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Sociophysiology of Relationships in Squirrel Monkeys. I. Formation of Female Dyads

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SALTZMAN, W., S. P. MENDOZA AND W. A. MASON. *Sociophysiology of relationships in squirrel monkeys. I. Formation of female dyads.* PHYSIOL BEHAV **50**(2) 271–280, 1991.—Physiological and behavioral consequences of formation of female-female relationships were investigated in adult squirrel monkeys. Plasma cortisol, heart rate, and behavior were evaluated during confinement in a test cage while animals were housed alone, during the first hour of isosexual pair formation, and while animals were housed as isosexual dyads. In addition, basal cortisol levels were assessed both before and after pair formation, as were behavioral and cardiovascular responses to social and nonsocial stimulus presentations. Basal cortisol levels underwent a marked and sustained reduction following formation of pairs, independent of both dominance status and the quality of social interactions between pairmates. In contrast, adrenocortical responsiveness was not altered by social conditions, apart from a modest and transitory difference between dominant and subordinate females in their initial response to pair formation. Heart rate declined sharply during each test session, but did not reliably differentiate social conditions, stimulus conditions, or dominance status. These findings contrast with results of a parallel study of male squirrel monkeys and suggest that isosexual relationships in males and females are associated with different sociophysiological processes.

Pair formation Relationships Cortisol Heart rate Dominance Sociophysiology Squirrel monkeys

PRIMATES are highly adapted for social life. Not only do they expend a great deal of time and energy in establishing and maintaining interindividual relationships, but their physiological functioning is finely tuned to the social environment. Through alterations in such physiological systems as the pituitary-adrenal axis, the pituitary-gonadal axis, and the autonomic nervous system, primates may regulate their metabolic, reproductive, and behavioral states in accordance with salient social phenomena [e.g., (1, 5, 9, 28, 36)]. However, primate social relationships vary across multiple dimensions, such as stability, mutuality, intensity and exclusivity. To the extent that different kinds of relationships place different demands on individuals and entail different social consequences, they may be expected to be associated with contrasting physiological profiles (23,26). Investigation of such sociophysiological contrasts offers a valuable means of understanding the diversity of primate social relationships and the nature and functional significance of the processes contributing to them.

This study is one in a series investigating sociophysiological processes in squirrel monkeys (*Saimiri sciureus*). These small New World primates exhibit a sexually segregated social structure: within the large, multimale/multifemale troops in which they live, adults associate primarily with members of their own age-sex class (3, 12, 21, 32, 42). Adult relationships with like-sex companions differ between males and females in a number of respects. Male-male relationships have been described as highly individualized and temporally stable. Agonistic interactions are prevalent among males, and dominance hierarchies are readily identifiable (3, 14, 25, 32, 41). Nevertheless, pairs of males may develop close affiliative relationships which may persist for several years and may include conjoint transfer between social groups (32,40). Relationships between females, in contrast, appear to be less well differentiated and more transitory. Females are strongly attracted to one another and engage in predominantly affiliative interactions, while interfemale agonism is generally infrequent and mild (3, 12, 22, 32). Dominance relations among females appear to be less prominent than those among males: although a number of investigators have detected dominance hierarchies among females, others have been unable to discern clear status relations (2, 3, 6, 8, 25, 29, 32, 41, 43). Moreover, female-female relationships are thought to be temporally unstable, with membership in female cliques changing frequently (40,42).

These differences between male-male and female-female relationships appear to be associated with contrasting physiological sequelae. Among male squirrel monkeys, formation of isosexual relationships alters activity in the pituitary-adrenal axis, the pituitary-gonadal axis, and the autonomic nervous system. These effects are dependent on relative dominance status attained. Dominant males typically exhibit higher plasma testosterone levels than their subordinate partners, and either higher or lower plasma cortisol levels, depending on the subspecies of monkeys (10, 24, 31, 34). Recent data also indicate that formation of male-male relationships is associated with a decline in heart rate which ap-

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pears to be mediated by an increase in parasympathetic activity (31). While this effect was seen in both dominant and subordinate males during the first hour of pair formation, it was significantly more pronounced in dominant than in subordinate animals following several weeks of cohabitation. Furthermore, the heart rate decline was apparent only in the presence of the male cagemate.

For female squirrel monkeys, at least two aspects of adrenocortical function appear to be altered by within-sex social stimulation. First, females have been found to induce in one another a dramatic and sustained reduction of basal cortisol levels (27, 29, 30). Secondly, females living in isosexual pairs have shown reduced adrenocortical responsiveness to handling and ether anesthetization compared to females living alone (16). Paradoxically, however, responsiveness to stressful circumstances is not altered by the immediate presence of familiar female companions (18,19). Responsiveness of the pituitary-adrenal system therefore appears to be altered by the availability of like-sex companions in the ongoing living arrangements, but not by their immediate presence during stressful circumstances. Investigations of the senstivity of female neuroendocrine function to qualities of isosexual social relationships have also produced mixed findings. While several investigators have suggested that such qualities as dominance status and agonism impinge on pituitary-adrenal activity, others have failed to find such an effect (16–18, 29).

It is not known whether socially induced changes in female andrenocortical function are accompanied by shifts in other physiological systems. It is possible, for example, that cardiovascular and/or autonomic activity are altered by isosexual stimulation, as they are in males. Moreover, as in male squirrel monkeys, autonomic activity in females may be more sensitive to qualities of isosexual relationships and immediate availability of a like-sex companion than is the pituitary-adrenal system. In this study, therefore, we evaluated the adrenocortical, cardiovascular, and behavioral effects of isosexual relationship formation in female squirrel monkeys, replicating a paradigm used with males in order to facilitate comparisons between the sexes (31). Plasma cortisol levels, heart rate and behavior were monitored before, during and after formation of isosexual pairs.

METHOD

Subjects

Subjects were 16 adult female squirrel monkeys (*Saimiri sciureus*) of Colombian, Peruvian and Bolivian varieties. Eight animals were captive-born, and the remaining 8 had been imported from South America at least 3 years before the study began. Two females were found to be pregnant during the course of the study.

Animals were housed indoors in standard basket-type primate cages ($0.73 \times 0.77 \times 0.73$ m). Opaque partitions between adjacent cages precluded visual and tactile contact between animals in different cages, but females had auditory and olfactory access to one another. All subjects were individually housed for at least 3 wk before data collection began and during the initial phase of the study. Subsequently, subjects were housed in pairs, with pairings made between animals which had not lived together previously. Pairmates were matched as closely as possible for age, weight, and provenience.

Diet consisted of New World monkey pellets. Feedings occurred twice daily at 0730 and 1300, and water was available ad lib. Room temperature ranged from 13 to 37°C; supplemental heat and cooling were provided at the temperature extremes. Lighting was controlled on a 12:12 h dark:light schedule.

Apparatus

Testing was conducted in a test cage (1.64 m high $\times$ 1.54 m long $\times$ 0.62 m wide) constructed of wood and poultry wire. The test cage was located in a room which contained no other animals. A set of 3 double perches was situated at either end of the test cage. Each set was approximately 20 cm from the end, with the perches at heights of 0.43, 0.84 and 1.24 m from the cage floor. An observation booth was located behind a 1-way vision screen 1.77 m from the test cage. Adjacent to one end of the test cage was a stimulus cage, 0.82 m high $\times$ 0.49 m long $\times$ 0.62 m wide. A double perch running the width of the stimulus cage was at approximately the height of the middle perch in the adjacent test cage, and the top of the stimulus cage was 0.23 m above the top perch in the test cage. The test cage and stimulus cage were separated by an opaque guillotine door, controlled from the observation booth; when this door was raised, the ends of the two cages were 6.30 cm apart and separated only by poultry wire. The openings in the wire were 2.54×3.81 cm, so that monkeys could reach from one cage into the other.

Two identical test cages were available for use in habituation and in Phase I. Before any data were collected, each subject was released alone into a test cage for 1 h on several occasions. This habituation procedure was repeated until each animal moved freely about the cage.

Design

Each subject was tested while living alone (Phase I), during the initial hour of isosexual pairing (Phase II), and while living with another female (Phase III). The sequence of data collection procedures in each of these phases is presented in Table 1. At the beginning and end of Phase I, a basal blood sample was collected from each female immediately following removal from her home cage and subsequently assayed for plasma corticosteroid concentrations. Midway through Phase I, each subject was confined alone in the test cage for 55 min, during which behavior and heart rate were recorded (cage test—alone condition); a blood sample was collected immediately following this test period and subsequently assayed for plasma corticosteroid levels. Several days before the cage test and again several days after, each female was tested in the stimulus test, in which behavior and heart rate were monitored in response to a series of stimuli presented in the stimulus cage.

In Phase II, 2 unfamiliar females were placed together in the test cage (cage test—pair formation condition). Behavior and heart rate were monitored and a blood sample was obtained as in the cage test in Phase I. Following pair formation, each dyad was released into a new home cage to live together for the remainder of the study. Data collection in Phase III replicated that in Phase I. Basal blood samples were collected at 3–4 days and 29–36 days following pairing. The cage test was performed once on each dyad (established pairs condition), 2–3 weeks following pair formation, with pairmates tested together; behavioral data, heart rate data, and a blood sample were collected as in Phases I and II. The stimulus test was conducted twice on each individual as in Phase I. Finally, food-competition tests were performed to assess dominance relationships within dyads. For each subject, at least 2 and no more than 14 days elapsed between consecutive experimental procedures. Time from beginning to end of data collection ranged from 56 to 129 days (mean = 87 days).

Cage Test

Subjects to be tested on a given day were fitted with heart rate harnesses and transmitters at 0730 h and immediately re-

TABLE 1

SEQUENCE OF EXPERIMENTAL PROCEDURES

Phase I—Monkeys Housed Alone
1. Basal Cortisol
2. Stimulus Test
3. Cage Test—Alone
4. Stimulus Test
5. Basal Cortisol

Phase II—Pair Formation
1. Cage Test—Pair Formation

Phase III—Monkeys Housed in Pairs
1. Basal Cortisol
2. Stimulus Test
3. Cage Test—Established Pairs
4. Stimulus Test
5. Basal Cortisol
6. Food-Competition Tests

turned to their home cages. Testing was conducted between 1230 and 1500 h. At the beginning of a test session, subjects were removed from their home cage(s) and released into the test cage(s). Behavior and heart rate were monitored simultaneously during alternate 5-min periods, beginning immediately following release, so that a total of 30 min of cardiac and behavioral data was collected on each subject. Data collection periods were separated by 5-min intervals during which no data were collected. After 55 min had elapsed, subjects were immediately caught and manually restrained while a blood sample was collected.

In Phase I of the study, each female was tested individually (alone condition). However, the 2 identical test cages were placed end-to-end in the test room and separated by an opaque partition, so that future pairmates were tested simultaneously without having visual or tactile access to one another. In Phases II and III, pairmates were released into the same test cage in rapid succession. This design ensured that all procedures, including capture and sampling procedures, were strictly comparable for all phases.

Stimulus Test

Subjects were fitted with harnesses and transmitters at 0730 h and returned to their home cages; testing was conducted between 1200 and 1600 h. At the beginning of a test session, a subject was released alone into the test cage and allowed to habituate for 10 min. At the end of this period, the first of 7 stimulus conditions was prepared in the stimulus cage and the opaque door between the two cages was raised. Exposures lasted 5 min each, during which behavior and heart rate were recorded simultaneously. Successive exposures were separated by 5-min periods during which no data were collected, the guillotine door remained closed, and the next stimulus condition was prepared. Following presentation of all 7 stimulus conditions, the opaque door was closed, the subject was caught, harness and transmitter were removed, and the animal was returned to her home cage.

Stimulus conditions included 1) a female monkey, the subject's future or current pairmate; 2) a male stranger; 3) the pairmate and male stranger together; 4) a cup of preferred food items (raisins and miniature marshmallows); 5) the pairmate with the cup of food; 6) a mirror suspended against the stimulus cage and facing the end of the test cage; and 7) the empty stimulus cage. Stimulus conditions paralleled those used in the identical study of males. They were selected to assess responsiveness of monkeys to a like-sex partner alone and with incentives (opposite-sexed conspecific, food) which were anticipated to elicit competition (31). The mirror was intended to simulate a like-sex stranger who remained unfamiliar throughout the course of the study, and the empty stimulus cage served as a control condition. Order of stimulus presentations was approximately balanced across subjects, but remained constant for each female thoughout the study, and was the same for each pair of cagemates. Different stimulus males were used for each dyad, but the same male was used for each pair of females throughout the study.

Behavioral Observations

Behavioral observations utilized checksheets with a predetermined list of behaviors. One-zero sampling was used to score behaviors which tended to occur in irregular clusters (locomotion, harness manipulation, urine wash, rump rub, sneeze, reach into stimulus cage). These behaviors were scored once if they occurred within a 15-s interval, as demarcated by an audible signal from a timer. Behavioral states of relatively long duration (huddle posture, proximity, contact, location, orientation toward stimulus) were scored on the 15-s signal. Behaviors occurring as discrete events (approach, leave, displace, grab/hit, genital display, arching/cage-shaking display) were scored each time they occurred. Interobserver agreement was assessed before data collection began. Agreement for all behaviors considered together was 94% for the cage test and 88% for the stimulus test. Table 2 lists the behaviors scored, definitions, and scoring methods.

Heart Rate Telemetry

Heart rate was monitored telemetrically using an elastic chest harness equipped with 2 surface monopolar electrodes and an FM transmitter [weight: 19 g; see (33) for details]. Cardiac signals were transmitted to an FM receiver and recorded either on electromagnetic tape or directly on a computer. Mean heart rate in beats per min was subsequently determined for each 5-min recording period.

In order to minimize the response to the heart rate harness during data collection, each female wore a dummy elastic chest harness for a total of 10 days before formal data collection began. Dummy harnesses were removed before the beginning of the study. On test days, subjects to be tested were manually captured and restrained while being fitted with a chest harness. As indicated, this was completed at least 4 h before testing to allow time for any effects of the harnessing procedure to dissipate. For the cage test, females to be tested together wore transmitters set at different frequencies, allowing cardiac data from both to be recorded simultaneously.

Blood Sampling and Cortisol Assay

Blood samples were collected between 1230 and 1500 h. Monkeys were manually captured and restrained while a 1 ml sample was withdrawn by femoral venipuncture. All samples were obtained within 4 min from cage opening (mean = 97 s). In Phases II and III, and in the cage test in Phase I, blood samples from pairmates were collected simultaneously.

Blood samples were centrifuged and the plasma fraction extracted and frozen at −20°C until assayed by a competitive binding technique modified from that of Bassett and Hinks (4). Although this assay measures both cortisol and corticosterone concentrations, comparison of values obtained by this method with those obtained by radioimmunoassay procedures specific for

TABLE 2

Behavior	Definition	Scoring Method
Huddle Posture	sitting quietly with tail up over shoulder	instantaneous
Proximity	pairmates within arm's reach (15 cm) of one another, either with or without contact, excluding tails	instantaneous
Contact	pairmates contacting one another with any part of body, excluding tails	instantaneous
Location	perch on which subject is located or to which subject is closest	instantaneous
Orientation	subject's face and body directed toward stimulus cage	instantaneous
Approach	move in a directed manner to within 15 cm of partner, with both animals remaining in position for at least 3 s	all occurrences
Leave	move out of proximity of partner after being in proximity for at least 3 s	all occurrences
Displace	cause physical relocation of partner, either with or without physical contact	all occurrences
Grab/Hit	common usages	all occurrences
Genital Display	face partner and present genitals to partner, with thighs spread and one leg usually raised	all occurrences
Arching/Cage-Shaking Display	shake cage and/or rise up with back arched, usually grasping substrate; may be accompanied by screech	all occurrences
Locomotion	physically relocate body by at least one body length	one-zero
Harness Manipulation	contact heart rate harness with hand, foot, or mouth, or rub harness against cage; includes pulling, biting, scratching, and touching harness	one-zero
Urine Wash	urinate, catch a few drops of urine in one hand, and rub palm of that hand on sole of ipsilateral foot; may repeat with opposite hand and foot	one-zero
Rump Rub	move anogenital region back and forth against substrate	one-zero
Sneeze	common usage; putative scent-marking behavior	one-zero
Reach	extend arm out of test cage into stimulus cage	one-zero

cortisol do not yield significant differences (13). Results are therefore presented with reference to cortisol. Intra- and interassay coefficients of variation were 4.1% and 8.6%, respectively.

Food-Competition Tests

Food-competition tests were performed to ensure that sufficient data were available to designate dominance status within each dyad. After all other experimental procedures had been completed, each subject was placed alone in the test cage on several occasions and trained to take a series of marshmallow pieces presented on a stick. This procedure was repeated until each animal reached the criterion of accepting the item within 15 s on each of 20 consecutive presentations. Cagemates were then released together into the test cage and presented with 10 marshmallow pieces at 15-s intervals; the identity of the monkey obtaining each item was recorded. Following a 5-min recovery period, another 10 marshmallow pieces were presented. This completed the test session. Each dyad underwent 5 test sessions for a total of 100 food presentations per dyad. The animal in each pair obtaining the majority of the food items across the entire test series was considered dominant. One female failed to reach criterion in the test cage but did so in the home cage; therefore, food-competition trials for this dyad were conducted in the home cage. In addition, one monkey failed to reach criterion but accepted more than 10 consecutive food items; this dyad was therefore given a total of 10 test sessions with 10 marshmallow pieces presented in each session.

Data Analysis

Physiological data were analyzed parametrically using analyses of variance and *t*-tests. As plasma cortisol levels rise considerably during pregnancy in this species (11), cortisol data from the 2 pregnant subjects were omitted. Basal and cage test cortisol data were analyzed separately with conditions treated as a within-subjects factor. In addition, because rank-related physiological differences in primates are typically found to occur within, but not between, social groups (10, 15, 24), and because pairmates in the current study were matched as closely as possible, dominance status was treated as a within-subjects factor in all analyses. The partners of the 2 pregnant subjects, therefore, could not be used in analyses of dominance effects on adrenocortical activity. In order to utilize as many subjects as possible for each analysis, basal and cage test cortisol values were each analyzed in 2 ways. First, a repeated-measures ANOVA was run using all 14 nonpregnant animals in order to detect any main effect of conditions. Secondly, a rank × conditions repeated-measures ANOVA was performed using data from only the 6 pairs of nonpregnant animals, in order to detect any main effect of dominance rank or rank × conditions interaction. Heart rate data from the cage test and stimulus test were submitted to separate analyses of variance. Cage test heart rates were analyzed using conditions, time and dominance status as within-subjects factors; for stimulus test heart rates, conditions, stimuli and dominance status were treated as within-subjects factors. Behavioral data were analyzed nonparametrically using the Friedman test for overall comparisons across conditions and the Wilcoxon signed-ranks test for paired comparisons between conditions and for comparisons between dominant and subordinate pairmates. Several behaviors (genital display, cage shake/arching display, urine wash, rump rub, sneeze) occurred only rarely and were omitted from analysis. Correlational analyses were performed using Pearson correlations for physiological measures and Spear-

man rank correlations for behavioral measures. Analyses of stimulus test data in Phase I and Phase III were based on the average of the 2 test sessions in each phase. Asymmetry in number of food items obtained during food-competition tests was evaluated by the binomial test for each dyad.

RESULTS

Behavioral Responses to Cage Test

Responses to the test cage in Phase I were bimodally distributed. The majority of subjects (N = 11) were relatively inactive, spending most of the test period in the huddle posture (mean = 82.2% of 15-s signals) and engaging in low levels of locomotion (mean = 11.7% of intervals). Five animals, in contrast, appeared to be highly agitated, engaging in frequent locomotion (mean = 76.5% of intervals) and little or no huddling (mean = 21.2% of intervals). As might be expected, these 2 measures were inversely related ($r = -.58$, $p<0.05$). Frequency of locomotion tended to decline across the 55 min in the test cage, whereas frequency of huddling increased. Comparison of each measure during the first and final 5 min in the cage indicated a significant decline for locomotion and a significant increase for huddling (p's<0.01, Wilcoxon).

Initial encounters between monkeys in the test cage (Phase II, pair formation) suggested that females were highly responsive to one another (see Table 3). In most dyads, affiliative interactions predominated. Pairmates were in proximity to one another on an average of 42.6% of 15-s intervals and in contact on an average of 36.1% of intervals; most of this contact (mean = 32.3% of intervals) involved social huddling, the predominant affiliative behavior exhibited by squirrel monkeys, in which both individuals assume the huddle posture while in passive contact with one another. In 5 dyads, agonism was negligible or absent; in 1 dyad (dyad 5; see Table 4), one individual directed sustained low-level agonism (grabs, displacements) at her partner; and in 2 dyads (dyads 1, 7), one female chased and attacked (grappled with, bit) the other. Agonism was consistently directional: in no dyad were both animals observed to perform antagonistic behaviors. Approaches and leaves, although infrequent, also tended to be asymmetric within pairs: females who initiated agonism performed 82.1% of all approaches but only 32.5% of leaves.

Frequencies of individual behaviors (locomotion, huddle) were highly variable during pair formation and did not differ reliably from those during the alone condition. As in the alone condition, locomotion tended to decline and huddling tended to increase over time. Comparisons of values for the first and last 5 min in the test cage indicated that differences were significant for both measures (p's<0.05, Wilcoxon).

Although frequencies of social behaviors did not differ significantly between Phases II and III, interactions between pairmates following 2–3 wk of cohabitation (Phase III, established pairs) tended to be more consistently affiliative. Mean scores for both proximity and contact were somewhat higher than during pair formation (n.s.; see Table 3): pairmates were in proximity on an average of 64.4% of intervals and in contact on an average of 54.4% of intervals. As in Phase II, most of this contact (mean = 47.6% of intervals) involved social huddling. No fighting occurred, and sustained agonism was seen in only a single dyad (see Table 4). Inasmuch as pairmates spent most of their time sitting in contact during the established pairs condition, individual activity levels were generally low. As in the alone and pair formation conditions, locomotion tended to decrease and huddling tended to increase over the 55 min in the test cage, resulting in significant differences between the first and last 5 min of testing for both measures (p's<0.01, Wilcoxon).

TABLE 3

SOCIO-SPATIAL BEHAVIORS DURING THE PAIR FORMATION (PF) AND ESTABLISHED PAIRS (EP) CONDITIONS*

	Proximity		Contact		Social Huddle	
Dyad	PF	EP	PF	EP	PF	EP
1	1	49	0	48	0	32
2	93	98	83	93	79	79
3	0	86	0	72	0	67
4	50	23	50	18	50	17
5	8	27	2	13	0	10
6	83	48	68	18	54	12
7	34	100	23	100	19	98
8	72	84	64	73	56	66

*Percent of 15-second signals.

Food-competition tests clearly identified a dominant female in each dyad (p's<0.05, binomial). Each dominant animal obtained the majority of food items in at least 4 out of 5 test sessions, and these females obtained an average of 81.8% of food items taken across all sessions. Within pairs, the animal considered dominant on the basis of food-competition trials also tended to perform the greater number of agonistic behaviors during the cage test (see Table 4). Notably, only 4 of the 8 dyads engaged in sufficient agonism during the cage test to permit assessment of dominance relations; however, directionality of agonism in all 4 of these pairs was consistent with dominance relations as determined by food-competition trials. Due to the low frequency of agonistic interactions, statistical evaluation of the differences between dominant and subordinate animals in initiation of agonistic behaviors was not appropriate. Other social and individual behaviors failed to differ in relation to dominance status during the pair formation and established pairs conditions. In the alone condition, however, females who eventually became dominant exhibited significantly more harness manipulation, an apparent displacement behavior, than did their future pairmates ($p<0.05$, Wilcoxon).

In order to determine whether responses to social conditions were influenced by temperamental variables, animals were divided into 2 groups on the basis of activity levels during the alone condition of the cage test. "Active" monkeys (N = 5, including two sets of pairmates) were defined as those which locomoted during at least half of the 15-s observation intervals, whereas "inactive" animals (N = 11) locomoted on fewer than half of the intervals. These 2 groups did not differ significantly during pair formation in either individual behaviors or initiation of social behaviors. However, differences between the groups reemerged after several weeks of cohabitation. Active females engaged in significantly more locomotion and harness manipulation and less huddling during the established pairs condition than did inactive females, and they performed significantly more grabs, displacements, approaches, and leaves (p's<0.05, Mann-Whitney). Finally, behaviors were compared between the 3 dyads which engaged in sustained agonism during pair formation (dyads 1, 5, and 7; see Table 4) and the remaining 5 dyads. In conjunction with their higher frequencies of displacements, dyads which were initially antagonistic engaged in significantly more locomotion and, correspondingly, significantly less huddling than the remaining dyads during the pair formation condi-

TABLE 4

INITIATION OF SOCIAL INTERACTIONS IN THE PAIR FORMATION (PF) AND ESTABLISHED PAIRS (EP) CONDITIONS AND SUCCESS IN FOOD-COMPETITION TESTS BY DOMINANT AND SUBORDINATE FEMALES

Dyad	Rank	Grab*		Displace*		Approach*		Leave*		No. Food Items Obtained†
		PF	EP	PF	EP	PF	EP	PF	EP	
1	α	8	0	22	0	0	1	0	0	66
	β	0	0	0	0	0	0	0	1	34
2	α	0	0	0	0	2	2	1	0	82
	β	0	0	0	0	0	1	1	3	0
3	α	0	0	1	0	0	1	0	8	70
	β	0	0	0	1	0	6	0	0	30
4	α	0	3	0	2	0	2	0	6	82
	β	0	0	0	0	0	3	0	0	18
5	α	1	0	75	5	11	4	1	2	77
	β	0	0	0	1	0	7	9	10	23
6	α	0	3	0	21	1	31	17	24	67
	β	0	0	3	5	20	10	3	17	33
7	α	40	0	123	0	13	0	8	0	88
	β	0	0	0	0	1	0	3	0	3
8	α	0	0	2	1	25	11	14	6	95
	β	0	0	0	1	11	6	23	9	5

*Number of occurrences during 30 min of observation.
†Maximum = 100 items.

tion (p's<0.01, Mann-Whitney). However, in accordance with the overall decline in agonism following several weeks of cohabitation, no differences were apparent between these 2 groups of dyads in the established pairs condition.

Heart Rate Responses to Cage Test

In each of the three 1-h exposures to the test cage, heart rate was initially high and declined rapidly, $F(5,70)=41.5$, $p<0.001$; (see Fig. 1). Heart rate did not differ significantly between the 3 cage test conditions. Furthermore, no differences were apparent between dominant and subordinate animals. Individuals' mean heart rates across each test session were positively correlated with scores for locomotion and negatively correlated with scores for huddling; however, the magnitude of these correlations tended to decline from the alone condition (locomotion: $r=.82$, $p<0.001$; huddle: $r=-.51$, $p<0.05$) to pair formation (locomotion: $r=.43$, $p=0.10$; huddle: $r=-.53$, $p<0.05$) to the established pairs condition (locomotion: $r=.45$, $p=0.08$; huddle: $r=-.36$, $p>0.10$). In parallel with differences in activity levels, active monkeys had reliably higher heart rates in Phase I than did inactive monkeys, $t(14)=3.8$, $p<0.01$; however, heart rates of active and inactive animals did not differ reliably in either Phase II or Phase III. Similarly, animals in dyads which were initially antagonistic had significantly higher heart rates during pair formation than did those in the remaining dyads, $t(14)=3.6$, $p<0.01$, but no differences were apparent between these groups of dyads during the alone or established pairs conditions.

Cortisol

Basal cortisol levels dropped significantly following pairing, from a mean of 109.1 μg/dl when animals were housed individually to a mean of 83.8 μg/dl when they were housed in pairs, $F(1,13)=7.4$, $p<0.05$ (see Fig. 2). This reduction occurred in 10 of 14 nonpregnant females. Cortisol concentrations did not differ reliably between the 2 basal samples collected within each phase, and values in each phase were highly stable within subjects (Phase I: $r=.74$, Phase III: $r=.80$, p's<0.01). Basal cortisol titers did not differ significantly between dominant and subordinate animals. Furthermore, no differences were found between active and inactive monkeys or between dyads which were and were not initially antagonistic.

In each phase of the study, females responded to 1-h confinement in the test cage with a dramatic elevation of plasma cortisol over their basal levels for the current housing conditions [alone vs. Phase I basal: mean increase = 152.1 μg/dl, $t(13)=12.3$, $p<0.001$; pair formation vs. Phase I basal: mean increase = 160.8 μg/dl, $t(13)=8.9$, $p<0.001$; established pairs vs. Phase III basal: mean increase = 163.3 μg/dl, $t(13)=4.1$, $p=0.001$]. The response to the test cage was influenced by both dominance status and social conditions, as revealed in a signifi-

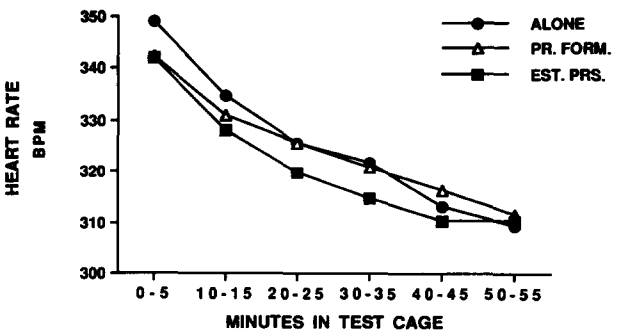

FIG. 1. Heart rate in beats per minute during confinement in the test cage under 3 social conditions: Alone, pair formation, and established pairs.

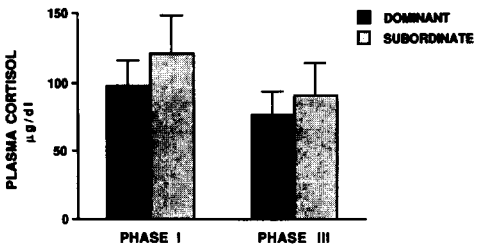

FIG. 2. Mean basal cortisol titers, ±SEM, of 7 dominant and 7 subordinate females when housed alone (Phase I) and when living in isosexual dyads (Phase III).

cant rank × conditions interaction, $F(2,10)=11.8$, $p<0.01$ (see Fig. 3). When analyzed separately, cortisol titers of dominant females declined significantly across cage test conditions, $F(2,10)=4.3$, $p<0.05$; values following the established pairs condition were significantly lower than those following the alone condition ($p<0.05$, Newman-Keuls), and pair formation values were intermediate. Subordinate females, in contrast, did not significantly differentiate cage test conditions. Cortisol values of dominant and subordinate females did not differ significantly in any of the cage test conditions, and adrenocortical responses to the test cage did not differ between active and inactive animals or between those in dyads which were initially antagonistic and those that were not.

In order to determine whether adrenocortical reactivity was altered by formation of isosexual relationships, the incremental response to the test cage was compared between Phases I and III. The magnitude of the cortisol elevation above basal levels did not differ between the alone and established pairs conditions. Furthermore, no differences were apparent between dominant and subordinate females.

Behavioral Responses to Stimuli

Females behaviorally differentiated stimulus conditions in both Phase I and Phase III. When monkeys were housed alone (Phase I), scores for huddling, harness manipulation, and reaching into the stimulus cage differed significantly across stimulus conditions (p's<0.01, Friedman). During Phase III, following formation of pairs, these behaviors again differentiated stimulus conditions, as did the number of scans on which females were found on the two perches adjacent to and in view of the stimulus cage (p's<0.01, Friedman). In both phases, females were highly responsive to stimulus conditions involving food, as evidenced by high scores for time spent next to the stimulus cage, frequent orientation toward and reaching into the stimulus cage,

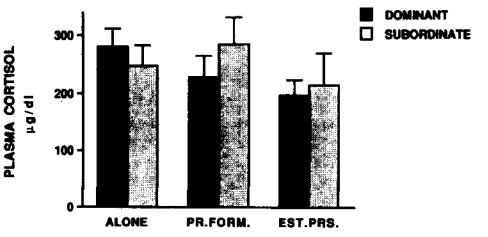

FIG. 3. Mean plasma cortisol concentrations, ±SEM, of 6 dominant and 6 subordinate females immediately following 55-min confinement in the test cage during Phase I (alone condition), Phase II (pair formation), and Phase III (established pairs condition).

and low scores for huddling during presentation of these conditions. As can be seen in Fig. 4, responses to stimulus conditions involving the female partner were not particularly pronounced in either phase. However, females appeared to be somewhat more attracted to one another in Phase III than they were in Phase I. Wilcoxon tests comparing behavioral responses to each stimulus condition in the 2 phases indicated that females oriented toward the female + male condition significantly more often in Phase III than in Phase I ($p=0.05$). In addition, they were adjacent to and in view of the stimulus cage during the female and female + male conditions significantly more often in Phase III (p's<0.05). No other differences betweeen the two phases were apparent in behavioral responses to stimuli.

Dominant animals tended to be more active during the stimulus test than their subordinate pairmates. In Phase I, for all stimulus conditions considered together, females who later became dominant engaged in significantly more harness manipulation than did females who became subordinate ($p<0.05$, Wilcoxon); in Phase III, these females had significantly higher scores for both harness manipulation and locomotion (p's<0.05, Wilcoxons) than did their subordinate partners.

Heart Rate Responses to Stimuli

Heart rate did not reliably differentiate stimulus conditions when monkeys were housed alone nor when they were housed in pairs. Any such effects may have been masked by an effect of time: heart rate declined significantly across successive stimulus conditions, $F(6,90)=5.5$, $p<0.001$. Furthermore, heart rate was significantly higher across all stimulus conditions in Phase III than in Phase I, $F(1,7)=11.7$, $p=0.01$. Cardiovascular responses to stimuli were not reliably influenced by dominance status.

DISCUSSION

The most striking response to female-female pair formation was a dramatic and sustained drop in basal cortisol concentrations. Circulating hormone titers declined by an average of 22.1% within the first 3–4 days following pair formation and remained suppressed for at least another month. The reduction in basal cortisol was notably insensitive to the quality of interactions between pairmates: dyads which initially engaged in considerable agonism exhibited as great a decline as those which did not, and subordinate females showed as great a drop in cortisol as their dominant partners. It therefore appears that like-sex conspecifics are sufficiently salient and important social stimuli for female squirrel monkeys that their presence can lead to long-term suppression of basal pituitary-adrenal activity, independent of the details of the animals' interactions with one another.

The physiological mechanisms mediating the reduction of basal cortisol are currently unknown. However, as the reduction appears to require more than 24 h for its complete expression and may persist for at least 1 year (29,30), it appears to involve a reorganization of the regulatory mechanisms of the hypothalamic-pituitary-adrenal axis. Elevated basal glucocorticoid titers observed in a variety of circumstances, including depressive disorder in humans, social subordination in male baboons, and advanced age in rats, have been associated with reduced sensitivity to glucocorticoid negative feedback, possibly mediated by a decline in the number of glucocorticoid receptors in the central nervous system (7, 35, 38, 39). It is possible that the shift in adrenocortical activity we have found in female squirrel monkeys represents the converse of this physiological condition. That is, isosexually induced reduction of basal cortisol may involve enhanced efficiency of glucocorticoid negative feedback

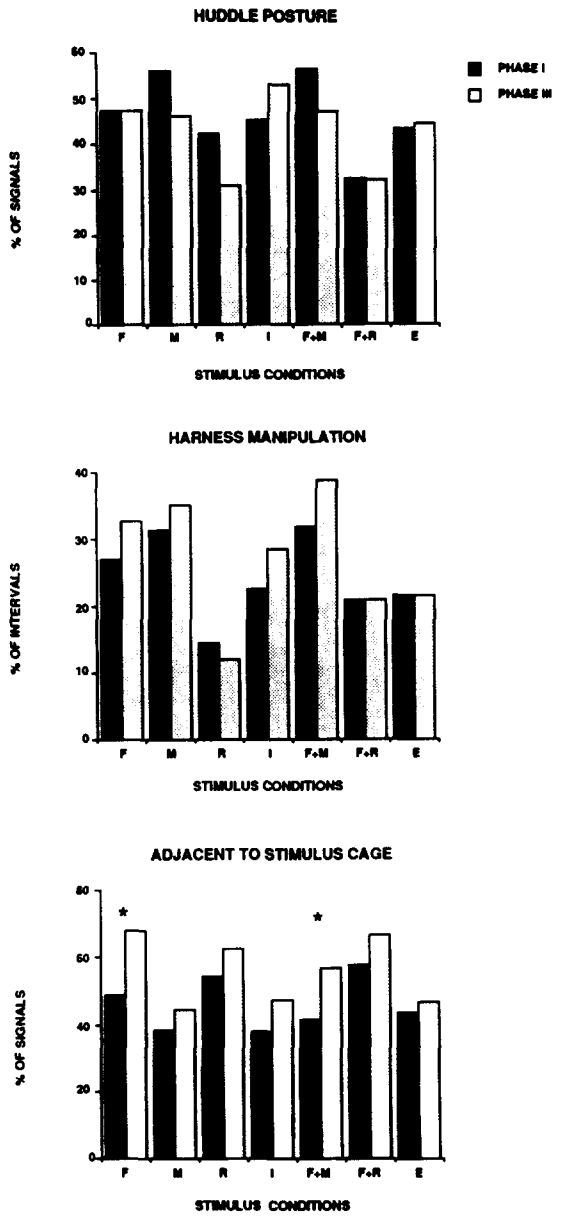

FIG. 4. Behavioral responses to 5-min stimulus presentations when females were housed alone (Phase I) or in isosexual dyads (Phase III). Stimulus conditions: F = female partner, M = male conspecific, R = preferred food items, I = mirror, F + M = female partner with male, F + R = female partner with preferred food items, E = empty stimulus cage. *Indicates significant difference between phases at 0.05 level (Wilcoxon test).

and, consequently, diminished release of corticotropin-releasing hormone from the hypothalamus and adrenocorticotrophic hormone from the pituitary.

In contrast to basal pituitary-adrenal activity, adrenocortical responsiveness to the test cage was highly stable across conditions. Females responded to each 1-h confinement in the test cage with a pronounced elevation of plasma cortisol, despite their repeated exposures to the cage both before and during the study. Responsiveness was also not affected by social conditions. Cortisol levels following test cage confinement tended to decline from the alone condition to the established pairs condition, but this effect was only significant for dominant animals and was completely accounted for by the reduction in basal cortisol levels following pair formation. Incremental responses to the test cage did not differ across conditions. Furthermore, dominance rank exerted only a transitory influence on cortisol levels: although a significant rank × conditions interaction was detected, it could be attributed to differential responses of dominant and subordinate females to their initial hour together. Thus, in keeping with findings by Hennessy (18,19), we found no evidence that adrenocortical responsiveness to a 1-h test situation is altered in female *Saimiri* by the availability of familiar female companions.

The absence of social modulation of the adrenocortical response to the test conditions contrasts with findings by Gonzalez et al. (16), who reported that both absolute and incremental responses to handling and ether anesthetization were smaller in isosexually paired female squirrel monkeys than in those housed alone. Several methodological differences may have contributed to this disparity, including the intensity and duration of stressors. The difference between the two studies in the time from termination of the stressor to blood sample collection may be particularly important. If, for example, singly housed females show reduced sensitivity to negative feedback effects of glucocorticoids, they would also be expected to show elevated cortisol for longer periods following termination of the stressor (37). In contrast, isosexually paired females would be expected to show enhanced negative feedback regulation and consequently a more rapid return to basal values. In the current study, blood samples were collected immediately following 1-h confinement in the test cage. As pituitary-adrenal activation probably continued throughout the test period [see (13)], differential effects of housing conditions on inactivation of the stress response would not have been detected. Blood samples in the study by Gonzalez et al., however, were collected 30 min following termination of the stressor. This amount of time would be ample for differences in negative feedback effects to emerge (20) and could account for differences in the stress responsiveness of grouped and singly housed females. In view of this possibility, social influences on the time course of the stress response in female squirrel monkeys offer an interesting avenue for further research.

Heart rate declined markedly during each confinement in the test cage. This pattern of response differs from that of squirrel monkeys exposed to a similar but completely novel test cage for the first time (13), suggesting that the response to the test cage was influenced by the habituation procedures. Like pituitary-adrenal responsiveness, however, heart rate was not sensitive to social conditions. Cardiac activity did not differ reliably between cage test conditions or between dominant and subordinate females, and although heart rate responses to stimulus exposures were greater following pair formation than before, there was no indication that heart rate was differentially responsive to conditions involving the female partner. It is clear, however, that heart rate can provide a sensitive measure of social variables in squirrel monkeys. Cardiac activity of male *Saimiri* tested under identical conditions was highly responsive to social stimulation (31). Heart rate showed an overall reduction following formation of male-male dyads, and this effect was more pronounced in dominant males than in subordinates.

Relationships formed by female squirrel monkeys were generally harmonious. This was apparent in 5 dyads during their initial hour together. The remaining 3 dyads responded agonistically to one another during initial encounters; after several weeks of cohabitation, however, all pairs engaged in at least moderate levels of affiliation and little or no agonism. Furthermore, there was no evidence of incompatability between females in the home cage. Periodic checks of animals following initial formation of

pairs revealed no signs of discord; no dyads had to be separated, and no animals sustained injuries at any point in the study.

In spite of the fact that females lived together amicably, continuous cohabitation was not an influential determinant of behavior or physiology in the test situation. Dyadic interactions were less agonistic and somewhat more affiliative following several weeks of cohabitation, but no significant behavioral differences were detected between the pair formation and established pairs conditions. Similarly, neither heart rate nor adrenocortical responsiveness reliably differentiated the two conditions. Responses to the stimulus test likewise indicated that familiarity between females was not an important factor in this situation. Heart rate was not selectively responsive to the familiar female companion, and behavioral responses to stimulus conditions involving the female partner gave only moderate indications of enhanced attraction after pair formation.

Another aspect of social relationships that might be expected to influence behavior and physiology is dominance. Success in food-competition trials reliably differentiated dominant and subordinate females in every dyad, and the outcomes of these trials were almost entirely consistent with directionality of agonistic interactions in the test cage. For half of the pairs, however, agonism was infrequent (0–5 occurrences) and relative status could not have been determined on the basis of agonistic interactions. The effect of dominance status on physiological measures was restricted to a slight difference in pituitary-adrenal responses to pair formation. Analyses of incremental responses to the same situation, however, did not reveal any status effects. Thus, although our findings confirm previous reports that female squirrel monkeys establish dominance relations with one another which are apparent in agonistic and competitive interactions (17, 25, 32, 41, 43), they also suggest that dominance relations among female *Saimiri* do not impose strong constraints on the behavior or physiology of individuals.

Comparison of the present results with those from previous studies of males demonstrates that male-male and female-female relationships among squirrel monkeys are associated with contrasting physiological profiles. In males, neuroendocrine and autonomic activity is sensitive to specific qualities of isosexual interactions, including relative dominance status (10, 17, 24, 31, 34). Socially induced alterations in neuroendocrine activity are most pronounced shortly following formation or disruption of social relationships, suggesting that physiological function responds to such social dimensions as familiarity, compatibility, or predictability (30,34). Among females, in contrast, basal pituitary-adrenal activity reflects the sustained availability of like-sex companions (16, 29, 30). Pituitary-adrenal activity does not respond to short-term presence or absence of companions, however, and neither neuroendocrine nor autonomic function is particularly sensitive to such relational dimensions as familiarity, dominance or the quality of social interactions in which females engage (18, 19, 29). These physiological contrasts appear to be associated with sex differences in the development and dynamics of intrasexual social relationships.

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