Seasonality in Squirrel Monkeys (*Saimiri sciureus*): Social Facilitation by Females

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SCHIML, P. A., S. P. MENDOZA, W. SALTZMAN, D. M. LYONS AND W. A. MASON. *Seasonality in squirrel monkeys (Saimiri sciureus): Social facilitation by females.* PHYSIOL BEHAV **60**(4) 1105–1113, 1996.—The extent to which social living arrangements influenced seasonal changes in physiology and behavior was examined in adult squirrel monkeys (*Saimiri sciureus*). Data were collected over 20 months (encompassing two breeding seasons) from animals that were housed in three mixed-sex social configurations that varied in the number of heterosexual and isosexual social partners. For both sexes, the presence of multiple females was found to facilitate reproduction. Females housed with other females were more likely to exhibit seasonal ovarian cyclicity and tended to have higher conception rates. Social facilitation of reproduction was particularly prominent for subordinate females. The presence of same-sex companions also resulted in reduced adrenocortical output in females during the first nonbreeding season. In males, the availability of multiple females increased plasma testosterone levels, except in the presence of more dominant males. Seasonal increases in male weight coincided with increased cortisol levels and were most prominent in social groups containing multiple females. The influence of multiple females on male seasonality occurred despite the finding that male–female interactions were infrequent and, in fact, occurred less frequently when isosexual partners were available. Unexpectedly, affiliative social interactions between same-sex and opposite-sex partners occurred less frequently during the breeding season. As expected, behaviors associated with sex tended to increase during the breeding season. Very little agonism was observed during the course of the study and there was no evidence of interanimal competition for mates.

Squirrel monkey   Cortisol   Estrogen   Progesterone   Testosterone   Reproduction   Seasonality
Social influences   Behavior   Social enhancement   Dominance

SQUIRREL monkeys (*Saimiri sciureus*), like many primates, characteristically engage in mating behavior during a discrete annual period. The onset of the breeding season in squirrel monkeys is signaled by substantial increases in body weight (fatting), particularly in males [10,15]. This change coincides with an increase in androstenedione, possibly of adrenal origin [40]. Other group members find males particularly attractive at this time, as evidenced by increased approaches by other males and females [5,24]. Shortly after peak fatting, gonadal hormone levels increase in males, ovarian cyclicity commences in females, and mating begins [23,24]. Cortisol levels are also higher during the breeding season [7], although the precise timing of increased glucocorticoid activity relative to other seasonal events is not known.

The transition into and out of the breeding season is more or less synchronized among group members [10]. Although ecological factors are undoubtedly important in timing seasonal transitions, there is considerable evidence in squirrel monkeys and other seasonally breeding animals that the coordination of reproductive changes between individuals is mediated by social stimulation [38,39]. In squirrel monkeys, formation of new social groups at most times of the year can increase gonadal activity to levels indicative of breeding readiness in both males and females [21,26,27] and group formation can alter the timing of subsequent breeding seasons [10,29].

Hormonal changes within the first few weeks following formation of new relationships indicate that both heterosexual and isosexual social stimulation can influence breeding readiness. For

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males, heterosexual stimulation increases testosterone levels, whereas isosexual stimulation, at least for subordinate males, can decrease testosterone levels [21,33]. In contrast, group formation studies indicate that for females, heterosexual social stimulation leads to increased gonadal hormone activity only when other females are also present [27]. Formation of female–female relationships does not, however, influence gonadal activity directly. These findings suggest that for males, same-sex social partners either have no effect or inhibit reproductive capacity, whereas for females, same-sex partners may actually facilitate reproductive capacity.

The present study examined this possibility by comparing behavior, seasonal transitions in gonadal hormone activity, and reproduction in squirrel monkeys living in three heterosexual social configurations that differed in the availability of same-sex companions. Data were collected for 20 months, encompassing two breeding seasons, beginning 5–6 months after the groups were initially formed. Moreover, because adrenocortical activity in squirrel monkeys can be altered by social companions [25], adrenal hormones may change seasonally [7,40], and because adrenocortical activity can have considerable influence on gonadal hormone production [6], cortisol levels were also monitored. The data presented are part of a larger study on the same subjects, some of which have been previously reported [19,28,29,33].

METHOD

Subjects

Subjects were 28 adult male and 38 adult female squirrel monkeys (Saimiri sciureus) of Peruvian origin. Two males and three females were laboratory born and raised with their mothers in groups. The remaining monkeys were wild born and imported as adults. At the beginning of the study, all monkeys had been in our laboratory for at least 13 months. All subjects were estimated to be at least 5 years of age and, hence, fully adult, at the time the study began. One male died during the 16th month of the study. The data from this male were deleted from the analyses.

Subjects were housed in two large indoor rooms with lights on from 0600 to 1800 h. Skylights in the ceilings of the animal quarters exposed the monkeys to sunlight and natural variation in day length. Large sliding doors were opened when the daytime ambient temperature was 22–33°C. Supplemental heat and cooling were provided to maintain room temperatures within this range.

All animals were maintained according to standard laboratory protocol, which included cage cleaning and feeding at approximately 0800 h and an additional feeding at 1330 h. They were fed standard New World monkey chow, supplemented with apples and raisins. Water was available ad lib.

Subjects were housed in three different social configurations. Eight males and eight females were housed in heterosexual pairs; 5 males and 15 females were housed in single-male, multiple-female groups (three females per group); and 15 males and 15 females were housed in multiple-male, multiple-female groups (three males and three females per group). Of the animals that were laboratory born, two females were housed in heterosexual pairs, and one female and two males were housed in multiple-male, multiple-female groups. Any offspring born during the study remained with their natal groups for 6–9 months, at which time they were removed and placed into peer groups.

All groups were housed in large, stainless steel cages (1.2 × 1.2 × 2.1 m) equipped with four perches extending the width of the cage, arranged in a stepwise fashion from the lower front to the upper back. The top, bottom, and front of each cage were welded wire, and the back and side walls were solid. Cages were arranged so that adjacent social groups could not see one another except through small openings where water spouts or fasteners were attached to the cages. No attempt was made to limit auditory or olfactory interaction. Each heterosexual pair occupied one cage; each single-male, multiple-female group or multiple-male, multiple-female group occupied two cages connected by a 30 × 30 cm opening.

Monkeys had been living in their assigned social groups for 5–6 months at the start of data collection. The social groups were formed as part of previous studies that examined the responses of the males and females to isosexual and heterosexual group formation [19,33]. Social living arrangements were maintained throughout the course of the study. Subjects were removed from their social groups occasionally for 1–2 h for routine testing, cleaning, or medical procedures. On seven occasions it was necessary to remove animals from the colony for extended medical treatment. The duration of these absences ranged from 1 to 15 days, and animals were returned to social groups as soon as it was determined to be medically safe to do so.

Design

Behavioral and endocrine changes through two breeding seasons were evaluated. The primary focus of the study was on the potential influence of same-sex companions on reproductive seasonality. Our social groups did not, therefore, reflect natural grouping patterns, but rather variations in availability of types of companions. Group sizes were minimized to avoid substantial differences in social density. Data were collected for 20 months, beginning in October, 1989. Behavioral observations consisted of two 5-min focal observations per subject per week, totalling 40 min per subject each month. On 3 days each month, blood samples were collected from each nonpregnant, nonlactating adult for determination of basal adrenocortical and gonadal hormone levels. To provide an adequate basis for evaluation of ovarian cyclicity, the three blood samples were collected within a 6–9-day period during each month of data collection. Once per month, animals were weighed and females were palpated to determine whether they were pregnant. All subjects were well habituated to the presence of observers and to the capture and handling techniques used in this study.

Blood Sampling and Endocrine Determinations

Blood samples were collected between 1130 and 1330 h. Subjects were captured in a transport cage, removed, and manually restrained while a blood sample (1 ml) was collected by femoral puncture using a heparinized syringe. Blood samples were collected serially from all subjects within each of the two colony rooms. All animals from a given social group were captured simultaneously and blood samples from cagemates were collected as rapidly as possible. Group order within a room was constant; room order was alternated. Average elapsed time from initial disturbance of a subject's cage to sample collection was 2 ± 0.02 min (mean $\pm$ SEM) and 98.7% ($N = 3143$) of the blood samples were obtained within 5 min of cage entry. Preliminary analysis of the data indicated that the time from room entry to collection of blood samples (total disturbance time) did not influence the results. Correlations between cortisol levels and disturbance time for each sample collection day ranged from −0.34 to 0.36 and were as likely to be negative as positive; the few significant correlations (three negative, two positive) were expected by chance.

Blood samples were spun in a refrigerated centrifuge and the plasma fraction extracted and frozen until assayed. Plasma concentrations of cortisol, progesterone, and estradiol were estimated for females, and plasma concentrations of cortisol and testoster-

one were estimated for males. Testosterone, cortisol, and progesterone assays were performed using coated tube radioimmunoassay kits, and estradiol assays were performed using double-antibody radioimmunoassay kits (Diagnostic Products Corporation, Los Angeles). Intra- and interassay coefficients of variation were, respectively, 7.01% and 8.32% for cortisol, 5.19% and 9.12% for testosterone, 8.37% and 11.28% for estrogen, and 6.88% and 7.88% for progesterone. The least detectable dose was 9.83 μg/dl for cortisol, 3.14 ng/dl for testosterone, 18.96 pg/ml for estradiol, and 6.81 ng/ml for progesterone.

Behavioral Observations

Behavioral data were recorded on checklists with a predefined list of behaviors [see [24,27] for definitions]. Each 5-min period was divided into 20 15-s intervals. The beginning of each interval was indicated by an audible signal. Instances of huddle posture, social contact, and social proximity were noted on the signal. Approach, grab, genital display, and anogenital exploration were recorded once for each 15-s interval in which they occurred. For directional behaviors performed or received by the focal animal (approach, grab, genital display, and anogenital investigation), the initiator and recipient were identified. Social huddling, an affiliative behavior, was scored post hoc if huddle posture and contact both occurred at the beginning of an interval. Mounting and fighting are infrequent, but highly visible, behaviors in squirrel monkeys. Therefore, these behaviors were scored whenever they occurred during observation of a group whether or not the focal subject was involved. Observations were conducted between 1400 and 1600 h, with the observer sitting quietly, in full view of the monkeys, approximately 1 m from the cage. Interobserver reliability exceeded 85% for all behavioral categories.

Data Analysis

Ovarian cyclicity was assessed as previously described [26]. Difference scores for estrogen and progesterone were calculated by subtracting the lowest from the highest of the three values each month. If the difference score exceeded 100 pg/ml for estrogen and 50 ng/ml for progesterone, or if the average of the three samples exceeded these values, a female was considered to be cycling.

Conceptions were estimated in two ways: 1) by subtracting 155 days from the birth date [13], and 2) by identifying the month prior to detection of pregnancy by palpation. The two methods agreed surprisingly well. The average interval between initial determination of pregnancy by palpation and birthdate was 128.9 days. Therefore, the assumption that conception occurred in the month previous to positive palpation provided the same estimate of month of conception as did gestation length. Any month in which a conception occurred was considered to be in the breeding season.

Seasonal changes in hormone concentrations and relations between hormones and behavior were evaluated using average monthly hormone values. Because hormonal data for females were not continuously available due to pregnancy and lactation, male and female endocrine data were analyzed separately. Male cortisol, testosterone, and body weight were analyzed by a 3 (social configuration) × 20 (months) ANOVA, with social configuration treated as a between-subjects variable and months as a within-subjects variable. Post hoc evaluations were performed using tests for simple effects and Newman–Keuls comparisons. Analysis of cortisol values for females focused on the nonbreeding season each year. Four months of continuous data from each nonbreeding season were selected when the maximum number of females were neither pregnant nor lactating. Because the fe-

male subject pool varied in number in each year of the study, separate analyses were performed for year 1 ($N = 25$) and year 2 ($N = 16$) of data collection. For each nonbreeding season female cortisol data were analyzed using a 3 (social configuration) × 4 (months) ANOVA. To evaluate the potential change in adrenocortical activity during the transition from nonbreeding to breeding, average cortisol values from the nonbreeding months were compared to the first month in which cyclicity was detected.

Data were further analyzed to evaluate any influence of dominance on hormonal activity or body weight. Where possible, within-sex dominance hierarchies were constructed using the frequency and direction of grabs and genital displays [8,21]. ANOVAs were performed with rank as a between-subjects factor and months as a within-subjects factor.

The influence of social living arrangements on the probability that females would undergo ovarian cyclicity and ultimately conceive was evaluated by χ^2 tests. Similarly, the influence of relative dominance rank on conception rates for females living in multiple-female social arrangements was evaluated by χ^2.

Analyses of social behaviors were based on the average number of interactions that each subject initiated or received each month. Interactions with same-sex and opposite-sex partners were analyzed separately. Behavior scores were corrected for the number of potential partners. Spatial measures (contact, proximity, social huddle) were analyzed using the dyad as the unit of analysis. ANOVAs were performed with social configuration as a between-subjects variable and Month as a within-subjects variable. Tests for simple main effects and Newman–Keuls comparisons were used for post hoc analyses where appropriate.

RESULTS

Conceptions/Births

As expected, the distribution of births was highly seasonal (Fig. 1). The initial birth peak (November–December, 1989) followed group formation by 6–7 months. Assuming a 155-day gestation period, these data suggest that a few females conceived in the early weeks following formation of heterosexual social units. The second and third birth periods took place in the months of August through December, 1990, and August through November, 1991. Estimates of the timing of conceptions indicated that the first breeding season included the months February through June, 1990, and the second breeding season commenced in Feb-
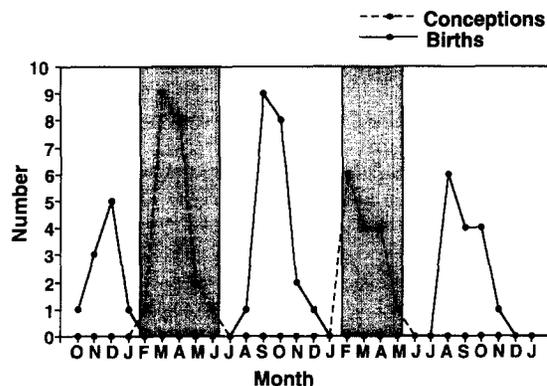
FIG. 1. Number of conceptions (dashed line) during each month of data collection. The breeding seasons are indicated with gray shading. Number of births (solid line) prior to and following data collection is also indicated.
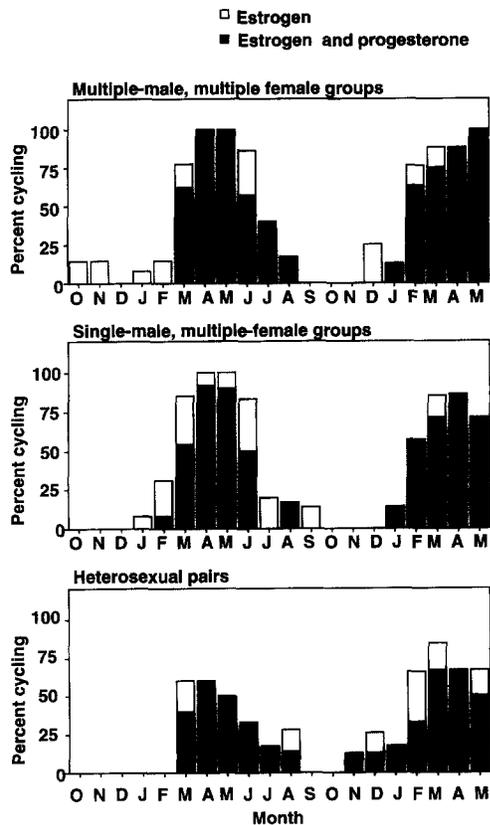
FIG. 2. Percent of females within each social configuration undergoing ovarian cycles during each month of data collection, as determined by plasma concentrations of estrogen or concentrations of estrogen and progesterone.

ruary and ended in May, 1991, when behavioral and endocrine data collection ended. No conceptions occurred after this time.

A total of 46 conceptions were detected and 36 infants (78.2%) survived to weaning. Females did not breed at maximum capacity. Assuming all females could conceive once during each breeding season, the overall conception rate during the two complete breeding seasons was 48.6% (37/76). Only 6/38 females (15.8%) became pregnant in two successive breeding seasons and 5/38 females (13.2%) never became pregnant during the course of the study.

Female Reproductive Measures

The number of females judged to be undergoing ovarian cyclicity also showed seasonal changes (Fig. 2). Conceptions occurred only in those months in which females were judged to be cycling. Hormonal data were available for 34 of the conceptions that occurred during the study. Of these conceptions, 16/34 (47.1%) took place during the first month that females were judged to be cycling. Only one female exhibited unusual cyclicity. This female showed no variation in progesterone, suggesting that ovulation did not occur; she did not conceive. For all other females, if conception did not occur, cyclicity persisted for 4–6 months after which the anovulatory pattern typical of the non-breeding season was resumed.

The likelihood that a female would conceive in either breeding season was influenced by whether she had conceived in the previous year, but not by social configuration. Six conceptions

occurred in heterosexual pairs (37.5% conception rate), 13 in single-male, multiple-female groups (43.3% conception rate), and 18 in multiple-male, multiple-female groups (60.0% conception rate) ($\chi^2 = 2.68$, NS). Conception rates were lower for females that conceived in the previous breeding season than for females that did not conceive in the previous year (previous conception: $N = 31$, 19.4% conception rate; no previous conception: $N = 45$, 68.7% conception rate, $\chi^2 = 18.02$, $p < 0.001$). This effect does not appear to be due to the immediate presence of the infant, as females that experienced a loss (e.g., stillbirth or neonatal death) in the previous birth season were also less likely to conceive when compared to other females without infants (lost infant: $N = 10$, 30.0% conception rate; $\chi^2 = 4.66$, $p < 0.05$), and not significantly different from females whose infants were still living with them at the beginning of the new breeding season (live infant: $N = 21$, 85.7% conception rate, $\chi^2 = 1.07$, NS).

The likelihood a female would undergo ovarian cycles was influenced by the social configuration in which she lived. During both years, almost all females (95.2%) housed with isosexual companions (those in multiple-female groups) exhibited hormonal profiles consistent with ovarian cyclicity. A much smaller proportion of females housed with only a heterosexual companion showed evidence of cyclicity (63.6%, $\chi^2 = 8.51$, $p < 0.01$).

Testosterone

Testosterone levels in males exhibited clear seasonal changes, $F(19, 456) = 6.46$, $p < 0.001$ (Fig. 3A). Testosterone levels were significantly elevated above nonbreeding values in April of
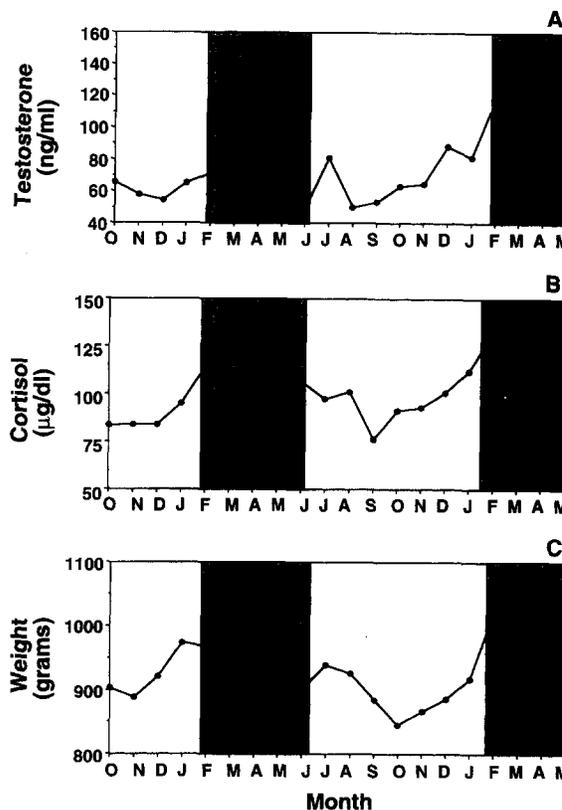
FIG. 3. Mean plasma testosterone levels (A), plasma cortisol levels (B), and body weight (C) of males for all social configurations during each month of data collection. Shaded areas indicate breeding seasons.
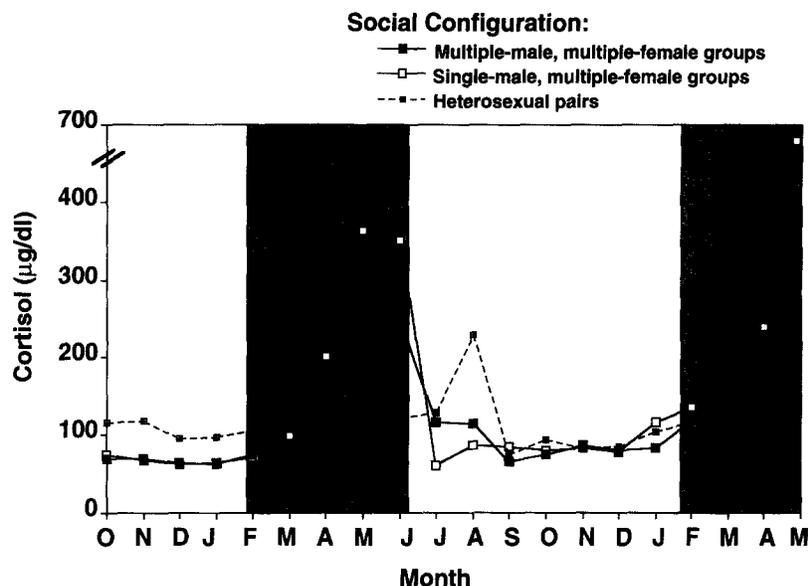
FIG. 4. Mean plasma cortisol levels for females in each social configuration during each month of data collection. Shaded areas indicate breeding seasons.

year 1 and in February, March, and April of year 2. In both breeding seasons, peak conceptions preceded maximum testosterone elevations by 1 month, and in both years, testosterone levels declined to nonbreeding concentrations before females had resumed an anovulatory pattern of gonadal hormone activity.

Social configuration also influenced overall levels of testosterone, $F(2, 24) = 3.65$, $p < 0.05$. Males in single-male, multiple-female groups had the highest levels of testosterone (118.16 ± 7.34 ng/ml). Males housed in heterosexual pairs had the lowest levels of testosterone (55.13 ± 4.52 ng/ml). Males housed in multiple-male, multiple-female groups had levels that were intermediate to the others (77.16 ± 4.40 ng/ml) and not significantly different from either. No interaction between month and social configuration was found, $F(38, 456) = 0.74$, NS.

Male Fatting

Male body weight showed pronounced seasonal variation, $F(19, 437) = 22.87$, $p < 0.0001$. Weights increased just prior to the breeding season each year and reached their highest level in the same months as peak conceptions—March of the first year and February of the second year (Fig. 3C). The decline in weight was as precipitous as the rise and reached nonbreeding levels prior to the end of the breeding season in each year. Peak weights preceded peak testosterone by 1 month during each breeding season. Weight changes were influenced by social configuration, $F(38, 437) = 2.22$, $p < 0.001$ (social configuration × Month interaction). This was largely due to males in heterosexual pairs: these males did not exhibit weight changes during the second year. Weight changes were prominent for males living in single-male, multiple-female groups or multiple-male, multiple-female groups during both breeding seasons, but peaks occurred in different months within each social configuration (all $p < 0.05$).

Adrenocortical Activity

Male adrenocortical activity exhibited a pronounced seasonal rhythm, $F(19, 456) = 11.77$, $p < 0.001$. In each year, high cortisol levels coincided with peak weights and preceded peak

testosterone levels by 1 month (Fig. 3B). Adrenocortical activity in males was not affected significantly by social configuration, $F(2, 24) = 1.35$, NS.

Female adrenocortical activity was influenced by social configuration as well as by season. During the first nonbreeding season, females living in heterosexual pairs had higher cortisol levels than did females living with other females, $F(2, 22) = 4.00$, $p < 0.05$ (Fig. 4). Female cortisol levels declined slightly during the first nonbreeding season, $F(3, 66) = 5.85$, $p < 0.01$. Cortisol levels increased substantially following the onset of cyclicity [year 1: $F(1, 28) = 14.44$, $p < 0.001$; year 2: $F(1, 16) = 10.63$, $p < 0.01$]. During the first year, females housed in heterosexual pairs maintained higher levels of adrenocortical activity during the first month of cyclicity than females housed with like-sex companions, $F(2, 28) = 4.53$, $p < 0.05$. During the second nonbreeding season, the effects of social configuration on adrenocortical activity did not reemerge, $F(2, 13) = 1.63$, NS. The extremely high cortisol values shown during the breeding season may reflect increased adrenocortical activity during initial stages of pregnancy.

Heterosexual Behavioral Interactions

Affiliative heterosexual interactions occurred more frequently when isosexual companions were not available (Fig. 5). Males living in heterosexual pairs approached females considerably more often than did males living in other social configurations during each month of data collection, $F(2, 24) = 6.04$, $p < 0.01$. Male approaches to females changed across months of the study in heterosexual pairs, but not in other social configurations, $F(38, 456) = 1.48$, $p < 0.05$ (months × social configuration interaction). Interestingly, male approaches to females in heterosexual pairs were most frequent during the nonbreeding seasons, with peak levels occurring in October and November during the first year and during November and December during the second year.

As with male approaches to females, females approached males considerably more often during each month of data collection when housed in heterosexual pairs than in other social

Social Configuration:

—■— Multiple-male, multiple-female groups
—□— Single-male, multiple-female groups
---■--- Heterosexual pairs

Male Approaches to Females

Female Approaches to Males
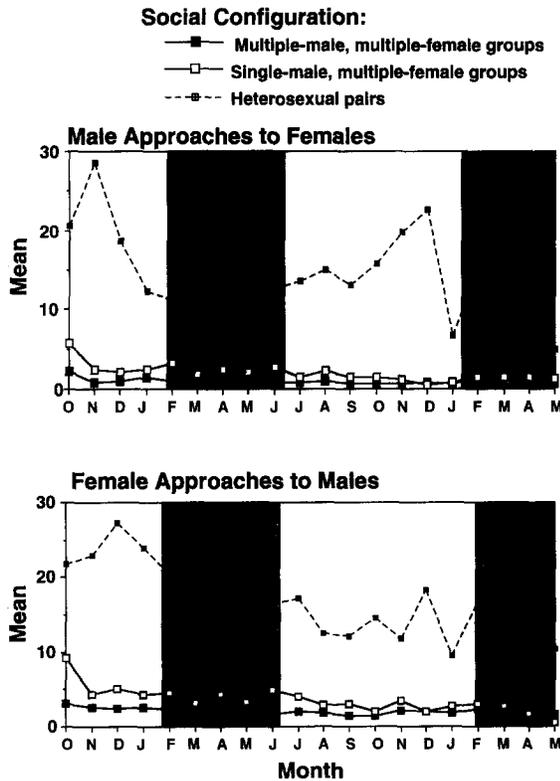
Month

FIG. 5. Mean number of 15-s intervals in which approaches were performed by males to females (top) and by females to males (bottom) in each social configuration during each month of data collection. Shaded areas indicate breeding seasons.

configurations, $F(2, 35) = 12.57$, $p < 0.001$ (Fig. 5). Female approaches to males also changed over time, especially for females living in heterosexual pairs, $F(38, 665) = 2.21$, $p < 0.001$ (months × social configuration interaction). This change had little to do with seasonality, however, and reflected a general tendency for female approaches to males to decline the longer the animals lived together.

Spatial measures indicated that males and females spent more time together when males did not have other males available [proximity: $F(2, 35) = 12.11$, $p < 0.001$; contact: $F(2, 35) = 6.31$, $p < 0.01$; social huddling: $F(2, 35) = 5.51$, $p < 0.01$]. All spatial measures exhibited similar patterns. Seasonal changes in the amount of time males and females spent together were also influenced by the social configuration [proximity: $F(38, 665) = 2.32$, $p < 0.001$; contact: $F(38, 665) = 2.10$, $p < 0.001$; social huddle: $F(38, 665) = 1.87$, $p < 0.01$]. Males living in either single-male, multiple-female groups or heterosexual pairs spent more time with females during the nonbreeding season than during the breeding season. Heterosexual proximity, contact, and social huddle was lowest for animals living in multiple-male, multiple-female groups and did not change seasonally.

Aggressive interactions between males and females tended to be limited to mild agonistic behaviors such as grabbing; no fights were observed at any point during the study. There was no indication that either seasonality or social configuration affected the frequency of heterosexual grabbing, whether initiated by males or by females. However, the overall frequency of grabs tended to decline during the study [male → female: $F(19, 456) = 2.36$, $p < 0.01$; female → male: $F(19, 665) = 2.75$, $p < 0.001$].

Seasonality effects on sexual interactions were most clearly evident for anogenital investigation, $F(19, 456) = 3.40$, $p < 0.001$ (Fig. 6). Peak levels of anogenital investigation of females by males occurred during the breeding season in March of both years. Animals living in different social arrangements did not differ in the frequency of anogenital investigation. Mounting was observed too infrequently for analysis.

Although less clearly associated with other seasonal indices, frequency of male genital displays towards females also changed across months, $F(19, 456) = 2.76$, $p < 0.001$ (Fig. 6). Genital displays tended to increase in months during which conceptions occurred, but were also frequent in some months during the nonbreeding season, especially for males living only with females [social configuration × month interaction, $F(38, 456) = 1.95$, $p < 0.001$].

Isosexual Behavioral Interactions

Spatial measures indicated that the tendency for males living in multiple-male, multiple-female groups to associate with one another increased following peak conceptions and during the nonbreeding season [proximity: $F(19, 279) = 3.49$, $p < 0.001$; contact: $F(19, 247) = 4.91$, $p < 0.001$; social huddle: $F(19, 247) = 5.03$, $p < 0.001$]. Generally, other male–male social interactions did not vary seasonally, except male–male grabs, which were elevated during 1 month of the nonbreeding season, $F(19, 279) = 2.40$, $p < 0.01$. No fights between males were observed during the course of the study.

Females approached one another more often during nonbreeding months than during breeding months, $F(19, 532) = 6.63$, $p < 0.0001$. Females also tended to spend the most time in asso-

Social Configuration:

—■— Multiple–male, multiple-female groups
—□— Single-male, multiple female groups
----■---- Heterosexual pairs

Anogenital Investigation

Genital Displays
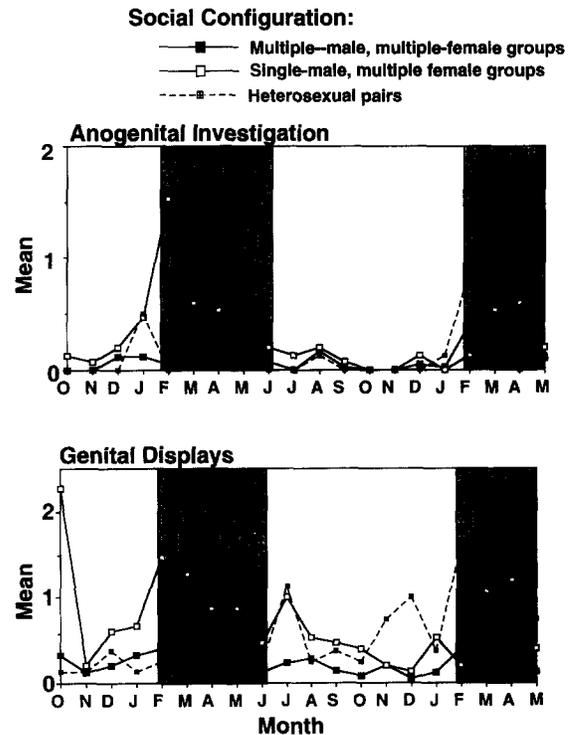
Month

FIG. 6. Mean number of 15-s intervals during which anogenital investigation of females by males and genital displays to females by males occurred within each social configuration during each month of data collection. Shaded areas indicate breeding seasons.

ciation with one another toward the end of the breeding season [proximity: $F(19, 532) = 11.50, p < 0.001$; contact: $F(19, 532) = 11.20, p < 0.001$; social huddle: $F(19, 532) = 10.54, p < 0.001$]. The presence of multiple males accentuated the tendency for females to associate with each other during nonbreeding months, as indicated by significant social configuration $\times$ months interactions [proximity: $F(19, 532) = 2.13, p < 0.01$; contact: $F(19, 532) = 2.12, p < 0.01$; social huddle: $F(19, 532) = 2.09, p < 0.01$]. Agonistic interactions between females also tended to increase during nonbreeding months [grabs: $F(19, 532) = 3.93, p < 0.0001$; genital displays: $F(19, 532) = 1.99, p < 0.01$]. No fights between females were observed.

Dominance

It was possible to construct dominance hierarchies for each of the male and female triads. On average, 92.8% of genital displays and grabs (range: 62–98%) were in accordance with a linear hierarchy. For the triad in which one male died, the deceased male had been the most subordinate and no changes in dominance rank occurred after his death.

Testosterone levels differentiated animals by rank, $F(2, 11) = 10.98, p < 0.01$. Newman–Keuls comparisons revealed that alpha males had significantly higher levels of testosterone (125.71 ± 5.53 ng/ml) than did either beta (56.71 ± 6.32 ng/ml) or gamma males (42.04 ± 7.27 ng/ml). Testosterone levels in beta and gamma males were not significantly different. Seasonal changes in testosterone were not influenced by rank, nor were male fatting, male adrenocortical activity, or male interactions with females.

Female dominance status reliably influenced conception rate. Dominant females were much less likely to conceive than subordinate females ($\chi^2 = 5.63, p < 0.05$) (conception rates: 30% for alpha females; 62.5% for beta and gamma females). Cortisol levels were not influenced by female dominance status, nor were female interactions with males, whether initiated by males or by females.

Several instances of isosexual mounting were observed and were generally in accordance with the dominance hierarchy. Thirty-three cases of male–male mounting were observed during the study of which 76% ($n = 25$) were performed by higher ranking males to lower ranking males. Five occurrences of female–female mounting were observed; all involved a higher ranking female mounting a lower ranking female.

DISCUSSION

Squirrel monkeys in this and previous studies have been found to show strong seasonal variations in physiology and behavior [3,5,12,14,15,24]. In the present investigation, breeding occurred during a 4–5-month period and approximately half of the females conceived each year. Most females (86.8%) conceived during the study. The factor most clearly influencing whether a female would conceive during a particular breeding season was whether she had done so in the previous year. This has been previously reported for free-ranging populations [30], but not for captive squirrel monkeys.

As expected, body weight and steroid hormone levels increased during the breeding season [23,24,40–42]. Our data replicate previous findings indicating that male weights peak approximately 1 month prior to the peak in testosterone levels [23,40]. Our results further suggest that seasonal elevations in male cortisol coincide with fatting and precede peak gonadal hormone production. This result was foreshadowed by the finding by Wiebe and coworkers [40] showing that seasonal increases of androstenedione (presumably of adrenal origin) occur earlier

than seasonal testosterone elevations. Elucidation of whether androstenedione, cortisol, or other products of the adrenal cortex contribute to fatting in squirrel monkeys awaits further research.

Female cortisol levels also increased during the breeding season. It appears that changes in female cortisol levels may coincide with gonadal hormone changes: all females showed an increase in plasma cortisol during the first month of ovarian cyclicity. This is consistent with the finding that estrogen can increase circulating cortisol levels in squirrel monkeys [9].

The present results confirm that female social companions enhance reproduction for other females. Females were more likely to undergo ovarian cyclicity in the multiple-female groups than in the heterosexual pairs. On the basis of retrospective analysis of colony records, we previously reported that females were less likely to conceive if they were housed in heterosexual pairs [26]. Although not significant, this trend was apparent in the current study as well. Surprisingly, social facilitation of reproduction was particularly apparent for subordinate females, which were significantly more likely to conceive than their more dominant companions. Because no effect of dominance was found on the likelihood of ovarian cyclicity, it is possible that the effect of dominance on conception may be mediated by altered behavioral interactions.

Testosterone levels were also enhanced by the number of females present, but were further influenced by relationships between males. Dominant males and single males living with three females had substantially higher testosterone levels than did subordinate males or males living in heterosexual pairs. Dominance relations among these males were formed when the animals were living as isosexual triads and, at least during the first 9 weeks of cohabitation, testosterone levels did not reflect the clear dominance status of the males [19]. When heterosexual social units were formed some 4 months later, differences between males emerged immediately [33] and did not diminish during the ensuing 2 years, as evidenced by the present data. These and earlier studies [21] suggest that the presence of females accentuates rank-related differences in testosterone levels, or alternatively, that dominant males prevent female-induced elevation of testosterone in subordinate males. Other studies have failed to find rank-related differences in testosterone in stable, multiple-male heterosexual groups [24,26]. The reason for these discrepancies is unclear at this time.

Seasonal fatting in males was also sensitive to the presence of social companions and to the duration of cohabitation. In both years, social living arrangements affected the timing of seasonal weight gain in males. Perhaps of most interest is the finding that males housed in heterosexual pairs did not exhibit significant peaks in weight during the second year. This suggests that male seasonal rhythms are responsive to the number of females present (or the total number of social companions) and that following an extended period of cohabitation, a single female may not provide sufficient social stimulation for males to sustain the full suite of seasonal changes.

During the first nonbreeding season, females housed with other females had lower levels of cortisol than those housed with only a male social companion. When cortisol levels rose with the onset of the breeding season, the effects of social configuration on female adrenocortical activity disappeared and did not reemerge at any subsequent point in the study. Male cortisol levels were not influenced by the presence of other males. We have previously reported socially induced reductions in adrenocortical activity, but only within the first few weeks after formation of isosexual dyads or triads [19,22,27,34]. From the present study, we know isosexual partners can influence basal cortisol levels beyond the initial stages of relationship formation, but such in-

fluences do not persist indefinitely. At the present time, we do not understand why some social influences on physiology subside over time, as observed with weight in males housed in heterosexual pairs and female adrenocortical activity. Social groups in this study were stable and undisturbed, quite different from the labile social groups in nature in this species, in which individuals are reported to transfer between groups [5] and seasonal changes in the degree of sexual integration also occur [2,30].

The presence of isosexual companions reduced the likelihood of heterosexual interactions. Male–female approaches, proximity, contact, and social huddling were more commonly observed in heterosexual pairs than in the other social conditions. This was also the case immediately following group formation [18,33]. These differences were attenuated during the breeding season when interactions between males and females in the heterosexual pairs tended to be less frequent. Affiliative interactions among like-sex partners also declined during the period of heightened sexual activity. Agonistic interactions were very infrequent throughout the study; however, mild antagonistic interactions between like-sex animals were most frequent during the nonbreeding season and there was no indication of intrasexual competition in either males or females.

In most studies of social influences on reproduction in mammals, heterosexual social partners are generally found to enhance reproductive potential [20,31,32,37] and isosexual social partners either have no effect or inhibit reproduction [4,16,35]. Male

squirrel monkeys follow this general pattern. For males, the presence of multiple females accentuates seasonal changes and dominant males inhibit gonadal hormone production in subordinates. Female squirrel monkeys, in contrast, do not conform to the expected pattern. For females, like-sex partners enhance reproductive potential: females living in multiple-female social groups are more likely to undergo ovarian cyclicity, than single females living with only a male companion. This finding is not altered by the number of males living with the multiple-female subgroups. Perhaps even more surprising is the finding that subordinate females were more likely to conceive than dominant females. This contradicts the well-accepted notion that social dominance functions to enhance reproductive success for dominant individuals [11]. Dominant females in many species have been reported to breed exclusively, or at a higher rate, than subordinates [1,4,16,17,43]. Apparently squirrel monkeys are an exception. Social facilitation by females appears to be the primary theme governing social influences on reproduction in Saimiri.

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