RESEARCH ARTICLE

Age Differences in Neophilia, Exploration, and Innovation in Family Groups of Callitrichid Monkeys

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The prevailing assumption in the primate literature is that young or juvenile primates are more innovative than adult individuals. This innovative tendency among the young is frequently thought to be a consequence, or side effect, of their increased rates of exploration and play. Conversely, Reader and Laland's [International Journal of Primatology 22:787–806, 2001] review of the primate innovation literature noted a greater reported incidence of innovation in adults than nonadults, which they interpreted as (in part) a reflection of the greater experience and competence of older individuals. Within callitrichids there is contradictory evidence for age differences in response to novel objects, foods, and foraging tasks. By presenting novel extractive foraging tasks to family groups of callitrichid monkeys in zoos, we examined, in a large sample, whether there are positive or negative relationships of age with neophilia, exploration, and innovation, and whether play or experience most facilitates innovation. The results indicate that exploration and innovation (but not neophilia) are positively correlated with age, perhaps reflecting adults' greater manipulative competence. To the extent that there was evidence for play in younger individuals, it did not appear to contribute to innovation. The implications of these findings for the fields of innovation and conservation through reintroduction are considered. Am. J. Primatol. 66:167–188, 2005. © 2005 Wiley-Liss, Inc.

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INTRODUCTION

Many animals respond to environmental stressors or ecological challenges by inventing a new behavior or using existing behaviors in a novel context (henceforth termed ''innovation'') [Kummer & Goodall, 1985; Lee, 1991; Lefebvre et al., 1997; Reader & Laland, 2001]. Such behavioral flexibility is thought to be vital to individuals that are forced to adjust to impoverished environments, or are members of opportunistic or generalist species [Box, 1991; Lee, 1991; Lefebvre et al., 1997]. Following Reader and Laland [2003], innovation is defined here as a process that results in new or modified learned behavior and introduces novel behavioral variants into a population's repertoire (innovation sensu process).

A number of characteristics have been put forward as causes or covariates of innovation. There is some evidence that innovation is correlated with neophilia and extractive foraging in animals [Day et al., 2003; Greenberg, 2003]. Exploration also has been regarded as a precursor to innovation since, combined with learning, it may enable an animal to gather information and develop new behaviors or novel means of exploiting the environment [Reader & Laland, 2003; Russell, 1983; Thorpe, 1956]. Several authors have also proposed or reported positive correlations of innovation with brain size, rates of genetic evolution, habitat invasions, construction of new niches, speciosity, and extinction risks [Laland et al., 1996; Lee, 1991; Lefebvre et al., 1997; Reader & Laland, 2002; Sol, 2003; Sol et al., 2002; Wilson, 1985, 1991; Wyles et al., 1983].

Many behavioral innovations in animals appear to be governed by the adage ''necessity is the mother of invention'' [Reader & Laland, 2001, 2003]. Because age is often related to social rank, and the latter is positively correlated with success in obtaining desirable foods in primate species [Cambefort, 1981; Goodall, 1986; Silk, 1987], younger individuals (who may also have higher metabolic costs) might be expected to exhibit a greater need for innovation. A contrasting theory, the ''spare time hypothesis,'' proposes that innovation is favored by a lack of environmental stressors or social distractions [Kummer & Goodall, 1985]. This led Kummer and Goodall [1985, p 209] to state that ''many innovations appear during childhood when a youngster…has much time for carefree play and exploration.'' In fact, several authors have predicted or reported that young primates are more likely to innovate than older ones [Boesch & Boesch, 1981; Cambefort, 1981; Fragaszy & Adams-Curtis, 1991; Hannah & McGrew, 1987; Hauser, 1988; Huffman, 1996; Itani, 1965; Kawamura, 1954; Kummer, 1971; Kummer & Goodall, 1985; McGrew et al., 1979; Nishida et al., 1983], while others have reported that young primates are more investigative toward novel objects [Bertrand, 1969; Glickman & Sroges, 1966; Menzel, 1965, 1969]. These and other well-known examples may reinforce the view that young or juvenile animals are the most innovative members of a group.

The purported increased exploratory and investigatory behavior of young animals has often been interpreted as reflecting the greater ''playfulness'' of these individuals [Bolig et al., 1992; Bramblett, 1978; Bronsen, 1965; Cebul, 1980; McGuire et al., 1994]. It has been suggested that play may facilitate creativity, leading to innovation [Siviy, 1998]. Fedigan [1972, p 362] proposed that animals play not ''just to practice species-specific behavior…but also to put out as many tests or probes of the environment as possible, to innovate.'' Smith [1982] challenged the hypothesis that play is favored by selection partly because it generates elevated rates of innovation, on the grounds that the rate of innovation is low in species (such as common chimpanzees) in which play is frequently

observed. Conversely, Reader and Laland [2002] reported elevated rates of innovation in that species.

However, there are several lines of evidence that conflict with the view that young animals are more innovative than their older conspecifics. In an extensive survey of the literature on primate innovation, Reader and Laland [2001] found proportionately more reports of innovation for adults than for nonadults. Reader and Laland interpreted this finding as most likely reflecting the fact that innovation frequently builds upon other skills and may require a degree of strength, experience, and competence that is more common in adults than nonadults. Consistent with this, young animals have been reported to be ''clumsy foragers'' compared to adults [e.g., Spear, 1984; Wunderle, 1991], since many tasks require considerable experience and practice [McLean, 1997].

Other reports have indicated that it is the older members of a population, individuals that have experienced various environmental fluctuations, that lead their groups out of potential difficulty in times of stress [Hauser, 1988; Kummer, 1971; McComb et al., 2001]. Older individuals may succeed with novel solutions where younger individuals fail, as the latter possess a relatively impoverished database of prior experiences and knowledge from which to innovate [Hauser, 1988; Nishida, 1987]. However, conservatism among adults due to the accumulation of various experiences has also been highlighted in primates [Cambefort, 1981; Goodall, 1986; Lee & Oliver, 1979; Menzel, 1969].

While many studies have provided information on the relationship between age and innovation in large terrestrial primates, relatively little is known about this subject in smaller arboreal species. Such information would be highly relevant to the study of neotropical primates, which are currently exposed to changing environments due to rapid deforestation. Several studies have reported age differences within the callitrichid family in response to novel objects, environments, and foraging tasks, with contradictory findings. Of 17 studies, three reported that the adults were the most innovative individuals in a group [Chamove & Rohrhuber, 1989; Millar et al., 1988] (Moore, unpublished results), while 10 suggested that juveniles were the most innovative [Buchanan-Smith et al., 1993; Price et al., 1989; Schneider, 1994; Scolavino & Vitale, 2000] (Detert, Eva, Matthews, Moore, O'Connell, and Uzu, unpublished results). Two of the studies reported that neither the youngest nor the oldest, but the intermediate-aged individuals in a group exhibited the most innovation [McGrew & McLuckie, 1986; Millar et al., 1988], while others reported no age differences in response to novel foods [Box & Smith, 1998] (Mark Prescott, personal communication). These studies have in common a small sample size, ranging from one to six groups (mean number of groups=2.4) and five to 56 individuals (mean number of individuals=16.4). Although these studies reflect a range of experimental situations, the small sample sizes suggest that the conflicting findings may in part reflect low statistical power. A larger study is needed in order to explore the innovatory tendencies of different age classes of callitrichids with greater reliability. In this study, seven novel extractive foraging tasks were presented to 26 captive family groups of callitrichids from three genera, totaling 108 individuals (which is more than double the sample size used in the previous studies).

We designed this study to clarify conflicting hypotheses relating age to innovation. If play promotes innovation, then as age increases evidence of exploration and innovation should decrease. Conversely, if competence, strength, maturity, or manipulative experience is required for success with novel tasks, then innovation/exploration and age should be positively correlated. Finally, if

age is only a factor in innovatory tendencies insofar as it covaries with social rank, no age differences in innovation should be expected, since callitrichids are largely egalitarian.

MATERIALS AND METHODS

Novel foraging tasks were presented to family groups of callitrichid monkeys. The tasks involved either opaque white plastic puzzle boxes that could be opened to gain access to familiar foods, or novel foods that required extractive foraging. Variables pertaining to neophilia (first individual per group to contact the task, and latency to first task contact), innovation (first individual per group to successfully manipulate the task), and exploration (latencies to, and frequencies of task manipulations; and attentiveness to the tasks) were recorded. This method of studying innovation by evoking it through the introduction of novel tasks was first advocated by Kummer and Goodall [1985], and has been successfully employed in a number of studies [Custance et al., 2001; Lefebvre, 2000; Reader & Laland, 2000].

Subjects

The subjects were 26 captive groups of callitrichids, totaling 108 individuals, of seven species. They were located in four different zoos, housed in different types of enclosures, group sizes, and compositions, with varying husbandry regimes (see Table I). The enclosures varied from the smallest indoor areas of traditional cages (approximately 4 m (l) × 2 m (w) × 2.5 m (h)) to the theoretically limitless areas of free-ranging enclosures. We standardized the visibility of the tasks to all subjects as far as possible by avoiding any enclosures (or parts of enclosures) that contained overly dense foliage. The individuals ranged in age from 1.5 months to 18.5 years, and were divided into age categories according to the classification scheme of Yamamoto [1993] (i.e., each stage corresponds to the birth of a new set of twins). The length of each stage equates to the reported interbirth intervals for *Callithrix* [Stevenson & Rylands, 1988], *Saguinus* [Snowdon & Soini, 1988], and *Leontopithecus* [Hoage, 1982]. Since Yamamoto's [1993] classification resulted in a disproportionate number of individuals assigned to the young-adult category, and there was a very wide range of ages in this one category, we split it into three categories: young-adult, adult, and old-adult (see Table II). Infants are weaned when they are 8–15 weeks old. Juveniles typically weigh 75–77% of adult weight [Hoage, 1982; Snowdon & Soini, 1988]. By the subadult stage, the animals are approximately 82% of adult weight, have an adult appearance, have mastered most of the adult behavioral repertoire, and achieve puberty. Young-adults are adult size, have reached sexual maturity, and are capable of reproduction if paired.

A callitrichid family group is made up of a reproductively active male and female, reproductively suppressed adult offspring, and infant offspring [Koenig & Rothe, 1991]. Since age is related to the social role or rank of the individual (Caldwell et al., unpublished results), we also categorized each animal according to its position within the family group. When twins were born, they were both assigned to the same offspring category. As can be seen in Table III, each age category contained individuals from two or more ''family position'' categories.

Whenever necessary for identification, individuals were marked with colored inks (International Market Supply, Cheshire, UK). This method caused no

TABLE I. Subjects by Genus, Species, Group Size, Enclosure Type, and Zoo*

Species	Group size	Enclosure type	Zoo
Leontopithecus (n=58)			
L. chrysomelas	3	Indoor-outdoor	Whipsnade
L. chrysomelas	2	Indoor-outdoor	Jersey
L. chrysomelas	2	Indoor-outdoor	Marwell
L. chrysomelas	5	Indoor-outdoor	Twycross
L. chrysomelas	4	Island	Jersey
L. rosalia	2	Indoor-outdoor	Marwell
L. rosalia	6	Indoor-outdoor	Twycross
L. rosalia	3	Indoor-outdoor	Jersey
L. rosalia	3	Island	Marwell
L. rosalia	7	Free ranging	Jersey
L. rosalia	2	Free ranging	Marwell
L. chrysopygus	2	Indoor-outdoor	Jersey
L. chrysopygus	6	Indoor-outdoor	Jersey
L. chrysopygus	7	Indoor-outdoor	Jersey
L. chrysopygus	2	Indoor-outdoor	Jersey
L. chrysopygus	2	Indoor-outdoor	Jersey
Saguinus (n=13)			
S. imperator	3	Indoor-outdoor	Marwell
S. imperator	3	Indoor-outdoor	Marwell
S. imperator	3	Indoor-outdoor	Twycross
S. oedipus	4	Indoor-outdoor	Twycross
Callithrix (n=37)			
C. argentata	8	Indoor-outdoor	Twycross
C. argentata	6	Free ranging	Whipsnade
C. argentata	8	Free ranging	Jersey
C. geoffroyi	7	Indoor-outdoor	Twycross
C. geoffroyi	3	Indoor-outdoor	Jersey
C. geoffroyi	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. See Day et al. [2003] for information regarding intergeneric differences; these are independent of any age differences reported in this paper.

TABLE II. The Distribution of Subjects Across the Age Categories*

Age categories	*Callithrix*		*Saguinus*		*Leontopithecus*		Total
	Months	n	Months	n	Months	n	
Infant	1–5	4	1–7	1	1–4	0	5
Juvenile	5–10	7	7–14	3	4–9	1	11
Sub-adult	10–15	5	14–21	0	9–12	2	7
Young-adult	15–50	10	21–50	5	12–50	12	27
Adult	50–100	8	50–100	2	50–100	26	36
Old-adult	100+	3	100+	2	100+	17	22

*The scheme follows Yamamoto [1993] but with the original ''young adult'' category divided into three categories.

TABLE III. The Distribution of Subjects According to Age Category and "Family Position"

Family position Age category	Non-breeding adult group	Parent	Offspring				
			1st	2nd	3rd	4th	5th
Infant			1		2	1	1
Juvenile			4	2	2	3	
Sub-adult				1	6		
Young-adult	1	3	6	11	4		
Adult	14	12	6	2	2		
Old-adult	5	15	2				
Total, n	20	30	19	16	16	4	1

distress, and a few minutes after application the subjects paid no attention to the marks.

Apparatus

Each group of subjects was presented with seven extractive foraging tasks. Four opaque white plastic puzzle boxes of various shapes, containing raisins, were used (see Fig. 1). When the boxes were closed, the subjects had limited visual and olfactory access to the food reward. For each task the subjects were given two equivalent color-differentiated and spatially-separated means of extracting the raisins (e.g., two doors). The colors used were valid for both di- and trichromatic individuals (N. Mundy, personal communication) and hence were appropriate for both male and female Callitrichid monkeys. The tasks were designed so that the animals could perform them using natural foraging actions, such as those employed for turning over leaves, exploring crevices, and rummaging in leaf litter [Peres, 1986; Garber, 1993]. The flip-top task consisted of a box (10×11.5 cm and 7 cm high. The top of the box was divided into two doors: one painted blue and one painted green (see Fig. 1a). The round-box task consisted of a round box (11 cm in diameter, 6.5 cm high), the top of which had two access holes (one painted blue and one painted yellow) that were of different sizes for the three genera (Fig. 1b). The cylinder task consisted of a cylinder 11 cm in diameter and 16 cm high. At a height of 8 cm, two access holes (one blue and one red) were placed opposite one another (Fig. 1c). The push-pull task consisted of a large transparent box, sized according to body size (for *Leontopithecus*: 32×22 cm and 24 cm high; for *Saguinus* and *Callithrix*: 22×15 cm and 16 cm high), with a hinged door that had to be pushed inward or pulled outward to enable the subject to enter the box and reach the raisins (Fig. 1d). The tasks were designed in such a way that at any one time only one option could be used to extract the reward. It was ascertained during pilot studies at Banham Zoo that individuals of all ages and species could physically obtain the food reward inside the box.

The three novel foods consisted of whole passion fruit, peanuts in the shell, and hard-boiled quail eggs in the shell. It has been reported that callitrichids eat bird eggs and hatchlings in the wild [Kleiman et al., 1988], and although in captivity peeled and chopped hen eggs are often provided, the whole intact quail eggs were always novel to the subjects. There was a lack of response to the passion fruit during pilot studies; therefore, immediately prior to presentation they were punctured with a sharp object to enhance olfactory stimulation.
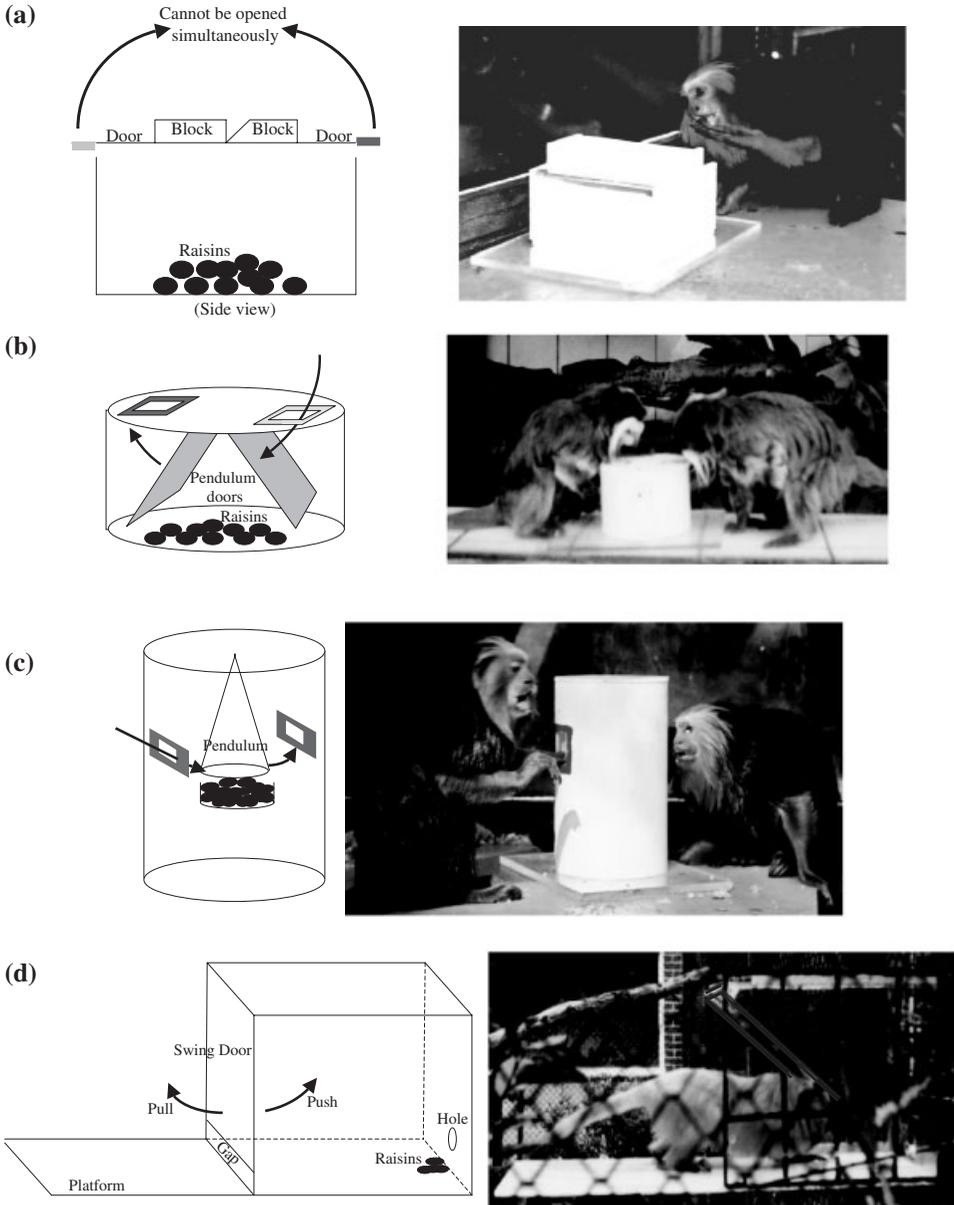
Fig. 1. Diagrams and photos of (**a**) the flip-top task used by a golden-headed lion tamarin, (**b**) the round-box task used by emperor tamarins, (**c**) the cylinder task used by golden-headed lion tamarins, and (**d**) the push-pull box used by a golden lion tamarin. Arrows indicate the movement of the devices that prevent simultaneous use of the task options.

Within each enclosure the food platform that according to the zoo-keepers was the most popular in the group was used as a platform for all task presentations. However, if this platform was not easily seen by the experimenters it was relocated. Before the task was presented, the experimenters defined an

area that included and surrounded the platform, within which the subjects were categorized as being ''at proximity to the task'' (an approximately 50 cm radius), and beyond which the subjects were considered to be ''at a distance from the task.''

Procedure

Using both instantaneous and focal behavior sampling, R.L.K. and R.L.C. collected data simultaneously on paper check sheets and a hand-held PSION computer containing an observation program.

Baseline data.
Three 20-min blocks of baseline feeding data were taken for each subject group to determine whether the behavior observed in the experimental trials was due to the novelty of the task or merely to the presence of food. The blocks were spread out such that one occurred prior to any task presentations, one occurred after the third or fourth task was presented, and one occurred after all tasks were presented. Each group was observed during at least one morning and afternoon feeding session to enable comparison with experimental data should a time-of-day effect be found. The food was placed on the platform used for novel task presentations. Data comparable to those taken during the task presentations were collected. The identity of each individual within the ''at proximity'' area, surrounding the food platform, was recorded at 10-sec intervals, as well as the latency between the introduction of the food and the first feeding of each individual. Also, the number of pieces of food (monkey pellet/fruit) each individual consumed during the period was recorded. We defined all individuals at proximity to the food platform as being ''attentive to the task'' on the grounds that such individuals were usually observed to look directly at the food platform.

Task presentation.
Before each task was presented, each group of subjects was provided with raisins to ensure that they were all familiar with this food. Each task was presented to each group once. The tasks were introduced into the enclosure by R.L.K. or a zookeeper (depending on the zoo involved). Observations began immediately and continued for 30 min or until all of the food had been extracted, whichever occurred first. Within each group, during half of the task presentations we recorded the behavior of animals ''at proximity to the task,'' and during the other half we noted the behavior of animals ''at a distance from the task,'' randomized as far as possible for task. No more than three tasks were presented to each group per day, with not less than 1 hr between presentations of tasks or routine feedings by the keeper. The order of presentation was pseudo-randomized within the puzzle boxes (which were always presented first for logistical reasons) and the novel foods, for each species. For each group there was a mixture of morning and afternoon presentations.

During the ''at proximity'' observations, we noted at 10-sec intervals which individuals were within the ''at proximity'' area. Since individuals within this area were usually oriented toward the task, an animal at proximity was said to be attentive to the task at proximity. During ''at distance'' observations we noted at 10-sec intervals which of the individuals outside the proximity area had their face orientated toward the task and were thus judged to be attentive to the task at a distance. Because of logistical reasons, the measure of attentiveness toward the task did not distinguish between instances when conspecifics were present but

not manipulating the task, and instances when no conspecifics were present. Also recorded, for each task presentation, was the latency within the group with which each individual first *contacted* 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 naturalistic tasks). The number of unsuccessful and successful manipulations, per individual, throughout each task presentation was noted.

Any additional behavior (e.g., aggression or scrounging) that might have influenced the performance of the novel extractive foraging behavior was also recorded.

Definitions and Derived Variables

We defined "aggression" as any instance in which an individual emitted a call deemed to be a sign of aggression by previous researchers (e.g., "cackling" [Stevenson & Rylands, 1988] or physically attacked a conspecific (e.g., "cuffing" or "snap-biting" [Stevenson & Rylands, 1988], and "slapping" [Kleiman et al., 1988]). Due to observer constraints, more subtle manifestations of aggression were not recorded. "Scrounging" was defined as any instance in which an individual acquired a food item that had been extracted by a conspecific, either by directly taking the item from the conspecific's hand or indirectly by picking up a discarded item from the substrate. Thus the individual that received food was designated the "scrounger," and the individual that provided food was the "producer." "Attentiveness to the task/food platform" is represented as a percentage of the total 10-sec intervals during which the task or food was in position.

Statistical Methods

Because there was no significant interaction between age category and task type, and there were insufficient data per task to analyze all tasks individually, data for all dependent variables were pooled across tasks. Following presentation of the data pertaining to the number of tasks with which individuals of each age group interacted, all of the analyses excluded instances in which individuals did not provide data for the variable in question. We checked all of the data for normality using Kolmogorov-Smirnov tests, and for homogeneity of variance using Levene's test. The data were natural-log-transformed when necessary to allow parametric statistical analyses. When it was not possible to use parametric statistics, nonparametric tests were used. All statistical tests were two-tailed. When multiple comparisons or tests were made, we controlled the familywise error rate by modifying the significance level of alpha, designated in the text as α^*. For each family of comparisons $\alpha^* = \alpha/c$, where $\alpha = 0.05$, and c corresponds to the number of comparisons. We performed power analyses (reported at $\alpha = 0.05$) of nonsignificant results using a medium-effect size estimate [Cohen, 1988]. Whenever possible, we reanalyzed significant results using ANCOVA with genus and "family position" as a covariate to ensure that the results were due to age rather than any effect of genera differences [Day et al., 2003] or social role/rank within the family group. In these analyses, data from groups containing only nonbreeding adults were excluded, since paired adults were not regarded as a family group. Because of the large number of statistical analyses performed in

this study, not all of the results are reported here. Further details are available from the authors on request.

RESULTS

Order in Which Individuals Interacted With the Task

Less than a quarter of the groups contained a specific individual that was consistently the first to contact and succeed with the novel tasks (see Table IV). In all but one case, these consistent ''innovators'' were adults.

We determined whether there were age differences in the number of times individuals were first in their group to interact with the novel tasks. We calculated the difference between the observed number of instances and the expected number given the frequency of individuals of each age category in the group. Groups in which there was only one age category represented, or there were no instances of the behavior in question were excluded. There were no significant age differences in the number of times individuals were the first in their group to contact or successfully manipulate the novel tasks. However, as shown in Fig. 2, there was a pattern whereby juveniles, infants, and adults were first in their group to contact and succeed with the tasks less than expected, and old-adults and young-adults did so more than expected.

We enhanced the power of the analyses by summing across adult and nonadult age categories. While there was no difference in the extent to which adults and nonadults were the first in their group to contact the tasks (ANOVA: $F_{1,56}=1.8$, $P=0.185$, $\alpha^*=0.025$, power$=0.75$), adults (mean$\pm$SE$=0.186\pm0.140$) were the first to successfully manipulate the task more often than nonadults (mean$\pm$SE$=-0.5\pm0.23$) (ANOVA: $F_{1,54}=6.49$, $P=0.014$, $\alpha^*=0.025$).

Frequency of Task Interaction

As can be seen in Fig. 3, there appears to be a positive correlation between the number of tasks interacted with and age; however, this was only significant for the number of tasks successfully manipulated (Pearson correlation: $\rho_{108}=0.221$, $P=0.021$, $\alpha^*=0.025$). Indeed, infants (Tukey: $P=0.004$) and juveniles (Tukey: $P=0.001$) successfully manipulated fewer tasks than did adults (ANOVA: $F_{5,107}=5.53$, $P<0.001$, $\alpha^*=0.025$). This result remained when family position was

TABLE IV. Groups in Which Specific Individuals Were Consistently the Only Ones in Their Group to Interact With Tasks First

Group no.	Non-adults present	First to contact (out of 20 groups)[a]		First to success (out of 16 groups)[a]	
		Age category	No. tasks	Age category	No. tasks
4	No			Old-adult	3
9	No	Old-adult	7	Old-adult	6
17	Yes	Juvenile	3		
18	Yes	Young-adult	6		
21	Yes	Young-adult	4		
22	No			Old-adult	3

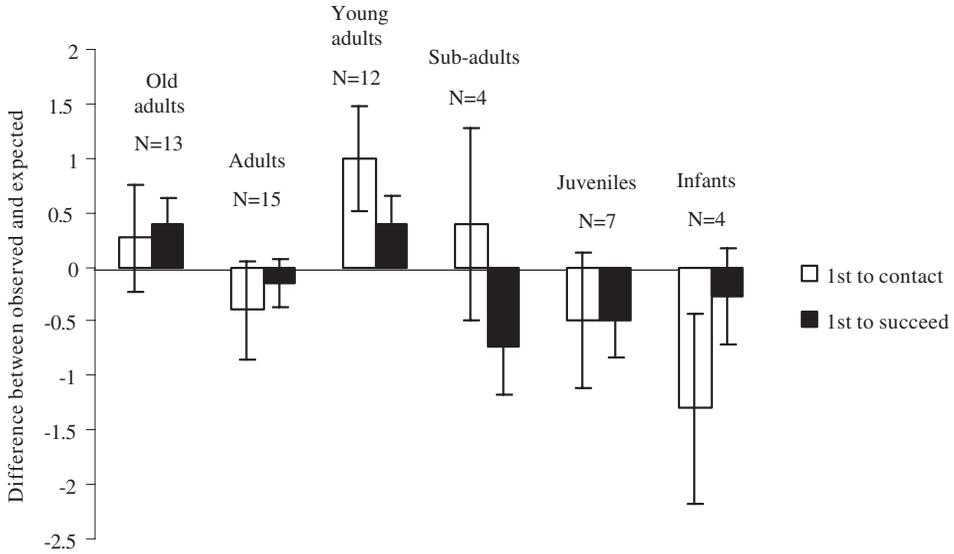[a]Only groups in which more than one task was interacted with were included.

Fig. 2. The number (mean ± SE) of times (observed − expected) individuals in each age category were the first to contact and successfully manipulate the novel tasks. Positive values indicate a greater than expected number of instances, while negative values indicate fewer than expected instances.
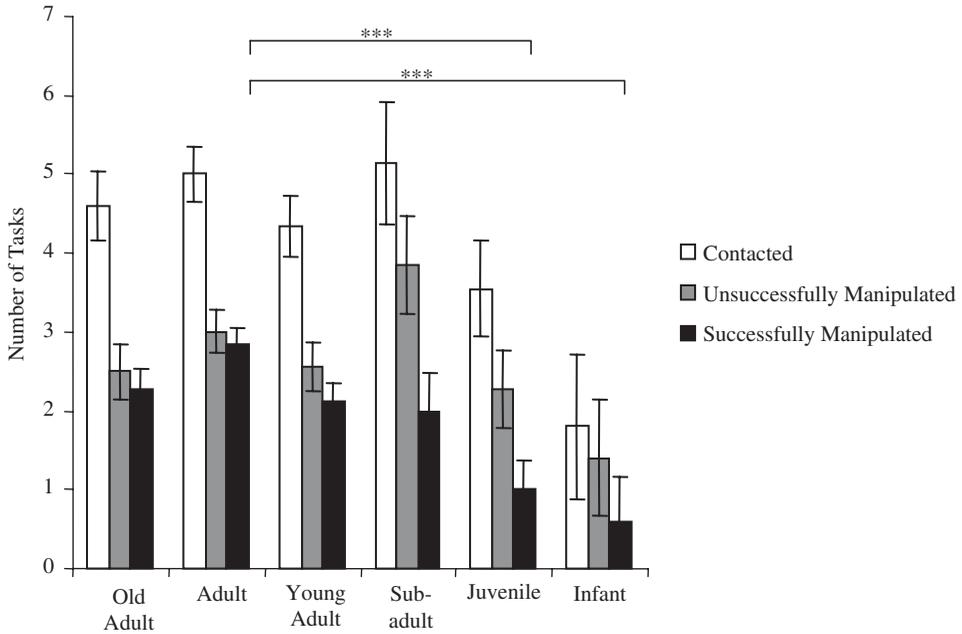

Fig. 3. The number (mean ± SE) of tasks with which individuals of each age category interacted at least once (***$P < 0.005$).

TABLE V. ANCOVA Results of All Variables so Analyzed

Dependent variable	Covariate to age category	
	Family position	Genera
Frequency of tasks successfully manipulated	$F_{5,85}=3.9$, $P=0.003$	$F_{5,85}=1.96$, $P=0.093$, power <0.2
Latency to first unsuccessful manipulation	$F_{5,70}=2.444$, $P=0.042$	$F_{5,92}=2.330$, $P=0.049$
Latency to first successful manipulation	$F_{5,67}=4.931$, $P<0.001$	$F_{5,89}=5.843$, $P<0.001$
Baseline scrounging events instigated	$F_{5,75}=6.615$, $P<0.001$	N/A
Baseline aggression received	$F_{5,75}=4.395$, $P<0.001$	N/A

included as a covariate, and approached significance when genera was included (see Table V).

There were no age differences in the average number of unsuccessful manipulations or total manipulations produced by individuals. However, there was a significant difference in the average number of successful manipulations produced ($\chi^2=17.738$, $df=5$, $P=0.003$, $\alpha^*=0.016$). Old-adults and adults produced more successes than young-adults and subadults (Mann-Whitney: $Z_{58,34}=-2.740$, $P=0.006$, $\alpha^*=0.025$), which in turn produced more than juveniles and infants ($Z_{34,16}=-2.161$, $P=0.031$, $\alpha^*=0.025$). There was a positive correlation between the age of individuals and the number of successful manipulations produced (Spearman: $\rho_{108}=0.271$, $P=0.005$). These age differences are unlikely to be explained by differences in the motivation to feed, since in the baseline condition there was no significant effect of age category on the percentage of time spent feeding (ANOVA: $F_{5,96}=2.022$, $P=0.082$, power$=0.30$).

The relative number of unsuccessful and successful manipulations produced within each age category differed. Old-adults and adults produced more successful manipulations than unsuccessful ones (Wilcoxon: $Z_{22}=-1.800$, $P=0.072$, $\alpha^*=0.01$; $Z_{36}=-2.580$, $P=0.01$, $\alpha^*=0.01$, respectively). Conversely, young-adults ($Z_{27}=-2.631$, $P=0.009$, $\alpha^*=0.01$), subadults ($Z_7=-1.524$, $P=0.128$, $\alpha^*=0.01$), juveniles ($Z_{11}=-1.836$, $P=0.066$, $\alpha^*=0.01$), and infants ($Z_5=-0.535$, $P=0.593$, $\alpha^*=0.01$) produced less successful manipulations than unsuccessful ones (see Fig. 4a). When old-adults and adults were combined and compared with the remaining younger categories, the older category produced significantly more successful manipulations than unsuccessful ones (Wilcoxon: $Z_{58}=-3.165$, $P=0.002$, $\alpha^*=0.025$), while the younger category produced significantly more unsuccessful manipulations than successful ones ($Z_{50}=-3.667$, $P<0.001$, $\alpha^*=0.025$) (see Fig. 4b).

Latencies of Task Interaction

There were no age differences in the latency to first contact the task. There were, however, significant age differences in the latency to first unsuccessful manipulation ($F_{5,93}=4.636$, $P<0.001$, $\alpha^*=0.017$), as old-adults and adults had significantly shorter latencies than subadults (Tukey: $P=0.043$, $P=0.010$) and juveniles ($P=0.046$, $P=0.008$). A similar pattern was observed with latency to first successful manipulation ($F_{5,90}=6.440$, $P<0.001$, $\alpha^*=0.017$), as old-adults and
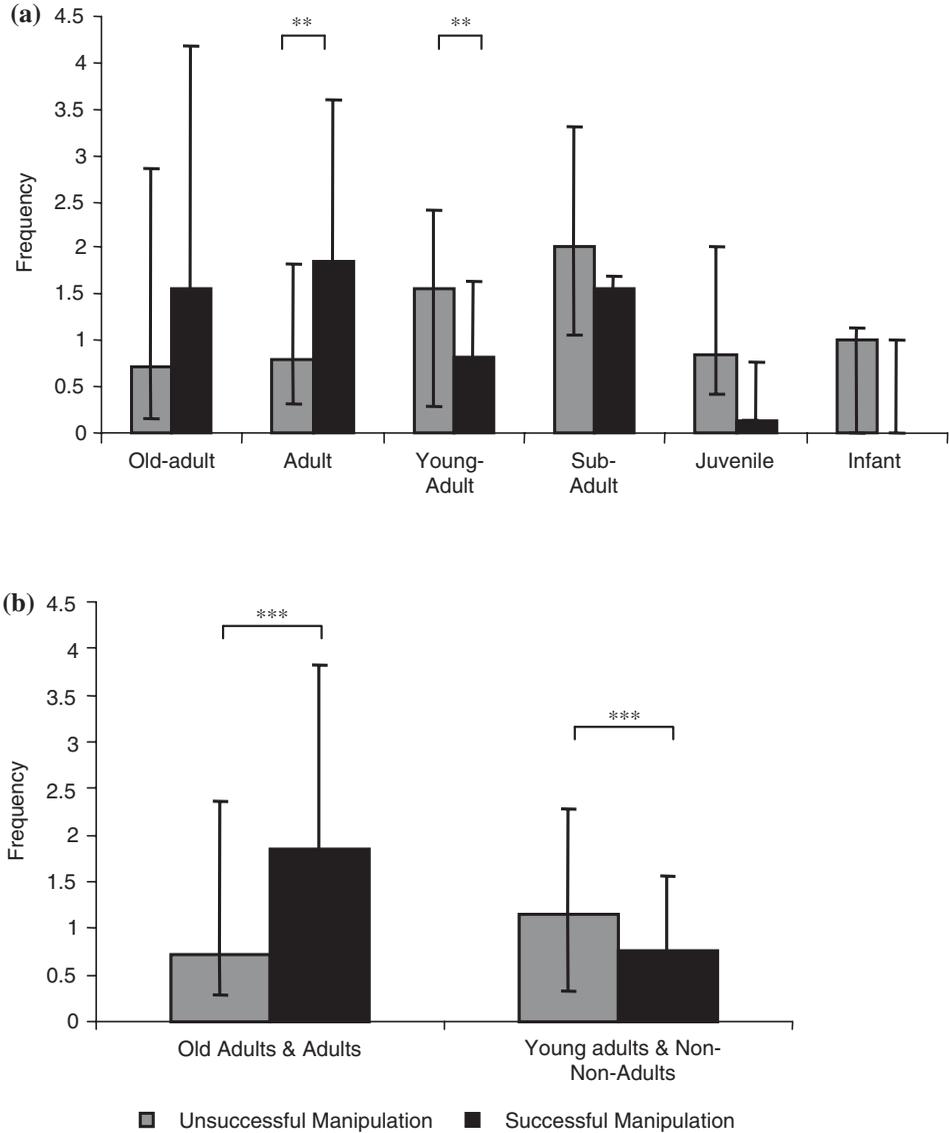
Fig. 4. The relative frequency (median±interquartile range), across all tasks, of unsuccessful and successful manipulations produced by individuals in **(a)** each age category and **(b)** the combined older category of old-adults and adults, vs. the combination of younger age categories (**P<0.025, ***P<0.005).

adults had significantly shorter latencies than subadults (Tukey: NS, $P=0.036$) and juveniles ($P=0.017$, $P=0.005$). However, the latency for infants was shorter than that for young-adults (Tukey: $P=0.016$), subadults ($P<0.001$), and juveniles ($P<0.001$). These findings remained significant when family position and genera were included as covariates (see Table V). These differences cannot be explained by differences in the motivation to feed, because in the baseline condition there was no effect of age upon the latency to first feed ($F_{5,95}=1.542$, $P=0.184$, power=0.30), although infants did take the longest to feed of all age groups.

Among those individuals that responded to the tasks, there were significant differences between the three older and three younger categories, as was demonstrated when adults and nonadults were compared. There was no significant difference between adults and nonadults in the average latency to first contact the novel tasks. Adults did, however, have significantly shorter latencies (mean$\pm$SE) than nonadults to first unsuccessful manipulation (adults: 294.5$\pm$30.6; nonadults: 622$\pm$57.4; $t_{97}=-4.568$, $P<0.001$, $\alpha^*=0.025$) and first successful manipulation (adults: 303.1$\pm$27.3; nonadults: 691$\pm$108.7; $t_{94}=-2.334$, $P=0.022$, $\alpha^*=0.025$).

Attentiveness to the Novel Task

As shown in Fig. 5a, there was a trend for attentiveness to increase as age decreased. Indeed, there was a significant negative correlation between absolute
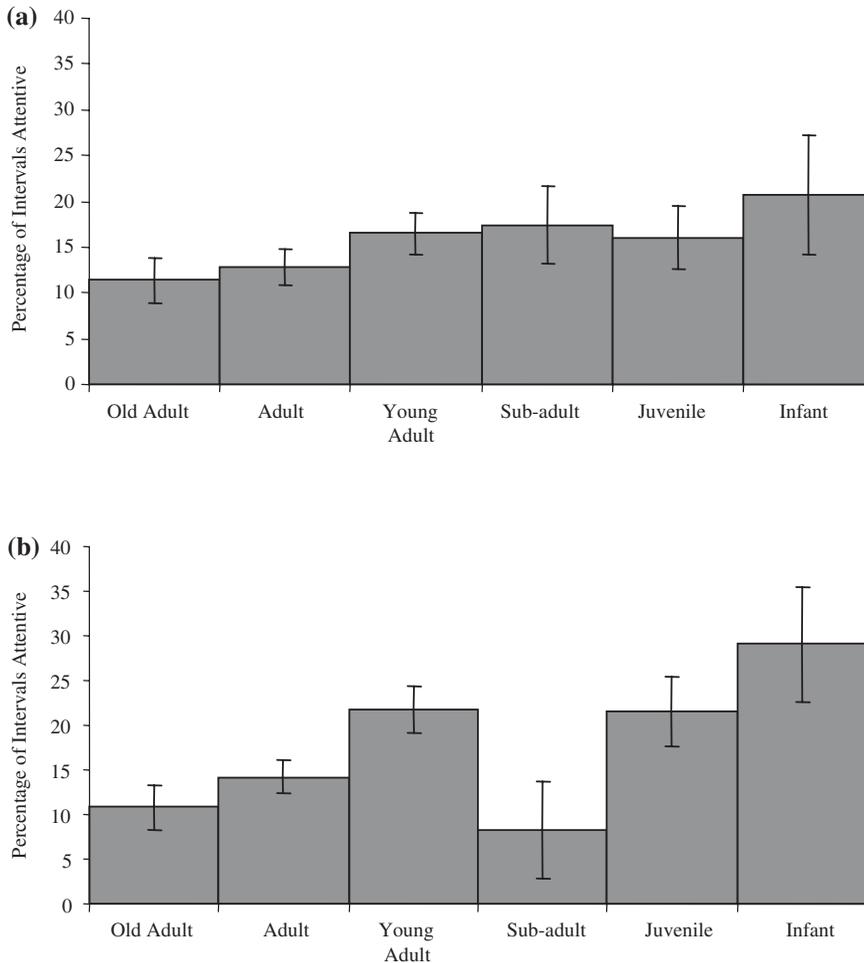

Fig. 5. The percentage (mean$\pm$SE) of intervals, across all tasks, in which individuals of each age category were attentive to the novel tasks (**a**) at proximity ($P=0.01$) and (**b**) at a distance ($P=0.032$).

age and percentage proximity to the task (Spearman: $\rho_{104}=-0.247$, $P=0.01$, $\alpha^*=0.016$). This result cannot be explained by differences in the motivation to feed, because in the baseline condition there were no significant age differences in the mean percentage of observed intervals during which individuals were present at the food platform (ANOVA: $F_{5,96}=1.508$, $P=0.194$, power=0.30). However, infants (mean$\pm$SE=7.8$\pm$3.5) were by far the least present of all the age groups (range=13.4$\pm$1.6 to 17.2$\pm$3.0). There was also a near significant negative correlation between absolute age and percentage distant attentiveness to the task (Spearman: $\rho_{87}=-0.230$, $P=0.032$, $\alpha^*=0.016$, power=2.8) (see Fig. 5b).

Scrounging and Aggression

There were no significant differences between the age categories in terms of the number of scrounging events instigated. This nonetheless differed from the baseline condition, where there were significant age differences in the number of scrounging events instigated (ANOVA: $F_{5,96}=6.223$, $P<0.001$), with infants scrounging more than animals of other ages (Tukey: $P<0.001$). In both the experimental and baseline contexts, there were no significant age differences in the number of aggressive events instigated. However, in the baseline condition there were significant differences in the number of times individuals were the recipients of aggression (ANOVA: $F_{5,96}=5.985$, $P<0.001$), since infants received more aggression than all other age categories (Tukey: old-adults, adults, young-adults, subadults, and juveniles; all at $P\leq0.001$). When family position was included as a covariate, the significant age differences in scrounging events instigated and aggression received in the baseline condition remained significant (see Table V).

DISCUSSION

Neophilia and Innovation

There was little evidence that within groups there was one individual that was consistently the most neophilic (first to contact) or innovative (first to successfully manipulate the task). The few individuals that were consistently neophilic or innovative were adults rather than nonadults.

While there were no age differences in the number of times individuals were first in their group to contact the novel tasks (neophilia), adults were the first to successfully manipulate the tasks (innovate) significantly more often than nonadults. Thus it would seem that in callitrichids, neophilia cuts across age boundaries, but older (sexually mature) individuals are more innovative than younger individuals.

An often-used proxy measure of neophilia is the latency to contact novel objects or tasks; however, within the individuals that contacted the tasks in this study, there were no age differences in latency to first contact. This finding provides further support for the assertion that temperament differences (in terms of neophobia) may cut across age boundaries. In this study, in contrast to a previous analysis [Day et al., 2003], neophilia was not positively associated with innovation. However, the current finding pertains to age groups, and should not be confused with an association between neophilia and innovation within genera or indeed individuals.

Our results regarding neophilia and innovation correspond with the findings of other callitrichid researchers. Box and Smith [1998] reported a lack of age differences in marmosets in response (in this study, proximity) to novel foods, and

in a study of wild *S. imperator* and *S. fuscicollis*, adults were found to be more innovative with a novel food task than nonadults (Israel Aragón Romero, personal communication). Adult callitrichids have also been observed to be the first to enter and explore unfamiliar environments [Chamove & Rohrhuber, 1989] (Moore, unpublished results); however, this is not consistently the case, as several studies have found nonadults to be the most neophilic in this context [McGrew & McLuckie, 1986; Price et al., 1989; Schneider, 1994] (Detert, Eva, Matthews, Moore, O'Connell, and Uzu, unpublished results). As the propensity to enter a novel environment and contact the novel objects it contains corresponds with our definition of neophilia, so does the lack of consensus in the latter studies correspond with our finding that neophilia cuts across age boundaries. Similarly, the finding by Millar et al. [1988] that *C. jacchus* and *S. oedipus* adults consistently contacted novel objects first, and Scolavino and Vitale's [2000] report of a ''prompt response'' of *C. jacchus* juveniles (in family groups) to novel foraging tasks are not inconsistent with our findings, because those studies were subject to the stochastic variation of five and four groups of callitrichids, respectively.

Exploration

Investigation of novel objects may increase the rate at which individuals encounter novel situations, enabling the learning of novel environmental affordances [Reader & Laland, 2003] and potentially resulting in behavioral innovation. The fact that older individuals contacted and successfully manipulated more of the novel tasks presented to them compared to younger individuals (infants and juveniles) indicates a greater propensity for exploration in the older individuals. This greater propensity for exploration corresponds with the finding (outlined in the previous section) that adult callitrichids are more innovative than nonadults. However, it appears that age and family position (birth order) were equally influential regarding the number of tasks individuals contacted.

When the overall performance of individuals that interacted with the tasks is considered, the results suggest that experience and competence allow older individuals to solve novel problems more effectively than younger individuals. Across tasks, adults performed their first unsuccessful and successful manipulations more quickly, and produced more successful manipulations than nonadults. Similarly, Millar et al. [1988] reported that *C. jacchus* and *S. oedipus* adults spent longer amounts of time in contact with novel objects, which may indicate increased exploration. In contrast, Scolavino and Vitale [2000] found *C. jacchus* juveniles to be the most efficient of four family groups at solving one of the novel extractive foraging tasks posed to them. Given the task specificity of this result, it does not contradict our findings regarding adult innovation.

The positive relationship between age and task success suggests that the greater life experience of individuals over 4 years old may enable them to outperform younger individuals. However, other developmental factors, such as improvements in manipulative skills, increased strength, and maturity with age, cannot be ruled out. Old-adults and adults combined produced more successful than unsuccessful task manipulations, while individuals in the younger age categories combined produced more unsuccessful than successful task manipulations. This suggests that there may be a developmental watershed at about 4 years, when prior manipulative experience generates sufficient competence in extractive foraging for individual callitrichids to efficiently translate unsuccessful manipulations into successful manipulations. In accordance with such a

competence hypothesis, Menzel and Menzel [1979] suggested that *S. fuscicollis* adults acquire information more efficiently, and can recognize and classify objects more quickly than nonadults.

While it is possible that the age differences reported in this study reflect the fact that older individuals monopolized access to the food, this is considered unlikely because old-adults, adults, young-adults, and subadults are of similar sizes and very little overt aggression was recorded during the task presentations. It is, however, possible that more subtle forms of task monopolization occurred. In addition, there was a negative relationship between proximity to the task and age. Caldwell et al. (unpublished results) reported a similar result in a study of common marmosets, in which co-action of dominants and subordinates at a novel foraging task was prevalent. We also consider it unlikely that the relatively poor performance of the nonadults with the tasks was due to neophobia or disinterest in the novel tasks. This is because there were no significant differences between adults and nonadults in the number of times they contacted a task first in their group, the number of tasks they contacted, or the latency to first task contacts. In addition, attentiveness to the tasks increased as age decreased.

It is possible that the inefficient conversion of unsuccessful manipulations into successful manipulations by younger animals was not solely due to a lack of experience or competence. However, it does not appear that the younger animals had problems completing the tasks due to physical size or strength. The few infants that attempted the tasks accomplished their first successful manipulations more quickly than the larger young-adults, subadults, and juveniles. In addition, if the infants directed their behavior toward acquiring food but were physically incapable of doing so, they might be expected to scrounge from their elders [Ferrari, 1987]. However, while infants scrounged more than individuals in the other age categories in the baseline condition, they did not do so in the experimental condition. Conceivably, the large number of unsuccessful manipulations compared to successful manipulations produced by individuals less than 4 years of age was a manifestation of play. In accordance with this notion is the report that play can arise in adult marmosets with the introduction of novel objects [Stevenson & Poole, 1976]. Hoage reported that in *Leontopithecus*, individuals frequently ''pick at and probe in an object or part of the environment'' [Kleiman et al., 1988. p 316]. Manipulative play is usually discerned by the absence of any extrinsic goal, and other criteria, such as repetition [Smith, 1982]. Thus, the apparent repetition of unsuccessful manipulations without progression to food extraction could outwardly appear to be play.

Although the apparent repetition of unsuccessful manipulations in callitrichids less than 4 years of age could be described as play, there are several reasons why this explanation for the performance of these individuals is unsatisfactory. First, if every behavior pattern exhibited by nonadults that lacks a clear alternative function is attributed to ''play,'' this term becomes devalued into a heterogeneous category for which play behavior cannot be predefined. Second, the play frequencies of offspring are said to drop around the time of puberty in animals, including callitrichids [Bronsen, 1965; Vorland, 1977]. In the current study, the behavior that could possibly be attributed to play (here, unsuccessful manipulations) was prevalent in subadults that had achieved puberty and young-adults that were sexually mature, as well as in younger individuals. Thus, although play in callitrichids may function as a precursor to and preparation for later physical abilities [Yamamoto, 1993], such as insect foraging [Izawa, 1978], the hypothesis that play may promote innovation in young animals is unsupported by these data.

Application to Reintroductions

While the success of reintroduction as a conservation strategy has been limited [Seddon, 1999], this only reinforces the need for research into how to increase the effectiveness of reintroductions [Cowlishaw & Dunbar, 2000]. Among other considerations, such as genus, species, sex, and enclosure-type differences [Day, 2003; Day et al., 2003], the age of animals when they receive any pre-release training may determine whether the experience is effective in enhancing post-release survival [Beck et al., 2002; Biggins et al., 1998]. In contrast to previous studies in which callitrichids were exposed to pre-release foraging tasks [Kleiman et al., 1986; Redshaw & Mallinson, 1991], the current results suggest that older individuals have an increased ability to acquire or exploit novel information compared to younger individuals. Further research into a possible sensitive or transitional period for learning in callitrichids could be used to enhance the efficacy of pre-release training by enabling the training to be focused on individuals when they are at their most receptive age. If the findings of this study prove robust, a further possibility for pre-release training would be to improve manipulative competence in callitrichids under 4 years of age. Individuals could be provided with experiences appropriate to scaffold manipulative competence from infancy, when their behavioral and neural development is plastic. Finally, since the relative performance of individuals when presented with novel tasks often influences decisions made about the composition of a release group [e.g., Valladares-Padua et al., 2000] and pre-release training, one must be sure that the results of such studies are robust. For instance, the results of this study may hold only for the specific tasks presented, and the results of previous studies may be unreliable due to the influence of stochastic effects associated with small sample sizes [Brown & Silk, 2002; Palmer, 2000].

CONCLUSIONS

The findings of this study are consistent with those of Reader and Laland [2001], and suggest that within primates, older individuals are more innovative and explorative than younger individuals, probably because of their increased manipulative competence. Thus, in addition to the ''necessity'' and ''spare time'' hypotheses proposed for the occurrence of innovation [Kummer & Goodall, 1985; Reader & Laland, 2001, 2003], it would be useful to consider the influence of age-related competence [e.g., Hauser, 1988; Reader & Laland, 2001]. Studies of the ontogeny of skillful behavior, such as tool use [Hauser et al., 2002; Tebbich et al., 2001], may shed light on the influences of age-related competence on innovatory propensities.

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