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RESEARCH ARTICLES

Annual Physiological Changes in Individually Housed Squirrel Monkeys (*Saimiri sciureus*)

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This study investigated whether annual changes in physiology occur in individually housed squirrel monkeys (*Saimiri sciureus*). Physiological measures were monitored for 20 months. Over the course of the study, all individually housed males and females exhibited clear annual changes in gonadal and adrenal hormone levels, and males exhibited species-typical changes in body weight. Females exhibited a typical pattern of hormonal changes, with elevations in gonadal steroids occurring during the same months as elevations in cortisol. Males, however, exhibited an atypical pattern, as elevations in hormone levels were not synchronized with each other; rather, elevations in testosterone occurred out of phase with changes in cortisol and body weight. The timing of annual events in individually housed subjects was compared to that in nearby social groups, in which the timing of the breeding season from year to year was determined by social group formations and was outside the naturally occurring breeding season. Elevations of ovarian and adrenocortical hormones in individually housed females were synchronized with indices of breeding in heterosexual social groups. Similarly, weight gain in males was associated with elevations in cortisol and, as with socially housed males, tended to precede seasonal breeding in the social groups. In contrast, annual testosterone elevations for individually housed males were not synchronized with breeding in nearby social groups. We conclude that direct physical interaction is not required for the annual expression of breeding readiness. Synchrony of seasonality among squirrel monkeys may be accomplished by distant social cues in females, but males may require physical interaction for complete synchrony of annual physiological changes. Am. J. Primatol. 47:93–103, 1999. © 1999 Wiley-Liss, Inc.

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INTRODUCTION

Like many other primates, squirrel monkeys (*Saimiri sciureus*) engage in mating activities during a brief period once each year. In the months just before the breeding season, males gain weight [DuMond & Hutchinson, 1967; Mendoza et al., 1978a], the so-called "fatting response" [Nadler & Rosenblum, 1972]. The breeding season is accompanied by increased heterosexual social interactions [Baldwin, 1968; Mendoza et al., 1978b], including heightened olfactory investigation of females by both sexes [Baldwin, 1970; Hennessy et al., 1978; Boinski, 1987b, 1992]. Circulating gonadal hormone levels increase during the breeding season [Mendoza et al., 1978a,b; Diamond et al., 1984; Wiebe et al., 1988], as do circulating concentrations of cortisol [Schiml et al., 1996].

The factors controlling the seasonal transition from nonbreeding to breeding status in squirrel monkeys are not fully understood. Ecological factors, such as shifts signaled by weather patterns or nutrient availability, are likely to be important; breeding typically occurs during the dry season, and infants are born during the rainy season, when food is most abundant [Baldwin, 1968; Boinski, 1987a; DuMond & Hutchinson, 1967; Mitchell, 1990]. In captive populations, social events have been shown to have strong effects on variations in breeding activity. Formation of heterosexual groups can induce breeding readiness [Coe & Rosenblum, 1978; Mendoza et al., 1979; Mendoza & Mason, 1991] and alter the timing of annual changes so that subsequent breeding seasons occur in the same calendar months as group formation [Coe & Rosenblum, 1978; Mendoza et al., in press]. Furthermore, as compared to animals living as heterosexual pairs, the presence of multiple females in a social group increases the proportion of females exhibiting ovarian cyclicity and heightens testosterone levels in males [Schiml et al., 1996].

Although physical interaction with social partners can alter seasonal measures in *Saimiri,* it is not clear whether tactile and close olfactory contact with other conspecifics is essential for the expression of seasonality. An absence of certain types of social cues results in atypical seasonal rhythms in other species. Gordon et al. [1978] found that isosexual groups of male rhesus monkeys exhibited seasonal patterns of testosterone that were diminished in magnitude when the males were isolated from all contact with females but showed normal variations in the magnitude and timing of testosterone cycles when provided with distant contact (visual, olfactory, auditory) with heterosexual social groups.

In this study, we investigated whether individually housed squirrel monkeys exhibit annual changes in circulating steroid hormone concentrations and male body mass. Because individually housed subjects had distant contact (auditory, olfactory) with social groups, we also describe the relationship of changes in the subjects to the breeding season of the nearby social groups in order to examine the possibility that cues emanating from the social groups may have influenced physiological measures in the subjects.

METHODS

Subjects

Subjects were nine adult male and eight adult female squirrel monkeys (*Saimiri sciureus*) of Peruvian and Colombian varieties living at the California Regional Primate Research Center in Davis, California. All animals were laboratory-born and raised with their mothers in social groups, with the exception of one female who was wild-born and brought into our laboratory as an adult 19

months prior to the beginning of the study. All animals were reproductively mature when the study began and ranged in age from 3–15 years. Subjects were housed in social groups of various compositions in indoor cages with outdoor access until approximately 1 week before data collection began, at which time subjects were separated from their social partners and placed into individual housing in an indoor colony room at the Primate Center, in which social groups of various compositions had been living for 5 months (see below). No physiological measures were collected from subjects before the animals were moved into individual housing.

Subjects were housed individually in stainless steel cages (.80 m × .80 m × .95 m) equipped with one upper and two lower perches extending the length of the cage. Cages had solid sides and backs and were positioned so that subjects did not have full view of any other monkeys and so that physical interaction between cages was not possible. No attempt was made to limit auditory and olfactory communication.

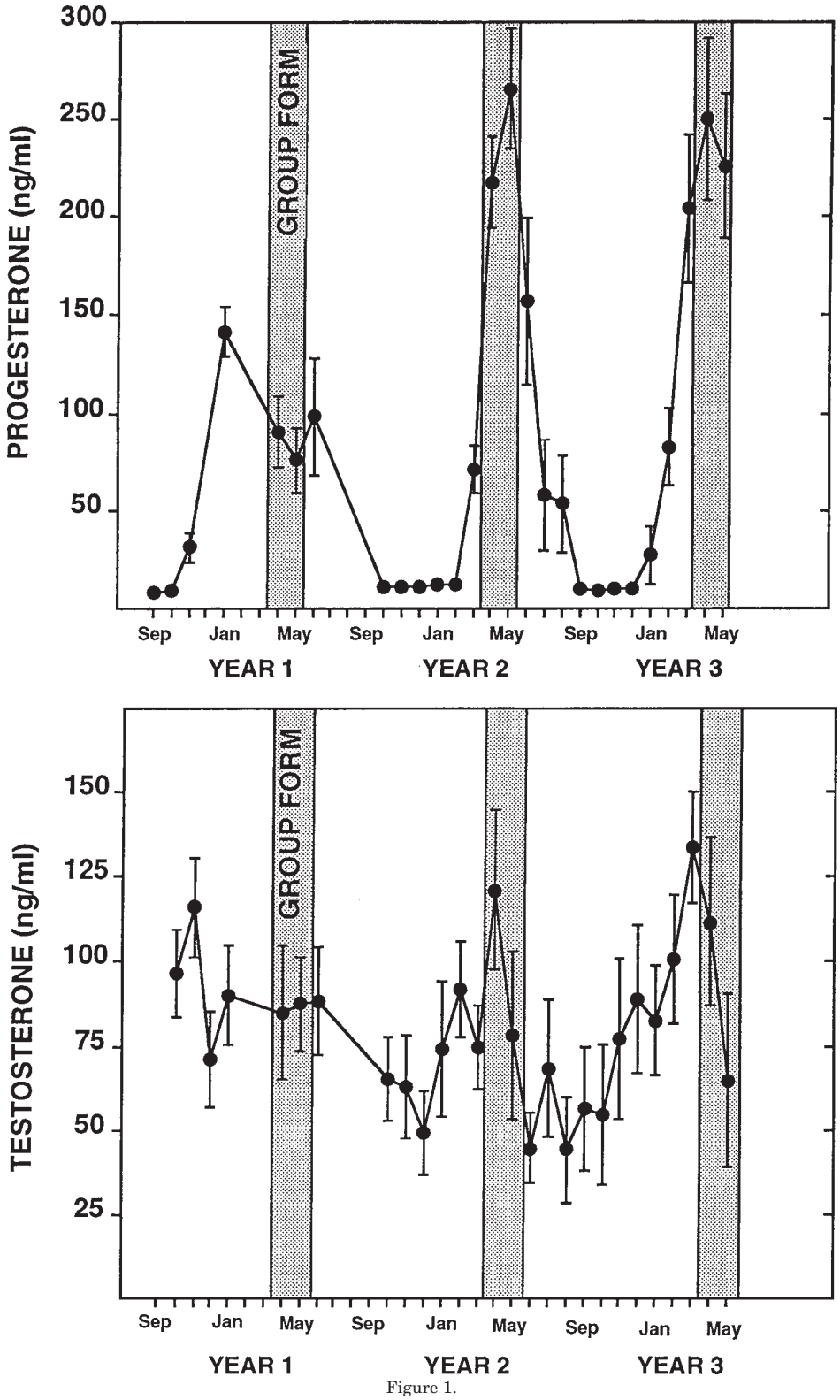
Animals were maintained according to standard laboratory protocol, which included cage cleaning and feeding at 0800 h and an additional feeding at 1330 h. They were fed standard New World monkey chow supplemented with apples and raisins. Water was available ad libitum. Lighting was on a 12:12 light/dark schedule, with lights on at 0600 h, and skylights in the ceilings provided exposure to sunlight and natural variation in day length. Large, sliding doors in the colony room were opened to screen doors to the outside when the daytime ambient temperature was 22–33°C. Additional heating and cooling were provided at other times to maintain room temperature within this range.

The colony room also contained 11 female and seven male squirrel monkeys housed in five heterosexual social groups, which subjects could hear, smell, and occasionally see. In an adjacent room, 27 female and 21 male squirrel monkeys were housed in 13 heterosexual social groups; subjects could hear and possibly smell but not see these animals. Breeding was induced in the colony's heterosexual social groups by group formation 5 months before individually housed subjects were moved into the colony room. Group formation altered the timing of subsequent breeding seasons in the social groups so that breeding was not timed according to the last freely occurring breeding season but rather was timed according to group formation (see Fig. 1). Individually housed subjects lived in a different building during the heterosexual group formations and presumably could not see, hear, or smell the group-housed animals at this time.

Once established, the living arrangements of all animals were maintained throughout the course of the study. The only additions to the colony room were births into the social groups. Subjects were removed from their cages occasionally for routine cleaning or medical procedures. On five occasions, health matters necessitated removal and hospitalization of a subject. The duration of these absences ranged from 1–2 days, and animals were returned to the home cage as soon as it was deemed medically safe.

Design

Data were collected for 20 months. Three blood samples were collected from each subject within a 6–9 day period each month. This provided an adequate sampling for the evaluation of cyclicity in females, as the ovarian cycle is approximately 8–9 days in length in this species [Ghosh et al., 1982]. In addition, males were weighed once each month. Prior to the outset of the study, all animals were well habituated to the capture and handling techniques used in the


PROGESTERONE (ng/ml)
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TESTOSTERONE (ng/ml)
150
125
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75
50
25
GROUP FORM
Sep
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YEAR 3

Figure 1.

study: animals were trained to enter transport boxes and were very familiar with the blood sampling procedures.

Blood Sampling and Hormone Assays

Blood samples were collected between 1130 and 1330 h. Blood samples were collected from all subjects on each blood-sampling day. Subjects were captured in a transport cage, removed, and manually restrained while a blood sample (1.0 ml) was collected via femoral venipuncture into a heparinized syringe. After blood samples were collected, animals were rewarded with an edible treat. Blood samples were collected serially from subjects in an order that remained the same throughout the study. Blood samples were stored on ice until samples were collected from all subjects. Samples were then centrifuged, and the plasma fraction was extracted and frozen until assayed. Blood samples were obtained from each subject within 1.52 ± 1.0 min (mean ± SE) of the initial disturbance to the home cage. This latency was well within the range reported to be before pituitary–adrenal activity rises due to sampling stress [Cook et al., 1973; Coover et al., 1979]. Of the 1,020 samples collected, all but 4 (<1%) were collected within 4 min from initial cage disturbance. Correlations between cortisol levels and latency between cage disturbance and sampling time ranged from –.45 to .66. Significant correlations occurred on 6 of the 60 sampling days.

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

Data Analysis

Ovarian cyclicity in females was assessed as described by Mendoza and Mason [1989]. Briefly, we calculated difference scores for estrogen and progesterone for each month by subtracting the lowest from the highest of each animal's three values for that month. If the difference exceeded 100 pg/ml for estrogen or 50 ng/ml for progesterone or if the average of the three samples exceeded these values, a female was considered to be cycling. For all other analyses, values from each of the three blood samples collected each month were averaged. Data from males and females were analyzed separately. Cortisol, testosterone, estrogen, progesterone, and male body weight were analyzed by one-way repeated measures analysis of variance (ANOVA), using month as the within-subjects variable. Post-hoc comparisons were based on Newman-Keuls tests [Winer, 1971].

The timing of annual changes in physiology in the subjects was compared to the timing of hormone elevations and breeding in the social groups housed in the same room. The breeding season (as defined by months in which conceptions

Fig. 1. Seasonal changes in progesterone and testosterone levels in group-housed squirrel monkeys before and for 2 years following heterosexual group formation. Months of group formations are indicated by the first shaded area, and the next two shaded areas demarcate periods occurring 12 and 24 months after group formations and denote breeding seasons. Data from Lyons et al. [1994], Saltzman [1991], and Schiml et al. [1996].

occurred [Schiml et al., 1996]) within these social groups occurred 12 and 24 months after group formations. As shown in Figure 1, gonadal hormones were elevated during these months relative to nonbreeding months.

RESULTS

Females

Gonadal hormone levels in individually housed females exhibited clear annual changes over the months of the study (estrogen: $F(19,133) = 7.97$, $P < .001$; progesterone: $F(19,133) = 7.19$, $P < .001$) (see Fig. 2). Progesterone levels peaked during April through June in the first year of the study and in April and May of the following year (Newman-Keuls, $P < .05$). Similarly, estrogen was high in May through July during the first year and in April and May of the second year (Newman-Keuls, $P < .05$).

Estimates of ovarian cyclicity (based on changes in estrogen and progesterone within a month) conformed well to the analysis of mean ovarian hormone levels. All eight females were judged to be undergoing ovarian cycles from April through June during the first year and again, beginning eleven months later, in March and April during the second year. One female began cycling in April of the first year and continued for the next 14 months. Excluding this female, once cyclicity began, it continued for an average of 6.29 months per year (range: 4–10 months).

Adrenocortical activity in females also exhibited annual variation ($F(19,133) = 7.18$, $P < .001$). High cortisol levels in females were observed in April through June during the first year and in April and May of the second year (Newman-Keuls, $P < .05$) (see Fig. 2).

As compared to the breeding season of the nearby social groups, ovarian and adrenocortical hormone levels in females housed alone peaked during the social groups' breeding seasons in both years and remained high during the initial months of the social groups' nonbreeding season (Fig. 2, shaded areas).

Males

Plasma testosterone levels of the nine males changed across months ($F(19,152) = 2.17$, $P < .01$) (Fig. 3), but, unlike ovarian hormones, elevations in testosterone were significant in only 1 month, July (Newman-Keuls, $P < .05$). Male weight exhibited two cycles ($F(19,152) = 4.48$, $P < .001$), peaking in March of the first year and in February and March of the second year (Newman-Keuls, $P < .05$) (see Fig. 3).

Plasma cortisol levels in males also varied across the period of data collection ($F(19,152) = 3.46$, $P < .001$), showing a conspicuous peak in January and February of the second year (Newman-Keuls, $P < .05$).

As compared to socially housed animals, elevations in testosterone were out of phase with the social groups' breeding seasons (Fig. 3, shaded areas). Weight gain in individually housed males preceded the social groups' breeding seasons in both years by 1 month. Cortisol levels of individually housed males were elevated during the first year of the study and then fell, rising to a peak prior to the social groups' second breeding season.

DISCUSSION

This study is the first report of annual changes in physiology and male body weight in individually housed squirrel monkeys. All animals showed marked elevations in gonadal and adrenal hormones, and males exhibited annual patterns

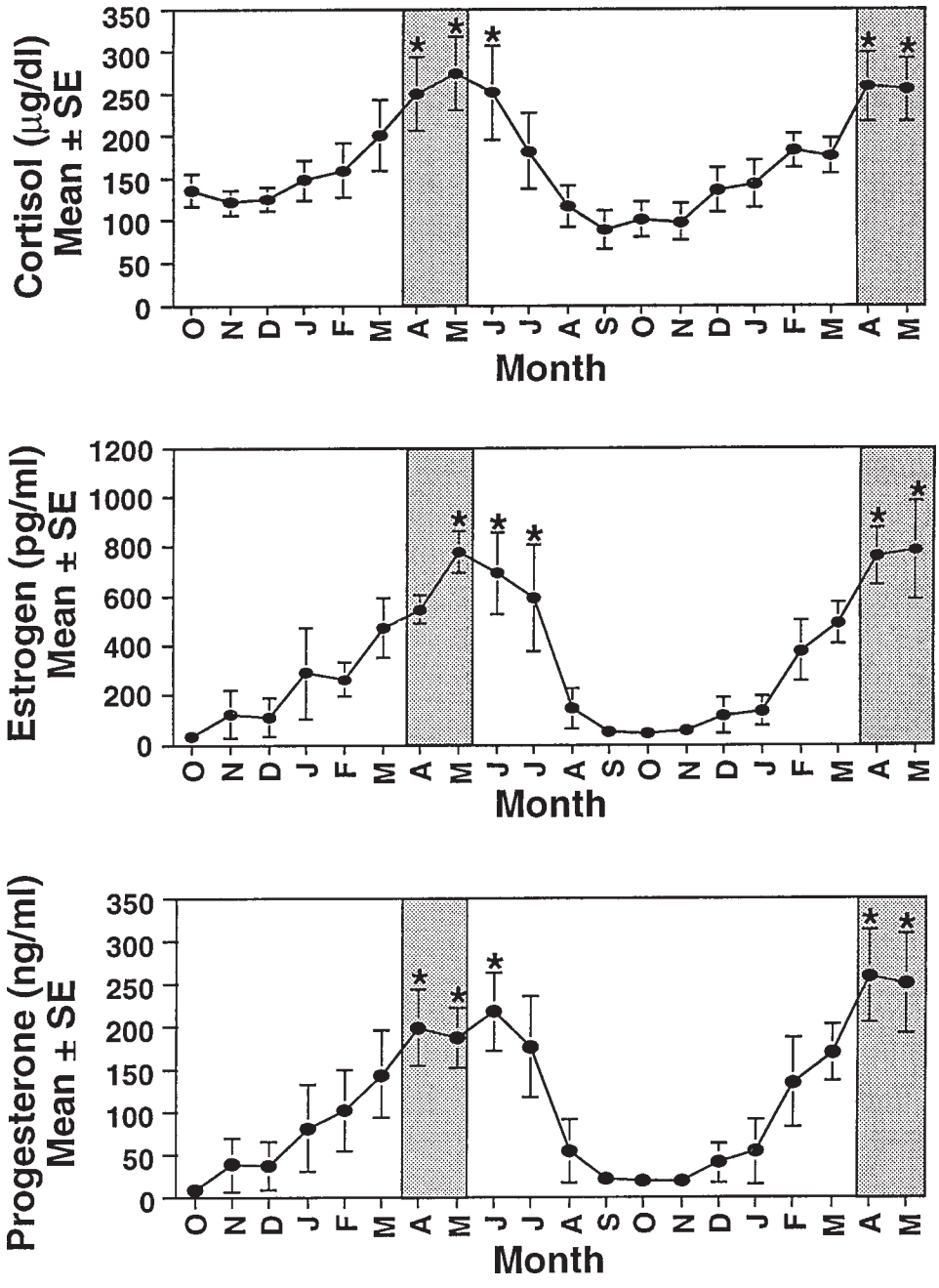

Fig. 2. Seasonal changes in cortisol, estrogen, and progesterone in female squirrel monkeys housed alone. Shaded areas demarcate breeding seasons in nearby social groups, as induced by group formation. Asterisks (*) indicate significant elevations as determined by Newman-Keuls comparisons ($P < .05$).

of weight gain and loss, demonstrating that physical social interaction is not required to produce annual fluctuations in hormones and body weight.

The cyclic elevations in the various physiological measures in individually housed subjects appear to be similar in magnitude and duration to those ob-

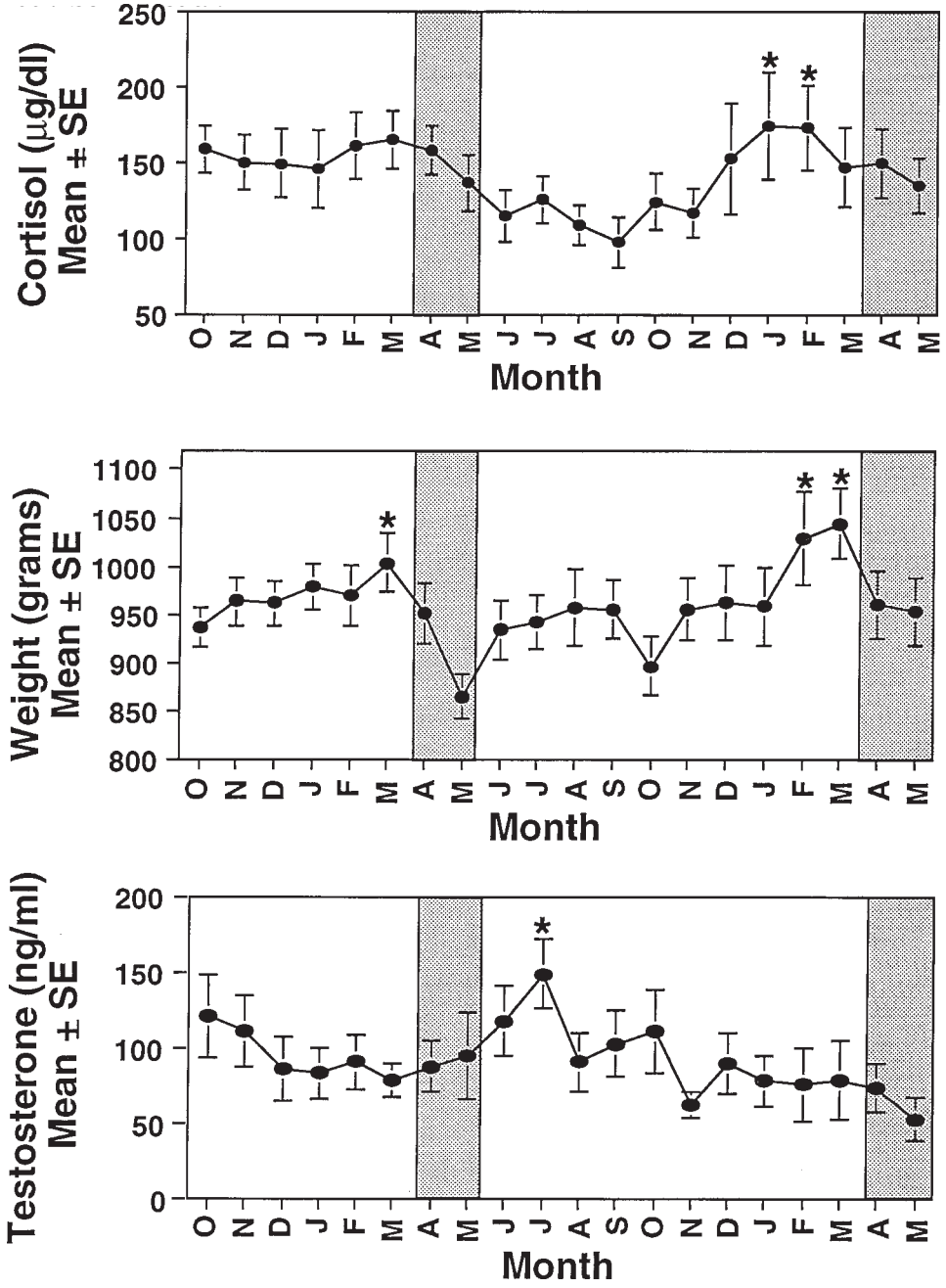

Fig. 3. Seasonal changes in cortisol, weight, and testosterone in male squirrel monkeys housed alone. Shaded areas demarcate breeding seasons in nearby social groups, as determined by group formation. Asterisks (*) indicate significant elevations as determined by Newman-Keuls comparisons ($P < .05$).

served in group-housed animals. Individually housed females underwent ovarian cycles for 4–10 months, slightly longer than socially housed animals, which cycle for 4–6 months (for those that did not become pregnant [Schiml et al., 1996]). Elevations in hormones and body weight persist for 1–3 months in socially housed

animals [Schiml et al., 1996], and individually housed animals exhibit a similar pattern.

In individually housed females, elevations in adrenal and ovarian hormones tended to occur in the same months. This is also observed in socially housed females [Schiml et al., 1996]. In contrast, annual changes in individually housed males were dissociated from one another. Although plasma testosterone levels did show an increase comparable in magnitude (a difference of approximately 100 ng/ml from seasonal peak to trough) to that observed in socially housed animals [Schiml et al., 1996], the increase was out of phase with the other cyclic changes occurring in the subjects. In socially housed males [Schiml et al., 1996], peaks in cortisol and male weight tend to coincide, even though this association was not as clear during the first year as during the second. The data suggest that hormone cycles in individually housed males were different between the first and second years of the study. During the second year, peaks in cortisol and weight were of a greater magnitude than in the first year. It is possible that over time, males became more sensitive to cues regulating annual changes and that this accounted for the year-to-year drift observed in the timing and magnitude of hormonal peaks.

Although no physiological data were collected from the individually housed subjects prior to the start of the present study, data collected from the animals housed in the social groups in the months prior to the start of this study indicate that the seasonal cycle in the social groups was different after group formation relative to before [Mendoza et al., in press] (see also Fig. 1). The data from the present study indicate that the individually housed subjects, particularly females, exhibited the same pattern of annual changes as the social groups after the annual pattern in the social groups had been shifted by heterosexual group formations. Elevations in plasma hormone levels in individually housed females coincided with both breeding seasons in the social groups. In contrast, all physiological measures in individually housed males were dissociated in time from breeding in the social groups. This was particularly true for testosterone, which peaked during only 1 month during the social groups' nonbreeding season. One possible explanation for these findings is that individually housed females were sensitive to cues, such as odor or vocalizations, from the social groups that acted distally, but males were less so.

In other species, social cues can dramatically alter seasonal expression. In lesser mouse lemurs, isolation can advance the onset but delay the peak in seasonal testosterone elevations in males [Perret, 1985] and can shorten the ovarian cycles in females [Perret, 1986] relative to seasonal changes in grouped animals. If distant communication (visual, auditory) is allowed, cycle length is increased in females [Perret, 1986]. While lesser mouse lemurs are normally solitary, animals that associate in groups also show evidence of socially induced alterations in seasonality. In talapoin monkeys, differences in the timing of the breeding season can be observed in animals sharing the same environment but residing in different social groups [Rowell & Dixson, 1975]. Pinealectomized ewes exhibit a delay in annual surges in luteinizing hormone (LH) when socially isolated but exhibit a normal rhythm if kept in a flock of intact ewes [Wayne et al., 1989]. In this case, social partners facilitate the synchronization of LH secretion in individuals incapable of responding to photoperiodic input.

Changes in day length modulate seasonal reproduction in many species [for review see Nelson et al., 1990], but the effects of photoperiod on seasonality have not been systematically examined for the squirrel monkey. While the synchrony between individually housed female subjects and socially housed females living

nearby may be due to light cues, this seems unlikely to have occurred only in females and not in males. DuMond and Hutchinson [1967] noted that squirrel monkeys brought from Iquitos, Peru, to Miami, Florida, exhibited an approximately 4 month drift in their breeding and birth seasons over the course of 6 years; the drift occurred within the first 4 years and then stabilized. These changes could have been due to photoperiod differences between Peru and Florida, but the authors suggest that the shift may have occurred as a result of differences in precipitation cycles [DuMond & Hutchinson, 1967]. Harrison and Dukelow [1973] found that in females, sensitivity to an ovulation induction regime changed over the course of the year and suggested that females were most sensitive to the regime during periods of high humidity and least sensitive during periods of low humidity. In natural [Boinski, 1987a,b] or seminatural [DuMond & Hutchinson, 1967; Baldwin, 1970] environments, births tend to occur during rainy months, during which changes in food and nutrient availability can also occur [Boinski, 1987a]. The present study did not systematically control or examine the effects of photoperiod or rainfall, but nutrient availability did not change over the course of the study, as the monkeys were fed a standardized diet.

Our results suggest that while direct contact with social partners is not required for the expression of seasonality in squirrel monkeys, it may be important for modulating the timing of annual changes within and among individuals, particularly in males. Direct contact may provide males with nonvolatile chemical cues [Wysocki, 1979] or tactile cues used for timing seasonal events. In contrast, females may be more sensitive to distant social cues, perhaps olfactory or auditory in nature, and may use these cues to time seasonal changes with those occurring in other animals. Therefore, instead of being a requisite for the occurrence of seasonal cycles, direct social stimulation is a factor that modulates and synchronizes the timing of annual changes within individuals, and in nature may serve to coordinate reproductive synchronization among members of a group [Baldwin, 1970; Boinski, 1987a; Mitchell, 1990].

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