

Synchronization of Ovarian Cycles Within and Between Social Groups in Golden Lion Tamarins (*Leontopithecus rosalia*)

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Synchronization of ovarian events has been reported in a number of primate species, with the temporal resolution of synchrony ranging from the occurrence of seasonal breeding within the annual cycle to a close matching of ovarian events within a single ovarian cycle. However, ovarian synchrony has not been reported in a New World primate. The temporal association of ovarian events was examined in female golden lion tamarins (*Leontopithecus rosalia*) living in the same or different social groups. Ovarian cyclicity was monitored by measuring the excretion of urinary estrogen metabolites. There was a high degree of synchronization in the occurrence of urinary estrogen peaks for females in different social groups (mean peak discrepancy = 2.1 days) and in females housed in the same social group (mean peak discrepancy = 1.3 days). Contrary to previous reports on callitrichid primates, daughters housed in their natal family group exhibited cyclic patterns of urinary estrogen excretion. These findings represent the first explicit demonstration of ovarian synchrony in a New World primate, and the tight coupling of ovarian cycles in female tamarins resembles the nature of menstrual synchrony in human females.

Key words: female sexual cycle, sexual cycle synchrony, reproductive suppression, Callitrichidae

INTRODUCTION

Group-living females of many mammalian species exhibit a tendency toward synchronization of ovarian cycles. The tendency of females in physical and/or olfactory contact with each other to become synchronized with regard to reproductive cycles has been reported in rodents [see review by Brown, 1985], marsupials [opposums: Fadem & Reyve, 1985], and a variety of nonhuman primates [ring-tailed lemurs: Jolly, 1967; chimpanzees: Wallis, 1985; various cercopithecines: Rowell & Richards, 1979].

To our knowledge, no one has explicitly analyzed reproductive cycles in New World primates for evidence of ovarian synchrony. This paper describes such an analysis for the golden lion tamarin (*Leontopithecus rosalia*; Primates: Family Cal-

Received May 29, 1986; revision accepted November 2, 1986.

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litrichidae). One of the difficulties in conducting research on reproductive synchronization in callitrichid primates is the lack of a clear, reliable index of ovarian cyclicity. Cycling female tamarins and marmosets do not show cyclic changes in perigenital swellings or color [Hampton et al, 1966]; there are no consistent changes in vaginal cytology across the reproductive cycle [Hearn, 1978]; there is no menstrual bleeding [Brand, 1981]; and there is a lack of a conspicuous behavioral estrus associated with the periovulatory phase of the cycle [Epple, 1975; Stribley et al, in press; Rothe, 1975]. Thus, in the absence of a measure of ovarian cyclicity, it is difficult to assess synchronization among females.

Recently, however, noninvasive methods for monitoring the reproductive cycle of female callitrichids based on the measurement of urinary estrogen excretion have been developed [Brand, 1981; French et al, 1983; Hodges et al, 1981]. A urinary estrogen radioimmunoassay has been developed and validated for monitoring ovarian cyclicity in female golden lion tamarins (*Leontopithecus rosalia*) [French & Stribley, 1985]. In the study reported here, the temporal association of ovarian events was examined among females living in separate cages but in close proximity to each other and among females living in the same cage.

METHODS

Subjects

Five adult female golden lion tamarins (*Leontopithecus rosalia*) served as subjects in this study. Two females were housed in separate large breeding cages, each with an unrelated adult male. The remaining three females constituted a family group (mother and two daughters) which also contained an adult male and an infant male. The older daughter (Ch) also participated in the study after removal from the family group and pairing with an unrelated adult male. The ages, housing condition, and date of pairing with the male mate are shown in Table I. The golden lion tamarin is an endangered species, and the University of Nebraska at Omaha is a signatory member of the International Cooperative Management Agreement.

Housing and Maintenance

The tamarins were housed in cages (1.0 × 2.0 × 2.1 m, minimum size; 2.0 × 2.0 × 2.1 m, maximum size) constructed of wood and wire mesh. Natural branches, nest boxes, and hanging objects were provided for the animals' use. Sawdust bedding was placed on cage floors for hygiene and to protect falling infants from injury. Sawdust was replaced every 1 to 2 weeks, and clean, unmarked branches were provided once every 3 to 4 months.

The animals were fed once a day with a varied diet of prepared marmoset diet (Hills, Topeka, KS), fresh fruit and vegetables, dairy products and eggs, peanuts, infant mice and gerbils, and meal worms. All cages were provided with identical foods daily. Fresh water was freely available.

Cages were maintained in a large colony room (40 m²) that was divided by solid walls into smaller subrooms. Each cage was physically and visually separated from the others, either by being located in a separate subroom or by suspending an opaque divider between cages. Acoustic and olfactory contact between all cages was possible. All subrooms in the colony shared a common air supply, and there were approximately six to eight air changes per hour in the room. The minimum average distance between cages was 0.3 m, and the maximum average distance between cages was 3.7 m.

Urine Collection and Hormone Analysis

Urine samples were collected daily (7 days per week) for each female. Sample collection occurred during the early to mid-morning (0700 to 1100 hours). A collection

TABLE I. Female *L. rosalia* at the University of Nebraska at Omaha

Female ISIS code ^a	Age at onset of study (yrs)	Pairing date	Housing condition
101187 (Al)	8	1977	Family group
104187 (Ch)	2	August 14, 1983	Family group pair
104659 (Em)	1.5	—	Family group
102801 (Ro)	4	September 8, 1983	Pair
100997 (Lu)	9	August 24, 1983	Pair

^aInternational Species Inventory System.

procedure that eliminated capture and restraint was adopted. Large stainless-steel pans were placed on the floor of the cage. Females were watched until they urinated on the pans. In cases of contamination of samples by urine from other animals, the sample was discarded and an additional, uncontaminated sample was immediately collected. After a female urinated (usually 0.5 to 3.0 ml), the sample was pipetted into a vial, centrifuged briefly at 1,500 rpm to remove detritus, and frozen at -40°C until assayed. All of the pans were washed after use each day with a mild detergent, rinsed with hot water, and allowed to air dry before use the next day.

Details of the urinary estrogen assay procedure and its validation can be found in French and Stribley [1985]. Briefly, urine was diluted in phosphate-buffered saline and hydrolyzed with β -glucuronidase-sulphatase, estrogens were extracted with anhydrous diethyl ether, and assay for estrogen was accomplished with an antiserum for estrone. In the golden lion tamarin, estrone is the predominant urinary estrogen in cycling and pregnant adult females. Estrone is excreted at 14- to 26-fold higher concentrations than estradiol- 17β [French & Stribley, 1985]. Procedural losses were monitored by the recovery of ^3H -labelled estrone, and unknown values were corrected for procedural losses. A urine pool from adult females was assayed in triplicate with each set of samples. Intra-assay variation, calculated as the mean coefficient of variation for the three samples in each assay, was 9.4%. Interassay variability was 13.0%. The estrogen concentration of each urine sample was divided by the creatinine concentration of the sample to control for variable fluid intake and output.

Cyclicity was determined with reference to the peaks in urinary estrogen excretion. Peaks were defined as elevated concentrations of estrogen with no higher values for four samples prior to and for four samples following the peak [French et al, 1983; French & Stribley, 1985].

Analysis of Data

Two analyses were performed to assess the hypothesis of synchronization of ovarian cycles: One parametric and one distribution-free test. Both analyses, however, assessed the null hypothesis that a female in the colony was exhibiting peaks in urinary estrogen cycles independently, or randomly, with respect to other females in the colony.

"Peak discrepancy" was the measure used to assess ovarian synchronization and was derived as follows: A peak in estrogen excretion was identified in one female, and the absolute difference, in days, to the nearest estrogen peak in all other females for whom there were data, was determined. For instance, in Figure 1, which presents the hormonal profiles for colony females throughout the course of the study, female Ch exhibited a peak in estrogen excretion on day 20. The peak discrepancy for female Em was 0 days, and the peak discrepancy for female Al was 1 day. The

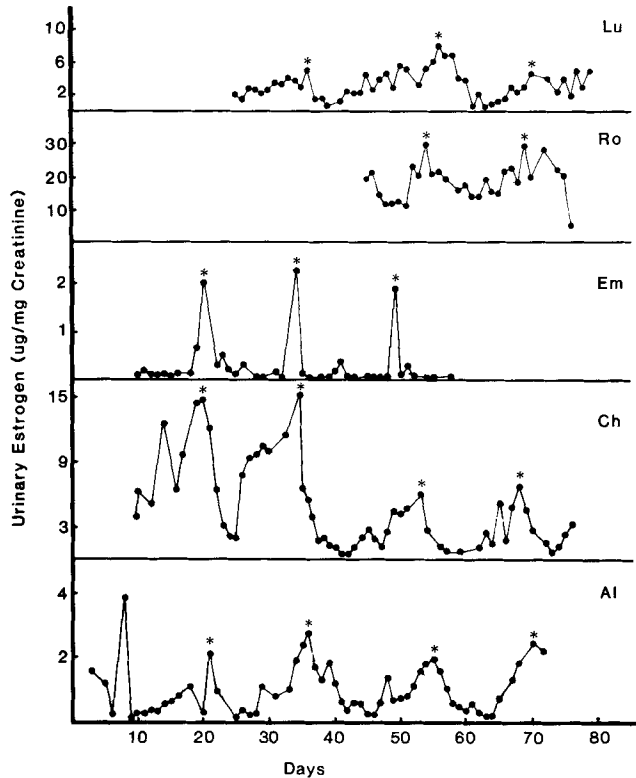


Fig. 1. Patterns of urinary estrogen excretion in five female golden lion tamarins during a portion of the study. Corrected values are expressed as μg estrogen per mg creatinine; note the different scales for individual females. Estrogen profiles are aligned according to calendar date. Asterisks indicate cycle peaks.

derivation of "peak discrepancy" is similar to the procedure used by McClintock [1971], Graham and McGrew [1980], and others to assess menstrual synchrony in human females ("menstrual onset discrepancy").

For the parametric analysis, a one-sample *t*-statistic was calculated to test the hypothesis of synchronization. Under the null hypothesis of no synchronization, the mean of the distribution of absolute peak discrepancy was estimated at 4.5 days. This value was based on the 19-day estrogen cycle in the golden lion tamarin [French & Stribley, 1985], and it was assumed that the distribution of absolute peak discrepancies should range from 0 to 9 days with a mean of 4.5 days.

In the nonparametric analysis, a χ^2 statistic was used to test the hypothesis that the distribution of peak discrepancies differed from a randomly determined distribution. Peak discrepancies were clustered into intervals of 2 days (0-1, 2-3, 4-5, 6-7, and 8-9 days). This analysis was conducted for all colony females, and also separately for between-cage synchronization (unrelated females) and within-cage synchronization (mother and two daughters). For all statistical comparisons, a significance level of 0.05 was adopted.

RESULTS

There was a high degree of synchronization in the occurrence of urinary estrogen peaks among female golden lion tamarins housed in a common colony facility.

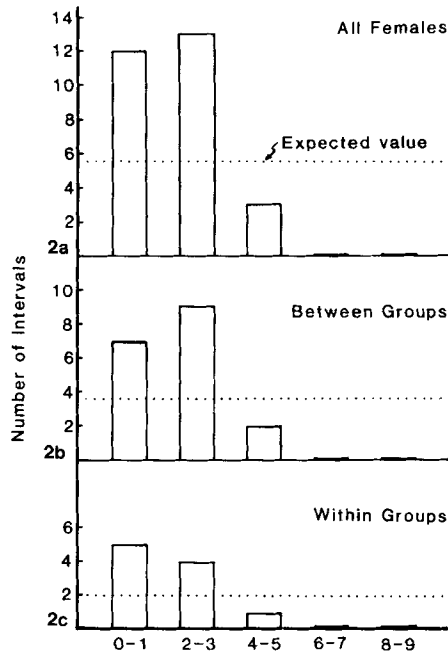


Fig. 2. Distribution of peak discrepancy intervals. Intervals are categorized into 2-day blocks. The values represent the number of peak discrepancy intervals for that time block. Dotted line represents expected value with random, asynchronous ovarian cycles. a: Peak discrepancy intervals for all females in the study. b: Peak discrepancy intervals for females housed in separate social groups. c: Peak discrepancy intervals for females housed within the same social group.

Figure 1 presents individual urinary cycles aligned on the basis of calendar date, and clear patterns of synchronization are apparent. Among all females in the colony, the mean peak discrepancy was 1.79 ± 0.26 days (mean \pm SEM). This peak discrepancy was significantly different from the peak discrepancy expected with random, nonsynchronized estrogen cycles [4.5 days; $t(27) = 8.74$, $p < 0.001$]. Figure 2a presents the distribution of peak discrepancy intervals for all females in the colony. No estrogen peak occurred more than 5 days from another female's peak, and 89% (25/28) of the peaks occurred within 3 days of another female's estrogen peak [$\chi^2(4) = 29.50$, $p < 0.001$].

Between Social Groups

Cycles from females housed in different cages were analyzed separately for ovarian synchronization. The mean peak discrepancy was 2.11 ± 0.35 days, which was significantly less than one would predict with random occurrence of estrogen peaks [$t(17) = 5.41$, $p < 0.001$]. Figure 2b shows the distribution of peak discrepancy intervals for females housed separately. There was a high degree of synchronization, with 89.9% (16/18) of the intervals being 3 days or less. The distribution of discrepancy intervals departed significantly from a random distribution [$\chi^2(4) = 19.22$, $p < 0.001$].

Within Social Groups

Daughters housed in their natal family group exhibited signs of regular ovarian cyclicity (see Fig. 1, females Ch and Em). Cycles for 22-month-old Ch resembled

normal adult female patterns of estrogen excretion, with smooth, sinusoidal patterns predominating. On the other hand, Em's pattern of urinary estrogen excretion was characterized by low basal levels and rapid elevations to peak concentrations (spikes), followed by a rapid return to basal levels.

There was a high degree of synchronization in estrogen excretion among the mother and her two daughters. The mean peak discrepancy was 1.30 ± 0.30 days, which was significantly shorter than the 4.5 days expected with randomly distributed cycles [$t(9) = 13.31, p < 0.001$]. Figure 2c presents the distribution of peak discrepancy intervals for the three females in the family group. Only one out of a total possible of ten intervals was greater than 3 days, and five of ten comparisons of peaks were within 1 day of another female's peak. The distribution of intervals departed significantly from a random distribution [$\chi^2(4) = 11.00, p < 0.001$]. The mean peak discrepancy for females within a social group did not differ significantly from that of females housed in different social groups [1.30 days vs 2.11 days, $t(26) = 1.55$, not significant (n.s.)].

The effect of proximity to another female on the degree of ovarian synchronization was assessed by correlating the distance between cages with the mean peak discrepancy for females housed in those cages. Females housed in the same cage were excluded from this analysis. The mean distance between cages ranged from 0.33 to 3.7 m, and the mean peak discrepancy among pairs of females ranged from 1.33 to 5.0 days. There was no relationship between physical proximity and degree of synchronization ($r = 0.017$).

DISCUSSION

Female golden lion tamarins housed in separate cages but with a common air supply exhibited synchrony of urinary estrogen cycles, with a mean peak discrepancy of 2.11 days. Females housed in the same social group exhibited even greater ovarian synchronization, with a mean peak discrepancy of 1.30 days. Both the mean peak discrepancy and the distribution of peak discrepancy intervals are significantly different than expected if females were exhibiting nonsynchronized, random ovarian cycles. These data represent, to our knowledge, the first demonstration of ovarian synchrony in a New World primate.

McClintock [1981] has identified four levels of reproductive synchronization, each distinguished by a different level of temporal resolution of the synchronization. Synchronization among females can occur for life span reproductive events, such as menarche or reproductive senescence; for annual reproductive events, such as breeding seasons; for specific reproductive events, as parturition or weaning; and for specific ovarian events, such as ovulation. Synchronization of reproductive variables has been documented at all levels of temporal resolution in primates.

Seasonal breeding patterns have been documented in many primate species [eg, Coe & Rosenblum, 1978; Nash, 1983; Wolf, et al, 1975; van Schaik & Noordwijk, 1985; Walker, et al, 1984]. Synchronization of reproductive activity within a breeding season has also been reported. Rowell and Richards [1979] reported a tendency for birth periods to be similar among captive female vervet monkeys (*Cercopithecus aethiops*). Fifty percent of the births among females housed close to each other occurred within a 3-month period.

Several authors have reported synchronous reproductive events within a breeding season. In an early report, Jolly [1967] noted a main estrous phase in ring-tailed lemurs (*Lemur catta*). She documented periods of time in which all of the adult breeding females in a troop showed full pink genitalia within 10 days of each other. Wallis [1985] examined deviations in the onset of perigenital swelling and the day of probable ovulation (maximal perigenital swelling) in female chimpanzees (*Pan*

trogodytes) housed in two separate groups of six and four females. Although the discrepancy in the day of probable ovulation was not affected by the social housing condition, the discrepancy in the days of onset of perigenital swelling was lower for group-housed females than for females housed in different groups.

The magnitude of both within-group and between-group synchrony in estrogen cycles reported here for the golden lion tamarin is greater than that previously reported for any nonhuman primate. Cycles in female tamarins were synchronized to within 1 to 3 days of cycles in other females. This resembles the temporal resolution of menstrual synchrony in human females. McClintock [1971] first reported systematic data on menstrual synchrony in dorm-living college women and found that menstrual onset discrepancy was reduced over the course of an academic year among close friends and roommates from approximately 6.5 days in October to 4.7 days in April. This finding has been independently confirmed in three studies [Graham & McGrew, 1980; Quadagno et al, 1981; Jarrett, 1984]. Significant synchronization of menstrual cycles in human females can occur in as short a period of time as 3 months. The female tamarins in this study had been housed together in a common colony room for varying periods of time from a minimum of 2 months to a maximum of 2.5 years at the start of urine collections. There did not appear to be a relationship between length of common housing and degree of synchrony. Therefore, in female tamarins, as in human females, significant socially mediated adjustments of ovarian cycles can occur within a relatively short period of time.

The most frequently proposed hypothesis regarding the proximate mechanisms producing ovarian synchrony among female mammals is that cycles are synchronized by olfactory cues [McClintock, 1978; Russell et al, 1980]. In rats, synchronization is accomplished through distinct effects of odors from females in different phases of the estrous cycle: Odors from a donor female in a preovulatory state shorten the cycles of recipient females, whereas odors from donor females in the periovulatory phase of the estrous cycle tend to lengthen the receiver's estrous cycle [McClintock, 1984]. Russell et al [1980] provided a direct test of the olfactory mediation hypothesis in human females. Ethanol extracts of axillary gland secretions collected from a donor female and painted on the upper lip of recipients for 4 months reduced menstrual onset discrepancy between the donor and recipients.

That ovarian synchrony in golden lion tamarins is mediated by olfactory cues is highly likely for several reasons. First, all marmosets and tamarins possess specialized sebaceous and apocrine skin glands [eg, Perkins, 1968, 1969; Sutcliffe & Poole, 1978] and exhibit a variety of behavior postures that serve to deposit odors on the substrate. Second, the odors have been implicated as important social signals in affiliative and aggressive interactions [Epple, 1975; French & Snowdon, 1981]. Third, another parameter of ovarian function in other species of callitrichids, ovulation suppression, appears to be socially mediated, probably by olfactory cues associated with the breeding female [Abbott, 1984; Epple & Katz, 1984; French et al, 1984].

If ovarian synchrony in golden lion tamarins is mediated by olfactory cues, the results of this study suggest certain characteristics of the pheromone(s) involved in the effect. First, because females living in separate cages, as well as in the same cage, all exhibited ovarian synchrony, physical contact with other females or their scent deposits may not be necessary to induce ovarian synchrony. Second, the absence of a correlation between distance among females and the degree of synchrony indicates that the effectiveness of the potential odor(s) is not influenced by differences in physical distance, at least across the range of distances examined in this study (0.33 to 3.7 m).

One of the surprising findings of this study was that subordinate daughters in the presence of a reproductively active female exhibited clear signs of reproductive activity. It is well established in saddleback tamarins (*Saguinus fuscicollis*) and cotton-top tamarins (*S. o. oedipus*) that subordinate females exhibit low and acyclic patterns of estrogen production and fail to breed [Epple & Katz, 1984; French et al, 1984; Ziegler et al, 1986; but see also Tardif, 1984, who reports signs of ovulation in some daughters housed in family groups]. In common marmosets (*Callithrix jacchus*), reproductive activity is also suppressed in subordinate females in peer groups (three unrelated males and three unrelated females [Abbott, 1984] and perhaps in daughters in family groups [Evans & Hodges, 1984]. In the present study, both female Ch and Em showed clear patterns of adult-like urinary estrogen excretion (Fig. 1). However, as in other marmoset and tamarin species, neither adult daughter acquired breeding status, exhibited any sexual behavior, or attracted high levels of investigatory behavior from males in the family group. It appears, then, that although the mechanisms of fertility suppression may differ among species and in different contexts (eg, physiological vs behavioral suppression), the outcome is equivalent: only one female produces viable offspring.

The significance of ovarian synchrony in golden lion tamarins is not clear. It may be that in golden lion tamarins, as in human beings, the adaptive significance of ovarian synchrony is not explicable in light of extant social and environmental conditions [McClintock, 1981; Kiltie, 1982]. Thus, ovarian synchrony may reflect an evolutionarily conservative trait that at some point in the past had functional significance for tamarins (eg, if, at some point in time, mating relationships were characterized by a polygamous, not monogamous, system). The occurrence of ovarian synchrony across diverse mammalian taxa is a testament to its pervasive and conservative nature, and its potentially fundamental importance in mammalian reproductive systems.

CONCLUSIONS

1. Female golden lion tamarins housed in separate social groups but in olfactory and acoustic contact exhibited synchronized ovarian cycles. The mean peak discrepancy in urinary estrogen peaks was 2.1 days.

2. Females housed within one social group (mother and two daughters) all exhibited cyclic patterns of urinary estrogen excretion. Ovarian cycles were synchronized among these females (mean peak discrepancy = 1.3 days).

3. There was no relationship between physical proximity of females and degree of synchronization, nor was the length of time a female had been housed in the colony a significant factor in synchronization.

4. This is the first known demonstration of social regulation of ovarian synchronization in a New World primate, and the close temporal matching of ovarian events in female tamarins resembles the degree of menstrual synchrony reported for human females.

ACKNOWLEDGMENTS

We thank L. Maitland for assistance in urine collections, and M. Carlson, J. Janovy, P. Kassmeyer, and L. Umstead for aid in colony maintenance. V. Dudley-Meier, B. Inglett, J. Klaric, and A. Salo provided useful comments on previous versions of this manuscript, and B. Easton was indispensable in the preparation of the paper. This work was supported in part by funds from the University Committee on Research, University of Nebraska at Omaha. The UNO Callitrichid Research Unit is fully accredited by AAALAC, and the research described in this report was conducted in compliance with the U.S.D.A Animal Welfare Act and the P.H.S. Policy on Laboratory Animals.

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