

REVIEW

Sociophysiology of Squirrel Monkeys

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Primate sociophysiology is an emerging discipline concerned with understanding the proximate mechanisms that contribute to the generation and maintenance of species-typical social systems. Studies of squirrel monkeys illustrate that sociophysiological processes are more varied than is commonly assumed with respect to both the effective social dimensions that influence physiological function and the nature of concomitant physiological effects. For adult squirrel monkeys, a major consequence of social stimulation is altered regulation of pituitary-adrenal, pituitary-gonadal, and autonomic function. In females, socially-induced physiological changes appear to be independent of specific interindividual relationships with other adults, whereas in males, many sociophysiological effects can be understood only when specific relational attributes are considered. In all instances, adult relationships are associated with distinctly different sociophysiological profiles than have been found for the mother-infant relationship and do not conform to the stress/buffering model within which they are often interpreted.

Key words: social relationships, *Saimiri*, stress, hormones, reproduction

INTRODUCTION

One of the earliest and most enduring findings in primatology is that primate species differ in the kinds of social systems they form [Carpenter, 1934, 1935]. Discovering the processes involved in the formation, maintenance, and transformation of species-characteristic modes of social organization has long been recognized as an important task for primatology [Carpenter, 1942]. This problem is traditionally viewed in terms of two interrelated levels of analysis. One level concerns the ultimate forces of natural selection involved in the evolution of primate societies, a topic that has received considerable attention following the seminal work of Crook [1970] and Crook & Gartlan [1966]. Ultimate processes involve phylogenetic time scales, population dynamics, and evolutionary forces that are usually construed in terms of socioecological pressures or constraints. The other level of analysis concerns the proximate social processes by which mutually inter-

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dependent individuals function in coherent, self-organized societies across life-span development.

Until quite recently, scientific disciplines concerned with social behavior have emphasized either the ultimate or the proximate sources of variation; it is becoming clear, however, that previously distinct disciplines are converging in their interests. Ethologists, traditionally concerned with innate behavior, are becoming increasingly interested in behavioral flexibility and modification. Sociobiology no longer considers only the ultimate explanations of behavior but is beginning to explore proximate mechanisms. Psychologists concerned with general principles governing the behavior of individuals have turned to neurophysiology on the one hand and to ecological and evolutionary theory on the other. A major consequence of these changes in the behavioral sciences is renewed interest in the evolution of proximate mechanisms that contribute to the generation and maintenance of primate social systems. This in turn has led to a proliferation of interdisciplinary research devoted to understanding social processes at multiple levels of organization, from physiological systems to ecosystems. Sociophysiological research exemplifies the utility of this multi-level approach and provides a descriptive base upon which the integration of traditionally distinct approaches can proceed.

The availability of conspecifics of a particular age-sex class, engagement in certain kinds of social interactions, and qualities of specific interindividual social relationships are all known to have physiological consequences for individual primates [Mendoza, 1984; Mendoza & Mason, 1989b]. In marmoset groups, for example, mating is restricted to a single adult pair; remaining adults are excluded from the reproductive process in large part by the social suppression of pituitary-gonadal activity induced by some as yet unknown attribute of the reproductive pair [Abbott, 1989; Abbott *et al.*, 1981]. Social interactions involved in the formation of dominance relationships can alter pituitary-adrenal, pituitary-gonadal, and autonomic activity in males of various primate species in a manner dependent on the relative rank attained by each individual [Bernstein *et al.*, 1974; Mendoza *et al.*, 1979; Keverne, 1983; McGuire *et al.*, 1983; Sapolsky, 1983; Glick, 1984; Mendoza, 1987]. For squirrel monkeys and macaques, the availability of the mother can reduce the infant's pituitary-adrenal response to stressful events such as capture and brief restraint [Smotherman *et al.*, 1979; Mendoza *et al.*, 1980; Coe *et al.*, 1985b]. These and other findings have firmly established that primate neuroendocrine systems are sensitive to social stimuli.

While the number of relevant empirical studies has increased in recent years, substantial conceptual gaps persist in our understanding of primate sociophysiology. As much primate life is characterized by and organized around specifiable, long-term social relationships, it is often assumed that the supportive or aversive qualities of established relationships represent the principal social domains which impinge on physiological processes. By reviewing information from a single, well-studied primate taxon, the squirrel monkey (*Saimiri* spp.), we hope to illustrate that sociophysiological phenomena are more varied than commonly assumed with respect to both the effective social dimensions that influence physiological functioning and the nature of these concomitant physiological alterations.

SQUIRREL MONKEY SOCIAL ORGANIZATION

Squirrel monkeys are typically born into mixed-sex, age-graded social groups composed of 10–50 individuals [Thorington, 1968; Baldwin, 1985; Boinski, 1987a]. The salient attributes of the social environment vary with age, gender, and, because squirrel monkeys are seasonal breeders, time of year. With the exception of

infants, squirrel monkeys associate predominantly with members of their own age/sex class [Baldwin, 1985]. The resulting sexually segregated social structure is also apparent under laboratory conditions [Mason & Epple, 1969; Coe & Rosenblum, 1974; Alvarez, 1975; Strayer et al., 1975], and available evidence indicates that females play an important role in the regulation of this grouping pattern. Adult females show greater attraction to each other than males do to males [Mason, 1971a, 1974b]. Moreover, females are generally more active than males in initiating agonistic interactions which contribute to the spatial relations between the sexes [Coe & Rosenblum, 1974]. If females do not assume this role, as is the case for some subspecies of squirrel monkeys, a sexually integrated social structure emerges [Mendoza et al., 1978b].

Interactions among females within a squirrel monkey group are not distributed uniformly. Females tend to cluster into smaller social units or cliques [Fairbanks, 1974; Leger et al., 1981; Tabor, 1986] and may act in concert with clique members to actively exclude other group members or to gain access to desired incentives [Leger et al., 1981]. Interactions among females within a clique are generally affiliative or passively benign; however, agonistic interactions are also more likely to occur between members of a clique [Leger et al., 1981]. Longitudinal studies of stable captive groups have shown that clique membership is often transitory [Tabor, 1986], and preliminary data on free-ranging monkeys indicate that females periodically transfer between groups [Boinski, 1987b]. In comparison to adult females, relationships among adult males are thought to be less affiliative [Coe & Rosenblum, 1974] but more stable [Scollay & Judge, 1981; Tabor, 1986; Boinski, 1987b]. Within-sex associations may also be described in terms of social status. Both sexes tend to form linear dominance hierarchies, but these appear to be more clearly demarcated among adult males [Baldwin, 1971; Mendoza et al., 1978b].

Infant squirrel monkeys are completely dependent on their mothers for the first 4–6 weeks of life [Rosenblum, 1968], and mothers generally restrict maternal behavior to their own infants [Boinski & Fragaszy, 1989]. Although occasional “aunting” by other females may occur, mothers in natural troops may vigorously resist attempts by other females to carry or physically interact with their infants [Baldwin, 1985; Boinski, 1987a]. Weaning occurs at 2–6 months post partum as infants begin to interact with other group members, especially other infants of the same birth cohort [Rosenblum, 1968; Boinski & Fragaszy, 1989]. While young monkeys of both sexes associate extensively with their mothers early in life, evidence from captive colonies suggests that affiliative bonds between mothers and daughters sometimes persist into adulthood [Leger et al., 1981; Tabor, 1986]. The sexually segregated group structure exhibited by adults emerges among juveniles at 2–3 years of age [Baldwin, 1969; Coe & Rosenblum, 1974], corresponding more or less with the onset of puberty [Coe et al., 1985a].

Throughout its life, the individual squirrel monkey participates in several classes of social associations, including mother-infant, within-sex, and heterosexual relationships. The picture emerging from ongoing research is that each of these classes entails a unique set of sociophysiological processes. Among the first sociophysiological phenomena to receive systematic attention is the interrelationship between mother-infant attachment and pituitary-adrenal function. This interplay represents one of the most thoroughly studied aspects of squirrel monkey sociophysiology, and because most of these findings have been reviewed elsewhere [Mendoza et al., 1980; Hennessy, 1985; Coe et al., 1985b; Levine & Coe, 1988], we address them only briefly here. This body of research illustrates how early investigations of the filial bond have influenced, and, to a certain extent restricted, our

conceptual views of the sociophysiology of squirrel monkey relationships occurring in adulthood.

MOTHER-INFANT FILIAL BONDS AND PITUITARY-ADRENAL RESPONSIVENESS

Mother and infant squirrel monkeys react to the disruption of their relationship with a substantial and rapid increase in pituitary-adrenal activity. Brief involuntary separation of 3-month-old infants from their mothers elicits an increase in plasma cortisol of up to 100% of baseline values in both mothers and infants within 30 minutes, and cortisol levels return to pre-separation baseline levels 1–6 hours following reunion [Coe et al., 1978; Levine et al., 1978; Mendoza et al., 1978d]. When infants are cared for by a familiar adult female during separation from the mother, infants show as great an increase in cortisol as when they are left alone [Coe et al., 1978]. Moreover, in stressful situations, the presence of an infant's mother, but not another familiar adult female, effectively inhibits or "buffers" the normally observed rise in infant plasma cortisol titers. The acute pituitary-adrenal response to disruption of the mother-infant bond is remarkably resistant to habituation, at least in infants. Hennessy [1986b] found that over the course of 80 mother-infant separations conducted between 12 and 31 weeks of age, each 2-hour separation reliably elicited an increase in infant cortisol titers. Inasmuch as *basal* cortisol levels in these repeatedly separated infants remained unchanged and did not differ from basal values in non-separated control infants, these recurrent reactions to mother-infant separation appear to occur around a roughly stable physiological set-point.

These findings, together with those from other studies and data from other species, confirm the initial interpretation that the effective social dimension triggering the acute physiological response to separation is not removal of maternal behaviors per se, but the disruption of a well-integrated and specific psychosocial attachment between mother and infant [Mason, 1971b; Mendoza et al., 1980; Swartz & Rosenblum, 1981]. This intense mother-infant bond and the clear-cut physiological consequences of its disruption have shaped our thinking about positive social relationships in adult primates. Many investigators proceed as if all affiliative social relationships resemble the attachment bond in form, structure and consequences, differing only in the intensity of participant involvement [e.g., Hofer, 1984; Mendoza, 1984; Panksepp et al., 1985; Levine & Coe, 1988]. At the risk of oversimplification, we will refer to this view of social relationships as the stress/buffering model.

The more salient sociophysiological phenomena of the stress/buffering model can be stated as follows: disruption of affiliative social relationships is stress-inducing; engagement in affiliative social relationships is stress-reducing; and individuals confronted with potentially stressful circumstances seek engagement in affiliative relationships as a coping strategy. Recognizing that not all associations among primates are affiliative, the stress/buffering model may be expanded to incorporate the negative counterparts of sociality. Engagement in relationships characterized by high levels of conflict or aggression is stress-inducing, and avoidance of these relationships, particularly in arousing circumstances, is employed as a coping strategy. Finally, since uncertainty, novelty, and lack of predictability are potent elicitors of a physiological stress response [Hennessy & Levine, 1979], interactions between individuals with no prior experience with one another (i.e., strangers) should induce stress, particularly if the interactions are characterized

by antagonism or aggression. Engaging in affiliative, sexual, or displacement behaviors under these circumstances should serve to modulate the stress response.

The stress response is characterized by a rapid activation of several physiological systems, the most well-studied being the pituitary-adrenal axis. The combined products of the stress-responsive systems lead to wholesale mobilization of bodily resources preparatory for action, and as such, the stress response is viewed as a transitory deviation from homeostasis. It is significant in this regard that heightened levels of cortisol, the most frequently used measure of the stress response, function in large part to inhibit other aspects of the physiological defense mechanisms and thus serve to reestablish homeostasis [Munck et al., 1984]. Consequently, the stress response is usually identified by the temporal characteristics of a rapid onset followed by gradual return to baseline values. In keeping with Selye's [1946] original conceptualizations, it is generally believed that conditions which elicit the stress response also produce discomfort or distress, and that frequent or prolonged activation of stress-response systems is detrimental to maintenance activities, reproduction, and health.

The stress/buffering model of social relationships has had broad appeal. For example, it is the most frequently invoked explanation of the repeated finding that the social environment is a determinant of human health [Cohen & Wills, 1985; House et al., 1988]. Similarly, the conviction that the stress/buffering model is applicable to nonhuman primates forms the basis for the current requirement in the animal welfare regulations that compatible conspecifics be housed together.

We began our investigations of squirrel monkey sociophysiology confident that the stress/buffering model was correct and sufficient. As in the mother-infant relationship, we anticipated that disruption of affiliative relationships among juvenile or adult monkeys would be stressful, as reflected in a rapid activation of stress-response systems such as the pituitary-adrenal axis. We further postulated that the physiological response to stressful events would be reduced or eliminated by the presence of familiar companions with whom an affiliative relationship had been established. Our initial study, designed specifically to demonstrate these sociophysiological phenomena, examined the response of female squirrel monkeys to involuntary separation from like-age/same-sex companions, relationships which might be expected to conform most closely to the mother-infant bond [Hennessy et al., 1982]. To our surprise, the results indicated that juvenile females did not show a specific response to separation from isosexual companions, nor did familiar companions reduce the adrenocortical response to stressful events such as capture, handling, or exposure to a novel environment. These results have since been extended to adult relationships. Hennessy [1986a] found that the adrenocortical response of adult females to a novel environment was not influenced by the presence of a familiar like-sex cagemate, and that the degree of affiliation displayed by the companions in the home cage did not influence the response to novelty. Similarly, disruption of established heterosexual relationships among adult squirrel monkeys does not induce behavioral or physiological indications of distress [Cubicciotti & Mason, 1975; Mendoza & Mason, 1986], nor do familiar heterosexual companions ameliorate the physiological response to novel conditions [Anzenberger et al., 1986; Cubicciotti et al., 1986]. These findings are clearly contrary to predictions based on the stress/buffering model; yet other studies indicate that availability of social companions does indeed alter pituitary-adrenal activity in juvenile and adult squirrel monkeys [Gonzalez et al., 1981, 1982; Hennessy, 1984; Coe et al., 1985a; Mendoza & Mason, 1986]. The apparent discrepancy in these studies led us to consider the possibility that the range of sociophysiological effects may be

broader than predicted by the stress/buffering model and, in adult squirrel monkeys, distinctly different from those evident in the mother-infant relationship.

ADULT WITHIN-SEX RELATIONSHIPS AND SOCIOPHYSIOLOGICAL REGULATION

The clearest evidence for sociophysiological effects that do not conform to the stress/buffering model is provided by a study of the adrenocortical response to group formation in adult squirrel monkeys [Mendoza & Mason, submitted]. We monitored pituitary-adrenal activity in 15 females while they were individually housed and following formation of female triads. The results revealed an unusual endocrine response. All females showed a reduction ($\bar{X} = 36\%$) in basal cortisol upon formation of female groups, an effect that took 2–6 days to develop and that persisted for at least 6–7 weeks. This drop in cortisol occurred despite the fact that these females were placed in entirely novel surroundings, a situation that has been shown to reliably elevate cortisol titers in adult squirrel monkeys [Hennessy et al., 1982; Anzenberger et al., 1986; Cubicciotti et al., 1986; Hennessy, 1986a]. Similar changes in adult female adrenocortical activity had been reported in previous group formation research [Gonzalez et al., 1981], but since pre-group formation assessments of cortisol levels in individually housed females were not obtained, these investigators reasonably assumed that cortisol titers following group formation were indicative of elevated, rather than reduced, pituitary-adrenal activity.

One possible explanation for this reduction in adrenocortical activity is that social support provided by like-sex companions "buffered" females from experiencing the full range of physiological responses normally observed when individuals are placed in novel cages. This seems unlikely for several reasons. First, adrenocortical activity when females were living together represented a clear suppression below pre-introduction levels, not merely an attenuated stress response. We also know that the immediate adrenocortical response of group-living females to confinement in a novel cage is not inhibited by the presence of a familiar female cagemate [Hennessy et al., 1982; Hennessy, 1986a]. Additionally, some of the females were subjected to considerable harassment from other group members. According to the stress/buffering model, these females should have exhibited elevated pituitary-adrenal activity, yet they showed reduced basal cortisol levels. Finally, our previous research has shown that undisturbed females living in heterosexual pairs exhibited a modest reduction of cortisol within 1 hour of visual exposure to another female [Mendoza & Mason, 1986], and the complete reduction over longer time scales has been replicated in subsequent research of the formation of female dyads and triads [Saltzman et al., 1988, 1989; Mendoza et al., 1989]. Separation of established dyads leads to an increase in cortisol but only after several (2–6) days of social isolation [Mendoza et al., 1989]. Clearly, the profile of the female adrenocortical response to isosexual stimulation departs significantly from the characteristic responses predicted by the conventional stress/buffering model, and was not detected in early studies since longitudinal evaluation of physiological responses to social stimulation have rarely been considered.

Male squirrel monkeys also exhibit socially-induced changes in basal adrenocortical activity, as first indicated by a study of social dominance and the response to stress [Coe et al., 1979]. Basal and stress levels of plasma cortisol were monitored in eight pairs of male squirrel monkeys, and basal values were found to be higher in the dominant member of each pair. In contrast, stress values (obtained 30 minutes following capture, exposure to ether, and basal blood sampling) did not differ between dominant and subordinate males. In another study we showed that differential basal adrenocortical activity emerged only after relationship forma-

tion and that differences between dominant and subordinate males were accentuated by introduction of females [Mendoza et al., 1979].

Differences in basal cortisol values between dominant and subordinate males cannot be readily interpreted within a stress model. The complete expression of this physiological differentiation appears to have a rather slow onset, ranging from days to weeks following introduction [Mendoza et al., 1979; Coe et al., 1985a], and although these rank-related differences are thought to disappear in stable groups [Mendoza, 1984; Steklis et al., 1986], they persist for at least several weeks following group formation. The slow onset and persistence of these endocrine response profiles differ from the more acute patterns of reactivity typically reported in stress research. Moreover, basal testosterone titers, typically suppressed in chronically stressful circumstances, were also higher in dominant animals. Finally, the presumed association between dominance status and psychosocial stress is further questioned by the finding that patterns of endocrine differentiation vary across taxa. Squirrel monkeys imported from Bolivia exhibit the endocrine pattern described above, whereas those imported from other regions of the squirrel monkey cline exhibit the more common primate pattern in which subordinate males have higher basal cortisol values and lower testosterone titers [Coe et al., 1983; Mendoza, 1987]. While there is no universal pattern of association between dominance status and endocrine profiles, male-male relationships consistently produce sustained physiological differences between individuals.

In considering physiological mechanisms that might mediate these socioregulatory effects in males and females, we selected the autonomic nervous system as a likely starting point for several reasons. Elevated adrenocortical activity in squirrel monkeys, relative to other primates, is not complemented by hypersecretion of adrenocorticotrophic hormone (ACTH) from the pituitary [Coe et al., 1978; Cassorla et al., 1982], and the squirrel monkey adrenal cortex is not particularly sensitive to ACTH [Kittenger & Beamer, 1968; Brown et al., 1970]. Moreover, negative feedback is not completely effective in reducing acute responses of the pituitary-adrenal system following stress [Mendoza & Moberg, 1985]. Reduced ACTH levels and minimal feedback regulation of adrenocortical reactivity suggest that the squirrel monkey adrenal cortex is regulated, in part, by mechanisms other than ACTH stimulation. A likely possibility is sympathetic stimulation of the adrenal cortex. Sympathetic contributions to adrenocortical activity have been documented for other species [Engeland & Dallman, 1975; Henry et al., 1976; Holzwarth et al., 1987], and sympathetic nerves innervating the squirrel monkey adrenal cortex are myelinated [Penney & Brown, 1971]. The possibility that sympathetic contributions are involved in the regulation of adrenocortical activity is complemented by the finding that squirrel monkeys also have unusually high levels of sympathetic activity which are relatively unimpeded by parasympathetic counter-influences [Kelleher et al., 1972; Byrd & Gonzalez, 1981; Mendoza & Mason, 1984].

Our preliminary analyses of within-sex effects on pituitary-adrenal and autonomic activity suggest that socioregulatory changes in adrenocortical functioning might involve alterations in autonomic activity in adult males but not in females. Using telemetrically obtained measures of heart rate and heart rate variability in freely moving monkeys as indices of sympathetic and parasympathetic activity [Porges, 1985], we found no significant changes in cardiac measures as a result of pair formation in females, despite the fact that these same individuals showed the previously described reduction in basal cortisol titers [Saltzman et al., 1988]. In contrast, differentiation of pituitary-adrenal activity induced by male pair formation was associated with corresponding changes in cardiac activity [Mendoza,

1987]. Although cardiac measures of autonomic activity cannot provide us with direct information about sympathetic influences on pituitary-adrenal regulation, these findings do suggest a promising avenue for future sociophysiological investigations of male-male relationships.

In summary, the above evidence demonstrates that pituitary-adrenal activity is sensitive to regulation by within-sex social stimulation in ways that transcend acute stress responsiveness or reactivity. For females, interactions with like-sex conspecifics induce dramatic and persistent reductions in plasma cortisol levels, an effect which appears to occur independently of specific attributes of within-sex social relationships. Male neuroendocrine activity, in contrast, is responsive to a readily identifiable attribute of interindividual social relationships. Relationship formation in males sets in motion a suite of physiological changes that accentuate differences between otherwise similar animals. Dominant and subordinate males differ not only in pituitary-adrenal activity, but also in autonomic and pituitary-gonadal activity. Neither hormone levels nor cardiac activity prior to formation of new relationships predict subsequent social status, so that male-male relationships appear to influence each monkey's neuroendocrine state, rather than individual differences in physiology determining the nature of inter-male social relationships [Mendoza et al., 1979]. For both sexes, relationships among adults are associated with sociophysiological processes that clearly differ from those operating in the mother-infant relationship. The functional significance of these within-sex sociophysiological processes is currently a matter of speculation; one possibility is that they impinge on reproductive performance.

ADULT HETEROSEXUAL STIMULATION AND BREEDING READINESS

Reproductive events in squirrel monkeys are limited to discrete periods once each year in both natural [DuMond, 1968; Baldwin, 1985; Boinski, 1987a,b] and laboratory environments [Kaplan, 1977; Coe & Rosenblum, 1978; Taub et al., 1978; Mendoza et al., 1978c; Dukelow, 1985; Williams et al., 1986]. Just prior to breeding, squirrel monkeys undergo "fattening," characterized by changes in body conformation (particularly in the upper torso), alterations in the appearance of the fur, and an increase (up to 35%) in body weight (DuMond and Hutchinson, 1967; Nadler & Rosenblum, 1972; Coe and Rosenblum, 1978; Mendoza et al., 1978a; Baldwin, 1985; Coe et al., 1985a; Williams et al., 1986; Boinski, 1987b). These seasonal changes in morphology correspond, at least in males, with annual variations in circulating thyroid hormones [Kaack et al., 1980] and androstenedione, possibly of adrenal origin [Wiebe et al., 1988]. Males and females tend to approach one another more frequently when fattened [Mendoza et al., 1978c; Williams et al., 1986] and have been described as more interactive and reactive at this time of year [Coe et al., 1983; Baldwin, 1985; Boinski, 1987b]. Within a few weeks of attainment of peak annual body weights, concentrations of gonadal hormones increase in both sexes, males show increased spermatogenesis, and females begin to exhibit 7–12 day ovarian cycles. Increases in investigatory behaviors, the species-typical genital display, and mating activities all coincide with heightened gonadal hormone levels [Mendoza et al., 1978c; Williams et al., 1986].

It is generally assumed that seasonal changes in reproductive physiology are triggered by ecological events and these in turn produce changes in sociosexual behavior. The sequence of events described above, however, suggests the intriguing possibility that increased social interaction which accompanies fattening may contribute to the subsequent physiological expression of breeding readiness. That

is, socially-induced changes in physiological systems may play an important role in regulating reproduction in squirrel monkeys. This hypothesis is supported by several interrelated lines of evidence.

A sudden increase in social stimulation, as when new heterosexual groups are formed in the laboratory, can induce breeding 6 months out of phase with the normal reproductive cycle [Mendoza et al., 1979]. Reproductive synchronization among group members established by induced breeding appears to be maintained across successive annual reproductive cycles [Baldwin, 1970; Coe & Rosenblum, 1978]. As a consequence, groups that are housed in adjacent cages under identical environmental conditions may differ reliably in the timing of major reproductive events [Mendoza & Mason, unpublished observations], as do neighboring *Saimiri* troops in natural habitats [Boinski, 1987a].

A further indication that social stimulation influences the annual reproductive cycle is provided by the finding that the minimal reproductive unit, a heterosexual pair, represents a suboptimal breeding unit for this species. Squirrel monkeys maintained for long periods in heterosexual pairs and in mixed-sex groups are clearly differentiated by measures of reproductive success [Mendoza & Mason, 1989a]. Our colony records indicate that many adult females living in heterosexual pairs (59%) never became pregnant, whereas very few group-housed females (8%) failed to do so. Moreover, when pair-housed females did conceive, only 39% produced viable young as compared with 70% for group-living females. These retrospective data suggest that some attribute of larger social units makes an important contribution to squirrel monkey reproduction.

This conclusion is supported by recent findings from sociophysiological investigations of breeding readiness in heterosexual pairs [Mendoza & Mason, 1989a] and larger mixed-sex groups [Mendoza & Mason, submitted]. Adult males and females living in previously established heterosexual pairs were separated from their partners and paired with a new partner of the opposite sex immediately before the onset of the anticipated breeding season. The question of primary concern was whether this procedure would facilitate the onset of breeding readiness in either sex. Breeding readiness was evaluated by measuring plasma testosterone in males, estrogen and progesterone in females, and social behavior among pair-mates.

In the hour immediately following the formation of new pairs, male testosterone levels increased, as did male-initiated sexual overtures. Males maintained this state of enhanced breeding readiness for 2 weeks, after which time both behavior and physiology returned to nonbreeding levels for most males. The behavioral and physiological changes in males were not complemented by similar changes in their female pairmates, suggesting that the primary reproductive deficit in heterosexual pairs is in some way attributable to females. Males also show diminished breeding readiness, however, inasmuch as sexual arousal and heightened gonadal hormone activity were not sustained by a single sexually quiescent female.

Given the apparent significance of female-female associations in squirrel monkeys, it seemed likely that the presence of female conspecifics (rather than males alone) might represent an important factor contributing to female breeding readiness. This seemed particularly likely since the onset of ovarian cyclicity is synchronized among most females, and mating activity is largely restricted to a period when most females are cycling [Coe & Rosenblum, 1978; Mendoza et al., 1978c]. In order to evaluate this possibility we utilized a group formation paradigm similar to that previously employed to induce breeding [Mendoza et al., 1979], and examined the response of females to formation of female triads and their subsequent response to introduction of a single male [Mendoza & Mason, submitted].

While the formation of female triads had clear and dramatic effects on basal cortisol levels (as described above), it had no consistent effect on ovarian activity. Both before and after triad formation a few females (4–5) were judged to be cycling, based on changes in estrogen and progesterone levels. Conversely, the introduction of a male to female groups had no effect on female adrenocortical activity, but triggered changes in ovarian activity. Shortly following introduction of a single male to each triad, 13 of 15 females exhibited ovarian cyclicity, and nine were impregnated during the 4 weeks of heterosexual cohabitation. These results stand in sharp contrast to the female's response to a single male when living without female companionship. Within-sex companions, therefore, appeared to prime females so that stimulation provided by the male rapidly induced breeding readiness.

While a complete understanding of heterosexual social influences on squirrel monkey physiology is not currently within our grasp, the existing empirical evidence supports a number of conclusions. Adult males and females do not appear to form affectional bonds with one another. Although they are not socially incompatible, in that heterosexual agonistic interactions are neither intense nor frequent, male-female dyads rarely engage in affiliative social interchanges; they do not appear to attend closely to each other's behavior; they seem to be uninfluenced by one another when engaged in nonsocial activities; and they show no evidence of pituitary-adrenal responsiveness upon involuntary separation [Mason, 1974a, 1975; Phillips & Mason, 1976; Fragaszy, 1985; Andrews, 1986; Mendoza & Mason, 1986]. Behavioral and physiological data collectively suggest, however, that one sociophysiological dimension of heterosexual interaction—the regulation of reproduction—is functionally significant for adult squirrel monkeys.

The details of these reproductive regulatory processes differ for males and females. For males, the initiation of breeding readiness is influenced, in part, by female social stimulation. Responsiveness to heterosexual stimulation is evident in single males housed in newly formed heterosexual pairs [Mendoza & Mason, 1989a], in single males placed in multi-female groups [Mendoza & Mason, submitted], and in the most dominant, but not subordinate, males living in multi-male, multi-female groups [Mendoza et al., 1979]. In the latter case, within-sex status relationships block the heterosexual effects for subordinate males. For females, on the other hand, within-sex stimulation appears to facilitate the full expression of breeding readiness in response to heterosexual stimulation. For both males and females, then, within-sex sociophysiological processes modulate the effects of between-sex social stimulation.

Under the appropriate conditions, breeding readiness can apparently be induced in adult males and females by any conspecific of the opposite sex. Thus, participation in physiologically significant social activities by adult males and females does not appear to require involvement in an individualized social relationship. Those social elements responsible for the observed effects on reproductive physiology remain to be identified, but it appears as though animals are responding to categorical dimensions such as maleness or femaleness.

DISCUSSION

Recent scientific work has established clear empirical evidence for causal links between social and physiological phenomena in a variety of primates. With the possible exception of rhesus macaques, we currently know more about the socio-physiology of squirrel monkeys than of any other primate. Various aspects of *Saimiri* pituitary-adrenal, pituitary-gonadal, neurochemical, autonomic, cardiovascular, and immune systems have been shown to be influenced by social context

and interindividual relationships [Mendoza et al., 1980; Mendoza, 1984; Coe et al., 1985a,b; Steklis et al., 1986; Levine & Coe, 1988]. Our comparisons of sociophysiological processes associated with distinctly different classes of squirrel monkey social relationships indicate that the effective attributes of the social environment that impinge on physiological functioning and the nature of these physiological alterations are more varied than we originally anticipated.

The mother-infant relationship is characterized by an intense and specific attachment bond which persists well beyond the stage of infant dependency. Disruption of this relationship produces an immediate and substantial physiological response which is long-lasting, but not indefinite. Engagement in the relationship not only truncates or reverses the physiological response to separation but can also buffer both mother and infant from experiencing the full range of physiological responses to environmental perturbations. The mother-infant relationship has often been taken as a prototypical social relationship in that other relationships are generally assumed to share the same stress-inducing or stress-reducing qualities exemplified in the attachment bond. Adult relationships demonstrate that this is not the case.

Adult males and females living in heterosexual pairs behave much as if they are living alone; they do not respond to separation from, or disturbance of, their heterosexual pairmate, and quite often do not reproduce. In larger social units, males and females do not frequently interact, yet they induce significant physiological changes in one another. In males, heterosexual stimulation produces sustained increases in adrenocortical activity, and for both sexes in appropriate social situations, heterosexual stimulation triggers changes in gonadal hormone activity indicative of breeding readiness. Availability of within-sex companions modulates this response to heterosexual stimulation and also alters physiological function directly. For males, responses to within-sex companions include long-term changes in pituitary-adrenal, pituitary-gonadal, and autonomic nervous systems; the pattern of response depends on each male's social status within the relationship. For females, within-sex stimulation produces tonic reductions in basal adrenocortical activity, a response that appears to be independent of the qualities of their relationships. Thus, each of the four types of relationships examined (i.e., mother-infant, male-female, male-male, and female-female) is associated with a different sociophysiological profile.

These findings have broad implications for sociophysiology. First, not all significant social influences are mediated through specific interindividual relationships. Hinde [1975, pp. 13, 15] has defined social relationships as "the content, quality and patterning of interactions" occurring "among two animals known to each other as individuals." While such differentiated relationships are clearly a prominent feature of primate social life, it is also evident that primates frequently respond to more generic dimensions of the social environment. Thus, two individuals may respond to each other not in terms of the history of interactions between them, but on the basis of such categorical attributes as age, sex, familiarity, or reproductive status [Mendoza & Mason, 1989b]. An important contribution of sociophysiological research has been to provide an empirical means of distinguishing between social associations which rely upon specific interindividual relationships and those that do not necessarily move beyond the categorical domain. In squirrel monkeys, the former are exemplified by mother-infant and male-male relationships, and the latter are illustrated by male-female and female-female associations.

Another implication of the findings reviewed here is that the concepts of stress responsiveness and social buffering are, by themselves, insufficient to account for

the totality of observed sociophysiological effects. In his work with rodents, Hofer [1978, 1981, 1983] distinguished between two broad classes of socially induced physiological changes: reactivity and regulation. Differences between the two processes are evident in simple and direct measures of latencies, rise times to peak intensities, and recovery times. These parameters reflect the idea that most responses have a specific onset, they rise in intensity, and they peak and subside across time. Socially-induced changes in physiological reactivity are characterized by acute, rapid responses that eventually return to a prior steady state or baseline. Reactive processes in physiological systems may be conceptualized as transient deviations from a set-point, and these acute changes are well-designed to function in maintaining the status quo. In contrast, socially-induced regulatory processes entail prolonged responses that require longer periods of time for their complete onset. Regulatory changes involve a sustained reorganization in the system itself, such as a resetting of homeostatic set-points. Reactive physiological processes fit readily into the conceptual framework of stress theory; regulatory changes do not. Instead, regulatory changes appear to represent a set of processes that are qualitatively different from those involved in acute reactivity.

Physiological changes produced by regulatory processes are likely to coincide with functionally different demands on individuals than are reactive changes. This idea is clearly illustrated by sociophysiological processes associated with relationships between mothers and infants, and those among adults. As the infant's principal source of nourishment, warmth, and protection from hazards encountered in a wide-ranging, arboreal, social group, the mother represents a critical resource to the infant. Correspondingly, her absence may represent, at least to very young infants, a life-threatening situation. Specific recognition of and responsiveness to the mother, as manifested in the filial bond, is therefore essential to infant survival and development. Involuntary separation disrupts this bond and elicits in both mother and infant a set of responses—including increased locomotor activity, elevated vocal repetition rates, and heightened plasma cortisol titers—that under normal circumstances serve to reinstate mother-infant proximity [Coe et al., 1985b]. Chief among the many physiological functions of glucocorticoids in primates is the alteration of metabolic, perceptual, and cognitive processes that collectively prepare an individual for dealing immediately with stressful or threatening circumstances [Munck et al., 1984; Sapolsky, 1986]. The acute reaction of the pituitary-adrenal system thus represents part of an integrated sociophysiological process that normally serves to maintain the ongoing mother-infant relationship critical to infant survival and maternal reproductive success.

In contrast, acute pituitary-adrenal reactivity to involuntary separation is not evident in relationships among adult squirrel monkeys. For example, removal of adult females from like-sex companions elicits a sustained cortisol rise only after a latency of several days [Mendoza et al., 1989], suggesting that female pituitary-adrenal function is not finely tuned to short-term changes in the immediate availability of other females. Indeed, acute reactivity would interfere with such essential activities as foraging, during which squirrel monkeys are typically dispersed [Boinski, 1988].

Psychosocial stress research is generally based on a homeostatic model that emphasizes the maintenance of physiological steady states. In contrast, the concept of regulatory change emphasizes functional shifts between different physiological states. In terms of their measureable response characteristics, within-sex social influences on adult squirrel monkey pituitary-adrenal activity more closely resemble regulatory changes. The functional significance of these regulatory shifts remains unknown. Possibilities include the regulation of reproduction in both

sexes, facilitation of female intergroup transfers, and establishment of stable relationships through status-related physiological differentiation among males [Mendoza, 1984; Saltzman et al., 1989; Mendoza & Mason, 1989b]. These all suggest directions for future research which may further illuminate our understanding of the processes underlying squirrel monkey social organization.

The integration of data on natural history, social behavior, and physiology affords a unique opportunity for achieving the task Carpenter [1942] considered central to primatology—understanding the processes involved in the generation and maintenance of species-typical social systems. In pursuit of this goal it will be important to keep in mind that the conditions and demands of one type of social association differ in meaningful ways from those evident in another, and the corresponding sociophysiological processes may differ as well. The research and concepts described in this report represent only a modest beginning toward understanding the diversity and unity of sociophysiological processes evident in primate social systems, including our own.

CONCLUSIONS

1. Sociophysiological processes operating in squirrel monkeys are distinctly different depending on the category of relationships considered.
2. The sociophysiological attributes of the mother-infant relationship, often considered prototypical, can be characterized within a stress/buffering model. Disruption of the relationship is stress-inducing; engaging in the relationship reduces or buffers the response to potentially stressful conditions.
3. Socially-induced physiological changes among adult squirrel monkeys include altered regulation of the pituitary-adrenal, pituitary-gonadal, and/or autonomic nervous systems. These sociophysiological processes do not conform to the stress/buffering model.
4. Female-female and male-female sociophysiological effects do not appear to be mediated by specific interindividual relationships, whereas male-male and mother-infant sociophysiological processes reflect qualities of specific interindividual relationships.
5. The range of sociophysiological processes is more varied than is commonly assumed. Effective social dimensions include categorical distinctions as well as individualized social relationships. Socially relevant physiological phenomena include regulatory changes as well as reactive changes characterized by stress responsiveness.

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