Anim. Behav., 1996, **51,** 657–674

Behavioural and endocrine predictors of dominance and tolerance in female common marmosets, *Callithrix jacchus*

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(Received 10 October 1994; initial acceptance 18 January 1995; final acceptance 19 July 1995; MS. number: A7121R)

Abstract. As a result of social subordination, female common marmosets undergo suppression of ovulation and inhibition of sexual behaviour. This study examined the possibility that subordination also results in decreased aggressiveness and increased submissiveness towards same-sex strangers. Thirty-two adult females were pre-assigned to eight mixed-sex social groups. The females' behavioural and adrenocortical responses to brief confrontations with each of three female strangers were assessed under two conditions: while subjects were pair-housed with a male and while they were living in established, mixed-sex groups. Only 22% of subjects threatened stimulus females in the heterosexual pairs condition, 47% submitted and 31% showed no agonism. These agonistic behaviour patterns reliably predicted whether a female would become dominant or subordinate in a mixed-sex group. When animals were housed in established social groups, both dominant and subordinate females either showed similar responses to stimulus animals as they did in the earlier condition or became somewhat less responsive. Plasma cortisol levels did not correlate with agonistic behaviour and were not elevated by stranger-encounter testing. Finally, in the first 10 days following group formation, subordinate females that had shown ovulatory cyclicity prior to group formation were significantly more likely to receive persistent aggression from their dominant female groupmate than subordinates that had been anovulatory. These results suggest that attainment of social status between female marmosets is closely related to pre-existing individual differences in agonistic behaviour, whereas tolerance between females depends upon ovarian function.

Dominant and subordinate individuals of many species show systematic differences in 'personality', as reflected in patterns of social behaviour, indices of emotionality and physiological responsiveness. For example, dominant individuals have frequently been described as more aggressive and less timid than subordinates (Fox 1972; Buirski et al. 1978; Benton & Brain 1979; Caine et al. 1983; Haug et al. 1986; Drummond & Osorno 1992) and often show lower reactivity of the stress-responsive hypothalamo-pituitary-adrenal endocrine axis (Sassenrath 1970; Ely & Henry 1978; Coe et al. 1982; Kaplan et al. 1986). Such correlations between social status and personality traits can arise through several mechanisms. First, behavioural or physiological attributes of individuals can influence the animal's likelihood of attaining dominant or subordinate status. For example, individual differences in aggressiveness are frequently thought to influence animals' relative likelihoods of attaining dominance (Ginsburg & Allee 1942; Wilson 1975; Slater 1986), and the ability to dominate conspecifics is heritable in some species, even when factors such as age and size are excluded as possible determinants of status (Dewsbury 1990; Moore 1990).

Alternatively, behavioural and physiological differences between individuals can emerge as consequences, rather than causes, of social status. Success in agonistic interactions increases aggressiveness in several species, described as the 'winning begets winning' or 'trained fighter' phenomenon; conversely, defeat in agonistic encounters results in increased submissiveness and reduced aggressiveness, producing 'trained losers'

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0003–3472/96/030657+18 $18.00/0

(see reviews by Jackson 1988; Chase et al. 1994). These behavioural consequences of agonism can be accompanied by physiological changes, leading to rank-related differences in such measures as circulating androgen concentrations, circulating glucocorticoid levels or autonomic nervous activity (see reviews by Miczek et al. 1991; Mendoza 1993). Overall, such socially induced behavioural and physiological changes appear to reinforce the status quo, with dominant individuals becoming more aggressive and subordinate animals becoming more fearful and submissive.

The present study focused on behavioural and hormonal correlates of dominance and subordination in female common marmosets. Social status in these small, New World monkeys has particularly dramatic consequences for reproductive physiology and reproductive success: in both wild and captive groups, reproduction is typically monopolized by a single, dominant female (reviewed by Stevenson & Rylands 1988; Abbott & George 1991). Subordinate females are usually anovulatory due to suppressed pituitary release of luteinizing hormone (Abbott et al. 1981, 1988) and serve as non-reproductive helpers, providing care for the offspring of the dominant female (Stevenson & Rylands 1988). In association with their suppressed reproductive function, subordinate females also have very low plasma cortisol levels compared to their dominant counterparts (Saltzman et al. 1994) and engage in little or no courtship or sexual behaviour (Epple 1967; Rothe 1975; Abbott 1984).

In addition to rank-related differences in endocrine activity and sexual behaviour, dominant and subordinate female marmosets may differ in their aggressiveness to strangers. Epple (1967, 1970) reported that subordinate females were less aggressive towards unfamiliar intruders in the home cage than were dominant females. Because social subordination imposes strict constraints on physiological functioning of female marmosets, and because both ovarian and adrenocortical hormones can influence aggressive and submissive behaviour (Leshner 1980; Monaghan & Glickman 1992), we speculated that subordination might also alter females' agonistic responses to strangers. Such generalized submissiveness or reduced aggressiveness might be expected to lower an animal's risk of incurring aggression or injury from other animals, but may also minimize its chances of gaining a dominant, breeding position in a social group. The objectives of this study, therefore, were to determine whether dominant and subordinate female marmosets differ in their agonistic and adrenocortical responses to conspecifics, outside of the familiar social group, and if so, to determine whether these differences represent causes or consequences of social status.

In a previous paper on the same group of marmosets used in the present study, we examined the interactions between attainment of social status, plasma cortisol concentrations, and ovarian activity before and after group formation (Saltzman et al. 1994). We demonstrated that adult females housed in heterosexual pairs showed marked differences in ovarian function, with 47% of animals undergoing regular, cyclic ovulatory activity, 28% showing anovulation, and the remaining 25% showing sporadic, or oligocyclic, ovulatory function. These patterns of ovarian activity were associated with differences in baseline plasma cortisol concentrations: cyclic females had significantly higher cortisol levels than anovulatory females, whether housed in heterosexual pairs or in established social groups. Moreover, ovarian activity prior to group formation appeared to be related to attainment of dominance status, because no anovulatory females became dominant. Social status could not, however, be predicted by inter-individual differences in age, body weight or baseline plasma cortisol.

In the present study, we characterized the same animals' behavioural dispositions and investigated the relationship of these dispositions to plasma cortisol, ovarian function and attainment of socal status. Using standardized tests in a neutral cage, we evaluated females' behavioural and adrenocortical responses to female strangers under two conditions: while subjects were housed in heterosexual pairs, and while each subject was either dominant or subordinate in a mixed-sex social group. Because female marmosets that become subordinate experience reduced or no reproductive success, and because adult marmosets tend to be highly aggressive towards same-sex strangers (Epple 1967; Evans 1983; Sutcliffe & Poole 1984; Harrison & Tardif 1989), we anticipated that all or most animals would initially behave aggressively towards unfamiliar females in stranger-encounter tests as well as in a new social group. When animals were housed in established groups, however, we hypothesized that only dominant females would continue to behave aggressively in

stranger-encounter tests, whereas subordinate females would show reduced aggression and/or increased submission towards strangers.

METHODS

Subjects

Subjects were 32 captive-born, young adult female common marmosets (mean ± SE age = 25 ± 2 months, range 16–54 months). Before data collection began, we pair-housed each subject with an adult male for at least 12 days (58 ± 10 days) and pre-assigned it to one of eight social groups. The four females pre-assigned to each group were unrelated and had not previously lived together, with the exception of two animals that were housed together in a group of six juveniles for 4 weeks, 8 months earlier. We used eight additional females from our breeding colony as stimulus animals. Stimulus females were housed with a male pair-mate and up to seven offspring, were 28–64 months of age, and were typically pregnant and/or lactating throughout the study.

Monkeys lived indoors in stainless steel cages, which contained perches and nestboxes and allowed visual, auditory and olfactory contact with marmosets in other cages. We housed male–female pairs in cages measuring approximately 89 × 85 × 85 cm or 75 × 70 × 69 cm. Social groups were formed in a complex of three adjoining cages (group formation cage; each segment 88 × 85 × 86 cm) separated by partial partitions, allowing monkeys to escape temporarily from physical and visual contact with one another. Each group either remained in this complex until the end of the experimental procedures or was moved to a new home cage (two adjoining cages, each measuring 89 × 85 × 85 cm, or a single cage measuring 61 × 91 × 183 cm) at least 2 weeks following group formation. Monkeys were fed daily at 1300–1500 hours, and water was available ad libitum. Additional details on animal management are provided by Saltzman et al. (1994).

Design

The experiment consisted of three phases. During the heterosexual pairs phase (approximately 2 weeks), each subject was housed with a male and underwent four stranger-encounter tests (see below) and four basal blood samples for determination of baseline plasma cortisol concentrations (see below). The group formation phase (3 days) began several days following conclusion of these procedures. We released the four female subjects and four adult males (which were unfamiliar to one another and had not been housed with any of the female subjects for at least 4 months) into the group formation cage and monitored behaviour and plasma cortisol levels for 3 days. The established groups phase (3 weeks) began 5 weeks after group formation. We collected behavioural data from established social groups to confirm the social status of each female, and then conducted stranger-encounter testing and basal blood sampling as in the heterosexual pairs phase.

Stranger-encounter Tests

To avoid home-cage effects on social behaviour, we conducted stranger-encounter tests in a relatively unfamiliar test apparatus consisting of two stainless steel mesh cages: a test cage (61 × 46 × 61 cm) to one end of which was affixed a smaller stimulus cage (18 × 25 × 20 cm; Fig. 1). In the month prior to the beginning of stranger-encounter testing, we released each subject into the test cage for approximately 1 h on three different occasions to facilitate habituation to the test set-up. Stimulus females underwent one brief adaptation trial (approximately 15 min) in the stimulus cage. We conducted habituation trials and stranger-encounter tests in a room in which no other animals were housed, but which was adjacent to the rooms housing the animals' home cages. During testing, therefore, monkeys had auditory access to the remainder of the colony.

At the outset of each test, the opaque partition was positioned between the two cages, and the stimulus and subject animals were manually captured from their home cages and immediately released into the stimulus cage and test cage, respectively. Following a 5-min adaptation period during which no data were collected, we collected behavioural data (see below) for a 5-min baseline period. We then removed the partition and collected behavioural data for an additional 15 min. At the conclusion of the test, we immediately captured the subject and collected a blood sample for plasma cortisol determination (see below). We then returned the subject and stimulus monkeys to their home cages.

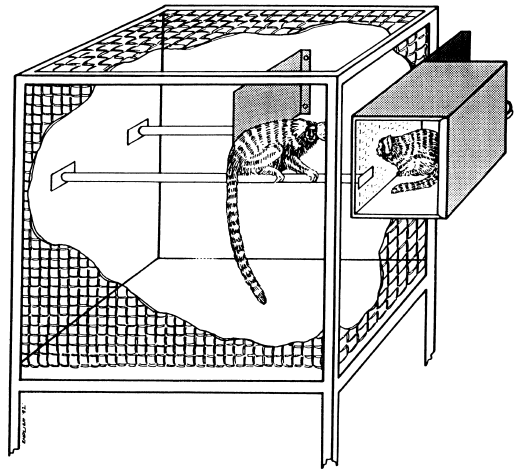


Figure 1. Illustration of stranger-encounter test set-up. The test cage and stimulus cage were separated by a mesh panel and by an opaque, remotely operated sliding partition; when the partition was removed, the animal in each cage could see and reach into the adjacent cage. The stimulus cage was designed to minimize movement of the stimulus animal towards or away from the subject. A perch traversed the width of the test cage, facilitating movement of the subject towards or away from the stimulus cage. A stainless steel 'privacy panel' (20 × 20 cm) projected from the back wall of the test cage, halfway along the width of the cage. A small perch (28 cm), parallel to the first perch, ran between the panel and the cage wall furthest from the stimulus cage, allowing the subject to move out of view of the stimulus animal.

A trained observer collected behavioural data from behind a one-way shade using a laptop computer and a predetermined list of behaviour patterns (Table I). For 'proximity to stimulus cage' and 'behind privacy panel', we scored both duration and number of bouts; for the remaining behaviour patterns, we scored frequency of occurrence. Inter-observer reliability scores averaged 0.89 for behavioural frequencies and 0.96 for behavioural durations (Spearman's rho, $N=8$ 15–20 min samples).

Each subject underwent four stranger-encounter tests during the heterosexual pairs phase: one test with each of three stimulus females, which were unfamiliar to and unrelated to the subject, and one control test in which no stimulus female was present (empty-cage condition). In the established groups phase, each subject again underwent four tests with the same stimulus animals and schedule of testing as in the earlier period. We used the same three stimulus females for all four subjects in each social group but not necessarily for subjects in different groups. Order of stimulus conditions was balanced across subjects within each group. We tested animals between 0900 and 1145 hours and balanced the time of testing across days and subjects. We tested each subject no more than once in any 2-day period, and no animal served as a stimulus in more than one trial on any day of testing.

Formation of Social Groups

On day 1 of the group formation phase, we simultaneously released four female subjects and four adult males into the group formation cage at 0930–1240 hours. For the next 2 h, three observers recorded individual behaviour patterns and social interactions on audio tape. Two observers similarly collected 1 h of behavioural data approximately 24 (day 2) and 48 h (day 3) following group formation. At about 0900 hours on days 1, 2 and 3 of group formation, we collected blood samples from all animals in the group for cortisol determination. Following blood sample collection on days 2 and 3, we inspected all animals for wounds, treated them as necessary, and returned them to the group formation cage. We permanently removed individuals from the group at any time following group formation if they received persistent aggression from higher-ranking animals of the same sex. Prior to group formation, we coloured each monkey's ear tufts to facilitate identification of individuals (Redken Deco Color, Canoga Park, California).

We classified each female as dominant or subordinate on the basis of submissive behaviour patterns (Saltzman et al. 1994). Because some subordinate females in two groups did not interact agonistically with all other subordinate females prior to removal of animals from the groups, we did not assign animals a numerical rank. We defined the dominant female as the female that received submission from each of her three female groupmates, and did not submit to them, in the last 30-min period in which we observed her to interact agonistically with each other female. We used these initial status designations to analyse data collected prior to and during group formation. For analyses of data collected during the established groups condition, we based

Table I. Behaviour patterns scored in stranger-encounter tests

Behaviour pattern	Definition
Aggressive behaviour	
Threat (erh-erh)	Low-pitched staccato chattering ('chatters given when angry': Epple 1968; 'erh-erh': Stevenson & Poole 1976; 'vocal threat': Abbott 1984)
Frown	Lower eyebrows while staring (Stevenson & Poole 1976)
Genital present	Orient anogenital region towards stimulus cage and raise tail to expose genitals (Stevenson & Poole 1976; Abbott 1984)
Ear-tufts flick	Rapid back-and-forth movement of ear tufts (Stevenson & Poole 1976)
Bristle-strut	Any combination of arching posture, strut locomotion and piloerection ('Katzbucke Imponieren': Epple 1967; 'arch-bristle locomotion': Stevenson & Poole 1976)
Attempt attack	Lunge at, or attempt to grab, bite or scratch, stimulus animal (Harrison & Tardif 1989)
Fight	Both animals grapple, including attempted or actual grabbing, biting, scratching or lunging
Submissive behaviour	
Vocal submit (ngä)	Relatively low-pitched, atonal, infantile squeal (Epple 1968)
Facial submit	Tufts flatten (lower ear tufts against side of head) and/or facial grimace (mouth partially open with corners of mouth retracted, exposing lower and sometimes upper teeth) and/or eyes slit (eyelids half closed) (Stevenson & Poole 1976; Abbott 1984)
Continuous submit	Continuous vocal or facial submit lasting ≥ 5 s
Investigative behaviour	
Look at stimulus cage	Look directly at or into stimulus cage
Sniff stimulus cage	Sniff at stimulus animal or at mesh directly in front of stimulus cage, or push face up to mesh
Reach into stimulus cage	Push, or attempt to push, fingers through mesh into stimulus cage
Other social behaviour	
Tongue in–out	Rhythmically move tongue in and out of mouth while facing stimulus cage (Epple 1967; Stevenson & Poole 1976)
Location	
Proximity to stimulus cage	Monkey's head within arm's reach (10 cm) of stimulus cage
Behind privacy panel	Monkey's head behind privacy panel, i.e. out of visual contact with stimulus animal
Individual behaviour	
Tsee-tsee/tsik-tsik	Series of loud, sharp, high-pitched calls (Epple 1968)
Long call	Long, high-pitched, whistle-like contact call ('phee': Epple 1968)
Anogenital scent-mark	Rub or drag anogenital region along substrate
Sternal scent-mark	Rub sternal region along substrate (Stevenson & Poole 1976)
Gouge	Gnaw at substrate or object (Epple 1970; Stevenson & Poole 1976)
Self-directed behaviour	
Scratch	Common usage; scratch at own body
Autogroom	Use hands and/or mouth to pick through fur
Tag manipulate	Hold, pull, bite or pick at ID tag or collar

designation of social status on behavioural data collected 5 weeks following group formation using the same 3-day schedule of observations as in the group formation period (see also Saltzman et al. 1994).

Blood Sample Collection, Hormone Assays and Termination of Pregnancies

To determine baseline plasma cortisol concentrations and to control for diurnal rhythms in cortisol levels across the testing period, we collected two basal blood samples from each subject during each week of stranger-encounter testing in both the heterosexual pairs phase and the established groups phase. On each day of basal sampling we collected samples at about 0900 and 1145 hours; these times roughly corresponded to the times at which stranger-encounter testing began and ended on each test day. After each sample, we returned the monkey to its home cage. Serial blood sampling performed in this manner does

not elevate plasma cortisol levels in marmosets (Saltzman et al. 1994). At least 6 days elapsed between successive days of basal blood sample collection, and we did not collect baseline samples on days of behavioural testing. We also collected blood from all subjects twice per week throughout the study, and for at least 7 weeks prior to group formation, for plasma progesterone determination to monitor ovarian activity.

We manually captured monkeys, briefly placed them in a restraint tube (Hearn 1977) and collected 0.1–0.3 ml blood by femoral puncture into a heparinized syringe. During the group formation and established groups phases, we captured all females in the same group and sampled them in rapid succession. For samples assayed for cortisol, the latency from initial entry into the cage to blood sample collection was less than 5 min and averaged 92 s. Blood samples were centrifuged at 2000 rpm for 10 min and the plasma extracted and frozen at -20°C until assayed.

We measured plasma progesterone concentrations directly, without extraction, using a heterologous enzyme immunoassay (Saltzman et al. 1994). The sensitivity of the assay at 90% binding was 4.5 pg, and the intra- and inter-assay coefficients of variation of a marmoset plasma pool (38% binding) assayed in duplicate on each plate were 2.79% and 12.12%, respectively ($N=126$ assays). We measured plasma cortisol concentrations using an antibody-coated-tube radioimmunoassay kit, GammaCoat (Incstar Corp., Stillwater, Minnesota; Saltzman et al. 1994). Assay sensitivity was 1.0 µg/dl, and intra- and inter-assay coefficients of variation of a plasma pool assayed in duplicate in each assay (40% binding) were 5.35% and 6.66%, respectively ($N=15$ assays).

To prevent term pregnancies, we injected subjects intramuscularly with 0.75 µg cloprostenol sodium, a prostaglandin $F2_\alpha$ analogue (Estrumate, Mobay Corp., Shawnee, Kansas), 14–30 days after each ovulation, defined as the day preceding a rise in plasma progesterone concentrations above 10 ng/ml (Harlow et al. 1983). This treatment causes luteolysis and the termination of the luteal phase or early pregnancy (Summers et al. 1985).

Analysis

Data are presented as $\bar{X} \pm$ SE. We characterized each female's ovarian activity as cyclic, acyclic or oligocyclic based on plasma progesterone concentrations in semi-weekly blood samples, using parameters provided by Harlow et al. (1983; see also Saltzman et al. 1994). Briefly, we classified females as acyclic if they showed no sustained (two or more successive samples) elevations of progesterone levels above 10 ng/ml. Cyclic females showed regular, sustained progesterone elevations, with luteal phase (progesterone >10 ng/ml) durations of at least 11 days ($\bar{X} - 2$ SD) and follicular phase (progesterone ≤ 10 ng/ml) durations of 13 days or less ($\bar{X} + 2$ SD); and oligocyclic females showed one or more luteal phase lasting less than 11 days and/or one or more follicular phase lasting more than 13 days. Females that were cyclic, oligocyclic and acyclic during the 37 days ($\bar{X}$ cycle length + 2 SD) prior to group formation showed no significant differences in body weight at the time of group formation, but did differ in age: cyclic females ($N=15$) were significantly older than acyclic females ($N=9$), and oligocyclic females ($N=8$) did not differ reliably from the other two groups. When animals were housed in established groups, all dominant females showed cyclic ovarian activity, and all subordinate females were acyclic (Saltzman et al. 1994).

We analysed cortisol data, as well as animals' weights and ages, by analysis of variance and *t*-tests; post-hoc comparisons used the Tukey HSD test (Systat version 5.2.1). We analysed behaviour patterns scored in stranger-encounter tests and during group formation nonparametrically using the Kruskal–Wallis one-way analysis of variance, the Mann–Whitney *U*-test, and the Wilcoxon matched-pairs signed-ranks test. Post-hoc comparisons following significant Kruskal–Wallis tests used the Tukey-type test described by Zar (1984), with Dunn's correction for unequal sample sizes. Because we generally performed three different between-groups analyses on behavioural responses to stranger-encounter tests and group formation (cyclic versus oligocyclic versus acyclic; aggressive versus non-agonistic versus submissive; dominant versus subordinate), we used the Dunn–Sidak correction to maintain a family-wise error rate of 0.05; this yielded a critical *P*-value of 0.017 for these analyses (Chandler 1995; Sokal & Rohlf 1995). For all other analyses, we assessed significance at the 0.05 level.

To determine the significance of the observed patterns of dominance attainment, we calculated

Table II. Mean (± SE) behaviour scores during exposure to stimulus females and to the empty stimulus cage in stranger-encounter tests while subjects were housed in male–female pairs ($N = 32$)

Behaviour pattern	Empty-cage condition	Stimulus-female condition	Stimulus-female versus empty-cage condition (Wilcoxon)		
			P	*z*	*N*
Investigative behaviour					
Look at stimulus cage*	34.1 ± 2.5	69.9 ± 3.3	<0.001	4.86	32
Sniff stimulus cage*	3.9 ± 0.5	11.0 ± 1.1	<0.001	4.49	30
Reach into stimulus cage*	0.1 ± 0.1	2.2 ± 0.7	<0.001	3.83	19
Location					
Proximity to stimulus cage†	139.8 ± 20.1	241.5 ± 25.3	<0.005	3.20	32
Behind privacy panel†	95.1 ± 23.7	63.1 ± 12.2	NS	− 1.21	30
Agonistic behaviour					
Threat*	Not observed	1.1 ± 0.6	<0.05	2.37	7
Bristle-strut*	Not observed	0.9 ± 0.3	<0.01	2.67	9
Facial submit*	0.03 ± 0.03	0.8 ± 0.2	<0.005	3.19	13
Vocal submit*	Not observed	0.8 ± 0.5	<0.05	2.02	5
Tongue in–out*	Not observed	0.8 ± 0.6	<0.05	2.53	8
Self-directed behaviour*‡	2.5 ± 0.6	4.1 ± 1.0	<0.05	2.35	30
Individual behaviour					
Scent-mark*	0.3 ± 0.1	0.9 ± 0.3	NS	1.81	12
Long call*	4.7 ± 1.5	3.9 ± 1.1	NS	− 0.58	20

N is the number of animals that performed each behaviour and therefore contributed data to the Wilcoxon test.
*No. of occurrences per 15 min, averaged across three stimulus-female tests or one empty-cage test.
†Total no. of s per 15 min, averaged across three stimulus-female tests or one empty-cage test.
‡Combined score for groom, scratch and tag-manipulate.

the probability that they occurred by chance alone, based on the distribution of animals (e.g. cyclic, oligocyclic or acyclic; aggressive, non-agonistic or submissive) in each of the eight social groups. For example, to compute the probability that no acyclic females became dominant, we first determined the probability, for each social group individually, that a cyclic or oligocyclic female became dominant, based on the relative numbers of cyclic/oligocyclic and acyclic animals in each group. We then calculated the product of these eight independent probabilites. We used a comparable procedure to calculate the significance of the observed pattern of dominance attainment with respect to animals' agonistic behaviour in stranger-encounter tests.

In the 5 weeks following group formation, we disbanded one group and removed 11 females from the remaining groups because of persistent intra-sexual aggression. These included 10 subordinate females and one dominant female that sustained severe wounds (CJ0038, group 2); in this latter group, a submissive female (CJ0010) therefore became dominant by default. We thus collected data from 17 females in seven established groups. However, we omitted data from two of these females from analyses of rank-related differences in behaviour and cortisol in established groups, because we could not confirm their ranks in observations of the group 5 weeks following group formation (Saltzman et al. 1994).

RESULTS

Heterosexual Pairs

Behavioural responses to stranger-encounter tests

As expected, exposure to a stimulus female markedly altered subjects' behaviour in stranger-encounter tests (Table II). Several behaviour patterns, including ear-tufts flick, genital present,

frown, fight and sternal scent-mark, were never performed in stranger-encounter tests. Others, including attempt attack, gouge and tsee-tsee/tsik-tsik, were performed too infrequently for statistical analysis.

The most striking result of stranger-encounter tests was the pronounced inter-individual variation in agonistic behaviour patterns (Fig. 2). Only seven of the 32 subjects (22%) threatened stimulus females. In contrast to these subjects, which were designated 'aggressive', 15 'submissive' subjects (47%) performed facial and/or vocal submits to stimulus females. The remaining 10 subjects (31%) neither threatened nor submitted to stimulus females and were designated 'non-agonistic'. No subject both threatened and submitted to stimulus females. Kruskal–Wallis tests comparing other behaviour patterns of aggressive, non-agonistic and submissive females did not reveal any additional significant differences.

Aggressive, non-agonistic and submissive females did not differ reliably in either age (31 ± 5 versus 22 ± 1 versus 26 ± 3 months, respectively) or weight (352 ± 11 versus 361 ± 20 versus 349 ± 9 g, respectively) at the time of group formation. To determine whether they differed in their patterns of ovarian activity prior to group formation, we performed the Fisher exact probability test in two ways. First, we compared aggressive and non-aggressive (non-agonistic + submissive) females with respect to the occurrence of cyclic/oligocyclic versus acyclic ovarian activity. This analysis indicated that aggressive and non-aggressive animals did not differ reliably in their patterns of ovarian activity. Second, we compared submissive and non-submissive (non-agonistic + aggressive) females with respect to the occurrence of cyclic/oligocyclic versus acyclic ovarian activity. This test revealed that submissive females were less likely than non-submissive animals to show cyclic or oligocyclic ovarian activity, and more likely to be anovulatory ($P < 0.05$). Although both cyclic and oligocyclic females were distributed more or less equally among the aggressive, non-agonistic and submissive categories, almost all of the acyclic subjects (seven of nine) submitted to stimulus females, and none threatened them (Fig. 3). This result might have been related to the younger ages of acyclic females than of cyclic or oligocyclic females.

To determine whether responses to stimulus females corresponded to the subject's ovarian status, we compared behaviour scores during exposure to stimulus animals between cyclic, oligocyclic and acyclic subjects. As indicated above, vocal submits (Kruskal–Wallis test: $H = 14.5$, $N = 32$, $P < 0.001$) differed significantly in association with patterns of ovarian activity, because acyclic females were the only animals to perform this behaviour (2.9 ± 1.5; Tukey-type test versus cyclic: $P < 0.005$; versus oligocyclic: $P < 0.01$). Conversely, acyclic females were the only group that never performed tongue in–out (cyclic: 1.4 ± 1.2, oligocyclic: 0.5 ± 0.4; Kruskal–Wallis test: $H = 3.94$, NS), a behaviour that has been described as serving a sexual, affiliative or aggressive function (Epple 1967; Stevenson & Poole 1976).

Cortisol responses to stranger-encounter tests

Plasma cortisol concentrations in blood samples collected immediately following stranger-encounter tests averaged 196.9 ± 15.9 μg/dl. To determine whether cortisol levels were significantly elevated following stranger-encounter tests as compared to basal levels, we performed a two-way ANOVA (basal versus post-test × 0900 hours versus 1145 hours), using each female's mean basal cortisol values at 0900 and 1145 hours and post-test values only for her two tests at the corresponding times of day. This analysis revealed that stranger-encounter tests did not significantly elevate cortisol levels above baseline values.

Cortisol values did not differ reliably across days or times of stranger-encounter testing or between stimulus-female and empty-cage tests. However, both basal (results presented in Saltzman et al. 1994) and post-test ($F_{2,29} = 8.17$, $P < 0.005$) plasma cortisol levels were strongly associated with patterns of ovarian activity. Post-test cortisol concentrations of acyclic females (113.9 ± 17.1 μg/dl) were significantly lower than those of both cyclic (239.5 ± 21.2 μg/dl; Tukey test: $P < 0.005$) and oligocyclic animals (210.3 ± 28.5 μg/dl; Tukey test: $P < 0.05$). A similar pattern was seen in basal cortisol levels, however, and ovarian activity did not significantly influence the differences between basal and post-test cortisol levels. No differences in basal or post-test cortisol concentrations were found between aggressive, non-agonistic and submissive females, even when acyclic females were excluded from the analyses.

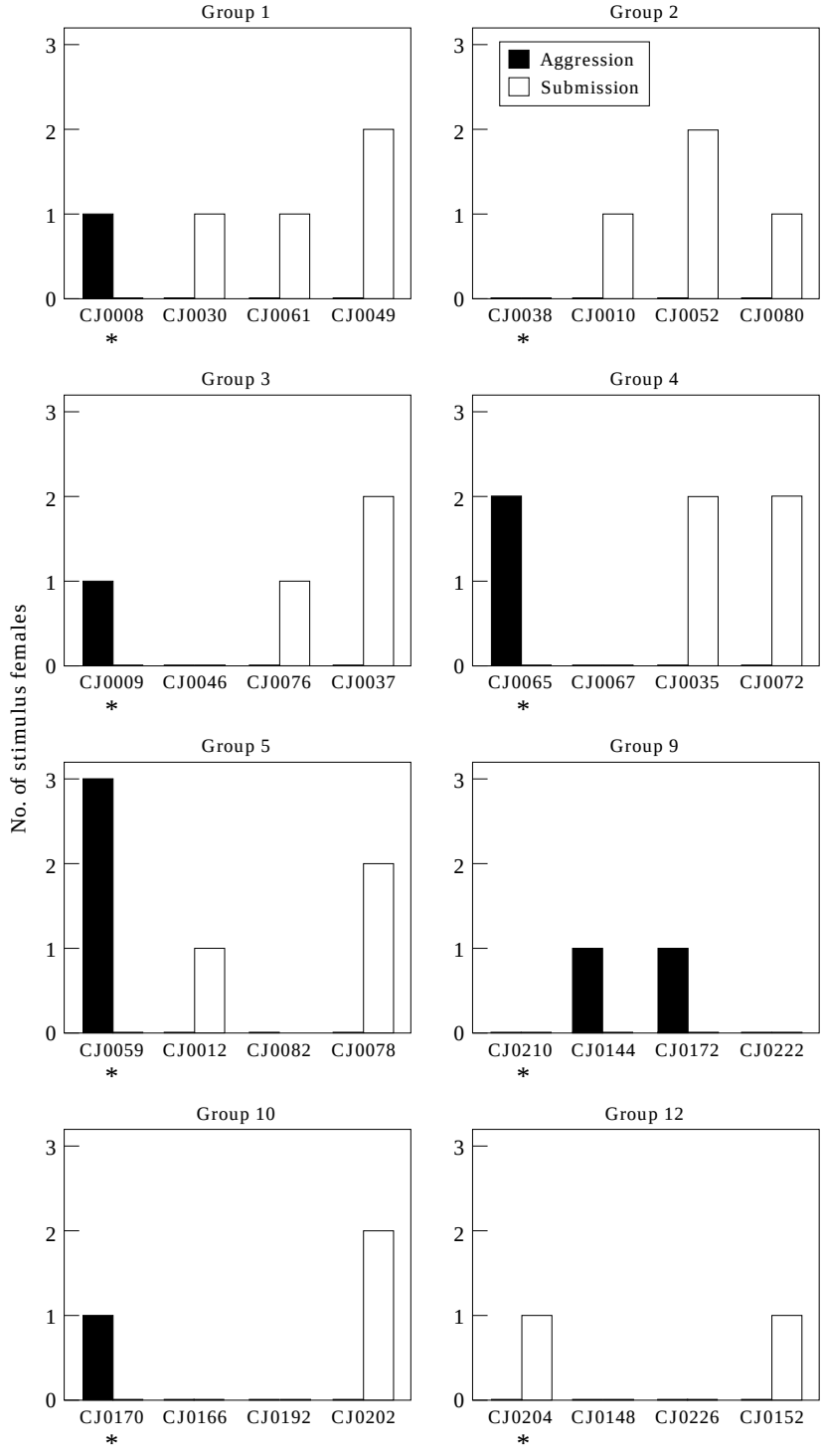


Figure 2. Number of stimulus females to which each subject directed aggression or submission in stranger-encounter tests prior to group formation. Asterisks indicate which female subsequently became dominant in each group.

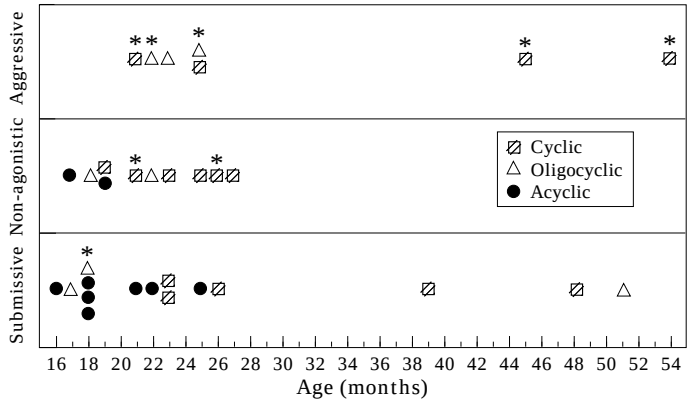


Figure 3. Relationships between age, agonistic behaviour in stranger-encounter tests prior to group formation and ovarian activity of individual female marmosets during the 37 days prior to group formation. Asterisks denote animals that became dominant.

Group Formation

In six of the eight groups, the female that was the most aggressive and/or least submissive in stranger-encounter tests attained the dominant position (Fig. 2). In five of these groups, only the dominant female had threatened any stimulus animals in stranger-encounter tests. In one group, the dominant female had not threatened in any stranger-encounter tests but was the only female in the group that never submitted to a stimulus animal. In the remaining two groups, either a non-agonistic female became dominant over several aggressive groupmates, or a submissive female became dominant over several non-agonistic groupmates.

Overall, based on the distribution of aggressive, non-agonistic, and submissive females across the eight social groups, the probability that the most aggressive and/or least submissive female would become dominant in at least six of eight groups was $P=0.01$. Because females showing acyclic ovarian activity were significantly younger than other females, which might have contributed to their likelihood of attaining subordinate status, we repeated the analysis with all acyclic females excluded; this yielded a probability of $P<0.05$. Thus, whether or not acyclic females were included in the analysis, a female's agonistic behaviour in stranger-encounter tests during the heterosexual pairs condition was a reliable predictor of her likelihood of attaining dominance in a newly formed social group. Consistent with their greater aggressiveness and lower submissiveness in stranger-encounter tests, females that later became dominant performed more threats to stimulus females (3.8 ± 2.1 versus 0.2 ± 0.2; Mann–Whitney *U*-test $U=148.5$, $N=32$, $P<0.005$) and reaches into the stimulus cage (4.7 ± 2.3 versus 1.3 ± 0.5; $U=154.0$, $N=32$, $P<0.01$) during the heterosexual pairs condition than did those that became subordinate. Finally, the probability that no acyclic female became dominant was $P=0.05$, suggesting that anovulatory females were reliably less likely to attain dominance than were females with cyclic or oligocyclic ovulatory activity.

Dominant and subordinate females showed clear behavioural differences as early as the first hour after group formation. As in our previous results for data collected during the first 3 days of group formation (Saltzman et al. 1994), dominant females performed more intra-sexual aggression (67.9 ± 16.8 versus 34.4 ± 14.1 bouts; Mann–Whitney *U*-test: $U=155.0$, $N=32$, $P=0.01$), performed less intra-sexual submission (0.5 ± 0.4 versus 32.2 ± 8.0 bouts; $U=8.5$, $N=32$, $P<0.001$) and received more intra-sexual submission (53.3 ± 11.8 versus 14.6 ± 3.8 bouts; $U=169.0$, $N=32$, $P<0.005$) than did subordinates. Dominant females also scent-marked more frequently (17.0 ± 5.9 versus 2.5 ± 1.1 bouts; $U=174.5$, $N=32$, $P<0.001$) and bristle-strutted in more 10-min intervals (5.0 ± 0.4 versus 1.6 ± 0.4; $U=167.5$, $N=32$, $P<0.005$) than did subordinates. Few behavioural differences emerged during the first hour of group formation between cyclic, oligocyclic and acyclic females or between females

that were aggressive, non-agonistic and submissive in stranger-encounter tests. Submission received from other females during the first hour of group formation was associated with ovarian activity (Kruskal–Wallis test: $H = 8.45$, $N = 32$, $P = 0.015$), because cyclic females received more submission than did acyclic females (37.5 ± 8.5 versus 8.1 ± 5.0 bouts; Tukey-type test: $P < 0.05$; oligocyclic animals: 17.6 ± 6.7, NS). In contrast, frequency of scent-marking during the first hour of group formation was associated with patterns of agonism in stranger-encounter tests (Kruskal–Wallis test: $H = 10.37$, $N = 32$, $P < 0.01$), because aggressive females performed significantly more scent-marks than did submissive females (10.9 ± 4.5 versus 3.7 ± 3.2; Tukey-type test: $P < 0.01$; non-agonistic females: 6.5 ± 2.8, NS).

Tolerance of subordinates by dominants

In considering the significance of the different agonistic styles observed in stranger-encounter tests, we speculated that those subordinate females that showed the most submissive and/or least aggressive behaviour might be the most likely to be tolerated by their dominant female groupmate. To evaluate this hypothesis, we inspected the data on removal of females from social groups. Eleven of the 24 subordinate females received intense, persistent aggression from their dominant female cage-mate within the first 10 days of group formation, necessitating their permanent removal from the group. We found no evidence that a female's likelihood of being targeted for persistent aggression was related to her agonistic style in stranger-encounter tests: seven of 14 submissive subordinates (50%), three of eight non-agonistic subordinates (37.5%) and one of two aggressive subordinates (50%) had to be removed. Further inspection of the data, however, suggested that the pattern of tolerance and intolerance shown by dominant females was related to the ovarian status of subordinate females: nine of 10 subordinates (90%) that had shown cyclic ovarian activity prior to group formation had to be removed from their groups, whereas only one of nine acyclic subordinates (11%) and one of five oligocyclic subordinates (20%) had to be removed. When acyclic and oligocyclic subordinates were considered together, they were significantly less likely to be removed than were cyclic subordinates (Fisher test: $P < 0.01$). In association with the significant age difference between cyclic, oligocyclic and acyclic females, subordinates that were tolerated by their dominant female groupmates were significantly younger than those that were not tolerated (20 ± 1 versus 30 ± 3 months, respectively; $t = 3.09$, df = 22, $P < 0.01$). Subordinates that were and were not tolerated did not differ reliably in body weight at group formation (345 ± 15 versus 365 ± 12 g, respectively).

Established Groups

Behavioural responses to stranger-encounter tests

We found no evidence that marmosets became either more aggressive or more submissive to stimulus animals as a result of living in a heterosexual group or attaining dominant or subordinate status (Table III). Of the two subjects that threatened stimulus animals following group formation, both were dominant females that had previously threatened stimulus animals in the heterosexual pairs phase (Fig. 4). Similarly, the five subjects that submitted to stimulus females in the established groups condition were all subordinate females that had also submitted to stimulus females in the heterosexual pairs condition. Thus, most females (11 of 17, 65%) showed the same agonistic style both before and after group formation, but animals were somewhat less likely to either threaten or submit to same-sex strangers when housed in established groups than when housed in heterosexual pairs. In addition, females bristle-strutted and reached into the stimulus cage less frequently in the established groups condition than in the heterosexual pairs condition (Table III). Among the 15 animals that could be unambiguously classified as dominant or subordinate in established social groups, dominants performed significantly more long calls than subordinates (22.8 ± 11.0 versus 0.9 ± 0.9, respectively; Mann–Whitney U-test: $U = 44.0$, $N = 15$, $P = 0.017$). Differences in facial submits (0.0 versus 0.4 ± 0.2; $U = 12.0$, $N = 15$, $P = 0.035$) and total submits (vocal + facial + continuous submits; 0.0 versus 1.4 ± 0.6; $U = 12.0$, $N = 15$, $P = 0.035$) also approached significance but exceeded our modified critical P-value (see Methods) because of the small numbers of animals performing these behaviour patterns.

Table III. Mean (± SE) behaviour scores during exposure to stimulus females in stranger-encounter tests while subjects were housed in established mixed-sex groups and in heterosexual pairs ($N = 17$)

Behaviour pattern	Heterosexual pairs, Stimulus-female condition§	Established groups, Stimulus-female condition	Heterosexual pairs versus established groups, Stimulus-female condition (Wilcoxon)		
			P	*z*	*N*
Investigative behaviour					
Look at stimulus cage*	70.9 ± 4.6	70.9 ± 6.3	NS	−0.07	17
Sniff stimulus cage*	11.0 ± 1.1	8.8 ± 1.2	NS	−1.79	15
Reach into stimulus cage*	3.2 ± 1.3	0.9 ± 0.4	<0.01	−2.80	11
Location					
Proximity to stimulus cage†	272.2 ± 37.2	208.5 ± 26.5	NS	−1.73	17
Behind privacy panel†	58.7 ± 17.1	65.1 ± 19.0	NS	0.73	17
Agonistic behaviour					
Threat*	1.2 ± 0.8	0.4 ± 0.3	NS	−1.21	5
Bristle-strut*	1.4 ± 0.6	0.4 ± 0.3	<0.05	−2.02	5
Facial submit*	0.8 ± 0.4	0.2 ± 0.1	<0.05	−2.25	8
Vocal submit*	1.5 ± 0.9	0.4 ± 0.2	NS	−1.21	5
Tongue in–out*	0.3 ± 0.2	0.8 ± 0.8	NS	0.37	4
Self-directed behaviour*‡	5.6 ± 1.7	3.0 ± 0.9	NS	−1.44	17
Individual behaviour					
Scent-mark*	1.0 ± 0.4	0.6 ± 0.2	NS	−0.77	13
Long call*	3.5 ± 1.5	8.6 ± 4.5	NS	−0.16	12

N is the number of animals that performed each behaviour and therefore contributed data to the Wilcoxon test.
*No. of occurrences per 15 min, averaged across three stimulus-female tests.
†Total no. of s per 15 min, averaged across three stimulus-female tests.
‡Combined score for groom, scratch and tag-manipulate.
§Data are presented only for animals that were also tested in the established groups condition.

Cortisol responses to stranger-encounter tests

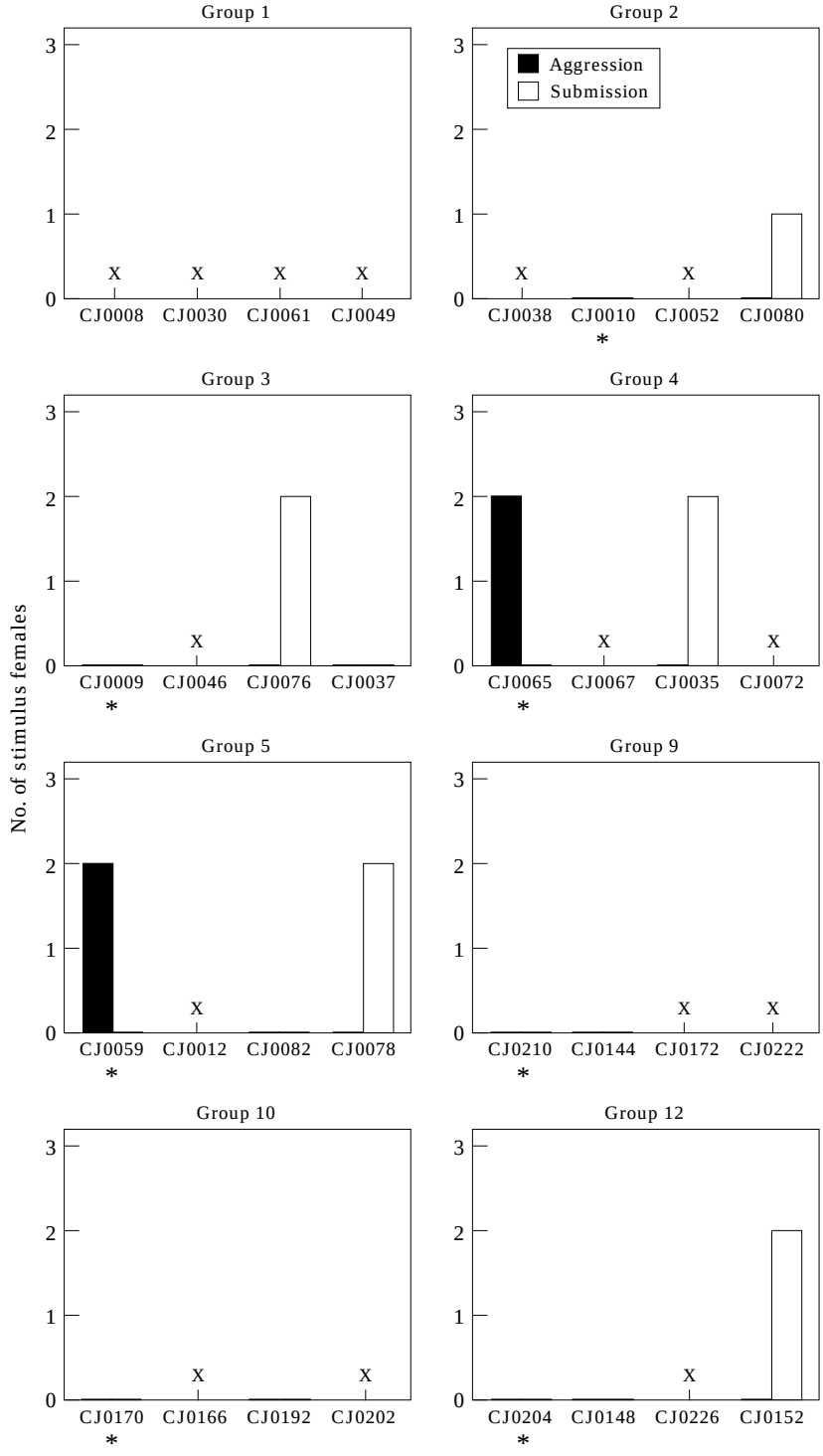
In the established groups condition, as in the heterosexual pairs condition, stranger-encounter tests did not significantly elevate animals' plasma cortisol levels above basal values. Plasma cortisol levels also did not differ reliably across days or times of stranger-encounter tests or between empty-cage and stimulus-female tests (overall mean: 157.0 ± 21.3 μg/dl). Consistent with the earlier association between cortisol concentrations and patterns of ovarian activity, however, both basal (Saltzman et al. 1994) and post-test cortisol levels were higher in dominant (cyclic) females than in their subordinate (acyclic) counterparts (post-test: 199.2 ± 32.2 versus 98.6 ± 12.1 μg/dl; $F_{1,13} = 11.41$, $P = 0.005$).

DISCUSSION

Agonism and Social Status

The results of this study demonstrate that dominant and subordinate adult female marmosets housed in mixed-sex groups differ in their agonistic responses to unfamiliar females. Dominant females tended to perform more aggression and less submission to stimulus females in stranger-encounter tests, and showed more intra-sexual aggression, less intra-sexual submission and more display behaviour during the first hour following group formation than did subordinates. We found no evidence that these differences resulted from or were exaggerated by the differential attainment of social status: animals showed similar behavioural

Figure 4. Number of stimulus females to which each subject directed aggression or submission in stranger-encounter tests 6–7 weeks following group formation. Xs indicate subjects that were removed from their group in the 5 weeks following group formation because of persistent intra-sexual aggression. Asterisks indicate which female was dominant in each group at the time of stranger-encounter testing.


Group 1
Group 2
Aggression
Submission
Group 3
Group 4
Group 5
Group 9
Group 10
Group 12
No. of stimulus females
0
1
2
3
X
CJ0008
CJ0030
CJ0061
CJ0049
CJ0038
CJ0010
CJ0052
CJ0080
CJ0009
CJ0046
CJ0076
CJ0037
CJ0065
CJ0067
CJ0035
CJ0072
CJ0059
CJ0012
CJ0082
CJ0078
CJ0210
CJ0144
CJ0172
CJ0222
CJ0170
CJ0166
CJ0192
CJ0202
CJ0204
CJ0148
CJ0226
CJ0152
*

responses to stimulus females during the heterosexual pairs and established groups conditions, or became somewhat less responsive when housed in a social group. A female's likelihood of attaining dominance in a group, however, was closely related to, and in fact could be predicted by, her previously demonstrated agonistic tendencies. Among female common marmosets, therefore, individual differences in aggressiveness and submissiveness are likely to be a determinant, rather than a consequence, of social status. Furthermore, because dominant females were not older or heavier than subordinates, and were usually wounded at least as extensively as subordinates during group formation, these behavioural differences seem to be more influential in attainment of dominance than age, body weight and fighting ability, factors that have frequently been identified as determinants of dominance in other species (Wilson 1975; Francis 1988).

Dominance between female marmosets is particularly important for reproductive success: subordinate females usually undergo ovulation suppression and therefore fail to breed (reviewed by Abbott & George 1991). We had anticipated, therefore, that all pair-housed females would actively contend for dominance when confronted with a same-sex stranger; i.e. that they would behave aggressively and would not readily submit. The magnitude of inter-individual variation in agonistic behaviour was thus particularly surprising. In contrast to previous studies, in which most adult female marmosets showed aggression towards female strangers (Evans 1983; Sutcliffe & Poole 1984; Harrison & Tardif 1989), almost half of the marmosets in this study submitted to unfamiliar females in stranger-encounter tests; subsequently, many of these submissive individuals did not appear to contend for dominance in a newly formed social group and instead submitted readily to their female cage-mates. Only a minority of subjects in the present study behaved aggressively towards unfamiliar females in stranger-encounter tests and in a new social group, and exhibited little or no submission to other females. Several features of our experimental design may have contributed to these findings. In contrast to previous studies, for example, stranger-encounter testing was performed in a neutral test cage, with the subjects out of visual and physical contact with familiar social partners. Furthermore, most of the subjects were fairly young adults, whereas stimulus animals were generally somewhat older and, unlike the subjects, were breeding. Finally, because we deliberately used a very small stimulus cage, stimulus females were unable to withdraw or hide from subjects and were therefore continuously present, possibly making them more 'intimidating'. In spite of these factors, stranger-encounter testing did not elevate plasma cortisol levels in subjects, suggesting that the testing procedures were not highly stressful.

Another unexpected finding of this study was that both dominant and subordinate females were less responsive to stimulus animals while living in established social groups than when housed in male–female pairs. In the established groups condition, females performed significantly fewer bristle-struts, facial submits, and reaches into the stimulus cage, and tended to perform lower frequencies of most other behaviour patterns, than in the heterosexual pairs condition. Moreover, nearly half (6 of 13) of the females that threatened or submitted to stimulus females in the heterosexual pairs condition did not respond agonistically to stimulus females when housed in established groups, and no animal showed aggression or submission to stimulus females in the latter phase that had not done so prior to group formation. One possible factor contributing to this decline in responsiveness is habituation to the stranger-encounter test paradigm or to the specific stimulus animals. This possibility seems unlikely, because 6–7 weeks elapsed between the two rounds of testing and subjects interacted with each stimulus animal for only 15 min in each condition. A more interesting possibility is that the animals' motivation to interact with same-sex strangers was dampened as a result of living in a mixed-sex social group. Similarly, female squirrel monkeys housed in mixed-sex groups were less attracted to same-sex strangers than were females housed in male–female pairs (Vaitl et al. 1978). In both species, therefore, absence of same-sex companions in the familiar social environment may increase females' motivation to interact with and establish a relationship with female strangers.

The significance of the agonistic styles revealed in this study and their utility in predicting status attainment should be interpreted cautiously. First, although individual differences in agonistic behaviour were strongly related to attainment of dominance, this relationship was not absolute. A female's likelihood of becoming dominant

depended not only on her own agonistic style but also on the agonistic styles of the females with which she was grouped. Second, the labelling of individual marmosets as aggressive, submissive or non-agonistic, and the finding that these categories of animals differed in their attainment of social status, does not imply that individual females were consistent in their agonistic responses to strangers. To the contrary, marmosets showed considerable within-animal variation in their responses to conspecifics: most of the aggressive and submissive animals threatened or submitted, respectively, to some but not all of the three stimulus females. Thus, aggressive, submissive and non-agonistic dispositions represent not absolute differences between individuals but differences in the probabilities that individual animals will behave aggressively or submissively under specific circumstances.

Finally, these agonistic tendencies cannot be assumed to represent stable, long-term characteristics of individual animals. For example, only 65% of animals showed the same agonistic style in the heterosexual pairs and established groups conditions. Moreover, although considerable inter-individual differences in agonism were apparent throughout the age range of subjects, the high incidence of submissiveness in younger, acyclic females suggests that these differences in part reflected an ontogenetic effect. Sutcliffe & Poole (1984) similarly reported that young, presumably anovulatory female marmosets were less aggressive and more submissive to same-sex strangers than older breeding females, and attributed this finding to a pattern of age-dependent social status observed in family groups of marmosets. It is also unknown whether inter-individual differences in agonistic behaviour are based on genetic or environmental differences (Wilson et al. 1994). However, 23 of the 32 subjects in the present study had at least one full sibling that also served as a subject, and only six of the 19 sister pairs showed the same type of agonistic behaviour in stranger-encounter tests prior to group formation, exactly the number predicted by chance.

Hormonal Correlates of Agonistic Behaviour

Activity of the hypothalamo-pituitary-adrenal (HPA) axis, measured by circulating glucocorticoid concentrations, has been found to be a good (Golub et al. 1979; McGuire et al. 1986) or poor (Mendoza et al. 1979; Goo & Sassenrath 1980) predictor of dominance status and has sometimes, but not always, been found to differ systematically between individuals with different 'personality' styles (Ader 1975; Suomi 1987; Ray & Sapolsky 1992). Among female marmosets, plasma cortisol levels were not predictive of social status (Saltzman et al. 1994), did not differ in association with agonistic style and were not elevated by stranger-encounter testing. Instead, as we have previously reported, cortisol concentrations were strongly correlated with ovarian function, presumably due to a stimulatory effect of oestrogen on HPA activity (Saltzman et al. 1994; see also Ziegler et al. 1995). Thus, although dominant females in established groups had significantly higher plasma cortisol levels than subordinates, this difference was probably caused by differential ovarian activity. The present results are thus consistent with our previous conclusion that adrenocortical activity in this species is not highly sensitive to psychosocial variables (Saltzman et al. 1994).

In contrast to HPA activity, patterns of ovarian activity were associated with styles of agonistic behaviour, although not in a straightforward manner. Acyclic (anovulatory) females were never aggressive and were usually submissive in stranger-encounter tests. Furthermore, they tended to perform high frequencies of intra-sexual submission and low levels of display behaviour in newly formed social groups, and they never became dominant. These results may have been related to the young ages of acyclic females in comparison with cycling animals. All of the acyclic subjects were past the average age of puberty (Abbott 1978), however, and three females that were aggressive in stranger-encounter tests and became dominant in their social groups were within the age range of acyclic, submissive animals. In contrast to acyclic marmosets, cyclic or oligocyclic females could show aggressive, submissive or non-agonistic behaviour in stranger-encounter tests, with roughly equal numbers of these animals displaying each type of agonistic behaviour. These results suggest that ovarian cyclicity may be a necessary but not sufficient condition for the expression of intra-sexual aggression in stranger-encounter tests under the conditions used in this study.

Patterns of ovarian activity corresponded not only to the patterns of agonism that marmosets

performed but also to the aggression that they received from other females. Among females that became subordinate in their social groups, those that underwent cyclic ovarian activity prior to group formation were specifically targeted for intense, persistent aggression by dominant females, whereas individuals undergoing oligocyclic or acyclic ovarian activity were usually tolerated by the dominant female, receiving relatively infrequent, low-level aggression. These results suggest that female marmosets are able to detect ovulatory activity in one another, and that dominant females are intolerant of those subordinates that may represent the greatest reproductive competition. The mechanism by which marmosets evaluate ovarian function in one another is unknown. Scent-transfer studies have shown that female marmosets can distinguish cyclic (dominant) from acyclic (subordinate) or ovariectomized female conspecifics using olfactory cues (Smith 1994). Moreover, the most common social behaviour seen immediately following group formation is sniffing, with many of these sniffs directed to another animal's genital region (unpublished data). Olfaction is therefore likely to be important in establishing patterns of tolerance between females based on ovarian function, although a possible role of behavioural cues cannot be excluded.

Reproductive and Social Strategies

The correspondence of different patterns of ovulatory activity with agonistic behaviour performed and received between females suggests that these ovarian patterns are associated with different relative costs and benefits, and perhaps with alternative reproductive/social strategies. Although little is known about how female marmosets attain group membership, dominance and reproductive success under natural conditions, available evidence suggests that several different strategies may be used. First, among *C. jacchus* and two closely related species, *C. flaviceps* and *C. intermedia*, post-pubertal females are thought to usually remain in the natal family, where they frequently serve as non-reproductive helpers (Stevenson & Rylands 1988; reviewed by Ferrari & Digby, in press). Second, recent findings that some wild groups of *C. jacchus* contain two breeding females suggest that some females may be able to reproduce while living with the natal family (Digby & Ferrari 1994). Third, on several occasions, adult or adolescent females have been observed to emigrate, to form new heterosexual groups, or to immigrate into established groups (Hubrecht 1984; reviewed by Ferrari & Digby, in press). Use of these different strategies seems likely to be associated with different agonistic styles and different patterns of ovarian activity among individual animals.

Our findings on agonistic behaviour, ovulatory activity, attainment of dominance and tolerance between female marmosets may have important implications for understanding reproductive strategies and social dynamics in other cooperatively breeding species in which reproduction is usually monopolized by a single female. Among captive naked mole rats, *Heterocephalus glaber*, for example, a similar association between aggressive behaviour and ovarian activity among subordinate females has recently been reported: a small number of subordinate females showed ovulatory activity and 'queen-like' aggressive behaviour while housed with a dominant, breeding 'queen' and were specifically targeted by the queen for aggression; upon removal of the queen, these same females were the most likely to actively contend for dominance (Margulis et al. 1995). The possibility that females differ in their likelihood of accepting subordinate status and reproductive suppression, and particularly the possibility that some females may actively seek out a subordinate position, is consistent with the reproductive suppression model proposed by Wasser & Barash (1983). This model indicates that under certain circumstances, female mammals, particularly young adults, can optimize their lifetime reproductive success by curtailing current reproductive efforts and deferring reproduction until a time when more auspicious conditions prevail.

ACKNOWLEDGMENTS

This research was supported by NIH grants RR00167 and HD07678. We thank J. Hayden and C. Conway for assistance in data collection; S. Brice and D. Wade for maintenance of the animals; W. D. Houser for veterinary care; P. Dubois for computer assistance; R. Pape and D. Zweifel for construction of marmoset housing and testing equipment; G. Scheffler, J. Scheffler and F. Wegner for assistance with hormone

assays; L. Endlich for artwork; and T. Havighurst for statistical advice. We are also grateful to J. P. Hailman, C. T. Snowdon, J. P. Hearn, L. C. Drickamer, J. A. French and P. L. Schwagmeyer for valuable comments on an early draft of the manuscript. Preparation of the manuscript was facilitated by the staff and resources of the Wisconsin Regional Primate Research Center Library. The animals used in this study were maintained in accordance with the recommendations of the *Guide for the Care and Use of Laboratory Animals* and the Animal Welfare Act and its subsequent amendments. All experimental protocols were reviewed and approved by the Graduate School Animal Care and Use Committee of the University of Wisconsin, Madison. The Wisconsin Regional Primate Research Center is accredited by AAALAC as part of the UW-Madison Graduate School. This is publication number 34-015 of the Wisconsin Regional Primate Research Center.

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