Social and Physical Maturation in Captive Lion Tamarins, *Leontopithecus rosalia rosalia* (Primates: Callitrichidae)

R. J. HOAGE

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ABSTRACT

Hoage, R.J. Social and Physical Maturation in Captive Lion Tamarins, *Leontopithecus rosalia rosalia* (Primates: Callitrichidae). *Smithsonian Contributions to Zoology*, number 354, 56 pages, 24 figures, 12 tables, 1982.—Among nonhuman primates, New World marmosets and tamarins (Callitrichidae) exhibit a unique combination of biological and behavioral traits, including monogamy, twinning, and infant caretaking by fathers and juveniles. Currently, little is known of the relationship between social and physical maturation in this species.

From February 1974 to January 1976, quantitative data were collected on the maturation of seven litters of lion tamarins (*Leontopithecus rosalia rosalia*) born at the National Zoological Park, Washington, D.C. Although a total of 22 tamarins were involved in the observations, the study focused on the ontogeny of eight males and six females in the first year of life.

Five maturational phases were distinguished: (1) Dependent Infant, (2) Advanced Infant, (3) Young Juvenile, (4) Advanced Juvenile, and (5) Young Subadult. Data were taken for six behavior categories: (1) infant carrying, (2) food sharing and stealing, (3) allogrooming, (4) scent marking and social sniffing, (5) sexual behavior, and (6) agonistic behavior. The data were examined for the first appearance of these behaviors and for the influence of three variables on maturing young: (1) parental reproduction, (2) the presence of older and younger siblings in the family group, and (3) the existence of same and opposite sex biases in social interactions within the family unit.

Infants were carried to 14 weeks after birth. Mothers were the principal carriers in the first three weeks, after which fathers dominated carrying; older siblings were involved to a limited extent.

Both food sharing and stealing were observed between individuals of both sexes and of various ages. Mothers in late pregnancy and immediately postpartum received food from older young as did both parents when carrying newborn infants. Older young and parents provided food for new infants, especially during weaning.

Same sex preferences occurred regularly in social interactions between young and other family members. Some opposite sex biases became evident in weeks 41–52, the Young Subadult Phase, when physical size and scent marking rates began to approach adult levels. Several 41 to 52-week-old males attempted to mount their mothers and one subadult female was repeatedly mounted by her father. However, intromission was never observed except between parental pairs.

Noninjurious agonistic encounters between (1) young subadults and same sex parents and (2) between subadults and siblings were seen to increase towards the end of the first year, yet older offspring are known to remain in relative harmony within the family unit up to 20 months of age. The extended residence of older young in the family group is believed to maximize the chances of survival and reproductive success of parents and infants, and also provides older offspring with the training necessary to maximize their own reproductive success once they have left the natal family unit. Supporting this conclusion was the finding that primiparous parents having the most experience interacting with younger siblings had the most success in rearing their own infants.

Contents

Social and Physical Maturation
in Captive Lion Tamarins,
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(Primates: Callitrichidae)

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Introduction

Since Harlow and others (Harlow and Harlow, 1965; Seay et al., 1964; Mitchell and Schroers, 1973) have demonstrated the importance of proper socialization in the development of normal sexual and parental behaviors in Old World macaques, the process of socialization has been described for a variety of Old World primates both in captivity and in the wild (Anthoney, 1968; Van Lawick-Goodall, 1968; Rowell et al., 1968; Chance and Jolly, 1970; Poirier, 1972). However, little attention has been given to the analysis of social and physical maturation in marmoset and tamarin monkeys (Callitrichidae), despite their importance in recent years to behavioral and biomedical research (Hearn, 1975; Wolfe et al., 1975). In contrast to numerous studies on African and Asian forms (Hall and DeVore, 1965; Kummer, 1968; Gartlan and Brain, 1968; Jay, 1965), there have been few studies on callitrichids that have outlined stages of development defined by both physical traits and the frequency of certain behaviors.

New World marmosets and tamarins exhibit a unique combination of behavioral and biological

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traits: (1) little or no sexual dimorphism (Lucas et al., 1937; Hershkovitz, 1949), (2) twinning (Hill, 1926, 1932; Wislocki, 1939), (3) monogamy with nuclear families composed of parents and offspring from successive births (Hampton et al., 1966; Epple, 1967; Dawson, 1977; Izawa, 1978; Box and Morris, 1980), (4) paternal and juvenile participation in infant rearing (Fitzgerald, 1935; Lucas et al., 1937; Christen, 1974; Epple, 1975b; Hoage, 1977), and (5) extended residence within family groups of nonbreeding older offspring who serve as parental assistants (Epple, 1970b, 1975a; Rothe, 1975; Kleiman, 1977b).

Focusing on captive groups of golden lion tamarins, *Leontopithecus rosalia rosalia*, this study investigates six specific classes of behavior that occur during maturation and that may prepare young for mating and infant rearing: (1) infant carrying; (2) food sharing and stealing; (3) allogrooming; (4) scent marking and social sniffing; (5) sexual behavior, and (6) agonistic behavior. A correlational summary between physical and behavioral traits is presented in Appendix I.

Where possible, I have compared results with equivalent data available on other members of the Callitrichidae (Appendix III). Final discussion centers on the unique configuration of callitrichid biological and behavioral traits relative to

other monogamous nonhuman primates and mammals. I conclude that the biological and behavioral adaptations of the marmosets and tamarins help maximize the chances of survival and reproductive success of three classes of individuals: parents, older offspring, and infants.

DESCRIPTION AND DISTRIBUTION OF THE CALLITRICHIDAE.—Together with the Cebidae (generally larger animals including five genera with prehensile tails), the small, squirrel-like marmosets and tamarins (weighing less than 800 g and measuring less than 60 cm long) make up the Platyrrhini or New World monkeys. Callitrichids are neotropical in distribution; the four genera (*Cebuella, Callithrix, Saguinus,* and *Leontopithecus*) range from Panama southward through the Amazon River basin to southeastern Brazil (Figure 1). They are diurnal, insectivorous, and frugivorous and forage in secondary growth and open forests in riverine habitats (Eisenberg, 1977). A possible fifth genus, the enigmatic Goeldi's monkey (*Callimico goeldii*), sometimes classified as a callitrichid (Napier and Napier, 1967), has been given its own familial status, Callimiconidae (Hershkovitz, 1970).

Among callitrichids curved, claw-like nails are
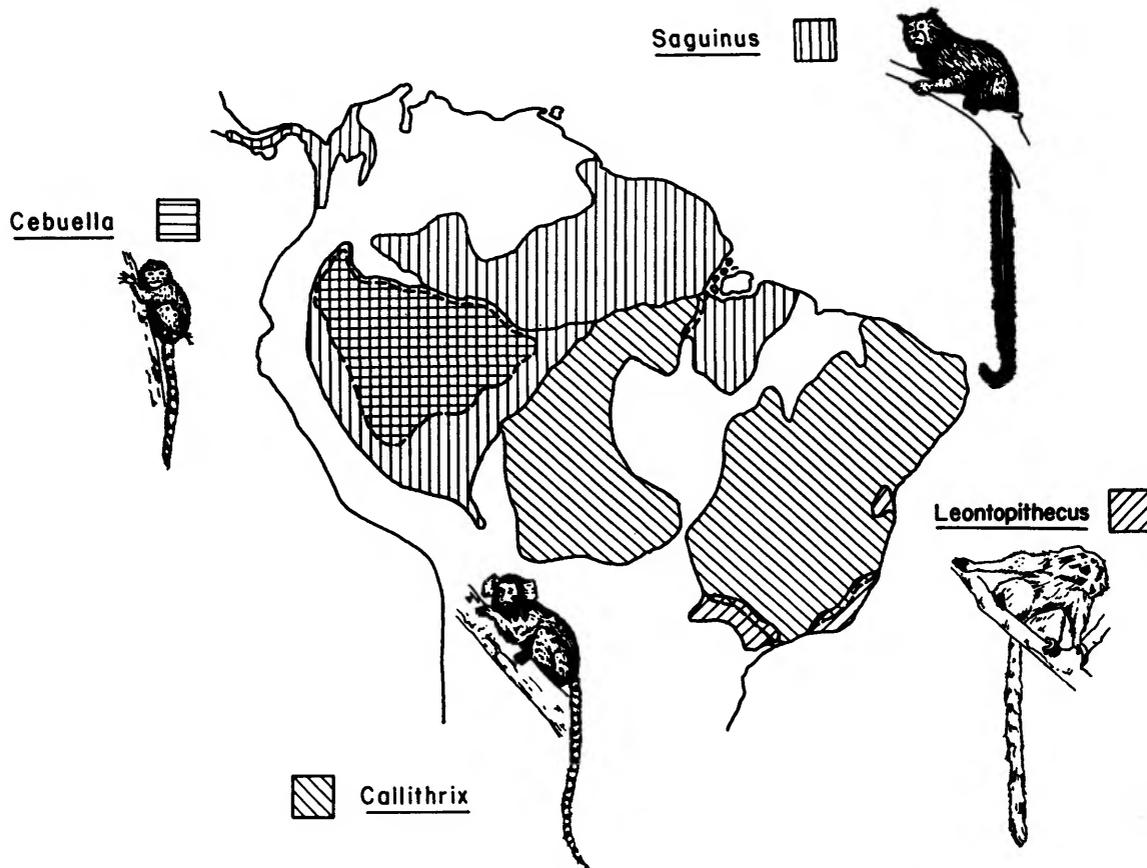
FIGURE 1.—Approximate pre-Columbian distribution of the four genera of the family Callitrichidae (after Hershkovitz, 1977:400); *Cebuella* (the pygmy marmoset, 1 species); *Callithrix* (the marmosets, 8 species); *Saguinus* (the tamarins, 22 species); and *Leontophithecus* (the lion tamarins, 1 species, 3 subspecies). (Drawing by S. Bruch.)

found on all digits except the big toes (halluces) which have flat nails. Scent glands on the sternum and in the circumgenital area are used in marking behavior. Tamarins in contradistinction to marmosets are "long tusked," having canines longer than incisors (Coimbra-Filho and Mittermeier, 1977).

THE GENUS *Leontopithecus.*—The genus comprises three subspecies: *L. rosalia rosalia, L. rosalia chrysopygus,* and *L. rosalia chrysomelas* (Hershkovitz, 1977:825) (Figure 2). Lion tamarins (500 to 800 g) are the largest callitrichids. Coimbra-Filho and Mittermeier (1973:55) and Coimbra-Filho (1977) report that in the wild these monkeys occupy the middle canopy of remnants of original Brazilian coastal forests and do not occupy secondary growth.

In recent decades, the habitats of all three forms have been greatly reduced by human encroachment. For the three lion tamarin subspecies combined, recent estimates list a total of only 600 to 1200 animals left in the wild (Coimbra-Filho and Mittermeier, 1973). Extinction in the wild is likely. Breeding and research centers have been established at the Tijuca Biological Bank, Rio de Janeiro (Magnanini et al., 1975), and at the National Zoological Park, Washington, D.C. (Kleiman, 1977b; Kleiman and Jones, 1977).

ACKNOWLEDGMENTS.—Predoctoral fellowships from the Smithsonian Institution and the Friends
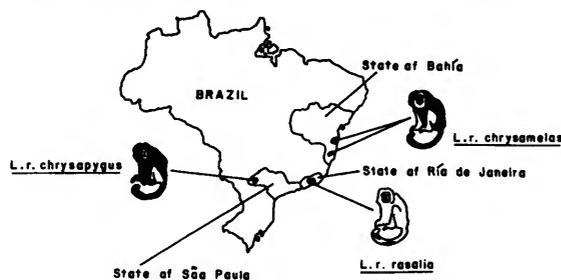
FIGURE 2.—Current distribution of the genus *Leontopithecus* within Brazil (after Coimbra-Filho and Mittermeier, 1972:19; Hershkovitz, 1977:808). The three subspecies are shown: *L. rosalia rosalia* (the golden lion tamarin), *L. rosalia chrysomelas* (the golden-headed lion tamarin), and *L. rosalia chrysopygus* (the golden-rumped lion tamarin). (Drawing by S. Bruch.)

Study Site and Methods

From February 1974 through January 1976, I studied the birth and maturation of seven litters of lion tamarins (*L. r. rosalia*) in four nuclear family groups at the National Zoological Park (NZP), Washington, D.C. Three successive litters were observed in one family, two in another, and one each in two others (Table 1). Each group consisted of an adult breeding pair and one to three sets of offspring. Among families in which

more than one litter was studied, family composition (except for the breeding pair) changed from one birth episode to the next as subadults were removed to form new groups. Within the four family groups, a total of 22 animals was involved in the observations. Observations were made irregularly on nine other animals in three additional groups. However, since none of these groups produced young that survived infancy during the period of data collection, they were not included in the analysis. I followed closely 14 young, 8 males and 6 females (referred to herein as the "focal tamarins"). Nine were studied through the first 52 weeks of life, two for the first 34 weeks, and three from weeks 41 through 52.

Two groups were on public display in the NZP Small Mammal House. Each family occupied a three-sectioned, 6.1 × 1.8 × 2.5 m, glass-fronted cage. All other groups were housed in an off-

exhibit research facility. This building included six rooms measuring 4.6 × 3.7 × 4.6 m for free-running animals and a seventh room of the same size with small holding cages. Each room had an adjoining outdoor porch area for use during warm weather. Families in both buildings were visually isolated from one another; but vocal and olfactory communication was possible between groups. Human observers were in full view of the animals at all times.

The enclosures in the Small Mammal House and the research facility contained diagonal and horizontal tree limbs, at least two nest boxes, and a wood chip substrate. The tamarins were fed twice a day with a diet of Science Diet Brand Marmoset Ration (Hill Packing Co., Topeka, Kansas), fruits, crickets, hairless mice, vegetables, and cottage cheese.

In the first four weeks after birth, quantitative

TABLE 1.—Family group composition for the 14 focal tamarins (italicized) included in seven litters born at the National Zoological Park between February 1974 and May 1975 (capital letters plus numerals designate groups with multiparous parents; subscripts indicate repeat litters for one parental pair; unsubscripted capital letters designate groups with primiparous parents; dashes indicate no individuals; individual lion tamarins are identified by sex, NZP accession number, and age in years)

Family group	Focal taramin litters	Father		Mother		Older sibling litters			
		NZP No.	Age	NZP No.	Age	NZP No.	Age	NZP No.	Age
A$_1$	♂M00863 ♂M00862[a]	♂33691	6.75	♀32721-B	6.00	♂M00715[b] ♂M00716[b]	0.75 0.75	– –	– –
A$_2$	♂M01006 ♀M01007	♂33691	7.33	♀32721-B	6.50	♂M00863	0.60	–	–
B$_1$	♀M00872	♂30571-A	>8.50	♀33692	>6.75	♂M00708[c] ♀M00709[b]	0.85 0.85	– –	– –
B$_2$	♂M00996 ♀M00997	♂30571-A	>9.00	♀33692	>7.25	♀M00872	0.45	–	–
B$_3$	♂M01186 ♀M01887 ♀M01888[d]	♂30571-A	>9.67	♀33692	>7.75	♀M00872 –	1.10 –	♂M00996 ♀M00997	0.67 0.67
C	♂M00885 ♀M00886	♂M00270	2.25	♀M00320	2.00	–	–	–	–
D	♂M01253	♂M00716	2.00	♀M00709	2.00	♂M00715	2.00	–	–

[a] Died day 3.
[b] Focal tamarins observed only in young subadulthood (weeks 41–52).
[c] Young tamarin that died 3 weeks after focal infant was born; ♂M00708 is not included as a focal animal.
[d] Stillborn.

data collection was limited to infant carrying behavior and the first appearance of behaviors in the five other categories selected for study.

Since infant carrying data were collected and analyzed in the earliest phase of this study, the methods used were somewhat different from the analytical procedures applied to the other behaviors. Specifically, infant carrying was observed beginning day 1 after birth, but unlike data collected for other behaviors, infant carrying time was recorded in minutes; summaries were made every seventh day. Carrying time was recorded up to week 12. After week 12, infants were infrequently carried.

From week 5 through week 52, quantitative data were collected for (1) food sharing and stealing, (2) allogrooming, (3) scent marking and social sniffing, (4) sexual behavior, and (5) agonistic behavior. For each of these five behavior classes, a 30-second interval was used to score both social interactions and individual behavior. A score of 1 was given to one or more occurrences of a specific behavior within each 30-second block of time. These scores are referred to as behavior rates and are adjusted to an average rate per hour of observation time.

Each of the 14 focal tamarins was observed an average of 45 minutes per week. A total of 273 hours of observation was accumulated. Data were recorded between 9:00 A.M. and 6:00 P.M. with an emphasis on afternoon hours. Data on physical growth (weights and body measurements) were also collected (Appendix II).

The data were examined for first appearance of specific behaviors and the influence of three variables on maturing young: (1) parental reproduction (mating, pregnancies, and birth of siblings); (2) older and young siblings present in the family group, and (3) same and opposite sex biases in social interactions within the family group. The examination of this last variable required an analytical format (Appendix V) that permitted the evaluation of preferential interactions between focal tamarins of each sex and other family members in three age/sex categories (Appendix VI).

Since data collection in weeks 1–4 was limited

to infant carrying and the initial appearance of behaviors, this study emphasizes data collected in weeks 5–16, 17–28, 29–40, and 41–52, which approximately correspond to maturational stages discernible by observations of physical, social, and sexual development. For nonhuman primates, the appearance of the first permanent teeth has been used as a marker for the end of infancy (Napier, 1972:66), while the appearance of the last permanent teeth has been considered a marker for the end of the juvenile stage (Simonds, 1974:93). The first permanent teeth in marmosets and tamarins usually erupt before week 16 after birth, while the last permanent teeth appear between weeks 40–48 (Johnston et al., 1970; Chase and Cooper, 1969; Immendorf, 1961). In the primate collection at the National Museum of Natural History (Smithsonian Institution, Washington, D. C.), there are four skulls with mandibles from L. r. rosalia subadults, ranging in age from 11 to 13.5 months (USNM 398200♂, USNM 534978♀, USNM 534283♀; and NZP 23671♂). The dentitions of these specimens show that the canines are fully erupted by approximately 13 months. Thus, the four 12-week phases outlined above roughly agree with the first and last of the general callitrichid dental stages. The four 12-week blocks, plus the first 4 weeks following birth were divided into the following phases: Dependent Infant (weeks 1–4), Advanced Infant (weeks 5–16), Young Juvenile (weeks 17–28), Advanced Juvenile (weeks 29–40), and Young Subadult (weeks 41–52). Green (1979:8), who also worked on lion tamarins at the National Zoological Park, has suggested the extension of this classification to describe Advanced Subadults (53–64 weeks of age) and Adults (65 weeks and over). Two reasons exist for accepting these categories: at 15 months (about 64 weeks) L. r. rosalia weights appear to be entirely within the upper and lower ranges of adult variation, and at 16 months (69 weeks) the earliest conception of a female lion tamarin at the NZP took place; for L. r. rosalia males, 17 months (73 weeks) was the time for the earliest impregnation recorded. These events took place only after the young adults were removed from their families. Thus, actual breed-

ing probably occurs only after offspring leave the natal group and may not be a normal behavior for both sexes until sometime after 65 weeks. Statistical tests follow Siegel, 1956; Ferguson, 1959; Downie and Heath, 1974.

Behavioral Definitions

INFANT CARRYING.—Carrying behavior was investigated from two perspectives: the transport of infant focal tamarins by other family members and the transport of newborn siblings by maturing focal tamarins. Carrying occurred when an infant's weight was supported by another group member and the infant was off the substrate (Figure 3); this included nursing positions while on the mother. Infants were recorded as independent or "off" if most of the body was in contact with the substrate and not supported by another animal. Active transport (i.e., moving while carrying an infant) was not the only criterion for carrying since a "carrier" could support an infant while lying down. Except when nursing or attempting to nurse, infants clung to the dorsum of the carrier.

FOOD SHARING AND STEALING.—Snyder (1972) was the first to apply the terms sharing and stealing to food transfers among *L. r. rosalia*; however, clear distinctions between the behaviors

FIGURE 3.—*Leontopithecus r. rosalia* father carries twin offspring. (Drawing by S. Bruch from a photo by L. Newman.)
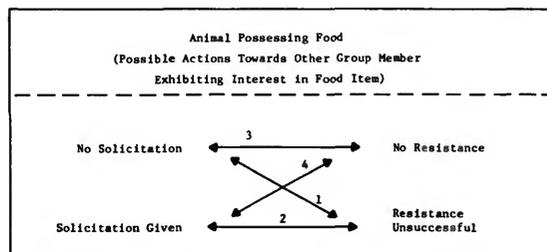
FIGURE 4.—Classification of food transfers among *Leontopithecus r. rosalia* at the National Zoological Park (1 = food stealing; 2 = quasi-food stealing; 3 = passive food sharing; 4 = overt food sharing).

were not provided. C.G. Wilson (1976) distinguished three forms of food sharing in lion tamarins but did not define food stealing.

During interactions involving food, a lion tamarin could succeed or fail in trying to acquire food. Taking successes only and using a scheme based on whether there was solicitation and/or resistance by the animal possessing food, four forms of transfer could result (Figure 4).

Food Stealing: A possessor of food does not solicit investigation by a second animal and unsuccessfully resists a theft attempt (Figure 5).

Quasi-food Stealing: A possessor initially solicits investigation by another, then unsuccessfully resists the attempt to take its food. (This type of interaction occurs very rarely.)

Passive Food Sharing: A possessor of food neither solicits nor resists another's attempt to take its food (Figure 6).

Overt Food Sharing: A possessor actively solicits another's approach and allows food to be taken without resistance. Solicitation may be simply a movement of the possessor of food toward a second animal, thereby attracting attention. However, complex signals have also been observed and filmed, including an approach together with a rasp vocalization and a stare at the intended recipient followed by the possessor sitting on its haunches while holding the food away from the body (with elbow bent). The possessor may then hold its head erect and look over and beyond the recipient while the latter takes the food (Figure
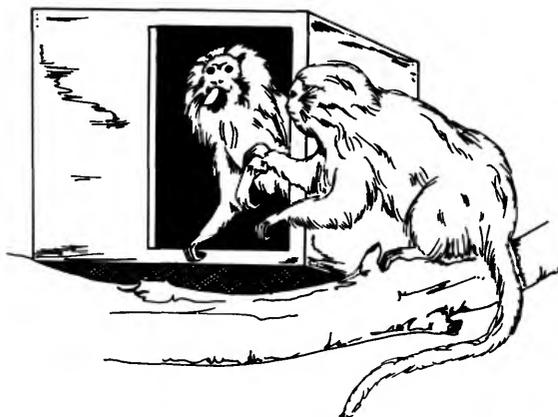
FIGURE 5.—Attempted food stealing. Without solicitation by the food possessor, a subadult male *Leontopithecus r. rosalia* attempts to steal a food item from its mother. (Original sketch by S. Bruch, modified by R.J. Hoage and P. Lesneski; from a photo by K.M. Green.)

8).[1] Although several solicitation signals can be used, usually only two or three occur in most instances. The criterion for solicitation in this study was the approach by a possessor of food to within one foot (30.5 cm) of another animal.

ALLOGROOMING.—Grooming was usually unidirectional; that is, one animal groomed another without the benefit of being reciprocally groomed (Figure 7). Simultaneous mutual grooming did not occur and reciprocal grooming (taking turns) was uncommon (see definitions in Sparks, 1967). Box (1975a) has observed similar patterns in *Callithrix jacchus*.

Grooming consisted of using the fingers to part the fur, allowing particles to be removed by the lips or teeth (the thumb is not opposable in callitrichids). Licking was not, in itself, considered grooming since in *L. r. rosalia* it appeared fre-

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[1] Initially labeled "food proffering," a form of overt food sharing; I observed and filmed such a series of signals in the early spring of 1974. A decade and a half ago, Graetz (1968:34) pointed out for *Saguinus oedipus geoffroyi* that the best way for a food possessor to transfer food was in the sitting position. Interestingly, such transfers were labled "steals."

FIGURE 6.—Passive food sharing of a *Leontopithecus r. rosalia* mother with her weanling infant. (Sketch by S. Bruch, modified by R.J. Hoage and P. Lesneski; from a photo by J. Skrentney.)
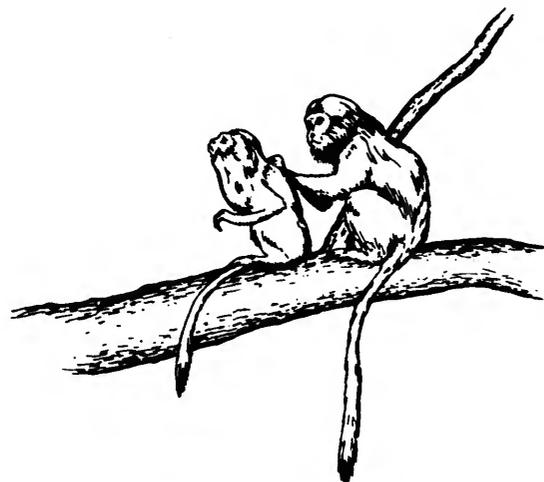
FIGURE 7.—Allogrooming in *Leontopithecus r. rosalia*. A young subadult male is shown grooming his infant brother. Typically, the tamarin receiving grooming remains passive. (Original drawing by S. Bruch, redrawn by Z. Slawinski.)
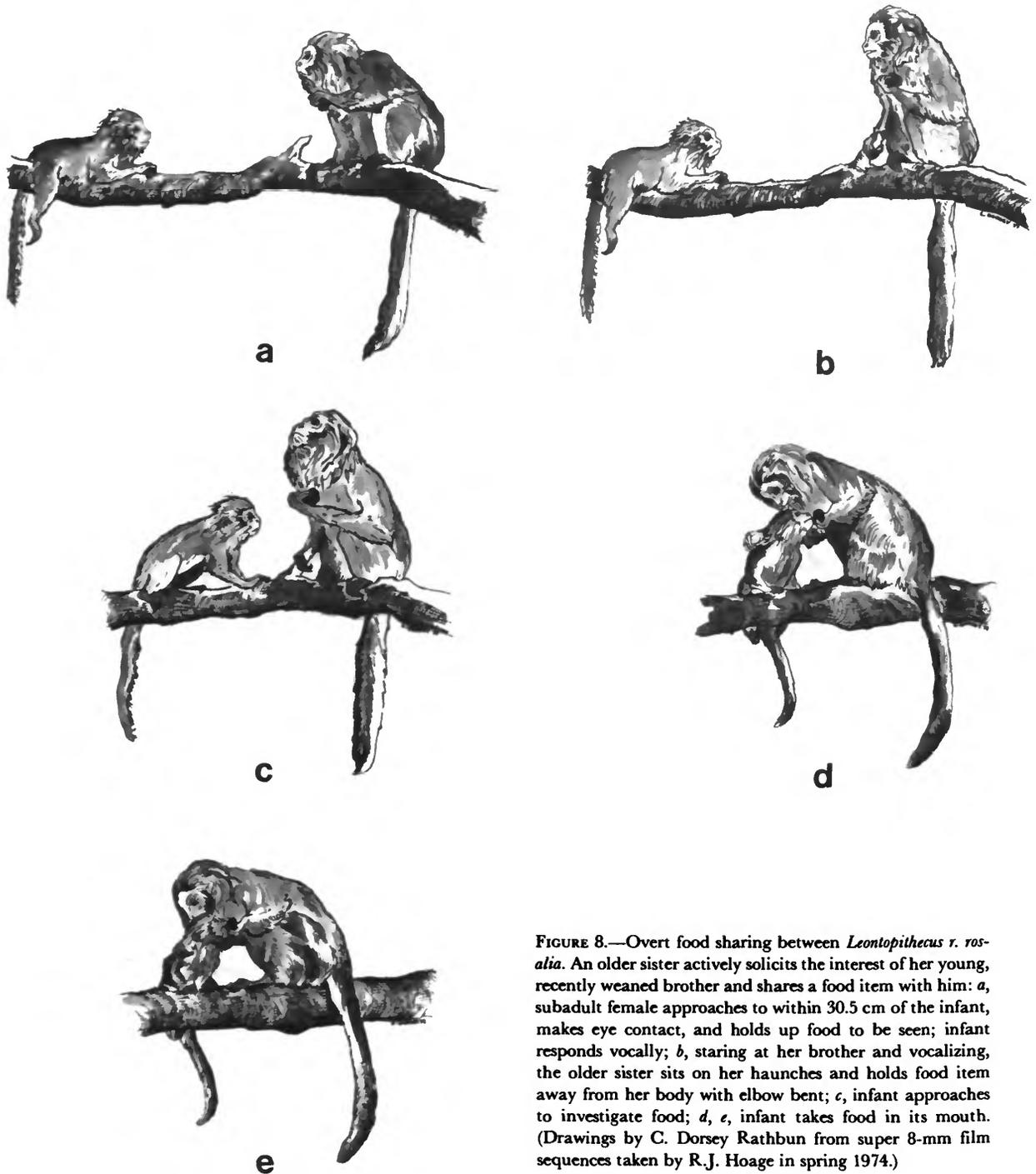
FIGURE 8.—Overt food sharing between *Leontopithecus r. rosalia*. An older sister actively solicits the interest of her young, recently weaned brother and shares a food item with him: *a*, subadult female approaches to within 30.5 cm of the infant, makes eye contact, and holds up food to be seen; infant responds vocally; *b*, staring at her brother and vocalizing, the older sister sits on her haunches and holds food item away from her body with elbow bent; *c*, infant approaches to investigate food; *d*, *e*, infant takes food in its mouth. (Drawings by C. Dorsey Rathbun from super 8-mm film sequences taken by R.J. Hoage in spring 1974.)

quently in anogenital investigation, especially of newborn infants.

SCENT MARKING AND SOCIAL SNIFFING.—For convenience, scent marking and social sniffing are classified together; they are not correlated. Descriptions of scent glands in New World monkeys have long been available (Wislocki, 1930; Epple and Lorenz, 1967). Locomotor patterns associated with scent marking in callitrichids have also been described (Epple and Lorenz, 1967; Moynihan, 1970). Two general types of scent marks have been delineated in *Leontopithecus*: circumgenital and sternal marking (Mack and Kleiman, 1978; Kleiman and Mack, 1980). For circumgenital marking, an individual may assume a sitting posture, with the anogenital region pressed down firmly upon the substrate, followed by side to side rubbing movements, or with his hands, may pull himself along in a sitting position, dragging his anogenital area over the substrate. Sternal marking occurs when an individual leans forward, presses the sternal gland to the substrate, and rubs side to side or slides forward (most often) or backward. Sometimes the hands are used to pull the marker along, a motion Moynihan (1970:16) has called "pull rubbing."

Social sniffing was recorded if the nose of an animal was thrust forward to within approximately 1 cm, or less, of another animal. Frequently sniffed areas of the body were associated with strong odors: food, urine, feces, and scent glands.

SEXUAL BEHAVIOR.—Two categories of sex-related behavior were considered: genital investigation (sniffing, touching, manipulating, mouthing, and licking) and mounting behavior (attempted mounting and full mounting with thrust positioning or with actual thrusts). Genital sniffing, included above in the soeial sniffing category, is also included under genital investigation. Licking did not include a mother's licking the anogenital area of a newborn infant to stimulate elimination. Mounting occurred when one animal approached another from the rear end and clasped the latter around the mid-section such that contact was made between the abdominal area of the mounter and the posterior area of the recipient. The mounting animal's feet remained on the branch or substrate. Mounting between immature tamarins and between parents and offspring was observed, but true copulations took place only among parental pairs.

AGONISTIC BEHAVIOR.—Overtly aggressive behavior, sometimes with serious fighting and injuries, has been recorded for callitrichids, both between and within family groups. Aggressive behavior between distinct families was not examined in this study since barriers between groups prevented direct interactions. Within family groups at the NZP, a number of instances of actual fighting and injury have been recorded between 1973 and 1978 (Kleiman, 1979). All involved interactions among the following: (1) members of recently formed groups of adults where one or more individuals were unrelated strangers, (2) parents and offspring, or (3) siblings of same or different litters in groups with consistently reproducing parents. Only one case of intragroup discord was actually observed in this study (p. 25). Among established family groups, harmonious interactions typically prevailed, but frequently one could observe a number of low intensity aggressive interactions. Four categories of agonistic behavior were distinguished.

Aggressive Chasing and Non-injurious Fighting: Occur when one animal initiates agonistic movement toward or contact with another animal. Movements without contact include pounces, lunges, and intense chasing; movements with contact include aggressive shoves, slaps, bats, grappling, and nips and bites.

Agonistic Facial Expressions: Involve primarily the eyes and the mouth. Staring with glaring eyes is often accompanied with swaying and head bobs. The open mouth, often with corners back forming a grimace and teeth showing, is frequently combined with staring.

Agonistic Postures: Consist of back arching, piloerection, and tail thrashing. Back arching and walking with piloerection have been considered a defensive threat by Epple (1967:63) and Moynihan (1970:40) and an indication of tension and ambivalence by Rathbun (1979:145). Piloerection occurred only when focal tamarins were

10

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY

moving and independent of carriers; it was very common among infants being dislodged or rejected by carriers. Piloerection is thought to signify some degree of disturbance to the animals (Stevenson, 1976a:435). Tail thrashing is characteristically displayed by infants being rejected by carriers.

Agonistic Vocalizations: Consist primarily of three types and are typically found in combination with one or more of the above behaviors: (1) warbles and trills; (2) screeches, rasps, and hisses; and (3) alarm chirps and clucks (see McLanahan and Green (1977) and Green (1979) for detailed analyses of *L. r. rosalia* vocalizations).

First Appearance of Selected Behavioral Patterns

INFANT CARRYING.—Infants are first transferred from their mothers to other group members (usually fathers first) at about 14 days after birth (Figure 9). They are usually carried from birth to about 12 to 14 weeks of age. When approximately 20 days old, they are first observed off of carriers. After 14 weeks, infants may attempt to board carriers when frightened, but they are rarely carried.

FOOD SHARING AND STEALING.—In the first 14 weeks, three trends can be detected (Figure 9). In weeks 4–5 infants are introduced to solid foods by investigating food in the mouth or hands of their carriers. Initial tasting, touching, and sniffing rapidly develop into taking bites or grabbing pieces of food brought to them by others. This behavior marks the beginning of weaning.

In the next four weeks (weeks 5–8), infants independently move to, and begin taking food from, other group members (usually from mothers first, followed by fathers and older male and female siblings). At first these encounters tend to involve sharing by older family members, but subsequently infants begin to steal food. By week 8 infants may feed alone at the food dish.

In weeks 8–14 older group members obtain food from infants, initially by stealing but later by the infants' sharing. When weaning is completed, usually between 11–15 weeks after birth,

nursing ceases and infants show the full range of food-related behaviors observed in older family members.

ALLOGROOMING.—Between weeks 1–3 after birth older group members groom infants. Beginning about week 4, infants initiate uncoordinated grooming movements, consisting of running the fingers through, and sometimes pulling on the fur of the groomee (almost always an older group member carrying the infant on its back). In contrast, tamarins older than 16 weeks show skilled motor coordination (Figure 9).

In the first week, mothers lick and groom the anogenital region of young when they cling ventrally. At the same time juvenile and subadult siblings are intensely interested in touching, sniffing, mouthing and patting neonates; often they will attempt to groom young carried by the mother. Although mothers may guard against such contact, older siblings usually succeed for brief periods.

Fathers, as well as older siblings, frequently use touching, nudging, and grooming to entice infants to move off mothers (or other carriers) and onto themselves. Fathers usually do not exhibit such interest until the second week, when mothers begin to transfer infants to them.

SCENT MARKING AND SOCIAL SNIFFING.—By 12 weeks of age, most infants perform circumgenital-like marking by sitting on the substrate and moving side to side (rubbing) or moving along forward or backward (dragging) (Figure 9). In these instances, contact is short and movement slight. Often such movements follow defecation and could be a cleaning action rather than true scent marking. (Moynihan, 1970:19, witnessed similar activity in *Saguinus oedipus geoffroyi.*) The first appearance of this behavior is the same for young males and females.

By the end of week 20, most young are performing more precise circumgenital rubbing. In only one case did this motion follow defecation. For both sexes of young, the first adultlike circumgenital drag marking typically appears by week 25. Again, in only one instance did it follow defecation. By week 38 sternal marking becomes noticeable, but not frequent, in most young. The first
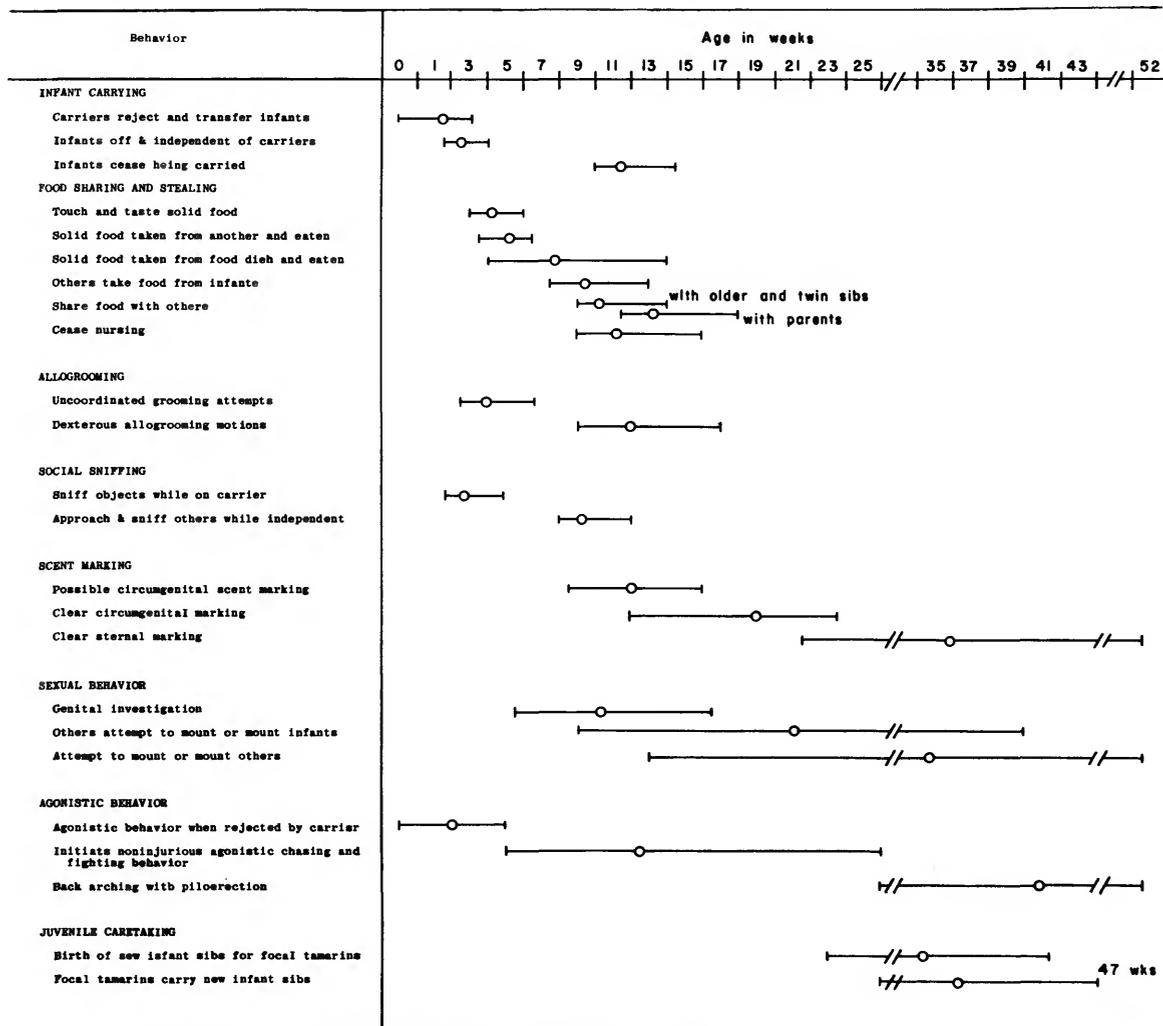
FIGURE 9.—First appearance in *Leontopithecus r. rosalia* of 24 kinds of behaviors
(bar brackets = range; circle = average).

occurrence of this behavior varied from 21 to 52 weeks of age and showed little difference between young males and females.

From birth through week 4, infants crawl over their carriers and lean out to sniff and taste objects in the environment. As early as week 6, with the onset of weaning, they begin to independently approach and sniff other family members (Figure 9). By week 11, all family members are approached and sniffed. Often these initial approaches and sniffs by young occur after food is held or has been eaten by another. Sniffing after weeks 5–16 is less involved with food.

SEXUAL BEHAVIOR.—Up to week 4, licking of the anogenital area of infants by mothers and other group members may have more to do with elimination and infant hygiene than with sexual interest. However, when young become independent of carriers, such genital investigation may indicate interest in individual and sexual identity.

Parents and older siblings tend to initiate genital investigation of independently locomoting infants in weeks 4–16 (Table 2, Figure 9). When young have twin sibs, the littermates initiate genital investigation of each other during weeks 8–32. Older family members frequently begin to mount young during weeks 8–27, while twin sibs show more variability in initiating mounting (weeks 14–42). Older sibs and mothers mount young sometime between weeks 8 and 15. Fathers mount young after week 20.

Young tamarins of both sexes (weeks 6–16) initiate genital investigation of parents and older sibs at about the same time. Young begin to mount parents and older siblings in weeks 24–52, but when a littermate is present, mounting between the two occurs as early as week 14.

With the birth of siblings, young (33–40 weeks) begin initiating genital investigation of younger brothers and sisters. Young tamarins (37–44 weeks) begin to mount younger siblings.

The focal tamarins (35–43 weeks) first had their genital areas investigated by younger siblings. The mounting of focal tamarins by younger sibs was recorded only three times. The focal tamarins were all 35–60 weeks old when the mountings occurred.

The first appearance of genital investigation and mounting behavior showed considerable

TABLE 2.—First appearance of sex-related behavior among captive *Leontopithecus r. rosalia* (young males and females are combined into one category since there were no significant differences between sexes)

Behavior initiator/recipient	Age of young (weeks)	
	Genital investigation	Mounting behavior
Parents/young	4–8	10–21
Young/parents	10–13	24–52
Older sibs/young	5–16	8–27
Young/older sibs	6–16	28*
Twin sibs initiate with each other	8–32	14–42
Younger sibs/young	35–43	35–60
Young/younger sibs	33–40	37–44

* Data available on only three animals.

variation among the different family groups and individual young. No consistent same sex or opposite sex biases were evident in these first sex-related interactions. The first occurrence of sexual behavior seemed to be related to such variables as group composition, especially the presence of a twin or older siblings, and whether or not the mother was pregnant. In general, genital investigation initiated by young tamarins occurred before mounting behavior.

AGONISTIC BEHAVIOR.—Dependent infants exhibited a number of agonistic behaviors, especially when being rejected or displaced by carriers. A carrier vocally signalled its intolerance toward young or scratched, pushed, pulled, or attempted to rub off a carried infant against a branch. Carriers also nipped or lightly bit young who proved persistent in their efforts to stay on. In response, neonates usually resisted with tail thrashing, nipping or biting, piloerection, and open mouth grimaces—all in conjunction with loud and frequent vocalizations (screeches, rasps, hisses, warbles, trills, and alarm chirps or clucks).

Noninjurious agonistic behaviors appear between young and other group members following the carrier rejection period. These behaviors occur during competition for food, aggressive play, grooming, approaches, and in sex-related encounters. When independent of carriers, young (weeks 5–27) initiate agonistic chasing and fighting with parents and older or twin siblings. Such behavior is initiated somewhat earlier with older and twin sibs than with parents. A littermate is frequently the target of first agonistic charges, pounces, and contacts. Because of their later arrival, younger siblings become the last targets of focal young (weeks 25–46). Young (5–34 weeks) receive agonistic charges and contacts from parents and older siblings. From younger sibs, young receive such interactions in weeks 37–52. Piloerection appears when infants resist rejection from carriers, and it is often seen among all ages when individuals are excited or aroused. It is difficult to discern any change in the frequency of piloerection when young become independent of carriers. However, piloerection with back arching and walking, ap-

pears much later (weeks 25–52). Rathbun (1979:138) observed a young male lion tamarin at the NZP to piloerect and back arch at 18 weeks of age; the earliest for a female was 43 weeks. The averge time of first occurrence comes in weeks 41–42 (Figure 9). In contrast, older group members (largely parents) begin to exhibit piloerection and back arching toward young in weeks 22–46, with an average at about week 29. Younger sibs did not initiate such behavior with focal tamarins during this study.

INFANT CARRYING BY OLDER YOUNG.—For most focal tamarins, younger sibs tended to be born in weeks 23–42 (Figure 9). In weeks 25–47 young first carried their baby brothers and sisters. On average, new infant sibs appeared in week 36 and were first carried by young in week 39, the period when focal tamarins were still advanced juveniles.

DISCUSSION.—In most respects, lion tamarins do not differ substantially from the ranges given for other marmosets and tamarins (Appendix III). However, lion tamarins exhibit some characteristics seen only in Goeldi's monkey (*Callimico goeldii*), including a close similarity in infant carrying patterns among mothers and fathers and the rate of increase in infant independence (Heltne et al., 1973; Hoage, 1977). Additionally, *L. r. rosalia* and *C. goeldii* have two of the longest periods of infant nursing (over 75 days). The similarity may be due to convergence since these species are larger than nearly all other marmosets and tamarins.

Young lion tamarins first scent mark and arch walk 8 to 24 weeks later than smaller callitrichid species, such as *Callithrix jacchus* (Sutcliffe, 1978). However, data for many species are required before clear differences in these behaviors can be determined across species.

The Influence of Parental Reproduction

During the maturation of focal tamarins, mothers, with somewhat varying degrees of regularity, copulated, conceived, sustained an 18-week pregnancy, delivered new infants, and began anew the weaning process (Tables 3, 4). These activities proved to be major stimuli for the focal tamarins of this study.

INFANT CARRYING BEHAVIOR

The results of earlier work (Hoage, 1977) on infant carrying patterns among adult and juvenile *L. r. rosalia* at the National Zoological Park are summarized below due to their relevance for the present study.

THE EFFECT OF THE NEWBORN.—Mothers were the principal infant carriers through week 3 but became secondary carriers in weeks 4–12. In contrast, fathers, secondary carriers through week 3, became principal carriers in weeks 4–12. Between weeks 13–16 infant carrying largely ceased as infants achieved 45% of the average adult weight. Among older siblings, juvenile females were tertiary carriers from the second to the seventh weeks and, after week 8, were only incidental carriers. Juvenile males were also tertiary carriers but exhibited a concentrated period of carrying between weeks 3 and 8. Thereafter they were only incidental carriers.

TABLE 3.—Number of *Leontopithecus r. rosalia* focal tamarins over five maturational phases experiencing the reproductive activities of their mothers

Maternal reproductive activities	Dependent Infant (weeks 1–4)	Advanced Infant (weeks 5–16)	Young Juvenile (weeks 17–28)	Advanced Juvenile (weeks 29–40)	Young Subadult (weeks 41–52)
No. whose mothers conceived	3	5	6	3	5
No. whose mothers in last half (9 weeks) of pregnancy	0	3	6	10	5
No. experiencing birth of sibling litters	0	0	3	9	4

Table 4.—Number of younger siblings born into and surviving in family groups with focal
tamarins already present (five maturational phases shown are for focal tamarins)

Activities of younger siblings	Dependent Infant $\left(\begin{array}{c} weeks \\ 1-4 \end{array}\right)$	Advanced Infant $\left(\begin{array}{c} weeks \\ 5-16 \end{array}\right)$	Young Juvenile $\left(\begin{array}{c} weeks \\ 17-28 \end{array}\right)$	Advanced Juvenile $\left(\begin{array}{c} weeks \\ 29-40 \end{array}\right)$	Young Subadult $\left(\begin{array}{c} weeks \\ 41-52 \end{array}\right)$
Number of younger siblings born	0	0	4	11	6
Younger siblings surviving infancy	0	0	2	6	2
Younger siblings dependent and largely carried	0	0	2	6	2
Younger siblings experiencing weaning	0	0	0	6	4

Experienced or multiparous mothers tended to carry singleton infants to day 16 postpartum without transferring them. The same mothers usually began to transfer or dislodge twins at about day 10 or 11 postpartum. The weight of one maturing infant seemed to be easier for the mother to bear than twins (Appendix II).

Prior Experience in Parental Care.— Among primiparous parents, those with the greatest length of previous exposure to infants had the greatest success with neonates (Hoage, 1977). This suggests that a minimum time of exposure to infants is probably necessary for juveniles to insure that they will be successful as primiparous parents. Exposure to infants in the first 11 weeks seems most critical; it is the period when juveniles learn to carry infants and to some extent begin to mimic the carrying patterns of the same sex parent. Also, juveniles first reject or dislodge carried infants without injury in this period. The likelihood of a primiparous pair having success in rearing their first litter is increased if, within their natal family units, they have had previous juvenile or subadult exposure to more than one birth and infant rearing episode.

Food Sharing and Stealing

Food Obtained from the Environment Compared to Food Obtained from Group Members.—To gain some idea of how much food was obtained from the environment (from food dish or through foraging) as opposed to that taken from individuals (through sharing and stealing), a special investigation was undertaken in summer 1977. Two family groups, one in the National Zoological Park Small Mammal House and one in the photographic room of the Hospital/Research Building, were observed intensely over a two week period (neither was a primary study group listed in Table 1). Each group was examined 15 minutes a day for 10 days. The two families were chosen for their similar age and sex compositions and because they had compositions comparable to those of the main study groups (Table 5). Data were collected on the total number of food items (excluding small pieces or droppings) obtained (grasped or held in the hands or mouth) from the environment or others during twenty 15-minute observation periods (10 per group). Data were not taken during intensive feeding periods (immediately after provisioning); observations began about one hour after feeding.

Mothers and fathers received only 10 to 11% of their food from others, subadults and advanced juveniles 15%, and younger juveniles got somewhat more (30%). Infants were the only group members taking more food from others than from the environment (90%). These percentages indicate that an inverse relationship exists between the age of young and the amount of food obtained from other group members.

TABLE 5.—Number of food items obtained by members of two family groups from the environment compared to food items obtained from family members (numbers in parentheses indicate percentage of food items obtained from family members)

Food source	Father (n = 2)	Mother (n = 2)	Subadult offspring (n = 2)	Juvenile offspring (n = 2)	Infant offspring (n = 2)	Totals (n = 10)
From the environment	27	31	50	40	2	150
From family members	3 (10)	4 (11)	9 (15)	17 (30)	21 (91)	54 (26)

FOOD TRANSFERS DURING WEEKS 5 TO 52.—As young aged they were less successful in acquiring food from others so that by weeks 29-40 they had only a 50% success rate (Figure 10). Also, acquisition through sharing decreased with age, while stealing increased to the point that in weeks 41-52 stealing was the major method by which young obtain food from others (Figure 11).

Two other important patterns are evident in Figure 11. First, overt sharing is a frequent method of delivering food to young only in weeks 5-16. Second, the yielding of food by young, especially through sharing, peaks in weeks 29-40, the period when mothers often are either in the last stage of pregnancy or have recently delivered.

FOOD ACQUIRED AND YIELDED BY YOUNG.— Transfers to young occur most frequently in weeks 5-16 (Figure 12), when weaning begins
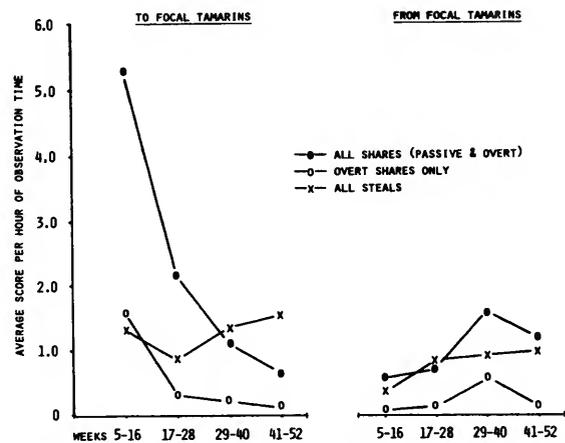
FIGURE 11.—Rates of food sharing and stealing among focal tamarins of *Leontopithecus r. rosalia.*
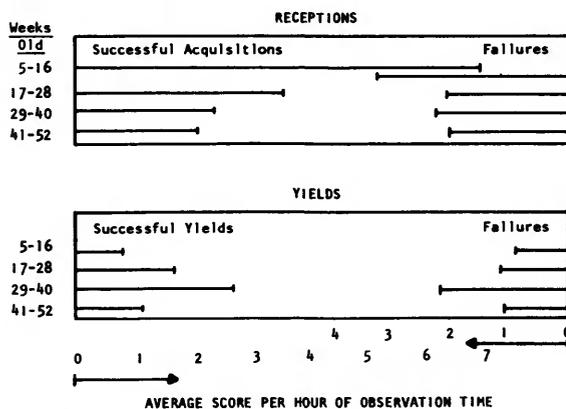
FIGURE 10.—Food transfer interactions among *Leontopithecus r. rosalia* focal tamarins; data are given only for young (males and females combined).
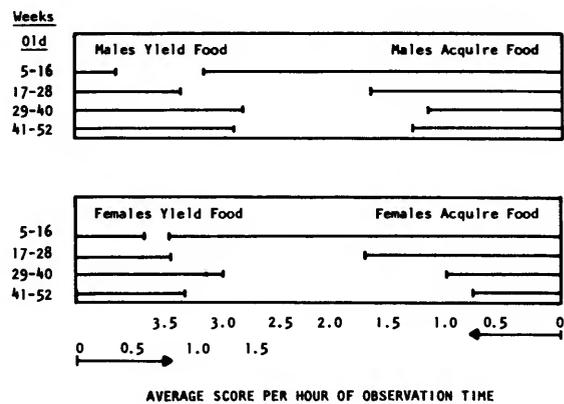
FIGURE 12.—Food transfers between *Leontopithecus r. rosalia* focal tamarins and other family members (data are given only for young males and females; the category of "others" combines parents and older and younger siblings).

and young gradually become independent of carriers. Young are principally food receivers rather than providers in the first two 12-week periods, but their receptions drop 50% during the second 12-week period. Young yield more than they acquire in weeks 29–52, making them net providers rather than receivers. This distinction in status between weeks 5–28 and 29–52 is an important diagnostic characteristic separating early and later youth. The combination of weeks 29–52 covers the period when many mothers are concluding their pregnancies and delivering infants (Table 3).

In weeks 5–16 females are more active in both acquiring and yielding food, but in the last two 12-week phases (29–40 and 41–52) males are more active than females. The meaning of these differences is not clear.

FOOD TRANSFERS BEFORE AND AFTER THE BIRTH OF SIBLINGS.—In order to examine the influence of mothers' pregnancies and births of new siblings on food transfers among young, I compiled data on food acquisitions and yields by focal tamarins during two periods prior to their mothers' deliveries (12-7 and 6-1 weeks) and two periods (1–6 and 7–12 weeks) postpartum (Table 6). These data were collected under a different protocol from that of the main behavior classes in this study: the numbers reflect total food transfers, not scores per 30-second intervals.

The data in Table 6 show that young receive significantly more food than they yield during interactions with mothers and fathers in 12-7 weeks before the birth of siblings. A change-over occurs in 6–1 weeks prepartum: acquisitions and yields by young tend to even out, especially with mothers, with whom young tend to give up more than they acquire even though total food-related interactions have decreased by 24%. Acquisitions and yields between young and older and twin sibs over the same two 6-week periods exhibit a 55% decline, but ratios of gain to loss remain stable.

In the first weeks postpartum, food transfers occur at a relatively low rate, about three per hour. When mothers and fathers carry infants, young yield more food to parents than they ac-

TABLE 6.—Focal tamarin food acquisition and yield ratios (acq:yld) during the 24 weeks surrounding the birth of a new litter of siblings (males and females combined; data indicate number of completed food transfers; 6 focal tamarins were observed for 46 hours in the prepartum period, 8 were observed for 73 hours during the postpartum period; dash indicates insufficient data for comparison)

Individual transferring food	Weeks prepartum		Weeks postpartum	
	12–7 (acq: yld)	6–1 (acq: yld)	1–6 (acq: yld)	7–12 (acq: yld)
Mothers not carrying newborn	42:4[a]	16:19	17:8[b]	10:5
Mothers carrying newborn	–	–	4:16[b]	0:0
Fathers not carrying newborn	16:7[b]	10:8	4:5	12:4[c]
Fathers carrying newborn	–	–	3:6	0:2[c]
Older or twin sibs not carrying an infant	29:32	13:15	5:4	9:9
Older or twin sibs carrying an infant	–	–	0:0	0:0
New infant siblings	–	–	3:16[a]	6:46[a]

Statistically significant relationships: [a] binomial test $p \leq .01$; [b] binomial test $p \leq .05$; [c] chi square with Yates correction $p \leq .05$.

quire. In contrast, when mothers are not carrying, young acquire twice as much from them as they yield. With fathers and older and twin sibs the ratio is about even. The difference in interactions when mothers are or are not carrying infants is particularly significant ($X^2 = 10.70$, $p \leq .01$). Pregnant mothers enjoy a special status 1 to 6 weeks before delivery and provide a stimulus that triggers a reaction in older offspring to become food providers for the mothers rather than receivers. To a lesser extent, this special status also applies to fathers when they carry newborn infants.

Food transfer interactions between parents carrying infants and focal young are few in weeks 7–12 after delivery. By 12 weeks after the arrival of new siblings, when the infants are seldom carried, focal tamarins again become predomi-

nantly food receivers, at least during interactions with parents (Table 6).

Transfer rates with older and twin sibs are depressed following new births. Food transfers to or from older and twin sibs carrying infants did not occur but food transfers with newborn siblings increased by 65% from weeks 1–6 to 7–12. In both periods focal tamarins yielded significantly more food to younger siblings than they received (Table 6).

The data indicate that the movement of food to and from focal tamarins is significantly altered by (1) mothers' pregnancies, (2) older family members (especially parents) carrying newborn infants, and (3) the arrival of younger siblings. Nevertheless, 7–12 weeks after infants are born, when carrying by parents declines, acquisition:yield ratios return to their early-to-midpregnancy levels.

Allogrooming

Allogrooming rates were the highest, most recurrent, and most sustained relative to the other behaviors examined. As indicated in Figure 13, infants in weeks 5–16 are only just becoming effective groomers; however, they are groomed quite frequently by others. Young are predominantly grooming initiators rather than receivers during the three subsequent 12-week phases. In contrast to these general trends, grooming initia-

tions by young females decline during weeks 29–40. The reason for this decrease is unclear.

Scent Marking and Social Sniffing

Figure 14 plots the development of scent marking behavior for young males and females through the four 12-week phases. Scent marking consistently increases from phase to phase, suggesting that rates of this activity may be a function of physiological maturation not greatly influenced by mothers' pregnancies and sibling births. Yet, the scent marking behavior of young in one family group provides evidence that certain inhibiting stimuli may nevertheless be present in family groups.

Up through weeks 29–40, all scent marking consists of circumgenital rubbing. Even in weeks 41–52, circumgenital rubs occur three to four times more than sternal rubbing. In the Young Subadult phase, circumgenital marking reaches its highest level. Even so, the levels are but 25% to 50% of the circumgenital marking rates of the parents. Subadults are actually only just beginning to sternal mark by weeks 41–52.

In group C, scent marking rates differed. When the mother (♀M00320) became ill and died, her daughter (♀M00886), a young subadult, dramatically increased both circumgenital and sternal marking (Figure 14). Female M00886's rates of

Figure 13.—Allogrooming interactions among *Leontopithecus r. rosalia* focal tamarins.
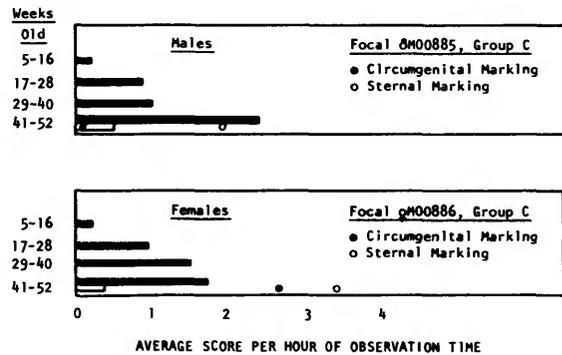
Figure 14.—Scent marking behavior among *Leontopithecus r. rosalia* focal tamarins (solid bar = average score for circumgenital marking; open bar = average score for sternal marking).
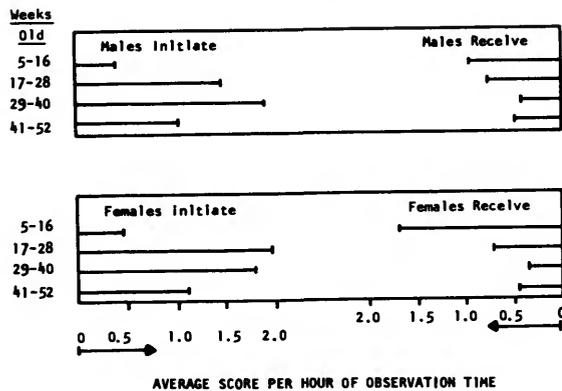
FIGURE 15.—Social sniffing interactions among focal tamarins of *Leontopithecus r. rosalia*.

circumgenital and sternal marking were well within the range of rates of equivalent marking behaviors observed in paried, adult female tamarins (Mack and Kleiman, 1978). During this period she was housed with her father (δM00276) and twin brother (δM00885). However, the twin brother had much lower rates than his sister for both behaviors. These patterns suggest the presence of parents of the same sex probably inhibit scent marking by maturing offspring.

Social sniffing occurred at a relatively lower rate than did other behaviors, such as allogrooming. The data in Figure 15 indicate that only in weeks 5–16 do young receive more sniffing than they initiate. For both sexes the highest initiation peaks occur in weeks 17–28 and 29–40 (Figure 15), periods when mothers frequently mate, conceive, and bear new young (Tables 3, 4).

SEXUAL BEHAVIOR

Genital investigation and mounting initiations occurred less frequently than did other behaviors. It is evident in Figure 16 that both sexes are predominantly initiators of genital investigation rather than receivers during all phases, except females in weeks 5–16. Most genital investigation receptions occur in weeks 5–16, when infants are becoming independent of carriers and when other family members can investigate them without provoking a negative response from the carrier.

Mounting occurs even less frequently than genital investigation. Young males are principally receivers in weeks 5–28, as are young females in weeks 5–16 and 41–52. Young increase their mounting initiations beginning week 17. As they mature from juvenile to subadult status, females initiate mounting less often than do males.

In weeks 17–28 when parents often mate, young males are mounted by older group members, especially brothers. Young females are mounted in weeks 41–52 when they are young subadults. When subadult males exhibit an increase in mounting initiations in weeks 41–52, they sometimes mount their mothers.

In weeks 41–52 when parents may mate, several fathers and at least one mother mounted young subadult females. Although mounting occurred,
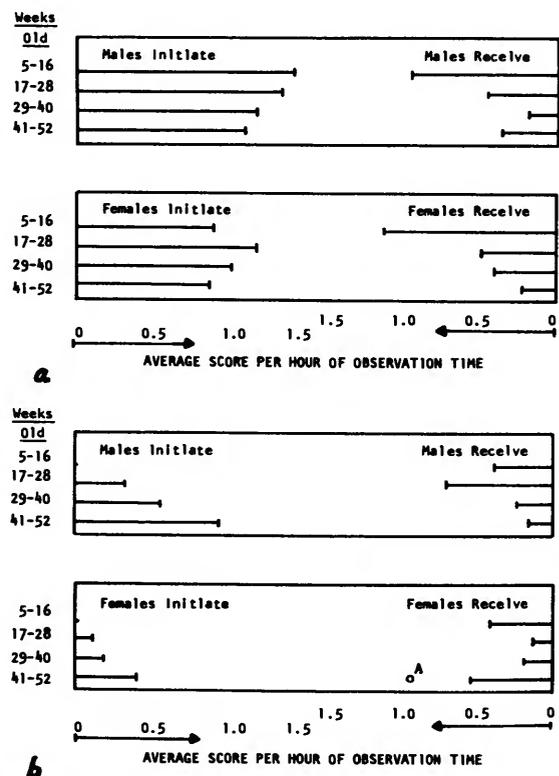
FIGURE 16.—Sexual interactions in *Leontopithecus r. rosalia*: *a*, genital investigation; *b*, mounting behavior (o^A = score for mounting behavior received by focal $\female$M00886, group C).

intromission was never observed except between the parental pair.

In group C, when the mother died, during weeks 41-52 for the twin offspring, the father mounted his young subadult daughter much more frequently than was the case in normal family groups (Figure 16). Occasionally he also mounted his son.

AGONISTIC BEHAVIOR

Agonistic behaviors occurred at a rate midway between those of grooming and sexual interactions. The data in Figure 17 show that the lowest levels of agonistic behavior between young and other group members occur in weeks 29-40 when most infant sibs are born (Table 4). Relatively high rates of agonistic behavior are received by young in weeks 5-16 when they are rejected and dislodged by carriers.

Agonistic behavior initiations and receptions involving young peak in weeks 41-52 when they achieve young subadult status. Clearly during the first year, life in the family group is most tense for young in weeks 41-52.

DISCUSSION

A few studies on other callitrichid monkeys provide comparable data on behavioral changes over the first year of life. The most data are

FIGURE 17.—Agonistic interactions among focal tamarins of *Leontopithecus r. rosalia*.

available on carrying (Appendix III). The greatest similarities are between *Leontopithecus r. rosalia* and *Callimico goeldii*, in which the fathers first carry infants in weeks 2-3 and older offspring first carry young in weeks 2-6. Although the data are limited, such callitrichids as *Cebuella pygmaea*, *Callithrix jacchus*, and various species of *Saguinus* do not seem to show this pattern. However, whether the father in *C. jacchus* becomes a major carrier or not sometimes depends on the number of juveniles present. If juveniles take over much of the infant transport burden, a father may become a secondary or tertiary carrier (Box, 1975b:426).

The degree of infant carrying by family members, including both parents and older offspring, seems to depend on age, sex, group composition, and prior experience rather than on species-specific differences. Thus, the suggestion that marmoset and tamarin fathers are the exclusive carriers of infants beginning within a few days after birth (Napier and Napier, 1967:199, 304; Jolly, 1972:248) may be incorrect for many species.

No equivalent data are known from other studies on marmosets and tamarins with regard to food sharing and stealing (Appendix III). However, accounts of food sharing and stealing are documented for a half dozen other higher primates (p. 31).

Some reports on grooming patterns involving immature callitrichids are available. Rothe (1978:247) reported that both sexes of *Callithrix jacchus* young between 17 and 34 weeks of age groomed mothers, fathers, and older brothers more than older sisters. In Rothe's study older female offspring formed a clique in which the members associated more with each other than with others in the group. In another investigation of *C. jacchus*, Box (1975b:430) found a grooming peak for juvenile males corresponding to weeks 17-28 (the Young Juvenile Phase in this study). Juvenile *L. r. rosalia* males in the same period exhibited a 3½-fold increase in grooming, which remained fairly constant over the remainder of the first year of life.

Although in this study there were insignificant differences in scent marking rates between sexes,
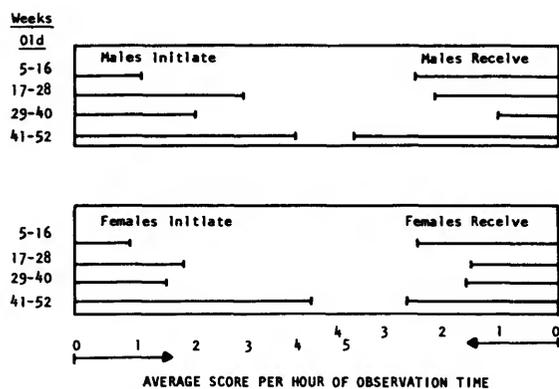
Kleiman and Mack (1980) did find a difference in sternal marking rates for NZP *L. r. rosalia*: young males began regular sternal marking during weeks 30–64 (average = 45 weeks); young females began during weeks 43–86 (average = 71 weeks). The sternal marking rates of young males living in family groups were sometimes observed to exceed those of the father or mother. However, young females living in family groups were rarely observed to sternal mark but began to regularly exhibit such behavior once removed at 15 to 20 months of age and paired with mates. The work of Kleiman and Mack does not contradict the data presented here since the latter emphasize the first appearance of sternal marking rather than its occurrence as a regular behavior. In this study, sternal marking was never a regular behavior for young of either sex.

The onset of regular marking behavior may indicate approaching adulthood among callitrichids (Epple, 1975a:214). Kleiman and Mack (1980:11) suggest that, because young *L. r. rosalia* females lag behind males in initiating regular sternal marking, they are behaviorally inhibited. Kleiman and Mack believe that the inhibition is due neither to a lack of mature scent glands nor to differing ages of maturity. The increased rate of sternal marking exhibited by the subadult female (♀M00886) in group C after the mother died supports this interpretation. Kleiman and Mack suggest that young males are not similarly inhibited.

In *Callithrix jacchus*, although not known to regularly scent mark, subordinate and juvenile group members show an increase in scent marking as the adult breeding pair increase their own scent marking in connection with copulations (Epple, 1967, 1970a, 1975a; Box, 1977b). *C. jacchus* adult pairs and their oldest offspring increase scent marking two weeks prior to the birth of new infants (Box, 1977b). Pregnant adult *L. r. rosalia* show increases in their scent marking until 1 month before delivery, but juveniles apparently do not (Kleiman and Mack, 1980). In one common marmoset family, the subadult male marked more than the subadult female (Box, 1977b). At

the National Zoological Park, 41- to 52-week-old male *L. r. rosalia* circumgenital mark somewhat, but not significantly, more than females, and both sexes sternal mark infrequently at roughly the same rate.

Sniffing behavior among marmosets and tamarins has usually been examined in conjunction with scent marking (Epple, 1975a) or sexual behavior (Kleiman, 1977a). Sniffing between adults has been the focus of such studies. Data on the ontogeny of sniffing behavior and on sexual behavior in other callitrichid species are not available.

Fighting between older twin offspring and between older and younger siblings has been reported in *Callithrix jacchus* by several investigators (Box, 1977b; Rothe, 1975; Stevenson, 1976a, 1976b; Sutcliffe, 1978) and by Kleiman (1979) in *L. r. rosalia*. However, the ontogeny of agonistic patterns involving such young have not been described.

The Influence of Older and Younger Siblings

Five major classes of behavior were compared between young living with older and younger siblings (Category A) and young living without older and younger siblings (Category B) (Figure 18). Eleven focal tamarins lived in family groups with either older or younger sibs or both. Three focal tamarins lived in families having no prior or subsequent sibling litters. Infant carrying behavior was excluded since Category B individuals had no siblings to carry.

FOOD TRANSFERS

Category B young exhibit rates of food acquisitions 1½ to 2½ times that of Category A young in weeks 29–40 and 41–52. Also Category A young show consistent declines in food acquisitions (not seen in Category B young) from weeks 5 though 52. For Category A young, food transfer receptions are lowest in weeks 29–40 and 41–52, when new infant sibs are becoming weaned and independent of carriers. In these two 12-week

blocks, Category B individuals generally have higher food yield scores, as well as higher food acquisition scores. The reason for this difference is unclear.

ALLOGROOMING

Category A young generally initiate and receive allogrooming more frequently than Category B young. Only in the last 12-week phase (weeks 41–52) do young in both categories exhibit similar rates, but only with respect to initiations.

SCENT MARKING AND SOCIAL SNIFFING

For Category A young an increase in marking (sternal and circumgenital combined) occurs in the final 12-week phase (weeks 41–52), which is twice that of Category B young in the same phase (Figure 18). The sudden increase may be related to one or more developments in the family group: (1) mothers often come into estrus, (2) parental scent marking and sexual behaviors often increase, (3) new infant siblings become young juveniles, and (4) focal tamarins become young subadults (Table 4 and Appendix I).

Social sniffing interactions show low rates over the four 12-week phases for both categories of young. There is little difference in scores between categories.

SEXUAL BEHAVIOR

GENITAL INVESTIGATION.—Category A young exhibit more initiations than Category B young during each of the four 12-week phases (Figure 18). An inverse correlation exists between receptions and initiations by Category B tamarins ($r = -.90$, $p \leq .05$; Pearson Coefficient of Correlation, after Downie and Heath, 1974:224), suggesting that when younger and older sibs are absent the rates of such behavior may be a function only of physical aging.

MOUNTING.—Category B young rarely initiated mounting at any time during the four 12-week phases, while Category A young exhibited some

initiations in all phases except weeks 29–40, the period when new infants are often born into family groups (Table 4). Category A individuals were mounted the least in weeks 29–40 and 41–52 while Category B young were mounted the most during the same two 12-week phases. In weeks 29–40 and 41–52 focal tamarins in Category B were mounted more than those in Category A. Possibly when young approach adulthood, parents that have produced only one litter may view them as potential competitors or mates. These mounting behaviors may also indicate dominance relationships, as well as sexual interest.

The levels of mounting exhibited by Category A young in each phase except weeks 29–40 may reflect stimuli from parental mating, mothers' pregnancies, and the appearance of independent younger sibs competing for food and status. None of these stimuli are present to influence the behavior of Category B young.

AGONISTIC BEHAVIOR

There are few differences in the scores between categories for agonistic behavior over the four 12-week phases (Figure 18). However, both Category A and B young decrease initiations and receptions in weeks 29–40. These similarities suggest that the presence of older and younger siblings is not essential for moderate to high levels of noninjurious agonistic behavior to occur between focal tamarins and other family group members. They also suggest that parents may be the most significant agonistic interactants for young.

SUMMARY OF DATA

Overall, young without older and younger siblings (Category B) initiated and received more agonistic behavior in the 24 weeks between weeks 29–52 than did young with older and younger siblings (Category A) (Figure 19). Category B offspring acquired and gave up more food than did Category A young.

Category A young initiated and received more
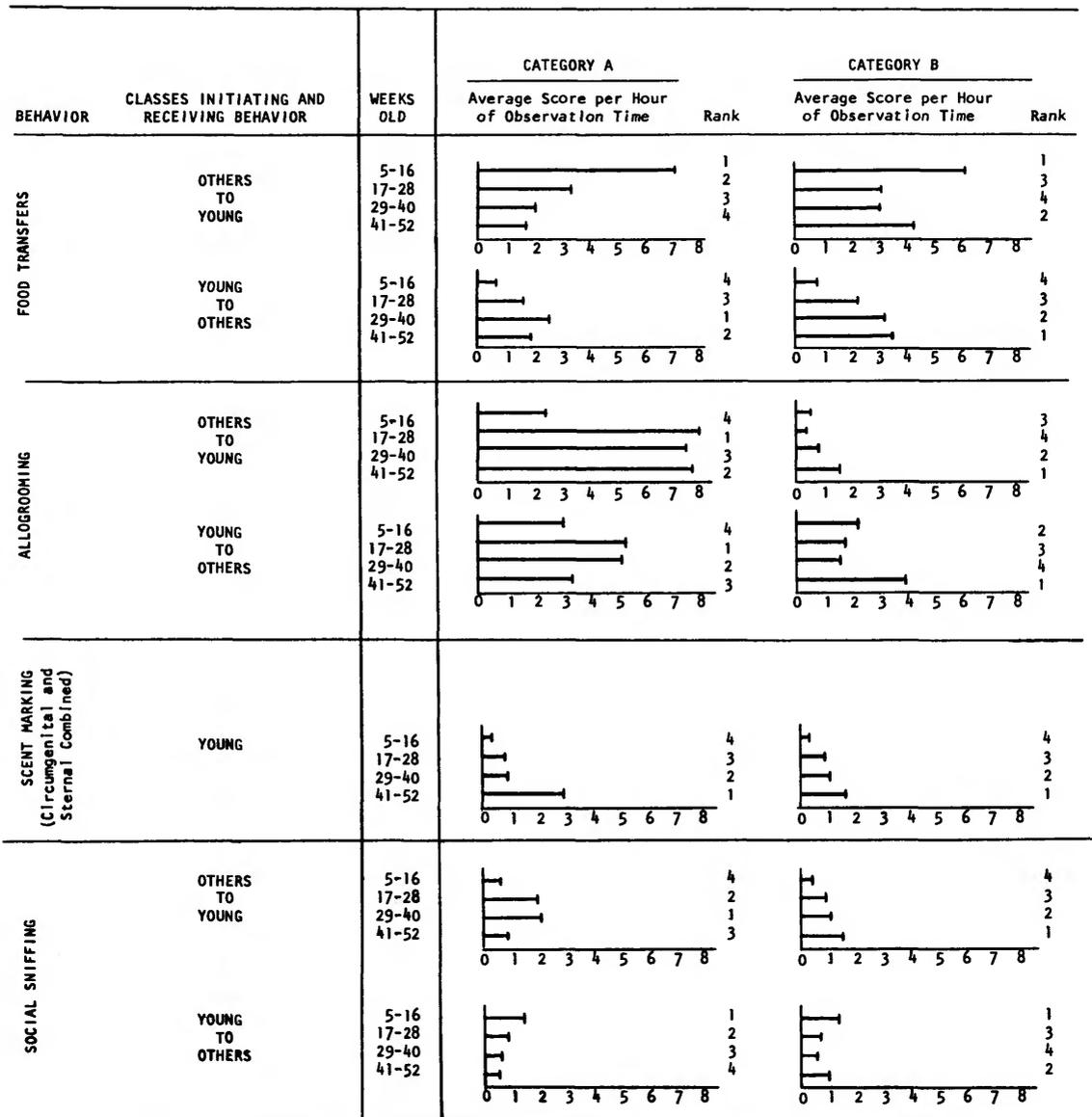
FIGURE 18.—Occurrence of selected behaviors among *Leontopithecus r. rosalia* focal tamarir ,
living in family groups (Category A = young living with older and younger siblings (n = 11);
Category B = young living without older and younger siblings (n = 3); scores are ranked
highest (1) to lowest (4) over the four age phases; ordinate scale = average score per hour of
observation).

BEHAVIOR	CLASSES INITIATING AND RECEIVING BEHAVIOR	WEEKS OLD	CATEGORY A		CATEGORY B	
			Average Score per Hour of Observation Time	Rank	Average Score per Hour of Observation Time	Rank
GENITAL INVESTIGATION	OTHERS TO YOUNG	5-16 17-28 29-40 41-52		1 2 4 3		1 2 3 4
	YOUNG TO OTHERS	5-16 17-28 29-40 41-52		4 1 3 2		4 3 2 1
MOUNTING BEHAVIOR	OTHERS TO YOUNG	5-16 17-28 29-40 41-52		1 2 4 3		4 3 2 1
	YOUNG TO OTHERS	5-16 17-28 29-40 41-52		1 3 4 2		-- -- -- --
AGONISTIC BEHAVIOR	OTHERS TO YOUNG	5-16 17-28 29-40 41-52		1 3 4 2		4 2 3 1
	YOUNG TO OTHERS	5-16 17-28 29-40 41-52		2 3 4 1		4 2 3 1

grooming and initiated more genital investigations than Category B young. In weeks 29–52 only, individuals with older and younger siblings initiated more scent marking and mounting than did young living with neither class of sibs. Young from family groups in which only one litter occurred were not exposed to and did not carry infants. Finally, although Category A young gave up and acquired less food than did Category B young, in weeks 29–40 Category A individuals became food providers, overall, rather than receivers. This did not happen with Category B young.

It seems that at least in the last two 12-week phases (weeks 29–52) without the presence of older and younger sibs, four types of behavior are inhibited in maturing tamarins (grooming, scent marking, genital investigation and mounting). At
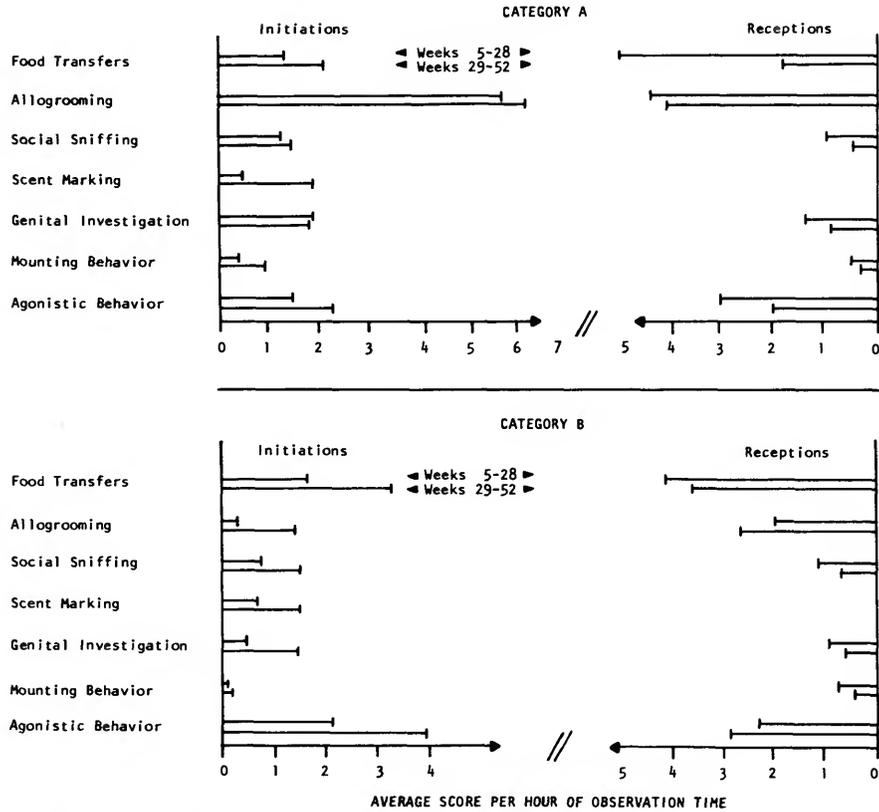
FIGURE 19.—Behavioral differences during early youth (weeks 5–28) and later youth (weeks 29–52) among *Leontopithecus r. rosalia* focal tamarins living with (Category A) and without (Category B) older and younger siblings. (The top bar for each behavior category = weeks 5–28; the second bar = weeks 29–52.)

the same time, two other behavior classes (agonistic behavior and food transfers) appear to be inhibited by the presence of older and younger siblings.

In sum, the presence of older and younger siblings appears to have an impact on the frequency of behaviors exhibited by focal young, especially in weeks 29–52 when new infant siblings appear in family groups. The presence of younger sibs seems to lower frequencies of agonistic encounters between focal tamarins and other group members.

In addition, reproductively active and successful parents clearly are models with whom offspring can interact, observe, and sniff, and who provide stimuli which, when learned or copied, presumably help maturing young become effective mates and parents. Parental pairs who had but one litter during the course of this study offered fewer stimuli to their offspring.

DISCUSSION

Scent marking in captive *Leontopithecus r. rosalia* young typically becomes common several months after the birth of a new litter of siblings, usually in weeks 29–52. But in two of three young males where the initiation of scent marking was delayed beyond 12 months of age, neither a littermate (twin sib) nor younger sibs were present in the

family group (Kleiman and Mack, 1980:12). This supports the obvious pattern apparent in weeks 41–52 (Figure 18), which shows that young living in groups without these sibs did not show a comparable increase in scent marking.

The lack of notable differences in agonistic behavior occurring in Categories A and B (Figure 18) suggests that parents, not siblings, are the most significant agonistic interactants. Hampton et al. (1966) came to a similar conclusion in their study of *Saguinus oedipus oedipus*. Moreover, Epple (1967:61), Snyder (1972:24–26), Ingram (1978), and Kleiman (1979) have observed in several captive callitrichid species that in some cases parents tolerated aggravating behavior from maturing young of the same sex less and less, to the point that such offspring may be driven from the group, attacked, or even killed. However, in this investigation, neither the expulsion of a subadult nor serious fighting was observed. One case of intense agonistic behavior, which involved two subadult males and, to some extent, their mother, was witnessed:

In family Group A₁, ♂M00716, a young subadult, had repeatedly mounted his twin brother, ♂M00715, and had exhibited aggressive play toward him. This behavior seemingly gave ♂M00716 dominant status. Some two months after the birth of a new sibling and during a subsequent maternal estrus, ♂M00716 exhibited a reversal in behavior. When ♂M00715 or even, at times, his mother approached ♂M00716, he began to exhibit desperate, panicky attempts to escape them. When ♂M00715 pounced or lunged in the direction of ♂M00716, the latter became frenzied and crashed headlong into the glass wall of the enclosure. As a result, ♂M00716 was removed from the family group for two weeks, after which he was successfully reintroduced, but no longer held dominant status over his brother.

Investigators working with other callitrichids have seen fighting between siblings. Fighting between older and twin offspring and between younger and older sibs has been reported in the common marmoset, *Callithrix jacchus* (Rothe, 1975:257; Stevenson, 1976a, 1976b; Box, 1977b; Sutcliffe, 1978), especially between male twins and between older and younger male sibs. In several instances fighting was sufficiently intense to cause one of the combatants to be expelled from the group (Box, 1977b; Rothe, 1975:257).

Among *L. r. rosalia* at the NZP, Kleiman (1979) has reported conflict between parents and offspring, fighting between older and younger sibs in family groups, sometimes with serious injuries, and intense aggression between twins, mainly of the same sex.

These reports suggest that agonistic behavior in *L. r. rosalia* and other callitrichids arises not just between parents and offspring but between offspring themselves. However, it is not yet known whether it is parent-offspring conflict, sibling conflict, or a combination of the two that results in the eventual peripheralization or expulsion of older offspring from the family group.

Sex Biases in Preferential Associations

SEX BIASES IN INFANT CARRYING

PREFERENCES OF OLDER GROUP MEMBERS.— When parents were observed carrying a single infant, in all four family groups in which heterosexual twins survived the first 12 weeks, fathers · carried sons more than daughters (three of four comparisons were significant) and, in three of the four groups, mothers carried daughters significantly more than sons (Table 7). In family group B₃, in which neither parent showed a strong preference, a subadult daughter and a pair of younger juvenile twins were present and frequently transported infants, thus relieving parents of much of their carrying duties. In group A₂, the only group for which there was sufficient data on the preferences of older siblings, the juvenile male preferred to carry his younger brother significantly over his younger sister (Table 8).

JUVENILE MIMICKRY OF PARENTS.—Juveniles have low infant carrying frequencies compared to parents. Among juveniles, females begin to carry first (in week 2 for new infants) when mothers are clearly the major carriers. Juvenile males begin to carry in week 3 when fathers are dramatically increasing their carrying time (Hoage, 1977). Carrying peaks for juvenile females in the third week after the birth of siblings. The third week postpartum is also the last week that mothers are

TABLE 7.—Data for the carrying of heterosexual twin offspring by parents (total carrying time was recorded in minutes, not scored in 30-second blocks; the time when both infants were carried by a parent is not included)

Parent	Minutes infants carried			Binomial test		Same sex pref.	Oppos. sex pref.
	♀	♂	Total	Z*	p≤		
Group A₂							
Mother	89.0	40.5	129.5	5.69	.001	yes	
Father	54.0	83.5	137.5	2.51	.006	yes	
Group B₂							
Mother	148.5	68.0	216.5	5.46	.001	yes	
Father	127.5	164.5	292.0	2.18	.015	yes	
Group B₃							
Mother	18.5	37.0	55.5	2.49	.006		yes
Father	92.5	103.0	195.5	0.75	.230	yes	
Group C							
Mother	132.5	36.0	168.5	7.40	.001	yes	
Father	26.0	180.5	206.5	10.70	.001	yes	

* p≤.05, binomial test after Downie and Heath (1974:141).

dominant infant carriers; male juveniles and fathers both peak during the infant's fourth week. When infants are three weeks old, juvenile males and females begin to show behavior patterns similar to mothers (and later of fathers) for dislodging or removing carried infants. From the fourth through the twelfth week, juvenile males carried infants about 9% more than did juvenile females, a pattern mimicking the behavior of fathers who, except for the first three weeks, carry infants more than mothers.

SEX PREFERENCES IN FIVE MAJOR BEHAVIORAL CATEGORIES

Forty-eight potential preferences, enumerated in Appendix V, were evaluated for each major

TABLE 8.—Carrying by juveniles of heterosexual twins in three family groups (data are in minutes; dash = insufficient data for comparison; J = juvenile; I = infant)

Interacting individuals	A₂	B₂	B₃	Total
J♀/I♀	–	7.0	4.5	11.5
J♀/I♂	–	4.5	8.0	12.5
J♂/I♀	54.0*	–	2.0	56.0
J♂/I♂	72.5*	–	1.0	73.5

* p≤.05, binomial test after Downie and Heath (1974:141).

category of behavior occurring during each 12-week phase after the Dependent Infant Phase. Significant results of these comparisons are summarized in Appendix VI.

SAME SEX PATTERNS.—In each of the four 12-week phases, except weeks 5–16, all significant preferences reflect same sex biases (Figure 20). Even during weeks 5–16, the majority of significant preferences are same sex biases. The most recurrent preferential associations occurred between young and parents of the same sex (Table 9). Between older or twin siblings and focal tamarins, as well as between focal tamarins and younger siblings, preferences of any kind were seldom seen.

Same sex interactions predominated over opposite sex interactions in each of the four 12-week phases for food transfers, allogrooming, social sniffing, and sexual and agonistic behaviors (Table 10). In fact, opposite sex biases occurred infrequently after weeks 5–16 (the Independent Infant Phase).

In weeks 5–16, focal tamarins were more initiators than receivers of significant same sex preferences (Table 11). While significant interactions were few over weeks 17–28 and 29–40, focal tamarins largely remained initiators rather than receivers of significant same sex preferences. In weeks 41–52, same sex biases increased for both

TABLE 9.—Sex biases in preferential interactions involving *Leontopithecus r. rosalia* focal tamarins (interactions between focal tamarins and younger siblings are omitted since they were not significant; numbers denote statistically significant cross-group comparisons listed in Appendix VI.)

12-week phase	Focal females interact with		Focal males interact with		Focal females interact with		Focal males interact with	
	Mother	Father	Mother	Father	Older or twin sisters	Older or twin brothers	Older or twin sisters	Older or twin brothers
5–16	5	1	2	1	0	0	1	1
17–28	1	0	0	1	0	0	0	1
29–40	2	0	0	3	0	0	0	0
41–52	5	0	0	5	0	0	0	0
Total interactions	13	1	2	10	0	0	1	2

focal tamarins and "others," but focal tamarins were initiators more than other group members.

Same sex preferences in food transfers and sexual behavior gradually declined over the four 12-week phases (Table 10). Significant same sex biases in social sniffing first appeared in weeks 29–40 and increased in weeks 41–52. Also, significant same sex involvement in allogrooming and agonistic behavior increased during weeks 29–40 and 41–52. Mounting was most prominent in weeks 5–16 and 41–52. Both heterosexual and homosexual mounting interactions were observed in these periods (Table 11). In weeks 29–52, the high incidence of same sex grooming interactions

initiated by others was very likely influenced by the presence of new infant sibs and by the maternal estrus period that typically follows. In weeks 41–52 the peak in agonistic interactions along with the peak in notable cases of mounting were

TABLE 10.—Sex biases of focal tamarins in five major behavioral categories (classes of individuals are not distinguished, see Table 9; numbers denote statistically significant cross-group comparison, see Appendix VI; numbers in parentheses denote the number of nonsignificant but notable instances of mounting behavior)

Behavior category	12-week phases				
	5–16	17–28	29–40	41–52	Total
Same sex biases					
Food transfers	4	1	1	0	6
Allogrooming	0	0	2	3	5
Social sniffing	0	0	1	2	3
Sexual behavior	3(2)	2(2)	(1)	1(2)	6
Agonistic behavior	0	0	1	4	5
Total	7	3	5	10	25
Opposite sex biases					
Food transfers	1	0	0	0	1
Allogrooming	0	0	0	0	0
Social sniffing	2	0	0	0	2
Sexual behavior	1(3)	0	(1)	1*(3)	1
Agonistic behavior	0	0	0	0	0
Total	4	0	0	0	4

FIGURE 20.—Sex biases in preferential associations between *Leontopithecus r. rosalia* focal tamarins and other family group members. Age class and sex of individuals are not distinguished (see Table 9).

* One significant case of opposite sex mounting was seen within family group C (p≤.05 binomial test, see Appendix VI).

TABLE 11.—Sex preferences of focal tamarins in five behavior categories expanded from Table 10 (interactions initiated by focal tamarins (sexes combined) are differentiated from initiations by others (ages/sexes combined); mounting data was insufficient for testing, except in one family group, thus sex-related interactions are here limited to genital investigation; numbers in parentheses indicate statistically nonsignificant, but notable instances of mounting behavior)

Behavior	12-week phases				Total
	5–16	17–28	29–40	41–52	
Same sex biases					
Focal tamarins initiate:					
Food transfers	2	0	1	0	3
Allogrooming	0	0	0	0	0
Social sniffing	0	0	1	2	3
Sexual behavior	2	2	0	1	5
Agonistic behavior	0	0	1	3	4
Total	4	2	3	6	15
Others initiate:					
Food transfers	2	1	0	0	3
Allogrooming	0	0	2	3	5
Social sniffing	0	0	0	0	0
Sexual behavior	1(2)	0(2)	0(1)	0(2)	1
Agonistic behavior	0	0	0	1	1
Total	3	1	2	4	10
Opposite sex biases					
Focal tamarins initiate:					
Food transfers	0	0	0	0	0
Allogrooming	0	0	0	0	0
Social sniffing	2	0	0	0	2
Sexual behavior	0(1)	0	0(1)	0(3)	0
Agonistic behavior	0	0	0	0	0
Total	2	0	0	0	2
Others initiate:					
Food transfers	1	0	0	0	1
Allogrooming	0	0	0	0	0
Social sniffing	0	0	0	0	0
Sexual behavior	1(2)	0	0	1*	1
Agonistic behavior	0	0	0	0	0
Total	2	0	0	0	2

* The one significant case of mounting behavior within a family group (see Appendix VI).

suggestive of the tension coupled with sexual interest apparently existing between parents and older offspring as the latter were nearing physical maturity.

IMPLICATIONS OF SPECIAL CASES.—Although same sex preferences tend to predominate across family groups, opposite sex biases do occur. Certain cases of same sex bias also deserve particular attention. Some selected cases of both are described below (see also Appendix VI).

In family group C, toward the end of weeks 41–52, the mother became severely ill and died. During the period when the mother was still alive, the focal female (♀M00886) yielded significantly more food to her father than to her mother. This pattern suggested a special interest, possibly sexual, on the part of this subadult female in her father.

In two family groups, during weeks 29–40 juvenile males preferred grooming pregnant or

newly parturient mothers over fathers. Why this did not happen in all groups with reproductively active mothers is not known, since such females might be expected to attract the interest of older offspring of both sexes.

Several significant opposite sex grooming and sniffing patterns were recorded. Although fathers preferred grooming sons over daughters in weeks 29–40, one father, in group B₃, preferred his daughter (a female twin) over his son (the male twin). This father had exhibited the same opposite sex bias before in weeks 17–28. The meaning of this preference is not clear since the young female had not yet reached subadulthood.

Young males exhibited a greater preference than did females for sniffing older or twin sisters in weeks 5–16. Young females sniffed fathers more than did young males in the same 12-week phase. As young achieve locomotor and feeding independence, such opposite sex biases may reflect general investigation of other group members or the sniffing of others to determine whether they possess food. In group C, however, after the death of the mother, the father sniffed his young subadult daughter significantly more than her twin brother. Having no access to other females, the adult male may have been investigating his maturing daughter as a potential mate.

During weeks 5–16, mothers initiated more genital investigation of young males than did fathers. Mothers also initiated more genital investigation with daughters than did fathers in the same 12-week period. Mothers in weeks 5–16 have been observed to inspect and lick the genitals of nursing infants with no apparent preference for either sex.

A number of conspicuous cases of heterosexual and homosexual mounting interactions occurred, although the data were insufficient for statistical analysis (Tables 10, 11, Appendix VI). The timing of the two types of mounting differed. During weeks 5–16 and 17–28 young males were homosexually mounted by older or twin brothers and, at times, by fathers. However, in only one instance did an older female (a mother) repeatedly mount a young female (her daughter). The daughter, in weeks 41–52, was a young subadult.

Such mountings may indicate same sex hierarchies within family groups. This possibility is supported by same sex biases seen in agonistic behavior during weeks 41–52 (Tables 10, 11).

Opposite sex mounting was most notable in group C in which the father began to mount his subadult daughter once his mate had died. Though not so striking as in group C, opposite sex encounters also occurred in other families. In weeks 41–52 the mounting of mothers in several groups by subadult male offspring (Table 11) point to a growing attraction by young males to their mothers, even though no true copulations were observed (Appendix VI).

Data on agonistic behavior suggest that weaning, rather than any kind of preferential bias, is probably the stimulus underlying agonistic interactions in weeks 5–16. For example, the 5 to 16-week-old focal male in group B₂ initiated agonistic behavior more with his mother than father, while in group B₃, the 5 to 16-week-old focal female, more than her twin brother, initiated agonistic behavior with the mother.

In general, opposite sex biases in agonistic behaviors are infrequent and show no clear patterns. Same sex preferences predominate and are most significant in weeks 41–52 when focal tamarins are subadults. Significant sexual biases in agonistic interactions occur more frequently between parents and young than between siblings (Table 9). The interactions occurring in group C illustrate the strained relationships between parents and like-sexed offspring:

With the death of the mother, the father (♂M00276) began to mount, though not copulate with, his 41 to 52-week-old daughter (♀M00886). At the same time, the father increasingly directed agonistic behavior at his daughter, but even more so at his son (♂M00885). The father was aggressive toward the twins during their play, huddling, and sometimes during ♂M00885's movements toward his father. Overall, the father directed significantly more agonistic behavior toward his son than toward his daughter (p ≤ .001, binomial test). The father appeared to be dominating his subadult son while investigating his daughter as a potential mate.

DISCUSSION

Some reports of same sex preferences are available in the literature on callitrichids. Common

marmoset mothers (*Callithrix jacchus*) nurse daughters more than sons; also fathers carry sons more than daughters (Ingram, 1977a:816–817, 1977b). *Callithrix jacchus* juvenile males may prefer to carry a male infant over a female (Box, 1975b:427). Young female *C. jacchus*, 8.5 to 26 weeks old, groom mothers more frequently than they groom their fathers (Woodcock, 1978:170). This same bias occurs in *Saguinus mystax* (Box and Morris, 1980:62). In *Saguinus fuscicollis*, aggression is common between parents and like-sexed offspring (Epple, 1972, 1975a:202). Aggressive same sex interactions are also reported for captive lion tamarins in a Florida facility (DuMond, 1971). Although aggression is infrequent among NZP *Leontopithecus r. rosalia*, when it does occur it is more serious between females than between males (Kleiman, 1979). Two females have been killed in recent years, apparently by mothers and sisters.

Opposite sex preferences in marmosets and tamarins are also recorded. In *C. jacchus*, fathers are the predominant groomers of daughters, and mothers are the principal groomers of sons (Woodcock, 1978:175–177; Rothe, 1971). In one family of *S. mystax*, the father groomed his daughter more than he groomed his son (Box and Morris, 1980:62). *Callithrix jacchus* male juveniles occasionally mount their mothers and adult males mount daughters, but without intromission (Abbott, 1978).

Same and opposite sex preferences may shift over time. In one group of *C. jacchus* with recently delivered heterosexual twins, the mother groomed her infant daughter more than her son (Box, 1975b:430). Later, however, when the infants were between 5 and 23 weeks old, the mother's preference reversed.

It must be recognized that in some instances one or more individuals can obscure preferential biases by initiating high levels of certain behavior with others, regardless of the sex of the recipients. For example, in this study, across groups in weeks 5–16, mothers yielded significantly more food to daughters than did fathers—an apparent same sex bias (Appendix VI). However, in the same 12-week period, mothers also gave up more food

to sons than did fathers—an apparent opposite sex bias. It is evident that the correct interpretation of this behavior is that in weeks 5–16 mothers yield more food to infants of both sexes than do fathers (mothers also take the initiative in weaning during this period).

In *C. jacchus*, fathers more than mothers tend to groom both male and female young in the first year of life (Woodcock, 1978:175–177). On the other hand, most offspring of each sex groom mothers more than fathers. The attraction of these young to their mothers, however, seems to depend on the mother's frequent pregnancies. Woodcock (1978:167) further suggests that, because in some large *C. jacchus* family groups the oldest offspring (between 13 and 20 months) are more involved with carrying newborn infants than are younger siblings (also Box, 1975b:426), younger infants and juveniles of each sex may exhibit more grooming of those individuals who carried them frequently during their first weeks of life.

Problems such as these were evident only occasionally in the numerous statistically significant cross-group comparisons listed for lion tamarins in this study. Clear preferences were usually apparent.

For young *L. r. rosalia* at the NZP, patterns of homosexual mountings in weeks 17–28 and occasionally in weeks 41–52, plus the increases in agonistic behavior in weeks 41–52, are suggestive of the existence of a dominance hierarchy, particularly among males. Agonistic encounters were especially strong between young and like-sexed parents but were seen sometimes between young and older and twin siblings. Investigators working with other callitrichid species have observed similar patterns. They have interpreted such behaviors as indicative of same sex hierarchies (Epple, 1967:61, 1972; DuMond, 1971; Snyder, 1972:30; Rothe, 1975:257). Undoubtedly within stable family groups of captive marmosets and tamarins, the parents would normally remain dominant until death or separation.

A final implication of the predominance of same sex biases in the socialization of *L. r. rosalia*

is that role modeling or sex-role identification may be taking place. However, until more precise manipulations can be made whereby a number of young can be raised without exposure to older animals of like sex, this idea remains a hypothesis to be tested.

The Callitrichid Biological and Behavioral Configuration

Among nonhuman primates, there is no family other than the Callitrichidae that exhibits the following configuration of traits: (1) little or no sexual dimorphism, (2) multiple births, typically twinning, (3) monogamous social structure, (4) nuclear families composed of parents and offspring from successive litters, (5) paternal and older offspring investment in the rearing of infants, (6) food sharing and stealing, (7) sexual biases in preferential associations during the socialization of young, and (8) extended residence within the family group of older offspring (past sexual maturity), who do not breed and who serve as parental assistants.

The behavioral traits were first determined from captive investigations and short-term field studies. The given configuration is supported by the recent advent of long-term field investigations, but these recent studies also indicate that some additional characteristics must be considered. For example, Dawson (1977:33) and Dawson and Dukelow (1976) observed a small number of subordinate subadults and adults living on the periphery yet attached to core groups (nuclear families) of *Saguinus oedipus geoffroyi*. It is likely that some of the peripheral animals were older offspring of the parental pair, but others may have been immigrants from neighboring groups. Although the origin of peripheral animals and their movement between groups is in need of further study, their existence suggests a mechanism for controling the size of each nuclear family.

Monogamy combined with paternal investment in the rearing of young has been reported for a number of primates, both in the field and in captivity. Among New World primates, *Callicebus moloch* (Mason, 1968; Moynihan, 1966), *Aotus trivigatus* (Moynihan, 1964), *Callimico goeldii* (Heltne et al., 1973; Lorenz, 1972), and *Pithecia monachus* (Napier and Napier, 1967) exhibit these traits. Among Old World primates, this social system has been found in the Hylobatidae (gibbons and siamangs) (Carpenter, 1940; Ellefson, 1974; Chivers, 1972, 1974), in *Presbytis potenziani* (Tilson and Tanaka, 1976), and in two lemuriformes: *Indri indri* (Pollock, 1975) and *Lemur mongoz* (Sussman and Tattersall, 1976).

According to one analysis of paternal investment among mammals, the monogamous marmosets, tamarins, gibbons, and siamangs show the highest paternal investment in the rearing of young (Kleiman, 1977a:55). Adult male siamangs carry young, sleep with them, and maintain close proximity to young during the day, thereby acting as a principal socializing agent in the first year of life (Chivers, 1972:123, 1974:214). Adult male gibbons are not known to carry young or exhibit an equivalent interest in the social development of offspring.

Outside the Callitrichidae, reports of food sharing or stealing (food transfers) are limited among nonhuman primates. Starin (1978) observed "begging" and food "taking" between family members in a wild South American titi monkey group, and Berkson and Schusterman (1964) and Schessler and Nash (1977) have described food sharing in captive gibbons. For nonmonogamous higher primates, reports of food transfer behavior have been equally rare, although food sharing or stealing has been described for *Ateles geoffroyi* (Dare, 1974), *Gorilla gorilla* (Schaller, 1963), *Pygathrix nemaeus* (Kavanaugh, 1972), and *Pan troglodytes* (Teleki, 1973; McGrew, 1975).

Among higher primates, only the Callitrichidae normally have multiple births. In the lemuriformes and lorisiformes, this characteristic is considered a conservative retention, while in the callitrichids it is considered a secondarily derived trait (Ford, 1980:31). Heterosexual callitrichid twins occur frequently since twins are characteristically dizygotic (Hill, 1926, 1932; Wislocki,

1939). This tendency affords an investigator a unique chance to observe differences in interactions according to sex.

Among monogamous anthropoid primates, preferential associations based on sex have not been a regular focus of socialization studies. Monkeys and apes, regardless of social structure, normally bear single young. The spacing of single offspring does not lend itself to easy analysis of differential socialization. Nevertheless, some sexual biases have been described for nonmonogamous genera, such as macaques and baboons. In captivity, male rhesus monkey infants are allowed more freedom and are treated more aggressively by their mothers than are female infants. Young females stay closer to, and are restrained more by, their mothers (Hansen, 1966; Mitchell, 1968; Jensen et al., 1968). Adult male baboons have been observed in captivity to groom and inspect the genitalia of male infants more than female infants (Rowell et al., 1968). Even so, these biases have not been described for as many behavior categories or for as long a period of time as has been reported in this investigation.

Monogamous nuclear families with extended residence of older offspring acting as parental assistants is uncommon in nonhuman primates, or even among mammals in general (Kleiman, 1977a). Rarer still are mammals whose offspring remain past puberty in the monogamous family unit, do not breed, and assist parents in raising siblings from more than one litter. Species reported to exhibit this pattern include African hunting dogs, *Lycaon pictus* (Van Lawick, 1970; Frame et al., 1979), coyotes, *Canis latrans* (Ryden, 1974; Bekoff and Wells, 1980), and the dwarf mongoose, *Helogale undulata* (Rasa, 1972, 1977; Rood, 1978, and pers. comm.).

Implications

This study indicates that, among captive *Leontopithecus r. rosalia* in the first year of life, preferential associations based on sex do exist and that same sex favoritism tends to dominate these biases. From such results one might infer that some form of identification or role modeling takes

place between fathers and sons, between mothers and daughters, and, perhaps to a lesser extent, between older and younger brothers and between older and younger sisters. Mimicry of same sex parental patterns is particularly suggestive of role modeling.

Subadult lion tamarins in weeks 41–52 exhibit a combination of behavioral and physical characteristics indicating approaching adulthood. First, for both sexes circumgenital scent marking becomes regular and sternal marking begins. Second, although opposite sex interactions appear infrequently in the first 40 weeks of life, they become more frequent in weeks 41–52. Young males sometimes mount their mothers. Furthermore, the father in one group mounted his daughter after his mate became ill and subsequently died. Third, agonistic interactions peak during weeks 41–52 for young males and females, and the frequency of such encounters is especially high between offspring and parents of the same sex. Finally, young subadults reach a size equivalent to the lower range of adult variation.

Since subadults are attracted to members of the opposite sex, incipient preparations for courtship or for securing a mate may begin in the natal social unit. At the same time, it is evident that subadulthood marks a period of growing tension between offspring and other family members, especially parents. Even so, the potential threat to the parental pair cannot be very strong since in *Callithrix jacchus*, *Saguinus fuscicollis*, and *Saguinus oedipus geoffroyi* nonbreeding offspring have remained in their family groups for two to three years without fighting with parents (Epple, 1975a:204; Rothe, 1975:257). NZP's *L. r. rosalia* have stayed in family units up to 20 months with no serious fighting. Yet, since the strongly bonded parental pair inhibit full sexual maturation and breeding status in young adults (Epple, 1975a:212; Rothe, 1975:266; Coimbra-Filho, 1969; Abbott and Hearn, 1978:162), it is not clear why offspring remain in their natal families when sexual maturity could be reached outside the group (see Appendix IV for first matings and conceptions in callitrichids.)

Certainly part of the answer is to be found in

the requirements of the monogamous relationship. Recent discussion has centered on attempts to define the relationship, its ecological correlates, and its relative success as an adaptive strategy (Eisenberg, 1966; Orians, 1969; Alexander, 1974). Of special interest have been the degree of male involvement and the ramifications such investment has for the rearing of offspring (Eisenberg, 1977; Eisenberg et al., 1972; Trivers, 1972, 1974; Kleiman, 1977a; Redican, 1976). When male involvement includes substantial assistance in the care and feeding of infants, it becomes a defining characteristic of what Kleiman (1977a:39) terms "obligate" monogamy, a specialized system in which offspring exhibit delayed sexual maturation in the presence of parents and remain in the family group providing aid in the rearing of young. Though perhaps a valid classification, specific behaviors of nonbreeding juveniles and subadults within such a system have yet to be delineated.

Among captive lion tamarins, adult males aid in all aspects of child rearing, but the continued residence of offspring in the family unit provides extra assistance. Besides supplying food to pregnant mothers, postpartum mothers, infant carriers, and newly weaned young, older offspring carry, play with, and babysit younger siblings, giving parents time to rest and feed. Probably, in the wild as in captivity, they also serve as potential resource and predator sentinels. In her long-term field study, Neyman (1977:58) observed that in the wild older *S. o. oedipus* juveniles, as well as parents, attempted to guard infants during encounters between groups. Such behavior on the part of young could be considered a case of "parental manipulation of progeny" (Alexander, 1974). However, this concept relies on the notion that such assistance increases the fecundity of the breeding pair at the expense of fertility in older offspring; the result is an increased investment of the helper class in the survivorship of infant siblings who share as many genes with them as would their own children (50%). According to Hamilton's (1964, 1972) "kin selection" theory, by improving the fitness of younger brothers and sisters, who will presumably be breeders, helpers

are ultimately improving the chances of their own genes appearing in the next generation. Continual investment would militate against the expulsion of older siblings from the group.

Such an explanation does not take into account the necessity of adequate socialization of current offspring required for the production and survival of subsequent generations. In higher primates, a large proportion of social behavior is learned. Only through adequate socialization can offspring practice and absorb the complexities of vital behaviors such as courtship, mating, grooming, infant carrying, and food sharing and stealing.

Certainly much is gained by remaining in the family group. While serving as parental helpers, older offspring acquire a great deal of parental experience. Among primiparous *L. r. rosalia*, success in rearing first-born infants depends on the length of infant handling exposure each parent had while living in its original family unit (Hoage, 1977). Coimbra-Filho and Mittermeier (1976) came to a similar conclusion when breeding *L. r. rosalia* with *L. r. chrysomelas*. Exposure to two litters in the juvenile and subadult phases appears to optimize this training. Without such experience, mated pairs have great difficulty in rearing first-born and, in some cases, subsequent litters. Thus, although infant caretaking behavior may seem to be a case of altruistic behavior, it also has direct advantages for older offspring, as well as for parents and infants.

Young lion tamarins at the NZP make no great sacrifices by remaining with the natal group. For instance, they do not give up the most nutritious or desirable food to the extent that they receive no part and become malnourished over time. Indeed, often while a potential recipient screams in frustration the "altruist" eats its fill or takes several bites before yielding the food. Such behavior does not conform to the evolutionary definition of altruism as genetically disadvantageous behavior rendered for the benefit of others (Hamilton, 1964, 1970; E. O. Wilson, 1975).

Finally, by remaining in the family unit, older offspring receive protection not available when alone, such as mutual warning calls, and assist-

ance and defense when faced with a predator. Here, too, since competition among members of the same family is usually minimal and does not regularly generate conflict, nonbreeding older offspring have access to food resources and, of course, the food transfer system based on sharing and stealing.

Thus, what appears to be in operation is neither altruism nor manipulation, but a maximization strategy. In such a scheme parents receive assistance from their offspring, who increase their own chances of survival while gaining practical experience in parental roles, experience which is vital to the survival of succeeding generations. Lastly, infants benefit from the protection and care provided by all older family members.

The key factor is the length of time offspring spend in the family group under normal circumstances. Employing Trivers' (1974) theory of parent-offspring conflict, at some time in the maturation process it is beneficial for parents to peripheralize an offspring, presumably at the moment when caring for the young begins to jeopardize the mother's future mating and success in subsequent infant rearing. Peripheralization should coincide with the time when the offspring is best suited both to survive on its own and to reproduce, thereby increasing the mother's genes in following generations.

With the reproductive potential to produce litters of twins twice a year (gestation is between 125 and 160 days in callitrichids, with *L. r. rosalia* averaging approximately 128 days), optimally a marmoset or tamarin mother could raise four offspring annually (this has, in fact, happened regularly in the *L. r. rosalia* colony at the NZP). With 100% infant survival, an eight-member family could arise in a matter of 18 months.[2] How-

ever, a 50% infant mortality rate has been reported for *Sanguinus o. geoffroyi* in Panama (Dawson and Dukelow, 1976). For *S. o. oedipus* in Columbia, an annual breeding appears to be the norm (Neyman, 1977). Therefore, given (1) the need for older offspring to be exposed to one or two litters of siblings, (2) inconsistent lengths of infant survival due to disease, falls, fluctuating resources, crowding, and predation, combined with (3) a possible 12-month interbirth interval, a nonbreeding older offspring could remain with the family group long after it has achieved physiological maturity.

Consequently, Trivers' (1974) view may be modified to include the idea that as long as the mother does not reproduce consistently, and the older offspring performs a useful function in the group (food and predator locating, infant carrying, and food sharing) and does not interfere with parental mating or food acquisition, there is no need for its expulsion from the nuclear family group.

Still, as the nuclear family grows, dispersal of older young would inevitably become necessary. As suggested in this study, peripheralization of older offspring can result from aggression between parents and older offspring and between offspring themselves. In lion tamarins at the NZP, such conflict is most often seen between individuals of the same sex and may be even more intense between same sex sibs than between parents and like-sexed offspring (Kleiman, 1979). Thus, hostility on the part of parents toward highly aggressive young may cause the latter to move out of the family group, while sibling conflicts may be responsible for the peripheralization of more subordinate offspring.

Serious fighting among lion tamarins at the NZP is not frequent. Although open, intense aggression does occur, the data presented in this research indicate that within family groups, expulsion or peripheralization seems to derive from a gradual buildup of tension in the form of low-intensity aggressive encounters between family members of the same sex.

Dawson (1977:31–35) and Dawson and Duke-

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[2] Despite having small family groups, these animals have a high reproductive potential, and when ecological factors are favorable, population growth and dispersion could be very rapid. Relative to other primate species, marmosets and tamarins have been labeled "r" selected (Eisenberg, 1977); see discussions of family growth potential in Ingram (1977a, 1977b), Dawson (1977), Dawson and Dukelow (1976), Eisenberg (1977), and Kleiman (1977b).

low (1976) have described a situation in the wild that indicates to what outcome this build up of tension may lead. He observed nuclear family-sized groups in *Saguinus o. geoffroyi*. Attached to these groups but living on the periphery were a number of adult or nearly adult individuals. Occasionally such individuals emigrated to other areas, joining neighboring groups. Sometimes, certain individuals reappeared, attached to their original groups.

These observations suggest that a mechanism exists in the wild, as well as in captivity, for moving older offspring out of the natal family unit and into a position to find mates and become reproductively active. Breeder status could be achieved by (1) replacing a deceased parent in the natal unit, (2) pairing with a mate from another group, thus starting a new family group, or (3) replacing a deceased breeder in a neighboring group. With such a mechanism a callitrichid family with a gradually expanding core of young can maintain equilibrium with its environment and meet the needs of its maturing offspring.

Appendix I

Summary of Maturational Phases
of *Leontopithecus rosalia rosalia*

Five maturational phases are summarized. Physical development is briefly sketched. The behaviors of family group members serving as probable stimuli for young are emphasized as is the response of young to such behavior. Additional behaviors of maturing young are also noted.

DEPENDENT INFANT PHASE

(1–4 weeks)

A healthy twin infant at birth weighs approximately 60 g (9% of average adult size); a singleton may weigh 5–10 g more. A 60 g infant would likely be 24.1 cm from head to tail (42% adult size), while head to rump length would be approximately 10.4 cm (38% adult size). During this phase, mothers may come into estrus within two to four weeks postpartum; pregnancies are uncommon, although the mothers of three focal tamarins conceived during this time.

Behavior of group members

1. Infant carrying: infants carried 90% of observation time.
   a. All older family members participate in carrying.
   b. Mothers, then fathers, become principal carriers; older male and female siblings are secondary or tertiary carriers.
2. Great sensory interest in new infants by older siblings (touch, sniff, mouth); less interest by fathers except when soliciting to carry.
3. Beginning week 3 infants are dislodged or rejected by mothers, then by older siblings; fathers do not regularly reject infants until weeks 5–16.

Behavior of young

1. Infants develop locomotor, visual, and eye-hand coordination while on carriers; use carriers as activity platform and seldom get off.

2. Great sensory interest (taste, touch, observe, and smell) in the environment; lean or reach off carriers.
3. In response to forceful rejection, infants exhibit first agonistic behaviors by vocalizing, biting, pouncing, slapping, lunging, and tail thrashing.

36

Advanced Infant Phase

(5–16 weeks)

Infants weigh, on average, 294 g by week 16, approaching 42% the adult average. By 10 weeks, total length may be about 39.5 cm (69% adult size) with head-to-rump length at approximately 17.0 cm (66% adult size). The mothers of five focal tamarins conceived in this period; three such young interacted with mothers during the last half of their pregnancies.

Behavior of group members

1. By week 5 after birth infants are carried 75% of the observed time; by week 12, 15%; and by week 14, less than 5% and then only by the father when frightened.
2. Infants are subjected to substantial agonistic behavior as a result of being rejected by carriers. Mothers are particularly intolerant of infants' attempts to nurse and to be carried; to a lesser extent older sibs are also intolerant; fathers begin rejecting infants in week 7.
3. Weaning begins early in week 5, nursing ceases around week 13.
4. Older family members yield food (through shares or steals) to infants in the weaning process; others also yield food to young more than at any other time.
5. Infants are sniffed more than in any other 12-week phase; infants receive more anogenital investigations than at any other time; also parents and older sibs first attempt to mount infants (infrequently).

Behavior of young

1. First sustained independent investigation of environment and of other group members.
2. As in weeks 1–4, in response to forceful rejection, infants exhibit agonistic behaviors by vocalizing, biting, pouncing, slapping, lunging, and tail thrashing.
3. First eating of solid foods independent of food transfers by others.
4. Food acquisitions from others peak; infants first share food to others after week 9.
5. Males initiate more anogenital contacts than in any other phase. Also, after week 9, first dexterous grooming of others.

Young Juvenile Phase

(17–28 weeks)

Young weigh, on average, about 509 g, about 72% of the adult mean. Mothers most frequently come into estrus and conceive in this phase (Table 3). Three young experienced the birth of new siblings in this phase (of 4 sibs born, 2 survived infancy).

Behavior of group members

1. Focal young are rarely carried.
2. Scent marking increases by mothers, whose hormonal [pheromonal] levels appear to be high.
3. Sexual behavior between parents can be observed and sniffed at close range by offspring.
4. Grooming between parents increases.

Behavior of young

1. Young become peers or playmates for twin and older siblings.
2. Focal males and females perform first (although irregular) circumgenital scent marking.
3. Females initiate more sniffing and anogenital investigation contacts than in any other phase.
4. Males initiate more allogrooming in this phase and in weeks 29–40 than at any other time.

ADVANCED JUVENILE PHASE

(29–40 weeks)

At 40 weeks young weigh approximately 540 g, nearly 77% the adult average. By 36.5 weeks, total length is approximately 53.9 cm (94% adult size), with head-to-rump length at about 23.3 cm (90% adult size). Nine advanced juveniles experienced the birth of new siblings in this phase (of 11 sibs born, 6 survived infancy). As in the Dependent Infant Phase, mothers may show a postpartum estrus within 4 weeks after delivery; however, pregnancies are infrequent (the mothers of three focal tamarins conceived at this time).

Behavior of group members	*Behavior of young*
1. New infants are usually born into family groups at this time. New infants show most of the activities listed in the Dependent Infant and Independent Infant phases.	1. As advanced juveniles, young tamarins exhibit most of the behaviors listed for older siblings in the Dependent Infant, Advanced Infant, and Young Juvenile phases: great sensory interest in infants; first carry, then reject infants; yield food, share food with infants (both sexes yield more food than at any other time); and infrequently mount infants (males only).
2. Other group members initiate more allogrooming of focal females than in other 12-week phases.	2. Males initiate more sniffing and allogrooming than in other phases.

YOUNG SUBADULT PHASE

(41–52 weeks)

Subadults weigh, on average, over 580 g, almost within the lower range of adult variation, but only about 82% of the size of an average 2-year-old, or older, adult. Although large and clearly nearing sexual maturity, within stable family groups, subadults do not become sexually active. They do not breed (69 weeks is the earliest conception on record for a newly mated female at the NZP). Mothers of five focal tamarins came into estrus and conceived in weeks 41–52. Five focal tamarins experienced mothers in the last half of pregnancies. Four focal tamarins experienced the birth of new siblings in this phase (of 6 sibs born, only 2 survived infancy).

Behavior of group members	*Behavior of young*
1. Younger siblings enter Young Juvenile Phase.	1. Young subadults exhibit many behaviors listed for older group members in Young Juvenile Phase.
2. Parental scent marking and sexual behavior increases. Parents allow offspring to observe and sniff at close range.	2. Circumgenital scent marking becomes regular for males and females; first appearance of sternal marking in young.

3. Peak for agonistic behavior initiated toward young subadults by others.

4. Although relatively infrequent, in one family the mother mounted her subadult daughter; in another the father mounted his subadult daughter (after his mate had died).

5. Grooming between parents increases.

3. First year peak for both sexes in initiating agonistic behavior; arch posturing and walking with piloerection first appears and becomes regular.

4. Females exhibited first occasional mounting behavior of others; males' infrequent mounting behavior peaks. In four families, subadult males targeted mothers for at least one mounting interaction during this phase.

5. Females exhibit more allogrooming than in other phases.

Appendix II

Weights and Body Measurements
of Immature and Adult *Leontopithecus rosalia rosalia*
at the National Zoological Park

Body measurements and weights were taken for 14 infants that died within five days after birth. Weights were obtained for 28 animals surviving beyond infancy (21 adults and 7 young). Body measurements were obtained for 2 older infants, 1 juvenile, and 1 adult (measurements were obtained only when animals had died or were immobilized for medical examination).

At birth, male and female lion tamarins differ little in weight (Table 12). Except for two infants (♀101593, 74.6 g, and ♂M00862, 53.8 g), all individuals in each litter class (singleton, twins, triplets) weighed within 5 g of each other.

Differences in size among litter classes are also reflected to some extent in body measurements

Table 12.—Data on full-term *Leontopithecus r. rosalia* infants born between February 1974 and March 1977 who died at birth or within 5 days after birth

Sex and number	Weight* (g)	Day of death	Singleton	Twin	Triplet
♀101593	74.6	Stillborn	X		
♀101525	66.5	Day 2	X		
♂101640	63.9	Stillborn	X		
♀M01210	63.2	Stillborn		X	
♂101622	61.3	Stillborn		X	
♀M01211	60.1	Stillborn		X	
♂M01248	59.4	Day 3		X	
♀M01249	58.2	Day 2		X	
♂M00862	53.8	Day 5		X	
♂102001	53.5	Day 5			X
♀M01188	52.1	Stillborn			X

* Range, 52.1–74.6 g; mean, 60.6 g; median, 60.1 g; standard deviation, 6.22 g.
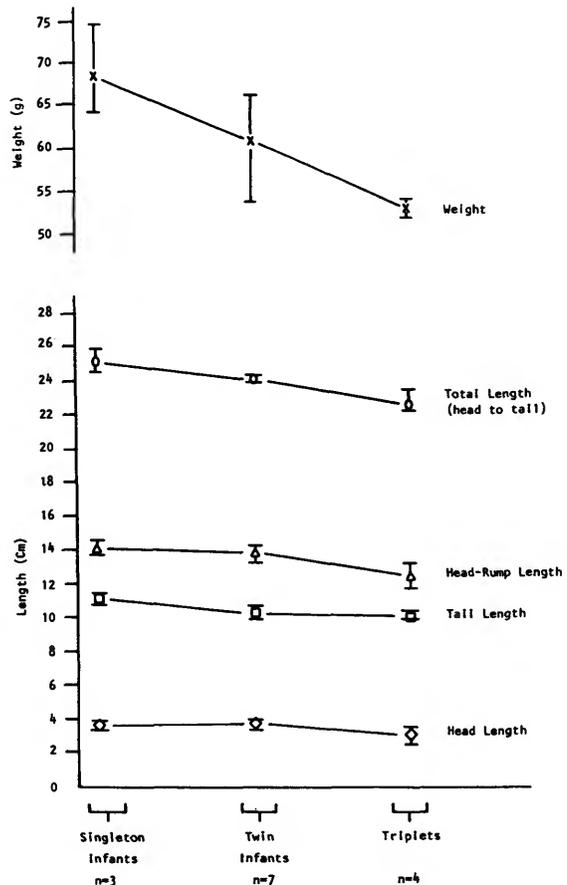
Figure 21.—Body weights and measurements for *Leontopithecus r. rosalia* infants at the National Zoological Park that were either born dead or died within 5 days after birth. All infants were considered full term. (Vertical bar bracket = ranges of weight or length; symbol = average weight or length).

40
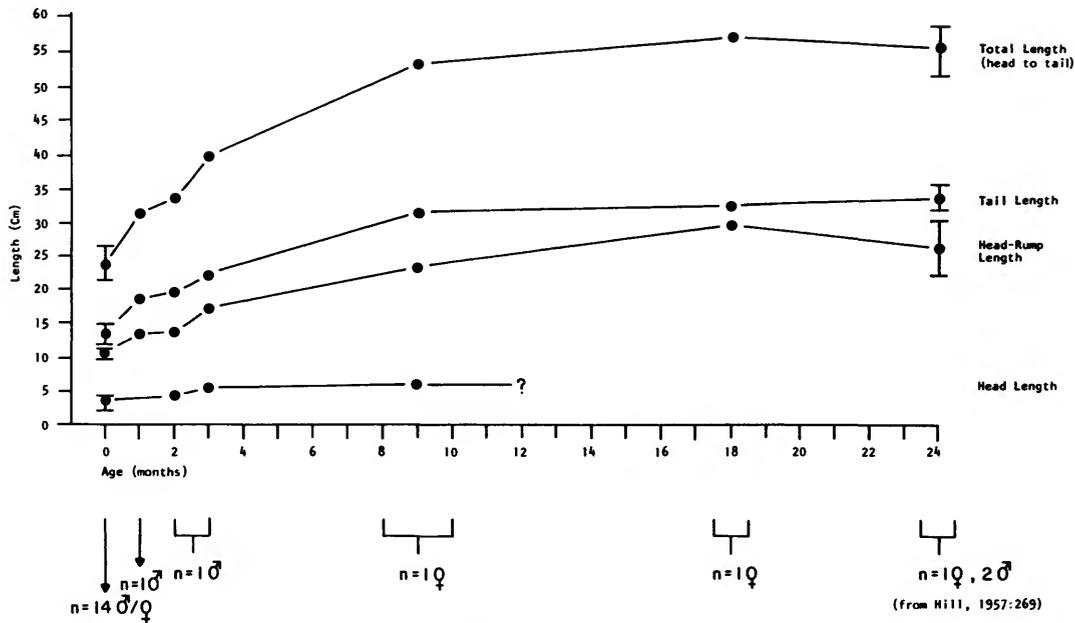
FIGURE 22.—Body measurements for *Leontopithecus r. rosalia* at the National Zoological Park. Measurements for 14 neonates are derived from Figure 21. Other measurements are derived from data taken for four additional NZP lion tamarins plus information provided by Hill (1957) for three fully adult animals (≥65 weeks old).

(Figure 21). Although a twin or a triplet may be smaller than a singleton, the burden on the mother (or any other carrier) is significantly less when carrying a singleton than when carrying twins or triplets.

The limited data indicate that young at 9 months are beginning to reach the lower ranges of adult variation and at 18 months have reached adult body measurements (Figure 22). Additional information is needed to corroborate these data.

Young lion tamarin females lag slightly behind males in weight gain up until 15 months of age (Figures 23, 24). It may be that immature males outcompete females for access to food; however, more data is needed for verification.

Adult males and females, 2 years of age or older, differ little in size (males range from 611 to 777 g, x̄ = 715 g; while females range from 588 to
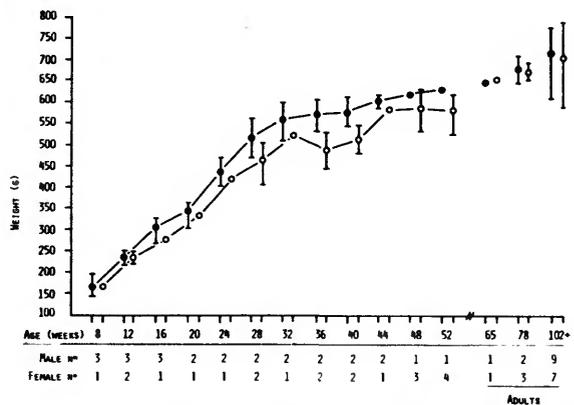
FIGURE 23.—Weights of maturing and adult (≥65 weeks) *Leontopithecus r. rosalia* from the National Zoological Park records (bar bracket = range in weight; solid circles = average weight for males; open circles = average weight for females).
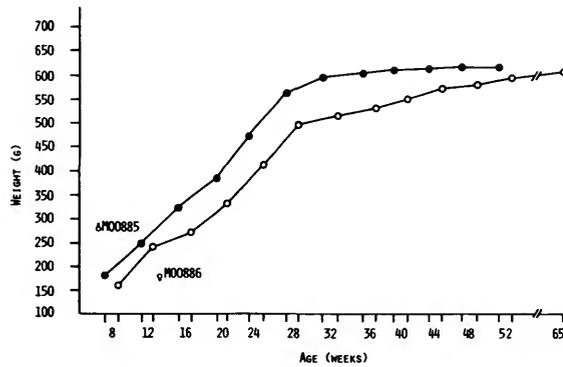
FIGURE 24.—Weight gain in one heterosexual part of *Leon-topithecus r. rosalia* twins.

794 g, x̄ = 703 g) (Figure 23). Maturing young in weeks 41–52 clearly overlap adults in weight range. On average, 41–52 week old subadults are 81% the size of adults 2 years of age and over. However by 1.25 to 1.5 years (65–78 weeks), young adults weigh from 648 to 711 g (x̄ = 668 g), well within the range of adult variation. These weights indicate that maturing young reach adult size sometime between 15 to 20 months of age. This is when most marmoset and tamarin species reach physiological sexual maturity (see Appendix IV).

Appendix III

Comparative Ontogeny of Selected Behaviors in Callitrichid Monkeys

(Behaviors were sought that match those listed in Figure 12 and Tables 3 and
4 for the young of *Leontopithecus rosalia rosalia*)

Behavior and species	First appearance of behavior	Source
INFANT CARRYING-RELATED BEHAVIOR		
Family member other than mother carries newborn infant		
Callithrix jacchus	1st day	Box, 1975b:426
Cebuella pygmaea	1st day	Christen, 1974; Ochs, 1964
Saguinus fuscicollis	1–10 days	Epple, 1974b:234
Saguinus midas	1st week	Christen, 1974
Callimico goeldii	2nd week	Heltne et al., 1973
	3rd week	Pook, 1978:6
Infants observed off and independent of carriers		
Callithrix jacchus	14–23 days	Epple, 1967:62, 1970b:62; Box, 1975b:427, 1977a:476
Saguinus fuscicollis	11–15 days	Epple, 1975b:228
Saguinus oedipus geoffroyi	21–23 days	Epple, 1970b:63
Saguinus oedipus oedipus	~23 days	Epple, 1967:62
Callimico goeldii	21–28 days	Heltne et al., 1973
	5–6 weeks	Pook, 1978:6
Leontopithecus rosalia	~25 days	Altmann-Schönberner, 1965:230
Infants rarely carried		
Callithrix jacchus	8–10 weeks	Epple, 1967:62
Saguinus oedipus geoffroyi	~21 weeks	Epple, 1970b:63
INFANT FEEDING-RELATED BEHAVIOR		
Touch, taste or smell solid food		
Leontopithecus rosalia rosalia	19 days	Altmann-Schönberner, 1965:233
Eat solid food obtained from the hands or mouth of group members		
Cebuella pygmaea	20–27 days	Christen, 1974
Callithrix jacchus	23–35 days	Stevenson, 1976b; Box, 1975c; Epple, 1967:62, 1970b:62
Saguinus midas niger	35–45 days	Christen, 1968
Saguinus oedipus geoffroyi	29–40 days	Epple, 1970b:63
	35 days	Graetz, 1968:34
Leontopithecus rosalia rosalia	26–35 days	Altmann-Schönberner, 1965:233; C.G. Wilson, 1976
Callimico goeldii	3rd week	Pook, 1978:6
Acquire food unaided from environment (from food dish or through foraging)		
Callithrix jacchus	~37 days	Stevenson, 1976b
Saguinus oedipus	29–35 days	Willig and Wendt, 1970
Saguinus midas niger	45–60 days	Christen, 1968

Behavior and species	First appearance of behavior	Source
Leontopithecus rosalia rosalia	~35 days	Altmann-Schönberner, 1965:230
Callimico goeldii	~38 days	Pook, 1978:6
Cease nursing		
Callithrix jacchus	52–85 days (~9 weeks)	Epple, 1967:62, 1970b:62
Saguinus oedipus geoffroyi	10 weeks	Graetz, 1968:34
Leontopithecus rosalia rosalia	~10 weeks	Altmann-Schönberner, 1965:230
Callimico goeldii	~14 weeks	Heltne et al., 1973
ALLOGROOMING		
Grooming (forms not distinguished: first uncoordinated attempts not distinguished from dexterous grooming)		
Callithrix jacchus	~43 days	Box, 1975b:432
Saguinus midas	~24 days	Christen, 1974
NASAL INVESTIGATION (SNIFFING)		
While being carried, infant leans off and sniffs objects and others		
Leontopithecus rosalia rosalia	~13 days	Altmann-Schönberner, 1965:234
SCENT MARKING		
"First" scent marking (type not distinguished)		
Callithrix jacchus	~30 days	Sutcliffe, 1978; Box, 1975b:432
SEXUAL BEHAVIOR		
Mounting behavior with no intromission		
Leontopithecus rosalia rosalia	~43 weeks	Altmann-Schönberner, 1965:235
AGONISTIC BEHAVIOR		
Initiate agonistic behavior when rejected by carrier		
Leontopithecus rosalia rosalia	13 days	Altmann-Schönberner, 1965:229
Aggressive movements and contacts		
Leontopithecus rosalia rosalia	~17 weeks	Altmann-Schönberner, 1965:230
General piloerection		
Callithrix jacchus	8 weeks	Sutcliffe, 1978
Bristle piloerection		
Callithrix jacchus	16–17 weeks	Sutcliffe, 1978

Appendix IV

Earliest Known Matings and Conceptions of Captive Callitrichid Monkeys

The time of first mating and conception is known for several callitrichid species. In his review of sexual maturation in marmosets and tamarins, Hershkovitz (1977:445) concluded that, in general, male and female marmosets (*Callithrix* and *Cebuella*) are fully grown and sexually mature by 18 months, while tamarins (*Saguinus* and *Leontopithecus*) reach similar status at 24 months. However, as the table indicates, *C. jacchus* females are physiologically capable of conceiving as early as 11 months of age and that *L. r. rosalia* females can conceive as early as 16 months, while *L. r. rosalia* males can impregnate females at 17 months.

Despite the fact that puberty may occur prior to 18 months among callitrichids, offspring are not reported to mate or conceive while living in their natal family groups, even after 18 months of age. For *Callithrix jacchus*, specifically, Abbott (1978) reports that there is a clear difference between puberty, when males are capable of ejaculation and females can ovulate (13 to 16.5 months), and sexual maturity, when copulations result in conceptions (17–20 months). Conceptions occurred only when animals were removed from their original family groups.

Species	Sex	Earliest mating or conception	Source
Cebuella pygmaea	♀	18 months, first mating; 24 months first litter	Christen, 1968, 1974
Cebuella pygmaea	♂	10 months, penis erection; attempts mating	Christen, 1968, 1974
Callithrix jacchus	♀	11 months, first conception	Hearn, 1978: 62
Callithrix jacchus	♀	11.5 months, first conception	Phillips, 1975
Callithrix jacchus	♀	11.5 to 30 months, first conceptions (average 19 months)	Abbott, 1978
Callithrix jacchus	♂	14.5 to 17 months, first copulation (average 15.5 months); copulations resulting in conceptions observed between 17 and 20 months	Abbott, 1978
Saguinus fuscicollis	♀	7 months; first conception	Epple (in Kleiman and Mack, 1980:12)
Saguinus oedipus geoffroyi	♀	15 months, first mating	Willig and Wendt, 1970
Leontopithecus rosalia rosalia	♀	14 months, first conception (average, 31.3 months)	Kleiman and Jones, 1977
Leontopithecus rosalia rosalia	♂	9 months, first mating with conception (average, 28.7 months)	Kleiman and Jones, 1977
Callimico goeldii	♀	11 months, earliest conception; sexual maturity reached at 13 to 14 months	Pook, 1978:6; Lorenz, 1972:102
Callimico goeldii	♂	reach breeding age at 15 to 18 months	Lorenz, 1972:102

Appendix V

Age- and Sex-Related Preferential Interactions between Young and Family Members

The 48 potential sex preferential interactions outlined here were evaluated for each of the major behavioral categories and for each of the four 12-week phases following the Dependent Infant Phase (weeks 1–4). The young in these interactions were the 14 focal tamarins. Significant results of these interactions are summarized in Appendix VI.

Interactions Initiated by Family Group Members

Parents

1. Mothers prefer daughters over sons
2. Mothers more than fathers initiate with daughters
3. Mothers prefer sons over daughters
4. Mothers more than fathers initiate with sons
5. Fathers prefer sons over daughters
6. Fathers more than mothers initiate with sons
7. Fathers prefer daughters over sons
8. Fathers more than mothers initiate with daughters

Older and Twin Siblings

9. Older and twin sisters prefer young females over young males
10. Older and twin sisters more than older and twin brothers initiate with young females
11. Older and twin sisters prefer young males over young females
12. Older and twin sisters more than older and twin brothers initiate with young males
13. Older and twin brothers prefer young males over young females
14. Older and twin brothers more than older and twin sisters initiate with young males
15. Older and twin brothers prefer young females over young males

16. Older and twin brothers more than older and twin sisters initiate with young females

Younger Siblings

17. Younger sisters prefer older sisters over older brothers
18. Younger sisters more than younger brothers initiate with older sisters
19. Younger sisters prefer older brothers over older sisters
20. Younger sisters more than younger brothers initiate with older brothers
21. Younger brothers prefer older brothers over older sisters
22. Younger brothers more than younger sisters initiate with older brothers
23. Younger brothers prefer older sisters over older brothers
24. Younger brothers more than younger sisters initiate with older sisters

Interactions Initiated by Young

With parents

25. Daughters prefer mothers over fathers
26. Daughters more than sons initiate with mothers
27. Daughters prefer fathers over mothers
28. Daughters more than sons initiate with fathers
29. Sons prefer fathers over mothers

46

30. Sons more than daughters initiate with fathers
31. Sons prefer mothers over fathers
32. Sons more than daughters initiate with mothers

With Older and Twin Siblings

33. Young females prefer older and twin sisters over older and twin brothers
34. Young females more than young males initiate with older and twin sisters
35. Young females prefer older and twin brothers over older and twin sisters
36. Young females more than young males initiate with older and twin brothers
37. Young males prefer older and twin brothers over older and twin sisters
38. Young males more than young females initiate with older and twin brothers
39. Young males prefer older and twin sisters over older and twin brothers

40. Young males more than young females initiate with older and twin sisters

With Younger Siblings

41. Older sisters prefer younger sisters over younger brothers
42. Older sisters more than older brothers initiate with younger sisters
43. Older sisters prefer younger brothers over younger sisters
44. Older sisters more than older brothers initiate with younger brothers
45. Older brothers prefer younger brothers over younger sisters
46. Older brothers more than older sisters initiate with younger brothers
47. Older brothers prefer younger sisters over younger brothers
48. Older brothers more than older sisters initiate with younger sisters

Appendix VI

Statistical Tests and Results

Presented are statistically significant results of the comparisons involving focal tamarins and other family group members outlined in Appendix V. Interaction numbers correspond with those in Appendix V. Cross-family group statistical tests: M = Mann-Whitney U-test (p≤.05); S = sign test (p≤.05). Specific, within-family group tests: B(1) = bionomial test (p≤.05) significant in only one family group; B(2) = binomial test (p≤.05) significant in two family groups. m = significant case of mounting behavior in one family group (group C); n = notable but not statistically significant case of mounting behavior (occurring in several groups); dash = no significant occurrence.

Behavioral biases	12-week phases			
	5–16	17–28	29–40	41–52
FOOD TRANSFERS				
Others transfer to young				
Same sex biases:				
1. Mothers prefer daughters over sons	M	–	B(2)	–
2. Mothers more than fathers transfer to daughters	M	M		
9. Older and twin sisters prefer young females over young males	B(1)	–	–	–
Opposite sex biases:				
4. Mothers more than fathers transfer to sons	M	B(1)	B(1)	
15. Older and twin brothers prefer young females over young males	B(1)	–	–	–
Young transfer to others				
Same sex biases:				
25. Daughters prefer mothers over fathers	M	B(1)	B(1)	–
26. Daughters more than sons transfer to mothers	M	–	M	–
45. Young males prefer younger brothers over younger sisters	–	–	–	B(1)
Opposite sex biases:				
27. Daughters prefer fathers over mothers	–	–	–	B(1)
ALLOGROOMING				
Others groom young				
Same sex biases:				
1. Mothers prefer daughters over sons	–	–	–	M
2. Mothers more than fathers groom daughters	–	–	–	M
5. Fathers prefer sons over daughters	–	B(2)	M	–
6. Fathers more than mothers groom sons	–	–	M	M
9. Older and twin sisters prefer young females over young males	–	–	B(1)	B(1)
13. Older and twin brothers prefer young males over young females	–	B(1)	–	–
Opposite sex biases:				
7. Fathers prefer daughters over sons	–	B(1)	B(1)	–

Behavioral biases	12-week phases			
	5–16	17–28	29–40	41–52
Young groom others				
Same sex biases:				
25. Daughters prefer mothers over fathers	B(1)	B(1)	B(2)	B(2)
26. Daughters more than sons groom mothers	–	–	–	B(2)
29. Sons prefer fathers over mothers	B(2)	–	B(1)	B(2)
Opposite sex biases:				
27. Daughters prefer fathers over mothers	B(2)	–	–	–
31. Sons prefer mothers over fathers	–	–	B(2)	–
SOCIAL SNIFFING				
Others sniff young				
Same sex biases:				
6. Fathers more than mothers sniff sons	–	–	–	B(1)
Opposite sex biases:				
4. Mothers more than fathers sniff sons	B(1)	B(1)	–	–
8. Fathers more than mothers sniff daughters	–	–	–	B(1)
Young sniff others				
Same sex biases;				
25. Daughters prefer mothers over fathers	–	B(2)	M	M
26. Daughters more than sons sniff mothers	–	B(1)	B(2)	S
30. Sons more than daughters sniff fathers	–	–	–	B(1)
37. Young males prefer older and twin brothers over older and twin sisters	B(1)	–	–	–
38. Young males more than young females sniff older and twin brothers	B(1)	–	–	–
Opposite sex biases:				
28. Daughters more than sons sniff fathers	M	–	–	–
31. Sons prefer mothers over fathers	B(1)	B(1)	–	–
40. Young males more than young females sniff older and twin sisters	M	–	–	–
GENITAL INVESTIGATION/MOUNTING BEHAVIOR				
Others initiate with young				
Same sex biases:				
1. Mothers prefer daughters over sons	–	–	–	n
2. Mothers more than fathers initiate with daughters	M	–	–	–
6. Fathers more than mothers initiate with sons	–	n	–	n
9. Older and twin sisters prefer young females over young males	B(1)	–	–	–
13. Older and twin brothers prefer young males over young females	n	n	–	n
Opposite sex biases:				
4. Mothers more than fathers initiate with sons	S	–	–	–
7. Fathers prefer daughters over sons	–	B(1)	–	B(1)m
11. Older and twin sisters prefer young males over young females	n	–	–	–
15. Older and twin brothers prefer young females over young males	n	–	–	–
Young initiate with others				
Same sex Biases:				
25. Daughters prefer mothers over fathers	–	–	–	B(1)
29. Sons prefer fathers over mothers	M	M	B(1)	M
38. Young males more than young females initiate with older and twin brothers	M	M	B(1)	–

Behavioral biases	12-week phases			
	5-16	17-28	29-40	41-52
Opposite sex biases:				
27. Daughters prefer fathers over mothers	B(1)	B(1)	–	–
31. Sons prefer mothers over fathers	n	–	n	n (3 cases)
AGONISTIC BEHAVIOR				
Others initiate with young				
Same sex biases:				
2. Mothers more than fathers initiate with daughters	–	–	–	B(1)
6. Fathers more than mothers initiate with sons	–	–	–	S
10. Older and twin sisters more than older and twin brothers initiate with young females	–	B(1)	–	–
14. Older and twin brothers more than older and twin sisters initiate with young males	B(1)	–	–	–
Opposite sex biases:				
4. Mothers more than fathers initiate with sons	B(1)	–	–	–
11. Older and twin sisters prefer young males over young females	–	B(1)	–	–
16. Older and twin brothers more than older and twin sisters initiate with young females	–	–	B(1)	–
Young initiate with others				
Same sex biases:				
25. Daughters prefer mothers over fathers	–	–	–	M
26. Daughters more than sons initiate with mothers	B(1)	–	–	–
29. Sons prefer fathers over mothers	–	–	S	S
30. Sons more than daughters initiate with fathers	–	–	–	M
37. Young males prefer older and twin brothers over older and twin sisters	–	B(1)	–	–
45. Older brothers prefer younger brothers over younger sisters	–	–	–	B(1)
Opposite sex biases:				
27. Daughters prefer fathers over mothers	–	B(1)	–	–
31. Sons prefer mothers over fathers	B(1)	B(2)	B(1)	B(1)
40. Young males more than young females initiate with older and twin sisters	B(1)	–	–	–

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