

# Response to Novel Objects and Foraging Tasks by Common Marmoset (*Callithrix jacchus*) Female Pairs

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**The authors analyze the effects of enrichment devices on the behavior of common marmoset female pairs, and determine which aspects of these devices are more likely to elicit explorative behaviors, and how their presence affects aggressive and stress-related behaviors. The results support the use of enrichment devices for captive primates and show that in marmosets, their effectiveness strongly depends on location within the enclosure and the presence of hidden food.**

The concept of boredom in captive animals is difficult to define, but most ethologists agree that insufficient environmental stimulation can lead to boredom<sup>1</sup>. Boredom, due to the absence of new or adequate stimuli, or both, is a major problem for laboratory and zoo nonhuman primates<sup>2,3</sup>. Enrichment devices, such as novel objects and foraging tasks, may improve the psychological well-being of animals, because these devices provide new or additional stimuli to the monkeys that may elicit exploration, manipulation, and attempts to gain food items from them<sup>4-6</sup>. As such, providing animals with enrichment devices on a regular basis should become the normal routine in captive settings.

Many studies on environmental enrichment have focused their attention on common marmosets (*Callithrix jacchus*<sup>7</sup>), which are frequently kept in laboratories and zoos. For research purposes or practical reasons, laboratories often house common marmosets in same-sex pairs, but neither male-male nor female-female pairs constitute a natural social grouping for this species. In the wild, common marmosets usually live in family units composed of a breeding pair, the older offspring, and sometimes a few unrelated individuals, all of whom participate in rearing the infants<sup>8,9</sup>. In captivity the dominant or breeding female often suppresses the ovulation of subordinate females by releasing pheromones by means of scent-marking<sup>10</sup>, although Ziegler and Sousa<sup>11</sup> have recently shown that this suppression may also occur at low rates. Moreover, female-female aggression is high among captive marmosets<sup>12,13</sup>. It is of utmost importance to provide enrichment for pairs or singly housed primates whose

social stimulation is restricted. However, if enrichment devices are to be effective in improving the well-being of captive animals by increasing explorative behavior and reducing abnormal behaviors, their presence should decrease the rates of aggression and stress-related behavior.

Despite the number of studies on environmental enrichment, we still understand little about which object properties are most effective in improving the well-being of the common marmoset. In addition, object properties may interplay with other variables that are known to affect responses, such as sex, social context, personality, and age<sup>14-16</sup>. This study examines the effects of age and object properties in female common marmosets living in an unnatural social group (*i.e.*, pairs). Object properties are of primary importance in determining responsiveness. Objects containing hidden food or those that are moveable or that respond to the primates in some way (*e.g.*, aurally responsive) elicit more exploration than those that do not<sup>17-21</sup>. Moreover, some arboreal species pay more attention to devices placed higher in the enclosure<sup>22,23</sup>. Finally, the social environment may affect the monkeys' response to environmental enrichment, although earlier studies on this topic and on the effects of novelty on the occurrence of stress-related behaviors have produced contrasting results. For example, cotton-top tamarins (*Saguinus oedipus*) living in unnatural social conditions react slowly to novelty and with increased signs of distress in comparison with those living in family groups<sup>24</sup>, whereas the presence of a foraging board elicits a strong response from individually housed rhesus monkeys and also reduces the occurrence of abnormal behaviors<sup>25</sup>.

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Environmental enrichment may have two alternative effects on common marmoset female pairs. Because the attention of the monkeys is focused on the devices, there may be a reduction in social tension within the pair, and an increase in exploratory behavior can improve the psychological well-being of the monkeys. Alternatively, the presence of enrichment devices may have deleterious effects on female pairs that are traceable to the unnatural social grouping. If environmental enrichment elicits high rates of exploratory behaviors, then aggression and stress-related behavior might increase as the monkeys try to monopolize the objects. This may be particularly true for enrichment devices containing highly palatable food. Indeed, some researchers have noted an increase in aggression in some species upon adding new, attractive objects to an enclosure, especially when including foraging tasks<sup>4,26,27</sup>. Moreover, Michels<sup>28</sup> has recently shown that frequency of aggression over food is higher among captive common marmoset females than among males. As such, it is important to examine whether the presence of enrichment devices (*i.e.*, foraging tasks) increases the occurrence of aggression within female pairs, and if it does, to avoid using such devices. Therefore, we aim here to analyze the response of common marmoset female pairs to artificial enrichment devices; we examine the effect on their response of the type of enrichment device (novel objects or foraging tasks) and the device's individual properties (*i.e.*, size, shape, aural responsiveness, and vertical position in the enclosure), as well as of the monkeys' age. Finally, we wish to determine if allo-grooming, aggressive, and stress-related behaviors are affected by the presence of the devices.

## Methods

### Study Animals and Housing

#### Conditions

The study animals were 32 common marmoset female pairs, housed at the Medical Research Council (MRC) Unit, Edinburgh, Scotland, in the upper level of two-tier cages measuring ~55 cm wide, 95

cm high, and 110 cm deep. We keep common marmoset females peacefully in pairs at the MRC by housing an older with a younger, usually unrelated, monkey. Majolo *et al.* provide details of the method of initial pairing, and the success rate of pairing common marmoset females<sup>29</sup>. All the cages contained a nest box, ample natural branches, and a bottle of water. We maintained the temperature at 22–23 °C and provided 12 h of light per day. Monkeys received food once a day at about 13:00 h (1:00 p.m.), and water was available *ad libitum*.

### Apparatus

For this study we chose three different novel objects for their different characteristics (*e.g.*, responsiveness) and not for their "naturalness". The first enrichment device (novel object A) consisted of a cup (~12 x 9 x 12 cm) filled with 10 small plastic test tubes. The second one (B) consisted of a plastic bottle (~17 x 9 x 9 cm) with a large hole on its side, filled with 10 pieces of cloth. The third one (C) consisted of four film cases (~9 x 6 x 9 cm), each containing a marble and joined together by plastic strings. Objects A and C were aurally responsive (*i.e.*, they made a noise when the monkeys touched them). Object B was silent. We used the same novel objects in Experiment 1 as foraging tasks, this time hiding 10 raisins within them (see later).

The monkeys usually ate raisins twice a week as part of their regular diet.

### Experiment 1

We designed Experiment 1 to test whether the kind of enrichment device (*i.e.*, novel object or foraging task) and relative age of the monkeys influenced their response to the objects and whether rates of stress-related and aggressive behaviors were affected by environmental enrichment. In Experiment 2 we examined the effect of object location on marmoset behavior. For Experiment 1, we collected data on 20 female pairs, using a between-subjects design. We presented novel objects to 10 of the female pairs and foraging tasks to the remaining 10 pairs (Table 1). We divided each cage into three equal parts (*i.e.*, low, middle, and high) and located the three objects accordingly. We placed object A in the center of the floor (low), attached object B horizontally to the middle of the cage door (middle), and hung object C from the ceiling by means of a string (high). We presented each object to each pair of monkeys once, on days 1, 3, and 5. We counterbalanced the order of presentation among the pairs (Table 1). The mean age of the pairs presented with novel objects did not differ from those presented with foraging tasks ( $25.8 \pm 2.2$  and  $23.1 \pm 2.1$  months, respectively, ANOVA:  $F(1,18) = 0.79$ , NS). The mean age of the older

TABLE 1. Procedure for Experiment 1<sup>a</sup>

No. of female pairs	Presentation order in the three observation days		
	First day	Second day	Third day
<b>Three novel objects</b>			
2	A	B	C
2	B	C	A
2	C	B	A
2	C	A	B
1	A	C	B
1	B	A	C
<b>Three foraging tasks</b>			
1	A	B	C
1	B	C	A
2	C	B	A
2	C	A	B
2	A	C	B
2	B	A	C

<sup>a</sup>Novel object or foraging task A, in low enclosure position; B, middle position; C, high position.

monkeys in each pair was  $31.3 \pm 2.2$  months, and  $17.6 \pm 1.0$  months for the younger monkeys.

### Experiment 2

We designed Experiment 2 to assess whether responsiveness to the enrichment devices was due to the object properties (*i.e.*, size, shape, or aural responsiveness) or to its location in the enclosure. We presented the same three novel objects as we had used in Experiment 1 to 12 different female pairs (Table 2). Here, we assigned the monkey pairs to three groups and presented each group with the same three objects in different locations. For example, whereas group 1 had confronted object A on the floor of the cage (low), group 2 confronted it attached to the cage door (middle) and group 3 saw it hung from the ceiling (high). We used the same procedure for objects B and C and counterbalanced presentation order among the pairs. Data collection involved the same methodology as in Experiment 1, except that observation sessions lasted only 10 min because most activity occurs immediately upon presentation of objects. The mean age of the female pairs in the three groups did not differ significantly (group 1 =  $17.9 \pm 3.6$ , group 2 =  $18.5 \pm 2.3$ , group 3 =  $19.8 \pm 2.6$  months  $\pm$  s.e.; ANOVA:  $F(2,9) = 0.17$ , NS), nor was the mean age of the five groups used in the two experiments significantly different (ANOVA:  $F(4,27) = 1.71$ , NS).

We collected all the data from a blind with a one-way mirror, and observation sessions occurred after cleaning and before feeding. To collect data, we used focal pair sampling<sup>30</sup> on checksheets for 20 min. We removed the objects at the end of the observation sessions. An additional 10 min observation session immediately preceded the presentation of each object so as to provide baseline rates of allo-grooming, stress-related, and aggressive behaviors. As measures of the responsiveness of the monkeys toward the enrichment devices, we used latency to explore (defined as touching, manipulating, or playing with the novel object or foraging task), time spent exploring, and latency to eat the first

TABLE 2. Procedure for Experiment 2<sup>a</sup>

Group no.	No. of female pairs	Presentation order of the three novel objects in the three observation days		
		First day	Second day	Third day
1	1	A (low)	B (middle)	C (high)
	1	B (middle)	A (low)	C (high)
	1	C (high)	A (low)	B (middle)
	1	A (low)	C (high)	B (middle)
2	1	A (middle)	B (high)	C (low)
	1	C (low)	B (high)	A (middle)
	1	C (low)	A (middle)	B (high)
	1	B (high)	C (low)	A (middle)
3	1	A (high)	C (middle)	B (low)
	1	B (low)	A (high)	C (middle)
	1	B (low)	C (middle)	A (high)
	1	C (middle)	B (low)	A (high)

<sup>a</sup>The experiment involved the same novel objects as in Experiment 1, but in different locations in the enclosures.

food item contained in the foraging tasks. We also recorded aggressive behavior (*e.g.*, frown, tufts or ears flick or forward, arch bristle locomotion, tail raised present, cackle, cuff, and bite) as well as scratching. Recent studies have shown that scratching is a reliable measure of stress in common marmosets<sup>31,32</sup>, as it is in Old World monkeys<sup>33,34</sup>. We recorded time spent exploring by using the instantaneous sampling method (20-s intervals), whereas we recorded behavioral events (*i.e.*, aggression and scratching) by using an all-occurrences sampling method<sup>35</sup>. Because allo-grooming had been rarely observed and had variable duration, we collected it by using the one-zero sampling method, with 20-s intervals<sup>36</sup>.

### Data Analysis

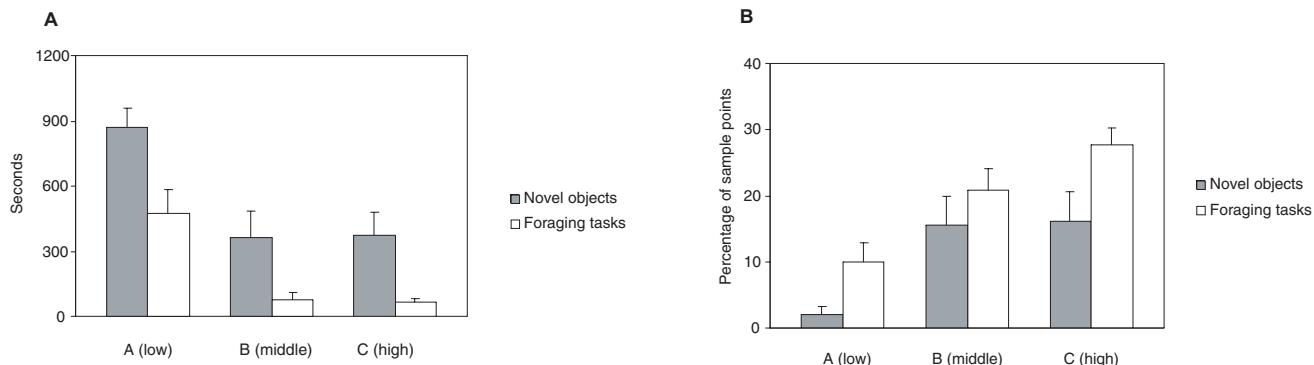
We used the mean scores per hour of each pair in the data analysis, except when making a comparison between the behavior of older and younger monkeys within each pair and when analyzing scratching at the individual level. We analyzed data using a series of mixed-design ANOVAs and repeated-measures ANOVAs. The between-subjects factor was enrichment type (novel object or foraging task), and the within-subjects factors were object (A, B, or C), height (high, middle, low), time (before and during object presentation), and relative age (older or younger in pair).

We ran Tukey post-hoc tests when we found a significant result<sup>37</sup>. We present only significant interactions. Although we considered presentation order in the data analysis to assess whether habituation toward the objects was a factor affecting the response of the monkeys, there was no significant result so for the sake of brevity we do not present these data. We ran a Pearson correlation to relate the baseline level of scratching (*i.e.*, frequency before the presentation of the objects) and its variation (*i.e.*, baseline level minus frequency of scratching during the presentation of enrichment devices). All the tests were two-tailed, and we set the level of significance at  $P < 0.05$ .

## Results

### Preference for Enrichment Devices

A 2 x 3 way ANOVA with enrichment type and object as factors showed that the latency to explore the foraging tasks was significantly shorter ( $F(1,18) = 16.73$ ,  $P < 0.01$ ) and time spent exploring them significantly longer than the novel objects ( $F(1,18) = 5.16$ ,  $P < 0.05$ ). The response of the monkeys to the three enrichment devices varied significantly in relation to kind of object (latency to explore:  $F(2,36) = 19.96$ ,  $P < 0.01$ ; time spent exploring:  $F(2,36) = 21.60$ ,  $P < 0.01$ ; Fig. 1A, B). Post-hoc tests showed that latency to explore



**FIGURE 1. Experiment 1 results. (A) Latency to explore and (B) percentage of time spent exploring the three novel objects (gray bars) and foraging tasks (white bars) (mean ± s.e.) in the three different cage positions.**

objects B and C (*i.e.*, middle and high in the enclosure, respectively) was significantly shorter than object A (*i.e.*, low,  $P < 0.01$ ). Moreover, monkeys explored both objects B and C for longer periods than A ( $P < 0.01$ ). There was no significant difference between results for objects B and C.

These results show that the monkeys interacted significantly more with the foraging tasks than with the novel objects. Because the monkeys responded to the devices differentially, the results also suggest that other variables such as object properties or height in the enclosure affect the responses toward them. However, the experimental design did not allow assessment of the relative importance of these characteristics, because the monkeys confronted each object in the same position.

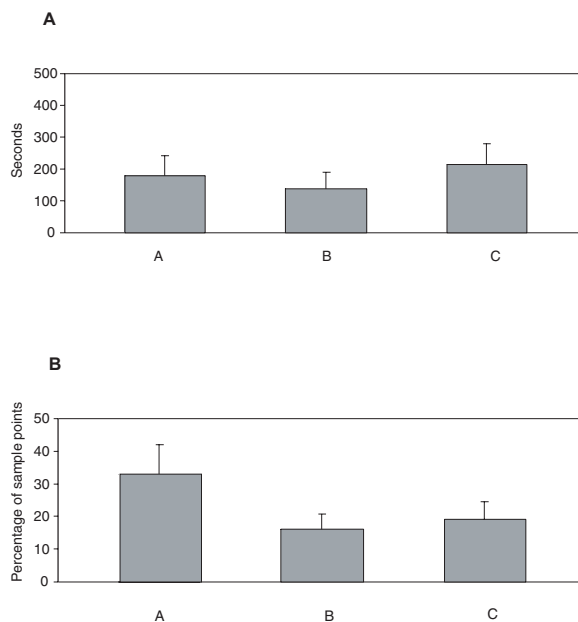
To this end, we ran two series of repeated-measures ANOVAs for Experiment 2. In the first one, we divided the data by object (*i.e.*, A, B, and C) regardless of their height in the enclosure. Neither latency to explore nor time spent exploring the objects differed significantly in relation to object (latency to explore:  $F(2,22) = 0.32$ , NS; time spent exploring:  $F(2,22) = 2.00$ , NS; Fig. 2A, B). Then, we divided the data according to the height of the object in the enclosure (*i.e.*, low, middle, and high), collapsing data across the three objects.

affected the latency to explore ( $F(2,22) = 25.84$ ,  $P < 0.01$ ) and time spent exploring ( $F(2,22) = 13.19$ ,  $P < 0.01$ ; Fig. 3A, B). Post-hoc tests showed that the monkeys explored the objects that were placed high or in the middle of the cage more quickly than those placed low in the enclosure ( $P < 0.01$ ). Moreover, the monkeys spent more time exploring the objects when they were placed in the middle or high in the enclosure than when placed low ( $P < 0.01$ ). There was no significant difference in the latency to explore and time spent exploring between objects placed in the middle and high in the cage.

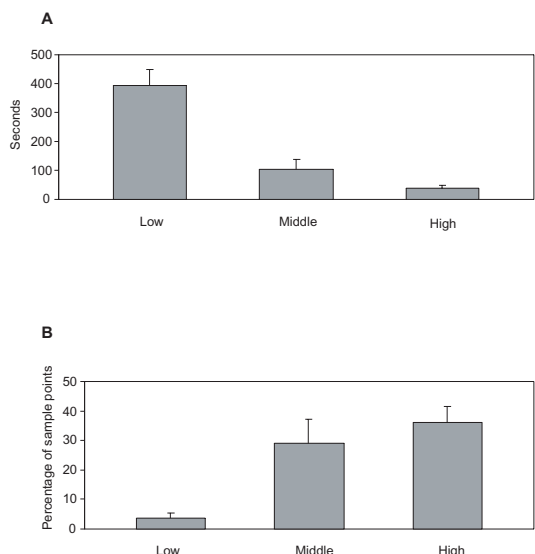
**Effect of Relative Age**

To test whether the response toward the enrichment devices varied between older and younger members of the pairs, we ran a series of repeated-measures ANOVAs and pooled together data from Experiment 1 for the three novel objects and foraging tasks. Latency to explore did not significantly differ between older and younger monkeys (mean for older monkeys,  $371.4 \pm 65.2$  s ± s.e.; mean for younger monkeys,  $368.2 \pm 68.9$  s ± s.e.;  $F(1,19) = 0.00$ , NS).

However, the younger monkeys explored the objects longer than did the older ones (mean for older monkeys,  $12.0 \pm 2.0$ ; mean for younger monkeys,  $19.0 \pm 2.0$ ;  $F(1,19) = 14.44$ ,  $P < 0.01$ ). Finally, we found no significant difference for latency to eat between older and younger monkeys within each pair (mean for older monkeys,  $474.11 \pm 94.03$  s; mean for younger monkeys,  $418.87 \pm 103.01$  s;  $F(1,9) = 0.48$ , NS).



**FIGURE 2. Experiment 2 results. (A) Latency to explore and (B) percentage of time spent exploring objects A, B, and C (mean ± s.e.).**



**FIGURE 3. Experiment 2 results. (A) Latency to explore and (B) time spent exploring the objects placed low, middle, and high in the cage (mean  $\pm$  s.e.).**

### Behavioral Effects of Environmental Enrichment

Female pairs never did allo-grooming while the enrichment devices were present. However, we also rarely observed this behavior when the objects were absent ( $0.47 \pm 0.19$  mean percentage of sample bouts).

Because the marmosets spent a considerable proportion of their time exploring the enrichment devices, one might expect them to fight so as to monopolize the objects, with this effect being stronger in female pairs confronting foraging tasks. To this end, we analyzed the frequency of aggression and scratching before and during the presentation of the enrichment devices. Scratching is a reliable measure of stress in common marmosets (see Methods). We ran two  $2 \times 2$  mixed-design ANOVAs using enrichment type and time as factors. We collapsed the data across the three novel objects and foraging tasks.

There was no significant difference in rates of aggressive behaviors before and during the presentation of enrichment devices ( $F(1,18) = 4.53$ , NS; Fig. 4), nor did enrichment type affect these rates ( $F(1,18) = 0.99$ , NS). The rate of scratching was significantly lower during object presentation

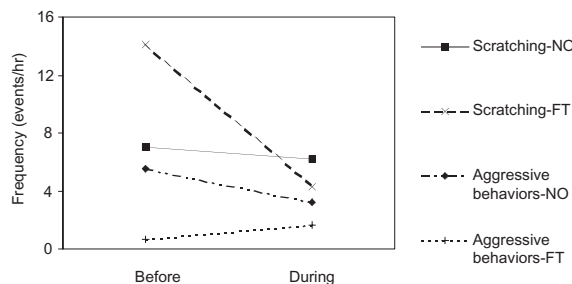
than before it ( $F(1,18) = 20.26$ ,  $P < 0.01$ ; Fig. 4), and this decrease remained stable throughout the 20 min observation sessions. We observed no significant difference between female pairs presented with foraging tasks and those presented with novel objects ( $F(1,18) = 1.26$ , NS), but there was a significant interaction ( $F(1,18) = 14.64$ ,  $P < 0.01$ ). The decrease in scratching was greater for foraging tasks than for novel objects. Finally, we found a significant positive correlation between the baseline level of scratching and the reduction in the occurrence of this behavior during the presentation of the enrichment devices ( $r_s = 0.87$ ,  $n = 40$ ,  $P < 0.001$ ).

### Discussion

All the monkeys explored the enrichment devices, but they began the foraging tasks earlier and continued them for longer periods than they devoted to the novel objects. The shorter latency to explore the foraging tasks suggests that the monkeys could smell the food hidden in the objects as soon as they approached them. Clearly, the presence of desired food in the foraging tasks accounts for the significant difference observed between foraging tasks and novel objects in time spent exploring, because this was the only factor that differed between them. Other studies have also shown that foraging tasks elicit the strongest responses in marmosets and tamarins<sup>18,38</sup>. As such, the foraging tasks are a more effective means of environmental enrichment than the novel objects in the short term for common marmosets. However, it is important to consider carefully the intensive use of foraging tasks containing desirable food items (such as raisins in this study),

because captive animals are often inactive<sup>3</sup>. The presence of highly calorific food in their diet may cause them to gain weight, be more inactive, and exhibit fewer behaviors. A solution to this problem may be to present the monkeys with foraging tasks containing food items from their daily diet. Data on rhesus macaques (*Macaca mulatta*) have shown that this practice increased the foraging effort (and thus reduced inactivity), reduced the waste of food, and stabilized the weights of the monkeys<sup>39</sup>. It is likely that this practice would have similar positive effects on common marmoset female pairs. The objects used in this study were not "natural", but they elicited high levels of curiosity in the monkeys, were easily obtainable, clean, cheap, and safe. As such, another potentially complementary approach may be to present the monkeys with two or three objects each day and to alternate unpredictably the presence and quantity of food items. Laboratory personnel should be able to implement this practice quickly and easily, and the marmosets would spend a large amount of time exploring the objects to determine whether or not they contain food. This situation is more similar to the natural foraging experiences of wild marmosets and can be easily achieved even with artificial devices.

Although the three objects used in this study differed from one another in size, shape, and aural responsiveness, the monkeys did not show any significant preference for any one of them. However, they explored the objects placed higher in the



**FIGURE 4. Experiment 1 results. Mean frequencies of scratching and aggressive behaviors per hour displayed before and during the presentation of the novel objects (NO) and the foraging tasks (FT).**

enclosure more than those on the ground, indicating that this factor greatly affects its attractiveness in common marmosets, as already noted by Millar *et al.*<sup>16</sup>. This result is not surprising because, in the wild, common marmosets occupy the lower strata of the canopy and rarely go to the ground where they might confront potential predators<sup>40</sup>. Therefore, exploring stimuli located in the upper part of the enclosure is a situation that resembles what wild common marmosets experience while foraging. As Reinhardt *et al.* argue, it may still be useful to place enrichment devices lower in the enclosure, because this might encourage animals to make greater use of available space<sup>41</sup>. It must be noted, however, that common marmosets spend the same amount of time in the upper part of their enclosure regardless of the height of food dishes<sup>42</sup>.

Neither latency to explore nor latency to eat significantly differed between older and younger monkeys. However, younger monkeys explored the enrichment devices for significantly longer periods than their older counterparts. This result indicates that the older monkeys lost interest in the objects substantially earlier than their younger social companions, as already noted in other studies<sup>43</sup>.

Environmental enrichment can only be effective if while decreasing boredom it avoids increasing rates of aggressive and stress-related behaviors. In this study, the presence of the enrichment devices did not affect the rates of aggressive behaviors, and scratching significantly decreased in their presence. Scratching and exploration are not mutually exclusive categories. The reduction in the occurrence of scratching was significantly greater in female pairs presented with foraging tasks than with novel objects, but this may be due to the higher baseline level of scratching in female pairs presented with foraging tasks (Fig. 4). However, though not conclusive, these data suggest that the presence of the enrichment devices may be beneficial for the psychological well-being of captive common marmosets, especially for monkeys with high baseline levels of stress.

Overall, these results support the importance of environmental enrichment for the psychological well-being of captive primates<sup>3</sup>. In particular, they are important because housing common marmoset females in same-sex pairs is an unnatural social grouping for this species, and the positive benefits of a social companion appear to be limited. Aggression among captive female marmosets is frequent, and moreover, female pairs exchange affiliative behaviors (*i.e.*, allo-grooming) only very infrequently. Therefore, enrichment devices may be extremely important for common marmoset female pairs (and probably for other captive primates living in similar unnatural social groupings), even if they are presented for relatively brief periods of time, because they reduce boredom through increases in exploratory behavior, decrease the occurrence of stress-related behavior, and do not affect aggression within the pair.

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### References

1. Wemesfelder, F. *Animal Boredom: Towards an Empirical Approach of Animal Subjectivity*. Thesis, University of Leiden, Utrecht, The Netherlands, 1993.
2. National Research Council. *The Psychological Well-being of Nonhuman Primates* (National Academy Press, Washington DC, 1998).
3. Novak, M.A. & Suomi, S.J. Psychological well-being of primates in captivity. *Amer. Psychol.* **43**, 765–773 (1988).
4. Clark, A.B. in *Primate Responses to Environmental Change* (ed. Box, H.O.) 91–114 (Chapman & Hall, Cambridge, UK, 1991).
5. Schapiro, S.J., Suarez, S.A., Porter, L.M. & Bloomsmith, M.A. The effect of different types of feeding on the behaviour of single-caged, yearling rhesus macaques. *Anim. Welfare* **5**, 129–138 (1996).
6. Snowdon, C.T. & Savage, A. in *Housing, Care and Psychological Well-Being of Captive and Laboratory Primates* (ed. Segal, E.F.) 74–88 (Noyes Publications, Park Ridge, NJ, 1989).
7. Scott L. in *Primate Responses to Environmental Change* (ed. Box, H.O.) 265–274 (Chapman & Hall, Cambridge, UK, 1991).
8. Digby, L.J. & Barreto, C.E. Social organization in a wild population of *Callithrix jacchus*. I. Group composition and dynamics. *Folia Primatol (Basel)* **61**, 123–134 (1993).
9. Koenig, A. Group size, composition and reproductive success in wild common marmosets (*Callithrix jacchus*). *Am. J. Primatol.* **35**, 311–317 (1995).
10. Abbott, D.H., Barrett, J. & George, L.M. in *Marmosets and Tamarins: Systematics, Behaviour and Ecology* (ed. Rylands, A.B.) 152–162 (Oxford University Press, Oxford, UK, 1993).
11. Ziegler, T.E. & Sousa, M.B.C. Parent–daughter relationships and the social controls on fertility in female common marmosets, *Callithrix jacchus*. *Horm. Behav.* **42**, 356–367 (2002).
12. Epplé, G. *et al.* in *Marmosets and Tamarins: Systematics, Behaviour and Ecology* (ed. Rylands, A.B.) 123–151 (Oxford University Press, Oxford, UK, 1993).
13. Rothe, H. & Darms, K. in *Marmosets and Tamarins: Systematics, Behaviour and Ecology* (ed. Rylands, A.B.) 176–199 (Oxford University Press, Oxford, UK, 1993).
14. Box, H.O. & Smith, P. Age and gender differences in response to food enrichment in family groups of captive marmosets (*Callithrix–Callitrichidae*). *Anim. Technol.* **46**, 11–18 (1995).
15. Clark, A.B. & Boinski, S. Temperament in non-human primates. *Am. J. Primatol.* **37**, 103–125 (1995).
16. Millar, S.K., Evans, S. & Chamove, A.S. Older offspring contact novel objects soonest in callitrichid families. *Biol. Behav.* **13**, 82–96 (1988).
17. Bayne, K.A.L. Nylon balls re-visited. *Lab. Primate Newslett.* **28**, 5–6 (1989).
18. Box H.O. in *Primate Responses to Environmental Change* (ed. Box, H.O.) 57–74 (Chapman & Hall, Cambridge, UK, 1991).
19. Poffe, A., Melotto, S. & Gerrard, P.A. Comparison of four environmental enrichment strategies in captive common marmosets (*Callithrix jacchus*). *Primate Rep.* **42**, 24–25 (1995).
20. Sambrook, T.D. & Buchanan-Smith, H.M. What makes novel objects enriching? A comparison of the qualities of control and complexity. *Lab. Primate Newslett.* **35**, 1–4 (1996).
21. Sambrook, T.D. & Buchanan-Smith, H.M. Control and complexity in novel object enrichment. *Anim. Welfare* **6**, 207–216 (1997).
22. Taylor, L.L. Promoting species-typical behavior in Coquerel's sifakas (*Propithecus*

- verreauxi coquerelli*). American Zoo and Aquarium Association Regional Conference Proceedings (1998), pp. 599–603.
23. Prescott, M.J. & Buchanan-Smith, H.M. in *Predator Sensitive Foraging among Primates* (ed. Miller, L.) 41–57 (Cambridge University Press, Cambridge, UK, 2002).
  24. Box, H.O. & Rohrhuber, B. Differences in behaviour among adult male, female pairs of cotton-top tamarins (*Saguinus oedipus*) in different conditions of housing. *Anim. Technol.* **44**, 19–30 (1993).
  25. Bayne, K.A.L. et al. The reduction of abnormal behaviors in individually housed rhesus monkeys (*Macaca mulatta*) with a foraging/grooming board. *Am. J. Primatol.* **23**, 23–35 (1991).
  26. Mc Gregor, P.K. & Ayling, S.J. Varied cages results in more aggression in male CFLP mice. *Appl. Anim. Behav. Sci.* **26**, 277–281 (1990).
  27. de Waal, F.B.M. Coping with social tension: sex differences in the effect of food provision to small rhesus monkey groups. *Anim. Behav.* **32**, 765–773 (1984).
  28. Michels, A.M. Sex differences in food acquisition and aggression in captive common marmosets (*Callithrix jacchus*). *Primates* **39**, 549–556 (1998).
  29. Majolo, B., Buchanan-Smith, H.M. & Morris, K. Factors affecting the successful pairing of unfamiliar common marmoset (*Callithrix jacchus*) females: preliminary results. *Anim. Welfare* (in press).
  30. Lehner, P.N. *Handbook of Ethological Methods* (Cambridge University Press, Cambridge, UK, 1996).
  31. Cilia, J. & Piper, D.C. Marmoset conspecific confrontation: an ethologically-based model of anxiety. *Pharmacol. Biochem. Behav.* **58**, 85–91 (1997).
  32. Johnson, E.O. et al. The biobehavioural consequences of psychogenetic stress in a small, social primate (*Callithrix jacchus*). *Biol. Psychiatr.* **40**, 317–337 (1996).
  33. Maestripieri, D., Schino, G., Aureli, F. & Troisi, A. A modest proposal: displacement activities as an indicator of emotions in primates. *Anim. Behav.* **44**, 967–979 (1992).
  34. Schino, G., Perretta, G., Tagliani, A.M., Monaco, V. & Troisi, A. Primate displacement activities as an ethopharmacological model of anxiety. *Anxiety* **2**, 186–191 (1996).
  35. Altmann, J. Observational study of behavior: sampling methods. *Behaviour* **49**, 227–267 (1974).
  36. Martin, P. & Bateson, P. *Measuring Behaviour* (Cambridge University Press, Cambridge, UK, 1993).
  37. Everitt, B.S. *Making Sense of Statistics in Psychology* (Oxford University Press, Oxford, UK, 1996).
  38. Molzen, E.M. & French, J.A. in *Housing, Care and Psychological Well-being of Captive and Laboratory Primates* (ed. Segal, E.F) 89–101 (Noyes Publications, Park Ridge, NJ, 1989).
  39. Bertrand, F., Seguin, Y., Chauvier, F. & Blanqu e, J.P. Influence of two different kinds of foraging devices on feeding behaviour of rhesus macaques (*Macaca mulatta*). *Folia Primatol.* **70**, 207 (1999).
  40. Stevenson, M.F. & Rylands, A.B. in *Ecology and Behavior of Neotropical Primates* Vol. 2 (eds. Mittermeier, R.A., Rylands, A.B., Coimbra-Filho, A.F. & da Fonseca, G.A.B.) 131–222 (World Wildlife Fund, Washington, DC, 1988).
  41. Reinhardt, V., Liss, C. & Stevens, C. Space requirement stipulations for caged nonhuman primates in the United States: a critical review. *Anim. Welfare* **5**, 361–372 (1996).
  42. Buchanan-Smith, H.M., Shand, C. & Morris, K. Cage use and feeding height preferences in captive common marmosets (*Callithrix jacchus jacchus*) in two-tier cages. *J. Appl. Anim. Welfare Sci.* **5**, 137–147 (2002).
  43. Voland, E. Social play behaviour of the common marmosets (*Callithrix jacchus* Erxl., 1777) in captivity. *Primates* **18**, 883–901 (1977).