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Prolactin and Paternal Care: Comparison of Three Species of Monogamous New World Monkeys (*Callicebus cupreus*, *Callithrix jacchus*, and *Callimico goeldii*)

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The authors explored whether prolactin is associated with paternal care in 3 monkey species: titi monkey (*Callicebus cupreus*), common marmoset (*Callithrix jacchus*), and Goeldi's monkey (*Callimico goeldii*). They compared prolactin levels in fathers before and after infant birth as well as between fathers and nonfathers. *C. cupreus* fathers carry infants almost exclusively, have higher prolactin levels than nonfathers, but show no prolactin increase after infant birth. *C. goeldii* fathers carry infants only after 3 weeks, show an increase in prolactin levels during the precarrying period, but do not have higher levels than nonfathers. *C. jacchus* fathers are the primary carriers, have higher prolactin levels than nonfathers, and show a trend for a prolactin increase after the birth of infants. In conclusion, species differences in the patterns of prolactin secretion were evident and reflect the different paternal roles.

Direct paternal care in which fathers actively engage in behaviors such as infant carrying and feeding is relatively uncommon yet can be found in a variety of animal taxa (Beck, 1998; Gross & Sargent, 1985; Ketterson & Nolan, 1994; Zeh & Smith, 1985), including mammals (Kleiman & Malcolm, 1981). As is the case with maternal behavior (Buntin, 1996; Pryce, 1992), paternal behavior is likely controlled by multiple mechanisms (Brown, 1993; Buntin, 1996; Schradin & Anzenberger, 1999; Ziegler, 2000). In females, prolactin is one of the important physiological agents regulating the onset of maternal behavior. Administration of prolactin to steroid-primed ovariectomized rats initiates maternal care (Bridges, Dibiase, & Loundes, 1985; Bridges & Mann, 1994), and mice deficient for prolactin receptors show deficits in maternal behavior (Lucas, Ormandy, Binart, Bridges, & Kelly, 1998). Not surprisingly, prolactin also appears to play a significant role in vertebrate paternal care (Schradin & Anzenberger, 1999; Ziegler, 2000).

In mammals, direct male parental care occurs only in about 10% of the more than 5,000 species, predominantly in rodents, carnivores, and primates (Kleiman & Malcolm, 1981). So far, studies on prolactin and paternal care have been carried out in only very few species. In dwarf hamsters, increased prolactin levels were found in fathers of the paternal Djungarian dwarf hamster (*Phodopus campbelli*) but not in fathers of a closely related nonpaternal species (*Phodopus sungorus*; Reburn & Wynne-Edwards, 1999). Increased prolactin levels have also been found in fathers of Mongolian gerbils (*Meriones unguiculatus*; Brown, Murdoch, Murphy, & Moger, 1995), California mice (*Peromyscus californicus*; Gubernick & Nelson, 1989), and wolves (*Canis lupus*; Asa & Valdespino, 1998). For human fathers, a possible prenatal increase of prolactin levels has also been reported (Storey, Walsh, Quinton, & Wynne-Edwards, 2000).

In two species of callitrichids (New World monkeys), the common marmoset (*Callithrix jacchus*) and the cotton-top tamarin (*Saguinus oedipus*), fathers were found to have higher prolactin levels than nonfathers (Dixson & George, 1982; Ziegler, Wegner, & Snowdon, 1996; for a possible negative effect of the hormone testosterone on infant carrying in the closely related black tufted-ear marmoset, *Callithrix kuhlii*, see Nunes, Fite, & French, 2000).

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In *S. oedipus*, prolactin levels of fathers increase before birth of infants (Ziegler & Snowdon, 2000), and prolactin levels seem to be influenced by paternal experience (Ziegler & Snowdon, 2000; Ziegler et al., 1996). Callitrichids live in family groups with one monogamous parent pair and siblings of different age classes (for departure from monogamy in callitrichids, see Ferrari & Ferrari, 1989; Rothe & Koenig, 1991). In callitrichids, mothers, fathers, and older offspring (helpers) take part in carrying the infants (Garber, 1997; Goldizen, 1987) and share food with them (Feistner & Price, 1991). Goeldi's monkeys (*Callimico goeldii*; for placement within Callitrichidae, see Dornum & Ruvolo, 1999; Horovitz, Zardoya, & Meyer, 1998; Hugot, 1998; Pastorini, Forstner, Martin, & Melnick, 1998), like other callitrichids, live in family groups, and the infants are reared cooperatively (Heltne, Wojcik, & Pook, 1981; Schradin & Anzenberger, 2001b). However, there are two marked differences between *C. goeldii* and other callitrichids: (a) Whereas all other callitrichids typically show twinning, *C. goeldii* has only a single infant (Martin, 1992), and (b) whereas marmoset and tamarin fathers begin carrying their infants shortly after birth (Welker & Schäfer-Witt, 1987), *C. goeldii* fathers start carrying their single offspring approximately 3 weeks after birth (Heltne, Turner, & Wolhandler, 1973; Jurke & Pryce, 1994; Schradin & Anzenberger, 2001b). Thus, *C. goeldii* provides an interesting system for the study of paternal care, especially in comparison with other callitrichids.

Paternal care is also found in two other New World primate taxa: owl monkeys (genus *Aotus*, family Cebidae; Dixson, 1994; Jantschke, Welker, & Klaiber-Schuh, 1998; Welker & Schäfer-Witt, 1987) and titi monkeys (genus *Callicebus*, family Atelidae; Fragaszy, Schwarz, & Shimosaka, 1982; Mason, 1966; Mendoza & Mason, 1986; Welker & Schäfer-Witt, 1987; for discussion of *Callicebus* systematics, see Dornum & Ruvolo, 1999; Horovitz et al., 1998), both of which live in family groups in which fathers carry infants. Titi monkeys are found in small family groups consisting of the adult breeding pair and one to three offspring, which can remain in the family group into adulthood (Mason 1966, 1968; Welker, Jantschke, & Klaiber-Schuh, 1998a). Like *C. goeldii*, titi monkeys have single offspring (Mason 1968; Welker, Jantschke, & Klaiber-Schuh, 1998b). However, titi monkeys are unusual in that the father is the primary caregiver, carrying infants within a few hours of birth and between 70% and 90% of the time. In contrast to callitrichids, siblings participate very little in infant carrying (Fragaszy et al., 1982; Mason, 1968; Mendoza & Mason, 1986; Welker & Schäfer-Witt, 1987), and mothers contribute little beyond nursing (Mendoza & Mason, 1986). Such high levels of paternal care in titi monkeys make them an interesting system for the study of endocrine correlates of paternal care in comparison to callitrichids.

Figure 1. Fathers of the three species studied carrying their infants: (a) *Callicebus cupreus* father and 2-week-old infant, (b) *Callimico goeldii* father and 5-week-old infant, and (c) *Callithrix jacchus* father and 5-week-old twins. Photographs are not shown to scale; body weights for captive *Callicebus, Callimico,* and *Callithrix* are about 1,000 g, 550 g, and 350 g, respectively. Photographs by Gustl Anzenberger.

To examine whether a relationship between prolactin and paternal care is a general New World monkey pattern, we measured urinary prolactin in coppery titi monkey (*Callicebus cupreus*), common marmoset (*C. jacchus*), and Goeldi's monkey (*C. goeldii*) fathers (see Figure 1). Although the cues that trigger changes in prolactin in males have not been identified, in the present research, we considered three possibilities: (a) Males may respond to cues presented by infants or pregnant or lactating females (Ziegler, Wegner, Carlson, Lazaro-Perea, & Snowdon, 2000; Ziegler et al., 1996); (b) males may respond to cues specifically related to the birth of infants (Dixson & George, 1982; Ziegler et al., 1996); and finally, (c) males may respond to the tactile cues provided during contact with infants (Dixson & George, 1982). These alternative possibilities need not be mutually exclusive, and there are other logical possibilities not considered here (e.g., changes in a male's hormonal state due to pair formation or distinctly male patterns of development).

On the basis of the results for *C. jacchus* (Dixson & George, 1982) and for cotton-top tamarins (*S. oedipus*; Ziegler et al., 1996), in which increased prolactin levels were found in fathers, we expected to find an increase of prolactin levels in fathers of all three species after the birth of their infants (Prediction 1). For *S. oedipus*, it has been reported that fathers have higher prolactin levels overall than nonfathers, independent of the presence of young (Ziegler et al., 1996). This suggests that there is a one-time change in prolactin, perhaps surrounding the birth of the first infant. If this finding generalizes to the other paternal New World primates, we would expect higher prolactin levels in fathers of all three species compared with nonfathers in a period without preambulatory infants (Prediction 2). Dixson and George (1982) found higher plasma prolactin levels were obtained in *C. jacchus* fathers that were carrying infants immediately before blood sampling as compared with fathers that were not carrying before blood sampling. They interpreted this result as an indication that prolactin increases in *C. jacchus* fathers because of tactile stimulation of the fathers. If this tactile stimulation hypothesis is correct, we would expect a positive correlation between paternal carrying and prolactin levels, and we would further expect prolactin changes to be most pronounced in *C. cupreus* and least pronounced in *C. goeldii* (Prediction 3).

Method

Subjects

Nine *Callicebus cupreus* fathers and 7 fathers of both *Callithrix jacchus* and *Callimico goeldii* were used to test whether prolactin levels increase after infant birth. All groups consisted of the breeding pair, the newborn infants, and previous offspring of different ages: 0–2 adult offspring in *C. cupreus* (*Mdn* = 1), 0–4 adult offspring in *C. jacchus* (*Mdn* = 2), and 0–1 adult offspring in *C. goeldii* (*Mdn* = 0); no subadult offspring in *C. cupreus*, 0–2 subadult offspring in *C. jacchus* (*Mdn* = 0), and 0–1 subadult offspring in *C. goeldii* (*Mdn* = 1). In addition, 8 of the 9 titi families had 1 adolescent offspring, 2 of the 7 marmoset families had 2 adolescent offspring, and 4 of the 7 Goeldi families had 1 adolescent offspring. The same males plus one additional *C. goeldii* father were used to examine the difference between fathers and nonfathers. All fathers were experienced; that is, they had already reared offspring prior to this study, except for one *C. goeldii* father who was a first-time father but had rearing experience as a helper. For comparison between fathers and nonfathers, 6 adult sons of *C. cupreus*, 12 adult sons of *C. jacchus*, and 7 adult sons of *C. goeldii* served as subjects (see below).

C. cupreus families were housed at the California Regional Primate Research Center at the University of California, Davis, according to standard laboratory protocol, as described in Hoffman, Mendoza, Hennessy, and Mason (1995). *C. cupreus* was previously considered synonymous with *Callicebus moloch* (Hershkovitz, 1963) but was recognized as a separate species by Hershkovitz (1990), Schneider et al. (1993), Kobayashi (1995), and Groves (1993, 2001). Previous research (e.g., Hoffman et al., 1995; Mendoza & Mason, 1986) using the animals from this colony has identified these titi monkeys as *C. moloch* on the basis of the taxonomy that existed at the time that the colony was established from wild stock. Families of *C. jacchus* and *C. goeldii* were housed at the primate station of the Anthropological Institute at the University of Zurich, Zurich, Switzerland. For a detailed description of housing of *C. goeldii*, see Schradin and Anzenberger (2001b), and for *C. jacchus*, see Schradin and Anzenberger (2001a).

Urine Collection

First morning-urine samples were collected. In *C. cupreus* and *C. jacchus*, this was done from 3 weeks prior to the birth of the infants until 6 weeks after birth. In *C. goeldii*, urine was collected 3 weeks before birth until 3 weeks after the onset of paternal carrying. The onset of paternal carrying occurs approximately 3 weeks after birth (Jurke & Pryce, 1994; Schradin & Anzenberger, 2001b); thus, the period of urine collection in *C. goeldii* paralleled exactly that used in the two other species. In *C. jacchus* and *C. goeldii*, which were kept in Zurich, Switzerland, urine was collected daily except weekends, whereas in *C. cupreus*, which were kept in Davis, California, samples were collected 3 to 5 days per week in 2-day intervals. To collect urine, the collector entered the animal room, turned on the light, and collected urine into a plastic cup as soon as each monkey began to urinate. All subjects were habituated to this procedure prior to the onset of the study. For some *C. jacchus* fathers, a urine collection apparatus, installed in front of the home cage, was used (Anzenberger & Gossweiler, 1993). In *C. jacchus* and *C. goeldii*, urine collection took place between 7 a.m. and 8 a.m. Curtains prevented normal daylight from waking up the animals before the collector entered the animal room. In *C. cupreus*, no curtains were available and the onset of urine collection thus depended on sunrise, taking place between 5:30 a.m. and 6:00 a.m. Sodium azide (0.03 mg/ml urine) was added as a preservative to all urine samples, and for *C. cupreus*, glycerol (33 μl/ml urine) was also added. Glycerol is known to prevent loss of immunoreactivity in some protein hormones (Livesey, Roud, Metcalf, & Donald, 1983). Glycerol was not added to *C. goeldii* and *C. jacchus* samples because urine collection in these two species started later than in *C. cupreus* and our tests showed that glycerol does not alter the immunoreactivity of prolactin. Samples for *C. jacchus* and *C. goeldii* were stored until analysis at −20°C; those from *C. cupreus* were stored at −70°C.

Potential differences in prolactin levels between fathers and adult sons during periods without preambulatory infants were investigated. For *C. cupreus*, urine samples from 3 weeks to 1 week before infant birth were used. For *C. jacchus* and *C. goeldii*, samples were collected at least 14 weeks after the last and 4 weeks before the next birth. Analysis was based on the average of at least five samples from each individual, which were collected and stored as described above. Within family groups, samples from fathers and adult sons were collected at the same time.

We measured prolactin levels from urine samples rather than plasma for the following reasons: (a) Collecting urine is a noninvasive and stress-free method of sampling. As prolactin is known to be stress responsive (Aidara, Tahiri-Zagret, & Robyn, 1981; Ziegler et al., 1996), a stress-free collection method is essential to reliably measure prolactin levels relating to fatherhood. (b) Plasma levels reflect actual prolactin levels. Therefore, short-term effects like stress influencing prolactin secretion might confound prolactin values. In contrast, urine levels provide an average value for prolactin secretion over the whole time of urine production. By using first morning urine, confounding effects like the circadian rhythm of prolactin secretion were kept constant. (c) A detailed study of the correlation of urinary prolactin and paternal behavior was done by Ziegler et al. (1996, 2000) on another neotropical primate species, the tamarin *S. oedipus.* By applying similar methods, we have ensured that the data of our study are directly comparable to the findings by Ziegler et al. (1996, 2000).

Hormonal Assay Procedures

Concentration procedure. Because the concentration of prolactin in urine is very low, urine had to be concentrated before assay (Keely & Fairman, 1994; Ziegler et al., 1996). This was accomplished using centrifugal filter units (10,000 nominal molecular weight limit, Ultrafree-4, Millipore, Bedford, MA); samples were concentrated by centrifugation at 3,010 g at 25°C until a final concentration of approximately 50 μl was achieved. Time of centrifugation depended on the amount of urine used and its initial concentration. Urine concentration, as measured by mean creat-

Table 1

Assay Validation for Urinary Prolactin (PRL) Values in the Three Different Species

Callicebus cupreus			*Callithrix jacchus*			*Callimico goeldii*		
Urine volume (ml)	Pool 1 (PRL)	Pool 2 (PRL)	Urine volume (ml)	Pool 1 (PRL)	Pool 2 (PRL)	Urine volume (ml)	Pool 1 (PRL)	Pool 2 (PRL)
2.5	1.8	1.3	0.25	0.4	—	0.5	0.5	0.6
5.0	2.5	2.5	0.5	0.6	0.7	1.0	1.0	1.2
7.5	5.7	3.3	1.0	1.0	1.5	2.0	2.0	3.0
10.0	7.6	4.3	2.0	2.3	2.9	4.0	5.9	7.6
15.0	12.8	8.3	4.0	6.0	6.0	8.0	14.5	15.4
20.0	17.1	10.2	8.0	11.5	10.6	14.0	—	23.0
			14.0	19.2	—	16.0	26.8	—

Note. Ascending volumes (in milliliters) of urine from a pool (two pools, each derived from urine from several individuals per species) yielded ascending estimates of PRL immunoreactivity, measured as picograms prolactin/tube. Dashes indicate missing data.

inine concentration (see below), varied greatly across the three species: being the most concentrated in *C. goeldii* (1.17 mg/ml urine), less concentrated in *C. jacchus* (0.71 mg/ml urine), and even less concentrated in *C. cupreus* (0.57 mg/ml urine). As a consequence, we used more urine for producing a concentrate when the concentration of the initial urine, and thereby prolactin concentration, was low (as measured by creatinine values). This method enabled us to measure prolactin reliably even in urine samples with very low prolactin concentration. For *C. goeldii* and for *C. jacchus*, daily urine samples were analyzed; for *C. cupreus*, samples were pooled (see below). For *C. goeldii*, we used 1 ml aliquots of urine in duplicate. For *C. jacchus*, we used aliquots of either 1 ml, 2 ml, or 4 ml in duplicate, depending on urinary creatinine concentrations. In *C. cupreus*, urine concentration and prolactin levels were low, with prolactin being undetectable in the 2 ml daily samples that were available. Therefore, to reliably measure prolactin in *C. cupreus* samples, we pooled urine into 3-week periods. Pooled samples contained on average 12.4 ml of urine in duplicate. After concentration, samples were mixed with 50 μl of phosphate-buffered saline (PBS) buffer (0.01 M $NaH_2PO_4 \cdot H_2O$, 0.14 M $Na_2HPO_4 \cdot H_2O$, 0.14 M NaCl, 0.01% thimerosal), which was added directly to the centrifugal filters. To compare prolactin levels in fathers versus adult sons in *C. jacchus* and *C. goeldii*, we pooled urine samples to obtain an average prolactin value for 5 days. For these assays, 4 ml in duplicate were used for each individual. In *C. cupreus*, we used the pooled samples from before infant birth, as described above.

Prolactin assay. Two commercial kits for measuring human prolactin were used: for *C. cupreus* and *C. jacchus*, COAT-A-COUNT Prolactin IRMA (Diagnostic Products Corporation [DPC], Los Angeles, CA) and for *C. goeldii*, PROL-CTK-4 IRMA (Sorin Biomedica, Saluggia, Italy). Two different kits were used because the Sorin Biomedica kit, used first for *C. goeldii*, did not work for the two other species. Most likely, the antibodies against human prolactin in this kit failed to bind to the species specific prolactin of *C. jacchus* and *C. cupreus* (Clarke & Bern, 1980). For *C. goeldii*, seven samples were measured with both kits leading to a highly significant correlation ($r_s = .964$, $N = 7$, $p = .018$), whereby the values measured with the DPC kit were on average 1.7 times higher. The DPC kit was modified by the addition of two standards, created by diluting the lowest standard provided. For both kits, 50 μl PBS buffer were added to each standard to make them comparable to the samples. Prolactin levels were calculated as pg prolactin/tube, which was later standardized for sample volume and concentration. All other steps in the assay were the same as described in the protocols provided by the suppliers.

Validation. Accuracy was determined twice for each species by adding the concentrate from a urine pool to each standard curve. Accuracy for *C. cupreus* was 98.7% ± 5.4% and 93.1% ± 8.4%; for *C. jacchus*, 108.2% ± 8.0% and 97.2% ± 3.9%; and for *C. goeldii*, 112.2% ± 14.5% and 93.3% ± 6.6%. The concentration procedure and prolactin assays were validated by serially diluting two pools of urine for each species (see Table 1). The sensitivities (minimal or least detectable dose [LDD]) of the modified assays were 15.5 pg/tube for the DPC kit and 56.7 pg/tube for the Sorin Biomedica kit. For any samples with values below the LDD, the LDD was used. Mean intra-assay and interassay coefficients of variation were determined (Rodbard, 1974) for one pool and a control serum (con6; DPCs) for *C. cupreus.* Within-assay variations were 6.1% and 4.4%, and between-assay variations were 8.3% and 6.6% ($N = 21$). In *C. jacchus* and *C. goeldii*, intra-assay and interassay coefficients were determined by using two pools of each species. Within-assay variations for *C. jacchus* were 5.0% ($N = 8$) and 7.5% ($N = 7$), and for *C. goeldii*, they were 9.9% ($N = 7$) and 8.3% ($N = 9$), respectively. Between-assay variations for *C. jacchus* were 19.1% ($N = 8$) and 31.6% ($N = 7$), and for *C. goeldii*, they were 24.7% ($N = 7$) and 20.7% ($N = 9$), respectively. Because of the high between-assay variation, the comparison between fathers and adult sons in both *C. jacchus* and *C. goeldii* was done using only one assay for each species. Injection of a serotonin agonist (fenfluramine; dose 0.5, 1.0, or 2.0 ng/ml) known to lead to prolactin secretion (Cowen, 1993) resulted in increased urinary prolactin levels in all six *C. jacchus* urine samples compared with basal levels (mean increase of 93%). This validation has been performed in the course of another study (Pryce, 2003),[1] which is why no such treatment was performed with the two other species.

Creatinine analysis. Creatinine concentration was used to measure urine concentration. To control for fluid variability of the urine, we divided creatinine concentrations (in mg/ml urine) into the prolactin values (Bös, Probst, & Erkert, 1993), resulting in prolactin levels given as picograms prolactin/milligrams creatinine. Urinary creatinine concentrations in *C. cupreus* were estimated using Taussky's method (Taussky, 1954); within-assay variation was 3.6%, and between-assay variation was 5.3%. For *C. jacchus* and *C. goeldii*, creatinine was measured in duplicates using the Creatinine Analyzer Model 2 (Beckman, Fullerton, CA). Intra-assay coefficient was 3.1% for 7 urine samples of *C. jacchus* and 8.3% for 10 urine samples of *C. goeldii.*

Behavioral Measures

For *C. jacchus* and *C. goeldii*, carrying behavior was measured using scan sampling five times per day, 5 days per week from the day of birth until the end of urine collection. Which group member(s) was carrying the

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[1] Special thanks go to C. Pryce for administration of fenfluramine to marmosets of his colony and subsequent collection of urine samples used for validation of the assay.

infant(s) was recorded at 8 a.m., 10 a.m., 12 p.m., 2 p.m., and 4 p.m. This method has been validated for cotton-top tamarins (*Saguinus oedipus*; Ziegler, Widowski, Larson, & Snowdon, 1990). In *C. goeldii*, the onset of paternal carrying was determined by additional observations during normal animal caretaking activities. As soon as the infant was observed the first time on the father's back, the day was recorded as the onset of paternal carrying. For *C. cupreus*, scans were recorded five times per day (7 a.m., 9 a.m., 11 a.m., 1 p.m., and 3 p.m.), 3 days per week from the day of birth until 6 weeks after birth. Paternal carrying was calculated as the percent of total observations; that is, in how many of the performed scans the father was the carrier of infants. Of the eight titi monkey families with adolescent and adult offspring, four had these offspring removed for 1 week following infant birth for colony management reasons. This procedure did not affect subsequent parental behavior.

Statistics

Because of small sample sizes and the nonnormal distribution of the data, nonparametric statistics were used (Siegel & Castellan, 1988), all being two-tailed. For *C. cupreus*, urine samples were pooled for the following three periods: (a) 3 weeks before birth, (b) Weeks 1–3 after birth, and (c) Weeks 4–6 after birth. In *C. jacchus*, prolactin levels were averaged for each male for the same three different periods. In *C. goeldii*, the following three periods were compared: (a) 3 weeks before birth, (b) from birth until the onset of paternal carrying, and (c) 3 weeks after the onset of paternal carrying. The onset of paternal carrying in *C. goeldii* represents a biologically relevant event that was expected to occur approximately 3 weeks following birth (Heltne et al., 1973; Jurke & Pryce, 1994) and is thus directly comparable with Weeks 1–3 used in the other two species. Comparisons within fathers were made using Friedman's two-way analysis of variance by ranks (abbreviated as Friedman test). All correlations were made using Spearman's rank correlation coefficient (r_s). For comparisons between fathers and adult sons (nonfathers) during the period without preambulatory infants, Mann–Whitney *U* tests were used (abbreviated as *U* test).

Results

Prolactin Levels in Fathers Following the Birth of Infants (Prediction 1)

Six *C. cupreus* fathers were observed carrying their infants the 1st day after birth; the other 2 were not seen carrying on this day during the time scans were made. Mean values for *C. cupreus* fathers were 33 pg prolactin/mg creatinine for the 3 weeks before birth, 41 pg prolactin/mg creatinine for Weeks 1–3 after birth, and 26 pg prolactin/mg creatinine for Weeks 4–6 after birth (see Figure 2, top panel). Data for 1 father were not available for the 3 weeks prior to the birth period because of an unacceptably high variation between the duplicates (22 pg vs. 95 pg). There were no differences in prolactin levels across the three time periods, Friedman test, $Fr(2, N = 8) = 3.25$, $p = .197$.

All 7 *C. jacchus* fathers started carrying their infants the 1st day after birth. Mean values for *C. jacchus* fathers were 76 pg prolactin/mg creatinine before birth, 102 pg prolactin/mg creatinine in Weeks 1–3 after birth, and 86 pg prolactin/mg creatinine in Weeks 4–6 after birth (see Figure 2, middle panel). There were no differences in prolactin levels across the three time periods, $Fr(2, N = 7) = 4.00$, $p = .105$.

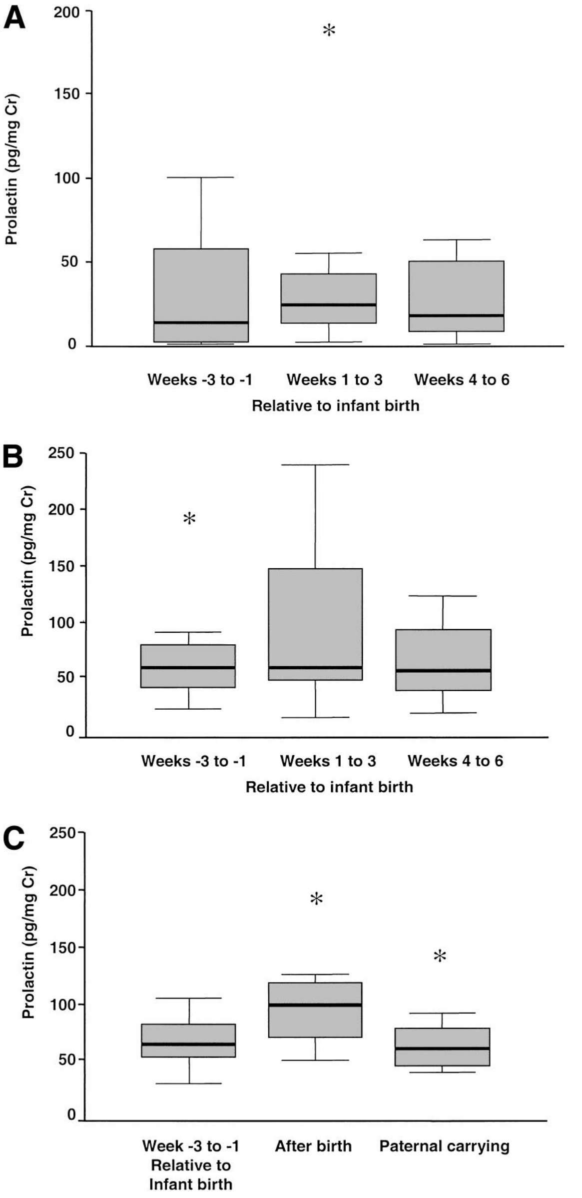

Figure 2. Urinary prolactin levels in fathers of *Callicebus cupreus* ($N = 9$; top panel) and *Callithrix jacchus* ($N = 7$; middle panel) for three periods: 3 weeks prior to birth, Weeks 1–3 after birth, and Weeks 4–6 after birth. Urinary prolactin levels in fathers of *Callimico goeldii* ($N = 7$; bottom panel) for three periods: 3 weeks prior to birth, birth until the onset of paternal carrying, and 3 weeks after the onset of paternal carrying. Medians (black lines) and quartiles as well as variability (bars) and outliers (*) are shown. Cr = creatinine.

In the 7 *C. goeldii* males, the onset of paternal carrying occurred 32 days after birth of the infants (1st quartile, $Mdn = 30$; 3rd quartile, $Mdn = 32$). Mean values of prolactin were 68 pg prolactin/mg creatinine before birth, 104 pg prolactin/mg creatinine following birth but before the onset of infant carrying, and 73 pg prolactin/mg creatinine following the onset of paternal carrying (see Figure 2, bottom panel). There was a significant difference in prolactin levels across the three time periods, $Fr(2, N = 7) = 10.57$, $p = .005$. Post hoc analysis showed that prolactin levels were significantly higher in the period between birth and the onset of paternal carrying than they were either before birth or after the onset of paternal carrying (Dunnett's test for nonparametric multiple comparisons, $p < .01$, for both comparisons; see Figure 2, bottom panel).

Prolactin Levels in Fathers Versus Nonfathers (Prediction 2)

C. cupreus fathers had significantly higher prolactin levels compared with their adult sons in the 3 weeks before birth (*U* test, $U = 8$, $m = 8$, $n = 6$, $p = .037$; see Figure 3). As to be expected given this result, age and prolactin were significantly correlated when the data of fathers and sons were combined ($r_s = .613$, $N = 14$, $p = .027$; see Figure 4, top panel). Multiple regression analysis could potentially assess the relative importance of paternal status and age in determining prolactin levels, but because of the small sample size and the nonnormality and heteroscedasticity of these data, multiple regression analysis in this case would lack both power and robustness (Darlington, 1990). However, if age is a significant determinant of prolactin levels, one would still expect a relationship between age and prolactin within the fathers alone, for which age varied considerably (see Figure 4, top panel). This was not the case, as a significant correlation between age and prolactin did not exist within fathers ($r_s = .196$, $N = 8$, $p = .603$) or even within sons ($r_s = .339$, $N = 6$, $p = .449$).

C. jacchus fathers had significantly higher prolactin levels in the period without preambulatory infants than did their adult sons ($U = 13$, $m = 12$, $n = 7$, $p < .02$; see Figure 3). As with *C. cupreus*, there was a significant correlation between age and prolactin levels when data of fathers and sons were combined ($r_s = .479$, $N = 19$, $p = .042$; see Figure 4, bottom panel) but not for fathers alone ($r_s = -.334$, $N = 7$, $p = .414$) nor for sons alone ($r_s = .019$, $N = 12$, $p = .981$).

Prolactin levels in *C. goeldii* fathers and adult sons were not different in the period without preambulatory infants ($U = 25$, $m = 8$, $n = 7$, $p > .7$; see Figure 3). There was no correlation between age and prolactin levels for data of fathers and sons combined ($r_s = -.066$, $N = 15$, $p = .805$), for fathers alone ($r_s = -.476$, $N = 8$, $p = .208$), or for sons alone ($r_s = .054$, $N = 7$, $p = .895$).

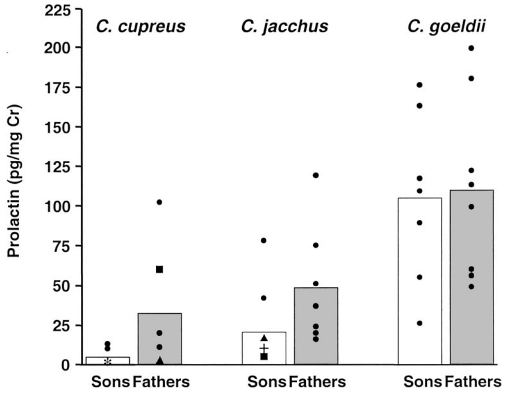

Figure 3. Comparison between urinary prolactin levels in fathers and adult sons of *Callicebus cupreus* (left), *Callithrix jacchus* (middle), and *Callimico goeldii* (right) for the period without preambulatory infants. Columns represent mean values. Solid circles represent data for single individuals, solid squares represent data for 2 individuals with similar data, solid triangles represent data for 3 individuals with similar data, the asterisk represents data for 4 individuals with similar data, and the plus sign represents data for 5 individuals with similar data. Cr = creatinine.

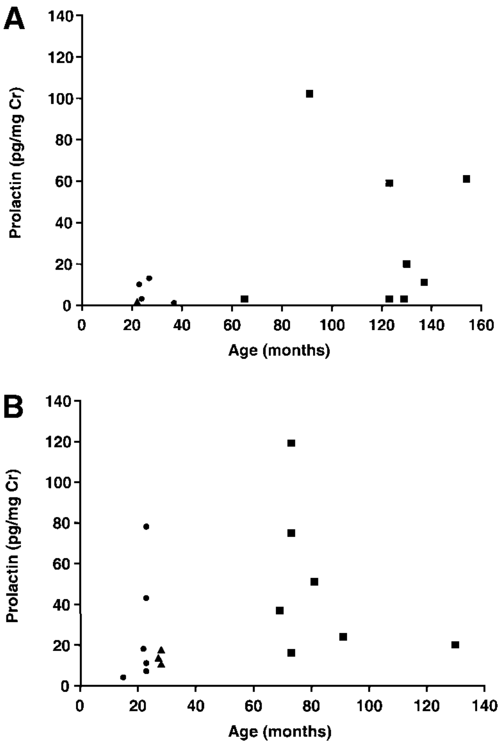

Figure 4. Relationship between age and social status (being an adult son or a father) versus urinary prolactin levels in *Callicebus cupreus* (top) and *Callithrix jacchus* (bottom). Solid circles represent data for sons, solid triangles represent data for 2 sons with similar values, and solid squares represent data for fathers. Cr = creatinine.

Prolactin Levels and Infant Carrying (Prediction 3)

There was no significant correlation between prolactin levels and percentage of paternal carrying in *C. cupreus* or *C. jacchus* for the first 3 weeks after birth ($r_s = .267$, $N = 9$, $p = .488$, for *C. cupreus*; $r_s = .018$, $N = 7$, $p = .965$, for *C. jacchus*) or for the first 6 weeks after birth ($r_s = .267$, $N = 9$, $p = .488$, for *C. cupreus*; $r_s = -.400$, $N = 5$, $p = .424$, for *C. jacchus*). In *C. goeldii*, an increase of prolactin levels preceded paternal carrying (see Figure 2, bottom panel) by several weeks, and the mean prolactin levels for the period before birth and the period of paternal carrying, when tactile stimulation of fathers occurred, were nearly identical (68 pg prolactin/mg creatinine vs. 73 pg prolactin/mg creatinine; see Figure 2, bottom panel).

Discussion

Differences were found in the pattern of prolactin secretion of fathers of three species of New World monkeys. Whereas *C. cupreus* fathers showed no significant increase in prolactin secretion after the birth of their infants ($N = 8$), there was a trend for an increase in *C. jacchus* fathers ($N = 7$) and a significant increase in *C. goeldii* fathers ($N = 7$; Prediction 1). In addition, *C. cupreus* and *C. jacchus* fathers were found to have significantly higher prolactin levels than were adult sons, independent of the presence of preambulatory infants, whereas no such difference was found in *C. goeldii* ($N = 7$; Prediction 2). Although we found higher prolactin levels in fathers, this difference may be due to factors other than fatherhood. The most likely alternative explanation is that prolactin levels increase with age. In fact, age and prolactin levels were significantly correlated in both *C. cupreus* and *C. jacchus* when both fathers and their adult sons were combined. However, this would be expected given that we already knew that there was a difference in both prolactin levels and age between fathers and sons. To control for the effect of being a father, we calculated the correlation between prolactin and age separately for fathers and sons, expecting to find a significant relationship if age is indeed more important than paternity. However, in neither species did we find any indication that prolactin and age are related when only fathers or only sons were considered (see Figure 4). A similar challenge was faced by Ziegler et al. (1996), who found that prolactin levels in male *S. oedipus* significantly correlated with age. However, they were later able to demonstrate that younger fathers had higher levels of prolactin than older nonfathers (Ziegler et al., 2000). Thus it seems that changing from a nonbreeding adult son, still living in the family group, to a breeding male is associated with increased prolactin secretion independent of age in *S. oedipus.* We believe that a similar phenomenon occurs in both *C. jacchus* and *C. cupreus.* The lack of a relationship between prolactin and age within fathers of variable ages in both *C. jacchus* and *C. cupreus* supports this idea. In neither the studies of *S. oedipus* nor in our study of *C. jacchus* and *C. cupreus* has a large enough sample size been available to assess the relationship between prolactin level and age via multiple regression.

We do not know when the increase in prolactin levels occurs in *C. cupreus* fathers; that is, whether prolactin increases with pairing or with the birth of their first infant. Prolactin levels increased in *C. jacchus* ($N = 7$) after infant birth in our study, but this trend was not significant. However, preliminary data of 3 *C. jacchus* males (Schradin, 2001) in which prolactin levels were followed from the time of being an adult subdominant helper until the birth of their first own infants indicate that prolactin levels as helpers were low, remained low after mating and pair-bonding, increased shortly before birth, and increased even more after birth of the infants (Schradin, 2001). Thus, pairing itself seems not to be the reason for an increase of prolactin levels in this species, but stimuli of a highly pregnant female might increase prolactin secretion (for *S. oedipus,* see Ziegler et al., 1996), and this secretion might be even intensified by infant stimuli. However, in *S. oedipus,* paternal prolactin levels are independent of whether infants survive, indicating that prolactin levels are not due to sustained cues from infants (Ziegler et al., 2000).

In contrast to the other two species, *C. goeldii* fathers compared with sons do not have higher prolactin levels in the period without preambulatory infants but show a significant increase of prolactin after the birth of their infants. The pattern of species differences is consistent with the notion that prolactin likely acts to prepare animals for periods of infant carrying. *C. cupreus* fathers carry infants from birth to weaning up to 90% of the time and even carry infants for significant periods until the birth of the next offspring (Mason, 1968; Mendoza & Mason, 1986; Welker & Schäfer-Witt, 1987). Sustained high levels of prolactin of *C. cupreus* fathers therefore could reflect the need to be continuously available to carry infants. Similarly, *C. jacchus* fathers assume the role of the primary carrier of newborn infants. Although they receive significant help from other group members (Goldizen, 1987; Yamamoto & Box, 1996, 1997), *C. jacchus* fathers, like *C. cupreus* fathers, need to be continuously prepared to carry infants. One would predict that *C. jacchus* and *C. cupreus* fathers do not need priming by prolactin, probably because they have always high prolactin levels and therefore should always be willing to carry infants, in contrast to *C. goeldii* fathers in which paternal response should not be constant but should increase after birth of their infants. Moreover, in *C. goeldii*, the mother rather than the father is the primary carrier (Heltne et al., 1973; Jurke & Pryce, 1994; Schradin & Anzenberger, 2001b). The increase in prolactin exhibited by *C. goeldii* fathers during the period immediately preceding the stage of infant carrying may be expected to facilitate the transition from nonparticipation to direct participation in infant care. This interpretation is consistent with findings from rodents and birds for which increased prolactin has been found to be important for the onset of parental care (Bridges & Mann, 1994; Bridges, Numan, Ronsheim, & Mann, 1990; Bridges & Ronsheim, 1990; Buntin, 1996).

It should be noted that carrying of infants cannot be equated with parental motivation, and we recognize that parental motivation may be high even for animals not directly participating in infant carrying. *C. goeldii* fathers, for example, are attracted by their infants immediately after birth and carry them when they are experimentally presented to them (Schradin, 2001; Schradin & Anzenberger, 2002). Many factors may contribute to differential carrying of infants in addition to parental motivation, including tolerance for prolonged contact, competition between animals for access to the infant, and the differential preference of the infant for various animals in the family. Therefore, paternal carrying might not be the only adequate measurement of paternal motivation, and an experimental approach might have been more conclusive. However, this was not possible as experimental manipulation could have had an influence on prolactin levels because prolactin is known to be stress dependent.

Because prolactin is stress responsive (Aidara et al., 1981), it is also possible that the presence of the infant in the group represents a stressor for male *C. goeldii* but not for *C. cupreus* and *C. jacchus.* Although we cannot completely eliminate this possibility, a previous study demonstrated that urinary cortisol levels are unrelated to parental care in *C. goeldii* (Jurke, Pryce, Hug-Hodel, & Döbeli, 1995). Similarly, in *S. oedipus*, both prolactin and cortisol were measured and fathers were found to have higher prolactin levels but not cortisol levels compared with nonfathers (Ziegler et al., 1996). In *C. cupreus*, baseline cortisol levels do not change after the birth of infants, but stress reactivity (in response to handling and bleeding) increases significantly in both fathers and their adult sons following birth of an infant (Reeder, 2001).

Dixson and George (1982) found that prolactin levels were higher when *C. jacchus* fathers were carrying infants immediately before blood sampling than when they were not carrying infants. Thus, they proposed that increased prolactin in *C. jacchus* fathers might be due to tactile stimulation by infants sitting on the fathers' backs. This interpretation was corroborated by a study by Mota and Sousa (2000), although it was based on a very small sample size. In contrast to this, we did not find any correlation between the amount of overall paternal carrying and prolactin levels in *C. cupreus* and *C. jacchus*, which would be expected if fathers that experienced more tactile stimulation secreted more prolactin. Similarly, there was no correlation between infant carrying and prolactin in *S. oedipus* (Ziegler et al., 1996). However, there is an important difference between the studies of Dixson and George and Mota and Sousa, respectively, and both Ziegler et al.'s (1996) and our study. Whereas in the first two studies blood samples were used, urine samples were used in the other two. Urinary prolactin estimates prolactin secretion for the prolonged period of urine production, whereas plasma prolactin estimates the amount of prolactin available at one point in time. Thus, a transitory and modest increase in prolactin increase due to tactile stimulation during infant carrying might be harder to detect using urine samples. In any event, the generally higher prolactin levels in *C. cupreus* and *C. jacchus* fathers compared with nonfathers found in our study in the period without preambulatory infants cannot be explained by the tactile stimulation hypothesis. Similarly, the significant increase in prolactin levels of *C. goeldii* fathers after the birth of their infants cannot be explained by tactile stimulation. *C. goeldii* fathers showed elevated prolactin levels in the period before infant carrying. No infants were sitting on the fathers' backs during the time of increased prolactin levels. Additionally, there was no increase of prolactin levels in the period of paternal carrying compared with the period before birth. Similarly, in *C. cupreus* fathers, prolactin levels did not increase during the period of infant carrying, thus tactile stimulation by carrying does not lead to detectable increased urinary prolactin levels in *C. cupreus* fathers either, who carry infants almost exclusively.

Although our results show an obvious connection between prolactin and paternal care in three species of New World monkeys, we do not know whether high prolactin facilitates paternal care and, if so, how it produces its effects. This study, like most studies of paternal care in fish, birds, and mammals, has demonstrated only a correlation between high prolactin levels and paternal care (Schradin & Anzenberger, 1999). Studies of maternal care in rats and both maternal and paternal care in fish and ring doves have demonstrated a causal link between prolactin and parental behavior (Blüm & Fiedler, 1964, 1965; Bridges & Mann, 1994; Bridges et al., 1997; Buntin, Becker, & Ruzycki, 1991; Kindler, Bahr, Gross, & Philipp, 1991; Ruiter, Bonga, Slijkhuis, & Baggerman, 1986). In these species, peripheral or intracranial injections of prolactin lead to parental behavior, and inhibition of endogenous prolactin secretion (via administration of bromocriptine, a dopamine receptor agonist) leads to a suppression of parental behavior. Additionally, prolactin receptor knock-out mice exhibit deficits in maternal behavior (Lucas et al., 1998). It has been demonstrated in parentally inexperienced and unpaired *C. jacchus* that bromocriptine administration decreases response toward infants (Roberts, Jenkins, Lawler, Wegner, & Newman, 2001). However, sampling in this study was rather heterogenous and included only 2 males. To date, there are no definitive studies establishing a causal relationship between prolactin and parental behavior in mammalian fathers. Our data indicate that this would be a promising avenue for future studies and further indicate that New World monkeys are excellent subjects for such research.

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