Social and Developmental Influences on Reproductive Function in Female Wied's Black Tufted-Ear Marmosets (*Callithrix kuhli*)

Tessa E. Smith, Colleen M. Schaffner,[1] and Jeffrey A. French

Nebraska Behavioral Biology Group and Department of Psychology, University of Nebraska, Omaha, Nebraska 68182

Although marmoset social groups may contain multiple adult females, reproduction is typically limited to one breeding female. A variety of endocrine and behavioral mechanisms have been identified that regulate fertility among female marmosets. In the present study, we assessed the mechanism(s) by which fertility is regulated in female black tufted-ear marmosets, *Callithrix kuhli*. The reproductive status of 10 daughters aged 2-24 months was evaluated by measuring concentrations of urinary pregnane-diol 3α glucuronide (PdG) and luteinizing hormone (LH). Concentrations of the two hormones were typically low in daughters less than 12 months of age, and the profiles suggested anovulation (mean PdG < 2 μg/mg Cr and mean LH < 6 ng/mg Cr). Concentrations of PdG rose dramatically in females older than 12 months. Eight subadult daughters commenced ovulatory function while still living with their family, and the remaining two failed to ovulate. The onset of ovarian function coincided with a change in the social environment in two females, but the remaining six females commenced spontaneous ovarian activity that was not associated with any social or environmental factor (mean age: 15.6 $\pm$ 1.6 months). Ovulatory function was monitored in five daughters while housed in their natal family group, while removed from the natal family group and housed singly, and while paired with an unrelated and unfamiliar male. The ovarian cycles of these females housed in the natal group were characterized by significantly shorter luteal phases and reduced PdG concentrations, relative to when the females were housed on their own, and relative to adult breeding females ($n = 6$). Stimulatory cues from unfamiliar males were not necessary to trigger regular ovarian function in females. In this species, the regulation of fertility in daughters is a complex combination of behavioral and endocrine factors. © 1997 Academic Press

[1] Current address: Department of Psychology, St. John's University, Collegeville, MN 56321-7155.

The social regulation of reproductive function is widespread among vertebrates, occurring in a variety of taxa and in species displaying diverse social systems (e.g., fish: Francis, Soma, and Fernald, 1993; birds: Wingfield and Moore, 1987; mammals: Bronson, 1989). The influence of social factors in reproduction is particularly pronounced in species that exhibit cooperative breeding—a social system in which group members deliver care to nondescendant offspring (Brown, 1987; Solomon and French, 1996). In many species that display cooperative breeding, reproductive activity within a group is typically limited to a single adult male and female (singular breeding). In other species, however, more than one individual of each sex in a group engages in reproductive attempts (plural breeding). This dimension has recently been formalized as "reproductive skew," which refers to variation in lifetime reproductive success among group members (Keller and Reeve, 1994; Sherman, Lacey, Reeve, and Keller, 1995). Skew can range from a value of 1.0 in cases where there is a strict reproductive division of labor, with physiologically or morphologically sterile castes, to a value of 0 in species where all adults within a group engage in breeding activity. Of particular interest are those species that lie between the two extremes of the reproductive skew continuum, both from the perspective of the evolution of reproductive life histories and from the perspective of the underlying mechanisms that produce reproductive skew within social groups.

The marmosets and tamarins of the primate family Callitrichidae provide useful taxa in which to study the mechanisms underlying reproductive skew, since it appears that both behavioral and physiological mechanisms control differential reproductive output among

females (Abbott, Barrett, and George, 1993; French, 1996). Field studies on wild callitrichid populations have revealed that breeding is typically limited to a single, behaviorally dominant female (see Sussman and Garber, 1987; French, 1996 for reviews). Laboratory studies have established that ovulation can be physiologically suppressed in subordinate females in the group. Subadult females in captive families of common marmosets (*Callithrix jacchus*), cotton-top tamarins (*Saguinus oedipus*), saddle-back tamarins (*S. fuscicollis*), and red-bellied tamarins (*S. labiatus*), housed under normal conditions in the presence of the mother and father, exhibit low and acyclic levels of urinary steroids (Epple and Katz, 1984; Evans and Hodges, 1984; French, Abbott, and Snowdon, 1984; Savage, Ziegler, and Snowdon, 1988; Kuderling, Evans, and Abbott, 1995).

As in other cases of socially mediated reproductive inhibition, the lack of reproductive capacity in subordinates can be produced either by the *presence* of inhibitory cues that delay or prevent the expression of ovulatory capacity in females (Drickamer, 1977; Faulkes, Abbott, and Jarvis, 1990) or by the *absence* of appropriate stimulatory cues that are necessary to initiate reproductive activity (Vandenbergh, 1967; Carter, Getz, Gavish, McDermott, and Arnold, 1980; Carter and Roberts, 1996). In female callitrichids, ovulatory suppression appears to be mediated in large part by inhibitory factors within the social group (Evans and Hodges, 1984; Savage *et al.,* 1988; Abbott and George, 1991). The dominant adult female appears to be a primary source of inhibitory cues, since removal of the breeding female from the natal group is associated with reproductive activation in daughters (French *et al.,* 1984; Heistermann, Kleis, Prove, and Wolters, 1989) and providing separated daughters (cotton-top tamarins and saddle-back tamarins) or subordinate females from social peer groups (common marmosets) with chemical cues from the adult female disrupts or delays the onset of ovulatory function (Epple and Katz, 1984; Savage *et al.,* 1988; Barrett, Abbott, and George, 1990; 1993; Smith, 1994). There is also evidence, however, that an absence of stimulatory cues from novel or unfamiliar males in the natal family environment might also contribute to the lack of competent reproductive function in subordinate female callitrichids. As in other species (e.g., mice: Vandenbergh, 1989; voles: Carter and Roberts, 1996; Solomon, Vandenberg, Wekesa, and Barghusen, 1996), the presence of unfamiliar males may stimulate female reproductive physiology in marmosets and tamarins, often overriding the influence of inhibitory cues (Carroll, 1986; Widowski, Ziegler, Elowson, and Snowdon, 1990; Price and McGrew, 1991; Rothe and Koenig, 1991; Wi-

dowski, Porter, Ziegler, and Snowdon 1992; Dietz and Baker, 1993; Saltzman *et al.,* 1997).

Within the marmoset genus *Callithrix,* there are approximately 10 recognized species (Stevenson and Rylands, 1988). However, our knowledge of the socioendocrinology of reproductive function in subordinate females is limited to a single species—the common marmoset. The present study addresses two issues in the regulation of singular breeding in Wied's black tufted-ear marmoset, *C. kuhli.* First, the ontogeny of reproductive function was assessed in daughters aged 2–24 months living under normal conditions in their natal group to determine if social factors affect reproductive development. Second, we experimentally evaluated the relative roles of inhibitory cues from natal family groups versus stimulatory cues from unfamiliar males in regulating reproduction function. Subadult females were removed from the family and housed alone, and following a period of at least 1 month, these same females were paired with an unfamiliar male. If factors in the family environment inhibited or regulated ovarian function in daughters, we predicted that the pattern of hormone excretion in daughters would change upon removal from the family. If cues from males had stimulatory effects on female ovarian function, we predicted significant changes in excretory profiles of reproductive hormones when females were paired with a male, relative to prepairing values.

METHODS

Subjects

The study involved 10 female black tufted-ear marmosets (*C. kuhli*) aged 2–24 months raised in their natal groups at the University of Nebraska at Omaha Callitrichid Research Center (*n* = 4 family groups). Family groups ranged in size from four to eight individuals and always contained the breeding pair and their offspring. The study also included six adult breeding females (mean age ± SEM, 3.5 ± 1.0 years) residing in a heterosexual pair (*n* = 4), in a two male:one female trio (*n* = 1), or with a male partner and three offspring (*n* = 1). All groups had been established for at least 6 months. Animals in all conditions were housed in large cages measuring 1.6 × 0.9 × 2.4 m, equipped with natural branches, a platform, and a nest tube. No more than two family groups or four pairs were housed in a single colony room. Marmoset groups within a colony room had olfactory and auditory contact but no visual con-

TABLE 1

Subject Identification and Parameters Relating to Onset of Ovarian Function and Experimental Manipulations

Female	Age at removal from family group (months)	Ovarian activity in family group	Factors associated with onset of ovarian activity	Age at onset of ovarian activity (months)
Ash	N/A	N	—	—
Que	N/A	N	—	—
Yaz	16.1	Y	Spontaneous	14.6
Thi	18.7	Y	Spontaneous	17.5
Sti	18.9	Y	Spontaneous	14.1
Una	22.9	Y	Spontaneous	21.5
Pix	24.8	Y	Spontaneous	9.8
Bon	N/A	Y	Mother died	13.5
Bas	N/A	Y	Mother removed	14.5
Wir	18.1	Y	Spontaneous	16.2

Note. N = No; Y = Yes.

tact. Further husbandry details are provided by Schaffner, Shepard, Santos, and French (1995).

Experimental Design

Reproductive Ontogeny. To investigate the development of reproductive function in female marmosets we monitored concentrations of urinary pregnane-diol 3α glucuronide (PdG; a progesterone metabolite) and luteinizing hormone (LH) in 10 female marmosets aged 2–24 months that were residing undisturbed in their family group. The longitudinal experimental design, ensured that data were available from females residing both in the presence and in the absence of older siblings. In this species, urinary LH provides an accurate marker of the periovulatory phase, and PdG concentrations rise immediately following the LH peak, reflecting luteal activity (French, Brewer, Schaffner, Schalley, Hightower-Merrit, Smith, and Bell, 1996). Samples were not available for all females in all age categories. To provide baseline data on the dynamics of ''normal'' nonconceptive ovarian cycles in adult female *C. kuhli,* we monitored levels of urinary PdG and LH across 12 ovarian cycles in six breeding females.

Experimental evaluation of the relative roles of inhibitory versus stimulatory cues in regulating reproduction function. To assess social factors that might regulate the reproductive condition of female marmosets, we monitored the reproductive status of five females under three social conditions. First, to assess the effect of potential inhibitory factors in the family environment on female ovarian function, levels of urinary PdG and LH were assessed in five females that were residing in the natal family group from the age of 2 months, until the ages of 16.1 to 24.8 months as indicated in Table 1. The five females were removed from their natal family group and housed alone in a cage for 4 to 5 weeks, during which time samples were also collected. To investigate whether the physical presence of an unrelated male affected female ovarian activity (either the onset of ovarian activity or the temporal and endocrine dynamics of existing ovarian cycles), we paired the same five females with an unfamiliar adult male immediately after the alone condition and monitored reproductive function via excreted hormones.

Sample Collection and Endocrine Measurements

Urine collection. Concentrations of urinary PdG and LH were measured in the first urine sample of the day, collected between 0600 and 0800 hr from all females 4 to 7 days a week. Urine samples were collected in a noninvasive manner from animals residing undisturbed in their social group. All females were trained to urinate for a desired food item and would usually urinate within 20 min of arising in the morning. Urine was collected in small hand-held aluminum pans held in the urine stream or on large stainless steel pans temporarily lining the floor of the cage. Urine samples (typically 0.2–1.0 ml) were transferred to plastic vials and centrifuged at 700 rpm for 2 min, and the supernatant was divided into two aliquots and transferred to clean vials. Dilute glycerol (1:7, glycerol: distilled water) was added to the aliquot destined for gonadotrophin analysis (10 μl glycerol per 100 μl urine) to prevent cryodegradation, and all samples were stored at −20°C until assayed.

Endocrine procedures. Concentrations of urinary PdG were determined using an enzyme immunoassay (EIA) previously characterized by Munro, Stabenfeldt, Cragun, Addiego, Overstreet, and Lasley (1991) and

adapted for *C. kuhli* as reported by French *et al.* (1996). Assay sensitivity at 90% binding was 78 pg. Intra-assay coefficients of variation for low- and high-concentration pools were 6.1 and 7.3% ($n = 22$), respectively. Inter-assay coefficients of variation for low- and high-concentration pools were 18.2 and 14.1% ($n = 22$), respectively. Concentration of urinary gonadotropin was measured with a LH/CG radioimmunoassay using an antibody characterized by Matteri, Roser, Baldwin, Lipovetsky, and Papkoff, (1987) and validated for *C. kuhli* in French *et al.* (1996). Intra-assay coefficients of variation for low and high pools were 15.3 and 9.9% ($n = 6$). Inter-assay coefficients of variation were 19.9 and 15.7% ($n = 11$) for low and high pools, respectively. To control for variable fluid intake and output, hormone concentrations were corrected for the creatinine concentration of each sample. Creatinine concentration was measured by a modified Jaffé end-point assay (Tietz, 1976) and has been described previously by French *et al.* (1996).

Statistical Analysis

Developmental data were analyzed using a one-factor ANOVA that contrasted mean concentrations of urinary PdG and LH for the 10 females, for six 3-month blocks. Data in this latter analysis were included only from females that were residing undisturbed in their natal family group. The onset of ovarian activity was defined as the time at which levels of urinary PdG exceeded 10 μg/mg Cr for at least 2 days. The luteal phase of an ovarian cycle was defined as the number of days that levels of urinary PdG were greater than 10 μg/mg Cr, and ovarian cycle length was calculated as the period from the start of one luteal phase to the start of the next luteal phase. The influence of social condition on cycle length, luteal phase length, and peak levels of PdG excretion was assessed by correlated samples *t* tests (family group vs alone) and independent samples *t* tests (family group vs breeding female, alone vs breeding females). Significance levels were set at 0.05 for all statistical tests.

RESULTS

Reproductive Ontogeny

There were significant changes across age in levels of excreted hormones among daughters residing in natal family groups. In daughters less than 12 months of age, concentrations of urinary PdG and LH were low (mean PdG < 2 μg/mg Cr and mean LH < 6 ng/mg Cr). The

hormone profiles of all daughters less than 12 months of age (except for one daughter; see Table 1) were not organized into regular ovarian cycles (Figs. 1a and 1b). In addition, for females for whom sufficient (i.e., near daily) samples were collected, no LH spikes were observed, confirming the anovulatory status of these females. There was a dramatic increase in concentrations of urinary PdG in daughters older than 12 months. Analysis of PdG concentrations across 3-month blocks for females residing undisturbed in their natal group revealed a significant effect of age [$F(7, 36) = 2.56$, $P < 0.05$; see Fig. 2a]. Concentrations of PdG in females older than 12 months of age were higher than those of females less than 12 months of age. Mean concentrations of urinary LH did not change significantly throughout development and remained low in all females aged 2–24 months [$F(7, 24) = 0.67$, NS; Fig. 2b].

Of the 10 daughters we monitored, 8 commenced ovarian function while still residing in their natal family group. These females were the oldest daughters in the family group at the time. The onset of ovarian activity in 2 daughters was associated with a documented change in the social environment. The onset of ovulatory function in these 13.5- and 14.5-month-old daughters was associated with the absence of the mother. For one daughter, the mother died, while in the case of the second daughter, the mother was temporarily removed for 48 hr as part of a separate experiment. In both daughters, the removal of the mother was associated with immediate increases in levels of urinary PdG above 10 μg/mg Cr within 10 and 2 days, respectively (Fig. 1c).

The remaining six daughters commenced cyclic ovarian function while housed in their natal groups, in the absence of any pronounced change in group composition or housing conditions (i.e., spontaneous onset of ovarian activity; see Fig. 1d). Figure 1e depicts levels of urinary LH and PdG for an ovulatory cycle for one daughter, illustrating raised levels of urinary PdG (> 10 μg/mg Cr) and a LH spike, confirming that ovarian function was organized into ovulatory events. Spontaneous onset of ovulation occurred in these females at a mean age ($\pm$ SEM) of 15.6 $\pm$ 1.6 months (range 9.8 to 21.5 months).

Experimental Evaluation of the Relative Roles of Inhibitory Versus Stimulatory Cues in Regulating Reproduction Function

Results from the ontogenetic phase of this study revealed that the onset of ovarian activity was common among daughters in family groups. Our experimental
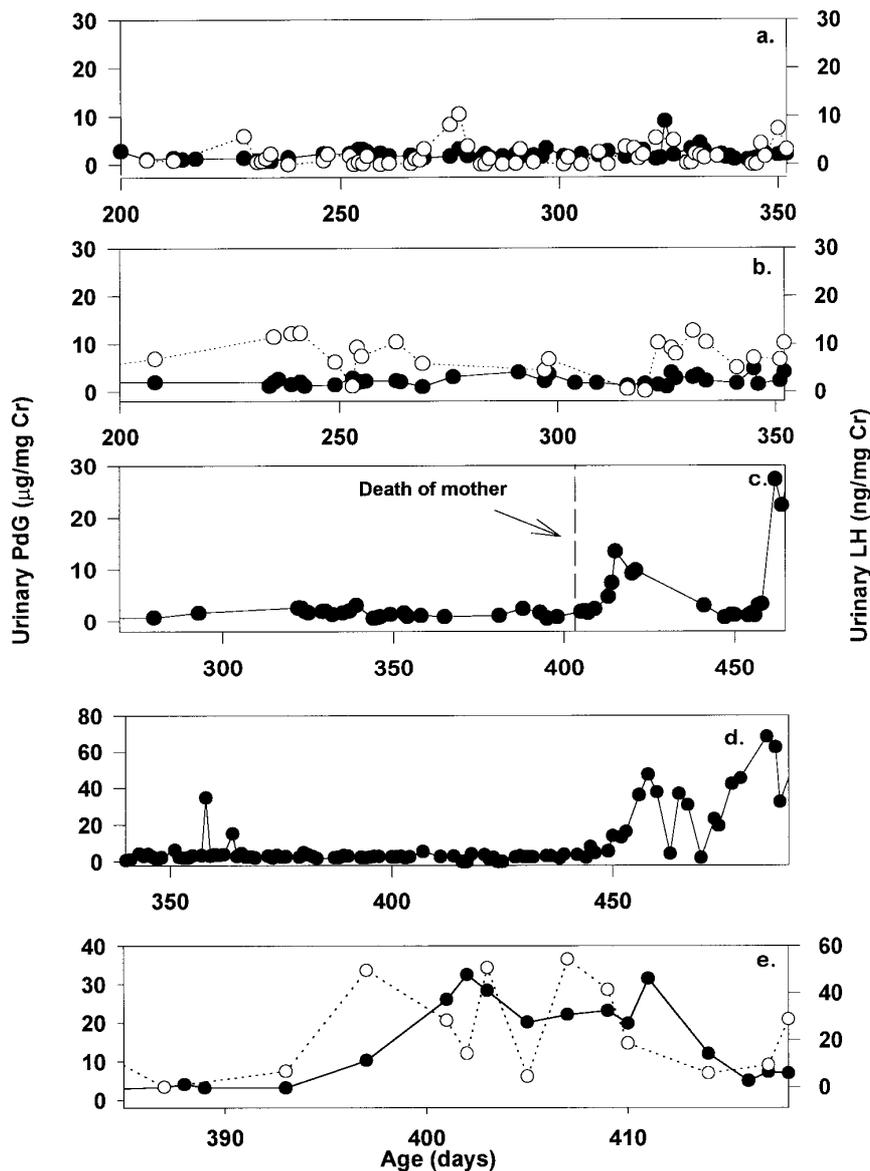
FIG. 1. Patterns of urinary excretion of pregnane-diol 3α glucuronide (PdG) and gonadotropin (LH) in: (a, b) two daughters living in their natal family group. Concentrations of both reproductive hormones are low and there is no evidence of ovulatory cycles. (c) One female for which onset of ovulatory cycles was associated with a change in the social envionment, i.e., death of the breeding female. (d) A daughter that commenced spontaneous ovulatory function while residing in the family group. Elevated levels of urinary PdG correspond to the luteal phase of an ovarian cycle. (e) A female who exhibited spontaneous ovarian function while in the natal family group. The periovulatory LH spike occurred at 397 days of age.

analysis of social effects on reproductive function thus focuses on potential social influences on quantitative and qualitative aspects of the ovarian cycles displayed by females. Social condition affected both the quantitative levels of excreted hormones and the qualitative features of the ovarian cycles. Figure 3 depicts representative endocrine profiles for a female exhibiting ovula-

tory cycles in her natal family group (Fig. 3a) and while housed on her own (Fig. 3b) and a nonconceptive ovulatory cycle from an established breeding female (Fig. 3c). Daughters housed in their family group exhibited significantly shorter luteal phases than when they were housed alone [Fig. 4a; $t(4) = 3.53$, $P < 0.02$]. In addition, peak concentrations of PdG excretion by females dif-
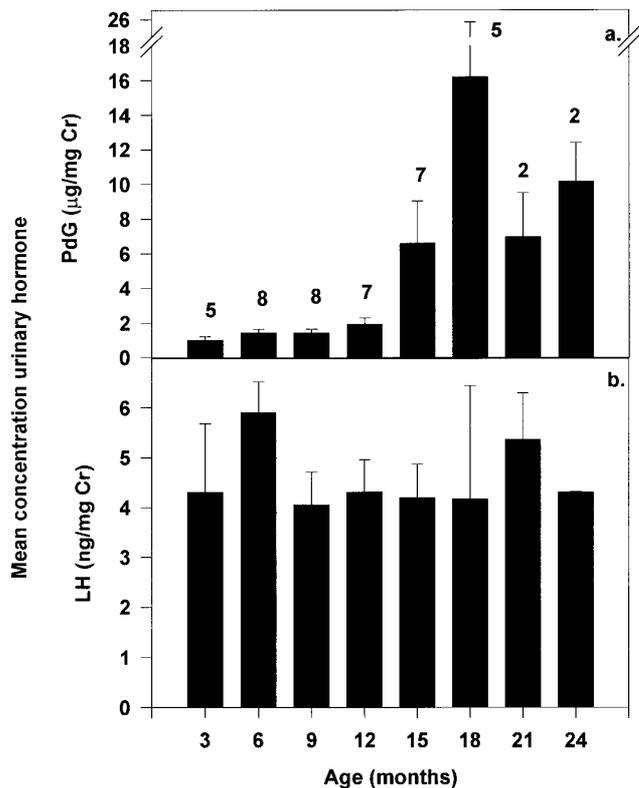
FIG. 2. Mean ± SEM concentrations of urinary PdG (a) and LH (b) across the first 24 months of life in female marmosets. Data are collapsed into 3-month blocks.

fered among social conditions, with significantly lower concentrations associated with cycles while females resided in their natal family group [Fig. 4b; $t(4) = 3.23$, $P < 0.03$]. Neither of the differences associated with the change in social condition appeared to be related to age differences among females, since correlations between age and luteal phase length ($r_s = 0.38$, n.s.) and between age and peak PdG concentrations ($r_s = 0.08$; n.s.) revealed no significant association among the two reproductive parameters and age.

Since all five females conceived on the first ovulation after pairing, no data on cycle dynamics are available for the heterosexual pair condition. In order to compare ovarian function in daughters in the two social conditions with normative, fully mature ovarian cycles, we contrasted the cycles of daughters with those from six adult females housed with a long-term male partner. The ovarian cycle exhibited by adult breeding females was (mean ± SEM), 25.5 ± 3.44 days long, with a luteal phase equal to 18.18 ± 1.3 days. Peak PdG values during the luteal phase were 80.27 ± 9.97 μg/mg Cr. Relative to these breeding females, daughters in family

groups had significantly lower peak PdG concentrations [Fig 4b; $t(9) = 3.54$, $P < 0.01$] and tended to have shorter luteal phases [$t(9) = 2.06$, $P = 0.07$]. Luteal length of ovarian cycles in daughters housed alone did not differ from those in breeding adult females [$t(9) = 0.89$, n.s.], although the differences in peak PdG concentrations between these two classes of females approached significance [$t(9) = 1.96$, $P = 0.08$]. The total length of the ovarian cycle did not vary among females in the three social conditions; daughters in family group vs daughters housed alone [$t(4) = 0.75$, n.s.], daughters in family group vs breeding females [$t(9) = 0.54$, n.s.], and daughters housed alone vs breeding females [$t(9) = 0.56$, n.s.].

DISCUSSION

In both captive groups (Schaffner *et al.,* 1995; French *et al.,* 1996) and wild populations (Rylands, 1989), the
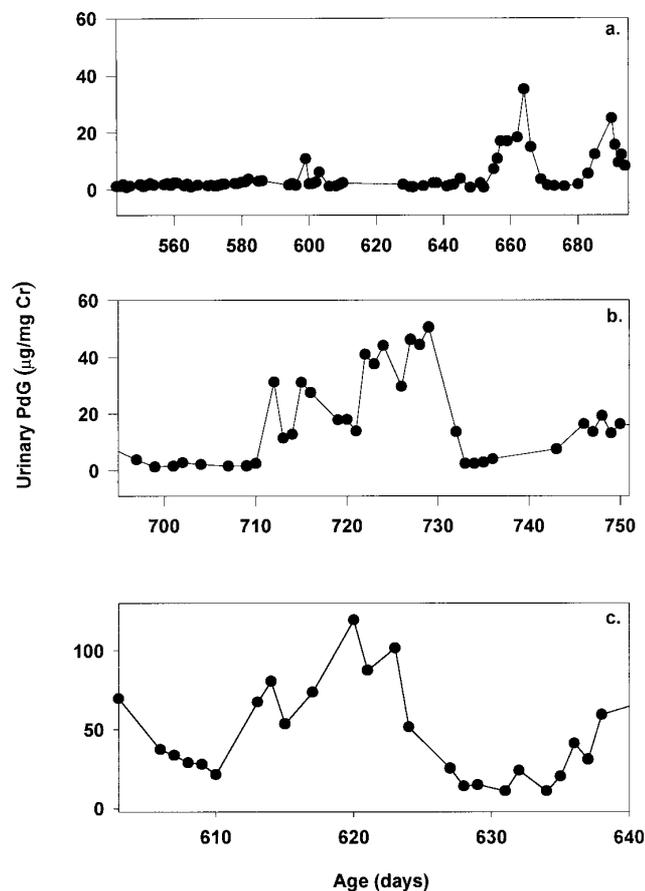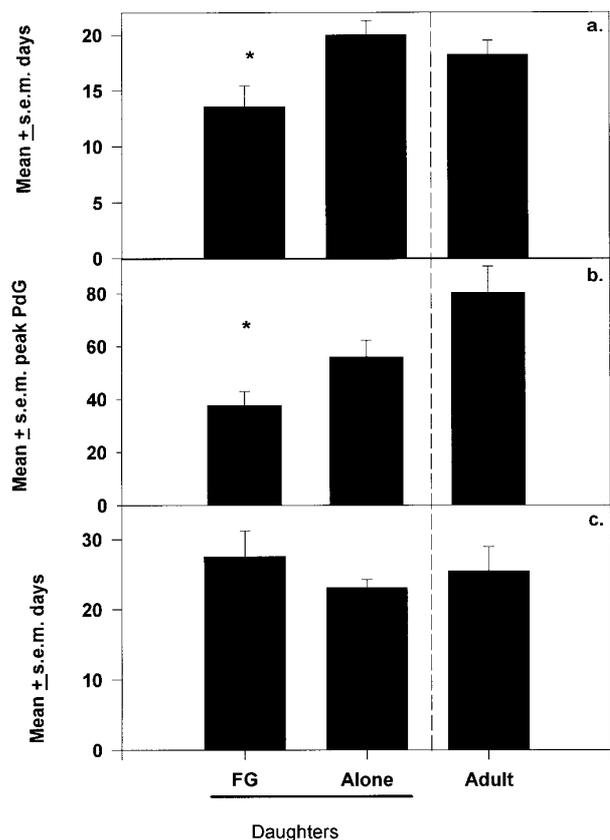

FIG. 3. Pattern of urinary PdG excretion in three females residing under different social conditions: (a) with the natal family group; (b) alone, and (c) as established breeding females.

FIG. 4. Mean ± SEM parameters of the ovarian cycle in ovulatory daughters residing in the family group (FG); the same daughters housed alone (Alone); and established adult breeding females (Adult). (a) duration of the luteal phase in days, (b) peak PdG values during the luteal phase (c) cycle length in days.

breeding system of *C. kuhli* appears to be similar to that of other callitrichids: production of offspring is limited to a single female. However, the results of the present study indicate that the mechanisms that produce singular breeding (and hence high reproductive skew) may not be purely endocrinological in nature. We found no simple relationship between social status within the group and ovarian competency. Of the 10 postpubertal daughters residing with their families, 8 exhibited ovarian function while still living in their natal group. In 6 of the 8 daughters, onset of ovarian function was spontaneous and not associated with any obvious environmental perturbations or social disruptions within the family group. Onset of ovarian activity in 2 daughters was, however, associated with a change in the social environment; namely, removal of the mother from the family group. The remaining two daughters showed no signs of ovarian function while housed in the family group. These females were, however, re-

moved from the family group at a relatively early age (around 14 months) and might have commenced ovarian function had they remained with their family for a longer period.

The result that 80% of subadult female tufted-ear marmosets ovulated while still living with their family contrasts with some earlier studies examining reproductive function in captive populations of other callitrichid species. These studies indicated that under normal conditions, postpubertal daughters in captive families of cotton-top tamarins, saddleback tamarins, and red-bellied tamarins are typically anovulatory (Epple and Katz, 1984; French *et al.,* 1984; Savage *et al.,* 1988; Kuderling *et al.,* 1995 also see Evans and Hodges; 1984). Our results are not surprising, however, in the light of studies with common marmosets that report a 50% incidence of daughters ovulating in the family group (Saltzman *et al.,* 1997; also see Abbott, 1984). In addition, subordinate female golden lion tamarins (*Leontopithecus rosalia*) and golden-headed lion tamarins (*L. chrysomelas*) exhibit regular ovulatory cycles, comparable to those of adult breeding females, despite still living with their family (French, Inglett, and Dethlefs, 1989; van Elsacker, Heistermann, Hodges, de Laet, and Verheyen, 1994). Female red-bellied tamarins also exhibit periodic rises in levels of urinary estradiol that, although being lower than concentrations in breeding females, might reflect ovulatory function (Kuderling *et al.,* 1995). Finally, signs of ovulatory activity in family-living female cotton-top tamarins were reported by Tardif (1984), particularly in cases in which there was a recent social disruption within the group.

Perhaps most relevant to our results are observations from the wild that document the presence of multiple reproductively active females in groups of common marmosets, golden lion tamarins, saddleback tamarins, moustached tamarins (*S. mystax*), and cotton-top tamarins (Terborgh and Goldizen, 1985; Savage, 1990; Dietz and Baker, 1993; Garber, Encarnacion, Moya, and Pruetz, 1993; Digby and Ferrari, 1994; for a review see French, 1996). In many cases where detailed field records were maintained (e.g., Digby and Ferrari, 1994), the two reproductively active females were mother and daughter, as was the case in the present study. Thus, while social effects on female reproduction are evidenced throughout callitrichid primates, there are considerable intra- and interspecific differences in the manifestation of these effects.

In the present study, even though older daughters were clearly ovulating while in the family group, they did not get pregnant. Interestingly, the only daughter in our colony that engaged in sexual behavior while in

her family group did so with a half-brother who had not been housed regularly in the family group. The failure of ovulating daughters living exclusively with family members to engage in sexual behavior and produce offspring is similarly observed in common marmosets, cotton-top tamarins, golden lion tamarins, and titi monkeys, *Callicebus moloch* (Abbott, 1984; French *et al.,* 1989; Heistermann *et al.,* 1989; Valeggia, Mendoza, and Mason, 1995; Saltzman *et al.,* 1997). Inbreeding in callitrichids has deleterious consequences on reproductive success and an incest taboo may be one behavioral mechanism that prevents consanguinous conception between dominant breeders and their offspring in family groups of callitrichids (Ralls and Ballou, 1982).

Although older daughters living with the family displayed signs of reproductive cyclicity, endocrine function did not appear to be totally free from the influence of social factors. Ovarian cycles in daughters living with their family were different from their cycles when the daughters were housed alone and were different from cycles associated with breeding adult females. The hormone profiles of family-living daughters were characterized by short luteal phases and lower peak concentrations of progesterone metabolite excretion. These profiles have been described as oligocycles (Saltzman, Schultz-Darken, Scheffler, Wegner, and Abbott, 1994), and they may be analogous to the menstrual cycles of human females diagnosed with luteal phase deficiency (LPD; Soules, McLachlan, Ek, Dahl, Cohen, and Bremner, 1989; Ayabe, Tsutsumi, Momeoda, Yano, Mitsuhashi, and Taketani, 1994). It was not until daughters were removed from their family group that they exhibited ovulatory cycles typical of adult breeding female *C. kuhli.*

We noted in this experiment that all daughters who exhibited ovulatory cycles in their natal family group were also the eldest daughters in the group. This result could be attributable to a simple developmental phenomenon; i.e., younger daughters simply did not reach the age at which ovulatory function normally commences in this species. Alternatively, younger daughters could be more susceptible to inhibitory influences from the breeding female or their older sisters. The design of our observations does not allow us to differentiate among these interpretations, however, and the resolution of this issue remains an interesting research goal for future study.

Several studies suggest that unfamiliar males play an important role in stimulating reproductive activity in female callitrichids (e.g., see Carroll, 1986; Widowski *et al.,* 1990; Price and McGrew, 1991; Rothe and Koenig, 1991; Saltzman *et al.,* 1997). In these studies, extensive contact between daughters and the unfamiliar male(s), including visual, olfactory, and tactile stimulation, was associated with the onset of ovulatory activity. While exposure to unrelated males may be an important modulator of reproductive function in subordinate female callitrichids, particularly younger females, our results indicate that male stimulation is not *necessary* to trigger female ovarian function in *C. kuhli:* eight daughters in our study commenced ovarian function spontaneously in the family group, without prolonged visual access to, or physical contact with, unrelated males.

In conclusion, our data have shown that female *C. kuhli,* residing in their natal family group, are not subject to strong endocrine regulation of ovarian function. Ovulatory function commences spontaneously, in a high proportion of females residing in their natal group. Even though daughters and subordinates among callitrichids rarely conceive offspring, reproductive activation as a subordinate might provide some future reproductive benefits when the subordinates eventually adopt a breeding position. Upon obtaining a dominant status within a group, female dwarf mongooses that engaged in breeding as subordinates had a shorter latency to produce their first litter and had larger litter sizes than females that had not engaged in breeding as subordinates (Creel, Monfort, Creel, Wildt, and Waser, 1995). Thus, in dwarf mongooses, reproductive activation as a subordinate is associated with poor immediate breeding outcomes, but enhanced future reproductive performance. These effects may be mediated by endocrine factors, particularly via higher estrogen concentrations in multiparous dominants versus primiparous dominants. The question of whether the first reproductive attempts of spontaneously ovulating daughters are more successful than those of daughters who were suppressed throughout their tenure in their natal family group has not been addressed in callitrichid primates. However, this represents yet another route whereby subordinates may ultimately benefit from a decision to remain in the natal group, suffer reduced reproductive success, and help rear nondescendant kin.

ACKNOWLEDGMENTS

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