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PARENT-OFFSPRING CONFLICT AND SIBLING COMPETITION IN A MONOGAMOUS PRIMATE

Members of the South American primate family Callitrichidae (marmosets and tamarins) are reported to live in nuclear or extended family groups (Epple 1975; Kleiman 1977*b*; Dawson 1977). Only a single dominant pair reproduces (monogamy), and both the father and older offspring (or other relatives) aid in the rearing of young. The mechanisms of dispersal of nonreproductive animals are not known. Field observations by Dawson (1977) and Neyman (1977) on the tamarins, *Saguinus oedipus geoffroyi* and *S. o. oedipus*, respectively, suggest that nonreproductive individuals may move in and out of their natal and neighboring groups before permanently joining a group and reproducing.

The following report details the probable cause and eventual results of several instances of familial conflict in captive lion tamarins (*Leontopithecus rosalia*) and suggests how and when dispersal might occur in wild populations of marmosets and tamarins. The observations also support the idea that monogamous species with helpers may share certain universal traits, including greater intrasexual aggression among females and a skewed sex ratio favoring males.

METHODS

The behavior of several lion tamarin family groups at the National Zoological Park has been followed closely since 1973. The housing, maintenance, and observation methods have been described elsewhere (Kleiman 1977*a*). This report will deal with the observed conflicts in four families, established in 1970 (group A and group D), 1975 (group B) and 1976 (group C). The composition of the families at the time of the conflict is summarized in table 1. A fifth artificial group (group E) is also included in table 1.

TABLE 1

COMPOSITION OF GROUPS OF LION TAMARINS AT THE TIME OF FAMILY CONFLICT

Group No.	Date	Mother	Father	Litter 1	Litter 2	Litter 3
A	15/4/74	32721-B	33691	M00715 ♂ M00716 ♂* (10 mo)	M00863 ♂ (2 mo)	
B						
1	28/10/76	M00872	M00276	101666 ♂* 101667 ♀ (3 mo)		
2	14/12/76	M00872	M00276	101666 ♂* 101667 ♀* (5 mo)		
3	25/6/77	M00872	M00276	101666 ♂ 101667 ♀ (11 mo)	101819 ♂* 101820 ♂* (6 mo)	102032 ♀ 102033 ♀ (1 wk)
4	11/5/78	M00872	M00276	101819 ♂ 101820 ♂* (17 mo)	102032 ♀† 102033 ♀ (12 mo)	102209 ♂ 102210 ♀ (3 mo)
C	16/2/78	M00940	M00863	101895 ♀† 101896 ♀ (12 mo)	102070 ♀ (7 mo)	102207 ♀ 102208 ♀ (2 wk)
D	31/5/78	33692	30571-A	101891 ♂ 101892 ♀* 101893 ♀* (15 mo)	102061 ♂ 102063 ♀ (10 mo)	102213 ♀ 102214 ♀ (3 mo)
E	12/3/76	M00872	M00276	M01007 ♀† (17 mo)		

* Injured animal.
† Death.

RESULTS

Group A.—The conflict in group A occurred approximately 2 mo following the birth of twins, of which one male survived. The older juveniles present were 10-mo old twin males, M00715 and M00716. On April 15, 1974, M00716 was found exhibiting behavior resembling a panic or escape response, including disoriented running back and forth in the enclosure which resulted in his crashing several times into the plate glass front of the exhibit. M00716 was separated from the group and reintroduced on the following day, only to exhibit the same frantic and disoriented locomotion. The escape response was especially noticeable when his twin, M00715, or the mother approached. Moreover, the two males engaged in two bouts of wrestling and biting before M00716 was again separated from the family. Two wk later M00716 was successfully reintroduced into the family with no further problem. Eventually, both males were jointly introduced to a young female where they remained without conflict through the birth and rearing of a single young to the female. M00716 was the sexually dominant male in this condition (Kleiman 1978*a*) and also exhibited more parental care than his brother (Hoage 1977).

Prior to the conflict, M00716 was the more dominant and assertive of the twins. For example, he was observed to mount his brother, father, and mother on

numerous occasions, a behavior seen rarely in M00715. Two days before the conflict there was increased sniffing and mounting of the female by the father, suggesting a possible heat period. Based on the date of birth of the next set of infants, the adult female did not conceive at this time, but 2 to 3 wk later, which is about the length of a normal estrous cycle (Kleiman 1977*a*). Thus, circumstantial evidence suggests that the female's reproductive condition might have triggered the fighting.

Group B.—Group B had four periods of conflict. In the first incident the male of a 3-mo-old heterosexual twin set was found with cuts and bruises on his nose and eyes. He was later observed to vocalize loudly and exhibit avoidance behavior when the father approached. On that day the adult male was also pursuing and frequently sniffing the adult female who was pregnant. This conflict between father and son occurred during the midpregnancy false estrous period common in *Leontopithecus* (Kleiman and Mack 1977), 53 days before the female's delivery. Six wk later (1 wk before the birth), both the male and female twins (now 5 mo) were observed to have cuts on their faces. It was not clear whether the twins had fought with each other or if there had been a conflict with the parents.

The subsequent litter contained two males, and the female became pregnant again soon after. Two females were born in June 1977, and 1 wk later both members of the now 6-mo-old twin male litter were observed with cuts and scratches on their faces. They were withdrawn from the family, but huddled and groomed with each other. The older 11-mo-old brother was observed arch-walking away from one of the young males (a signal of tension and possible hostility, Moynihan 1976; Rathbun, in press), and also pursuing and sniffing the mother. The father was also following and sniffing the female, suggesting that the female was in estrus, a common event 7 to 10 days postpartum (Snyder 1972; Wilson 1977), although in this case no conception occurred. Later in the afternoon one of the males was observed arch-walking away from his twin brother and then shrieking when approached by other family members.

During the 2 mo preceding this birth, the eldest male (101666) had been most socially active, frequently chasing and wrestling with his twin sister as well as arch-walking and scent-marking. His high activity level on the day when his younger twin brothers were found with facial wounds suggested that he might have been responsible for the wounds, especially since he was so actively pursuing and being thwarted by his mother.

The fourth conflict in group B was more dramatic. A 12-mo-old female (102032) was found cowering in a corner on the ground one morning. Before her removal, the mother was seen standing over her briefly. Upon examination, 102032 was found to have numerous puncture wounds and to be in severe shock; she died within a few hours. Her older brother (101820) had superficial facial wounds and remained isolated from the family during the day. Several times the father was observed to arch-walk away from him. The litter of twin males was later removed from the family group.

The conflict occurred 55 days prior to the mother's delivery, suggesting that she was in the midpregnancy false estrus, although no sexual behavior was observed. The female that died was thought to be dominant over her twin sister.

Group C.—The family conflict in group C began with fighting between two

12-mo-old female twins, approximately 2 wk after the birth of twins, on the day when the new infants were first being transferred from the mother to the father for carrying. Female 101895 was observed exhibiting frequent arch-walking as well as chasing her twin sister from a family group huddle. She also fought twice with her sister, including wrestling and biting on the ground. After each fight 101895 rejoined the family huddle, but female 101896, who had several cuts on her forehead, remained ostracized the entire day and frequently shrieked.

At 0730 hours, the following morning, the assertive twin sister, 101895, was found on the cage floor with three of the four family members standing over her. She was covered with numerous puncture and slashing wounds on the face, mouth, arms, and thighs and died 30 min later. During that day conflict developed between the 6½-mo-old female (102070) and her older sister, with the older sister being chased by the young sister. However, the ostracized female (101896) eventually rejoined the family during group huddles, and the following day the family appeared calm, and both young females were observed carrying the new infants.

In this particular case, the twin sister conflict may have been triggered by the presence of and initial transfer of the 2-wk-old infants from the mother to the father. However, copulations were observed 2 days after the death of female 101895, suggesting that the mother was approaching estrus at the time.

Group D.—On May 31, 1978, the eldest sibling females of a litter of triplets were both found exhibiting signs of panic, racing around the cage and crashing into its glass front. One female (101893) was charged by one of the parents and cowered on the floor during the incident. Both females had minor cuts and scratches and were separated from the family group into a neighboring cage. For the remainder of that day and the next, the mother frequently approached the door dividing the juvenile females from the family group and attempted to reach the daughters through the cracks in the door.

The adult female and adult male had copulated the previous day, and he was still pursuing and sniffing her on the day of the conflict as well as the subsequent day. The mother gave birth 51 days after the conflict, suggesting that she was exhibiting the midpregnancy false estrus.

Group E.—This artificial group is included because it documents another subadult female death. Female M01007 was removed from her family as a juvenile when she suffered a broken leg. Before a reintroduction was possible her father died and the family group was dissolved. At 12 mo of age, she was introduced to a young mature pair with the idea that she could gain experience of parental care after they reproduced. There was no conflict in the trio over a period of 5 mo. However, on the day of birth of the elder female (M00872), M01007 was severely attacked and did not survive. The death in this trio contrasted with 10 other trios containing two males and a female in which there was only one fight with a serious injury, and no deaths (Kleiman 1978*a*).

DISCUSSION

In marmosets and tamarins relations among family members are generally described as being peaceful, even when offspring are past the age of sexual maturity

(Epple 1975). For example, Rothe (1975, personal communication) has maintained common marmoset (*Callithrix jacchus*) young with the parents 6 or 7 yr beyond the normal age of puberty with only occasional conflict, even when some family groups reached the abnormally large size of 18 to 20 individuals. However, family conflicts have been described, and it appears as though sibling competition is more common than parent-offspring conflict (Epple 1975; Sutcliffe 1978; Rothe 1975, 1978; Stevenson and Poole 1976). Sibling competition is often expressed as "twin fights" which appear to be short-lived and resolved rapidly. Two of the conflicts reported here involved mainly siblings, three involved parents and offspring, and one included both sibling and parent-offspring conflict.

The observations in this report suggest some proximate causes of both sibling and parent-offspring conflict. The mother's estrus appears to affect the behavior of both male and female offspring, from very early ages. A male as young as 3 mo (group B) was clearly affected by his mother's heat period and may have fought his sister or been attacked by his father. In six of seven cases of family conflict, it was known or suspected that the mother was in heat. Two of the conflicts were 1 to 2 wk postpartum and three other conflicts occurred 7 to 8 wk prior to delivery during or near the midpregnancy false estrus period (Kleiman and Mack 1977).

In one case (group C), the presence of young infants and the first transfer from the mother to the father may have added to the tension. In general, young female marmosets and tamarins become involved in parental care earlier than males (Hoage 1977; Box 1977*a*; Ingram 1977), and often attempt to "steal" babies before the adult female is prepared to transfer them. The twin sisters of group C may have been aroused by the imminent infant transfer (as well as the mother's imminent estrus), and fought after being thwarted in their attempts to obtain an infant.

Two further facts are of interest. First, in three cases the more assertive individual of a twin pair was eventually most seriously affected by the conflict, suggesting that the parents and other members of the family may intervene to suppress high levels of assertiveness in their offspring. Although two females have been killed by family members in the captive condition, with the mothers heavily implicated in the deaths, such extreme behavior would probably be unusual in the wild; more likely, the expulsion or emigration of the dominant offspring would result, with an increase in the likelihood of mortality from other causes. Bekoff (1977) has suggested for coyotes (*Canis latrans*) that the most dominant and most subordinate individuals of a litter may be most likely to disperse first since they are the least interactive animals in the group. For the tamarins, parental intolerance of assertive offspring may promote dispersal of dominant young, but subordinate offspring may be forced to emigrate as a result of sibling competition.

A second important point is that aggression is apparently more serious in females than males and has more serious consequences. Other captive studies have indicated that intrasexual aggression among unfamiliar adults is greater in females than males (Epple 1975). The severity of attacks on young females occurs even though juvenile females in family groups appear to be both behaviorally and physiologically suppressed. Juvenile males may be quite socially uninhibited; they begin scent marking and arch-walking earlier and more frequently than females

(Kleiman and Mack, in press; Rathbun, in press) and may follow and attempt to mount the mother during her estrus without serious repercussions. They also appear to be more assertive in play bouts, doing more wrestling and chasing than female siblings. The greater activity of juvenile males in families has been noted in other callitrichid species (e.g., the common marmoset, *Callithrix jacchus,* Box 1977*b*), and suggests that fathers (and families) permit more assertive behavior by males than by females. Hearn (1977) has shown that female common marmosets are physiologically suppressed in that they do not exhibit an ovarian cycle as long as they are housed in the presence of the mother. Thus, the lower levels of social activity initiated or performed by juvenile females may be physiologically caused and may function to prevent tension between the mother and other female relatives, especially daughters.

The fact that intrasexual aggression in female marmosets and tamarins is more damaging than in males (Epple 1975, 1977; this study), resembles the descriptions of social behavior in African wild dogs (*Lycaon pictus*) (Lawick 1971, 1973; Frame and Frame 1976, 1977; Malcolm, personal communication) which are also monogamous. Female intrasexual conflict is more serious than male intrasexual conflict, resulting in forced expulsion and emigration of females or destruction of their pups, if they happen to become pregnant and give birth (Lawick 1973). Although the sex ratio at birth heavily favors males, the sex ratio of packs is even more skewed towards males (Kleiman and Eisenberg 1973), suggesting heavier mortality in juvenile and subadult females. Captive *Leontopithecus* also have a sex ratio at birth heavily skewed towards males. Between 1973 and 1977, 106 males, 95 females, and 7 young of unknown sex were born (Kleiman 1978*a*), a ratio of 1.12. Female emigration and a skewed sex ratio in favor of males have also been described in groups of the monogamous Florida scrub jay, *Aphelocoma c. coerulescens* (Woolfenden and Fitzpatrick 1977), which is also a species where older offspring remain with the parents and act as helpers at the nest. Thus, there may be some traits common to monogamous species that develop extended families and use offspring or other nonreproductive relatives as an aid in child-rearing. These include greater intrasexual aggression among females than males, a skewed sex ratio favoring males, and forced emigration of females by siblings and/or parents. This, in turn, suggests that the potential for reproduction by subordinate females is of greater consequence to the family than reproduction by a male and that the rearing of more than one litter per family group might seriously jeopardize the fitness of all related individuals. The generality of these traits, especially the degree of similarity between birds and mammals, can only be determined by further observations on monogamous species in which helpers occur.

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ON THE POPULATION BIOLOGY OF APHIDS

Janzen (1977) presented the view that one should differentiate between "evolutionary individuals" and physical individuals when considering parthenogenetically reproducing organisms, such as dandelions and aphids. His argument is based upon the assumption that the offspring of parthenogenetically reproducing organisms are genetically identical to their parent. If this assumption is true, Janzen's argument is reasonable, and he makes some valuable points concerning the study and interpretation of the population biology of such organisms. However, the evidence in the literature on aphids does not support the hypothesis of genetically identical offspring, and therefore Janzen's interpretation of the population biology of aphids is inappropriate.

There are two kinds of evidence relevant to this problem: the existence of selectable variation within parthenogenetic lines of aphids, and a possible genetic mechanism to account for this variation. First, there are a number of studies that have shown selection to be effective within parthenogenetic lines of aphids. Cognetti demonstrated a positive response to selection for lack of wing development in *Myzus persicae* (Cognetti 1961), and for parthenogenetic reproduction under conditions favorable to sexual reproduction in *Brevicoryne brassicae* (Cognetti 1965). Pagliai (1965) was able to select for the number and kinds of hairs on the cauda of the pea aphid, *Acyrthosiphon pisum*. Dunn and Kempton (1966), Needham and Sawicki (1971), and Sudderuddin (1973) have all shown the loss of insecticide resistance in parthenogenetic lines of *Myzus persicae* no longer sub-