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Food distribution effects on the behaviour of captive common marmosets, Callithrix jacchus

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Abstract

Common marmosets, Callithrix jacchus, are widely used by research laboratories and are commonly provided with food in bowls. These centralised, unchallenging sources of food result in high foraging success for low foraging effort. Foraging devices, which require more skill and effort for foraging success, may broaden the behavioural profiles of marmosets by including more elements of their natural ethogram, reflecting improved welfare. The behaviour of eight female common marmosets was examined as a function of four different food distributions: food centrally located in a stationary bowl; food in a bowl that changed location each day; food centrally located in a stationary bowl, in addition to hidden food in a clustered food source (cluster feeder) or hidden food in dispersed food sources (dispersed feeders). Both the cluster and dispersed feeder distributions increased foraging, and there was a trend for reduced scratching and grooming in the presence of the feeders compared with the bowl-only treatments. The cluster feeder increased the amount of time a marmoset spent in a large room annexed to the home rooms more than the dispersed feeders, and this effect was sustained throughout the day after the feeders had been removed. Both feeders increased activity and movements within all areas of the annexed room compared with the bowl-only treatments; therefore, both feeder types improved the welfare of the captive marmosets more than the provision of food bowls.

Keywords: activity, animal welfare, Callithrix jacchus, environmental enrichment, foraging, space use

Introduction

Common marmosets, *Callithrix jacchus*, are widely used by research laboratories and are often kept in environments that are impoverished compared with their natural habitat. Consequently, the welfare of animals kept in such environments may be compromised. One of the main welfare concerns relates to the marked difference between the foraging effort and foraging success of captive and wild animals. Typically, in a captive environment, the marmosets' standard rations are fed at routine times, in an easily consumed form and usually from a bowl (Poole *et al* 1999) even though their natural foraging strategies include searching, processing and consuming food that is spatially distributed, embedded or hidden (Rylands & de Faria 1993).

Food bowls are centralised, unchallenging sources of food that result in low foraging effort but high foraging success, and captive common marmosets typically weigh more than their wild counterparts (Araújo *et al* 2000) possibly as a result of this feeding method. However, the use of foraging devices can increase foraging effort and lower foraging success because more time and skill is required to obtain the same quantity of food (Kleiman *et al* 1986). Foraging devices are also more ecologically relevant to common marmosets than food bowls because they are analogous to natural foraging strategies (Rylands & de Faria 1993).

Wild callitrichids — marmosets and tamarins — spend up to 60% of their daily time budget actively foraging (Poole 1990). Wild common marmosets feed on spatially-clustered exudate sources (Maier et al 1982; Scanlon et al 1989) and on fruits and insects that are dispersed throughout their habitat (Rylands & de Faria 1993). They are also able to adapt to varying terrains, habitats and food availability (Ferrari 1993; Rylands & de Faria 1993); therefore, captive common marmosets may benefit from different feeding strategies that encourage a greater use of the space available. Most research on the use of space within captive marmoset enclosures has examined the subjects' preferences for infrastructure at different heights within a cage or preferences for different feeding heights. Marmosets have shown a preference for the upper parts of a cage versus the lower parts (Ely et al 1998), as well as food bowls (Hannaford 1996; Buchanan-Smith et al 2002) and foraging objects located in relatively elevated parts of the cage (Morrissey 1994; Majolo et al 2003). However, the provision of food bowls (Buchanan-Smith et al 2002) or enrichment devices, such as branches and perches (Kitchen & Martin 1996), or verandas (Ely et al 1998), in less preferred areas can alter the marmosets' preferences for the use of space and increase their overall use of the space available.

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Figure I



The provision of space does not necessarily improve welfare, and Chamove and Rohrhuber (1989) argue that any space provided in the name of *enrichment* or *improvement* needs to be 'usable' space. At the University of New England (UNE) Animal House, large rooms have been designed for marmosets that are accessible from the home rooms. These large rooms have been designed to be usable spaces and are furnished in a similar manner to the home cages with a proportionally larger number of furnishings, such as perches, platforms, nest boxes, tubes, tunnels, tyres and hanging objects. However, preliminary data on baseline room-use indicated that the marmosets spent only 21% of their daily time budgets in the large rooms; therefore, the large rooms may not be as 'usable' as the home rooms.

Foraging devices are more ecologically relevant to common marmosets than food bowls; therefore, including these devices within the large rooms may make the quantitatively larger space more qualitatively usable for the marmosets than providing food bowls alone. An increased use of the large rooms when the foraging devices are present would indicate that the marmosets value the foraging devices and that the room has become more usable, while a broadening of the marmosets' behavioural profiles to include more elements of their natural ethogram would indicate enhanced welfare (Stevenson & Poole 1976; Poole 1988; Buchanan-Smith 1994).

Activity, foraging, scratching and grooming were measured to assess changes in the marmosets' behavioural repertoires. The foraging devices may improve the marmosets' welfare by increasing activity and foraging, and reducing potentially stereotypic, self-directed behaviours. As a consequence of the low effort:high foraging success quotient from feeding bowls, captive animals spend less time foraging and eating than their wild counterparts, are less active and possibly have more 'vacuum' periods in which to perform other, maladaptive behaviours, such as scratching and grooming (Anderson & Chamove 1984). These behaviours can indicate compromised welfare when their frequency

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becomes excessive and irrelevant to the surrounding circumstances (Broom 1986, 1991; Maestripieri *et al* 1992): scratching has been shown to be a reliable measure of stress in captive marmosets (Johnson *et al* 1996; Cilia & Piper 1997), and self-grooming may also indicate stress. For example, marmosets that were isolated — an anxiogenic situation (Norcross & Newman 1999) — self-groomed twice as frequently as those living in groups (Rothe 1971). A decrease in these self-directed behaviours may indicate an improvement in welfare (Maestripieri *et al* 1992; Schapiro *et al* 1996; Cilia & Piper 1997); therefore, the promotion of activities that induce species-typical behaviours may improve the welfare of captive animals, not least because there are fewer 'vacuum' periods.

The current study was designed to determine if four different food distributions had an effect on the behaviour of captive marmosets, which would indicate improved welfare. It was predicted that the provision of a foraging device and a food bowl would increase the usability of the large room (as determined by an increased use of the space) and enhance welfare by increasing activity and foraging, and reducing scratching and grooming, more than a food bowl alone would.

Materials and methods

Subjects and housing

Eight adult, female common marmosets, *Callithrix jacchus*, (mean \pm standard error: 9.83 \pm 0.17 years) were observed in pairs (two mother/daughter pairs; two sister/sister pairs) at the UNE Animal House marmoset colony. Female pairing is not a natural family grouping; however, because of capacity limitations and intra-group aggression, the UNE marmosets, like those in other captive facilities (Clarke 1994), could not stay in their complete original family groups. The subjects had not been previously exposed to any manipulanda, for example swinging discs, such as those used in the current study. Each study pair was housed in a home cage (5.3 m³ average volume),



which contained one nest box $(0.29 \times 0.15 \times 0.18 \text{ m}, \text{length} \times \text{width} \times \text{height})$, one tyre, one hanging mirror, one hay tray and multiple perches, tubes and platforms. Cages were swept out and hosed down three times per week.

Figure 1 shows the marmoset housing arrangement. Marmosets from the same family were maintained within the same home room. All marmosets within the UNE Animal House were in auditory and olfactory contact, and occupants of the same room also had visual contact. Each enclosure consisted of a home cage within the respective home room, large room (LR) and outdoor cage. The current experiments were carried out over a four-month period during the winter and spring of 2003. As a result of the weather, the experimental procedure allowed access to the home rooms and LRs only. Cage groups from each home room had exclusive, but rotating, access to their respective LR via the runway system.

LRs 1 and 2 were $3.0 \times 3.0 \times 2.6$ m (length × width × height) and LR 3 was $3.4 \times 3.0 \times 2.6$ m (length × width × height). Each LR was visually divided into three equal vertical divisions of 0.85 m (High, Middle and Low) to allow the assessment of the marmosets' vertical use of the room. Oneway mirrors facing into the LRs from each ante-room allowed the experimenter to observe the marmosets in the LRs. LRs and home cages were similarly furnished. Each LR included one nest box ($0.29 \times 0.15 \times 0.18$ m, length × width × height), one tyre, one hanging mirror, one hay tray, one sand box, and four times as many perches, tubes and platforms than there were in the home cages. The quantity of each type of furnishing was equivalent across the three LRs.

Animal husbandry and diet

The temperature in all marmoset rooms was maintained between 18°C and 28°C. Both the home rooms and LRs were lit using fluorescent lights that were programmed on a 12 h:12 h light:dark cycle (light: 0730h–1930h). Ultraviolet light (350–390 nm) in each home room supplemented the marmosets' vitamin D intake for 60 min between 1300h and 1400h. During pre-experimental and non-experimental conditions the marmosets were fed varied foods in bowls once per day, in their home cages, between 1200h and 1300h. During experimental conditions the marmosets were fed varied foods in bowls and/or foraging devices according to the experimental condition. As with the pre-experimental standard husbandry procedure, bowls remained in the cages or rooms to allow the marmosets to feed freely throughout the day; bowls were then removed, cleaned and refilled the next day. Apart from short periods in which the bowls were cleaned and refilled, the marmosets were not food deprived; there was always food left in the bowls after each 24 h ad libitum feeding. The marmosets' bodyweights were maintained during the experimental periods. Water was available ad libitum at all times in all home cages and LRs. The Basic daily ration comprised specially prepared monkey cake and meatloaf, Pedigree® Principal[™] Active Maturity dog pellets (MasterFoods Australia New Zealand: Raglan, NSW, Australia) and apple. Additional foods provided on a rotational system included egg, peanuts, cheese, cereal, voghurt, and seasonal fruit and vegetables. Penta-vite® (Roche: Dee Why, NSW, Australia), a liquid human infant dietary supplement, was soaked into wholegrain bread to provide a vitamin supplement and fed once per week.

Apparatus

A motion sensor camera (Logitech® QuickCam® Pro 4000 internet camera) recorded the marmosets' movements in and out of the LR during the 12 h light cycle. The camera started taking pictures (still-image capture resolution: up to 1280×960 pixels) as soon as movement was detected and for as long as detectable movement continued. The QuickCam® integrated software annotated each picture with date and time (in hours, minutes and seconds) for subsequent analysis.

Eight identical glazed, ceramic dog bowls (550 ml volume, 5.5×11 cm, depth \times diameter) were used as food bowls. All food bowls were rotated and cleaned daily with dishwashing liquid, so that no individual bowl was consistently marked with a particular scent; Figure 2 illustrates the cluster and dispersed feeders.

Table I	Food dispenser (ie bowl and/or feeders)	, food contents and	locations per condition.
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Condition	Home cage	Large room
Empty room (also pre-experimental standard husbandry procedure)	Bowl (B + A)	-
Stationary bowl	Bowl (B + A)	Bowl (B + A)
Moving bowl position	Bowl (B + A)	Bowl (B + A)
Cluster feeder	Bowl (B)	Bowl (B) + cluster feeder (A)
Dispersed feeders	Bowl (B)	Bowl (B) + dispersed feeders (A)

Procedure

Procedures were undertaken in accordance with the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (NHMRC 1997) and the Policy on the Care and Use of Non-human Primates for Scientific Purposes (NHMRC 2003) and were approved by the UNE Animal Ethics Committee (AEC 03/050).

Marmoset pairs were observed in their respective LRs during three non-experimental conditions and four experimental conditions. Non-experimental conditions consisted of 'empty room' (ER) conditions 1, 2, and 3 and were interspersed between the four experimental conditions: (1) stationary food bowl (Bowl condition); (2) moving bowl position (MBP condition); (3) cluster feeder (CF condition); and (4) dispersed feeders (DF condition). The conditions were tested in the following order for all subjects: (1) ER 1: (2) Bowl; (3) MBP; (4) ER 2; (5) CF; (6) ER 3; and (7) DF. No additions or modifications were made to the LRs during the ER conditions; the LRs were maintained in their original, pre-experimental states with no food provided within them. The ER conditions were used as intermediate checks to see if the sequence of testing conditions produced an order effect. ER 1 was primarily intended to determine baseline measures of the marmosets' behaviours. The marmosets were observed under ER conditions during four testing sessions while all four experimental conditions were monitored during six testing sessions. Morning and afternoon testing sessions were equally represented.

All testing was performed within periods of time and not on a fixed schedule because presentation variability has been documented to limit habituation (Kuczaj *et al* 2002). Twenty-minute testing sessions were completed in the morning between 0845h and 1115h, and afternoon sessions were completed between 1400h and 1630h. These time periods accommodated the general maintenance and animal husbandry practices of the UNE Animal House, and only the experimenter had access to the UNE Animal House during the testing sessions.

Throughout all the experimental conditions a food bowl was available in the home cage and in the LR. Both bowls contained the same type and amount of food. Table 1 depicts the food dispenser (ie bowl and/or feeders), food contents and location(s) per condition. As with the regular husbandry practices, food bowls were left in the home cages and LRs throughout the day, and were cleaned and replenished during the next day's feeding time. All bowls were weighed before and after feeding to measure the amount of food removed (either consumed or dropped) as a measure of preference for feeding in the home cage versus the LR.

Bowl conditions: bowl and moving bowl position

At the start of this study we were interested in the possible effect of changing the bowl's position within the LR. However, because a food bowl in the LR was not part of the standard husbandry procedure, the bowl was initially presented in the LR continuously. Once the marmosets had learned that there was a bowl present in the LR, its position was changed.

A food bowl was first introduced in the LR during the Bowl condition. This condition was the control for the other three experimental conditions because they built upon the Bowl condition procedures. In the MBP condition the location of the LR food bowl was rotated through four different positions at the same height level in the LR, approximately 1 m above the floor and 0.75 m from each corner of the room, to determine if bowl position in the LR had an effect on the marmosets' behaviour. All bowl positions were in the Middle division of the LR. Bowl position per day and marmoset pair was determined using a Latin Square design. In the Bowl and MBP conditions the food bowls contained the Basic and Additional foods as outlined in the *Animal husbandry and diet* section (Table 1).

Feeder conditions: cluster feeder and dispersed feeders

Before the marmosets were tested with the cluster feeder, all marmosets were verified as being cognitively and physically capable of manipulating the feeder discs and completing the task that would be presented to them in the feeder experiments, that is to swing a disc to the left or right to uncover a food reward. Before being offered any feeder in the LR, each subject was given the opportunity to use the feeder by being given individual access to the dispersed feeder with a Perspex disc propped, first, completely open, second, half-open, and finally, closed. Then the subject graduated to a dispersed feeder with an opaque testing disc and was tested through the same disc stages until the subject successfully retrieved the food immediately behind the closed opaque disc in one trial. Once a subject met this criterion, the marmoset progressed to the CF condition.

The CF and DF conditions were similar to the Bowl condition except for the addition of either the cluster feeder or the dispersed feeders. Because the feeders were present

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only during testing sessions, and the marmosets' regular husbandry procedure was to have *ad libitum* food access, the Basic diet was not provided in the feeders. The Basic diet provided a balanced nutritionally sufficient food source but was pre-processed and offered few analogues to natural foraging behaviours. For these reasons, equal amounts of the Basic diet were offered in the home cage and LR food bowls *ad libitum*, as with the regular husbandry procedure, to ensure the marmosets had continuous access to sufficient food. The relevant feeders were loaded with the normal daily amount of Additional foods (as described in *Animal husbandry and diet* section) — the more ecologically relevant elements of the ration (Table 1).

During the first day of testing all 12 holes were filled with food for both the cluster and dispersed feeders. During the remaining three testing days 10 holes were filled to provide a level of unpredictability, similar to that experienced by wild common marmosets when foraging (Kleiman *et al* 1986); vacant holes were randomised for each testing session. Before the start of each session, the relevant feeders were loaded with food and placed within the LR. The cluster feeder was suspended approximately 1.3 m from the floor and the dispersed feeders were spread equally throughout all three vertical divisions of the LR; the feeders were removed at the end of each session.

During testing sessions the experimenter (SJ Bjone) continuously recorded the marmosets' behaviours within the LR using an all-occurrences sampling method (Altmann 1974). For each 20 min session a timer was used to record the beginning and end of each behaviour to obtain the time spent performing each behaviour. For example, a subject's entrance and exit times were used to determine the duration of each visit and the total time spent in the LR per testing session.

The testing sessions determined the short-term effects of food bowl or feeder presence, while motion sensor photographs helped to ascertain if the food bowls or feeders had a longer-term effect during the 12 h light cycle. The internet camera with motion sensor software recorded the marmosets' entries to and exits from the LR during the 12 h light cycle. Motion sensor photographs were taken for one day per pair during the ER conditions and two days per pair during the experimental conditions; however, the marmosets moved too quickly past the camera to permit individual identification. Therefore, total time in the LR, number of entries, and entry duration were calculated for each pair and not for each individual subject. It was not evident that one individual of a pair influenced the movements of the other cage mate because there were times when both cage mates were present, neither was present and just one was present in the LR.

Overall room use — as a measure of activity — was assessed using the number of times the marmosets moved into a different vertical room division: High, Middle and Low (similar to Bayne *et al* 1992; Bayne *et al* 1994).

As further measures of activity, the overall time spent sitting, sitting and eating or sitting next to a light were recorded. Overall sitting included any type of sitting, regardless of the location or other behaviour being performed. Sitting and eating was recorded when a marmoset sat, processed food and ate. Sitting that occurred within one body length from either of the two fluorescent lights on the ceiling of the LR was recorded because prior observations indicated that the marmosets were motivated to enter the LR so that they could interact with a light. Sitting next to a light did not include any eating, and sitting and eating did not include any time spent performing this behaviour while next to a light.

The number of scratching events and the amount of time spent grooming were also recorded. Scratching was recorded when a marmoset used a hand or foot to rhythmically rub its coat or skin; grooming was recorded when a marmoset used a hand and/or tongue to part hair and pick at hair or skin.

Foraging included searching for, processing and eating food. In the current study 'searching' was represented by the time spent interacting with a bowl or feeder, whereas 'processing and eating' food was recorded as time spent eating.

Statistical analyses

The Statistical Package for the Social Sciences (SPSS®) was used to analyse the data. Each individual subject's records were averaged for each behaviour per experimental condition, creating a subject mean per 20 min testing session for each experimental condition. The frequencies of behaviours were recorded and/or the total amount of time the behaviour was exhibited per 20 min testing session (time in min). Because the same subjects were evaluated for each experimental condition, a repeated-measures ANOVA was used to determine whether there was a significant difference between the experimental conditions for one dependent variable, and a multivariate ANOVA was used for more than one dependent variable (Tabachnick & Fidell 2001). Although there were inter-individual differences in response intensity to the experimental conditions, all individual subjects and testing pairs showed similar patterns of behaviour to the experimental conditions.

The degrees of freedom for all experimental condition analyses were df = 3,21 and df = 3,9 for the analysis of motion sensor data. Sphericity was checked for all repeatedmeasures ANOVA using Mauchly's check as provided by SPSS®. If sphericity could not be assumed, Greenhouse-Geisser values were used and the repeated-measures ANOVA's P value was labelled with a 'G-G' (Tabachnick & Fidell 2001). The Bowl condition was the control for all other experimental conditions. Simple contrasts using the Bowl condition as the control compared with the other three experimental conditions and Tukey's Honestly Significant Difference were used to determine the significance of the differences between experimental conditions (Keppel 1991). Significance levels were set at $\alpha = 0.05$. The strength of association was represented by partial eta-squared $(p\eta^2)$ (Tabachnick & Fidell 2001).

The ER conditions, in addition to spacing between experimental conditions, were used as intermediate checks to determine whether the sequence of testing conditions



Figure 3

0

Bow

Time spent in the LR during testing sessions; conditions with different letters are significantly different (at P < 0.05).

Experimental condition

Moving bow

position

Cluste

feeder

h

Dispersed

feeders



Time spent in the LR during the 12 h light cycle; conditions with different letters are significantly different (at P < 0.05).

produced an order effect. Repeated-measures ANOVAs were used to determine whether there was a significant difference in each behaviour for ER conditions 1, 2, and 3. Because these conditions were checks, they served their purpose by *not* being significantly different. There were no significant differences in all behaviours reported in this paper for ER conditions 1, 2 and 3, except for scratching events. This exception will be discussed in the *Results*.

Results

Room use was assessed using two data sets: data recorded during the 20 min testing sessions, and data collected from the motion sensor photographs taken during the 12 h light cycle. The number of entries into the LR and the time spent in the LR were analysed using both data sets to determine the time distribution between the home cage and the LR. Space-use within the LR was assessed using the number of movements into the vertical room divisions during the testing sessions.

There was a significant difference in time spent in the LR between conditions ($p\eta^2 = 0.765$, P = 0.001) (Figure 3). The time spent in the LR was significantly higher during both CF and DF than during the Bowl condition (CF: $p\eta^2 = 0.761$, P = 0.002; DF: $p\eta^2 = 0.837$, P = 0.001). However, there was no significant difference between conditions in the number of entries into the LR (G–G, P = 0.303).

The motion sensor camera recorded entries to and exits from the LR during the 12 h light cycle. These data were collected to determine if the food bowls or feeders had a long-term effect during the 12 h light cycle (0730h–1930h). From these data the total time spent in the LR and the number of entries were determined for each day's 12 h light cycle. The time spent in the LR per day was significantly different across conditions ($p\eta^2 = 0.579$, P = 0.043). Unlike the time in the LR per testing session, the time spent in the LR per day was significantly higher during the CF condition than during both Bowl conditions and was nearly significant to the DF condition. Therefore, the CF condition had a longer effect than either food bowl condition, even though the cluster feeder was only present during 20-40 min a day, and the bowls were continuously available. Although it was not quite significant, on average the marmosets spent approximately 3 h more in the LR per day during the CF condition compared with the DF condition (Figure 4). The number of entries per day was not significantly different across the conditions (P = 0.137), indicating that the marmosets stayed longer per entry.

Significantly more movements were made within the LR during both feeder conditions compared with the Bowl condition $(p\eta^2 = 0.628, P = 0.001)$. The DF condition involving the 12 individual dispersed feeders elicited the highest number of movements, or activity, compared with all other experimental conditions. Movements into the three vertical divisions of the room were also analysed using a 3×4 repeated-measures ANOVA. The interaction between vertical division and experimental condition was significant $(p\eta^2 = 0.426, df = 6.42, P = 0.001)$, indicating there was a significant difference in the number of movements into the vertical divisions across the experimental conditions. Across experimental conditions there was a significant difference in the number of movements into the High (G–G, $p\eta^2 = 0.444, P = 0.021)$, Middle $(p\eta^2 = 0.706, P = 0.001)$ and Low $(p\eta^2 = 0.586, P = 0.001)$ room divisions. Figure 5 shows the significant differences between experimental conditions for each vertical division.

Three different variations of sitting behaviour were recorded: sitting overall, sitting and eating, and sitting next to a light. Time spent sitting overall was not significantly different across the experimental conditions (P = 0.123). However, there was a trend for less sitting during the feeder conditions (CF and DF) than during the Bowl conditions (Figure 6). The type of sitting also shifted from passively sitting next to a light during the Bowl conditions to sitting

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and eating during the feeder conditions (CF and DF). Figure 6 also reveals a decreasing trend for sitting next to a light (P = 0.097), while sitting and eating significantly increased ($p\eta^2 = 0.742$, P = 0.001) during the feeder conditions (CF and DF) when compared with the Bowl conditions.

The self-directed behaviours — scratching and grooming — occurred most to least frequently as follows: ER conditions, Bowl conditions (Bowl and MBP), and feeder conditions (CF and DF). The number of scratching events was significantly higher during ER 1 than ER 3 ($p\eta^2 = 0.468$, P = 0.012), but neither scratching events nor grooming time was significantly different across the experimental conditions (scratching events: P = 0.652; grooming time: P = 0.196).

Feeder use was analysed using a two-tailed paired *t*-test. The marmosets spent significantly more time with the cluster feeder than the dispersed feeders (df = 7, P = 0.010), whereas they had significantly more interactions with the dispersed feeders than with the cluster feeder (df = 7, P = 0.003). The 12 dispersed feeders required more interactions to obtain the same amount of food, whereas the cluster feeder maintained the marmosets' attention for fewer, but longer interactions; therefore, the duration of interaction per feeder was longer in the CF condition.

A 2×2 repeated-measures ANOVA was used to analyse the time spent with the two types of feeders versus the food bowl, which was also available during the feeder conditions (CF and DF). When given a choice between easily accessed food in a bowl and food from a feeder that required manipulation and/or locomotion, the marmosets predominantly chose to interact with the feeders more than the bowls $(p\eta^2 = 0.824, P = 0.001)$. There was also a significant interaction between the type of food device (bowl or feeder) and the experimental conditions ($p\eta^2 = 0.597$, P = 0.015), as well as a significant difference in the time spent with the feeders across the experimental conditions ($p\eta^2 = 0.661$, P = 0.008). Therefore, the marmosets spent significantly more time with the cluster feeder than with the dispersed feeders and significantly more time with either feeder than with the food bowl (Figure 7)

Even though the food bowls contained the Basic food ration plus Additional foods during the Bowl conditions and the Basic food during the feeder conditions (CF and DF), there was no significant difference in the time spent with the food bowl across the four experimental conditions (P = 0.574). Similarly, there was no significant difference in the weight of food eaten from the LR and home cage bowls across the experimental conditions (P = 0.089). Therefore, it is unlikely that the amount of time spent with the feeders compared with the bowls was due to the type of food hidden within them.

In addition to the amount of food eaten by weight for each day, the time spent eating and the number of eating bouts were recorded during each testing session. Both behaviours changed significantly across the conditions (Time: $p\eta^2 = 0.819$, P = 0.001; Events: $p\eta^2 = 0.784$, P = 0.001). Both behaviours were significantly higher during both feeder conditions (CF and DF) than during both Bowl conditions (Figure 8).





Number of movements into the High, Middle and Low divisions of the LR; conditions with different letters within each room division are significantly different (at P < 0.05).





Time spent performing the three sitting behaviours as a percentage of the total time spent in the LR.

Discussion

The main objective of the current study was to find methods of improving the quality of life, or welfare, of captive common marmosets. Improvements can include increased activity and foraging behaviours. Throughout the study there were no indications that a behaviour exhibited by any subject was increasing or decreasing to an extent that might indicate apathy or distress. The results indicated that both cluster and dispersed types of feeders increased the activity and time spent within the LR as well as foraging, when compared with both Bowl conditions.

Figure 7



Time spent with feeders and bowls for the cluster and dispersed feeder conditions; bars with different letters are significantly different (at P < 0.05).



Time spent eating under four different experimental conditions; conditions with different letters are significantly different (at P < 0.05).

The presence of the cluster feeder or dispersed feeders increased the amount of time spent in the LR on a short-term basis (during testing sessions), indicating that the marmosets valued the feeders, and the room was more usable. The only significant increase in time spent in the LR during the 12 h light cycle occurred during the cluster feeder condition when each marmoset pair spent, on average, nearly 9 h in the LR compared with an average of approximately 4 h during both Bowl conditions. Therefore, not only did the cluster feeder have a significant effect when present during testing

sessions, but also it had a lasting effect throughout the whole day, even though the feeder was present for only 20–40 min in any one day. The presence of the dispersed feeders did not produce a similar significant long-term effect. However, the time spent in the LR did increase by 50% for each marmoset pair, from an average of 4 h during each light cycle during both Bowl conditions to 6 h during the dispersed feeder condition; similar feeder interaction times were documented by Scott (1991).

Varying the presentation of objects, and therefore reducing predictability, has been shown to increase object interaction in a variety of animals ranging from dolphins to macaws (Kuczaj *et al* 2002). However, in the current study, altering the location of the food bowl did not increase the time spent in the LR during the testing sessions. Similar to the short-term testing session data, changing the position of the food bowl did not increase the amount of time spent in the LR during the 12 h light cycle.

In the current study both types of feeder increased the activity within the LR, as assessed by movements made into each of the three vertical divisions and the amount of sitting. The marmosets moved more frequently within the LR when the feeders were present than when the stationary bowls were present. Even though common marmosets prefer to feed from higher areas (Hannaford 1996; Buchanan-Smith *et al* 2002), they will also feed from lower sites within a room. This study revealed that marmosets will take advantage of feeding sites at multiple vertical dimensions and, as a result, their activity increases.

Although the amount of time spent sitting overall did not decrease significantly during the feeder conditions (CF and DF), sitting occupied decreasing fractions of the total time budgets in the LR from the stationary bowl to moving bowl to cluster feeder to dispersed feeders conditions. This indicates that time budgets in the LR shifted from sitting to more active endeavours, such as feeder manipulation. Furthermore, the type of sitting changed. This is probably more relevant than time spent sitting overall because sitting could be performed in combination with other behaviours, such as eating.

The type of sitting changed from sitting next to a light during the Bowl conditions, to sitting and eating during the feeder conditions (CF and DF). Both sitting next to a light, and sitting and eating included a degree of inactivity because the subjects were not physically moving around the LR. However, sitting and eating also included an active behaviour, eating, whereas sitting next to a light was entirely passive. The marmosets consistently sat down while eating during the stationary bowl, moving bowl, and cluster feeder conditions. During these conditions the time spent sitting and eating was essentially equivalent to the time spent eating. However, during the dispersed feeder condition this equilibrium shifted so that the marmosets were not always sitting while eating. Therefore, the subjects were 'eating on the run', and the dispersed feeder condition added a locomotory element to eating.

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In addition, there was a trend toward reduced scratching and grooming — two potentially undesirable behaviours — in the presence of either feeder type when compared with either bowl condition. This finding complements that of Schapiro et al (1996) who documented a decrease in grooming when foraging devices were present. In the current study the reductions were not significant for the experimental conditions, whereas there was a significant decrease in scratching from ER 1 to ER 3. The decrease in scratching from ER 1 to ER 3 could have been attributable to seasonal changes in pelage, because the experimental conditions were tested over 80 days from October to December 2003, or it may be a long-term effect of increased activity throughout the experimental conditions. The reductions in scratching and grooming were not significant during the experimental conditions, possibly because the UNE marmosets did not have a history of stereotypical grooming or scratching and therefore already had low baseline rates; the effects of the feeders may be more pronounced in animals prone to such behaviours. Nevertheless, the reduction in scratching and grooming, although not significant, suggests enhanced welfare.

The present study found that when given a choice between a feeder and a food bowl, which required no work to obtain the food, marmosets predominantly chose the feeders (similar to O'Connor & Reinhardt 1994; Reinhardt 1994). Time spent in the LR during each day indicated that the marmosets were most influenced by the clustered food distribution because, after having encountered the cluster feeder in this room, they spent significantly more time in the room during this treatment. Similarly, during testing sessions the marmosets spent more time interacting with the cluster feeder than with the dispersed feeders. Possibly, the marmosets utilised the clustered food distribution more because they did not want to make the physical effort to travel to 12 different locations to obtain the same amount of food or they did not want to travel to all of the areas where the 12 dispersed feeders were located.

It is unlikely that the marmosets did not see all 12 dispersed feeders and therefore did not know there were more feeders to visit, because the dispersed feeders were placed in fixed locations throughout the dispersed feeders condition's testing sessions. In addition, each animal visited all 12 dispersed feeders at some point. There was no increase in bowl use from the cluster feeder to the dispersed feeder conditions; such an increase might indicate a lack of effort to move and feed from the dispersed feeders. Given that the UNE marmosets have rarely been fed from ecologically relevant food sources and have been continually fed from single food bowls, the sole cluster feeder may have been a gradual progression from the regular husbandry practice.

In different ways both feeders were successful in increasing foraging relative to either bowl condition. Foraging was assessed using the amount of time spent interacting with a feeder or bowl and the time spent eating, which included the processing and consumption of food. The marmosets spent more time interacting with the cluster feeder compared with

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the dispersed feeders, but there was no significant difference in eating during the feeder conditions. By these definitions the marmosets foraged more during the cluster feeder condition than the dispersed feeders condition. However, when presented with the dispersed feeders, the marmosets were required to move around the room to obtain the amount of food that they could have obtained from the cluster feeder without any locomotion; this locomotion could also be classified as searching. Therefore, although the marmosets foraged more from the cluster feeder, they had to expend more foraging effort to exploit the dispersed feeders.

Both feeders increased foraging and activity, and there was a trend towards reduced scratching and grooming in the presence of the feeders, compared with the bowl only conditions. Consequently, each feeder may merit the label 'enrichment', and caregivers of primate colonies should assess the benefits of each feeder type for their animals.

Animal welfare implications

The current study has shown that two types of feeders cluster or dispersed — improved the welfare of eight female common marmosets by broadening their behavioural repertoires toward their natural ethogram through increased activity and foraging, and decreased scratching and grooming. Many captive animal facilities maintain common marmosets in isosexual groupings (Clarke 1994); therefore, the use of either feeder would be a viable method for improving the welfare of female marmosets and possibly other captive animals in zoological parks, reintroduction programs or research facilities.

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