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GENDER DIFFERENCES IN MARMOSETS AND TAMARINS: RESPONSES TO FOOD TASKS

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ABSTRACT: The study of behavioural gender differences among Callitrichid primates has been generally neglected. We describe evidence from experimental studies in which adult female tamarins (*Saguinus*) and marmosets (*Callithrix*) demonstrate priority of access to food that is spatially and temporarily restricted. Differences in behavioural strategies between both reproductive and non-reproductive females, and males, are consistent with differences between the genera in their feeding ecology and social organisation. They are also functionally plausible. A recent study gives preliminary data to show that, although mated females in family groups of common marmosets demonstrate priority of access to food sources, overall there are differences in responsiveness that may be influenced by factors such as the time of feeding, energy content and preference of food.

Gender differences among the primates in their feeding behaviour include examples in which adult females demonstrate a priority of access to food (eg Jolly, 1984; Richard, 1987). This is unusual among primates and raises a number of interesting theoretical questions. For example, considerations of functional hypotheses to account for such phenomena include reproductive exclusivity within a small number of adult males and females. The case is most easily explained in the context of monogamy, as in some lemurs and in which paternity is relatively certain. The argument is that male deference to a breeding or potentially breeding female will benefit the future survival of the offspring of that female (eg Richard, 1987).

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The aim of the present paper is to discuss aspects of female priority of access to food among species of tamarins and marmosets. Moreover, in the majority of our experiments at Reading, we have used very simple food tasks in which different species could reach in and take pieces of fruit. These tasks are a kind of embedded food situation that is part of the natural feeding behaviour of these animals. Hence, we have made use of environmental challenges that provide controlled experimental conditions to probe natural behavioural propensities of responsiveness. They are useful for probing differences among species as well as specific behaviour within species.

One experiment in particular led to significant and interesting results, not least because it had a 'respectable' sample size (Box *et al.* 1995). We have presented a series of perspex food boxes (see Figure 1) that measured 15 x 6 x 10cm, with an ample supply of small pieces of chopped apple, into the home cages of 14 pairs of male and female tamarins (*Saguinus* spp.) for 20 min at a time. The idea was to construct simple tasks that varied in complexity and stimulated ongoing interest and activity in the monkeys.

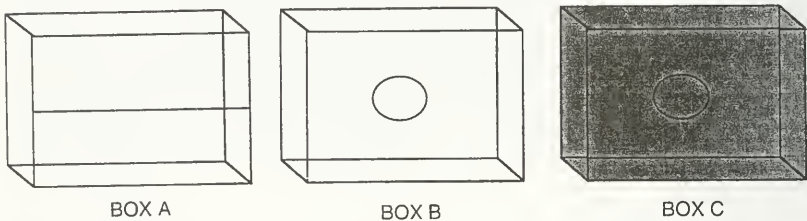


Figure 1. Plastic foraging boxes.

There were 5 pairs of male and female saddle backs (*Saguinus fuscicollis*), 5 pairs of male and female red bellied (*S. labiatus*) and 4 pairs of male and female cotton tops (*S. oedipus*). Baseline observations of activities were made before the experiment began, as well as before each presentation of a food task. These included frequencies and durations of huddling and proximity within the pairs, of feeding, drinking and locomotion in addition to frequencies of scent marking and aggressive behaviour. When the boxes were present, categories of behaviour also included directly approaching the tasks when looking at them, investigation (looking at and manipulating the boxes), attempts to remove food, and successes at removing the food from the boxes. The tasks were presented in a counterbalanced order, and all behaviour was recorded in real time with an on line computer system. The results were calculated using ANOVAS in which the main

variables were the species, the different boxes, and the gender of the tamarins.

It was interesting to note that the saddle backs showed a significantly different profile of responsiveness compared to other species. They were more 'cautious' in their behaviour, as shown by the fact that they approached the boxes less frequently and for less time than either of the other species. Interestingly, these observations contrast with observations of the species in nature, in response to food baited traps and at least in the context of associations with another species of tamarin (Box, pers observation cited Box, 1984; Buchanan-Smith, 1990). Species differences of these kinds are useful to help to build up a body of information that is relevant to the comparative behavioural ecology of the group, as well as towards their management in captivity. However, with reference to our experiment, it was the results on gender differences across all three species of tamarins that raised theoretically interesting questions. We found that the females attempted the tasks more often and for longer than the males, and with greater success in obtaining food. It was also important to find that all the animals were able to solve all the tasks. Again there were no significant differences between the males and females in the amount of time that they spent in investigating the tasks generally, and there were no obvious motivational differences in terms of their energy requirements. Males and females are of equivalent body size, and the females were not pregnant at the time. The crux of the matter was that the significant differences in behaviour between males and females related specifically to successful foraging from the food tasks.

It is also relevant to note here that additional evidence in this context was given in that we also found subsequently (Box and Rohrhuber, unpublished data) that the same adult pairs of animals that were used in the present study showed no gender differences in behavioural responsiveness in daily trials in which they had limited daily access to large unfamiliar outside areas to which their home cages were tunnelled. In other words, responses to new spatial opportunities differed from those given to new foraging opportunities.

In the food task study we concluded that females showed priority of access to the food which, in that case, was a preferred food. Moreover, we found no evidence for overt competition between males and females in the food task situation. Females did not defend the preferred food. There was some increase in aggression within the pairs when the food tasks were present, but there was no aggressive behaviour in the areas around the food boxes. In fact, males often sat

near the females when they were feeding from the boxes and 'looked on'. We described the males as deferring to the females when they fed. There are some other, if few, experiments that concur with these results, and interestingly, within the context of tamarin family groups as in cotton tops (Tardif and Richter, 1981). These also show female priority of access in food 'tasks'.

From a functional perspective it is interesting to consider that deference to a breeding female is advantageous in the context of the communal rearing system of callitrichids that support the energetic demands of multiple births, postpartum oestrous and pregnancy, together with lactation. It is also advantageous in that there is a small number of potentially breeding partners. From a male perspective, we may consider behaviour that is consistent with the protection of his genetic investment including mate guarding and vigilance. From the female perspective, priority of access to preferred and restricted sources of food may be a critical strategy in terms of their energetic demands. Further, it is also the case that non-breeding females may show priority of access to food, as in our experiment with tamarins. Hence, it is also relevant to consider that, apart from the direct energetic influences of reproductive status, females may have different characteristic propensities in foraging situations than males. These differences may become accentuated with regard energetic demands, but females may behave differently from males *per se* in some feeding situations. Moreover, it has also been of interest to discuss differences in behavioural strategies among males and females of species of different genera, and to find that these are consistent with differences between them in terms of their social organisation and feeding ecology (Box, 1997) when supplemental food is presented in spatially and temporarily restricted conditions. In essence, marmosets have been found to defend food assertively (cf Box, 1997), and it is relevant in this context to consider the following (cf Box 1997).

First, that marmosets and not tamarins have specialised dentition for gauging holes in plant material to feed on exudates. Exudates are highly nutritious foods that frequently require energy to obtain. Moreover, and importantly, such food is defensible. Second, that marmosets have home ranges that are smaller than those of tamarin species, and their mating systems tend more towards monogamy. These factors are consistent with the behaviour of marmosets in which adult females obtain priority of access to important static sources of food, by competitive strategies, and the males are relatively secure in their reproductive fitness and inclusive fitness. Third and by contrast,

the natural co-operative nature of tamarin social interactions (Caine, 1993) is consistent with their larger home ranges and relatively unstable social units in which there are more adult males, and paternity is comparatively uncertain. Further, tamarins do eat plant exudates, but this feeding is opportunistic, and does not involve defensible food at particular sites; food is generally more widely scattered. We may consider then that the adult males of different genera may behave differently with regard to female priority of access to food. Male tamarins for instance, may show a greater diversity of functions with regard to feeding situations than do marmosets. These strategies may include mating opportunities. Possibilities will vary according to species and social context. From the perspective of breeding females of all species, however, priority of access may be a critical strategy in terms of their energetic demands. However, it is also clear that non breeding females of different genera may show priority of access to food. Hence, we should consider that, apart from the direct influence of reproductive status, males and females have different characteristic propensities of responsiveness in such as foraging situations. Overall, the results of our research showed robust findings which opened up a whole range of ideas for further study (see Box, 1997).

We have recently extended the work on gender differences in feeding strategies within our long standing collaboration among a number of Brazilian institutions and Reading University in the UK. We plan food task experiments with species of lion tamarins (*Leontopithecus spp*) supervised by Sr Alcides Pissinati at the Rio de Janeiro Primate Centre. Species of this genus have not been examined in the present context and pose some interesting questions (Box, 1997). Further, studies with common marmosets are in progress in captivity at the Universidade Federal do Rio Grande do Norte (UFRN) and at two field sites, namely, that of the UFRN at Nisia Floresta supervised by Dr Maria de Fatima Arruda and at that of the Universidade Federal Rural de Pernambuco (UFRPE) at Tapacura supervised by Dr Maria Adelia Monteiro de Cruz. For instance, because one aspect of central interest in considering gender differences among common marmosets is the relative assertiveness of adult females over desirable food that is restricted in time and space, it is of interest to consider this with reference to an energy model for priority to access to food in captivity. Hence, we consider the influence of reproductive status and assertiveness over food. The behaviour of adult males and females are observed at times of different reproductive energy expenditure. For example, given the energy demands of lactation, we may expect that

reproductive females will demonstrate more evidence of priority of access to food at these times – as by greater assertiveness in aggressive defensive behaviour. A series of preliminary studies has begun at the UFRN to test a number of such hypotheses. We indicate one such study here that raises a number of questions for future research.

METHOD

Subjects

Observations were made on 10 family groups. Five of these contained adult pairs that lived with between two and four offspring, and they produced infants during the observation period. The reproductive pairs of the other 5 similarly sized families did not produce offspring for some time during the course of the study. Importantly, and in contrast to studies mentioned earlier, these observations were made to food that was routinely given to the marmosets. This adds an additional dimension to measures of responsiveness in this domain. The use of novel foods and unfamiliar food tasks certainly require care that we do not confound responses in obtaining food, with differences between males and females in their responses to unfamiliar objects - as by exploration for example.

Procedure

In this study, each family was fed three different kinds of food each day, in the same order, and in a bowl that measured 13cm in diameter. The first meal of the day consisted only of fruit. The second morning meal was a mixture of fruit and cereals or fish fry. A third meal of bread, milk and vitamins was given later in the early afternoon. Each group of marmosets was observed 6 times a week with 2, 10 min observations for each type of meal. The method of sampling behaviour was by continuous recordings spoken into a tape recorder and subsequently transcribed on to data sheets. With reference to the current context, aggressive behaviour was recorded when individuals characteristically vocalised, cuffed, chased or bit another animal in the immediate vicinity of the food source. Note that all such behaviour occurs in short bouts and was, therefore, at this pilot stage, recorded as frequencies and not in durations. With regard to the reproductive status of the breeding females, the 'non-reproductive' families were observed

over a total of 4 consecutive weeks. Observations on families that produced infants during the study were made for 4 consecutive weeks after the births and for one (2 families) or two (3 families) weeks before it.

RESULTS

Figure 2 shows total mean weekly frequency scores of aggressive behaviour for the adult pairs together with those of their offspring of various ages. From these preliminary data and analyses by 2-way ANOVAS (age and reproductive status), the following points are worthy of emphasis. First, that the adult pairs of all the families were consistently more aggressive in the presence of food than other group members ($df = 3,69$ $F = 12.11$, $p = 0.0001$). Second, that within the adult pairs, the females were consistently more aggressive than males (LS means $p = 0.023$). Moreover, the females that gave birth during the study, were more aggressive than those that did not. Third, that these females were more aggressive over the food after a birth than before it. We may also note a non significant trend of increasing aggressiveness from non-reproductive females, to reproductive females before a birth, to reproductive females after a birth. It was also interesting to find that both males and females of the mated pairs (including those that did not reproduce around the period of the study) increased their aggressiveness in the presence of food compared with their offspring - that included a variety of ages. Hence, both parents may assert social status in the context of the food sources, with the females being more assertive with regard to their energy requirements (see also Box *et al.* 1995).

We have also noted (Lopes unpublished data) that the aggressiveness of the reproductive male in the presence of food was not addressed to his mate, but to his offspring. This raises questions as to whether the male aids his female in defence of food, for example, and more so at particular times of her reproductive cycle.

The results as depicted in Figure 2 fit the general expectations that we outlined earlier. It was also important, however, to look at the behaviour of the animals in the context of their different meals. Figure 3 shows relevant data. Hence, observations on the first meal of the day showed that all the mated females - both reproductive and non reproductive, were more aggressive over the food than any of the other animals (2 way ANOVA $df = 3,69$, $F = 12.74$, $p = 0.0001$). This meal has a special reference in two respects. First, it was the first meal after

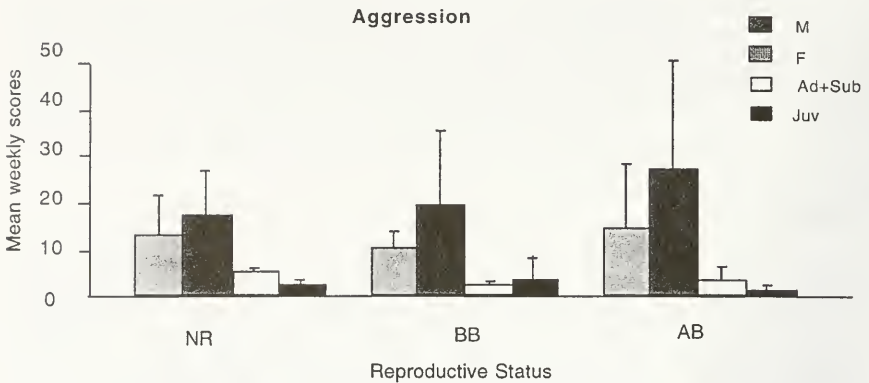


Figure 2. Total mean weekly frequency scores of aggressive behaviour for the adult pairs of marmosets that were non-reproductive (NR) and reproductive both before (BB) and after a birth (AB) together with the scores for the offspring of various ages.

a period without food, and second, it contained high energy food in the form of fruits. It was also of interest, however, to find that aggressive responsiveness to the foods was not consistent across the meals and times of day. Hence, reproductive females were more aggressive than non-reproductive females over food in the second meal, but there were no significant differences between either the non-reproductive and reproductive females, or between the reproductive females in the periods before and after a birth. In this condition, mated females overall were more aggressive in the presence of food than all other animals (2 way ANOVA $df = 3,69$ $F = 10.56$, $p = 0.0001$). Further, responses to the third meal were different from either of the first or second meals. In this case, the non-reproductive females were more aggressive than they were in the other meals. Again, and although it was not statistically significant, the mated males were more aggressive in these conditions than in either of the other meals.

Further, the aggressiveness of both the mated males and females did not differ significantly either between themselves or among the conditions of reproductive status, namely, non-reproductive, before a birth and after a birth ($df = 3,69$ $F = 6.67$, $p = 0.0006$ (LS means males and females, $p = 0.1842$). This pilot study then suggests some additional perspectives for captive studies. Hence, although in this case the meals were not presented in a counterbalanced order, the results do indicate the potential influence of temporal and nutritional factors. These will repay additional study and help to refine functional hypotheses of priority of access to food among these animals.

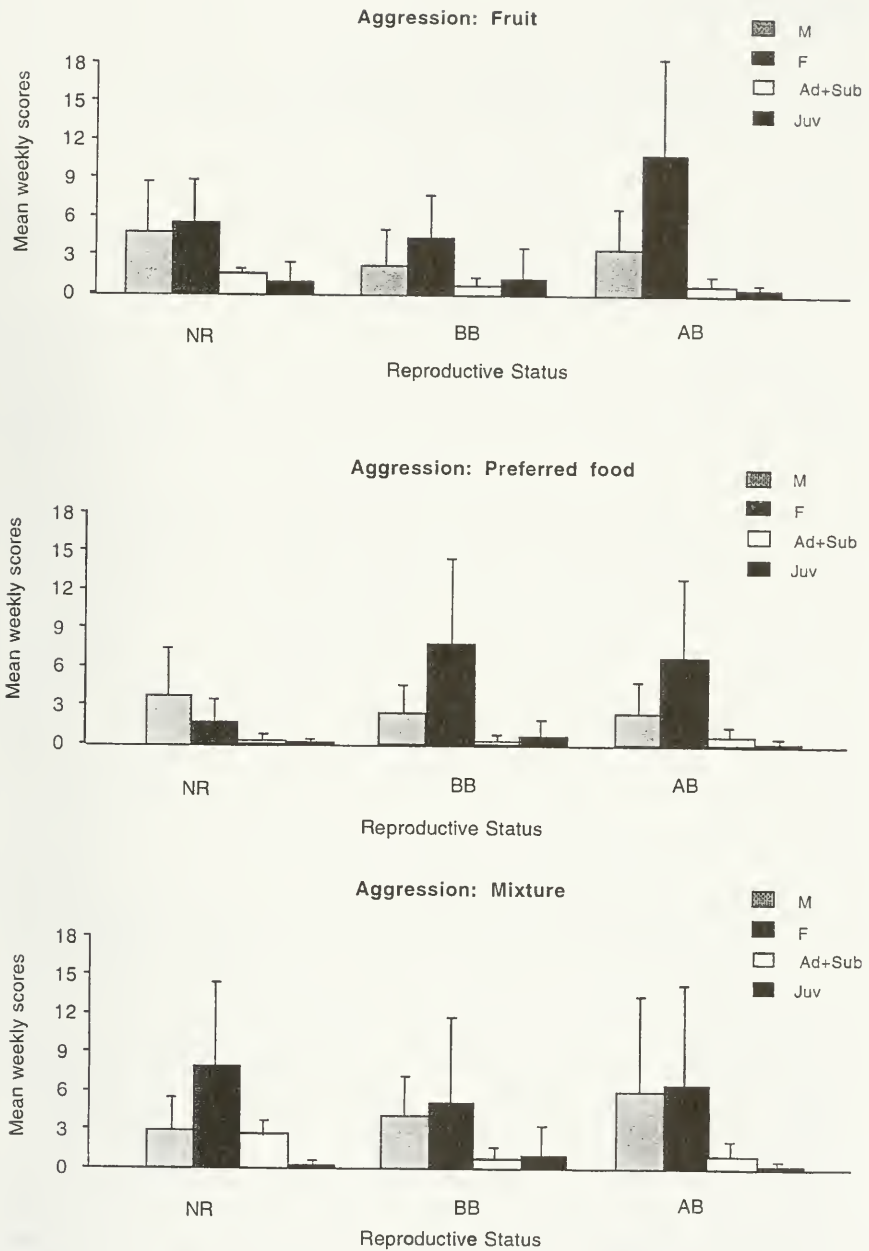


Figure 3. Total mean weekly frequency scores of aggressive behaviour for the adult pairs of marmosets that were non-reproductive (NR) and reproductive both before (BB) and after a birth (AB) together with the scores for the offspring of various ages – in the context of their different meals.

DISCUSSION

We wish to make two general points. First, to emphasise the value of environmental challenges as experimental techniques to provide controlled conditions to probe a range of comparative propensities of biobehavioural responsiveness among a wide diversity of animals. There are many good examples since the pioneering work of Alison Jolly in 1964, and Glickman and Sroges in 1966. The use of simple food tasks as described in the present, and related papers (Box *et al.* 1995; Box, 1997) provide additional cases.

The second general point is that compared with the vast majority of primate species discussions about behavioural differences between male and female callitrichids have been relatively neglected. Certainly, males and females look very similar and they behave similarly in many respects, and a lack of interest in this area is understandable. There are exceptions, of course, especially with reference to the behavioural and physiological control of reproduction in males and females (e.g. Abbott, 1991; Abbott and George, 1991; French and Inglett, 1991). There are also less systematic and small scale but nevertheless significant gender differences that deserve attention. For example, in captivity there is investigative behaviour of unfamiliar objects (Box, 1988) and spontaneous leaving of family groups (McGrew and McLuckie, 1986) and exploratory behaviour in an unfamiliar environment (Price, 1992) in all of which females have been found to be more responsive. In contrast, male tamarins have been observed to be less exploratory – initially at least, and more likely to be vigilant than females in unfamiliar environments (Price, 1991; Savage, 1990). A similar observation has been reported for common marmosets living in an unfamiliar area in captivity (Box, 1984) and by Koenig, (1998). See also Buchanan-Smith in this volume. There are also differences in vocal behaviour (Benz *et al.* 1980) and histological differences in scent glands that have implications for chemosignalling systems (Epple, 1994). Further, and again with potential reference to feeding, a proportion of all females of diurnal NWM species studied, are found to be trichromatic whereas males are consistently dichromatic (Jacobs, 1995). This suggests for example, that females may more easily discriminate and select among potential sources of foods than do males.

Recent work on female priority to food opens up additional perspectives. In all, we may consider that a neglect of behavioural gender differences in this group is a significant omission in our understanding of their biology. At this stage it is perhaps of particular

interest to emphasise gender differences between species of different genera. Once again, and as in previous studies, our present work with common marmosets is consistent with differences among marmosets (*Callithrix*) and tamarins (*Saguinus*) in their feeding ecology and social organisation.

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