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Social determinants of reproductive failure in male common marmosets housed with their natal family

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Postpubertal male common marmosets, *Callithrix jacchus*, engage in little or no sexual behaviour while living with their natal families. The social mechanisms underlying this phenomenon have not been identified but have been assumed to include reproductive suppression by dominant males and/or avoidance of mating with closely related females. We evaluated these two possible components of male reproductive failure. Seven postpubertal males and their fathers underwent a series of 45-min sex tests, in which the son, the father, or the son and father together were allowed to interact freely with the mother/mate or with an unfamiliar, unrelated adult female. We measured testosterone, luteinizing hormone and cortisol concentrations in blood samples collected from males immediately following each test, and in basal blood samples collected on three different occasions. Sons, but not fathers, engaged in very low rates of sexual behaviour when tested with the mother/mate. When tested with unrelated females, however, sons engaged in significantly more sexual behaviour than they had when tested with their mothers and showed no differences from their fathers. When sons and fathers were tested together, both males performed significantly less sexual behaviour than when tested alone with a female; however, they showed no overt competition for females and engaged in little agonism. Hormone levels did not differ significantly between fathers and sons. These results indicate that avoidance of mating with familiar females and possibly father–son competition, but not specific, rank-related suppression, contribute to reproductive failure among postpubertal male marmosets living with their natal family.

In singular, cooperatively breeding species, individuals of both sexes may remain with their natal group into adulthood, forgoing attempts at direct reproduction and instead helping to rear the offspring of the dominant, breeding pair (Solomon & French 1997). Studies of numerous avian and mammalian cooperative breeders have demonstrated that such reproductive failure may be mediated by inhibition of sexual behaviour and/or by suppression of reproductive endocrine function (reviewed by Mumme 1997). Less attention has been given to the specific social factors that trigger these inhibitory processes; however, two possible factors have been implicated. First, several investigators have attributed reproductive failure in helpers to rank-related reproductive suppression, in which sexual behaviour and/or reproductive physiology in subordinate animals is suppressed as a result of interactions with or cues from dominant individuals (e.g. Abbott & Hearn 1978; Jarvis 1981; Emlen & Wrege 1992; Creel et al. 1997). Second, reproductive failure in subordinate cooperative breeders may also result from avoidance of mating with close relatives (reviewed by Jennions & Macdonald 1994; Mumme 1997). These two potential determinants of reproductive failure are not mutually exclusive but differ in their likely ultimate causes and proximate mechanisms. However, the relative contributions of rank-related reproductive suppression and incest avoidance have rarely been examined systematically.

We have been investigating the proximate causes of reproductive failure in the common marmoset, *Callithrix jacchus* (Callitrichidae), a singular, cooperatively breeding New World monkey. Free-ranging groups contain 3–15 individuals, which appear to comprise primarily members of an extended family and often include several adults of each sex (Ferrari & Lopes Ferrari 1989; Ferrari & Digby 1996). However, only one or two dominant females breed in each group (Hubrecht 1984; Stevenson & Rylands 1988; Digby & Ferrari 1994; Digby 1995; Mendes Pontes

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& Monteiro da Cruz 1995); subordinate females, at least in captivity, undergo suppression of ovulation and inhibition of sexual behaviour (Abbott 1984a; Evans & Hodges 1984; Saltzman et al. 1997a, c). Although genetic paternity analyses have not yet been performed conclusively, behavioural data from both wild and captive populations suggest that reproduction is also usually monopolized by a single dominant male within each group (Rothe 1975; Abbott 1984a, 1993; Digby 1999). Reproductive failure of subordinate adult males cannot be attributed to sexual inadequacy or reproductive incompetence. In a free-ranging population, subordinate males were observed to mate with females in neighbouring groups (Digby 1999), and in captivity, mature sons that were briefly removed from their families and paired with an unfamiliar female engaged in sexual behaviour and ejaculated normal, motile spermatozoa (Abbott 1984a; Anzenberger 1985). Thus, subordinate males are reproductively competent both behaviourally and physiologically, but appear to be inhibited, at least behaviourally, by some element within the familiar social group.

Studies using laboratory groups of unrelated adults suggest that one cause of reproductive failure in subordinate male marmosets is rank-related reproductive suppression. Although both dominant and subordinate males in these groups may copulate, subordinate males engage in markedly fewer sexual interactions and are substantially less likely to achieve intromission or ejaculation than dominant males (Epple 1967; Rothe 1975; Abbott 1984a, 1993; Abbott et al. 1992). These differences may be caused, in part, by dominant males aggressively interfering in subordinate males' sexual interactions (Epple 1967; Rothe 1975; Abbott 1984a). Behavioural differences between dominant and subordinate males in groups of unrelated adults may be accompanied by hormonal differences: dominant males were found to have significantly higher circulating concentrations of testosterone and luteinizing hormone (LH) than subordinate males (Abbott et al. 1992; Abbott 1993; but see Abbott 1984a) and, in vitro, testicular tissue from dominant males produced greater concentrations of androgens, both under baseline conditions and when stimulated by human chorionic gonadotropin, than testicular tissue from subordinate males (Sheffield et al. 1989). Thus, in groups of unrelated adults, subordinate males show impairments in both sexual behaviour and reproductive physiology. Because sons typically are subordinate to their fathers (Rothe 1975; Abbott 1984a; Sutcliffe & Poole 1984b), a similar mechanism may contribute to reproductive failure in sons living with their natal families.

Incest avoidance, in addition to rank-related reproductive suppression, has been implicated in reproductive failure among common marmosets housed with their natal families. Replacement of the original breeding male in a family by an unrelated male can stimulate the onset of ovulatory cyclicity, sexual behaviour and conceptions in daughters (Abbott 1984a; Rothe & Koenig 1991; Kirkpatrick-Tanner et al. 1996; Saltzman et al. 1997a, b, c). Moreover, although mother–son, father–daughter and brother–sister incest has been reported to occur in this species (Epple 1970; Abbott 1984a; Anzenberger & Simmen 1987; König et al. 1988; Adler & Jämmrich 1991; N. J. Schultz-Darken, W. Saltzman & D. H. Abbott, unpublished data), König et al. (1988) found that unrelated animals that had been introduced previously into family groups, rather than offspring of the original breeding pair, preferentially attained the breeding position, following the death of the same-sex breeder. Finally, G. Anzenberger, A. Hotz & M. Keller (unpublished data) found that formation of new male–female pairs led to sexual behaviour and pregnancy in pairs of unfamiliar animals but not in brother–sister or parent–offspring pairs. Together, these findings suggest that reproductive failure among males housed with their natal families may result from the absence of unrelated females within the social group, rather than or in addition to rank-related suppression imposed by the father.

In the present study, we evaluated the influence of rank-related suppression and incest avoidance on reproductive performance in male common marmosets. To accomplish this, we characterized the behavioural and hormonal responses of adolescent/young adult males to familiar, related females and also to unfamiliar, unrelated females, both in the presence and in the absence of their father. We predicted that if rank-related suppression is an important cause of reproductive failure, sons should show less-pronounced sexual responses to females in the presence of the father than in his absence, and should engage in less sexual behaviour than the father when both males interact with a female together. Alternatively, if incest avoidance is a significant determinant of sons' reproductive performance, then sons should show a reduced sexual response to related females, compared to unrelated females.

METHODS

Animals and Housing

Subjects were 24 captive-born common marmosets, including seven adolescent to young adult males (sons) along with their mothers and fathers, and three additional adult females. The sons lived with their parents and up to five siblings; each was the eldest son currently living with the family. The additional females lived with a mate and up to four offspring. At the time of their first test, the sons were 15.5–24.8 months of age ($\bar{X} \pm \mathrm{SE} = 18.8 \pm 1.4$ months), fathers were 47.3–143.2 months (88.2 ± 11.1 months) and adult females (including mothers) were 49.3–94.3 months (72.3 ± 5.0 months).

Six of the seven families and all of the additional females occupied cages made of aluminium and wire mesh (61×91 cm and 183 cm high). Each cage contained a stainless steel nestbox, perches, and a variety of wood and rope accessories. These animals were able to engage in visual, auditory and olfactory contact with marmosets in other cages. The remaining family occupied a large room (254×292 cm and 221 cm high), which was enclosed by glass on two sides and contained two stainless steel nestboxes and several tree branches spanning

the length of the room. This latter family had limited auditory contact, and no visual or olfactory contact, with other conspecifics, except for approximately 3 h every 2 weeks during cage cleaning, when they were housed in a standard cage in a room containing other marmosets. All animals lived indoors, with lights on from 0600 to 1800 hours and the temperature and humidity at approximately 27°C and 50%, respectively. We fed marmosets Zu/Preem Marmoset Diet (Premium Nutritional Products, Inc., Topeka, Kansas) daily between 1300 and 1500 hours, with daily supplements of fruit, calcium, vitamin D_3 and vitamin C in plain yogurt. Water was available ad libitum.

Design

We tested each son–father pair once in each of six conditions. For each test, we initially released a female into the test cage (see below), followed by one or both male(s); we then allowed the animals to interact freely for 45 min. In three of the conditions, we tested one or both male(s) with the familiar mother/mate (hereafter termed the mother): (1) son–mother (SM); (2) father–mother (FM); (3) son–father–mother (SFM). For the remaining three conditions, we tested one or both male(s) with an unrelated, unfamiliar female: (4) son–unrelated female (SU); (5) father–unrelated female (FU); (6) son–father–unrelated female (SFU). Immediately following each test, we captured the male(s) and collected a blood sample (see below).

We conducted tests in a cage identical to those used for regular housing, in a room containing no other animals but permitting some auditory contact with conspecifics in other rooms. On three occasions during the 2 weeks prior to the subjects' first test, we released each male and each female alone into the test cage for 45–60 min to facilitate habituation to the cage and room. We coloured subjects' ear tufts to facilitate identification of animals during tests (Saltzman et al. 1996).

Throughout each test, a single, trained observer collected behavioural data on all subjects from behind a one-way viewing screen. We scored sexual, aggressive and affiliative behaviours from a predetermined ethogram (Table 1) on a laptop computer, recording the frequency, the initiator, and, where appropriate, the recipient of each behaviour. In addition, each time a male's genitals were in clear view, but no more than once every 30 s, we recorded whether the penis was fully erect, partially erect or not erect.

Four of the seven mothers and the three additional females each served as the unrelated stimulus female for another family. Prior to this experiment, males had never lived with the unrelated stimulus females with which they were tested. To maximize the frequency of sexual and social behaviours during tests (Abbott 1986), we removed all unrelated stimulus females and mothers/mates of test males, along with any daughters or infants ($\leq$2 months of age) present in their families, from their home cages between 1500 and 1700 hours on the afternoon prior to each test day. Each female and her removed offspring were housed together overnight in a cage identical to the ones used in normal housing conditions, in a room separate from their family. All animals were returned to their home cages immediately following testing the next day. Whenever possible, females were tested in the follicular phase of the ovarian cycle (see below). Animals engaged in sexual behaviour even when females were not in the periovulatory phase, consistent with previous findings that female common marmosets copulate and are receptive to males throughout the ovarian cycle and pregnancy (Kendrick & Dixson 1983).

We tested each family twice per week, between 0900 and 1115 hours, every 3–4 weeks, for 3 consecutive months. During each week of testing, we tested a son and/or his father on 2 consecutive days, once with the mother and once with the unrelated female. We did not use any animal in more than one test on a given day, and, with one exception, we tested each male with a particular female no more than once every 3 weeks. We used the same female in all three 'unrelated female' tests for each family, and we approximately balanced the order of test conditions across the seven families.

Ethical Note

As described above, to minimize novelty and stressfulness of the sex test procedure, we allowed each animal to adapt to the test environment on three occasions prior to testing. Agonistic interactions between male and female marmosets, and between fathers and sons housed together, are usually infrequent and mild; therefore, the sex tests did not seem likely to result in severe agonism or wounding. This expectation was confirmed by our results (see below), as no wounding, virtually no contact aggression, and very little noncontact aggression was observed. Moreover, fathers and sons showed only moderate cortisol elevations following sex tests (see Results), indicating that the tests may have been moderately but not severely stressful. Finally, removal of adult females, as well as their daughters and infants, from the family prior to each sex test was necessitated by the experimental design. To minimize the stressfulness of this procedure, we housed separated animals in cages that were as similar as possible to the home cage, and we minimized the length of the separation period. We found no behavioural, physical, or physiological evidence that overnight separation from the family adversely affected the animals' social relationships or health.

Blood Sampling, Hormone Assays and Somatometric Measurements

We used blood samples collected from males to determine plasma testosterone, LH and cortisol concentrations. In addition to samples collected immediately after each test, we collected three basal blood samples from each male at 2-week intervals on nontest days, at the same time of day as post-test samples (0945–1115 hours). At this time we also weighed each male, measured the length and width of each testis in the scrotum using calipers, and measured the crown–rump and knee–heel

Table 1. Behaviours scored

Behaviour	Definition
Sexual behaviours	
Full mount	Climb on partner's back from behind and grip partner around waist and legs, with genital region in close proximity to partner's genitals or tail; may be accompanied by pelvic thrusting (Kendrick & Dixson 1984)
Mount attempt	Grasp partner and begin to climb onto partner's back without successfully achieving mount position
Intromission	Grasp female tightly during mount and perform slow, deliberate pelvic thrusts; mount may end abruptly and may not lead to ejaculation
Ejaculate	Grasp female tightly during mount and perform slow, deliberate pelvic thrusts; usually accompanied by female looking back over her shoulder at male and attempting to disengage, and usually followed by rapid termination of mount and penile throbbing
Freeze	Remain immobile in crouched posture while looking straight ahead, in the absence of tufts back or tongue in-out
Tufts back	Draw ear tufts back while staring at partner; often accompanied by narrowing of eyes, in the absence of tongue in-out
Tongue in-out	Rhythmically move tongue in and out of mouth while facing or interacting with partner (Epple 1967; Stevenson & Poole 1976; Kendrick & Dixson 1984)
Mount interference	Approach, touch, frown at, threaten, or otherwise interact with mounting/copulating pair of animals
Full erection	Penis is rigid and straight
Partial erection	Penis is protruding from prepuce but not fully erect
No erection	Penis is not protruding from prepuce
Aggressive behaviours	
Erh-erh	Low-pitched, staccato chattering (Epple 1968; Stevenson & Poole 1976; Lipp 1978; Abbott 1984a)
Ear-tufts flick	Rapid back-and-forth movement of ear tufts (Epple 1967; Stevenson & Poole 1976; Lipp 1978)
Frown	Lower eyebrows while staring (Stevenson & Poole 1976)
Cuff	Swift, superficial blow or scratch performed aggressively (Stevenson & Poole 1976; Abbott 1984a)
Chase	Pursue partner, with one or both animals displaying aggression and/or submission
Fight	Grapple aggressively with partner(s), involving biting, clawing and wrestling (Lipp 1978; 'attack': Abbott 1984a)
Attack	Lunge at or pounce on partner aggressively; may or may not result in fight (Abbott 1984a)
Snap bite	Direct a single short, sharp bite at partner (Stevenson & Poole 1976; Abbott 1984a)
Genital present	Raise tail to expose genitals to partner
Submissive behaviours	
Vocal submit (ngä)	Relatively low-pitched, atonal, infantile squeal (Epple 1968)
Facial submit	Flatten tufts (lower ear tufts against side of head) and/or facial grimace (partially open mouth with corners of mouth retracted, exposing lower and sometimes upper teeth) and/or slit eyes (eyelids half closed) (Stevenson & Poole 1976; Abbott 1984a)
Investigative behaviours	
Sniff	Push face against or towards partner, excluding anogenital region
Nuzzle	Move face along partner with face contacting partner's body
Anogenital inspect	Orient face against or towards anogenital region of partner, or use hands or mouth to investigate anogenital region of partner; includes anogenital groom

length (Abbott & Hearn 1978). We calculated each male's testicular volume from his mean testicular length and width, using the formula for the volume of an oblate spheroid (see Abbott & Hearn 1978). We collected blood samples from females twice during each week in which they were tested, as well as once during the preceding week and once during the subsequent week, to determine plasma progesterone concentrations.

For the collection of blood samples, we manually captured animals from the home cage or test cage, briefly restrained them in a marmoset restraint tube (Hearn 1977) and collected 0.3 ml of blood into a heparinized syringe by femoral puncture. To minimize the hormonal response to the blood sampling procedures, we collected all blood samples from males in less than 4 min from cage entry (2.08 ± 0.03 min). We refrigerated blood samples at 4°C until centrifuging them for 10 min at 2000 rpm, and separated and stored the plasma at -20°C.

We measured plasma cortisol concentrations in duplicate aliquots using an antibody-coated tube radioimmunoassay kit, Gamma Coat™ (Incstar® Corp., Stillwater, Minnesota; Saltzman et al. 1994). The assay sensitivity was 0.1 ng/tube, and the intra- and interassay coefficients of variation (CVs) for a plasma pool assayed in duplicate were 4.74 and 9.68%, respectively. We measured plasma LH concentrations in single, 75-µl aliquots, using radioimmunoassay (Saltzman et al. 1998). Assay sensitivity was 0.1 ng/tube, and intra- and interassay CVs were 3.44 and 4.57%, respectively. We measured plasma progesterone concentrations directly in duplicate aliquots by a heterologous enzyme immunoassay (Saltzman et al. 1994). Assay sensitivity was 4.5 pg/tube at 90% binding, and

the intra- and interassay CVs were 2.79 and 12.12%, respectively.

We assayed plasma testosterone in duplicate 10-µl aliquots, without chromatography, following the method described by Robinson et al. (1975). At 50% binding, the antibody cross-reacted 47.1% with dihydrotestosterone (DHT), 7.7% with 4-androsten-3β,17β-diol, 5.8% with 5α-androstan-3α,17β-diol, 4.87% with 5α-androstan-3β,17β-diol, 0.465% with 5α-androstan-3,17-dione, 0.45% with androstenedione, 0.088% with epiandrosterone, 0.045% with 20α-dihydroxyprogesterone, 0.035% with dehydroepiandrosterone and less than 0.03% with hydrocortisone, cortisone, oestrone, oestradiol, progesterone, 17α-hydroxyprogesterone, desoxycorticosterone, cholesterol, pregnenolone and corticosterone. Despite the antibody's high cross-reactivity with DHT, testosterone is likely to be the principal androgen measured, as it is substantially more abundant than DHT in the plasma of male marmosets (Hodges et al. 1983). The recovery of testosterone standards (Sigma, St Louis, Missouri) added to 10 µl of a marmoset plasma pool (N=8) was 96.45 ± 0.98%. Serial dilution of a testosterone-spiked marmoset plasma pool (20.0–0.625 µl; N=6) gave a displacement curve parallel to that obtained with testosterone standards. The sensitivity of the assay at 90% binding was 4.8 pg/tube. The intra-assay CVs for two marmoset plasma pools assayed in quadruplicate on each plate (32 and 57% binding) were 2.41 and 2.66%, respectively, and the interassay CVs were 6.44 and 5.75%, respectively.

We gave females an intramuscular injection of 0.75 µg cloprostenol sodium (Estrumate, Mobay Corp., Shawnee, Kansas), a prostaglandin F2α analog, 5–6 days prior to each day on which they were tested; injections occurred 14–30 days after ovulation, defined as the day preceding a sustained rise in plasma progesterone concentrations above 10 ng/ml (Harlow et al. 1983). This treatment results in luteolysis and termination of the luteal phase or early pregnancy (Summers et al. 1985). Of the 42 sex tests conducted, the majority were performed when the female was in the follicular phase, approximately 4–13 days prior to ovulation. One female was pregnant throughout the study, and four tests were conducted with females in the luteal phase of the ovarian cycle. No female was in the periovulatory period (−3 through +3 days from ovulation) during testing, and no behavioural differences were apparent between tests in which females were and were not in the follicular phase.

Analysis

For each behavioural test, we determined the proportion of observational scans in which each male had a full, partial or no erection. For five males (two sons, three fathers), no observational scans were recorded in one to three tests because the genitals were never in view. Therefore, we omitted these animals from statistical analyses of erections.

To reduce heterogeneity of variance, we subjected observational scan data to arcsine transformation, frequencies of other behaviours to square-root transformation, and hormonal data to log transformation (Sokal & Rohlf 1995). We analysed behavioural data by two-way ANOVAs (SYSTAT version 5.2.1), with groups (fathers, sons) treated as a between-subjects factor and test conditions (alone with unrelated female, with other male+unrelated female, alone with mother, with other male+mother) treated as a within-subjects factor. Following significant groups × conditions interactions, we performed separate one-way ANOVAs to compare each group's responses to the four test conditions, and unpaired t tests to compare fathers' and sons' responses within each test condition. Following significant main effects of conditions, we performed pairwise comparisons using post hoc univariate f tests. For each hormone measured in males (testosterone, LH, cortisol), we first compared plasma concentrations across the three basal blood samples using a one-way ANOVA. Hormone levels did not differ significantly across basal samples; therefore, we calculated a mean basal concentration for each animal, which we compared with the four test conditions using a groups × conditions ANOVA. For all tests, significance was assessed at the 0.05 level (two tailed). Hormonal and behavioural data are presented as backtransformed means ± 95% confidence limits, and somatometric data are presented as $\bar{X}$ ± SE.

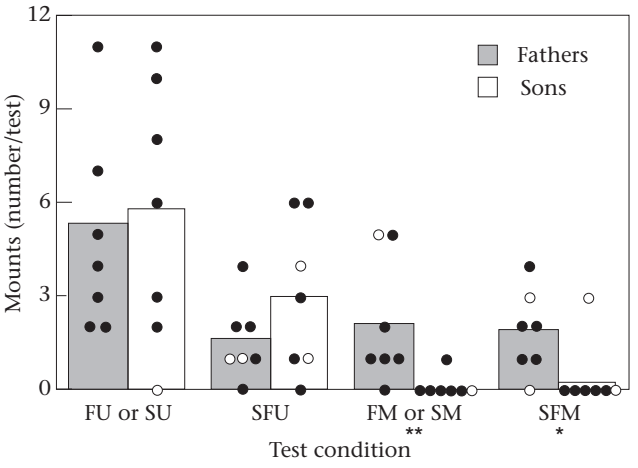

Figure 1. Mounts (full mounts and mount attempts combined; backtransformed means plus individual animals' scores) performed by fathers and sons in each test condition. FU or SU: Father or son alone with unrelated female; SFU: son and father together with unrelated female; FM or SM: father or son alone with mother; SFM: son and father together with mother. ●: Scores from tests in which the female was in the follicular phase of the ovarian cycle; ○: scores from tests in which the female was pregnant or in the luteal phase. *P<0.05, sons versus fathers in SFM; **P=0.01, FM versus SM.

RESULTS

Sexual Behaviour

The number of mounts (full mounts and mount attempts) performed by males showed both a main effect of test condition (ANOVA: $F_{3,36}$=15.16, P<0.0001) and a group × condition interaction ($F_{3,36}$=3.92, P<0.05; Fig. 1). Although fathers and sons showed no differences when tested with the unfamiliar female, sons performed fewer

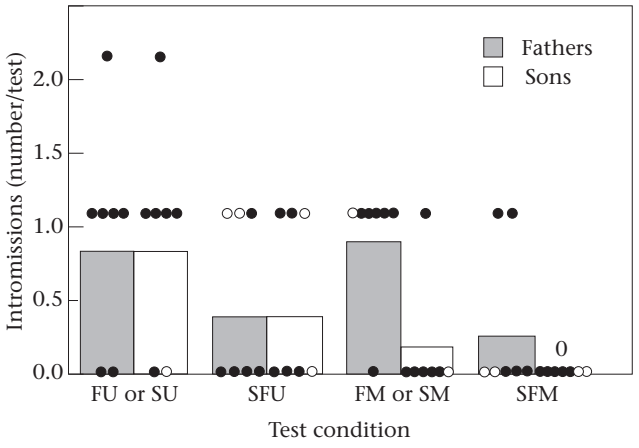

Figure 2. Intromissions (backtransformed means plus individual animals' scores) performed by fathers and sons in each test condition. Test conditions and symbol designations as in Fig. 1.

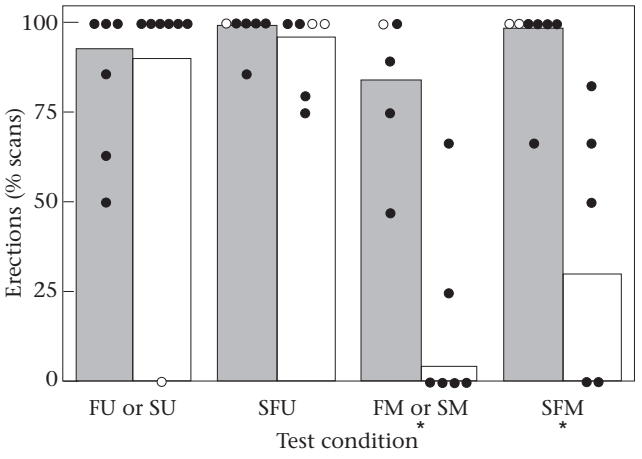

Figure 3. Percentage of observational scans (backtransformed means plus individual animals' scores) in which fathers (▨) and sons (□) displayed full or partial erections in each test condition. Test conditions and other symbol designations as in Fig. 1. *P<0.005, FM versus SM, sons versus fathers in SFM. No data were available from some animals in some tests because the animals' genitals were never visible to the observer (see text).

mounts than their fathers when tested with the mother (unpaired t tests: SM versus FM: $t_{12}=-3.03$, $P=0.01$; sons versus fathers in SFM: $t_{12}=-2.47$, $P<0.05$). When we analysed their data separately, sons showed a significant difference across test conditions (ANOVA: $F_{3,18}=11.26$, $P<0.0005$), performing more mounts with the unrelated female than with the mother (univariate f tests: SU versus SM: $P<0.005$; SU versus SFM: $P<0.05$; SFU versus SM: $P<0.01$; SFU versus SFM: $P=0.05$). Sons also showed a higher frequency of mounts when tested individually with the unrelated female than when tested together with the father and the unrelated female (univariate f tests: SU versus SFU: $P<0.05$). Fathers, like sons, showed a significant change across test conditions (ANOVA: $F_{3,18}=6.19$, $P<0.005$): they performed more mounts when alone with the unrelated female than in all other conditions (univariate f tests: Ps<0.05). When both males were tested together, neither fathers nor sons consistently had initial access to unrelated females: four sons and three fathers performed the first full mount or mount attempt. Finally, only two mount interferences occurred. In both instances, a full mount between a father and an unrelated female ended when the son sniffed or huddled with the mounting pair.

Intromissions occurred infrequently and showed only a main effect of test condition (ANOVA: $F_{3,36}=5.60$, $P<0.005$; Fig. 2). Together, fathers and sons performed fewer intromissions when both males were tested together with the mother than in all other conditions (univariate f tests: SFM versus SM+FM: $P=0.01$; SFM versus SFU: $P<0.05$; SFM versus SU+FU: $P<0.005$). The number of intromissions was also significantly lower when both males were tested together with the unrelated female than when they were each tested alone with the unrelated female (univariate f test: SFU versus SU+FU: $P<0.05$).

Ejaculations ($N=10$) occurred too infrequently to permit statistical analysis. We therefore compared the number of males that ejaculated in each condition. More fathers ejaculated when tested alone with either female (FU: three of seven males; FM: three of seven males) than when tested together with the son and either female (SFU: one of seven males; SFM: none of seven males). Sons ejaculated at low rates when tested with an unrelated female (SU: one of seven males; SFU: two of seven males) but never ejaculated with their mother.

For analyses of penile erections, we summed the proportion of observational scans in which males had full or partial erections. This yielded a main effect of group (ANOVA: $F_{1,7}=8.44$, $P<0.05$), a main effect of test condition ($F_{3,21}=5.92$, $P<0.005$) and a group × condition interaction ($F_{3,21}=3.08$, $P<0.05$; Fig. 3). When tested with an unrelated female, sons and fathers showed no difference in occurrence of erections. When tested with the mother, however, sons had erections in significantly fewer observational scans than did their fathers (unpaired t tests: SM versus FM: $t_9=-4.28$, $P<0.005$; sons versus fathers in SFM: $t_{10}=-3.98$, $P<0.005$). When we analysed data from sons and fathers separately, sons, but not fathers, showed a significant difference across test conditions (ANOVA: $F_{3,12}=7.15$, $P<0.01$): in general, sons showed more erections when tested with an unrelated female than when tested with the mother (univariate f tests: SU versus SM: $P<0.05$; SFU versus SM: $P<0.005$; SFU versus SFM: $P<0.005$).

Courtship Behaviour

The frequency of tongue in-outs (usually considered a form of sexual solicitation: Epple 1967; Kendrick & Dixson 1984) performed by males to females showed a significant main effect of test condition (ANOVA: $F_{3,36}=6.80$, $P<0.001$), but not of group. Males performed more tongue in-outs when tested alone with an unrelated female (backtransformed mean with 95% confidence limits: SU+FU: 2.74 (5.74, 0.72)) than in all other conditions (SFU: 0.15 (0.41, −0.07); SM+FM: 0.52 (1.34, −0.06); SFM: 0.11 (0.24, −0.01); univariate f tests: Ps<0.05).

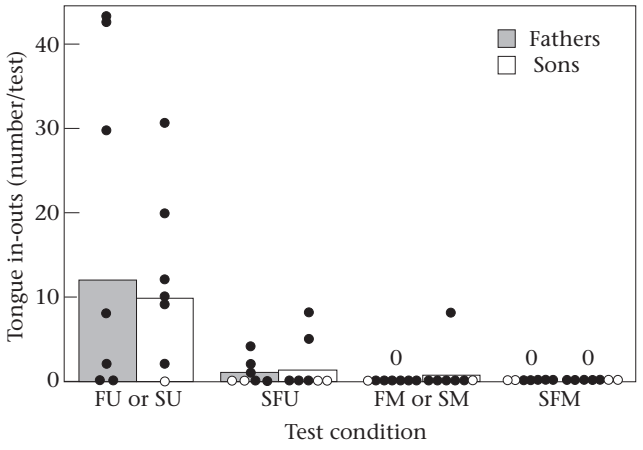

Figure 4. Tongue in-outs (backtransformed means plus individual animals' scores) received by fathers and sons from females in each test condition. Test conditions and symbol designations as in Fig. 1.

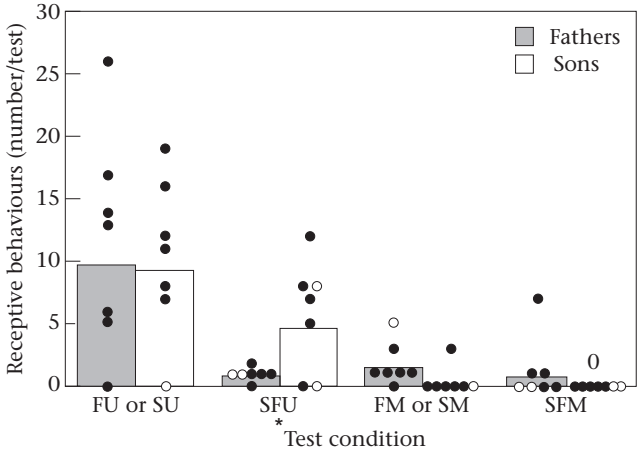

Figure 5. Receptive behaviours (tufts back and freeze combined; backtransformed means plus individual animals' scores) received by fathers and sons from females in each test condition. Test conditions and symbol designations as in Fig. 1. *P<0.05, sons versus fathers in SFU.

Females never performed tongue in-out to males when fathers and sons were tested together with the familiar mother/mate (SFM); therefore, this condition was excluded from analysis. The frequency of tongue in-outs received by males from females, like those performed by males, showed a significant main effect of test condition (ANOVA: $F_{2,24}$=15.13, P<0.0001; Fig. 4) but not of group. Males received a greater number of tongue in-outs when tested alone with an unrelated female than in the remaining conditions (univariate f tests: SU+FU versus SFU: P<0.005; SU+FU versus SM+FM: P<0.005).

The female behaviours of tufts back and freeze were combined for analysis ('receptive behaviours'). The frequency of receptive behaviours received by males from females showed a main effect of test condition (ANOVA: $F_{3,36}$=21.94, P<0.0001) and a group × condition interaction ($F_{3,36}$=2.92, P<0.05; Fig. 5). When males were tested together, sons received more receptive behaviours from unrelated females than did fathers (unpaired t test:

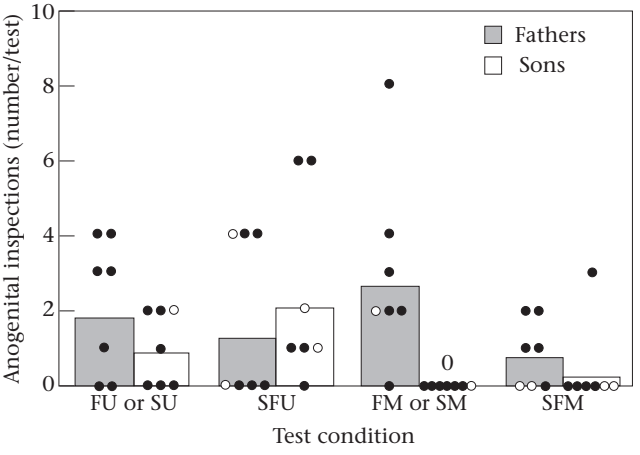

Figure 6. Anogenital inspections (backtransformed means plus individual animals' scores) performed by fathers and sons towards females in each test condition. Test conditions and symbol designations as in Fig. 1.

sons versus fathers in SFU: t_{12}=2.45, P<0.05). No differences between sons and fathers occurred in the single-male conditions. Sons never received receptive behaviours from the mother when tested with her and the father; thus, this condition (son in SFM) was omitted from all further analyses. When analysed separately, the number of receptive behaviours that sons and fathers each received differed by test condition (ANOVAs: sons: $F_{2,12}$=15.16, P<0.001; fathers: $F_{3,18}$=9.00, P<0.001). Fathers received more receptive behaviours when tested alone with an unrelated female than in the remaining conditions (univariate f tests: FU versus SFU: P=0.01; FU versus FM: P<0.05; FU versus SFM: P<0.05). Sons received more receptive behaviours from unrelated females than from mothers (univariate f tests: SU versus SM: P<0.005; SFU versus SM: P<0.01), and more from unrelated females when tested alone than when tested with the father (SU versus SFU: P=0.05).

Intersexual Investigative Behaviour

The frequency of sniffs performed by males to females did not differ between groups or across test conditions (backtransformed mean with 95% confidence intervals: 9.72 (12.11, 7.58)). The frequency of nuzzles performed by males to females differed across conditions (SU+FU=6.52 (11.56, 2.84), SFU=4.56 (10.19, 1.01), SM+FM=1.16 (2.74, 0.11), SFM=1.84 (3.58, 0.58): $F_{3,36}$=8.01, P<0.0005) but not between groups. Together, sons and fathers performed more nuzzles to the unrelated female than to the mother (univariate f tests: SU+FU versus SM+FM: P<0.001; SU+FU versus SFM: P<0.01; SFU versus SM+FM: P=0.01; SFU versus SFM: P<0.05). Females sniffed and nuzzled males too infrequently to permit statistical analysis.

Male anogenital inspections of females showed a significant group × condition interaction (ANOVA: $F_{3,36}$= 3.79, P<0.05, Fig. 6): sons never performed anogenital inspections of the mother when tested alone with her,

Table 2. Plasma cortisol, testosterone and LH concentrations (backtransformed means with upper and lower 95% confidence limits) of sons and fathers (N=7 per group) immediately following each behavioural test and under baseline conditions at the same time of day

Hormone	Animals	Baseline*	SM/FM	SFM	SU/FU	SFU
Cortisol (μg/dl)	Sons	95.58 (116.76, 78.24)	194.12 (223.04, 168.95)	211.64 (267.26, 167.58)	232.93 (271.80, 199.62)	226.64 (277.96, 184.79)
	Fathers	107.65 (157.81, 73.44)	185.99 (222.84, 155.24)	191.17 (245.61, 148.79)	195.02 (223.79, 169.95)	208.46 (266.12, 163.29)
Testosterone (ng/ml)	Sons	11.12 (15.92, 7.77)	12.83 (16.59, 9.93)	16.34 (23.04, 11.59)	11.96 (17.52, 8.17)	15.26 (20.50, 11.36)
	Fathers	14.48 (24.00, 8.74)	14.06 (25.86, 7.64)	12.89 (27.74, 5.99)	11.64 (22.89, 5.92)	11.67 (20.02, 6.80)
LH (ng/ml)	Sons†	4.03 (5.05, 3.22)	3.71 (5.75, 2.39)	5.04 (8.27, 3.07)	5.35 (7.21, 3.97)	4.00 (5.64, 2.83)
	Fathers	2.82 (4.00, 1.99)	2.84 (4.49, 1.79)	2.87 (4.75, 1.74)	2.76 (3.79, 2.01)	4.67 (9.03, 2.42)

Behavioural test conditions: SM/FM: son–mother and father–mother; SFM: son–father–mother; SU/FU: son–unrelated female and father–unrelated female; SFU: son–father–unrelated female.
*Mean concentration from three baseline blood samples.
†LH concentrations could not be determined for one son due to insufficient plasma volumes.

whereas all but one father did so. Moreover, when examined separately, sons, but not fathers, showed a significant change across conditions (ANOVA: $F_{3,18}$=5.22, P<0.01). In general, sons performed more anogenital inspections to unrelated females than to their mothers (univariate f tests: SU versus SM: P<0.05; SFU versus SM: P<0.05; SFU versus SFM: P<0.05).

Intersexual Agonism

Agonistic behaviours occurred very infrequently and therefore were combined into three categories for analysis: aggressive display (erh-erh+ear-tufts flick), contact aggression (cuff+attack+snap bite), and submission (facial submit). We did not observe vocal submission, frowns, genital presents, fights or chases in any tests. Most of the aggressive displays and contact aggression were received by males from females. (Two sons and three fathers received aggressive displays from five unrelated females and two mothers, while three sons and two fathers received contact aggression from four unrelated females and one mother.) One son and two fathers performed aggressive displays to unrelated females, and no males performed aggressive displays to the mother. Males never performed contact aggression towards females. Submission was performed by a single son, which submitted both to his mother and to an unrelated female.

Male–Male Agonism

Males engaged in almost no agonism with one another. Fathers and sons performed no aggressive displays towards each other and only one bout of contact aggression (snap bite by a father). A single son accounted for all submissive behaviour performed.

Hormones

Plasma cortisol levels did not differ significantly between fathers and sons but did differ across conditions (ANOVA: $F_{4,48}$=22.87, P<0.0001, Table 2). Together, fathers and sons had significantly higher cortisol concentrations following each test condition than under baseline conditions (univariate f tests: Ps<0.0001). Males also had higher plasma cortisol levels when tested with an unrelated female than when tested alone with the mother (univariate f tests: SU+FU versus SM+FM: P=0.001; SFU versus SM+FM: P=0.07). Plasma testosterone and LH concentrations did not show a significant main effect of group or condition, or a group × condition interaction (Table 2). The absence of clear LH or testosterone responses to sex tests might have reflected the relatively short duration of the tests (45 min).

Somatometric Measurements

Sons were significantly heavier than fathers (mean weights: $\bar{X} \pm$ SE=403.4 ± 15.4 versus 356.0 ± 11.3 g, respectively; unpaired t test: t_{12}= − 2.48, P<0.05) and tended to have longer crown–rump distances (18.3 ± 0.2 versus 17.8 ± 0.2 mm, respectively; t_{12}= − 2.09, P=0.06) but not knee–heel lengths (7.3 ± 0.2 versus 7.3 ± 0.1 mm, respectively). Mean testis volume did not differ reliably between groups (sons: 678.5 ± 38.5 mm^3; fathers: 777.4 ± 42.0 mm^3). Thus, sons had a lower testis-volume-to-body-weight ratio than fathers (1.69 ± 0.10 versus 2.19 ± 0.13 mm^3/g, respectively; unpaired t test: t_{12}=3.16, P<0.01).

DISCUSSION

The results of this study confirm that adult male marmosets housed with their natal families show impaired reproductive performances, under some circumstances, compared to their fathers. Our findings also suggest that these reproductive impairments may largely reflect incest avoidance: sons engaged in fewer sexual behaviours with their mothers than with unfamiliar, unrelated females,

and engaged in fewer sexual behaviours than the father only when tested with the mother. In contrast, we found limited support for the hypothesis that fathers impose rank-related reproductive suppression on their sons. First, sons did not have lower reproductive hormone levels or higher cortisol levels than their fathers, either under baseline conditions or following sex tests. Second, when tested with an unrelated female, sons did not show less sexual behaviour than their fathers. Third, although sons engaged in less sexual behaviour with unrelated females in the father's presence than in his absence, a parallel effect was also seen in fathers. Male–male competition may thus reduce sexual behaviour of both fathers and sons, but it cannot account for the specific reproductive deficits observed in sons. Incest avoidance, in contrast, appears specifically to curtail sons' reproductive activity, leading to asymmetrical reproductive performances by sons and fathers.

Effect of Incest Avoidance on Sons' Reproductive Performance

The importance of incest avoidance in determining the sexual performance of marmosets housed with their natal families has been emphasized by a number of studies. König et al. (1988) examined patterns of reproduction in marmoset families following the death of one of the original breeders and found that if an unrelated animal was present in the group, this animal, rather than an offspring of the remaining breeder, preferentially filled the vacant breeding position. More recently, Anzenberger et al. (unpublished data) found that parent–offspring and brother–sister pairs engaged in virtually no sexual interactions and did not reproduce even when removed from the remainder of the family, in contrast to pairs of unrelated adults. Finally, we have shown that adult female marmosets undergoing ovulatory cycles do not engage in sexual behaviour or conceive while housed with the intact natal family, but are likely to breed if the father is replaced by an unrelated adult male (Saltzman et al. 1997a, b, c; see also Abbott 1984a; Hubrecht 1989; Rothe & Koenig 1991; Kirkpatrick-Tanner et al. 1996); moreover, anovulatory adult daughters can be stimulated to commence ovulatory cyclicity by replacement of the breeding male (Saltzman et al. 1997b). Thus, limited access to unrelated adults of the opposite sex appears to be a critical factor constraining reproduction in marmosets living with their natal families. This conclusion is consistent with findings of pronounced inbreeding depression in both captive and wild populations of callitrichid monkeys (Ralls & Ballou 1982; Dietz & Baker 1993). However, in the present study, we were not able to assess independently the effects of familiarity and relatedness on males' responses to females.

Although sons in the present study both performed and received fewer sexual and courtship behaviours (mounts, penile erections, tongue in-outs, receptive behaviours) when tested with their mothers than when tested with an unrelated female, and although sons never ejaculated with their mothers, sons and mothers did not completely avoid sexual interactions with one another. Two sons mounted their mothers, and one of these intromitted with his mother and received both proceptive and receptive behaviours from her. These findings are compatible with previous observations suggesting that incest avoidance is not expressed consistently in this species (Anzenberger & Simmen 1987; König et al. 1988; Adler & Jämmrich 1991). Inbreeding may be most likely to occur when animals have no opportunities to outbreed. König et al. (1988) found that incestuous mating occurred, following the death of one of the original breeders, in five of 16 families in which no unrelated individual was available to fill the breeding vacancy. Similarly, in our own colony, two sons have been known to impregnate their mothers shortly following the death of the father, before an unrelated male was introduced into the family (W. Saltzman, N. J. Schultz-Darken & D. H. Abbott, unpublished data).

Effects of Male–Male Interactions on Sexual Behaviour

The results of this study did not support the hypothesis that marmoset fathers impose specific, rank-related reproductive suppression on their eldest sons. When both males were tested together with an unrelated female, sons neither performed nor received significantly lower levels of sexual or courtship behaviours than their fathers. Furthermore, we found no evidence that fathers actively interfered in their sons' sexual interactions or that males overtly competed for access to females. These results are consistent with the low levels of agonistic behaviour typically reported to occur in marmoset families (Rothe 1975; Abbott 1984a; Sutcliffe & Poole 1984b; Digby 1995). However, they contrast with findings from groups of unrelated adult marmosets, in which dominant males may aggressively disrupt subordinate males' sexual interactions with females and in which subordinate males engage in lower frequencies and intensities of sexual behaviour than dominant males (Epple 1967; Rothe 1975; Abbott 1984a, 1993; Abbott et al. 1992).

Male–male competition might have been more obvious in the present study if tests were conducted when females were in the periovulatory (i.e. fertile) period. In some species, both dominant and subordinate males mate with females during nonfertile periods, but dominant males monopolize matings when the female is most likely to conceive (Baker et al. 1993; de Ruiter et al. 1994). Another likely explanation for the disparity between the present findings and those from groups of unrelated adults is that males may be more tolerant of close male relatives than of unrelated (and less familiar) male groupmates. This possibility is supported by a recent study by Schaffner (1996, unpublished data), in which female black tufted-ear marmosets, *C. kuhli*, were introduced into established pairs of either unrelated or related (father–son or brother) males. Following introduction of a female, all pairs of unrelated males had to be separated within 4 days due to severe agonism, whereas all related pairs remained together for at least a year. As in the present study, pairs of related males housed with a female showed low levels of agonism

and no significant differences in their sexual interactions with an unrelated female. Similarly, in a wild population of golden lion tamarins, *Leontopithecus rosalia*, pairs of brothers living in non-natal groups were more stable over time than pairs of unrelated males (Baker et al. 1993). Thus, high tolerance between closely related males may lead to polyandrous mating patterns in callitrichid groups containing an unrelated female (but see Goldizen et al. 1996).

Although we found no evidence for specific, rank-related suppression of sexual behaviour in sons, both sons and fathers engaged in less sexual behaviour when males were tested together than when they were tested alone with a female. This pattern was seen most clearly in males' interactions with unrelated females: fathers and sons performed significantly fewer mounts, intromissions and tongue in-outs with the unrelated female, and were somewhat less likely to ejaculate, in the two-male condition than in the one-male condition. In addition, they received significantly fewer tongue in-outs and receptive behaviours from the unrelated female when both males were present. These results are similar to Anzenberger's (1985) findings that both fathers' and sons' sexual interactions with an unfamiliar female were reduced when either the male's or the female's family was present or visible.

One possible explanation for these findings is that fathers and sons may have been mutually inhibited by each other's presence. It is also possible, however, that they were simply distracted by one another, or that they had less access to the female because she was dividing her time between both males. This latter possibility is supported by several lines of evidence. First, males' sexual behaviour was consistently reduced by the presence of another male only in tests with an unrelated female, in which both males usually engaged in sexual activity; in fact, for both mounts and intromissions, the total number performed by the father and the son when the males were tested together with an unrelated female was similar to the average number performed when either male was tested alone with the unrelated female. In tests with the mother, in contrast, sons did not typically engage in sexual behaviour, and their presence did not generally alter the father's sexual interactions with the mother. Thus, the mere presence of another male was not sufficient to inhibit or distract a male and lower his rate of sexual interactions. Moreover, the proportion of observational scans in which males had penile erections did not differ between the one-male and two-male conditions, suggesting that males' arousal levels were not reduced by the presence of another male, as might be expected if males were simply distracted by one another. Another possible explanation for the reduced frequency of sexual behaviours in two-male tests is that females may have been behaviourally inhibited by the presence of two unfamiliar males. This possibility is supported by the finding that unrelated females consistently performed fewer total receptive or proceptive behaviours to fathers and sons together in the two-male condition than they did to either male when tested alone with him. Whatever the exact cause, it is clear that the presence of a familiar male reduces sexual behaviours performed and received by both fathers and sons.

Effect of Novelty on Males' and Females' Sexual Behaviour

An unexpected finding of this study was that both males and females showed a sexual preference for unfamiliar animals over the familiar mate. In single-male tests, in which the father's interactions with females were not influenced by the son, fathers performed more mounts to unrelated females than to the mother (familiar mate) and received higher numbers of proceptive and receptive behaviours from unrelated females than from the mother. Thus, both males and females showed a clear willingness to mate with unfamiliar individuals and even seemed to prefer them to the familiar mate. Moreover, agonistic behaviours occurred very infrequently between males and unrelated females. The females' low aggressiveness and high sexual responsiveness towards unfamiliar males contrast with results from several previous reports, in which mated male marmosets typically performed sexual solicitation towards unfamiliar, mated females, but females responded with virtually no sexual or courtship behaviours, little or no affiliation, and often moderate to high levels of aggression (Evans 1983; Sutcliffe & Poole 1984a; Anzenberger 1985).

The reasons for the disparity between these earlier findings and the present results are not clear. One possible explanation is that females in the present study were usually in the follicular phase of the ovarian cycle during behavioural testing, whereas those in the previous studies were pregnant. This is unlikely, however, to account fully for the behavioural differences observed. Female common marmosets are receptive to males and copulate throughout the ovarian cycle and pregnancy (Kendrick & Dixson 1983); in the present study, no systematic behavioural differences were evident between females that were in the follicular phase and those that were in the luteal phase or pregnant during testing (see also Anzenberger 1985). Another factor that may have reduced females' xenophobic responses to males in the present study is that animals were tested in a neutral (but somewhat familiar) test cage, out of visual, auditory and olfactory contact with familiar groupmates. In contrast, behavioural tests in previous studies were typically conducted in cages adjacent to, and sometimes in view of, the animals' familiar social groups (Evans 1983; Sutcliffe & Poole 1984a; Anzenberger 1985). Finally, females' willingness to mate with unfamiliar males in the present study might have been enhanced by our procedure of separating males and females from opposite-sexed groupmates at least 16 h before each test. However, Abbott (1984b) found that females living in mixed-sex groups of unrelated adults readily mated with unfamiliar males several minutes following removal from the familiar social group. Whatever the reason for the disparity between the present and previous findings, it is clear that mated female common marmosets do not consistently avoid sexual interactions with extragroup males.

Absence of Hormonal Differences between Fathers and Sons

Fathers and sons in this study showed no differences in circulating testosterone or LH concentrations either under baseline conditions or immediately following sex tests. Previous investigations of reproductive hormones in dominant and subordinate male callitrichids have yielded mixed findings. Similar to the present results, Abbott & Hearn (1978) found that postpubertal male common marmosets housed with their natal families had circulating testosterone levels similar to those of their fathers. In groups of unrelated adult common marmosets, subordinate males had significantly lower plasma levels of both testosterone and LH than dominant males (Abbott et al. 1992; Abbott 1993; but see Abbott 1984a); however, when rank-2 males, comparable to the eldest sons used in the present study, were examined separately from lower-ranking males, their testosterone levels did not differ reliably from those of dominant animals. Finally, in families of black tufted-ear marmosets, adult sons have significantly lower urinary testosterone levels than their fathers (French & Schaffner 1995). The source of these differences between studies and between species is unclear. However, the finding that callitrichid sons do not consistently have lower reproductive hormone levels than their fathers is in keeping with the general pattern among mammalian (and avian) cooperative breeders that physiological suppression is usually expressed more weakly in males than in females, possibly in association with sex differences in costs of reproduction and in certainty of parentage (Mumme 1997). It may also be relevant that, in at least one wild population of common marmosets, intergroup encounters occurred frequently and most subordinate adult males copulated with extra-group females (Digby 1999). Thus, males may benefit from remaining in a state of breeding readiness, even if no unrelated females are present in the males' own social group, in order to take advantage of possible mating opportunities outside of the group.

Plasma cortisol concentrations, like reproductive hormones, did not differ reliably between marmoset fathers and sons in the present study. Reproductive suppression in cooperative breeders has often been attributed to psychosocial stress; however, recent studies of mammalian and avian cooperative breeders have revealed that subordinate, nonbreeding males usually have circulating or excreted glucocorticoid levels that are similar to or lower than those of dominant, breeding males (Mays et al. 1991; Wingfield et al. 1991; Creel et al. 1996, 1997; Schoech et al. 1997; but see Faulkes & Abbott 1997). This pattern indicates that reproductive inhibition in non-breeders cannot be attributed to increased hypothalamic–pituitary–adrenal activity, and suggests that these subordinate animals are not subjected to chronic stress (Abbott et al. 1997).

In conclusion, the results of this study indicate that reproductive failure in male common marmosets housed with their natal families is mediated by inhibition of sexual behaviour and not by suppression of reproductive hormones. Furthermore, our findings indicate that this behavioural inhibition results from avoidance of mating with highly familiar and/or related females, and possibly from father–son competition for females, rather than from specific, rank-related reproductive suppression imposed by the father.

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