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RESEARCH ARTICLE

Changes in Locomotor and Foraging Skills in Captive-Born, Reintroduced Golden Lion Tamarins (*Leontopithecus rosalia rosalia*)

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The behavior of reintroduced, captive-born animals is understudied, limiting the scientific understanding and utility of reintroduction as a conservation tool. This work describes changes in locomotor and foraging behaviors in captive-born golden lion tamarins over the first 18 months after their release into the wild. The subjects included 73 individuals living in and around the Poco das Antas Biological Reserve in Brazil between 1984 and 1996. The differences between animals that survived 6 months after release and those that did not indicate that initial deficiencies in locomotor and foraging abilities are related to survival. Behavioral changes in both juvenile and adult individuals during the first 6 and 18 months after release appear to be primarily related to locomotor abilities; however, the effect of provisioning on foraging abilities is unknown. Juvenile animals showed a larger number of changes relative to adults during the first 6 and 18 months, suggesting that placing tamarins into complex environments early in development may promote the expression of natural behaviors and increase survival opportunities after their release. However, when this is not possible, the best mechanism for reintroducing adult members of this species involves intensive post-release support rather than pre-release training, which confers few behavioral advantages. Recommendations for future reintroductions with this and other species include introducing animals to complex environments early in development, and collecting data systematically. Am. J. Primatol. 62:1–13, 2004.

Key words: reintroduction; acclimatization; conservation; captivity and behavior; environmental complexity

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INTRODUCTION

Reintroduction became a popular conservation tool in the last century, although only limited success has been achieved in establishing viable wild populations [Beck et al., 1994]. Our understanding of why reintroductions fail is hampered by a lack of post-release data on the survivorship and, particularly, the behavior of reintroduced animals. Most previous behavioral descriptions have been anecdotal; for example, many authors simply described the behavior of reintroduced animals as being similar to or deficient as compared to wild conspecifics [Moore & Smith, 1991; Soderquist & Serena, 1994]. Data on behavioral deficiencies in a variety of species could be helpful to researchers developing general recommendations for particular taxonomic groups. For example, herbivorous grazers, such as antelope, might not show large locomotor deficiencies and thus pre- and post-release training might be focused on other skills, such as foraging. Arboreal primates, on the other hand, might experience difficulty in locomoting on the thin, flexible substrates found in the wild, and consequently reintroductions with this taxonomic group would be structured differently.

In addition to simply documenting deficiencies, behavioral data can also highlight the time required for behavioral acclimatization, and differences in acclimatization rates for various behaviors (we use the term "acclimatization" here to describe increased competency in an environment, which may or may not represent true adaptation in the sense of increased behavioral similarities between wild and reintroduced populations). For example, studies of reintroduced Arabian oryx (*Oryx leucoryx*) found that changes in locomotor skills and some social behaviors occurred soon after release, whereas adaptations in foraging, social organization, and dominance patterns took several years [Tear et al., 1997]. Similarly, the time required for behavioral change in ringtailed lemurs (*Lemur catta*) following release into a natural, non-native habitat varied from 1 to 22 months, depending on the behavior [Keith-Lucas et al., 1999]. A knowledge of such patterns is important for structuring post-release programs that will maximize both survival and natural adaptive processes. For example, certain aspects of post-release support, such as assistance in navigation/orientation, might be eliminated relatively quickly, while others, such as provisioning or antipredator protection, may be needed for longer periods of time.

The goal of this study was to examine behavioral changes in captive-born, reintroduced golden lion tamarins. Specifically, we knew from comparisons with their wild-born offspring that captive-born individuals possessed deficiencies in locomotor and foraging skills, even 2 years after their release [Stoinski et al., 2003] (Table I). Therefore, we were primarily interested in examining the pattern of these specific behavioral changes over a similar time period, and what this might tell us about structuring the pre- and post-release environments for future reintroduction candidates. We also wanted to evaluate the effect of pre-release preparation (i.e., allowing the animals to range free in a seminatural environment) on post-release behavior. No survival differences have been observed between animals with such experience and those without [Beck et al., 2002]; however, both groups receive extensive post-release care, such as provisioning and medical assistance [Beck et al., 2002], which may mask survival differences. Thus, we were interested in evaluating whether there were behavioral differences between the two groups.

TABLE I. Categories Used in Data Collection and Their Relevance to the Study

Behavior	Definition/Significance	Change as a function of generation time Stoinski et al. (2003)
Substrate	**Locomotor abilities**	
Natural substrates <2 cm in diameter	Flexible substrates needed for travel between trees	Decrease from captive-born to second-generation
Natural substrates 2–5 cm in diameter	Semi-flexible substrates needed for travel between trees	Decrease from captive-born to second-generation
Natural substrates >5 cm in diameter	Non flexible natural substrates often used for resting	Increase from captive-born to second-generation
Artificial substrates	Non flexible substrates provided by humans; includes feeding platforms and nestbox	Decrease from captive-born to second-generation
Ground	Substrate not frequently used by wild tamarins	Decrease from captive-born to second-generation
Falls	**Locomotor abilities**	
Falls (all occurrences)	Animal falls to the ground	Decrease from captive-born to second-generation
Near falls (all occurrences)	Animal falls but catches itself before reaching the ground	Decrease from captive-born to second-generation
Activity	**Locomotor abilities**	
Inactive	Stationary	Increase from captive-born to second-generation
Locomotor	Moving from point A to point B	Decrease from captive-born to second-generation
Rest	Lying down	Increase from captive-born to second-generation
Height off ground	Locomotor abilities	Increase from captive-born to second-generation
Foraging/foraging	**Foraging/foraging abilities**	
Eat/drink	Includes both provided and natural foods	No change
Eat provided food (all occurrences)	Any food provided by human observers	No change
Eat natural food (all occurrences)	Anything occurring naturally in the environment	No change
Micromanipulate	Typical foraging behavior for animal prey; involves searching through environment with fingers	Decrease from captive-born to second-generation

Unless otherwise indicated, data collected through instantaneous scans.
Note: Changes as a function of generation time are the trends from captive-born to first-generation to second-generation and are thought to represent the actual pattern of acclimitization to the environment.

MATERIALS AND METHODS

Subjects

Since 1984, 153 captive-born golden lion tamarins have been reintroduced into areas in and surrounding Poco das Antas Biological Reserve, Rio de Janeiro, Brazil. Of these, 73 individuals were used as subjects in the current study. Individuals that were not included as subjects were those that were not part of regular data collections, and those that did not receive post-release support in the form of provisioning and medical treatment [Beck et al., 2002]. The majority of the subjects (91%) were released during the wet-season months (October–April) or just prior to the wet season (September). Of the remaining individuals, 4% were released just after the wet season (May) and another 4% were released in the dry-season months of June–August. The animals were generally fed 3–4 days per week throughout the study period. Provisioning consisted mainly of bananas placed on a constructed platform, and commercially prepared primate chow presented in PVC pipes.

The animals were shipped to Brazil following 1) the guidelines established in the Golden Lion Tamarin Husbandry Manual (Golden Lion Tamarin Management Committee, unpublished data), 2) the IATA Live Animals Regulations, and 3) all CITES regulations for Appendix I species. Before they were released, all animals weighing >450 g were fitted with radio collars. These collars enabled researchers to locate the group initially, but they were not needed to follow individual animals; therefore, sampling of individuals was not dependent upon their wearing a radio collar. Animals were trapped and marked with Nyanzol dye approximately two times a year.

Data Collection

The data used in this study were collected between 1984 and 1996. A team of six to eight Brazilian observers was trained and reliability-tested by the field coordinator. Interobserver reliabilities were obtained through independent, simultaneous data collection by a field coordinator and the data collector, and required an interobserver agreement of ≥ 0.80 for five sessions.

On average, observations were conducted several days a week throughout the 12-year period, using focal animal sampling [Altmann, 1974]. Focals were 10-min observations and consisted of instantaneous point sampling every minute and all-occurrence sampling (frequency only) of particular behaviors [Altmann, 1974]. We selected a subset of categories that we believed were particularly relevant to our hypotheses concerning locomotor and foraging abilities. For the instantaneous sampling, we included substrate (natural and artificial), height off the ground, behavior (foraging and feeding), and activity (see Table I). These data are summarized as percentage of time. All-occurrence behaviors (events) included in the analyses were "eat provided plant/animal," "eat natural plant/animal," and "falls/near falls." Each instance was considered a single event (e.g., if a tamarin ate an invertebrate, that would be considered one instance of "eat natural animal") and is presented as rate per hour.

Analyses

Behavioral change over time

To look at changes across time, we conducted two sets of analyses. First, we looked at changes over the first 6 months. The data were divided into monthly time periods (months 1–6), and 31 individuals with enough data from each time period (10 focals) were used in the analyses. These individuals were divided into two age groups. The first group consisted of animals that had been reintroduced between the ages of 6 and 18 months (juveniles; n=13; mean age at reintroduction=12±0.5 month; range of age at reintroduction=7–17 months). Since golden lion tamarins do not reach their adult weight until approximately 24 months of age [Dietz et al., 1994], all of the individuals reintroduced as juveniles were able to have experience in the wild before they became fully adult. The second age group consisted of individuals that were more than 24 months old at the time of reintroduction (adults; n=18; mean age at reintroduction 5±0.2 years; range: 2.5–9.4 years). For both age categories, an average of 11 focals were collected per individual per time block. In cases where multiple observations were collected for an animal during a single day, a daily mean was calculated for each behavior. An overall mean rate and/or percentage of time for each behavior was then calculated for each animal for each time period. Repeated-measures analyses of variance (ANOVAs) (two-tailed) were used to assess significant changes over time, followed by post-hoc comparisons across all time periods to look for trends (e.g., linear, quadratic, etc).

The second analysis focused on changes over the first 18 months after release. Forty-three individuals were included, with the same age categories as described above (juveniles; n=20; mean age at reintroduction=11.8±1 months; range of age at reintroduction=6–17.7 months; adults; n=23; mean age at reintroduction=4.7±0.5 years; range=2.2–9.4 years). The data were divided into three discrete time periods: time 1 represented 1–6 months in the wild, time 2 represented 7–12 months in the wild, and time 3 represented 13–18 months in the wild. These time periods were selected to ensure that sufficient data (at least 10 days of observation) was available on enough animals to permit analysis. On average, 46 focal observations were collected per subject per time block. The data were summarized as above. We performed repeated-measures ANOVAs (two-tailed), followed by post hoc tests to discover which of the individual time periods differed.

Effects of pre-release experience

To assess any differences as a function of the pre-release environment, we used data from 61 animals for which sufficient data (at least five observations per month) were available for the first year after release. Twenty-three subjects (14 adults and nine juveniles) received pre-release experience in the form of being allowed to range free on zoo grounds for 3–6 months prior to shipment. Allowing the animals to range free provided them with opportunities to locomote on natural substrates of varying diameters, forage for and consume naturally occurring foods, and engage in interspecific interactions (including interactions with aerial predators), and also exposed the animals to a variety of temperature and weather conditions (for a complete description, see Bronikowski et al. [1989], Stoinski et al. [1997], and Beck et al. [2002]). The remaining 38 individuals (23 adults and 15 juveniles) were taken to Brazil straight from traditional, caged, captive environments (i.e., food provided at fixed times, access primarily to inflexible substrates, fixed travel routes, etc. [Beck et al., 2002]).

Comparisons between the groups were made using data from the first 6 months after release. Additionally, we compared individuals with and without free-ranging experience in time periods 1 (1–6 months) and 2 (7–12 months) to determine whether free ranging had an effect on the initial rate of acclimatization. Independent sample t-tests (two-tailed) were used for these comparisons.

Behavioral differences between animals that did and did not survive to 6 months

Only 65% of reintroduced golden lion tamarins survive 6 months after they are reintroduced (Beck et al., 2002). To assess behavioral differences as a function of survivorship, we compared behavioral data from the first 6 months after release for 28 individuals that survived (average age=5.3 ± 0.4 years; 13 females and 15 males) and 12 individuals that did not survive (average age=5.4 ± 0.8 years; five females and seven males). Comparisons were conducted only on adult animals to control for any confounds of age. Mean values were obtained for each individual using only data that were collected during the first 6 months post-release and over a similar time period from release (average day since release of data collection:=day 78 ± 4 for surviving animals, and day 53 ± 7 for nonsurviving animals). Independent t-tests were then used to compare means.

All statistical tests were performed using Systat© 7.0. All data that did not meet normality assumptions were transformed. Results were considered significant at probabilities of ≤ 0.05, and considered to be trends at probabilities of > 0.05 and < 0.1.

RESULTS

Behavioral Changes in Reintroduced Adults and Juveniles During the First 6 Months

During the first 6 months, adults showed significant changes in the use of natural substrates of 2–5 cm diameter ($F (5, 85)=10.1$; $P<0.01$), artificial substrates ($F (5, 85)=10.9$; $P<0.01$), inactivity ($F (5, 85)=6.6$; $P<0.01$), and locomoting ($F (5, 85)=4.2$; $P<0.01$); Fig. 1). Post hoc tests revealed that time spent on natural substrates, inactive, and locomoting showed an overall linear increase, whereas time spent on artificial substrates showed an overall linear decrease.

Juveniles showed significant changes in time spent on natural substrates of 2–5 cm and > 5 cm diameter ($F (5, 60)=4.0$; $P< 0.01$ and $F (5, 60)=3.3$; $P=0.01$), artificial substrates ($F (5, 60)=12.7$; $P<0.01$), micromanipulating ($F (5, 60)=3.4$; $P=0.01$), resting ($F (5, 60)=2.4$; $P=0.05$), and inactive ($F (5, 60)=8.6$; $P<0.01$); Fig. 1). Specifically, the animals showed an overall linear increase in time spent on natural substrates, time spent inactive, and micromanipulating, and an overall linear decrease in time spent on artificial substrates. Although time spent resting did change significantly, post hoc tests revealed no significant pattern across the 6-month period. There was a trend for juveniles to increase their time spent eating provided food ($F (5, 60)=2.3$; $P=0.054$).

Behavioral Changes in Reintroduced Adults and Juveniles During the First 18 Months

An examination of the data from the first 18 months in adults revealed significant changes in the use of natural substrates of 2–5 cm in diameter, artificial substrates, inactivity, frequency of falling, and micromanipulating (Table II). Specifically, adult animals showed an increase in time spent on natural substrates ($F (2, 44)=3.7$; $P=0.03$), inactive ($F (2, 44)=4.9$; $P=0.01$), and micromanipulating ($F (2, 44)=4.7$; $P=0.01$). Conversely, adult animals showed a decrease in time spent on artificial substrates ($F (2, 44)=19.8$; $P<0.01$), and in

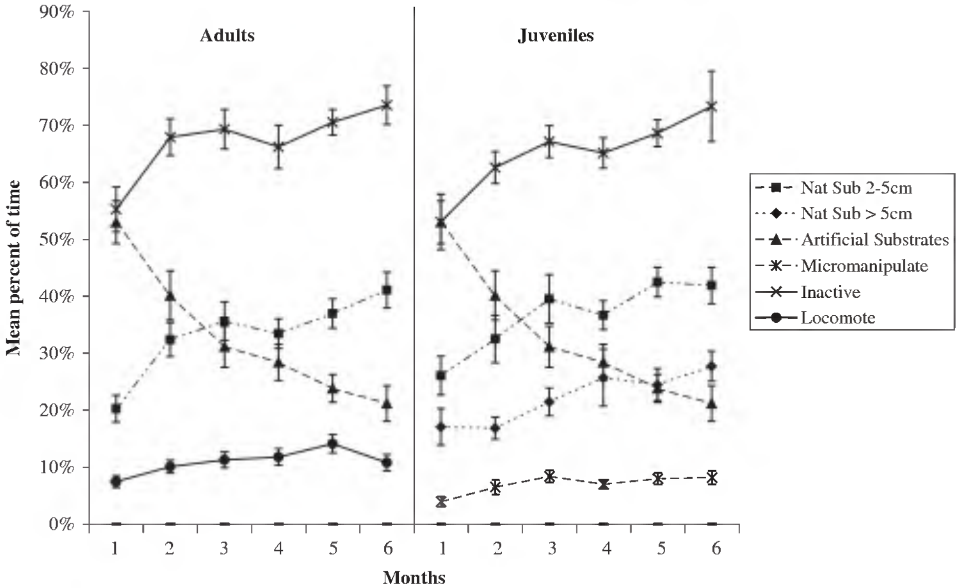

Fig. 1. Behavioral changes over the first six months in adult and juvenile animals. Post hoc tests revealed the dominant trend to be linear for all behaviors. Significant changes for the adult category were observed in the percent of time spent: on natural substrates >5 cm in diameter, on human-made substrates, inactive, and locomoting. Significant changes for the juvenile category were observed in the percentage of time spent on natural substrates 2–5 cm in diameter, on natural substrates >5 cm in diameter, on artificial substrates, micromanipulating, inactive, and resting. However, changes in the percent of time spent resting for juvenile animals are not presented as post hoc comparisons did not show any significant patterns.

frequency of falling (F (2, 44)=5.0; P=0.01). Post hoc analyses revealed that the majority of changes occurred between times 1 and 2, with artificial substrates being the only variable that showed changes between times 2 and 3.

For juveniles, overall tests including all time periods showed significant decreases in time spent on artificial substrates (F (2, 38)=20.4; $P<0.01$) and the ground (F (2, 38)=3.9; P=0.03), time spent locomoting (F (2, 38)=7.1; $P<0.01$), and frequency of falling (trend only; F (2, 38)=3.0; P=0.06; Table II). Increases were observed in ranging height (trend only; F (2, 38)=2.6; P=0.06), time spent on substrates >5 cm in diameter (F (2, 38)=3.6; P=0.04), time spent resting (F (2, 38)=5.7; $P<0.01$), and time spent inactive (F (2, 38)=24.3; $P<0.01$). As with the adult animals, the majority of changes occurred between time periods 1 and 2, with the exceptions of time spent on artificial substrates, which continued to decrease into time period 3, and time spent inactive, which continued to increase into time period 3.

Effects of Pre-Release Experience

Comparisons across groups showed very few behavioral differences in the first 6 months based on pre-release experience. Animals with free-ranging experience "nearly fell" less frequently, and spent more time micromanipulating than animals without this experience (Table III).

Both groups showed a similar number of changes (although in different behaviors) between time periods 1 and 2. In both groups, the same pattern of

TABLE II. Behavioral Differences Within the First 18 months After Reintroduction in Adult and Juvenile Reintroduced Tamarins

	Period 1	Period 2	Period 3
ADULTS			
Locomotor skills			
Natural substrates 2–5 cm	$31.1\% \pm 2.8\%^{a}$	$39.2\% \pm 3.1\%^{b}$	$42.1\% \pm 4.1\%^{b}$
Artificial substrates	$23.8\% \pm 4.4\%^{a}$	$11.5\% \pm 2.2\%^{b}$	$8.4\% \pm 2.0\%^{c}$
Fall	0.03 ± 0.01^{a}	0.007 ± 0.004^{b}	0.004 ± 0.004^{b}
Inactive	$60.8\% \pm 4.0\%^{a}$	$65.4\% \pm 3.9\%^{b}$	$66.6\% \pm 3.8\%^{b}$
Foraging/feeding			
Micromanipulate	$3.6\% \pm 0.7\%^{a}$	$5.1\% \pm 0.9\%^{b}$	$4.8\% \pm 0.7\%^{b(t)}$
JUVENILES			
Locomotor skills			
Natural substrates >5 cm	$24.7\% \pm 1.7\%^{a}$	$29.8\% \pm 2.7\%^{b}$	$31.1\% \pm 3.2\%^{b}$
Artificial substrates	$22.0\% \pm 3.4\%^{a}$	$15.1\% \pm 2.7\%^{b}$	$8.2\% \pm 1.8\%^{c}$
Ground	$1.0\% \pm 0.02\%^{a}$	$0.5\% \pm 0.2\%^{b(t)}$	$0.5\% \pm 0.2\%^{b}$
Height (trend only)	$4.9\ m \pm 0.2\ m^{a}$	$5.2m \pm 0.2mb^{(t)}$	$5.3m \pm 0.2m^{b(t)}$
Rest	$5.6\% \pm 1.5\%^{a}$	$9.2\% \pm 2.0\%^{b}$	$11.2\% \pm 2.2\%^{b}$
Inactive	$63.5\% \pm 1.6\%^{a}$	$71.0\% \pm 1.4\%^{b}$	$74.7\% \pm 1.3\%^{c}$
Locomote	$16.5\% \pm 1.2\%^{a}$	$14.5\% \pm 0.8\%^{b}$	$13.6\% \pm 0.7\%^{b}$
Fall (trend only)	0.04 ± 0.01^{a}	0.02 ± 0.008^{b}	$0.01 \pm 0.008^{b(t)}$

Percentages refer to mean percent of time (instantaneous data) while numbers without percentages (with the exception of height) represent mean frequency per hour (all occurrence data). Probability values are considered significant $p \leq 0.05$ and trends at $p > 0.05$, < 0.1. Periods with different letters are significantly different. A (t) signifies that the difference is a trend only.

results was seen in time spent on artificial substrates (decrease), time spent inactive (increase), frequency of falling (decrease), and height in canopy (increase; trend only in animals with free-ranging experience). In addition, free-ranging animals showed increases in time spent on natural substrates >5 cm in diameter, and in time spent eating and resting. Animals that had no free-ranging experience showed increases in time spent on natural substrates <2 cm (trend only) and 2–5 cm in diameter, and micromanipulating.

Behavioral Differences Between Adult Animals That Survived 6 Months and Those That Did Not

Adults that survived <6 months spent less time on natural substrates 2–5 cm (trend only) and >5 cm in diameter, and locomoting, and spent more time on artificial substrates, specifically in the nestbox. Additionally, there was a trend for animals that did not survive to spend less time micromanipulating (Table IV).

DISCUSSION

Behavioral changes in reintroduced golden lion tamarins were evident in locomotor and, to a lesser extent, foraging skills. The primary changes occurred within the first year and represented an improvement in locomotor skills, as demonstrated by less frequent falling, increased time spent on natural substrates, decreased time spent on artificial substrates, and traveling at greater heights.

TABLE III: Behavioral Differences in Animals That Received and Did Not Receive Pre-Release Training

Category	Free-ranging experience		Without free-ranging experience		Significance
Comparison 1: within six months of release					
Nearly fall	0.003±0.003		0.03±0.01		t=2.04; df=59; p=0.046
Micromanipulate	6.2%±0.8%		3.7%±0.4%		t=−2.7; df=59; p=0.009
Comparison 2: between time periods 1 and 2					
Locomotor skills					
	Time 1 (n=23)	Time 2 (n=23)	Time 1 (n=38)	Time 2 (n=38)	
Natural sub < 2cm	6.0%±1.4%	5.6%±1.1%	*4.9%±1.3%*	5.9%±1.5%	NFR: t=−1.8; df=37; p=0.072
Natural sub 2–5 cm	33.3%±3.0%	35.1%±2.3%	**34.6%±1.9%**	**44.8%±2.3%**	NFR: t=−4.8; df=37; p<0.001
Natural sub > 5 cm	**26.4%±2.5%**	**33.4%±2.7%**	29.5%±2.4%	28.7%±2.5%	FR: t=−5.3; df=22; p<0.01
Artificial substrates	**27.3%±4.8%**	**17.9%±3.0%**	**35.9%±2.9%**	**14.6%±2.3%**	FR: t=−2.7; df=22; p=0.013 NFR: t=−5.0; df=37; p<0.01
Ground	0.4%±0.1%	0.1%±0.1%	**0.7%±0.1%**	**0.2%±0.1%**	NFR: t=2.1; df=37; p=0.046
Inactive	**59.9%±3.3%**	**69.8%±3.2%**	**63.5%±2.5%**	**69.5%±2.6%**	FR: t=5.9; df=22; p<0.001 NFR: t=3.2; df=37; p=0.003
Rest	**7.8%±2.5%**	**14.2%±3.3%**	8.8%±2.1%	8.5%±1.7%	FR: t=−3.7; df=22; p=0<0.01
Falls	**0.03±0.01**	**0.00±0.00**	**0.02±0.005**	**0.009±0.004**	FR: t=3.2; df=22; p=0.004 NFR: t=2.3; df=37; p=0.025
Height	*5.5 m±0.4 m*	5.8 m±0.4 m	**4.7 m±0.3 m**	**5.0 m±0.3 m**	FR: t=−1.7; df=22; p=0.094 NFR: t=−2.3; df=37; p=0.028
Foraging skills					
Eating	**3.9%±0.4%**	**4.8%±0.4%**	4.4%±0.3%	4.8%±0.4%	FR: t=2.2; df=22; p=0.041
Micromanipulate	6.2%±0.8%	5.3%±0.8%	**3.7%±0.4%**	**5.3%±0.8**	NFR: t=−2.2; df=37; p=0.032

Comparison 1 shows significant behavioral differences in individuals with different pre-release experience. Comparison 2 contrasts change within a class of experience across time periods 1 and 2 (e.g. did the time spent on artificial substrates by animals with free-ranging experience change between periods 1 and 2?). For these comparisons, values in bold are significantly different between time periods 1 and 2 and values in italics represent trends. Percentages refer to mean percent of time (instantaneous data) while numbers without percentages (with the exception of height) represent mean rate per hour (all occurrence data). Probability values are considered significant at $p \leq 0.05$ and trends at $p > 0.05$, <0.1. FR, animals with free-ranging experience, NFR, animals without free-ranging experience.

TABLE IV: Behavioral Differences Between Animals That Did and Did not Survive to 6 months After Reintroduction.

Category	Individuals surviving >180 days (n=28)	Individuals surviving <180 days (n=12)	Significance
Locomotor skills			
Natural sub 2–5 cm	33.3%±2.5%	24.7%±5.4%	t=1.8; df=38; P=0.079
Natural sub 5 cm	28.6%±2.9%	19.7%±4.5%	t=2.0; df=38; P=0.052
Artificial sub (nestbox only)	18.3%±3.2%	32.2%±10.0%	t=−2.2; df=38; P=0.036
Locomote	13.7%±1.2%	9.3%±1.5%	t=2.4; df=38; P=0.022
Foraging skills			
Micromanipulate	3.9%±0.6%	2.5%±0.6%	t=1.7; df=38; P=0.09

Percentages refer to mean percent of time. Probability values are considered significant at $P \leq 0.05$ and trends at $P > 0.05$, < 0.1.

Foraging skills, or at least foraging efforts, also appeared to improve in adults, as shown by an increase in time spent micromanipulating. The relatively few changes related to feeding/foraging as compared to locomotion may reflect a slower rate of change for these behaviors, or may be a result of provisioning, which would decrease the animals' need to become proficient foragers.

The notion that the observed changes represent acclimatization and are beneficial is supported by the comparisons of individuals that survived 6 months with those that did not. For example, animals that did not survive 6 months spent more time on artificial substrates compared to surviving individuals. Thus, the decreased time spent on artificial substrates by both adult and juvenile animals over the first 18 months represents a shift away from a less adaptive behavioral profile. Additionally, such a change represents a movement in the behavior of captive-born, reintroduced animals toward that of the better surviving, wild-born members of the reintroduced population (e.g., descendants of captive-born, reintroduced individuals [Beck et al., 2002; Stoinski et al., 2003]).

Juveniles showed a larger number of significant changes in the first 6 and 18 months as compared to adults. Although some of the changes may reflect increased weight/maturation (e.g., increased time on natural substrates >5 cm in diameter), many are in the opposite direction of what would be predicted based on weight gain (e.g., increased height in canopy, decreased time on the ground). Thus, we believe the majority of these changes actually represent acclimatization to the environment for the same reasons cited above (i.e., they shifted the behavior of juveniles toward individuals born in the wild), and indicate that animals benefit from being reintroduced before they reach maturity.

There were few differences between the animals with and without free-ranging experience. The increased time spent micromanipulating, and the decreased frequency of "nearly falling" in individuals that had ranged free suggests that they had slightly better locomotor and foraging skills than those without such experience. However, the lack of drastic differences between these groups upon release, and the similar number of changes within the first year suggest that there are few long-term benefits from free ranging, which is consistent with our finding of no survival differences between the two groups [Beck et al., 2002].

Recommendations for Reintroduction

We now know that changes in both locomotor and foraging abilities in captive-born golden lion tamarins continue well into, and in some cases beyond, the first year after release. Additionally, the few behavioral differences between animals with and without free-ranging experience suggest that this preparation, as it has been structured, provides few benefits. Combining these two results leads us to conclude that the current protocol of extensive post-release support for reintroduced tamarins is probably essential for their survival, particularly in the first 6 months. One potential problem with post-release support, however, is its longevity. What is beneficial to the tamarins in the short term might not promote long-term survival and adaptation. For example, extensive provisioning may impede the development of foraging skills [Yeager, 1997]. Thus, a balance between short-term strategies designed to maximize immediate survival and long-term strategies designed to maximize natural adaptive processes is needed. The current data show that the majority of behavioral changes occur within the first year after release; thus, it may be appropriate to decrease post-release support after this time to ensure a more rapid adjustment to the wild.

In addition to maximizing survival, the goal of reintroduction should be to produce a population that is behaviorally similar to truly wild animals. Unfortunately, for golden lion tamarins, direct comparisons between the reintroduced and wild populations are limited by substantial methodological differences (i.e., data are collected at different times of the day, and captive-born tamarins are provisioned). However, we can examine whether changes in the behavior of reintroduced tamarins over time reflects a convergence in behavior between the two groups. We know that the percentage of time spent locomoting (21–43%), feeding (15.3–21.6%), and foraging (9.2–30%) [Dietz et al., 1994] is substantially higher in wild tamarins than in the current subjects at all points in the study. However, what is perhaps more significant is that only one of these behaviors was observed to increase in the current subjects as a function of time in the wild: time spent foraging increased in animals reintroduced as adults during the first year after release. For the remaining behaviors (and for foraging in animals reintroduced as juveniles), the time spent in the behavior either stayed the same or decreased over time. Thus, despite the methodological differences, we can conclude that over time some behaviors in reintroduced animals are not approaching those of wild individuals. The same result was obtained in a previous study when generation time was used as an independent variable [Stoinski et al., 2003]. Thus, although we interpret the current data as suggesting that the reintroduced tamarins are becoming acclimated to the wild, this does not mean they are developing behavioral profiles similar to those of truly wild tamarins. This is an important point to consider for any reintroduction program, and it highlights the need for periodic assessments of behavior and subsequent adjustments in procedures to facilitate true adaptation as opposed to acclimatization.

In terms of more general recommendations, two additional areas of interest are pre-release training and post-release evaluation. Many reintroduction programs develop structured training regimes for animals before they are released into the wild. Examples include teaching predator avoidance by associating a model or real predator with some aversive stimuli, exposing animals to food as it might be found in the wild (i.e., intact fruits or live prey), or forcing animals to use novel travel routes [Beck et al., 2002]. Much of this training is focused on adult animals after they have been selected for reintroduction, and it is often unsuccessful at increasing post-release survival rates [Beck et al., 2002].

The data from this study demonstrate one reason why the "training" experience given to golden lion tamarins in the form of living in a complex, free-ranging environment does not confer behavioral benefits: it is likely that the experience does not occur early enough in life. The majority of golden lion tamarins do not range free until they reach maturity; however, our results indicate that juveniles adjust to complex environments more rapidly. Other reintroduction projects have also found benefits from early exposure to complex environments [e.g., Biggins et al., 1998; Miller et al., 1990, 1998; Vargas and Anderson, 1998], and thus it would appear that any type of pre-release experience aimed at facilitating adaptation to the wild should begin as early in life as possible. This may not only enhance behavioral acclimatization, it may be essential for survival. Failure to introduce animals into a complex environment at a young age may permanently affect their ability to transition to the wild. Some animals, such as carnivores and birds, must learn particular behaviors during a sensitive period of development; after this period, behavioral traits may still develop, but not as efficiently [Miller et al., 1998]. Additionally, in many mammals, neural development continues after birth, and early enriched environments have been linked to changes in brain morphology, including increased number and complexity of synaptic connections, and increased cortical thickness and weight [Shepherdson, 1994; Miller et al., 1998]. The behavior of animals exposed to enriched environments from a young age reflects these morphological changes. For example, rats (*Rattus norvegicus*) raised in enriched environments avoid predator models better than rats raised in impoverished environments [Renner, 1988]. Thus, reintroduction programs should expose potential reintroduction candidates to complex environments as early in life as possible.

A second consideration for reintroduction programs is the methodology for post-release evaluation. One limitation of the data analyses in this study was that variable amounts of data were collected on different individuals, and data were missing for certain animals for some time periods. Many sophisticated techniques used for the analysis of developmental data are based on the assumption of systematic sampling over time (K. El Sheshai, personal communication). Thus, to effectively assess changes over time in captive-born animals, an a priori data collection method should be established to ensure that the data are recorded at equal time increments for all subjects. Obviously, it may prove logistically impossible to obtain data from every animal for every predetermined time period, especially as the reintroduced population becomes large and independent. However, attempts should be made, especially in the early stages, to monitor as many animals as possible and to ensure that data are obtained from a comparable number of individuals in each subgroup. We were also limited in our comparisons of reintroduced animals and truly wild tamarins because of methodological differences. Whenever possible, it would be beneficial to collect identical data from both populations so that direct comparisons could be made.

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