



# Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys

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In a comparative study of neophilia, innovation and social attentiveness we exposed individuals in seven callitrichid species, from three genera, to novel extractive foraging tasks. The results revealed consistently shorter response latencies, higher levels of successful and unsuccessful manipulation, and greater attentiveness to the task and to conspecifics in *Leontopithecus* (lion tamarins) than in both *Saguinus* (tamarins) and *Callithrix* (marmosets). This is consistent with the hypothesis that species dependent upon manipulative and explorative foraging tend to be less neophobic and more innovative than other species. Furthermore, *Callithrix* appeared to be less neophobic than *Saguinus*; if *Callithrix* is regarded as the greater specialist, this result is inconsistent with the hypothesis that neophobia is associated with foraging specialization. We consider the relevance of our findings to taxonomic relationships, and to technical and Machiavellian intelligence hypotheses and discuss the implications for captive breeding and reintroduction strategies.

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Flexibility of behaviour enables animals to cope with environmental change (Fragaszy & Mason 1978; Clark 1991). Innovation, the capacity to invent new behaviour, is thought to be an important component of this behavioural plasticity, vital to individuals in both generalist and opportunistic species (Lefebvre et al. 1997) and to those animals forced to adjust to impoverished environments (Box 1991; Lee 1991; Lefebvre et al. 1997). The acquisition of information through behavioural innovation and the subsequent social transmission of information may have significant fitness consequences, as well as implications for the invasion of habitats and construction of new niches (Lee 1991; Laland et al. 1996; Sol et al. 1999). In addition to being influenced by sex, age, social status and ecological context (Reader & Laland 2001), rates of innovation and social learning may be dependent on behavioural characteristics (such as neophobia, alternative foraging strategies, territoriality; see Lefebvre 2000) as well as perceptual, learning and cognitive differences.

Several authors have proposed links between opportunism, cultural transmission, brain size and the rate of genetic evolution (Wyles et al. 1983; Wilson 1985, 1991; Lefebvre et al. 1997; Reader & Laland 2002). For instance, Wilson (1985) proposed a behavioural drive hypothesis, which suggested that through their enhanced innovation and social learning, large-brained vertebrates expose themselves to novel selection pressures, which drives evolutionary rates. Recently, this hypothesis has received empirical support. The incidence of behavioural innovation has been used as a measure of behavioural plasticity, confirming the predicted link between opportunism and relative brain size (Lefebvre et al. 1997; Sol et al. 1999; Reader & Laland 2002).

Many behavioural dimensions such as bold–shy, fearless–fearful, or neophilic–neophobic in response to novelty have been used to draw inferences about ‘temperament’, ‘response style’ and the ‘psychological basis of plasticity’ in animals (Cowan 1977; Greenberg 1983; Box 1988; Kagan et al. 1992; reviewed by Clarke & Boinski 1995; Gosling 2001). We use the axis of neophilia–neophobia to avoid this diversity of terminology (Gosling 2001). Highly neophilic animals are quick to approach and explore a novel stimulus, while highly neophobic animals are slow to do so. This dimension has been found to be an appropriate characterization in a taxonomically diverse array of species and has been associated with ecological specializations (Glickman &

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Sroges 1966; Cowan 1977; Greenberg 1983, 1990; Clarke & Boinski 1995). For example, Greenberg (1983, 1984, 1990) found that variation in neophobia was related to the degree of foraging specialization (and omnivory) in migrant birds, with neophobia associated with morphological and behavioural specialization. Within primates, species dependent upon, but not anatomically adapted for, manipulative and explorative foraging are among the least neophobic (Vitale et al. 1991; Clarke & Lindburg 1993). This latter hypothesis is called the extractive foraging hypothesis (this apparently differs from Parker & Gibson's (1977) technical intelligence, extractive foraging, hypothesis which we discuss later). However, the costs of innovation, both energetic and increased susceptibility to risks such as predation or the exploitation of hazardous foods, may themselves result in foraging specialization or neophobia (Bandura 1977; Johnston 1982; Hart 1993; Milinski 1993; Clarke & Boinski 1995). Thus dietary generalists face a conflict between exploring new but potentially dangerous opportunities and using only familiar options that may be of lower quality or that may be limited by future environmental change (Rozin's 1976 'omnivore's paradox').

Several comparative studies have supported the notion that alternative responses to novelty correspond to differences in species-typical lifestyles (Glickman & Sroges 1966; Parker 1974; Torigoe 1985; Gosling & John 1999). For example, within *Macaca*, Clarke & Lindburg (1993) suggested that the greater neophilia of liontails, *M. silenus*, compared with cynomolgus, *M. fascicularis*, is consistent with the comparatively diverse, omnivorous diet and the greater use of extractive foraging in liontails. Social predispositions of primates also influence responsiveness to the physical environment. For example, the monogamous and territorial titi monkey, *Callicebus moloch*, is more socially attentive when faced with novel foraging tasks than the group-living, nonterritorial squirrel monkey, *Saimiri sciureus* (Phillips & Mason 1976; Fragasz & Mason 1978).

Reader & Laland (2001) found that approximately half of the recorded reports of primate innovation and social learning relate to the foraging domain, which raises the possibility that innovation and social learning are linked to technical and ecological intelligence hypotheses. Such hypotheses include the extractive foraging hypothesis (Parker & Gibson 1977). Species that detect and extract hidden food items, but lack specialized anatomy to do so, are thought to have high sensorimotor coordination and intelligence because of the identification and manipulative skills required to locate and process hidden foods (Parker & Gibson 1977; Dunbar 1992; Byrne 1995). Although Parker & Gibson (1977; Gibson 1986) restricted their hypothesis to the use of tools for extraction, we refer to the more general interpretation of the hypothesis as advocated by Dunbar (1992, 1995) and Byrne (1995, personal communication). Alternatively, the cognitive mapping hypothesis (Milton 1988) highlights the challenge of locating patchily distributed but potentially predictable food sources and thus the need for a mental representation of the environment for efficient navigation. Similarly, based on the assumption that gregari-

ous species rely more on social-learning processes than solitary species (e.g. Roper 1986; Lee 1991; Lefebvre & Giraldeau 1996; Lefebvre et al. 1996), it has been argued that social learning plays an important role in social intelligence hypotheses (or Machiavellian Intelligence as broadly interpreted) as it enables animals to exploit the expertise of others (Humphrey 1976; Jolly 1988; Whiten & Byrne 1988, 1997; Russon 1997).

The Callitrichidae are an ideal family in which to test the above hypotheses, as considerable differences exist between genera (Table 1). The Callitrichidae are small, arboreal, neotropical primates consisting of five genera: *Cebuella* (pygmy marmoset), *Callimico* (Goeldi's monkey), *Saguinus* (tamarins), *Callithrix* (marmosets) and *Leontopithecus* (lion tamarins). *Callithrix* and *Saguinus* rely mostly on visual foraging (Garber 1993) and *Leontopithecus* use a manipulative extractive technique (Coimbra-Filho 1981; Peres 1986). The genera also differ in foraging specialization, as only *Callithrix* are anatomically adapted to gummivory (Coimbra-Filho & Mittermeier 1978). Although gummivory is a form of extractive foraging, owing to the anatomical specialization required for extraction, it has not been classed as extractive foraging in the sense of the extractive foraging hypothesis of Parker & Gibson (1977), or the hypotheses relating extraction to opportunism and neophilia (Vitale et al. 1991; Clarke & Lindburg 1993).

The examination of behavioural differences between species also has practical implications. The results are important on economic, conservation and welfare levels, as behavioural differences impinge upon health, veterinary care and reproductive output of captive animals (Box 1988; Poole 1991). As different responses to novelty affect the survival chances of animals under new conditions, such as the postrelease environment (Lee 1991), it may prove important for reintroduction technologies to recognize the possibility that closely related species may vary in ways important in prerelease training programmes (Box 1991; Custance et al., in press). These issues are highly relevant to the Callitrichidae, as large numbers are held in captivity for research purposes and because of their conservation status.

Thus there is both a theoretical and a practical need to explore the response of the Callitrichidae to environmental change, a recommended methodology being the presentation of novel extractive foraging tasks (Kummer & Goodall 1985; Box 1997). We exposed seven callitrichid species to novel extractive foraging tasks, akin to natural or artificial fruits (Whiten et al. 1996). We reasoned that neophilia will be associated with innovation and hence we predicted (1) that individuals with low response latencies to novelty (neophilia) will also be quickest to learn the novel tasks (innovation; Lefebvre 2000). We tested (2) the extractive foraging hypothesis (Vitale et al. 1991; Clarke & Lindburg 1993), predicting that *Leontopithecus*, as manipulative extractive foragers, should be the most neophilic (or least neophobic) of the genera, while *Callithrix* and *Saguinus* should both show lower levels of neophilia. We also evaluated (3) the extractive foraging hypothesis of Parker & Gibson (1977), predicting that *Leontopithecus* should be quickest of the

**Table 1.** Main intergeneric differences between *Leontopithecus*, *Saguinus* and *Callithrix* in the wild

Genera	Common name	Habitat	Weight (g)	Range		Reproductive suppression	Prey foraging style	Diet	Anatomical features
				Group size	size (ha)				
<i>Leontopithecus</i> Sources: 1, 3, 6, 9, 10, 11	Lion tamarins	Mature or primary forest only	ca. 650	Smaller than <i>Callithrix</i>	>20–40	Behavioural	Manipulative extractive foraging for concealed prey	Opportunistic exudate consumption (gum, sap), small animals, fruit	Elongated fingers, Long-tusked, unable to gouge actively for exudates
<i>Saguinus</i> Sources: 3, 4, 5, 7, 11	Tamarins	Can survive in secondary or successional forest and primary forest	320–564	Smaller than <i>Callithrix</i>	20–40	Physiological	Primarily visual, stalk and pounce, foliage gleaning	Opportunistic exudate (gum, sap) consumption, small insects and fruit	Long-tusked, unable to gouge actively for exudates
<i>Callithrix</i> Sources: 2, 3, 4, 8, 9, 11, 12	Marmosets	Can survive in secondary or successional forest and primary forest	300–450	Largest and most stable	<20–40	Physiological	Primarily visual, stalk and pounce, foliage gleaning	Large reliance upon exudates, small insects, fruit	Short-tusked (canines and incisors of equal length, enabling gouging)

Sources: (1) Baker (1991); (2) Coimbra-Filho (1981); (3) Ferrari & Lopes Ferrari (1989); (4) French (1997); (5) Garber (1993); (6) Kleiman et al. (1988); (7) Peres (1991); (8) Rizzini & Coimbra-Filho (1981); (9,10,11) Rylands (1989, 1993, 1996); (12) Stevenson & Rylands (1988).

genera to learn the novel tasks, while *Callithrix* and *Saguinus* should both be less effective learners. We considered (4) the foraging specialization hypothesis (Greenberg 1983), which predicts that *Callithrix* might be more neophobic than *Saguinus* and *Leontopithecus*, if the former is regarded as showing the greatest level of foraging specialization, in the form of gummivory. Finally, we evaluated the evidence for: (5) the cognitive mapping hypothesis (Milton 1988), which predicts that *Leontopithecus* with the largest home ranges will be the most neophilic and innovative, while *Callithrix* with the smallest home ranges will be the least innovative; (6) the social intelligence hypothesis (sensu Dunbar 1992, 1995) which predicts, to the extent that social attentiveness reflects social learning, that *Callithrix* with the largest group sizes will show the greatest level of social attentiveness; and (7) the social learning hypothesis (Boyd & Richerson 1985; Laland et al. 1996), which predicts, if social attentiveness reflects social learning, that *Callithrix*, which is subjected to the least environmental variability (owing to reliance upon nonseasonal exudates) will show the least social attentiveness. These predictions are summarized in the Discussion.

## METHODS

### Subjects

We studied 26 captive groups of callitrichids, totalling 108 individuals. The subjects were located in four zoos, housed in a variety of enclosures, group sizes and compositions, with varying husbandry regimes (Table 2). Within these groups there were 56 males, 50 females and two of unknown sex (age range 6.5 months to 18.5 years). The sex ratios (male:female) within each genus were: *Leontopithecus* 32:26; *Saguinus* 7:5; *Callithrix* 17:19. All of these approximate a 1:1 ratio. The age of individuals in each genus differed markedly (median and interquartile range): *Leontopithecus* 71 months (44–105 months), *Saguinus* 41 months (13–70 months) and *Callithrix* 18 months (8–68 months), a point to which we return in the Results. Where necessary for identification, individuals were marked with coloured inks (International Market Supply, Congleton, Cheshire, U.K.). This method caused no distress and after a few minutes the subjects ignored the marks.

### Apparatus

We presented each group of subjects with four artificial tasks, which involved opening a box to gain access to food, and three natural tasks, which involved extractive processing of an unfamiliar food. The artificial tasks consisted of opaque white plastic boxes of different shapes containing raisins. When the boxes were closed the subjects had limited visual and olfactory access to the food reward. For each task the subjects had two equivalent, colour-differentiated and spatially separated means of extracting the raisins, for instance two doors. The colours used were valid for both di- and trichromatic

individuals (N. Mundy, personal communication) and hence appropriate for both sexes of callitrichid monkey. The tasks were designed so that they could be solved with natural foraging actions such as those used when turning over leaves and loose or rotting bark, exploring crevices and knotholes and rummaging in leaf litter (Peres 1986; Garber 1993). Task 1 consisted of a box of dimensions 10 × 11.5 cm and 7 cm high; the top of the box was divided into two doors, one painted blue and the other green. Task 2 consisted of a round box of diameter 11 cm and height 6.5 cm, the top of which had two access holes (of differing sizes for the three genera), one painted blue and the other yellow. Task 3 was a cylinder of diameter 11 cm and height 16 cm; at a height of 8 cm two access holes were placed opposite one another, one coloured blue and the other red. Task 4 consisted of a large transparent box (for *Leontopithecus*: 32 × 22 cm and 24 cm high; for *Saguinus* and *Callithrix*: 22 × 15 cm and 16 cm high), with a hinged door which the subject had to push inwards or pull outwards to reach the raisins. The tasks were designed in such a way that at any one time only one option could be used to extract the reward. Pilot studies at Banham zoo showed that individuals of all ages and species could physically obtain the food reward inside the tasks.

The natural tasks consisted of whole passion fruit, peanuts in their shells and hard-boiled quails' eggs in their shells. Callitrichids are reported to eat birds' eggs and hatchlings in the wild (Kleiman et al. 1988) and, although in captivity peeled and chopped hens' eggs are often provided, whole intact quails' eggs were always novel. As there was a lack of response to the passion fruit during pilot studies, immediately prior to presentation we punctured them with a sharp object to enhance olfactory stimulation.

Within each enclosure the food platform that, according to the zoo-keepers, was the most popular among the group was used as a platform for all task presentations. However, if the experimenters could not easily see this platform we moved it to a more suitable location. Prior to task presentation the experimenters defined an area including and surrounding the platform within which subjects would be categorized as 'in proximity' to the task (ca. 50 cm radius), beyond which subjects were considered to be 'at a distance' from the task.

## Procedure

### Baseline data

We obtained three 20-min blocks of baseline feeding data for each subject group to determine whether the behaviour observed in the experimental trials was due to the presence of the novel task and not just to the presence of food. These observation periods were spread such that one occurred before any task presentations, one after approximately half of the task presentations and one after all task presentations. Each group was observed during at least one morning and afternoon feed to enable comparison with experimental data if a time of day effect was subsequently found. The food was placed on the platform

**Table 2.** Subjects by genus, species, group size, enclosure type and zoo

Species	Group size	Enclosure type	Zoo
<i>Leontopithecus</i>	N=58		
<i>L. chrysomelas</i>	3	Indoor–Outdoor	Whipsnade
<i>L. chrysomelas</i>	2	Indoor–Outdoor	Jersey
<i>L. chrysomelas</i>	2	Indoor–Outdoor	Marwell
<i>L. chrysomelas</i>	5	Indoor–Outdoor	Twycross
<i>L. chrysomelas</i>	4	Island	Jersey
<i>L. rosalia</i>	2	Indoor–Outdoor	Marwell
<i>L. rosalia</i>	6	Indoor–Outdoor	Twycross
<i>L. rosalia</i>	3	Indoor–Outdoor	Jersey
<i>L. rosalia</i>	3	Island	Marwell
<i>L. rosalia</i>	7	Free-ranging	Jersey
<i>L. rosalia</i>	2	Free-ranging	Marwell
<i>L. chrysopygus</i>	2	Indoor–Outdoor	Jersey
<i>L. chrysopygus</i>	6	Indoor–Outdoor	Jersey
<i>L. chrysopygus</i>	7	Indoor–Outdoor	Jersey
<i>L. chrysopygus</i>	2	Indoor–Outdoor	Jersey
<i>L. chrysopygus</i>	2	Indoor–Outdoor	Jersey
<i>Saguinus</i>	N=13		
<i>S. imperator</i>	3	Indoor–Outdoor	Marwell
<i>S. imperator</i>	3	Indoor–Outdoor	Marwell
<i>S. imperator</i>	3	Indoor–Outdoor	Twycross
<i>S. oedipus</i>	4	Indoor–Outdoor	Twycross
<i>Callithrix</i>	N=37		
<i>C. argentata</i>	8	Indoor–Outdoor	Twycross
<i>C. argentata</i>	6	Free-ranging	Whipsnade
<i>C. argentata</i>	8	Free-ranging	Jersey
<i>C. geoffroyi</i>	7	Indoor–Outdoor	Twycross
<i>C. geoffroyi</i>	3	Indoor–Outdoor	Jersey
<i>C. geoffroyi</i>	5	Indoor–Outdoor	Jersey

Islands consisted of a heated hut placed on an island surrounded by water, and free-ranging subjects had a heated hut in a wooded area within the zoo grounds, but were not physically contained. All enclosures contained some form of environmental enrichment.

used for task presentations. We collected baseline data comparable to data taken during the task presentations. We recorded the identity of all individuals in proximity to the food platform at 10-s intervals, the latency to the first feed of each individual, the number of pieces of food (monkey pellet/fruit) each individual consumed during the period and the identity of individuals at proximity when a conspecific was eating at the food platform. We defined all individuals in proximity to the food platform as 'attentive to the task' on the grounds that all such individuals were observed to look directly at the food platform. Similarly, we defined all individuals in proximity to the food platform when a conspecific was eating at the food platform as 'socially attentive', on the grounds that all such individuals were observed to be watching these conspecifics.

#### Task presentation

Prior to task presentation we gave each group of subjects raisins to ensure that they were all equally familiar with this food reward. Each of the seven tasks was presented to each group only once. Tasks were introduced into the enclosure by R.D. or a zoo-keeper (depending upon the zoo). Observations began immediately and continued for 30 min or until all of the food reward had been extracted, whichever occurred sooner. Within each

group, during half of the task presentations we recorded the behaviour of subjects in proximity to the task and during the other half their behaviour at a distance from the task, randomized as far as possible for each task. No more than three tasks were presented to each group per day with not less than 1 h between presentations of tasks or routine keeper feeds. The order of presentation was pseudorandomized within the artificial tasks (which were always presented first for logistical reasons) and the natural tasks for each species. For each group there was a mixture of morning and afternoon presentations.

Data were collected simultaneously by R.D. and R.C., using paper check sheets and a PSION containing an observation program. During in proximity observations, the observers noted at 10-s intervals which individuals were within the proximity area. As individuals within this area were oriented towards the task, an animal in proximity was said to be attentive to the task in proximity. During at distance observations the observers noted every 10 s which of the individuals outside the proximity area had their face oriented towards the task, and so were judged to be attentive to the task at a distance. Also recorded were the latencies within the group with which each individual first made contact with the task (touched the task with the hand or mouth), first unsuccessfully manipulated the task in some way (moved part of the



artificial task or the whole natural task but did not eat), and first successfully manipulated the task (extracted a raisin or ate from the natural tasks). The number of unsuccessful and successful manipulations, per individual, throughout each task presentation was noted. During in proximity observations the observers recorded the identity of all individuals within the proximity area (and thus attentive) during manipulations of the task by conspecifics. During at a distance observations they recorded the identity of all individuals that were outside the proximity area and judged to be attentive (by face orientation) towards a conspecific manipulating the task. In this way subjects were defined as socially attentive when in proximity or at a distance, to either an unsuccessful or successful manipulation by a conspecific.

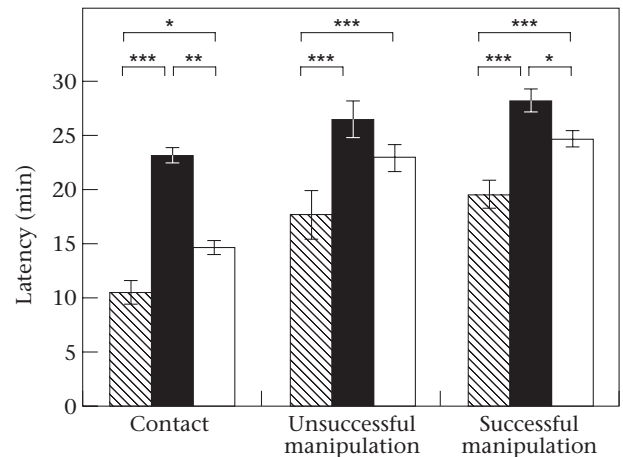
## Statistical Methods

As there were no significant differences between genera in responsiveness to the different tasks and as there were insufficient data per task to analyse them individually, we pooled data for all dependent variables across tasks. All data were checked for normality, with Kolmogorov–Smirnov tests, and log transformed where necessary to allow parametric statistical analyses. Where this was not possible nonparametric statistical tests were used. The number of intervals for which individuals were attentive to the task or food platform (in proximity or at a distance) was taken as a percentage of the total intervals that the task or food was in position, to account for different observation periods. The number of intervals that individuals were attentive to a manipulating or feeding conspecific was taken as a percentage of their opportunity to attend to a manipulating or feeding individual in that observation period (the number of unsuccessful manipulations, successful manipulations or feeds in the group minus those produced by the individual in question). Where multiple comparisons or tests were made, we controlled the familywise error rate by reducing the significance level of alpha, designated below as  $\alpha^*$ . For each family of comparisons or tests  $\alpha^* = \alpha/c$ , where  $\alpha$  equals 0.05 and  $c$  corresponds to the number of comparisons or tests. Power analysis (reported at  $\alpha = 0.05$ ) upon the baseline data was performed using a large effect size ( $\Phi' = 0.40$ ) as defined by Cohen (1988), owing to the large effects seen in the corresponding experimental data. We used two-tailed statistical tests.

## RESULTS

### Latencies

In the experimental condition there were significant effects of genus on latency to the first contact (ANOVA:  $F_{2,105} = 15.304$ ,  $P < 0.001$ ,  $\alpha^* = 0.013$ ), latency to the first unsuccessful manipulation ( $F_{2,105} = 17.109$ ,  $P < 0.001$ ,  $\alpha^* = 0.013$ ) and latency to the first successful manipulation ( $F_{2,105} = 29.504$ ,  $P < 0.001$ ,  $\alpha^* = 0.013$ ; Fig. 1). The pattern was consistent for all these parameters, with *Leontopithecus* having shorter latencies than both

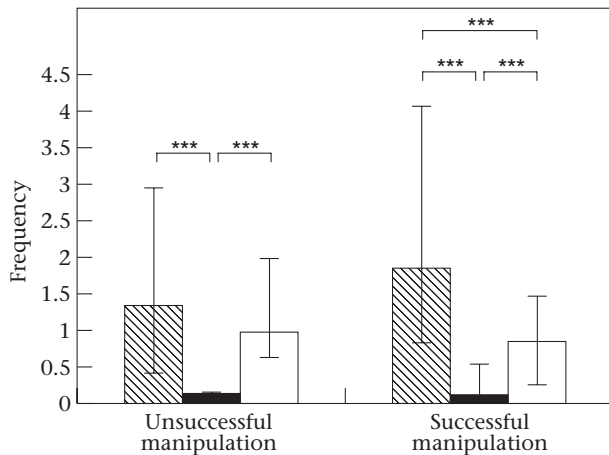


**Figure 1.** Mean latency  $\pm$  SE (min) to the first contact, unsuccessful manipulation and successful manipulation of the novel task by *Leontopithecus* (▨; lion tamarins), *Saguinus* (■; tamarins) and *Callithrix* (□; marmosets). ANOVA: \*\*\* $P < 0.005$ , \*\* $P < 0.025$ , \* $P < 0.05$ .

*Callithrix* (Tukey: contact:  $q_{3,105} > 3.40$ ,  $P < 0.05$ ; unsuccessful manipulation:  $q_{3,105} > 5.365$ ,  $P < 0.001$ ; successful manipulation:  $q_{3,105} > 5.365$ ,  $P < 0.001$ ) and *Saguinus* (Tukey: contact:  $q_{3,105} > 5.365$ ,  $P < 0.001$ ; unsuccessful manipulation:  $q_{3,105} > 5.365$ ,  $P < 0.001$ ; successful manipulation:  $q_{3,105} > 5.365$ ,  $P < 0.001$ ), while *Callithrix* had shorter latencies than *Saguinus* (Tukey: contact:  $q_{3,105} > 4.25$ ,  $P = 0.01$ ; unsuccessful manipulation:  $q_{3,105} < 3.40$ , NS; successful manipulation:  $q_{3,105} > 3.40$ ,  $P < 0.05$ ).

To determine whether these differences reflect differences in the latency of the first individual in each group to respond or in the subsequent response of the conspecifics to the first individual, we reanalysed these data, using the first individual within each group to make contact with the task for each task presentation. There was an effect of genus on the latency of the first individual to make contact with the novel object (ANOVA:  $F_{2,23} = 6.288$ ,  $P = 0.007$ ,  $\alpha^* = 0.013$ ) and as before *Saguinus* showed longer latencies ( $\bar{X} \pm \text{SE} = 15$  min, 38 s  $\pm$  4 min, 22 s) than both *Leontopithecus* (3 min, 52 s  $\pm$  1 min, 24 s; Tukey:  $q_{3,23} > 4.64$ ,  $P < 0.01$ ) and *Callithrix* (5 min, 42 s  $\pm$  1 min, 50 s;  $q_{3,23} > 3.58$ ,  $P < 0.05$ ), while there was no difference in latency between *Leontopithecus* and *Callithrix* ( $q_{3,23} < 3.58$ , NS).

In the baseline condition there was also a significant effect of genera on the mean  $\pm$  SE latency to the first feed (ANOVA:  $F_{2,98} = 6.732$ ,  $P = 0.002$ ): *Leontopithecus* had shorter latencies (1 min, 15 s  $\pm$  14 s) than both *Saguinus* (2 min, 2 s  $\pm$  30 s; Tukey:  $q_{3,98} > 3.40$ ,  $P < 0.05$ ) and *Callithrix* (2 min, 16 s  $\pm$  17 s;  $q_{3,98} > 4.28$ ,  $P < 0.01$ ), although in contrast to the experimental condition there was no difference between *Callithrix* and *Saguinus*. These differences were less marked than with the experimental tasks. For example, when the difference in latency between the first feed in the baseline and the first contact of the novel task was analysed, there was a significant intergeneric effect (ANOVA:  $F_{2,98} = 11.178$ ,  $P < 0.001$ ) such that *Saguinus* had significantly longer latencies than

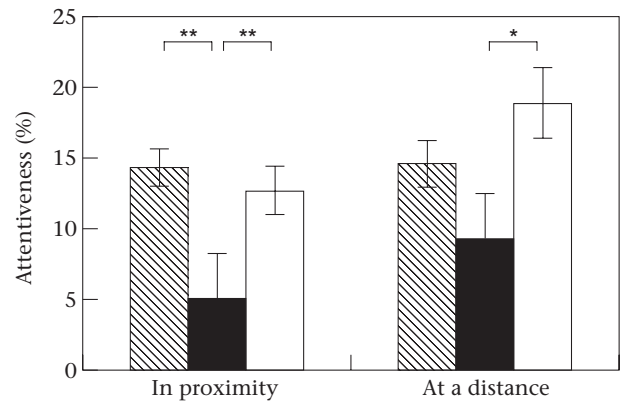


**Figure 2.** Median frequency (and interquartile ranges) of unsuccessful and successful manipulations per individual for *Leontopithecus* (▨; lion tamarins), *Saguinus* (■; tamarins) and *Callithrix* (□; marmosets). Mann–Whitney: \*\*\* $P < 0.005$ .

both *Leontopithecus* (Tukey:  $q_{3,98} > 5.365$ ,  $P < 0.001$ ) and *Callithrix* ( $q_{3,98} > 4.28$ ,  $P < 0.01$ ). Similarly, when the difference in latency between the first feed in the baseline and the first success with the novel task was analysed, there was a significant intergeneric effect (ANOVA:  $F_{2,98} = 18.358$ ,  $P < 0.001$ ) such that *Leontopithecus* had shorter latencies than both *Saguinus* (Tukey:  $q_{3,98} > 5.365$ ,  $P < 0.001$ ) and *Callithrix* ( $q_{3,98} > 5.365$ ,  $P < 0.001$ ), and *Callithrix* had shorter latencies than *Saguinus* ( $q_{3,98} > 3.40$ ,  $P < 0.05$ ). Hence we can be reasonably confident that the experimental findings cannot be explained by the differences between genera in their latency to feed in non-novel situations.

### Manipulation Frequency

There were also significant differences between genera in the number of both unsuccessful manipulations (Kruskal–Wallis:  $\chi^2_{25} = 15.715$ ,  $P < 0.001$ ,  $\alpha^* = 0.006$ ) and successful manipulations (Kruskal–Wallis:  $\chi^2_{25} = 30.602$ ,  $P < 0.001$ ,  $\alpha^* = 0.006$ ) produced per individual (Fig. 2). These results were due to more unsuccessful and successful manipulations in *Leontopithecus* than *Saguinus* (Mann–Whitney:  $U = 118$ ,  $N_1 = 58$ ,  $N_2 = 13$ ,  $P < 0.001$ ;  $U = 79$ ,  $N_1 = 58$ ,  $N_2 = 13$ ,  $P < 0.001$ ,  $\alpha^* = 0.006$ ) and *Callithrix* ( $Z = -0.806$ ,  $N_1 = 58$ ,  $N_2 = 37$ , NS;  $Z = -4.06$ ,  $N_1 = 58$ ,  $N_2 = 37$ ,  $P < 0.001$ ,  $\alpha^* = 0.006$ ), and in *Callithrix* than *Saguinus* ( $U = 88$ ,  $N_1 = 37$ ,  $N_2 = 13$ ,  $P = 0.001$ ;  $U = 111$ ,  $N_1 = 37$ ,  $N_2 = 13$ ,  $P = 0.004$ ,  $\alpha^* = 0.006$ ). In the baseline condition there were no significant differences between genera in the percentage of intervals in which individuals were eating (ANOVA:  $F_{2,99} = 2.525$ ,  $P = 0.085$ ,  $\Phi = 1.97$ , power = 0.86). With relatively high power to the analysis of baseline data we can be fairly sure that there were no genuine differences between genera in the amount they ate. Direct comparison of the amount of feeding in the baseline and the frequency of manipulations in the experimental conditions was not possible given the differences between these dependent variables, and the fact that far fewer food



**Figure 3.** Mean percentage of opportunities  $\pm$  SE used to attend to the novel task in proximity and at a distance by *Leontopithecus* (▨; lion tamarins), *Saguinus* (■; tamarins) and *Callithrix* (□; marmosets) individuals. ANOVA: \*\* $P < 0.025$ ; \* $P < 0.05$ .

items were available in the baseline than during the experiment. Analysis of covariance with the baseline data as a covariate was not possible as the data involved were not normal.

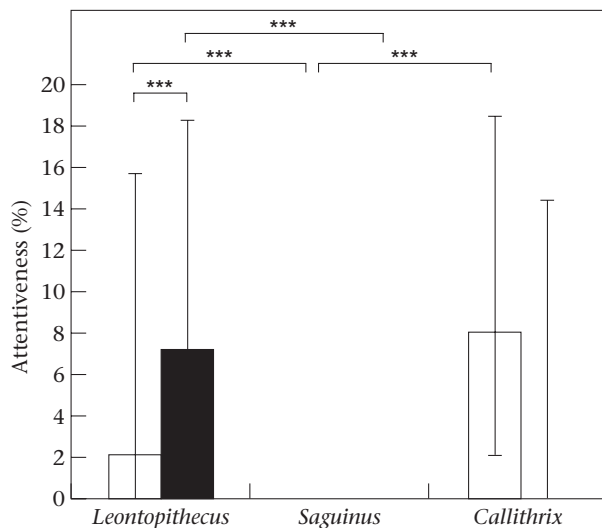
In line with prediction 1, there was a negative correlation between latency to the first contact with the novel tasks and the frequency of successful manipulations (Spearman:  $r_s = -0.703$ ,  $N = 108$ ,  $P < 0.0001$ ), and a positive correlation between latency to the first contact and latency to the first success with the novel tasks (Pearson:  $r_{106} = 0.785$ ,  $P < 0.0001$ ).

### Attentiveness to the Task

There were significant effects of genus on attentiveness in proximity to the task (ANOVA:  $F_{2,102} = 5.778$ ,  $P = 0.004$ ,  $\alpha^* = 0.025$ ) and at a distance (ANOVA:  $F_{2,85} = 3.360$ ,  $P = 0.039$ ,  $\alpha^* = 0.025$ ). The results (Fig. 3) are largely due to a lower level of attentiveness in *Saguinus* than *Leontopithecus* (Tukey: proximity:  $q_{3,102} > 4.28$ ,  $P < 0.01$ ; distance:  $q_{3,25} < 3.40$ , NS,  $P = 0.062$ ) and *Callithrix* (proximity:  $q_{3,102} > 4.28$ ,  $P < 0.01$ ; distance:  $q_{3,85} > 3.40$ ,  $P = 0.05$ ). In the baseline condition there was no significant effect of genera on the mean percentage of observed intervals that individuals were present at the food platform (ANOVA:  $F_{2,99} = 1.019$ ,  $P = 0.365$ ,  $\Phi = 1.97$ , power = 0.86).

### Attentiveness to Conspecific Manipulations

There were significant differences between genera in the level of attentiveness to conspecifics in proximity (Fig. 4) during unsuccessful (Kruskal–Wallis:  $\chi^2_{25} = 16.293$ ,  $P < 0.001$ ,  $\alpha^* = 0.005$ ) and successful manipulations (Kruskal–Wallis:  $\chi^2_{25} = 15.345$ ,  $P < 0.001$ ,  $\alpha^* = 0.005$ ), but not for attentiveness to conspecifics at a distance. *Saguinus* used a lower percentage of their opportunities to be in proximity to the task during an unsuccessful manipulation than both *Leontopithecus* (Mann–Whitney:  $U = 170$ ,  $N_1 = 13$ ,  $N_2 = 58$ ,  $P = 0.001$ ,  $\alpha^* = 0.005$ ) and *Callithrix* ( $U = 69$ ,  $N_1 = 13$ ,  $N_2 = 37$ ,  $P < 0.001$ ,  $\alpha^* = 0.005$ ). Similarly, during successful conspecific manipulations *Saguinus* were in



**Figure 4.** Median percentage (and interquartile ranges) of opportunities used to attend, in proximity, to conspecifics performing an unsuccessful (□) or successful (■) manipulation of the novel task by *Leontopithecus* (lion tamarins), *Saguinus* (tamarins) and *Callithrix* (marmosets). Mann–Whitney; \*\*\* $P < 0.005$ .

proximity a lower percentage of the time than both *Leontopithecus* (Mann–Whitney:  $U = 112.5$ ,  $N_1 = 12$ ,  $N_2 = 57$ ,  $P < 0.001$ ,  $\alpha^* = 0.005$ ) and *Callithrix* ( $U = 136$ ,  $N_1 = 12$ ,  $N_2 = 37$ ,  $P = 0.023$ ,  $\alpha^* = 0.005$ ), while *Callithrix* was in proximity during successful conspecific manipulations a lower percentage of the time than *Leontopithecus* ( $Z = -2.132$ ,  $N_1 = 37$ ,  $N_2 = 57$ ,  $P = 0.033$ ,  $\alpha^* = 0.005$ ). When attentiveness overall is considered (by summing attentiveness to successful and unsuccessful manipulations both in proximity and at a distance), there were no significant differences between genera, as *Saguinus* compensated for the low level of attentiveness in proximity by being attentive at a distance. Although not significant, *Saguinus* ( $\bar{X} \pm \text{SE} = 13.1 \pm 2.5\%$ ) and *Leontopithecus* ( $11.3 \pm 1.2\%$ ) had higher and more similar overall levels of attentiveness than *Callithrix* ( $9.4 \pm 1.5\%$ ).

*Leontopithecus* was the only genus to show more attentiveness (in proximity) to successful conspecific manipulations than unsuccessful ones (Wilcoxon:  $Z = -3.168$ ,  $N = 58$ ,  $P = 0.002$ ,  $\alpha^* = 0.005$ ; Fig. 4). *Saguinus* was the only genus to show a different level of attentiveness to conspecifics between proximity and distance, using more opportunities to observe from a distance than in proximity for unsuccessful (Wilcoxon:  $T = 0$ ,  $N = 13$ ,  $P = 0.017$ ,  $\alpha^* = 0.005$ ) and successful ( $T = 1$ ,  $N = 12$ ,  $P = 0.027$ ,  $\alpha^* = 0.005$ ) conspecific manipulations.

In the baseline condition there was also a significant effect of genera upon the mean percentage of conspecific feeds during which individuals were in proximity (ANOVA:  $F_{2,99} = 9.295$ ,  $P < 0.001$ ) such that *Leontopithecus* were in proximity significantly more ( $\bar{X} \pm \text{SE} = 19 \pm 1.2\%$ ) than *Callithrix* ( $11 \pm 1.5\%$ ; Tukey:  $q_{3,99} > 5.365$ ,  $P < 0.001$ ) but not *Saguinus* ( $15 \pm 2.5\%$ ). This corresponds to the experimental data. Unfortunately an analysis of difference scores was not possible because of the incompatibility of the baseline and experimental measures and an

analysis of covariance was inappropriate because of the non-normal nature of the experimental data.

Although individuals within *Leontopithecus* were significantly older than those within *Callithrix* (ANOVA:  $F_{2,105} = 10.041$ ,  $P < 0.001$ ) we believe the reported results were caused by intergeneric differences. This is because when the older *Leontopithecus* individuals were excluded from the data, such that there was no significant difference in age between genera, the reported trends remained with an equal degree of significance. Further statistical analyses established that the differences between genera presented here could not be accounted for by other variables such as group size, enclosure type or zoo.

## DISCUSSION

Our study investigated the behaviour of three of the four species of *Leontopithecus*, two of the 15 species of *Saguinus* and two of the 20 species of *Callithrix*. While a comparative experimental study incorporating 26 populations of seven primate species is a considerable undertaking, it is important to bear in mind that our conclusions relate exclusively to those species studied and must be regarded as tentative.

The results support Lefebvre's (2000) hypothesis that there is a positive association between neophilia and innovation. This association is also implied in the hypothesis relating extractive foraging to innovation (Clarke & Lindburg 1993) and thus the results would also appear to support this hypothesis.

We found consistently shorter response latencies, higher levels of successful and unsuccessful manipulation, and greater attentiveness in *Leontopithecus* than *Saguinus* and *Callithrix*. This is consistent with the hypothesis that species dependent upon manipulative and explorative foraging tend to be less neophobic and more innovative than other species (Vitale et al. 1991; Clarke & Lindburg 1993; Table 3). The manipulative foraging style of *Leontopithecus*, involving probing for concealed prey with their slender hands and fingers (Hershkovitz 1977; Coimbra-Filho 1981; Kleiman et al. 1988; Rylands 1989), may account for their better performance in the study. There are, however, several reasons to believe that the response of *Leontopithecus* to the novel tasks was due to their greater exploratory and neophilic tendencies, over and above their greater specialization towards 'blind' microhabitat exploitation (Bicca-Marques 1999), as predicted by Clarke & Lindburg (1993) and Vitale et al. (1991). However, motivational differences (possibly related to body size) between genera cannot be ruled out, owing to the similar patterns found in the baseline condition. Although we found no differences between genera in the latency to feed, the time spent feeding or in proximity to the food platform during the baseline condition (despite high power), *Leontopithecus* did appear to show more social attentiveness in the baseline than *Callithrix*, a pattern that is mirrored in the experimental results.

The morphology of *Leontopithecus* hands cannot be seen to be responsible for their superior performance



**Table 3.** Predicted results according to the hypotheses discussed and level of support in observed data

Hypotheses	Neophilia	Innovation	Social attentiveness	Predictions supported?
1 Neophilia associated with innovation (Lefebvre 2000)	—	—	—	Yes
2 Extractive foraging (sensu Clarke & Lindburg 1993)	L>C>S	L>C>S	—	Yes
3 Extractive foraging (sensu Parker & Gibson 1977)	—	L>C>S	—	Yes
4 Foraging specialization (Greenberg 1983)	L&S>C	L&S>C	—	No
5 Cognitive mapping (Milton 1988)	—	L>S>C	—	Partially
6 Social intelligence (sensu Dunbar 1992)	—	C>S&L	C>S&L	No
7 Social learning (Laland et al. 1996)	—	—	L&S>C	Partially

L: *Leontopithecus*; C: *Callithrix*; S: *Saguinus*.

upon latency to make first contact, unsuccessful manipulation and attentiveness to the task and conspecifics. The overall performance of *Leontopithecus* matched the response style of a 'bold' or 'neophilic' genus. These results correspond to those of Hardie & Buchanan-Smith (2000), who found that *Saguinus fuscicollis*, an extractive forager (Buchanan-Smith 1990; Peres 1991; Garber 1993; Hardie 1997; Bicca-Marques 1999), touched novel foraging objects more rapidly than *S. labiatus*, a visual seize and capture forager (Buchanan-Smith 1990; Hardie 1997).

Our results also reveal a difference in response between *Callithrix* and *Saguinus*. Despite exploiting a similar niche to *Saguinus* (Rylands 1996), *Callithrix* was consistently more neophilic. *Saguinus* appeared more neophobic than *Callithrix* (and *Leontopithecus*) as the first individual per group to make contact with the task did so significantly more slowly and tended to observe the novel task and conspecifics from a distance. The suggestion that *Saguinus* is comparatively neophobic is supported by the fact that in the baseline condition there were no differences between the genera in latency to first feed, making it likely that the behavioural differences were due to neophilia rather than feeding ecology or life history differences. This result appears to be inconsistent with Greenberg's hypothesis (that neophobia correlates with foraging specialization), as *Callithrix* might be expected to show the greatest level of neophobia, owing to its comparative foraging specialization, in the form of gummivory (Table 3). However, it may be inappropriate to regard *Callithrix* as specialized because it may exploit many different exudate species, possibly in different ways. Similarly, it would be premature on the basis of these results to conclude that all *Saguinus* species are neophobic and all *Callithrix* species neophilic as only two species of each genus were studied, and parity among species within a genus cannot be assumed (Box 1988). For example, the *Callithrix* genus is divided into two clades differing in dependence upon gummivory, home range size and resource variability (Hershkovitz 1977; Rylands et al. 2000). Also, within *Saguinus* (a visual forager) one species (*S. fuscicollis*) uses extractive foraging (Buchanan-Smith 1990; Peres 1991; Garber 1993; Hardie 1997).

Are the differences in 'temperament' between genera better explained by life history variables or phylogeny? On the basis of shared derived traits, Rosenberger (1984)

and Ford (1986) have proposed that *Callithrix* species are more closely related to *Leontopithecus* than to *Saguinus*. Therefore it should possibly be of no surprise that *Callithrix* and *Saguinus* differ in response styles, despite their commonalities of habitat, insect foraging and reproduction.

An alternative explanation for intergeneric differences is that they reflect cognitive abilities. If this supposition is correct, the results may reflect upon the technical and social intelligence hypotheses. *Leontopithecus* falls within the category of an 'unskilled extractive forager' (Dunbar 1995, after Gibson 1986) or 'simple object manipulator' (Parker & Gibson 1977). We believe this description to be accurate as, although the hands of *Leontopithecus* are specialized (being longer and narrower) compared with nonmanipulative *Saguinus* and *Callithrix* species (Bicca-Marques 1999), this does not lessen the skills (sensorimotor-coordination and intelligence for identification, location and processing of hidden foods) required of *Leontopithecus* in the sense of Parker & Gibson's (1977) hypothesis. Thus, evidence for the extractive foraging hypothesis (Parker & Gibson 1977; Gibson 1986) may be found in the observation that *Leontopithecus* tended to make fewer unsuccessful manipulations than successful ones (Fig. 2), although not significantly so, possibly revealing a more efficient conversion of trial and error to learning than the other genera. Although our interpretation of 'extractive foraging' is not restricted to tool use, there is a recent observation of extractive tool use by captive, free-ranging *L. rosalia* (Stoinski & Beck 2001). Furthermore, as *Callithrix* is classified as a 'specialized extractive forager' and the *Saguinus* species studied as 'nonextractive foragers' (see Dunbar 1995) by Parker & Gibson's hypothesis, the experimental results of increasing innovation from *Saguinus* to *Callithrix* to *Leontopithecus* correspond to the hypothesis that extractive foraging may have promoted the evolution of intelligence, in the form of an ability to respond to environmental change (Table 3).

Similarly, *Leontopithecus*, with their lack of gummivory and the largest home ranges of callitrichids, which are not only related to their larger body size (Rylands 1993), may conform to Milton's (1981, 1988) cognitive mapping hypothesis (Table 3) and to hypotheses relating opportunism to relative brain size (Lefebvre et al. 1997; Sol et al. 1999; Reader & Laland 2002) as they must cope with

patchily but predictably distributed fruits. Indeed, the travel patterns of callitrichids imply the use of spatial memory and 'detailed knowledge of the distribution of particular plant species' (Garber 1989; Tarou & Maple 2000). The superior performance of *Leontopithecus* in our study corresponds to the results of Platt et al. (1996) when comparing *Leontopithecus* and *Callithrix* on spatial and visual memory tasks.

Dunbar (1992, 1995) found evidence of a relation between group size, but not extractive foraging or range size, and absolute brain or relative neocortex size. A related hypothesis is that gregarious species rely more on social-learning processes than solitary species (e.g. Roper 1986). Our results may also address these hypotheses to the extent that attentiveness to conspecifics provides an indication of social-learning propensity (Humphrey 1976; Whiten & Byrne 1988, 1997). In the wild, *Leontopithecus* and *Saguinus* have similar group sizes (Rylands 1993) with *Callithrix* occurring in the largest groups (Rylands 1984; Ferrari & Lopes Ferrari 1989; Table 1). However, individuals within *Leontopithecus* showed more circumstantial evidence of social learning, in our study, as they alone observed more successful than unsuccessful manipulations, although this could represent attentiveness to the food. Furthermore, both *Saguinus* and *Leontopithecus* showed slightly (nonsignificant) higher overall levels of social attentiveness than *Callithrix*. Thus in so far as the data on social attentiveness reflect on hypotheses concerning group size, sociality and social learning, they are inconsistent with them.

Deaner et al. (2000) suggested that social and ecological demands could have evolved in tandem. Other researchers have suggested that species living in an environment of intermediate variability, using more dispersed foods or more complex foraging methods, may be more likely to evolve and use social learning (Giraldeau et al. 1994; Laland et al. 1996). To the extent that social attentiveness indicates a social-learning propensity, this hypothesis might account for the higher levels of social attentiveness observed in *Leontopithecus*, as they appear to show more complex extractive foraging than individuals in other genera. This result corresponds with Omedes & Carroll (1990) who found that a *Leontopithecus* species interacted socially more often than *Callithrix* or *Saguinus* species. Similarly, the higher resource variability experienced by *Leontopithecus* and *Saguinus*, owing to their inability to rely upon nonseasonal exudates (like *Callithrix*), may account for the higher (nonsignificant) levels of overall social attentiveness observed (Table 3).

Our results have several implications for callitrichid conservation. As callitrichids frequently come across novel exploitable foods in the rain forest (Kleiman et al. 1988), determination of the extent to which captive species or genera succeed in exploiting novel foods will assist in the formulation of species- or genera-specific prerelease training protocols for reintroductions (Box 1991). The degree of social attentiveness of different species or genera may reflect their use of social learning (Cambefort 1981; Coussi-Korbel & Frigaszy 1995), and indicate the viability of using skilled 'demonstrators' in prerelease training (Box 1991). In a recent review of the

primate social learning literature, Custance et al. (in press) found that the use of skilled, rather than unskilled, demonstrators significantly increased the likelihood of social learning in observers.

In conclusion, this study supports the hypotheses (Parker & Gibson 1977; Vitale et al. 1991; Clarke & Lindburg 1993) that species dependent upon manipulative and explorative foraging tend to be more attentive, innovative and neophilic than other species and that species subject to environmental variability, more dispersed foods (larger home ranges) and using more complex foraging methods are more socially attentive than other species (Laland et al. 1996). The other hypotheses discussed are either not supported by the data or received mixed support. Further work is required to validate the observed intergeneric differences, including novel contexts other than foraging. It would be especially interesting to study the response of *Saguinus* species thought to be manipulative foragers (*S. fuscicollis*, *S. nigricollis* and *S. tripartitus*, see Bicca-Marques 1999) to determine whether the apparent neophobia of the *Saguinus* species studied is due to the lack of extractive foraging shown by these species in the wild. Similarly, to determine whether the comparatively poor performance of the *Saguinus* species studied was due to greater neophobia or cognitive differences, one could expose them to novel tasks in a transparent box before testing. If the poor performance was due to neophobia, their subsequent performance should improve with this prior exposure.

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