinus midas midas was observed for two 80-min observation sessions, one occurring prior to noon and the other after noon, five times weekly for 6 weeks. Observations began the week of October 28, 1990 and ended the week of December 2, 1990. Observations were made under the same conditions as those described in Phase 1.

The behavior sampling procedures employed in Phase 2 were the same as those in Phase 1 with one modification; a third scan sampling procedure was added in order to assess infant carrying behavior. During each 10-min period of continuous sampling an audible tone occurred at 1-min intervals. At the tone, the observer scanned both on-exhibit enclosures, beginning with the focal enclosure, and gave the adult male and each juvenile a score of 0, 1, or 2 based upon the number of infants that the animal was carrying at that instant. The observer gave the adult female a score of 0, 1, or 2 for both nursing and carrying based upon the number of infants that she was nursing and/or carrying at that instant. The adult female was considered to be nursing an infant if the infant was positioned ventrally or ventrolaterally on the adult female; the female was considered to be carrying an infant in any other position upon the adult female. If an animal was in the off-exhibit area and, therefore, not visible during the scan, the observer could oftentimes give such an individual a score based upon process of elimination. When this was not possible, the observer scored the animal as not visible.

Reliability of Behavioral Observations

Cohen's Kappa (Cohen, 1960) was used to assess both interobserver and intraobserver reliability for continuous and scan sampling methods used in this study. All behavioral observations conducted during the course of this study were performed by the author. The co-coder that served as the standard for the calculation of interobserver reliability was, therefore, not a participant in this study.

Interobserver reliability was assessed using a 30-min videotape of the family group which was coded by both the observer and a co-coder. The observer coded the videotape twice at the midpoint of the study (once for continuous sampling and once for scan sampling of behavior) and twice at the end of the study while a co-coder also coded the videotape twice, once for each sampling method. By comparing the observer's records with the co-coder's records, the interobserver reliability for continuous sampling of behavior was determined to be $\underline{K} = 0.79$ at the midpoint of the study and $\underline{K} = 0.79$ at the end of the study. Interobserver reliability for scan sampling of behavior was determined to be $\underline{K} = 0.90$ at the midpoint of the study and $\underline{K} = 0.88$ at the end of the study.

Intraobserver reliability was assessed by comparing the observer's coding of the videotape performed at the midpoint of the study with that performed at the end of the study. Intraobserver reliability for continuous sampling of behavior was determined to be $\underline{K} = 1.0$ while that for scan sampling of behavior was $\underline{K} = 0.82$.

DATA ANALYSIS

The data were compiled on a weekly basis and converted to hourly rates or percentage of time spent. When making individual comparisons, each individual contributed a score on a weekly basis. When making age-graded comparisons, each age-class contributed a score on a weekly basis. It is important to note that, due to the discrepancy in age-class membership during Phase 1 (2 adults, 3 subadults, 2 juveniles), the frequencies that adults and juveniles groomed and received grooming from subadults were multiplied by a factor of 2/3. In addition, the frequencies that the adults, subadults, and juveniles acquired food from subadults were also multiplied by 2/3. Hourly rates were then calculated based upon these adjusted scores.

The weekly scores contributed by age-classes were calculated by two basic procedures. For example, the mean hourly rate per individual (averaged within an age-class) was calculated as follows: sum of occurrences of a behavior for all individuals in a given age-class/ total number of observation hours/ number of individuals comprising the age-class. Similarly, the mean percent time per individual spent in a behavior (averaged within an age-class) was calculated as follows: sum of scans in a behavior for all individuals in a given age-class/ total number of scans taken for animals in the age-class X 100.

Nonparametric statistical tests (Kruskal-Wallis rank-sum test, Friedman ANOVA by ranks, Mann-Whitney U test, and Wilcoxon signed-rank test) were utilized in this study. All values presented are for two-tailed tests. For descriptions of the individual tests refer to Siegel (1956).

RESULTS

ACTIVITY BUDGETS

Tables IV and V present the mean percentage of time per individual that animals of each age-class spent in various behaviors during Phases 1 and 2 of the study, respectively. In general, there were few obvious differences in activity budgets between age-classes. Juveniles did, however, spend significantly more time playing than animals of any other age-class (Kruskal-Wallis, $H(2) = 12.7$, $p \leq .005$, Phase 1 and Mann-Whitney, $U(6,6) = 0$, $p \leq .01$, Phase 2). Adults spent more time engaged in scent marking than subadults or juveniles, although, due to a large number of 0 scores, this difference was not significant. In addition, during Phase 2, adults spent significantly more time engaged in scent marking and infant carrying than juveniles (Mann-Whitney, $U(6,6) = 4.5$, $p \leq .05$, and $U(6,6) = 0$, $p \leq .01$, respectively).

SOCIAL GROUPING

Figure 2 shows that social groups of all possible sizes occurred during both Phases 1 and 2 of the study and that groups of some sizes occurred more often than others (Kruskal-Wallis, $H(6) = 23.1$, $p \leq .001$, and $H(3) = 13.2$, $p \leq .005$, respectively). During Phase 1, the mean percent of recorded social groups containing 1 individual was greater than that for groups containing 2,3,4,5,6, or 7 individuals (Mann-Whitney, $p \leq .05$ for each pairwise comparison).

With respect to these groups of 1, there was also a significant difference in the amount of time that each animal spent as a solitary individual (Kruskal-Wallis,

TABLE IV

PERCENT TIME PER INDIVIDUAL THAT ANIMALS OF EACH AGE-CLASS SPENT IN VARIOUS BEHAVIORS: PHASE 1

	Age-class		
Behavior	Adult	Subadult	Juvenile
Mounting			
<u>M</u>	0.0	0.0	0.0
<u>MDN</u>	0.0	0.0	0.0
<u>SD</u>	0.0	0.0	0.0
Thrusting			
<u>M</u>	0.1	0.0	0.1
<u>MDN</u>	0.0	0.0	0.0
<u>SD</u>	0.3	0.0	0.3
Scent Marking			
<u>M</u>	0.4	0.1	0.0
<u>MDN</u>	0.4	0.0	0.0
<u>SD</u>	0.4	0.2	0.0
Sniffing			
<u>M</u>	0.4	0.2	0.0
<u>MDN</u>	0.0	0.0	0.0
<u>SD</u>	0.6	0.3	0.0
Huddling			
<u>M</u>	3.7	2.1	6.0
<u>MDN</u>	3.6	1.9	6.1
<u>SD</u>	1.5	0.7	3.2
Allogrooming			
<u>M</u>	2.0	2.9	1.0
<u>MDN</u>	2.1	2.4	0.4
<u>SD</u>	1.4	2.0	1.4
Huddling + Allogrooming			
<u>M</u>	0.4	1.5	1.0
<u>MDN</u>	0.0	0.0	0.0
<u>SD</u>	0.6	1.1	0.6

TABLE IV

PERCENT TIME PER INDIVIDUAL THAT ANIMALS OF EACH AGE-CLASS SPENT IN VARIOUS BEHAVIORS: PHASE 1 [continued]

	Age-class		
Behavior	Adult	Subadult	Juvenile
Autogrooming			
_M_	0.6	0.7	0.4
MDN	0.7	0.8	0.0
_SD_	0.5	0.6	0.6
Playing *			
_M_	0.2	0.8	5.8
MDN	0.0	1.0	5.4
_SD_	0.6	0.6	2.5
Gnawing			
_M_	0.7	1.1	1.1
MDN	0.7	1.0	1.4
_SD_	0.4	0.9	0.7
Eating/Drinking			
_M_	6.3	3.3	4.6
MDN	6.1	2.2	4.3
_SD_	2.4	3.4	3.8
Food Transferring			
_M_	0.0	0.3	0.4
MDN	0.0	0.0	0.0
_SD_	0.0	0.4	0.6
Foraging			
_M_	0.2	0.5	0.2
MDN	0.0	0.3	0.0
_SD_	0.4	0.7	0.4

TABLE IV

PERCENT TIME PER INDIVIDUAL THAT ANIMALS OF EACH
AGE-CLASS SPENT IN VARIOUS BEHAVIORS:
PHASE 1
[continued]

	Age-class		
Behavior	Adult	Subadult	Juvenile
Stationary			
M	30.2	24.4	23.4
MDN	30.4	24.8	22.9
SD	4.5	5.8	4.9
Locomoting			
M	9.5	9.9	9.3
MDN	9.7	10.0	9.3
SD	2.6	2.4	3.5
Pacing			
M	0.6	0.0	0.0
MDN	0.4	0.0	0.0
SD	0.8	0.0	0.0
Other			
M	1.2	0.3	0.4
MDN	1.4	0.8	0.0
SD	1.1	2.0	1.7
Not Visible			
M	43.5	52.2	46.4
MDN	43.9	52.2	45.4
SD	7.9	7.0	11.2

* $p \leq .005$

TABLE V

PERCENT TIME PER INDIVIDUAL THAT ANIMALS OF EACH AGE-CLASS SPENT IN VARIOUS BEHAVIORS: PHASE 2

	Age-class[a]	
Behavior	Adult	Juvenile
Mounting		
M	0.0	0.0
MDN	0.0	0.0
SD	0.0	0.0
Thrusting		
M	0.0	0.2
MDN	0.0	0.0
SD	0.0	0.6
Scent Marking *		
M	1.8	0.1
MDN	1.0	0.0
SD	1.8	0.3
Sniffing		
M	0.6	0.2
MDN	0.7	0.0
SD	0.5	0.3
Huddling		
M	13.7	7.2
MDN	13.2	6.4
SD	7.9	4.4
Allogrooming		
M	1.5	3.9
MDN	1.4	3.6
SD	0.9	2.9

TABLE V

PERCENT TIME PER INDIVIDUAL THAT ANIMALS OF EACH AGE-CLASS SPENT IN VARIOUS BEHAVIORS: PHASE 2 [continued]

	Age-class[a]	
Behavior	Adult	Juvenile
Huddling + Allogrooming		
_M_	0.0	0.0
MDN	0.0	0.0
_SD_	0.0	0.0
Autogrooming		
_M_	0.8	0.9
MDN	0.7	1.1
_SD_	0.5	0.8
Playing **		
_M_	0.0	6.6
MDN	0.0	6.4
_SD_	0.0	2.6
Gnawing		
_M_	1.1	2.0
MDN	0.4	2.0
_SD_	2.1	1.5
Eating/Drinking		
_M_	8.1	7.7
MDN	7.5	7.5
_SD_	2.6	1.0
Food Transferring		
_M_	0.1	0.7
MDN	0.0	0.7
_SD_	0.3	0.6

TABLE V

PERCENT TIME PER INDIVIDUAL THAT ANIMALS OF EACH AGE-CLASS SPENT IN VARIOUS BEHAVIORS: PHASE 2

[continued]

	Age-class[a]	
Behavior	Adult	Juvenile
Foraging		
<u>M</u>	0.5	0.8
<u>MDN</u>	0.4	0.3
<u>SD</u>	0.6	1.0
Infant Transferring		
<u>M</u>	0.6	0.5
<u>MDN</u>	0.4	0.0
<u>SD</u>	0.7	0.8
Infant Carrying **		
<u>M</u>	45.7	7.9
<u>MDN</u>	45.0	8.6
<u>SD</u>	4.6	4.4
Stationary		
<u>M</u>	38.0	32.6
<u>MDN</u>	37.0	33.2
<u>SD</u>	2.7	6.6
Locomoting		
<u>M</u>	11.1	16.0
<u>MDN</u>	11.0	16.1
<u>SD</u>	3.0	4.7
Pacing		
<u>M</u>	0.6	0.0
<u>MDN</u>	0.7	0.0
<u>SD</u>	0.5	0.0

TABLE V

PERECENT TIME PER INDIVIDUAL THAT ANIMALS OF EACH AGE-CLASS SPENT IN VARIOUS BEHAVIORS: PHASE 2

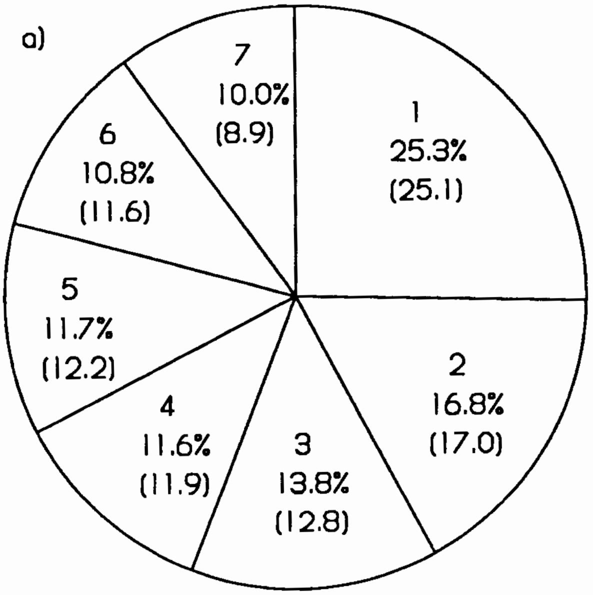
[continued]

	Age-class[a]	
Behavior	Adult	Juvenile
Other		
M	2.6	3.1
MDN	2.5	3.3
SD	1.6	1.3
Not Visible		
M	19.1	17.5
MDN	21.1	15.7
SD	8.0	7.0

[a] Infants are not represented because they engage in very little active behavior at this young age.

* $p \leq .05$

** $p \leq .01$



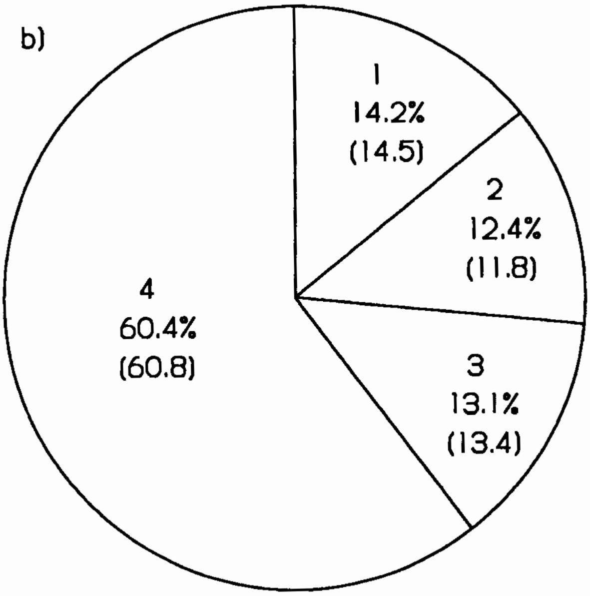


Figure 2. Mean (median) percent of recorded social groups that contained a) from 1-7 individuals during Phase 1 and b) from 1-4 individuals during Phase 2. (Only adults and juveniles were recorded during Phase 2.)

$U(6) = 34.4$, $p \leq .001$) (see Figure 3). The adult male spent more time as a solitary individual than any other animal except S♂(Mann-Whitney, $p \leq .01$ for each pairwise comparison). Although the adult male spent more time alone than S♂, this difference was not significant. In addition, members of some age-classes were more likely to spend time as solitary individuals than others (Kruskal-Wallis, $H(2) = 12.7$, $p \leq .005$). Figure 3 shows that both adults and subadults spent significantly more time alone than juveniles (Mann-Whitney, $p \leq .01$ for both pairwise comparisons).

During Phase 2, however, the mean percent of social groups containing all 4 individuals was greater than that for groups containing 1, 2, or 3 individuals (see Figure 2) (Mann-Whitney, $p \leq .01$ for all pairwise comparisons). Figure 3 shows that there was once again a difference between individuals in the amount of time spent alone (Kruskal-Wallis, $H(3) = 11.6$, $p \leq .01$). The adult male spent significantly more time alone than any other individual except the adult female (Mann-Whitney, $p \leq .01$ and $p \leq .05$ for comparisons with J1 and J2 respectively). Although the adult male spent more time alone than the adult female, this difference was not significant. The adults, once again, spent more time as solitary individuals than juveniles (Mann-Whitney, $U(6,6) = 2.5$, $p \leq .05$).

Two interesting changes in social grouping were observed from Phase 1 to Phase 2. In Phase 1, there was no difference between the time that the adult male and female spent in the same social group (i.e., in the same enclosure) as compared to different social groups. During Phase 2, however, the amount of time that the adult male and female spent in the same social group was significantly greater than the amount of time that they spent apart (Mann-Whitney, $U(6,6) = 0$, $p \leq .01$) (see Figure 4). In addition, the adult male spent

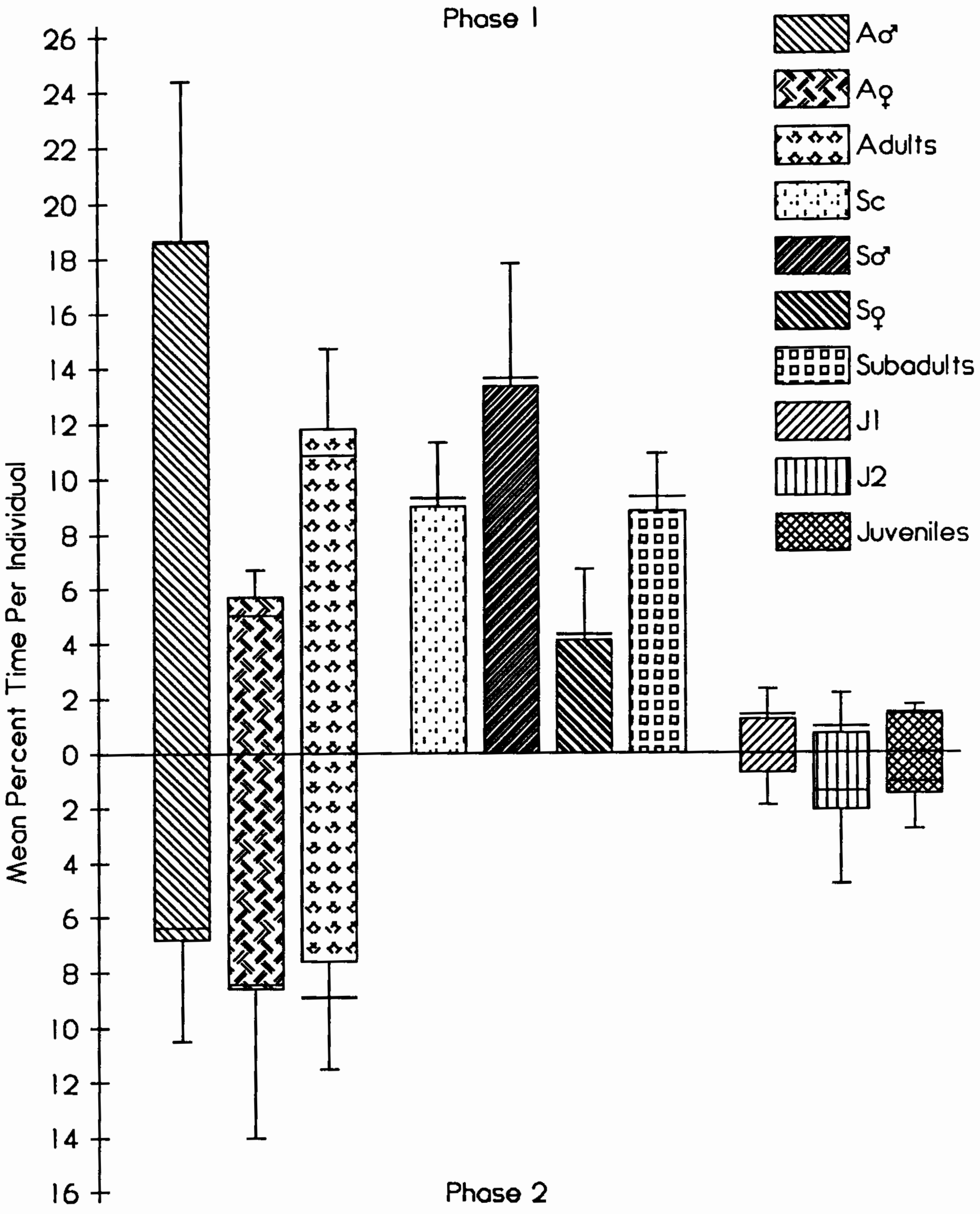


Figure 3. Mean (+ SD) percent time that animals spent as solitary individuals during Phases 1 and 2. (Contrasting horizontal bar indicates the median value.)

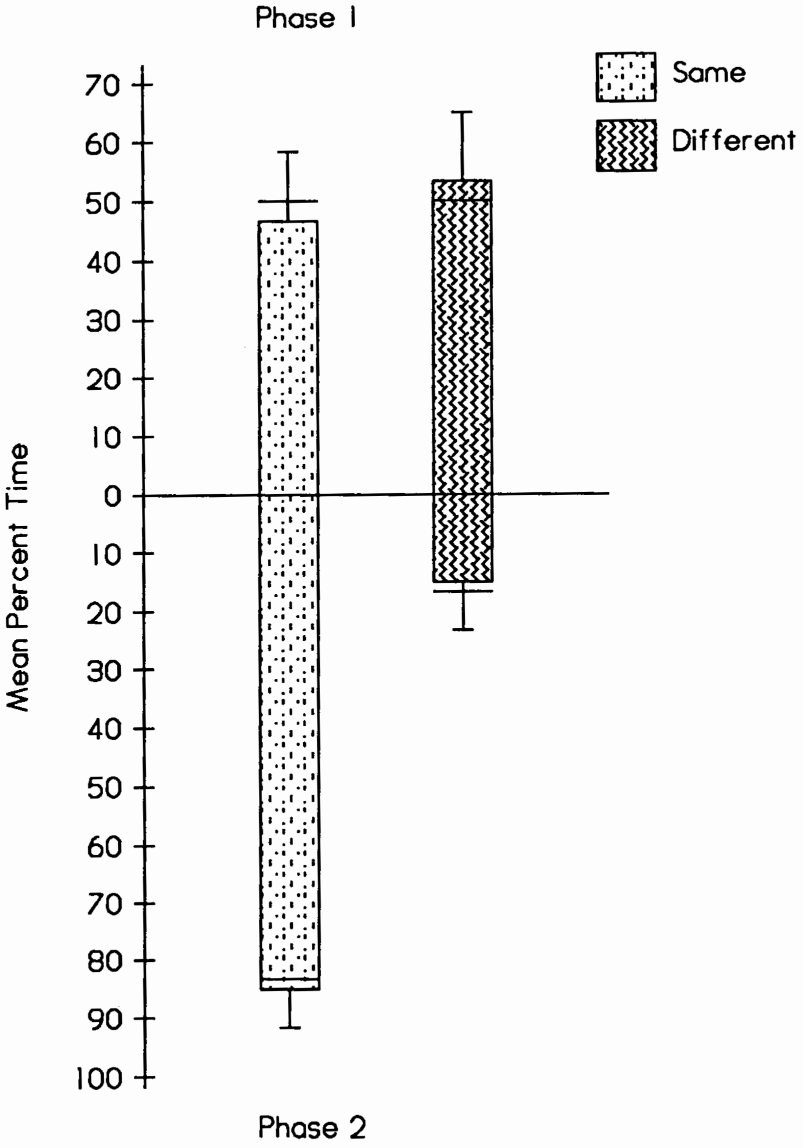


Figure 4. Mean (+ SD) percent time that the adult male and female spent in the same and differing social groups during Phases 1 and 2. (Contrasting horizontal bar indicates the median value.)

significantly less time as a solitary individual during Phase 2 as compared with Phase 1 (Wilcoxon, $T(6) = 1$, $p \leq .05$).

SCENT MARKING

Figure 5 presents the mean hourly rates of scent marking observed during Phases 1 and 2 of the study. There was a significant difference between age-classes in the hourly rate of scent marking during both phases (Kruskal-Wallis, $H(2) = 15.2$, $p \leq .001$, Phase 1; Mann-Whitney, $U(6,6) = 0$, $p \leq .01$, Phase 2). In Phase 1, adults scent marked at a significantly greater rate than subadults or juveniles while subadults scent marked at a greater rate than juveniles (Mann-Whitney, $p \leq .01$ for all pairwise comparisons). Adults also scent marked at a higher rate than juveniles in Phase 2 (Mann-Whitney, $p \leq .01$). In addition, the adult female scent marked more than the adult male during both phases of the study (Wilcoxon, $T(6) = 0$, $p \leq .05$ for both pairwise comparisons). There was no difference in the rates of scent marking exhibited by J1 and J2 during Phase 2. Only one striking difference in scent marking behavior occurred from Phase 1 to Phase 2; the adult female scent marked at a significantly higher rate during Phase 2 as compared with Phase 1 (Wilcoxon, $T(6) = 0$, $p \leq .05$). The juveniles, nonetheless, displayed a significant increase in scent marking over the course of the study ($r^2 = 0.47$, $F(1,10) = 10.65$, $p \leq .01$) (see Figure 6).

SOCIOSEXUAL AND AFFILIATIVE BEHAVIORS

Mounting and thrusting were infrequent behaviors. The adult male was, however, the animal most actively involved in these behaviors. During Phase 1, the adult male initiated a total of 6 mounts and 5 thrusts all of which were directed towards the juveniles. During Phase 2, the adult male initiated a total of

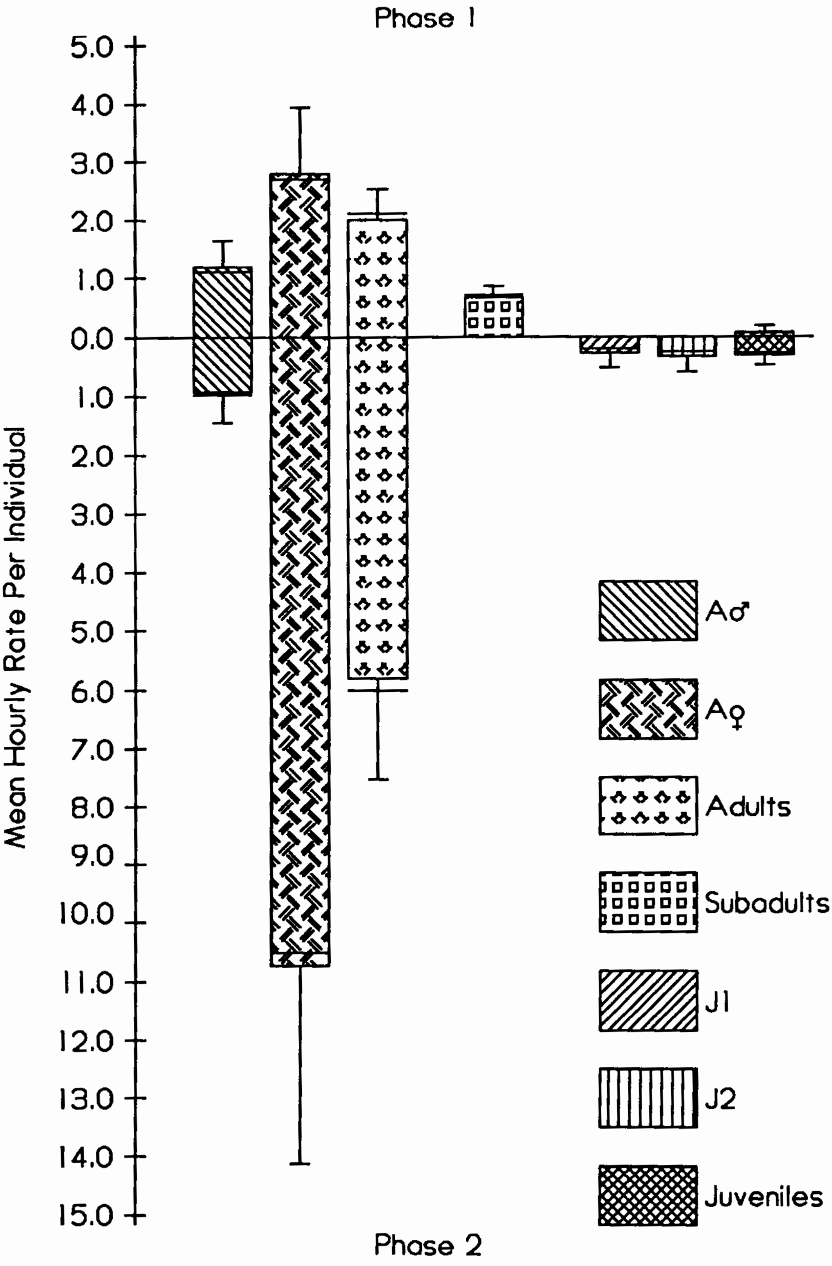


Figure 5. Mean (+ SD) hourly rate per individual of scent marking during Phases 1 and 2. (Contrasting horizontal bar indicates the median value.)

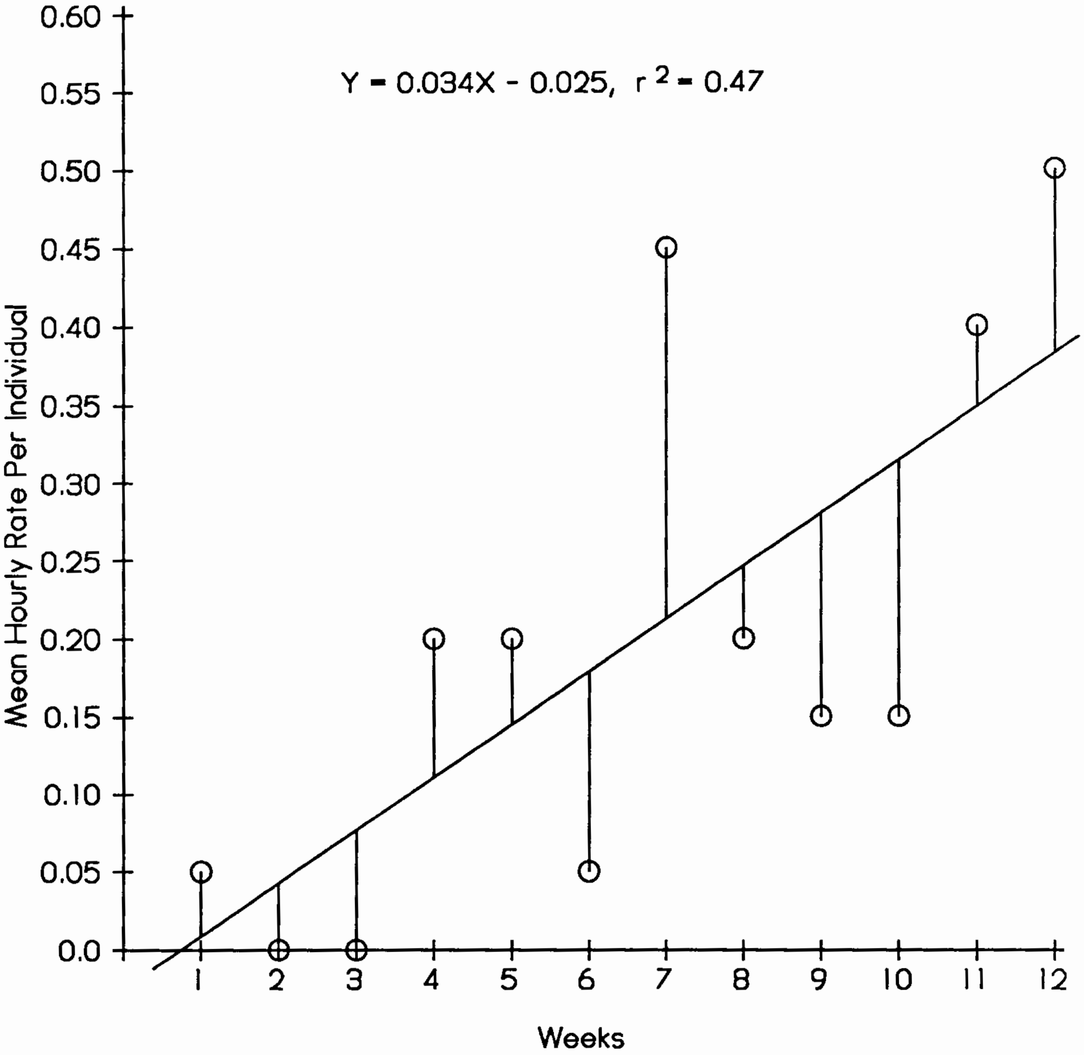


Figure 6. Mean hourly rate per individual that juveniles engaged in scent marking during Weeks 1-12.

5 mounts and 1 thrust all of which were, once again, directed toward the juveniles.

Juveniles demonstrated a general increase in sexual behavior over time ($r^2 = 0.24$) although this trend was not statistically significant (see Figure 7). Juveniles were not observed to initiate sexual behavior until Phase 2. During Phase 2, J1 initiated a total of 5 mounts, 3 involving the adult female and 2 involving J2. Interestingly, each time J1 mounted the adult female the adult female pushed J1 off almost immediately, and thrusting was not observed. J1 was observed to thrust on two occasions, and both of these thrusts were directed towards J2.

No sexual encounters involving a subadult were observed during Phase 1. In addition, neither a mount nor a thrust between the adult male and female was observed during the course of this study.

Figures 8 and 9 depict the grooming relationships between juveniles and animals of each age-class during Phases 1 and 2 of the study, respectively. During Phase 1, juveniles groomed adults the most and subadults the least, although these differences were not significant. There was, however, a significant difference in the rates at which juveniles received grooming from members of each age-class (Friedman, $\chi^2_r(2) = 7.6$, $\underline{p} \leq .025$). Juveniles received grooming from subadults and juveniles at approximately the same rate while they received significantly less grooming from adults than subadults (Wilcoxon, $\underline{p} \leq .05$). Juveniles also received less grooming from adults than juveniles, however, due to the small sample size, there was no basis for statistical comparison.

During Phase 2, there was a significant difference in the rates that juveniles groomed members of each age-class (Friedman, $\chi^2_r(2) = 10.3$,

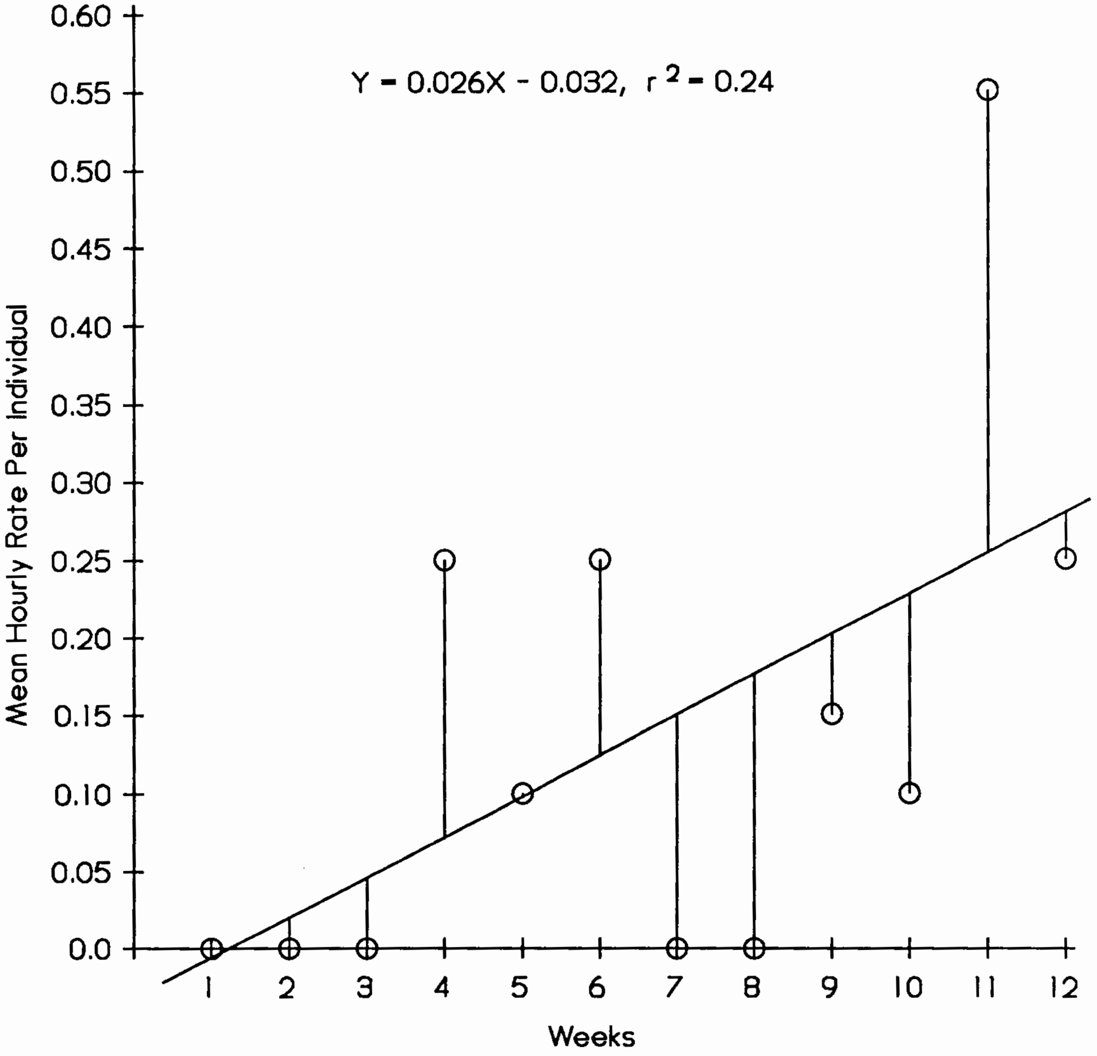


Figure 7. Mean hourly rate per individual that juveniles engaged in sexual behavior (mounts + thrusts) during Weeks 1-12.

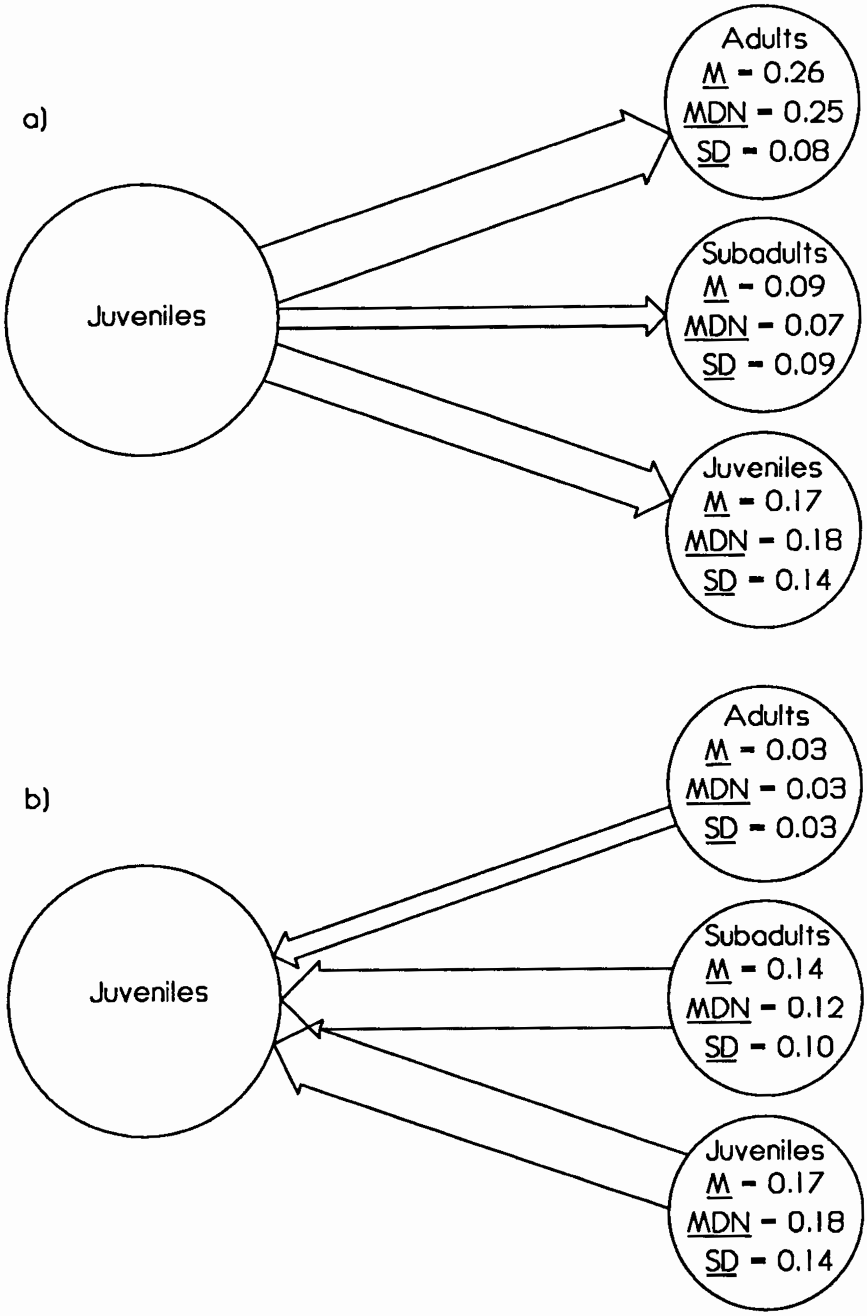


Figure 8. Mean hourly rates per individual that juveniles a) groomed and b) received grooming from animals of each age-class during Phase 1.

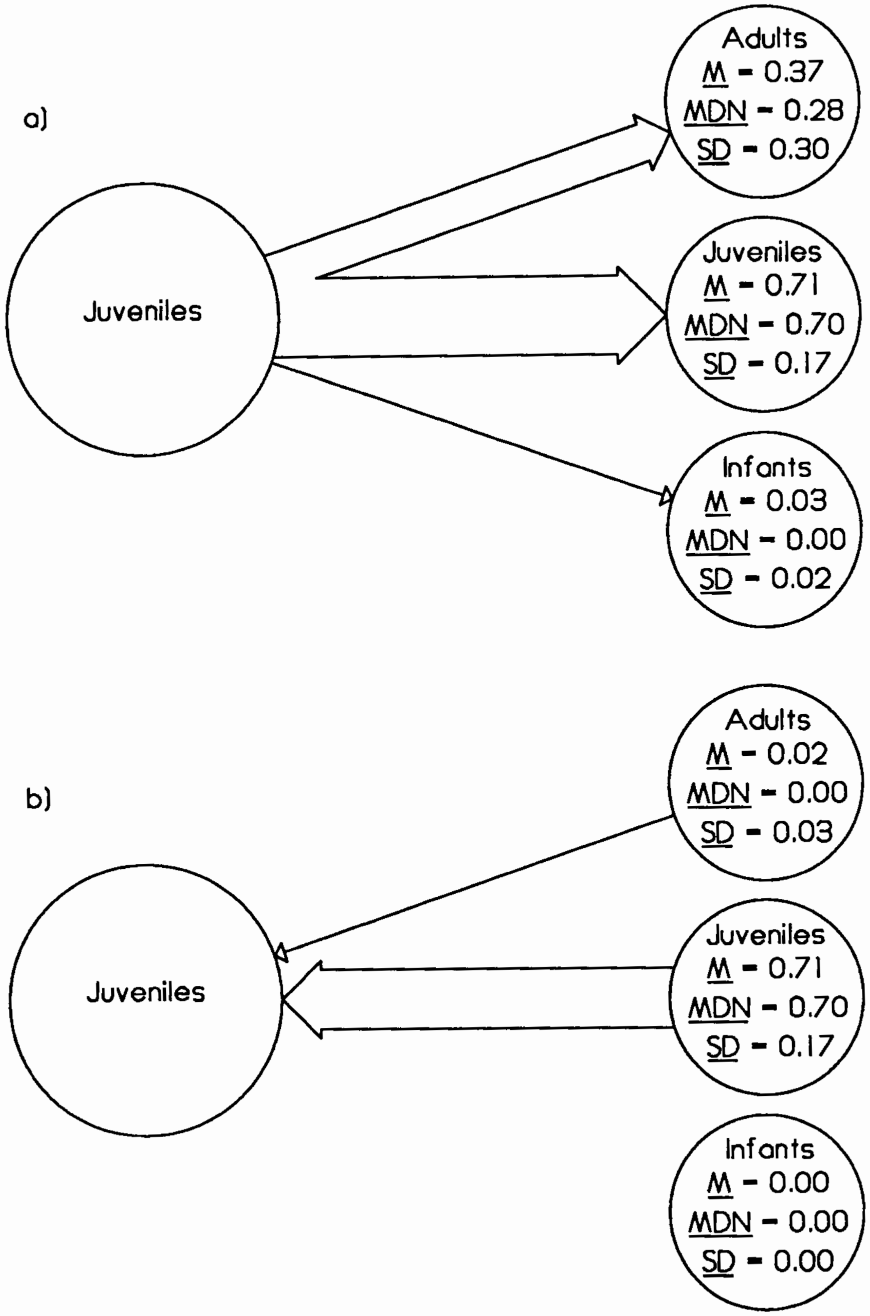


Figure 9. Mean hourly rates per individual that juveniles a) groomed and b) received grooming from animals of each age-class during Phase 2.

$p \leq .01$). Juveniles groomed juveniles and adults significantly more than they groomed infants (Wilcoxon, $p \leq .05$ for each pairwise comparison). While juveniles groomed juveniles at a higher rate than they groomed adults, this difference was not significant. Juveniles also received significantly more grooming from juveniles than adults (Wilcoxon, $T(6) = 0$, $p \leq .05$). It should be noted that infants, although the recipients of grooming, were not observed to groom others at this young age. In addition, juveniles showed a general increase in initiating grooming over the course of this study ($r^2 = 0.44$, $F(1,10) = 9.68$, $p \leq .01$) (see Figure 10).

Figures 11 and 12 depict the grooming relationships between adults and animals of each age-class during Phases 1 and 2 of the study, respectively. During Phase 1, the adults groomed subadults the most and juveniles the least, although these differences were not significant. There was, however, a significant difference in the rates at which adults received grooming from members of each age-class (Friedman, $\chi^2_r(2) = 9.3$, $p \leq .01$). Adults received significantly less grooming from adults than either subadults or juveniles (Wilcoxon, $p \leq .05$ for each pairwise comparison). While adults received more grooming from subadults than juveniles, this difference was not significant.

During Phase 2, adults groomed infants the most and juveniles the least, however, differences in these rates were not significant. Adults did, however, receive significantly more grooming from juveniles than adults (Wilcoxon, $T(6) = 0$, $p \leq .05$).

As noted with allogrooming, animals of all ages participated in huddling. Tables VI and VII display the occurrence of huddles of varying compositions during Phases 1 and 2 of the study. During Phase 1, juveniles displayed a preference in huddling partners (Friedman, $\chi^2_r(2) = 7.0$, $p \leq .05$). The mean

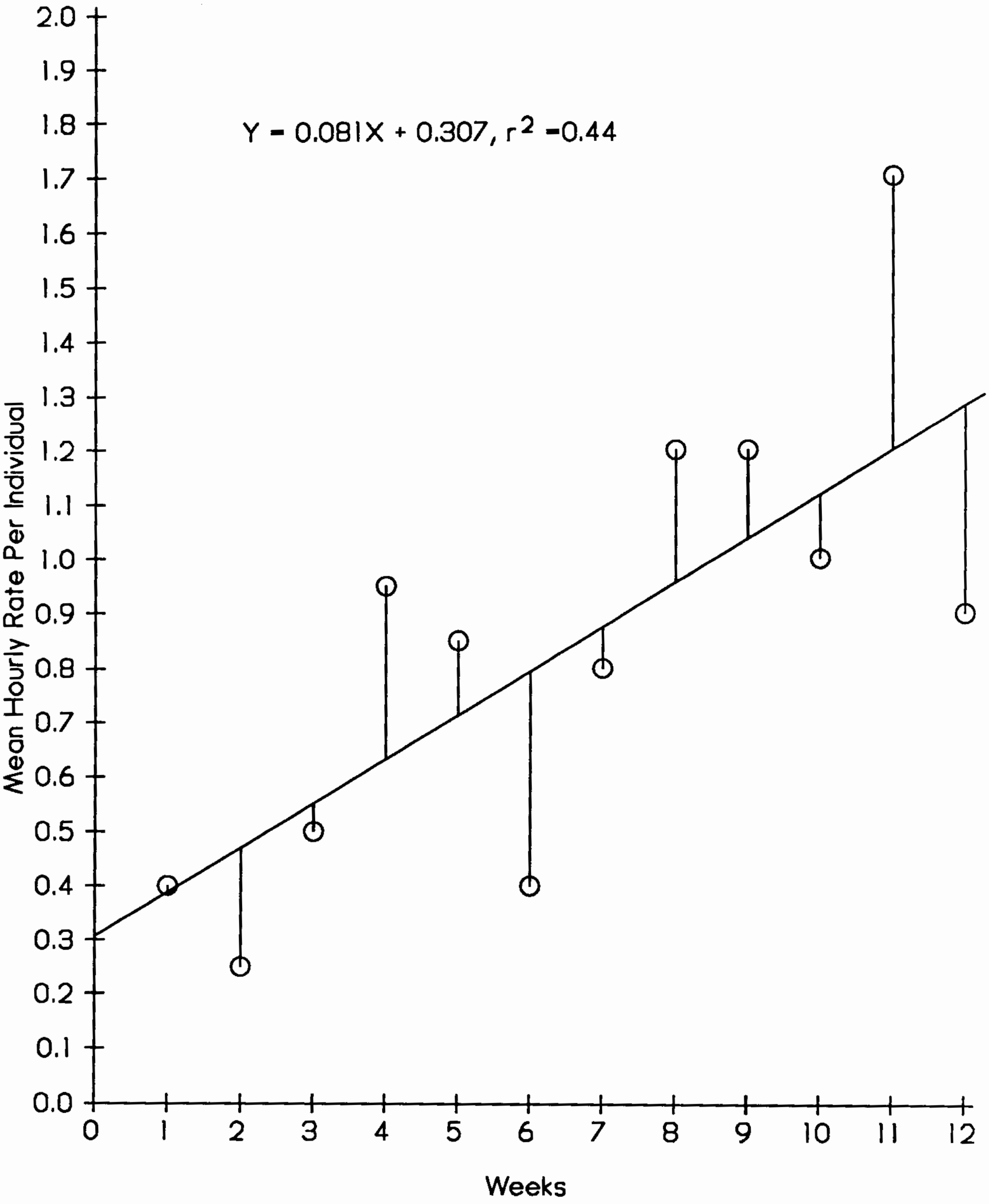


Figure 10. Mean hourly rate per individual that juveniles initiated grooming during Weeks 1-12.

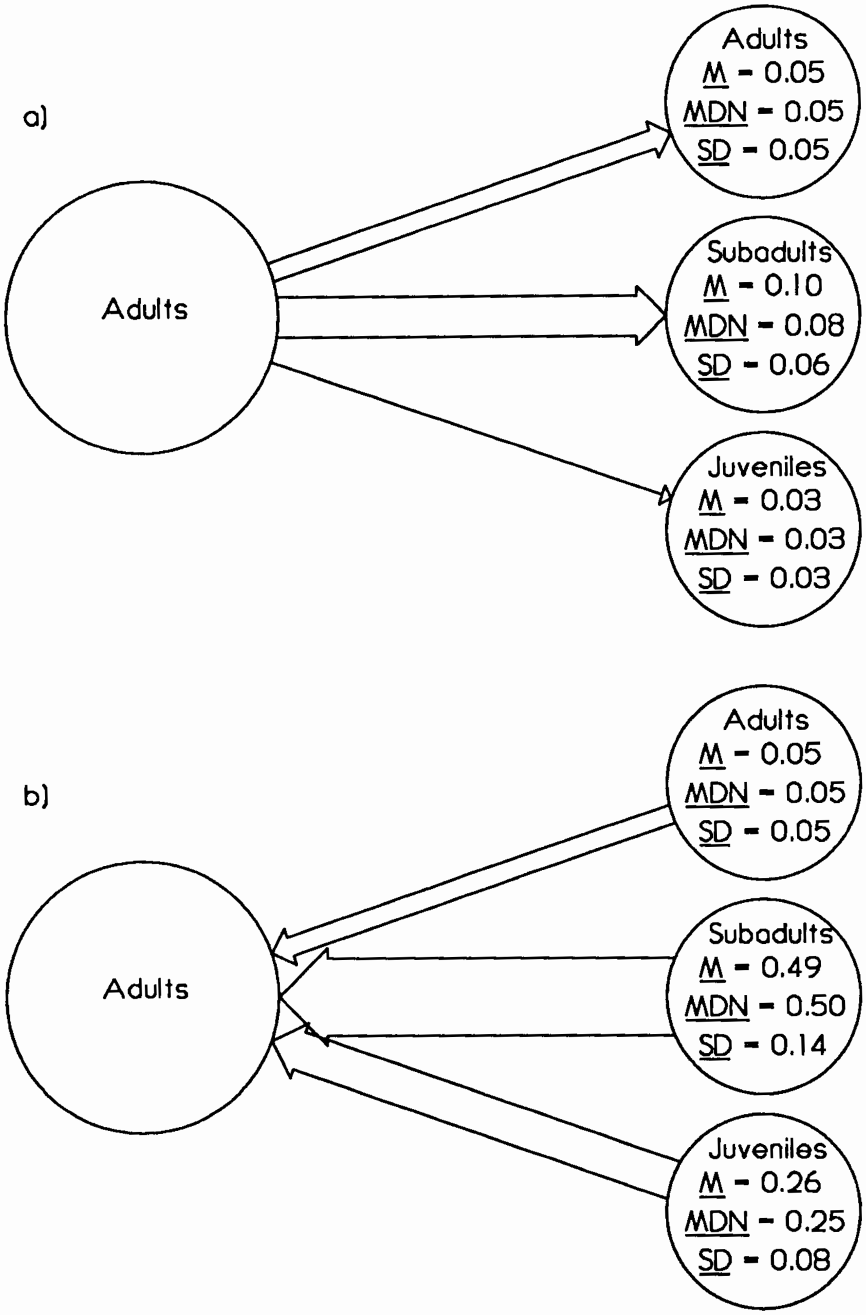


Figure 11. Mean hourly rates per individual that adults a) groomed and b) received grooming from animals of each age-class during Phase 1.

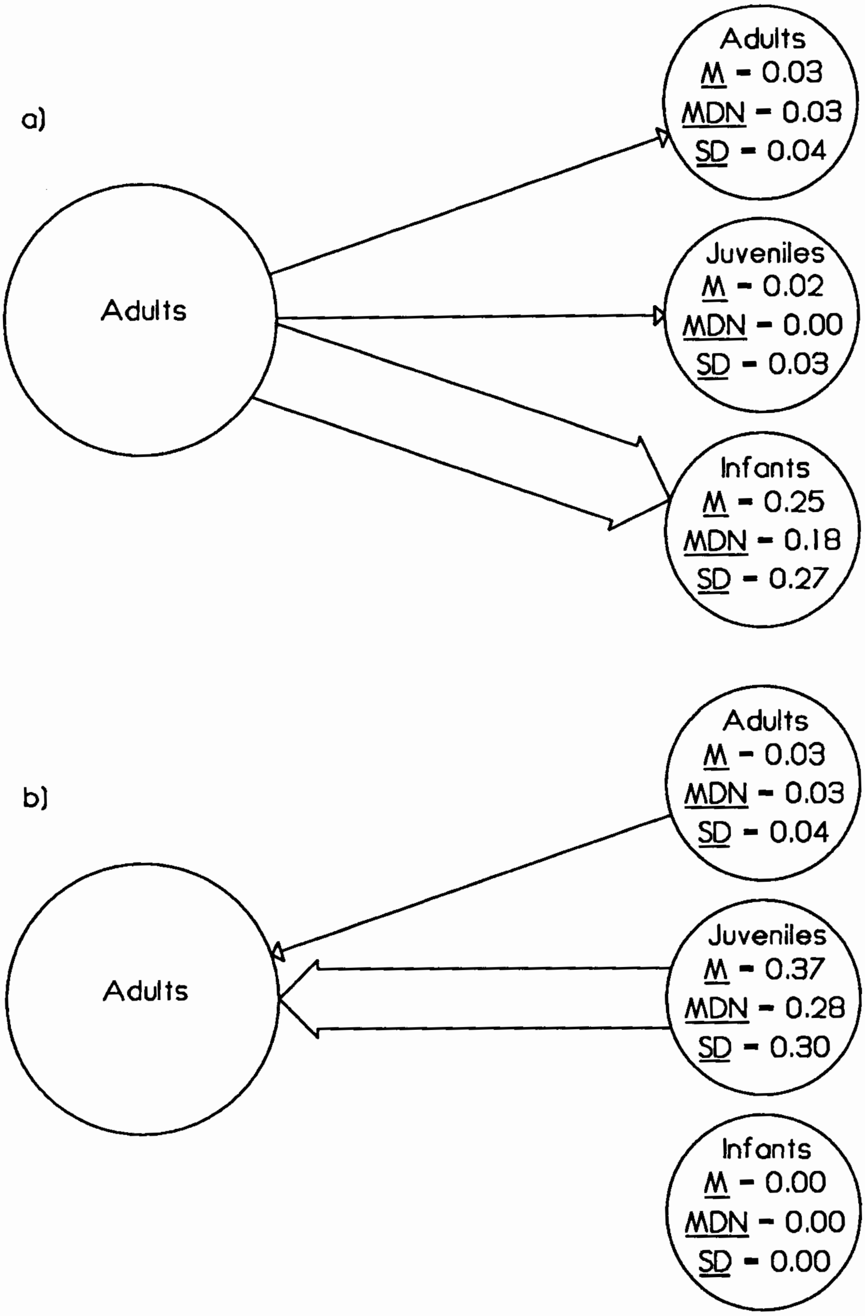


Figure 12. Mean hourly rates per individual that adults a) groomed and b) received grooming from animals of each age-class during Phase 2.

TABLE VI

OCCURRENCE OF HUDDLES OF VARYING COMPOSITIONS DURING PHASE I

Composition of Huddle	% of total observed huddles
A♂ A♀ S J J	0.9
A♂ A♀ S J	0.9
A♂ A♀ J J	2.8
A♂ J	0.9
A♀ S S S J J	2.8
A♀ S S J J	11.9
A♀ S S J	4.6
A♀ S J J	17.4
A♀ S J	8.3
A♀ S	1.8
A♀ J J	19.3
A♀ J	16.5
S S S J J	0.9
S J J	0.9
S J	2.8
J J	6.4

TABLE VII

OCCURRENCE OF HUDDLES OF VARYING COMPOSITIONS DURING PHASE 2

Composition of Huddle	% of total observed huddles	% of specific huddles with at least 1 infant present	
		on an adult	on a juvenile
A♂ A♀ J J	12.1	100.0	20.0
A♂ A♀ J	7.3	100.0	22.2
A♂ A♀	41.1	100.0	----
A♂ J J	1.6	100.0	0.0
A♂ J	3.2	100.0	0.0
A♀ J J	10.5	61.5	23.1
A♀ J	10.5	46.2	46.2
J J	13.7	----	11.8

percent of huddles containing both a juvenile and an adult (*M* = 84.9, *MDN* = 86.5, *SD* = 10.6) was significantly greater than the mean percent of huddles containing a juvenile and a subadult (*M* = 52.6, *MDN* = 57.8, *SD* = 14.4) or a second juvenile (*M* = 61.9, *MDN* = 62.3, *SD* = 20.4) (Wilcoxon, $p \leq .05$ for both pairwise comparisons). Although the mean percent of huddles containing both juveniles was greater than that for huddles containing a juvenile and a subadult, this difference was not significant. Thus, a juvenile was more likely to be found huddling with an adult rather than a subadult or juvenile. Furthermore, a juvenile was more likely to be found huddling with the adult female than the adult male; Figure 13 shows that the mean percent of huddles containing the adult female was significantly greater than that for the adult male (Wilcoxon, $T(6) = 0$, $p \leq .05$).

During Phase 2, however, there was no significant difference between the mean percent of huddles containing a juvenile and an adult (*M* = 41.1, *MDN* = 39.0, *SD* = 18.9) as compared to both juveniles (*M* = 36.3, *MDN* = 35.9, *SD* = 13.8). Thus, during Phase 2, a given juvenile was equally as likely to be huddled with another juvenile as an adult. In addition, the juveniles demonstrated a gradual decline in huddling with time ($r^2 = 0.11$) (see Figure 14). This trend was not statistically significant.

Adults also displayed preferences in huddling partners. These preferences were significant during Phase 1 (Friedman, $\chi^2_r(2) = 12.0$, $p \leq .005$). The mean percent of huddles containing both an adult and a juvenile (*M* = 84.9, *MDN* = 86.5, *SD* = 10.6) was significantly greater than the mean percent of huddles containing an adult and a subadult (*M* = 48.3, *MDN* = 45.6, *SD* = 15.5) or a second adult (*M* = 5.3, *MDN* = 0.0, *SD* = 10.7) (Wilcoxon, $p \leq .05$ for both pairwise comparisons). In addition, the mean percent of huddles containing both

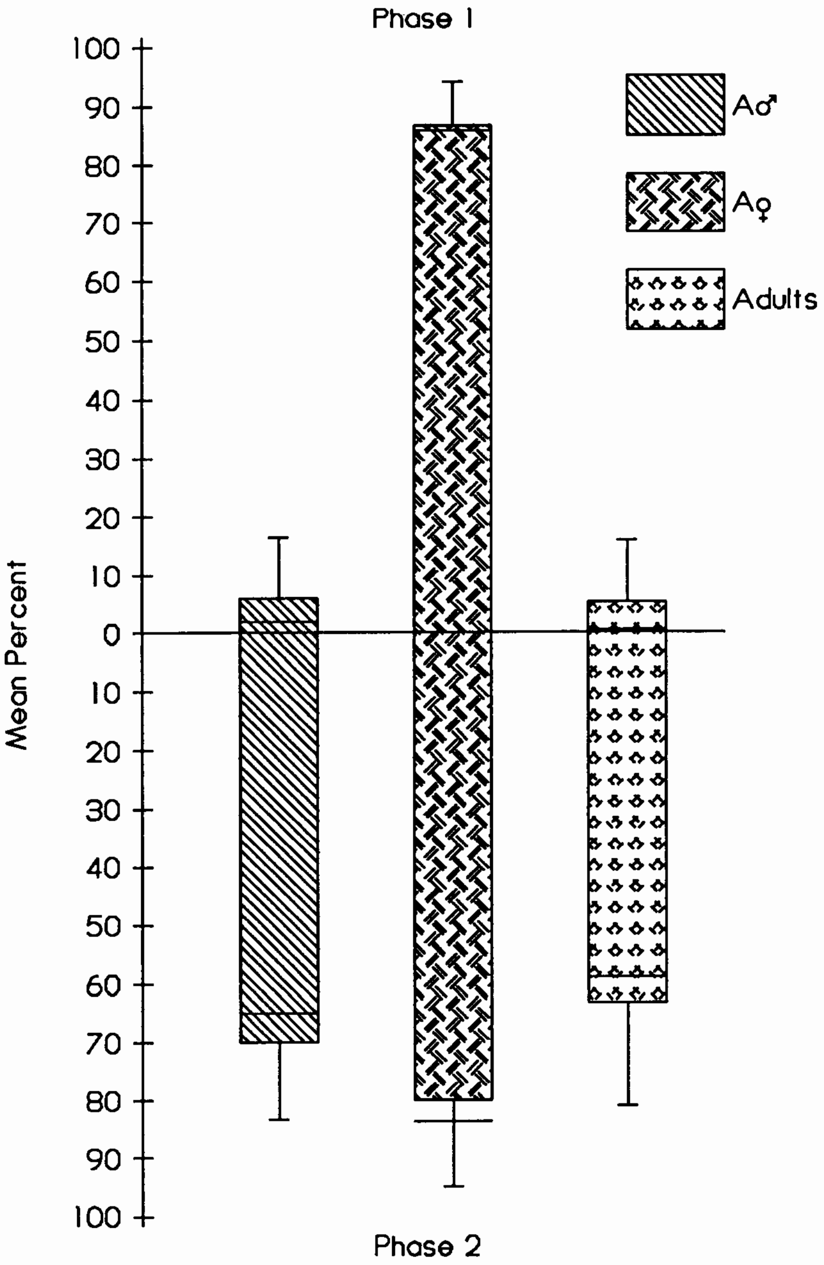


Figure 13. Mean (+ SD) percent of observed huddles that contained the adult male, the adult female, and both the adult male and female during Phases 1 and 2. (Contrasting horizontal bar indicates the median value.)

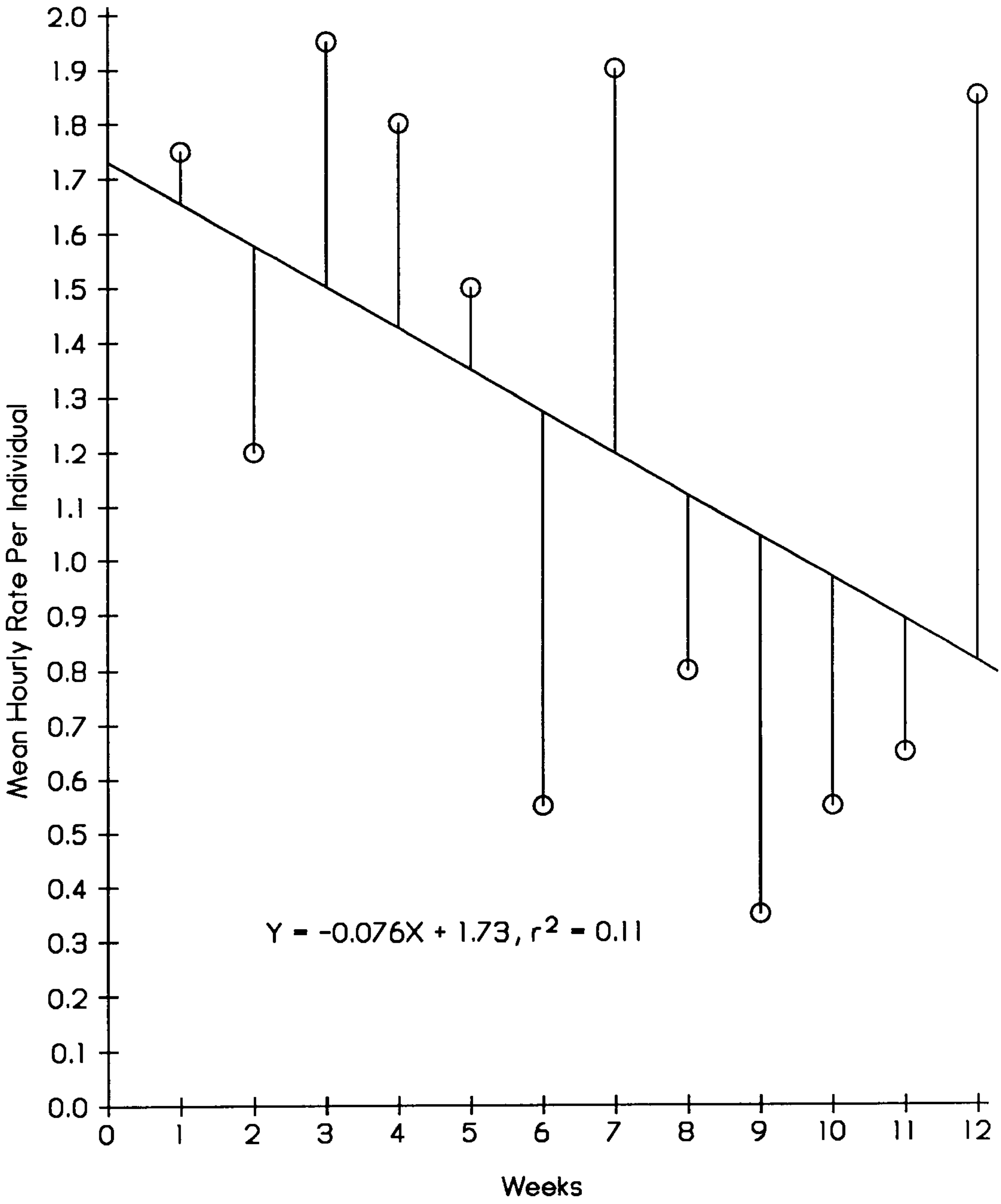


Figure 14. Mean hourly rate per individual that juveniles engaged in huddling during Weeks 1-12.

an adult and a subadult was significantly greater than that containing both adults (Wilcoxon, $p \leq .05$). Thus, an adult was most likely to be found huddling with a juvenile and least likely to be found huddling with another adult. During Phase 2, however, the mean percent of huddles containing an adult and a juvenile ($M = 43.5$, $MDN = 37.7$, $SD = 19.5$) was much less than that for huddles containing both adults ($M = 63.3$, $MDN = 58.9$, $SD = 17.7$); due to the large variability, however, this difference was not significant.

The adult male and female exhibited several interesting changes in huddling behavior from Phase 1 to Phase 2. As Figure 13 shows, the mean percent of huddles containing the adult male was significantly greater in Phase 2 as compared with Phase 1 (Wilcoxon, $T(6) = 0$, $p \leq .05$), and, contrary to Phase 1, there was no significant difference between the mean percent of huddles containing the adult male as compared with the adult female.

Furthermore, the mean percent of huddles containing both the adult male and female was significantly greater during Phase 2 as compared with Phase 1 (Wilcoxon, $T(6) = 0$, $p \leq .05$) (see Figure 13). Interestingly, among those huddles containing only the adult male and female, there was virtually no difference in the mean percent of huddles initiated by the adult male ($M = 49.1$, $MDN = 42.5$, $SD = 32.0$) as compared with the adult female ($M = 50.9$, $MDN = 57.5$, $SD = 32.0$). Also worthy of mention is the fact that the observer never noted the adult male and female huddled together, during Phase 2, without at least 1 infant present on either of the pair (see Table VII).

INFANT CARETAKING

Table VIII displays the food transfer activity during Phases 1 and 2 of the study. Virtually all of the food transfers observed during Phase 1 consisted of the juveniles taking food from others. There was a significant difference with respect to the age-classes from which juveniles took food (Friedman, $\chi^2_r(2) = 12.0$, $\underline{p} \leq .05$). Juveniles took food from subadults at a higher rate than from any other age-class while they took food from juveniles at a lower rate than from any other age-class (Wilcoxon, $\underline{p} \leq .05$ for all pairwise comparisons). Attempts made by the juveniles to take food from the adult female were extremely rare, and none of these attempts were successful. The adult female was the only other animal that made frequent attempts to take food from others, however, only a single attempt was successful.

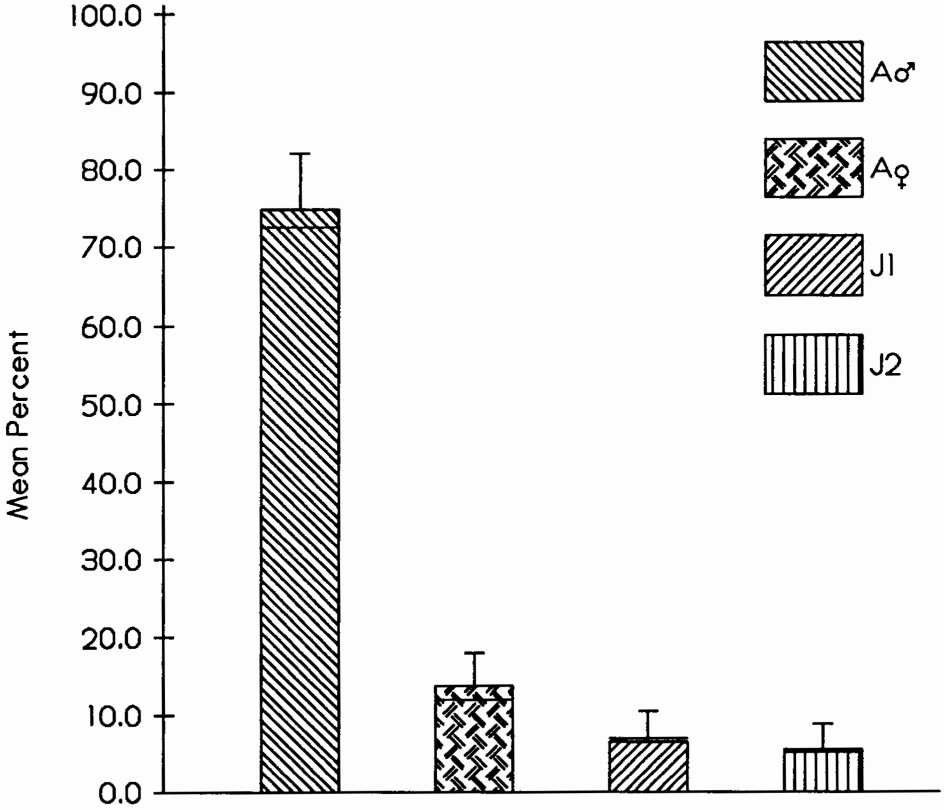
Food transfer was all but nonexistent during Phase 2. Attempts by any animal to take food from others were rare, and few attempts were successful. The observer first noted the infants eating solid food when they were 38 days old, and they acquired the food by taking it from the food dish while being carried by the adult male.

Figure 15 presents each individual's mean percent of the group's total infant carrying score. The contribution to infant carrying across individuals differed greatly (Kruskal-Wallis, $\underline{H}(3) = 18.9$, $\underline{p} \leq .001$). The adult male had a greater infant carrying score than any other individual (Mann-Whitney, $\underline{p} \leq .01$ for all pairwise comparisons). The adult female had a significantly greater infant carrying score than both J1 and J2 (Mann-Whitney, $\underline{p} \leq .05$ and $\underline{p} \leq .01$, respectively). Furthermore, the mean percent of the adult female's infant carrying score attributed to nursing was 65.4% ($\underline{MDN} = 61.4$, $\underline{SD} = 19.4$) while

TABLE VIII

MEAN HOURLY RATE PER INDIVIDUAL OF FOOD TRANSFER FOR ANIMALS OF EACH AGE-CLASS: PHASES 1 AND 2

	Recipient			
Tender	Adult	Subadult	Juvenile	Infant
	Phase 1			
Adult				
M	0.00	0.03	0.23	----
MDN	0.00	0.02	0.20	----
SD	0.00	0.04	0.10	----
Subadult				
M	0.04	0.01	0.50	----
MDN	0.00	0.00	0.57	----
SD	0.05	0.01	0.16	----
Juvenile				
M	0.00	0.01	0.01	----
MDN	0.00	0.00	0.00	----
SD	0.00	0.02	0.02	----
	Phase 2			
Adult				
M	0.01	----	0.03	0.04
MDN	0.00	----	0.03	0.00
SD	0.02	----	0.04	0.10
Juvenile				
M	0.03	----	0.04	0.02
MDN	0.03	----	0.03	0.00
SD	0.03	----	0.05	0.04
Infant				
M	0.01	----	0.00	0.00
MDN	0.00	----	0.00	0.00
SD	0.02	----	0.00	0.00



<u>Figure 15</u>. Each individual's mean (+ SD) percent of the group's total infant carrying score during Phase 2. (Contrasting horizontal bar indicates the median value.)

that attributed to strictly carrying was 34.6% (MDN = 38.7, SD = 19.4). This difference, however, was not significant. Juveniles were first observed carrying infants when the infants were only 5 days old; there was essentially no difference in the infant carrying scores of J1 and J2.

Infants were first observed to locomote independently when 30 days old. The adult female was far more tolerant of the infant's excursions than the adult male. When an infant ventured off on its own, the adult male was observed to retrieve it almost immediately whether the infant cried out or not. Although increasing in independence daily, the infants were still being carried most of the time at 6 weeks of age.

INCIDENTAL OBSERVATIONS

Two incidental observations are worthy of mention. First, aggressive interactions were extremely rare in this group. However, there were several occasions where the adult male and Sc, one of the subadult males, were involved in chasing and tongue-flicking bouts. During these interactions, one of the individuals, usually the adult male, began chasing the other. After a few chases around the enclosure, the individuals sat stationary on opposite sides of the enclosure, faced each other, and began flicking their tongues rhythmically.

Finally, both juveniles and the adult male were observed to nurse from the adult female on four occasions 2 days prior to parturition. Such behavior may, therefore, be indicative of imminent parturition.

DISCUSSION

This study gathered both general and specific information about the behavior of a captive family group of Saguinus midas midas. The study focused primarily upon the socialization of juvenile tamarins with regard to those behaviors known to be associated with reproductive success among members of the Callitrichidae. It was hypothesized that juveniles and adults participate in scent marking, mounting, thrusting, huddling, allogrooming, food transferring, and infant carrying. This hypothesis was supported. It was further hypothesized that both juveniles and adults participate in mounting, thrusting, huddling, and allogrooming more with adults than animals of any other age-class. The hypothesis concerning juveniles was supported while that pertaining to adults was not. Finally, it was also hypothesized that the adult female displays the highest rate of scent marking among members of the family group. This hypothesis was also supported.

BEHAVIOR

Activity Budgets and Social Grouping

With respect to the general behavior of these animals, the data clearly show that the tamarins in this family group spent their time engaged in a wide variety of activities ranging from social interactions to solitary behaviors. Yet, the group appeared to be fairly homogeneous with respect to behavior between age-classes. Adults, subadults, and juveniles engaged in virtually all of the recorded behaviors, and the amount of time spent in each behavior did not vary considerably between the age-classes.

The greatest difference observed in the activity budgets of the three age-classes occurred with respect to play behavior. Although individuals of all ages participated in this behavior, juveniles spent more time than both adults and subadults engaged in this behavior. This is not surprising. Play behavior has been proposed as an important means of socialization among young primates (Loizos, 1967; Poirer & Smith, 1974).

A surprising finding in light of the fact that these tamarins engage in a fair amount of social behavior is that a social grouping comprised of a single individual was observed more often than any other group size during Phase 1. (About 25% of all recorded social groups during Phase 1 contained a single individual.)

Because adult and subadult males were observed as solitary individuals more often than any other animals, one might suggest that this may, potentially, be important with respect to a territorial defense role among tamarins. While free-ranging members of both sexes participate actively in territorial behaviors, there is a tendency for male callitrichids to be more involved in physical encounters with neighboring groups or outsiders (Fedigan, 1982). This suggests that the time that males spent as solitary individuals away from the remainder of the group, in this study, may be indicative of a vigilance role. Obviously, field studies are needed to support this conjecture.

A less surprising finding with respect to social grouping patterns involved the juveniles. While adults were most likely to be observed as solitary individuals, juveniles were least likely to be found as such. While the juveniles were no longer at an age where they required the presence of others for locomotion or nourishment, they were at an age where socialization was important to their normal development. Socialization cannot take place in social groups comprised of a single individual, thus it seems logical that the juveniles spent very little time as solitary animals.

Scent Marking

Scent marking, although not a direct social interaction, is believed to be important in maintaining both the territory and breeding structure of a callitrichid group (Epple & Katz, 1984; Fedigan, 1982). Marmosets and tamarins are highly territorial and actively defend their territories against neighboring groups. Both the adult male and female are active in territorial behaviors (Fedigan, 1982). In addition to this territorial role, researchers (e.g., French et al., 1984) have shown that the single breeding female within a group maintains her breeding status via physiological suppression of ovulation among all subordinate females in the group. This suppression is believed to occur at the endocrine level and is presumed to be mediated through scent marking. It is not surprising, then, to find that the adult female in this family group exhibits the highest rate of scent marking, for she presumably uses this behavior to fulfill two crucial roles. (Box [1975a], however, reports that Callithrix jacchus males scent mark more than females.) By the same token, it is not surprising that juveniles exhibit the lowest rate of scent marking; juveniles of this age within a family group may be too immature to successfully function in either a defensive or reproductive role.

The precipitous increase in scent marking exhibited by the adults during Phase 2 of the study is also worthy of discussion. Although both adults were active in scent marking during Phase 2, only the adult female displayed an increase in this behavior. It is conceivable that the adult male scent marks primarily as a means of defending the group's territory. If this is the case, the adult male may maintain a relatively constant rate of scent marking across time. In light of the roles that scent marking plays with respect to the adult female, discussed previously, one might suggest that the female's increase in scent marking may serve two roles. Such an increase may serve to either intensify the territorial boundaries of the group in order to protect the infants from potential intruders or strongly reinforce her status as the breeding female. In all likelihood, the increase in the adult female's scent marking probably serves both functions.

Sociosexual and Affiliative Behaviors

Although not highly active in scent marking, the juveniles within this family group participated quite frequently in affiliative and sociosexual behaviors known to be important with respect to pair-bonding (see e.g., Epple, 1975a). As hypothesized, the active socialization of juvenile tamarins into these behaviors appeared to occur primarily through interactions with the adults. During Phase 1, all observed sexual encounters involving a juvenile also involved an adult. In addition, juveniles directed most of their grooming toward adults and were most likely to be huddled with an adult than an animal from any other age-class. Another study has reported, however, that juvenile Saguinus fuscicollis spend most of their time engaged in social interactions with same-aged siblings (Cebul & Epple, 1984). Why, then, do these juveniles appear to engage in social interactions more with older family members than same-aged siblings? It is supposable that in order to engage in a rather specialized social interaction an individual must either be knowledgeable about the behavior or engage in the interaction with an individual that is. Because juveniles may be thought of as being born relatively naive with respect to these specific social interactions, it seems logical that they would engage in these behaviors more often with older animals that are already well versed in such interactions as compared with naive juveniles.

Further, it is interesting to note that, during Phase 2, juveniles were involved in affiliative behaviors with each other as much as they were involved in these behaviors with adults during Phase 2. This change in the pattern of social interaction may have been due to the fact that the subadults were no longer present to serve as partners in social interactions. In addition, it may have been due to the fact that the adults were consumed with infant caretaking responsibilities and did not have time to be "bothered" by the juveniles. (There were many instances where juveniles approached adults that were carrying infants only to be threatened away by the adults.) The change in behavior may have also been due to a natural maturation process; the juveniles may have been quite proficient in these affiliative behaviors by the end of Phase 1 and simply sought to engage in these behaviors with each other during Phase 2. In all probability, the changes observed in affiliative social interactions among juveniles from Phase 1 to Phase 2 were precipitated, in part, by each of these possible causes.

In addition to active participation in sociosexual and affiliative behaviors, a second means of socialization of juveniles into these behaviors may occur passively. Juveniles may further learn about these social interactions important in pair-bonding by observing a pair-bonded male and female (i.e., via observational learning). In other words, the adult male and female may serve as passive role models for the juveniles. Assuming that this is a possible means of socialization, the relationship between the adult male and female in this family group becomes of great interest.

Surprisingly, during Phase 1 of the study the adult male was fairly "aloof" with respect to all members of the group including the adult female; the adult male spent more time alone than any other animal. As suggested previously, this could be related to a vigilance role which might require that the adult male remain at the fringes of the group. Whatever the reason, the fact remains that the adult male and female spent as much time in different social groups as the same social group. Furthermore, contrary to what was hypothesized, the adults rarely groomed each other or huddled together. And, finally, not a single sexual encounter was observed between the adult mated pair.

Considering that marmosets and tamarins are believed to be pair-bonded, this lack of association between the adult male and female seemed surprising at first. Several studies have shown, however, that sexual and affiliative interactions between an adult mated pair decrease rather rapidly with the duration of pairing (Evans & Poole, 1984; Ruiz, 1990; Kleiman, 1977; Savage, Ziegler, & Snowdon, 1988). When first paired, frequent sexual and affiliative interactions appear to be important in the formation of the pair-bond. After an adult male and female are paired for several weeks, though, such interactions diminish. At that point, sexual behavior is believed to play more of a reproductive rather than a bonding role. When one considers that this male and female have been paired for approximately 4 years, their apparent lack of close association does not seem quite so unusual.

This relative lack of association was not, albeit, permanent. Recall that, during Phase 2, profound changes in the association of the adult male and female occurred.

During Phase 2, the mated pair began spending more time in the same social group and more time huddling together than observed during Phase 1.

It is plausible that this increase in huddling and proximity was a direct result of the birth of the infants. One might argue, nonetheless, that these changes in behavior were due to the separation of the subadults rather than the birth of the infants. Although one cannot say that the separation of the subadults did not contribute to this increase in affiliation between the adults, it seems likely that the birth was the primary catalyst for these changes in behavior. The major evidence in support of this derives from observations of huddling; not once did the observer note the adult male and female huddled together without at least one infant present on either of the pair.

What may be the significance of this change in affiliative behaviors among the mated pair? One might envision the birth of the infants as an event which precipitates an opportunity for reinforcement of the existing pair-bond. Due to the great energy demands upon the postpartum female, primarily a consequence of lactation and infant carrying, paternal help in the rearing of infants is essential for infant survival (see Goldizen, 1988, for discussion). By spending time engaging in behaviors which reinforce the pair-bond, the adults may be "reassuring" each other that they will combine their efforts in helping to care for their offspring. Such joint cooperation between the adult male and female would greatly enhance the survival of the infants. In addition, such reassurance and reinforcement of the pair-bond at this time may also help to secure future copulations between the mated pair. (Price [1990] has also suggested that breeding male tamarins may use infant carrying as part of a courtship strategy and a means of securing copulations.) Thus, the relationship between the birth of infants and reinforcement of the pair-bond seems a natural one.

Infant Caretaking

The participation of juveniles in scent marking and certain behaviors important to pair-bond formation has been discussed. Let us now turn our attention to infant caretaking behaviors.

Several studies have shown that young callitrichids need experience in infant caretaking with their younger siblings in order to be competent parents for their own future offspring (Epple, 1975b; Hoage, 1978; Kirkwood et al., 1983; Tardif et al., 1984). One component of infant caretaking is the transfer of food objects between individuals. In this family group, juveniles took food from subadults more often than from any other age-class. This large contribution to food transfer displayed by older siblings parallels similar findings in *Saguinus oedipus* (Feistner & Price, 1990). However, this trend contradicts findings reported by Heymann (1990) who reported that juvenile *Saguinus mystax* take food most often from the adult male. Transfer of food objects among juveniles was rarely observed, and this is also in agreement with trends noted by Cebul and Epple (1984) in *Saguinus fuscicollis* and Feistner and Price (1990) in *Saguinus oedipus*. Thus, gaining experience in provisioning food appears to occur across age-classes, from older siblings to younger siblings.

Another interesting observation regarding food transfer among this family group of *Saguinus midas midas* is contrary to reports of other tamarins. The juvenile tamarins in this group, unlike the captive *Saguinus fuscicollis* described by Cebul and Epple (1984), made few attempts to take food from the adult female, and none of these observed attempts were successful. Recognizing that pair-bonded adult female marmosets and tamarins are either pregnant, lactating, or both for much of their adult lives, their energy demands must necessitate that they consume all of the food that they can possibly acquire. It seems reasonable, then, that the adult female was "reluctant" to give up food to the juveniles when other group members were present to share food with them.

The second component of infant caretaking assessed in this study was infant carrying. This is an extremely important component of caretaking, for young callitrichids are constantly carried by others for approximately the first 30 days of life (Cebul & Epple, 1984). As hypothesized, all individuals in this family group contributed to infant carrying. The participation of all group members in infant carrying has also been reported in Saguinus fuscicollis (Epple, 1975b; Vogt, Carlson, & Menzel, 1978), Saguinus mystax (Heymann, 1990), Leontopithecus rosalia (Hoage, 1978), and Callithrix jacchus (Box, 1975b, 1977). Contrary to another report of Saguinus midas (Christen, 1974), infants in this family group were not carried exclusively by their mother during their first few days of life. In fact, juveniles were observed carrying infants when they were merely 5 days old.

Although all individuals participated in infant carrying, the adult male performed the largest share of this duty. This trend has also been observed in groups of Saguinus mystax (Heymann, 1990), Saguinus fuscicollis (Cebul & Epple, 1984; Epple, 1975; Vogt et al., 1978), Saguinus midas (Christen, 1974), Leontopithecus rosalia (Hoage, 1978), and Callithrix jacchus (Box, 1975b).

While the adult male performed most of the infant carrying, the contributions of the adult female and juveniles were not negligible. Goldizen (1987b) calculated that in order to meet the energy demands placed upon a lactating adult female Saguinus fuscicollis in the wild, the adult female must limit her infant carrying to approximately 20% of the time for a twin litter. Interestingly, the adult female Saguinus midas midas in the present study group was observed to amass an average of 13.8% of the group's total infant carrying score, a figure similar to the 20% calculated by Goldizen.

Although the juveniles did not perform a large part of the infant carrying relative to the adult male, their combined contribution almost equalled that of the adult female. Clearly, the juveniles gained valuable experience in infant carrying while also aiding the adult male and female.

SOCIALIZATION

The main focus of this study was the socialization of juvenile tamarins with regard to behaviors relevant to reproductive success among the Callitrichidae. Juveniles are born relatively naive with respect to these specialized behaviors. Nevertheless, successful reproduction among these primates requires that individuals somehow learn and become proficient in the proper execution of these behaviors.

Participation and Observation

As previously mentioned, socialization may occur through two processes: active participation and/or passive observation. The data presented here show that juvenile tamarins engage in scent marking, mounting, thrusting, allogrooming, huddling, food transferring, and infant carrying. Active participation, therefore, seems to play a significant role in familiarizing young juveniles with each of these behaviors. Furthermore, because many of the social interactions involving juveniles in this study also involved older individuals, most often adults, it appears that the adult mated pair, and to a lesser degree older siblings, contribute significantly to the active socialization of young juveniles with respect to behaviors important in successful reproduction. It seems logical that juveniles would best learn the appropriate context and sequence of these behaviors via interactions with adults (given that the adults are already skilled in such social interactions).

Having addressed both means of socialization, participation and observation, one may also suggest that participation is the most stable form of socialization within this family group. This is especially true with respect to sociosexual and affiliative behaviors. While the adult male and female may be in close association only a portion of the time, and, hence, serve as role models only a portion of the time, juveniles have the opportunity to interact with other individuals on a daily basis.

Development of Behavior

Because socialization is believed to be a process through which young individuals learn about behavior (Fedigan, 1982), one would expect to see the development of allogrooming, huddling, scent marking, mounting, thrusting, food transferring, and infant carrying over time among these juvenile tamarins. Allogrooming and huddling, both affiliative behaviors believed to be important in pair-bonding, displayed differing trends over the course of this study. While the juveniles engaged in both of these behaviors from the onset of Phase 1, they showed an increase in the initiation of grooming and a decrease in huddling across time. Allogrooming is a rather specialized behavior, and it seems reasonable to propose that individuals would initiate grooming more as they gradually acquired the skills through practice. Huddling, on the other hand, appears to require relatively less skill, and, hence, less practice. Additionally, huddling may be supposed to provide "security" for young individuals. As juveniles mature and become more independent, their need for security assumably decreases. This decreasing need for security may, undoubtedly, manifest itself in several ways including a decrease in huddling.

Although the trends in allogrooming and huddling differed considerably, both behaviors appear to be important early in the life of these juvenile tamarins. (Recall that these behaviors were already present at the onset of this study.) Scent marking and sexual behavior, however, seem to be important somewhat later in the life of these tamarins. This study chronicled the emergence of these behaviors. Because of the relatively late onset and nature of scent marking, mounting, and thrusting, one might suggest that they are triggered by a hormonal process. Although this is most likely true, the contribution of socialization with respect to the development of these behaviors should not be altogether dismissed.

Finally, the emanation of infant caretaking by the juveniles was also documented in this study. The juveniles began carrying their infant siblings when merely 5 days old. Thus, practice in infant carrying began almost immediately, given the opportunity, among these juveniles. Little food transferring from juveniles to infants, however, was observed during this study. This was presumably due to the fact that the infants began eating solid food during only the last few days of Phase 2. As their consumption of solid food increased, the occurrence of food provisioning between juveniles and infants most likely increased as well.

Consequently, the data presented here support the notion that time spent in the natal group is beneficial, if not necessary, for the adequate development of behaviors important in successful reproduction among callitrichids. Both active participation and passive observation likely play a role in the socialization of young tamarins. Only future experimentation can determine the relative contribution of each of these processes.

SUMMARY AND RECOMMENDATIONS

In summary, this study has demonstrated that adult, subadult, and juvenile members of a rarely studied species, Saguinus midas midas, participate in a wide variety of behaviors which appear to be important to animals of all age-classes. Furthermore, this study has also shown that the behavior of this rarely studied species is similar to that of other callitrichids. This study has also demonstrated that even individuals of a highly social species spend time alone when given the opportunity. (The fact that this group had access to several enclosures is unusual, and other zoos may want to consider utilizing such enclosures.) Additionally, this study has suggested that the birth of infants may afford the mated pair an opportunity to reinforce the existing pair-bond.

The main focus of this study, nonetheless, was the socialization of juveniles into behaviors relevant to reproductive success among the Callitrichidae. The data reported here support the contention that the socialization process somehow fosters, among young primates, the development of behaviors crucial to the life of a species. Moreover, this study has suggested that active participation may be the most stable form of socialization within this family group and that interactions with adults play a major role. Data from the present study coupled with that presented by others (Epple & Katz, 1980; Tardif et al., 1986) lead the author to make two suggestions. The first is that the ability to competently engage in these behaviors may be a prerequisite for pair-bond formation just as pair-bond formation appears to be a prerequisite for reproduction and infant caretaking experience appears to be a prerequisite for infant survival. Secondly, although young tamarins participate in these rather specialized behaviors, 6-month old juveniles are not yet adequately socialized in these behaviors and should not be removed from their natal group. The ability of such young juveniles to form a pair-bond and reproduce successfully may be dependent upon pairing with an adult conspecific that is adequately socialized in such behaviors.

In light of the great variability both among individuals and species of the Callitrichidae, more work is needed to delineate just how young marmosets and tamarins learn these behaviors important in pair-bond formation and infant caretaking. More work is also needed in order to determine at what age young callitrichids can be removed from their natal groups and expected to form adequate pair-bonds with other young conspecifics. Future experimentation and manipulation with similar species, where possible, would best serve to clarify these issues. Information such as this would be useful to zoos as well as other institutions and may enhance the success of captive breeding programs for all species of the Callitrichidae.

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