Social Structure of the Squirrel Monkey (*Saimiri sciureus, Iquitos*): Relationships among Behavior, Heart Rate, and Physical Distance


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Abstract. The relationships between heart rate, behavior, and physical distance were assessed in squirrel monkeys forming a stable colony. For many specific behaviors, heart rate is elevated from baseline 2 min before the behavior and depressed afterwards. Heart rate during a specific behavior is often related to rank by either a U or inverted U: high and low ranking animals show similar heart rates but those of midranking animals are depressed or elevated. The findings are interpreted in terms of the possible evolitional effects on endocrine output of long- and short-term stress.

Key Words: Rank on dominance orders, endocrine functioning, autonomic nervous system, breeding season, arousal.

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Problem

Among the less well understood mechanisms of animal behavior are those which determine the various forms of social organization of different species. Although morphologically-determined capacities are an essential determinant of a biologically successful society, there are many examples of species having similar morphological characteristics which develop very different forms of social organization. This divergence of patterns of socialization is evident among the primates: in this order species sharing the same biosphere closely resemble one another morphologically but have developed distinct patterns of social behavior [Allee, 1939; Andrew, 1963a, b; Huxley et al., 1954; Lack, 1954; Mayr, 1963; Scott, 1945].

If the supposition is correct that the form of organization developed gives the species a selective advantage, it is necessary to analyze the factors leading to the selection of one form of organization over another. Two major questions are evident: how is a form of social organization developed by a species and how does the form of social organization developed affect individual members of the species?

The first question is not answerable experimentally unless one can control and observe speciation among animal forms on which selective pressures operate in such a way that the form of social behavior developed has an important survival value. Because of the obvious difficulties in answering this question experimentally, the usual procedure is to provide indirect answers by recreating the significant pressures and describing their probable relation to the form of social organization of the species. This procedure contains all of the logical problems and theoretical deficiencies associated with the postulation of untestable intervening variables.

The second question restates the implication that although a form of social organization may be beneficial to the species (as judged by survival of the species), the form may be disastrous to individual members of the species whose morphology or behavior is unsuited to the form of socialization developed. The question has the advantage of being answerable since we can trace behavior patterns to such factors as lifespan of the animal, reproduction, and aggression [Carpenter, 1942, 1945; Collias, 1950; Hederig, 1950].

However difficult it may be to stipulate the precise conditions required for a society to be said to exist, it is evident that the formation of societies is a major characteristic of mammalian behavior. Minimally, we can stipulate two conditions requisite for the establishment of a society: (1) interactions take place between members of the species, and (2) more important, inter-
actions between the members of the society lead to organized relationships. The complexity of social behavior is evident from both the large number of methods devised to study it and also the variety of social patterns that have received both theoretical and experimental attention, including maternal behavior, aggression, and dominance relationships [Carpenter, 1942; Chance and Mead, 1952].

A number of lines of inquiry suggest that a fruitful approach to the analysis of primate socialization would be to compare the various forms of behavior with concurrent physiological functioning. The convincing evidence that population density affects physiological state, mate selection, reproduction, phenotypes and, eventually, whether and in what form a species survives led us to examine the endocrine states accompanying group formation. In the case of the squirrel monkey, the nature and quantity of endocrine output differs markedly between animals which have formed colonies and those which have not and the endocrine output of individual animals is related to the animal’s rank on the dominance order [Candland and Leshner, 1973; Leshner and Candland, 1972].

Both the experimental evidence regarding the relation of socialization to survival of a species and the evolutionarily-derived assumptions suggesting that socialization itself possesses survival value (in so far as it reduces aggression and yields more time for foraging, mating, and other activities which enhance the probability of survival) imply that it is essential to consider the physiological changes that accompany socialization. This study reports the relationship among (a) patterns of behavior, especially dominance (b) heart rate, an autonomic measure responsive to endocrine secretion commonly believed to reflect emotional arousal, and (c) the physical distance maintained by individual members of a colony of squirrel monkeys whose social organization was continuously revised during a 9-month span by the periodic introduction of unfamiliar animals into the established colony.

Method

Subjects. Five male and four female squirrel monkeys (Saimiri sciureus, Iquitos) are described. The animals were estimated by weight and dentition to be between

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6 The taxonomy and nomenclature of the squirrel monkey remains unsettled. I have followed Cooper’s suggestion [1968] of using the source of supply following the name. For a useful discussion, see Clarkson et al. [1968].
4–5 years of age at the onset of the year-long study. They were housed in the laboratory for 6 months prior to the first observations. During the first 2 months, they were placed in isolation for standard TB and parasite tests. For the remaining 4 months they were housed in individual cages while dominance orders were determined using a round-robin pair comparison procedure with five repeated measures emphasizing penile displays and submissive gestures [Candland et al., 1970]. A linear order was found among the males which remained highly reliable over the 4-year period when these animals were observed. No consistent dominance relationships were observed among females. Intrasex determinations were not made.

Births and weight records date the fatted-male season to be between mid-November and February [Dumond and Hutchinson, 1967]. The males weighed between 750 and 960 g at the onset of the study (September) and between 755 and 986 g by the end of the observations reported here (May). Individual weights increased between 23 and 45 % during the fatted season, although a consistent relationship was not found between percentage weight gain and rank on the dominance order. Corresponding weights for females were 570–698 g at the onset of the study and 567–700 g at the conclusion.

**Housing conditions.** One month after the completion of the dominance tests (September), the animals were introduced individually into a simulated environment consisting of a room 4 × 4 × 3.5 m. A gridwork, consisting of 2.5 × 2.5 cm wood slats placed at 28-cm intervals, was numbered and color-coded to permit observers to identify the

![Fig. 1. The environment in which squirrel monkeys resided during the observations and telemetered heartrate measures.](image-url)
location of individual animals. One section of the gridwork was raised 10 cm from the floor and a second, of the same size, was raised 46 cm providing a split-level walkway arrangement. The floor was covered with cedar chips. Figure 1 shows the housing facility.

The temperature of the facility was 77 ± 3 °F during the study. The relative humidity varied between 35 and 65%. The lighting was two banks of fluorescent lights. The first was directly over the room and provided from 8 to 32 ft-c on the sides and from 8 to 12 ft-c on the floor of the room. The second bank was outside the housing and cast 4 ft-c on the wall most brightly lighted and 2 ft-c on the dimmest wall. The differences in reflectance within the room were due to the lights being outside the room and casting shadows. The second and dimmer bank came on at 05.30 EST and turned off at 18.00. The first (overhead) lights turned on at 06.00 and off at 17.30. This arrangement permitted a simulation of daybreak and nightfall. The light-dark ratio approximated the seasonal diurnal cycle of Iquitos, but it was not possible to approximate the humidity conditions.

Transmitting and recording heart rate. Heart rate was transmitted by Onyx TSBC transmitters attached to the animals’ backs. The heartbeat signals were detected by E & M self-adhering electrodes placed on either side of the sternum. Electrodes and transmitters were covered by a band of surgical tape. The signals were broadcast over different wavelengths between 88 and 102 mHz. They were received by FM tuners which relayed the signal into three types of monitors: (a) an oscilloscope used to provide a visual display of the signal for tuning purposes, (b) printout counters which cumulated the number of signals in 15 second blocks, and (c) an Esterline-Angus discrete recorder which provided a permanent record of the heartbeat. The printout record was compared to the Esterline-Angus record in order to eliminate data resulting from spurious records caused by detuning and interference.

Colonization. A colony was formed by placing animals periodically in the living area. The observations included recording simultaneously (a) the heart rate of selected animals, (b) behavioral patterns, and (c) the location of each animal. This permitted the analysis of relationships among heart rate, behavior, and physical distance at the time of the behavior.

Placement in colony. The animals were placed in the living area at 2- to 3-week intervals in the following order: 1 ♂, 1 ♂, 2 ♂, 2 ♀, 3 ♂, 3 ♂, 4 ♂, 4 ♂, 5 ♂. The dominance ranks previously determined were used to determine the order of introduction, alternating males and females from animals of high rank to those of low rank. Although females did not show a reliable linear order, one female was observed to be dominant over other females (1 ♀) and a second was seen to be clearly submissive to all other females (4 ♀). The ranking of males on the dominance order was consistent during the tenure of the observations and during the 3 years after the completion of the study. Although mid-ranking females can not be distinguished in dominance, the order derived from observation of both males and females while undergoing colonization is used to present results with the understanding that conclusions based on female rankings are merely suggestive.
Observations. Three 20-min observations were made twice a week. The observations took place in the morning, afternoon, and early evening although the precise time varied by as much as an hour and one half. In order to obtain additional information on the general behavior patterns of the animals, at various times they were observed by closed-circuit TV. Observations over the duration of the study showed that the animals had three distinct resting periods, one from 09.30 to 10.30, one from 11.30 to 12.30, and one from 15.30 to 16.30. On some occasions, the formal observation period interrupted the animals’ resting time [Candland et al., 1972].

After entering the room in which the living area was built, the observers waited between 5 and 10 min before beginning the formal observations. Each observer was assigned to one animal. A counterbalanced schedule was used in order to approach the ideal of having each observer record the behavior of each animal equally often. During each minute of the 20-min period, the observer recorded the occurrence of any of the selected behaviors and the location of the animal at the time. Heart rate was recorded in a separate room. The observers synchronized time over closed circuit TV with the staff that was telemetering the heart rate.

The major behaviors, recorded and coded for computer analysis, were as follows:
- Penile display; penile display received; biting (self-biting of hands or feet); holding (holding another animal); holding received; huddling (sitting with the head lowered and the tail wrapped around the body); scratching (self-scratching); stretching (stretching between grids, sometimes on the back [backrolling], but most commonly on the stomach in an upright position); urine washing is included in this category because the observers could not reliably distinguish urine washing from stretching. These behaviors accounted for 80–90% of the identifiable waking behavior of the squirrel monkey. Other behaviors were recorded as qualitative observations, but because of their rarity they are not included in the statistical analysis.

Heart rate records. During each observation session, the heart rate from two animals was recorded. The selection was made according to the following priorities: an animal placed in the room for the first time, pairs that had been interacting, animals from whom few data had been collected. Although an attempt was made to record heart rate from each animal equally often, this was impossible both because animals were in the colony for different durations depending on the order in which the animal was introduced and because females were much less active than males. The frequency of behavioral interactions among males favored their selection for heart rate recording during the formal observations.

At 09.00 on each observation day, the animals who were to have their heart rate recorded were removed from the colony by net and outfitted with the electrodes and transmitters. This procedure stressed the animal. Pilot data show that the increase in heart rate caused by this procedure dissipated in one hour or less. Nonetheless, the observation that heart rate returns to its baseline within an hour does not remove the possibility that heart rate viability was increased by the electrode placement procedure.

Following placement of the transmitter, the animal was returned to the living area; no observations were made for at least one hour. At the conclusion of the evening session, the telemetry equipment was removed from the animal.
Results

The results are separated into (a) behavior patterns described quantitatively, and qualitatively, (b) the relation between heart rate and the behavior patterns and (c) the relationship of physical distance between animals’ heart rate, and behavior patterns.

Behavior Patterns

Frequency of behaviors as a function of rank. Of the total number of behaviors observed, the following specific behaviors took place at the percentage shown: scratching (34%), holding (21%), holding received (20%), stretching (19%), biting (2%), penile display (1%), penile display received (1%).

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Fig. 2. Frequency of the basic behavior patterns showing the influence of rank on behavior for males. PD = Penile display given; PDR = penile display received; H = holding; HR = holding received; Sc = scratching; St = stretching; B = biting; Hu = huddling; GM = genital manipulation.

Fig. 3. Frequency of female behavior. For abbreviations, see figure 2.

The number of holds should equal the number of holds received. The 1-percent difference is observational error and may be considered an estimate of observer reliability since different observers watched different animals and recorded independently.
(1%), huddling (1%), and genital manipulation (1%). These percentages mask striking behavioral differences attributable to sex and to rank. Figures 2 and 3 show the frequency of the nine basic behaviors differentiated by sex and rank. Several trends appear:

Among males, the higher the rank, (a) the lower the frequency of penile displays received, holds, and holds received and (b) the higher the frequency of scratching, stretching, biting, genital manipulation, and penile displays (note the exception of 3♂, whose behavior is idiosyncratic in other respects). Among females, the higher the rank, (a) the lower the frequency of penile displays received and holds received, and (b) the higher the frequency of scratching, stretching, and biting.

Table I shows the degree of statistical significance of the basic behaviors when the sexes are compared. Comparison of bold face numbers suggests that males show a significantly greater frequency of penile displays, holding, and scratching, while females show a significantly greater number of holdings received and penile displays received. The frequency of stretching, biting, huddling, and genital manipulation is approximately the same for both sexes.

Two of these findings are unexpected from data collected both in the field [THORINGTON, 1968] and in a partially naturalistic environment [BALD-

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<td>Genital manipulation</td>
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Table I. Frequency of basic behaviors in males and females

1 Figures in italics indicate the higher frequency when sexes are compared.
2 Because of zero variance for females, binomial test for significance meaningless.
3 n.s. = Not significant at p < 0.05.
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Both observed penile displays received and holding received; however, the finding that the frequency is sex-related is not reported in their field studies. Although in our sample the male does display to other males, most male displays are directed toward females. Similarly, although the male 'holds' significantly more frequently than females \( p = <0.05 \), the females rather than the males are recipients of the holding.

**Frequency of behavior as a function of the reproductive cycle.** This section describes the frequency of the more important basic behaviors as a function of the season. Because unfamiliar animals were introduced throughout the observations, it is impossible to distinguish definitively the effects of season from the effects of introduction.

**Displays.** Figure 4 shows the frequency of penile displays given and received from October through May. The top part of the figure, penile displays given, shows that although 3 \( \sigma \) gives the highest number of total displays (fig. 2), a number of displays occur when 1 \( \sigma \), 2 \( \sigma \), and 3 \( \sigma \) are introduced to the colony. 4 \( \sigma \) and 5 \( \sigma \) do not display when introduced to the colony, either because of their low rank or because of the possible presence of an already organized order. After introduction to the colony, males display at a constant rate, suggesting that the order is settled. By comparison with the

![Penile displays given and received](image)

*Fig. 4.* Frequency of displays given (top panel) and received by males (bottom panel) as a function of season. Numbers indicate rank of males.
bottom part of the figure, penile displays received, it may be seen that 1 ♂ and 3 ♂ give most of their displays to females. Low ranking males 4 ♂ and 5 ♂ give few or no displays upon introduction, but are displayed to frequently.

Figure 5 shows displays per month received by females. 1 ♀ received only one display when introduced into the area (from 1 ♂) and received no displays afterwards. Lower ranking males introduced into the colony did not display to her. 2 ♀ received eight displays upon introduction, mostly from 1 ♂. She received displays for 4 months, primarily from 2 ♂ and 3 ♂. Both 3 ♀ and 4 ♀ received numerous displays when introduced into the colony, but not afterwards. This suggests that circumstances other than the season affect displays but that frequency of display is determined in part by the season. The introduction of females results in displays from males. The number of such displays increases both with low rank of the female and coincidently with the size of the colony and the number of males. The factors which account for the displays toward females are undeterminable from the design of this study, although the fact that 4 ♂ and 5 ♂ gave few or no displays indicates that the greater number of males may not be important since the displaying is done only by the three high ranking males.

It is instructive to review situations accompanying the large number of displays given to 2 ♀: (1) 1 ♂ is placed in the living area, (2) 1 ♀ is placed in the area and received a single display from 1 ♂, (3) 2 ♀ is placed in the area
and receives eight displays from 1 ϕ. The increase in displays to 2 ϕ shows that colonization requires more interactions (i.e., more displays?) when a second female is introduced to a pair. It is noteworthy that marmosets and squirrel monkeys display behavioral patterns which appear to have similar functions (i.e. the penile display in the squirrel monkey and the scrotal display in the marmoset). Among some subspecies of marmoset, the introduction of a stranger into an area inhabited by an established pair leads to fighting [EPPEL, 1970a, b; EPPEL and LORENZ, 1967].

**Scratching.** 1 ϕ, 2 ϕ and 1 ϕ (who rank high on their respective hierarchies and who have lived in the area for the longest time) show a lessening in the frequency of scratching between December and March. Because the lower ranking animals of both sexes were introduced into the colony after March, there was no opportunity to determine whether or not they showed a similar decrease. It was observed, however, that they did not show the increase in scratching during April and May exhibited by animals of higher rank. This suggests that high, but not low, ranking animals show a dramatic seasonal depression in the frequency of scratching. It is suggestive that the lessening of scratching occurs during the mating season.

**Stretching.** The class of behaviors termed stretching has been of interest to students of squirrel monkey behavior. The reason for the interest is that the squirrel monkey exhibits several similar stretching patterns in both field and laboratory so frequently that the behaviors are obviously important, but their functions are unclear. For example, during the mating season (and evidently at no other time), males rub one leg in a tonic fashion across a branch [DUMOND, personal commun]. In the field, squirrel monkeys often roll on their backs. In the laboratory, males stretch across two grids or place one leg slowly over a grid and withdraw it rapidly. In the environment used for these observations, both sexes stretched over the gridwork; sometimes, the stretching resembles casual sprawling, but at other times it is an intense activity. CASTELL et al. [1969] have described ‘Rückenwälden’ (back-rolling) in detail. Components of this behavior are included under ‘stretching’ in our analysis. Urine washing, which entails sprawling and stretching the legs, is a well-studied, if poorly understood, part of squirrel monkey behavior [CASTELL and MAURUS, 1967]. Because of the difficulties of separating these behaviors, we have classified them as stretching, although it is very likely that they will be found with further study to be behaviors of very different functions.
Stretching occurs at a consistent rate (between 19 and 20% of all quantitative behaviors) each month, with the notable exceptions of 1 ᵃ, 2 ᵃ, and 1 ᵇ, all animals of high ranks. These animals exhibit a very high proportion of stretching following the month when they were introduced into the area. 1 ᵃ, for example, shows 38% of all quantitative behavior as stretching during October. Data for 2 ᵃ and 1 ᵇ are more striking: 43 and 41%, respectively. Analysis of observers' comments shows that 1 ᵃ, 2 ᵃ, and 1 ᵇ stretched in different but characteristic ways. 1 ᵃ most commonly stretched across the grids with the hind feet and right arm: the left arm was raised stiffly at a 45° angle from the body plane. 2 ᵃ stretched over grids using all limbs. The majority of his stretching was clearly back-rolling. 1 ᵇ stretched her arms and legs across grids only briefly. Lower ranking animals did not show a significantly higher frequency of stretching when first placed in the area and, at the end of the observations in May, no low ranking animal showed a frequency of stretching of more than 3% of all quantitative behavior. The data imply that frequency of stretching is a function of high or low rank. Apparently, it is related to rank on the order and is most common, for animals of high rank, when an unfamiliar animal appears. Stretching is apparently related to the establishment or maintenance of rank.

_Holding and holding received._ Table I showed that holding and holding received were the most common behavior of these squirrel monkeys. One-third of the males' quantitative behavior and one-half of the females' consisted of either holding or holding received. Males hold more frequently and females are held more frequently, implying that the commonest form of this behavior is for the male to hold the female.

Figure 6 shows the frequency of holdings received as a function of sex, rank, and month. Among males, the three top-ranking animals are rarely recipients of holding. Low ranking 4 ᵃ and 5 ᵃ, however, receive more holds, especially when introduced into the area. Among females, receiving of holding is related to order; the higher the apparent rank the fewer holds received. An identical plot of the frequency of holding reveals no pattern, either in terms of season or rank, except that throughout the year (or as the size of the colony increases) there was a tendency for the number of holdings to increase. The importance of holding and holding-received appears to lie in the analysis of which animals held which animals, a relationship considered under the qualitative behavior of the animals which follows this section.
Other quantitative behaviors. The remaining behaviors recorded—huddling, biting, and genital manipulation—were rare compared to other behaviors (fig. 1, 2). In general, analysis by individual animal and month does not reveal noteworthy patterns. The following cases were exceptions. Both 1 ♂ and 1 ♀ bit themselves often (65 and 40 times) when introduced into the area. Few animals self-bit and those who did, with the exception of 1 ♂ and 1 ♀, bit rarely and without apparent relation to rank or season. It is uncertain whether the self-biting observed in 1 ♂ and 1 ♀ is related to either their being alone in the living area or to their rank. Nonetheless, no other animal, regardless of rank, showed significant self-biting when introduced into the area. An identical pattern is found for genital manipulation. 1 ♂ and 1 ♀ manipulated frequently when introduced into the area; the other animals did not show the behavior when introduced into the living area and later manipulated only occasionally and without relation to factors such as season or rank.

Behavior: Qualitative Observations

Although the quantitative data presented in the preceding section provide a description of the relationships between rank, behavior, and time of year, the use of descriptive statistics obscured the behavior patterns of individual animals. This section considers sequences of behavior, emphasizing the behavior of individual animals when an unfamiliar animal is introduced.
While 1 ♂ was in the area alone, his behavior was restricted to scratching and stretching. When 1 ♀ was introduced, 1 ♂ began biting and genital manipulation. Although these behaviors are the lowest in overall frequency, it is noteworthy that they did not appear until another animal was present and like scratching and stretching, they are self-directed behaviors. Huddling was first seen 2 days after the introduction suggesting that strangers do not huddle immediately, but that a period of acquaintance is required for self-directed activities to be replaced by activities involving another animal. When huddling began, biting and genital manipulation ceased. Considering behavior involving interactions between animals, 1 ♂’s immediate reaction to the introduction of 2 ♂ was stretching and genital manipulation followed within 2 minutes by a penile display of long duration. 1 ♂ gave a total of 17 displays to 2 ♀ within 15 min, followed by a display to 1 ♀. 1 ♂ and 2 ♀ then huddled. With the introduction of 2 ♂, 1 ♀ again exhibited genital manipulation and biting followed by a penile display. Following the display, 1 ♂ held 2 ♀, although he occasionally left this position to display to 2 ♂.

The introduction of 3 ♂ brought an immediate display from 1 ♂. 3 ♂ then displayed to both 1 ♂ and 2 ♂. The displays continued for 2 days, by which time 3 ♂ had ceased to display to 1 ♀ and displayed to 2 ♀ briefly and rarely. The introduction of 3 ♀ did not evoke penile displays. She was held by all animals except 1 ♂ who then held 4 ♀. The introduction of 4 ♂ and 5 ♂ evoked identical behavior from 1 ♂: he held each, gave a penile display, and held again.

The general sequence is (a) when placed into a novel area alone, the squirrel monkey shows a higher than usual frequency of stretching and scratching, (b) when an unfamiliar animal is introduced, self-directed activities are evident, such as biting and genital manipulation, (c) the penile display is the initial behavior directed toward another animal, (d) huddling and holding often follow the initially frequent penile displays.

The way in which the colony arranged itself is of special importance to the discussion of physical distance in the third section of results; however, it is also of importance to an interpretation of the qualitative social dynamics of this colony. 1 ♂ spent most of his time with 1 ♀ and 2 ♀. His most frequent behavior was to rest between them with an arm around one or the other, and he often held 1 ♀. No other animal was held by 1 ♂. 2 ♂ interacted only with 3 ♀, except for rare occasions when he was observed huddling with 1 ♂.

Footnote: In June 1972, 1 ♀ died during a hurricane, 2 ♀ appears to have taken her place on the deference order.
This occurred only during the night, when the females usually slept on the floor while the males remained on the gridwork above. 3 ♂ often attempted to hold 1 ♀ and 2 ♀; however, he was chased away by 1 ♂. 1 ♂ often slapped 3 ♂. The slap came only when 3 ♂ had harassed 1 ♀ and 2 ♀ for some time; it came with little warning and was severe. It always resulted in 3 ♂’s leaving the area. Some behavioral measures, including penile displays and holding, would suggest that 3 ♂ should have been classed as the second ranking male. It is possible that a change in the order was taking place during the observations. Many of 3 ♂’s holds were rebuffed, suggesting that the absolute frequency is misleading. Similarly, many of his penile displays were given at such a distance that the intended recipient appeared not to see them. Again, the quantity of behavior could be misleading for his numerous displays were ineffective. Finally, 2 ♂ had clear priority over 3 ♂ in location, food selection, drinking, and holding.

4 ♂ and 5 ♂ were associated with 3 ♀ and 4 ♀. These four animals, the lowest ranking males and females, remained on the floor under the grids most of the day. Other animals rarely huddled with them or held them, except during the night when all females and one or both low ranking males often stayed together. When introduced to the colony, both 4 ♂ and 5 ♂ remained on the floor for 10–14 days before being seen on the gridwork.

The colony as a group behaved in a fashion similar to that reported by field observers [Candland et al., 1972]. In the morning, the animals ate and drank, were active for an hour or two, napped, were active again for two to three hours, ate and drank, napped, ate and drank, were active for an additional two hours, and huddled approximately half an hour before darkness. The most obvious difference between this colony and groups observed in the field was that these animals napped three times during the day, while free-ranging animals are reported to nap but twice.

**Heart Rate and Behavior**

Before examining the relation between the specific behavior patterns recorded in these observations and heartrate, it is instructive to consider two interpretative problems.

First, it is difficult to establish a baseline for most physiological measures. This is especially true for measures of autonomic nervous system activity and

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8 Later catecholamine and corticosteroid measures [Leshner and Candland, 1972; Candland and Leshner, 1973] suggest that 3 ♂ was third-ranking in aggression and related responses, at least at the time of urinalysis one year after the observations reported here.
endocrine circulation. The most satisfactory estimate of baseline is the average and range of many measures taken under a variety of conditions as close as possible to free-ranging conditions for members of the species. Because these observations involved an extensive range of conditions, the mean heart rate for each animal throughout the duration of the experiment is used to represent baseline.

Second, in attempting to relate behavioral patterns to heart rate, it is reasonable to determine heart rate both before and after the observation of the behavior. The problem is setting time-limits on the measurements. Because heart rate is a continuously available variable, it is theoretically possible to examine heart rate for long periods before and after a specific behavior throughout the lifetime of the animal. Obviously, some arbitrary time is selected to terminate observations, however arbitrary the selection may be. In this analysis, we recorded heart rate for the period from 2 min before the behavior through 2 min afterwards. If an identifiable behavior follows a change in heart rate before or beyond this arbitrary range, the relationship is not detectable. It is unlikely that a change in heart rate extends beyond the 4-min segment selected.

This section emphasizes the relationship between heart rate and two other factors: the specialized behavior patterns and rank on the dominance order.

![Graph showing heart rate for squirrel monkeys by sex and season.](image)

*Fig. 7. Heart rate for all squirrel monkeys as a function of sex and season.*
Of general interest is the relationship between heart rate, sex, and time of year shown in figure 7. Except for the months associated with the fatted season, the heart rate of females is significantly more rapid than that of males. Tests of statistical significance between the sexes for different months (t, two-tailed) are all significant beyond the 0.001-level except for January, when they are significant at the 0.05-level. The level of confidence in December, when the male heart rate is higher, is beyond the 0.01-level. The mean female telemetered heart rate throughout 9 months including the breeding season is 296 bpm; for males, the figure is 282.

The general difference in heart rate reflects rank within the sexes as well as the difference among sexes. Table II shows the range of heart rate for males and females as a function of rank within the two orders. It is apparent that the ranking squirrel monkey of each sex shows appreciably lower heart rate than other animals. For 1♂, no heart rate measure is ever within the range of animals of lower rank. Because this study is concerned with a single group, there is no meaningful statistic to permit inferences regarding the probable level of confidence of the observed differences between the heart rate of the highest ranking squirrel monkeys and that of other animals of the same sex. Nonetheless, the large number of heart rate measurements taken, the fact that they were taken under a variety of conditions over 9 months, and the fact that they were telemetered and thus more free of contamination by stress or anesthetic than other measures, suggests that the differences in heart rate are of sufficient importance to require verification.

Figure 8 shows the changes in heart rate among the male squirrel monkeys both before and after receiving display. The four males receiving displays (alpha was never displayed to) show heightened heart rate before the display and lowered heart rate immediately after the display. If heart rate change during a display were arranged according to rank, the midranking males show the highest heart rate prior to receiving a display, implying that the onset of a display affects the heart rate of midranking animals more than that of high or low ranking males.

Table II. Range of heart rate for males, females, and as a function of rank within sexual order

<table>
<thead>
<tr>
<th>Rank</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>216-268</td>
<td>255-304</td>
</tr>
<tr>
<td>2-5</td>
<td>272-336</td>
<td>270-342</td>
</tr>
</tbody>
</table>
Fig. 8. Changes in heart rate among male squirrel monkeys before and after receiving a penile display. The point marked 0 is the time of the occurrence of the display. The numbers identify the rank of the animal. The alpha-male (1) is never displayed to.

Fig. 9. Change in heart rate before and after the giving of the penile display.

Fig. 10. Changes in heart rate before and after the initiation of holding.
Figure 9 shows the change in heartrate for male squirrel monkeys giving the penile display. It is evident that heartrate is elevated prior to the display and depressed afterward.

Figure 10 shows the absolute change in heartrate both preceding and following holding behaviors. The decrease for males in heartrate between -2 and +2 min is slight and statistically insignificant. The decrease for females is significant statistically at the 0.001-level (t, two-tailed). Although females have a higher baseline heartrate than males, the males show a higher heartrate than females when holding. Several interpretations of this finding are available and the choice one makes depends upon the assumptions made regarding the nature of the baseline measure (see Section: Significance). Holding lowers the degree of autonomic reactivity in females (but not, apparently, in males). In males, the prospect of holding leads to an increase in the level of autonomic reactivity.

When heartrate before, during and after initiating holding is related to rank on the dominance order, the plot shown in figure 11 results. Both sexes

![Graph](image)

**Fig. 11.** The relationship of heartrate to rank when initiating holding as a function of rank on the order. Observations from males and females are combined, there being no female of fifth rank.

**Fig. 12.** The relationship between mean heartrate and rank on the order for squirrel monkeys while the recipient of a hold. Functions for males and females are shown separately,
show remarkably similar functions. The function is the shape of a U, with high ranking animals of each sex showing little change in heartrate from baseline measures and midranking animals showing depressed heartrate. The implication is that holding leads to the greatest degree of autonomic change in midranking animals and the least degree of change in animals of extreme rank. It is possible that heartrate differs according to whether an animal is initiating or receiving holding. Figure 12 shows heartrate as a function of rank and sex for animals being held. It is evident that sex is not an important determinant: except for the alpha-animals, the heartrate for both sexes is remarkably similar. Because female heartrate is generally higher than that of males, the male heartrate while being held is elevated compared to that of females. When heartrate is examined as a function of rank, we find an inverted U-shaped function. Midranking animals being held show the highest heartrate, while midranking animals initiating the holding show the lowest heartrate. For squirrel monkeys of both high or low rank, either initiating holding or being held has equivalent effects on heartrate; however, for midranking squirrel monkeys, the heartrate is elevated when being held and depressed when initiating holding.

Figure 13 shows the relationship between mean change in heartrate before and after stretching. The functions are similar for males and females: heart-

![Graph showing changes in heartrate before and after stretching.](image1)

*Fig. 13.* Changes in heartrate before and after stretching. Functions for males and females are shown separately.

![Graph showing relationship between heartrate, physical distance, and specific behavior patterns.](image2)

*Fig. 14.* Relationship between heartrate, physical distance and specific behavior patterns.
rate is elevated before the behavior and depressed afterwards. Heart rate during stretching, biting, huddling, and genital manipulations do not vary with the behavior for either males or females.

Behavior, Heart Rate, and Physical Distance

Analyses of the relation of animals to their environment, including reactions to other animals and to inanimate stimulation, have yielded different but nonetheless useful measures of this relationship. Among these measures are (1) evaluation of preference for or withdrawal from specified stimuli, including other animals, (2) measurement of physical distance between groups or individual animals as a function of known variables, such as spacing or grouping, and (3) assessment of the animals' perceptions of physical distance, known as social distance. These assessments have led to analyses of constructs such as critical distance and flight distance. Our observations apply to the second form of measurement.

From these observations it was possible to record the physical distance between any two animals along with both heartrate and behavior. The use of number and color-coded grids permitted translating their locations into distance. Figure 14 presents the difference in heartrate for each major behavior as a function of the distance between the male animals involved in the behavior. The effect of distance is clearest in behaviors involving distance, especially penile display and penile display received. For the display, the nearer the two animals, the higher the heartrate. In the recipient, proximity lowers the heartrate. Certain behavior, including holding and huddling, require the animals to be in proximity with one another, although figure 14 shows measures at distances up to 0.2 m. The recording of heartrate at these distances occurs because the huddle or hold is often so brief that the heartrate measure includes heartrate immediately before and after the behavior. It is apparent that distance has little effect on the level of heartrate during holding or huddling.

Significance

There are two strategies available to us: to concentrate on reliability by using many groups (thereby decreasing the number of observations on each) or to concentrate on validity by increasing the number of observations on one group. The nature of the questions posed suggested the latter approach.

The findings suggest three relationships. First, for many forms of behavior, heartrate is elevated during the 2 minutes before the behavior and depressed
during the 2 minutes afterwards. Second, when heart rate during a particular behavior is related to rank on the order, either a U or an inverted U-shaped function results. In both cases, high and low ranking animals show similar heart rates while the heart rate of mid-ranking animals is either depressed or elevated. Third, if heart rate reflects autonomic arousal, some behaviors described in this report (e.g. displays, holding) clearly affect the level of arousal while other behaviors do not. Some behaviors acquire the potential for reducing arousal or, as in the case of heart rate, for reversing heart rate toward baseline [CANDLAND, 1971; DUFFY, 1962]. Holding is an obvious candidate because of its ontogenetic associations with maternal care. The penile display, to the contrary, would not appear to be directly responsible for acquired changes in heart rate because it has few, if any, characteristics of learned behavior.

Measurement of heart rate or of any other quantification of autonomic nervous system (ANS) activity is to use a discrete measure to describe a continuous process. Heart rate is a representation of both ANS activity and the level of endocrinious discharge. The secretion of catecholamines and 17-OHCS influences heart rate, and, it is almost certain that secretions of both the adrenal medulla and the adrenal cortex are (a) controlled over the long term by the schedule, type, and intensity of external events and (b) temporarily affected by stressful events, although the characteristics of the short-term stimulation eventually may produce long-term effects and (c) controlled by whatever genetic factors determine the rate and nature of endocrinious activity. The relationship, if any, between heart rate and either longevity or reproductive potential is uncertain. Without such knowledge, the relationship between heart rate and evolutionary processes remains murky. Nonetheless, the substantial number of established relationships between heart rate and factors known to be associated with longevity and possibly with reproduction is sufficient to convince us that heart rate, representing ANS and endocrine activity, reflects at least a general pattern of health, response to stress, and reproductive potential. Our evidence that rank on the social order is reflected in heart rate and endocrine functioning supports this belief [CANDLAND et al., 1969; CANDLAND et al., 1970; CANDLAND and LESHNER, 1973; LESHNER and CANDLAND, 1972]. Interpretation of data reported here is suited to a model of stress emphasizing the two factors: short-term stressors and their long-term effects on baseline physiological functioning.

There is ample evidence that position on the male dominance rank is related to reproductive success and survival. This is especially true of primates, an order in which complex forms of socialization often prohibit some
males from copulating. The squirrel monkey is an example of a primate whose natural social order prevents some adult males from breeding [Baldwin, 1969, 1971; Dumond, 1967; Thorington, 1968]. Among adult males, endocrinous responses before the social order is determined show the following relationships: (a) 17-hydroxycorticosteroids — a U function with eventually low ranking males showing highest output, (b) catecholamine level — the higher the rank, the lower the output and (c) for 17-ketosteroids, a U-shaped function, with low ranking animals showing the greatest output, alpha the next largest amount, and midranking males the lowest [Leshner and Candland, 1972]. These findings demonstrate long-term effects on physiological functioning. The same endocrine measures and, likely, others may reflect short-term changes when the dominance order is undergoing re-evaluation. Before adult males establish a dominance order, the higher the 17-OHCS excretion, the higher the rank on the eventual order. After the competition required in the establishment of a dominance order, the relationship is reversed; i.e. high ranking males show lowest 17-OHCS output. If total urinary catecholamines are measured from adult males before they are permitted to establish an order, eventually low ranking males show the highest output, alpha-male the next highest amount, and midranking males the lowest. After the order is established, the relationship between catecholamine output and rank is reversed. When male squirrel monkeys establish a new dominance order, 17-OHCS levels and catecholamine levels require at least 9 weeks to return to their previous relationship. Evidently, the long-term effects reflect the outcome of dominance contests, probably because they represent a history of adaptation and habituation to stress, while the immediate effects of the stress inherent in a re-arrangement of the dominance orders markedly changes endocrines output for approximately 2 months [Candland and Leshner, 1973].

The manner in which squirrel monkeys were introduced into the colony in this study is consistent with the technique used to measure long- and short-term endocrine responses to stress. Although heartrate may be considered a highly general reflection of endocrine secretion, total catecholamine output is known to affect both heartrate and behavior.

The formation of the suspected closed link between behavior, heartrate, and physiological functioning would require simultaneous measurement of the circulating hormone (e.g., catecholamines), heartrate, and behavior, accompanied by analysis of the component catecholamines. The assumed chain is supported by the nature of two relationships (heartrate and behavior, heartrate and catecholamine secretion) but lacks the third (catecholamines
and behavior). If, as appears likely, the endocrine system is affected by the nature, frequency, and spacing of stimulation external to the body, it follows that it should be possible to specify the conditions that lead to alteration. Attempts to determine the conditions which lead to alteration have shown that the autonomic nervous system is trainable following the principles of operant training [Miller, 1969]. The evidence for both short- and long-term effects of stimulation on endocrinous secretion supports our suggestion that some aspects of the endocrine system seem susceptible to operant training and classical conditioning. Susceptibility of these two physiological functions to conditioning, suggests that measures like heartrate which are reflective of the ANS and endocrine functioning, in so far as they show the conditioned aspects of physiological functioning, are instructive in identifying behaviors which reduce or increase the level of physiological arousal. These relationships are of special interest because of their importance to individual members of the species, to the development of social organization within the species, and to the ultimate survival of the species. The significance of several examples of these relationships follows.

Baseline level of heartrate is both sex-related and predictive of rank on the dominance order. A difference in heartrate between males and females is common among mammals. We found female heartrate to be higher except during the breeding season, when male heartrate was significantly higher. The importance of this finding lies not so much with the additional evidence that heartrate is sex-related, but with the finding that it varies with the season and is reflected in rank on the dominance order for males. The low heartrate of dominant animals (and the comparatively high heartrate of low ranking animals) is reflected precisely by catecholamine measures. Just as there is no overlap in heartrate between alpha-male and monkeys of lower rank, so the total urinary catecholamine excretion of males is 1.6 μg/day for alpha and between 2.6 and 3.1 for other males monkey. It is reasonable to suggest that eventual rank on the order is determined by (a) sex, (b) baseline level of physiological arousal and (c) the influence of stress, both long and short term, on the baseline level.

Heartrate during holding should be of special evolulational significance. Holding has obvious survival value for the animal confronted with the need to thermoregulate. Except for scratching, it is the behavior most frequently observed in the squirrel monkey. Figure 11 showed the heartrate during holds for each squirrel monkey as a function of rank. The similar function for males and females implies that whatever behavioral selection pressures exist in connection with holding are not sexually dimorphic. They are related, none-
theless, to rank on the order and presumably to the order and presumably to the role assumed by members of social groups. The heart rate of mid-rank- ing squirrel monkeys initiating holding is low compared to baseline heartrate and to the heartrate of monkeys occupying other positions on the order. Alpha-animals show higher heartrate, although the level is near baseline. These data suggest that holding greatly lowers the level of arousal of mid-ranking animals, but slightly raises it for alpha-animals. The hypothesis is testable by using holding as the reinforcing agent in a task requiring the acquisition of a new response. Presumably, mid-ranking animals should acquire the new response more readily and more efficiently. Additionally, if holding is highly reinforcing to mid-ranking animals, we may expect them to prefer holding to other behaviors. From table I we see that although holding and holding received account for approximately 32% of all males' behavior and 51% of all females' behavior, the frequency is linear with rank and not curvilinear, as might be expected if holding is more reinforcing to mid-ranking animals than to others. The apparent discrepancy between theoretical prediction and observation has several possible explanations, all critical both to the interpretation of these findings and to the interpretations of other studies on animal behavior; namely (a) heartrate does not reflect arousal, (b) physiological arousal is not related to acquired behavior and (c) holding (for example) has reinforcing properties under some circumstances, but the reinforcing quality would not necessarily be reflected when holding (or any other behavior) is measured as a free operant. Any attempt to relate physiological processes to behavior in naturalistic situations (in which the observer records rather than regulates the behavior) must assume explanation (a) in principle, for it states only that the physiological measure reflects an internal state associated in some way with behavior. Regarding explanation (b), the evidence that physiological arousal is regulated in part by the nature and schedule of external events is so overwhelming that it is difficult to suggest that the present case is an exception. In the absence of evidence (c) that free operant responses are related to reinforcing value, the most cautious course is to assume that they are unrelated, at least by way of heartrate. As satisfying logically as this disassociation may be, it prohibits drawing any parallels with behaviors occurring in the free situation and prevents making assumptions regarding their reinforcing or survival value to the animal. These concepts, nonetheless, have proved so powerful in the interpretation of animal behavior that it appears shortsighted to dismiss them. It is wisest to accept the suggestion that the frequency of freely given responses does not necessarily indicate the reinforcing potential of the behavior.
That midranking animals show either elevated or depressed heartrate depending on whether they are initiating holding or being held (fig. 11, 12) suggests that heartrate and whatever other internal processes it may reflect are influenced by whether the behavior is actively initiated or passively accepted. This possibility is suggested by the effects of distance on heartrate during specific behaviors (fig. 14). The heartrate of a squirrel monkey receiving a penile display increases with the distance between the two animals. Conversely, the heartrate of the displaying monkey decreases with distance. The greater the distance, the lower the heartrate. Distance may mean the recipient does not perceive the display and it would be unwarranted to attribute the slight increase in heartrate to any specific aspect of the behavior. For the displaying animal, the decrease in heartrate with distance is dramatic. Displays given with the recipient ten cm away are accompanied by heartrate at baseline levels, but displays given at greater distances are below baseline. It is not unreasonable to believe that proximity heightens the level of arousal.

The relationship of heartrate to behavior is paradoxical [Candland, 1971; Bridger and Reiser, 1959; Lacey and Lacey, 1962]. Both tachycardia and bradycardia have been shown to reflect apparently identical forms of stimulation, leading some to believe that heartrate is highly idiosyncratic.

The relationships between heartrate and behavior reported in this study are summarized in terms of elation or depression in table III. A number of factors follow a pattern, namely, a heartrate higher than baseline before

| Table III. Relation of heartrate to baseline immediately before and after observed behaviors¹ |
|-----------------------------------------------|-----------------------------------------------|
| Behavior                               | 2 min before behavior | 2 min after behavior |
|-----------------------------------------------|-----------------------------------------------|
| Penile display given                      | above baseline (9)                              | below baseline (9) |
| Penile display received                   | above baseline (8)                              | below baseline (8) |
| Stretching                               | above baseline (13)                             | below baseline (13) |
| Holding (initiated)                       | unchanged (10)                                  | decreases (10)    |
| Holding (received)                        | unchanged (ns)                                  | unchanged (ns)    |
| Other observed behaviors (scratching, biting, huddling, genital manipulation) | unchanged (ns)                                  | unchanged (ns)    |

¹ Numbers in parenthesis indicate figure number for reference; ns indicates not shown, but described in the text.
the behavior and a heartrate lower than baseline afterwards. Some behaviors fail to influence heartrate, but none recorded in this study are accompanied by lower heartrate prior to the behavior and higher heartrate afterwards. It is possible that the consistent pattern reflects nothing more than the compensatory attribute of the cardiovascular system. That the system is compensatory in nature fails to explain why the pattern is above and then below baseline, but never the reverse. Further, if the low heartrate following the behavior were only compensatory for the high heartrate preceding the behavior, we would expect the degree below baseline to be nearly the same as the degree above baseline. Even if it were possible to show that the degree of post-behavior heartrate reduction is a reflection of the heartrate increase before the behavior, the initial increase cannot be explained as a compensatory mechanism. A characteristic pattern relating heartrate to behavior appears to be that for many, but not all, behaviors heartrate increases before the behavior and decreases afterwards. The pattern of elevated heartrate prior to specific behavior patterns may be related to differences to behavioral and physiological responses accompanying the detection and recognition of stimuli and to physiological responses accompanying the orientation and defense reflexes.

The relationship between heartrate and rank on the order is in the shape of a U during holding and in the shape of an inverted U during penile displays received and holding received. These functions parallel those found from the heartrate of high and low ranking animals, in contrast to mid-ranking animals. Mid-ranking animals are either higher or lower than animals occupying extreme ranks. This function is similar to that for heartrate and dominance rank during the establishment of dominance orders in both chickens and squirrel monkeys in studies reported previously [Candland et al., 1969; Candland et al., 1970]. Candland and Leshner [1973] have shown that the changes are probably related to catecholamine output. It is noteworthy that behaviors which may be classed as individualistic (e.g., scratching, biting, genital manipulation) show neither the U-function nor the elevation of heartrate prior to their occurrence. Only behaviors which appear to involve other animals (penile displays, holding) show the U-shape relation to rank and the elevation preceding the behavior. Evidently, individualistic behaviors and those involving other animals have different effects on both the endocrine and autonomic nervous systems.

Footnote 9: Figures 11 and 12 show the first and third relationships. The second, penile displays received, is recoverable from figure 8, although there are no data for alpha since he was never the recipient of a display.
Summary

Because of the broad evolutionary significance of socialization as reflected by the quality and quantity of behavior and on the functioning of the autonomic nervous system and the endocrine system, we measured telemetered heart rate, kind and frequency of behavior, and physical distance from a colony of five male and four female squirrel monkeys (Saimiri sciureus) for 9 months. The following are the general findings:

(1) Both seasonal (breeding versus nonbreeding) and sexual differences in the frequency of basic behaviors are reported;

(2) telemetered heart rate over the duration of the observations shows differences related to season, sex, and rank on the dominance order;

(3) heart rate during both the giving and receiving of the penile display, a display believed to be related to the establishment of dominance among males, is related to the physical distance between the two males;

(4) heart rate is elevated during the 2 minutes before most behaviors and lower than baseline afterwards. Some possible interpretations are described, and

(5) the relationship between heart rate and rank on the order for several behaviors recorded is in the shape of a U or an inverted U. It is suggested that these characteristic functions reflect the effects of both long- and short-term stress on catecholamine output.

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