

RESEARCH ARTICLE

Social Learning and Mother's Behavior in Manipulative Tasks in Infant Marmosets

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High levels of social tolerance are considered to promote social learning, as they allow direct observation of a manipulating conspecific and facilitate scrounging. Owing to tolerance toward infants, infancy is thought to be especially suited for learning socially transmitted behaviors. Despite this, few studies have investigated social learning of infants, particularly in manipulative tasks where observation might be most helpful. Here, we investigated (1) the influence of social learning on task acquisition in infant marmosets, and (2) whether the mother augments her behavior in a way that may enhance social learning by her infants. We tested infant and juvenile marmosets in four different complex foraging-related tasks, featuring large living insects (two tasks) or artificially embedded prey (two tasks). Each individual observed the mother solving two of the tasks and served as a control in the other two tasks. Observers manipulated more and succeeded sooner than control animals, suggesting that observing the mother promoted learning either directly or by decreasing neophobia. Moreover, the data suggest that learning in 11–15 week-old infants might be promoted actively by the mother. She solved the tasks, consumed less food, and consumed it later than when foraging with older offspring or alone. Furthermore, the results indicate the possible importance of the third and fourth month of infancy as the crucial ontogenetic period for social learning in marmosets, corroborating recent observations of free-living common marmosets. *Am. J. Primatol.* 71:503–509, 2009. © 2009 Wiley-Liss, Inc.

Key words: social learning; infants; vertical transmission; marmoset; foraging

INTRODUCTION

Over the last few decades, researchers have invested considerable effort in exploring the psychological processes that underlie social learning [e.g. Dautenhahn & Nehaniv, 2007; Heyes & Galef, 1996], but how age or context influence whether or what animals learn from others remains largely unexplored. When considering the important question of the functional significance of social learning, the common assumption is that learning from others is inherently adaptive. Instead of costly individual learning, conspecifics provide information about location, quantity, or quality of food sources. They may do so actively by emitting specific signals, or passively by producing cues and signs in the course of their own foraging activity [Galef & Giraldeau, 2001].

However, copying others indiscriminately is not adaptive [Boyd & Richerson, 1985; Giraldeau et al., 2002]. Instead individuals should use social learning selectively, choosing carefully from whom to learn and when to learn, at other times learning individually by directly sampling the environment. In other words, whether social learning confers fitness advantages or not depends on *when* to learn socially and from *whom* [Laland, 2004].

Social learning is probably especially adaptive for an individual that is naïve, i.e. has much to learn in a short time, while starting to forage independently. By scrounging information, one can quickly and safely acquire necessary skills and knowledge, especially if allowed to follow models closely. Therefore, a social setting with a high degree of tolerance should be advantageous for social learning, as naive individuals might be able to combine observation with interaction with the demonstrator and task-related objects [Coussi-Korbel & Fragaszy, 1995]. As mothers are usually very tolerant toward their infants [Fragaszy & Visalberghi, 1989], infancy appears especially suited for learning socially transmitted behaviors [King, 1994], especially from the mother.

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Marmosets (*Callithrix jacchus*) are cooperative breeders living in extended family groups with the breeding female being the mother of all individuals except the breeding male(s) [Stevenson & Rylands, 1988]. These monkeys show marked tolerance toward each other while feeding, and frequently attend closely to the foods others are eating [Ferrari, 1987; Kaspar et al., 2008]; they maintain spatial and behavioral cohesion with their social partners [Digby & Barreto, 1993]. Furthermore, several studies have demonstrated that foraging in this species is strongly influenced by social facilitation, local and stimulus enhancement, and even imitation [Bugnyar & Huber, 1997; Caldwell & Whiten, 2003, 2004; Day et al., 2003; Snowdon, 2001; Voelkl & Huber, 2000, 2007; Voelkl et al., 2006].

Concerning the onset and duration of social learning, the only data from the field suggest that the age around 3–4 months is of special importance in common marmosets [Schiel & Huber, 2006]. During this period infants show an increased interest in the foraging activities of sub-adult and adult group members. This finding is compatible with reports of the start of sophisticated hunting techniques at around 3 months of age, when fine visual object discrimination develops [Missler et al., 1992]. However, exactly which factors contribute to the special importance of this ontogenetic phase remains to be investigated.

The aim of this study was to investigate the time course of social learning and contributing factors in a laboratory experiment with captive marmoset infants. In order to examine the acquisition of non-trivial manipulative foraging skills, we designed two complex foraging tasks; one required killing large insects, another required extracting embedded food. We assessed the infants' performance in these tasks either (i) immediately after closely observing and interacting with the mother while she solved them, or (ii) when alone with the insect or the apparatus, but with the mother present behind a wire-mesh partition.

In addition to the infants' behavior, we also became interested in the mother's behavior after observing what seemed to be signs of active provision of information to the offspring. One notable behavior was vocal communication, which drew the infants' attention to food items. Rapaport and Ruiz-Miranda [2002] observed two tamarin mothers and one father emitting "food calls" during foraging, which were immediately followed by approach and foraging behavior by 31–36-week-old infants at the same site. Interestingly, when the infants quickly extracted a prey item, the parents did not attempt to take it from their offspring. This behavior could be considered as tutoring, if not as "teaching" according to Caro and Hauser's definitions [1992].

To know the precise social learning mechanisms at play would again require data from rigorous tests,

but our experiments attempted to provide a starting point in this direction. We recorded the vocalizations of all subjects during the experiments, and analyzed the interactions between mother and offspring in detail. We also included tests with the mother either in the presence of offspring or alone.

METHODS

Subjects

Our main subjects were two sets of 11-week-old infant twins from the same marmoset family. Complementary tests were carried out with an 8-month-old juvenile twin pair again from the same family.

The mother's behavior was tested in trials with the four young infants, the juvenile twin pair, as well as an additional pair of infants born toward the end of the study.

All marmosets were born in captivity and housed in indoor cages (250 × 250 × 250 cm) at the Faculty of Life Sciences, University of Vienna, Austria. Cages were equipped with ropes and branches. The marmosets were fed fruits, vegetables, and protein supplements once per day. The temperature was 28–34°C during the day and the night. The humidity ranged from 70–90%. Our research was carried out in accordance with animal care regulations and applicable national laws.

Apparatus

All trials took place in a test cage (70 cm length, 36 width, and 108 cm height), which was visually isolated from the marmoset home cage. A small compartment in the top right-hand corner of the test cage was used to confine the mother during *Ob-phase-2* and *Non-Ob* trials (see below).

We investigated social learning in two foraging categories with two comparable tasks in each category:

Insect catching: Subjects had to catch either a grasshopper (*Locusta migratoria*) or a male cricket (*Gryllus bimaculatus*) of approximately 4 cm length. Insects were placed on the test cage floor and covered with an opaque plastic bowl until the trial started.

Artificially embedded prey: Subjects could retrieve mealworms out of paper-covered film cans or out of a small glass bowl filled with wood shavings. The film can setup consisted of two plastic film cans baited with two mealworms each. The cans were covered with parchment paper, which was fixed to the rim with tape. Subjects could extract the mealworms from the can after ripping off the paper. We used two cans for the setup as the opening of a filmcan is too narrow to allow joint exploration by two marmosets.

The glass bowl measured 6 cm in diameter, 4 cm in height. Four mealworms were placed into the

bowl, which was then filled up with wood shavings. Subjects were required to dig mealworms out of the substrate. As marmosets are more likely to approach objects when they are positioned above the floor [Majolo et al., 2003; Millar et al., 1988], we placed them on a 10×15 cm platform attached to the wall 40 cm above the floor.

Procedure

Preliminary to testing, all subjects were fed with chopped grasshoppers, crickets, and mealworms to avoid food neophobia. All subjects were habituated to the test cage. The mother was trained in each foraging task until she successfully completed three consecutive trials.

To control for similarities in genetics and rearing environment between twin pairs, we used a cross design within each category (prey-catching and embedded food), that is, one twin of each pair was the observer in cricket-catching and the non-observer in grasshopper-catching, and vice-versa (Fig. 1). As the tasks were comparable, this setup allowed to test each infant in a within-subject design.

During Non-Observer trials (*Non-Ob*), the infants were in the presence of the objects for 10 min. Meanwhile the mother sat in an adjoining compartment, where she was visible, but had no access to the objects.

Observer trials consisted of two phases. During the first 5 min, referred to as Observer phase 1 (*Ob-phase-1*), mother and offspring were in the test cage together, allowing the infant to observe, scrounge food, and manipulate the object alongside the mother as she solved the task. After 5 min, the marmosets were lured into an adjoining compartment with a small piece of banana. The test cage was equipped with a new, intact object out of view of the

marmosets. Infant and mother were separated by a guillotine door. About half a minute after the end of *Ob-phase-1* the infant was lured into the test cage again for Observer phase 2 (*Ob-phase-2*), when it was exposed to the task alone for another 5 min, whereas the mother remained in the adjoining compartment.

The four main subjects were tested once in each of the four tasks when they were 11, 15, 19, and 23 weeks old. We did not start testing earlier as visual object discrimination is not fully developed in younger infants [Missler et al., 1992]. Also, repeated parental deprivation during the first month of life can cause severe changes in infant marmoset behavior [Dettling et al., 2002]. The juvenile twin pair was tested once in each task at the age of 35, 39, and 43 weeks.

Additionally to infant testing, we investigated whether the mother changed her behavior to facilitate learning for her infants. Using the can opening task, we asked whether her behavior changed in the presence of an infant (experimental condition) compared with when encountering the same task alone for the same amount of time (control condition). We used the can opening trials from our main study (conducted with two infants, one trial each at 11, 15, 29, and 23 weeks), and additional trials with a third generation of infants of the same family (one trial each at the age of 11 and 15 weeks). The four control trials were conducted during the 4 weeks when the second infant generation was tested.

All trials were videotaped with a digital camera (Sony DCR-TRV 25E) with 25 frames per second. The camera was focused on subjects, and audio comments were recorded to describe their behavior in detail. All experiments were conducted between 10 a.m. and 12 a.m., shortly before feeding time.

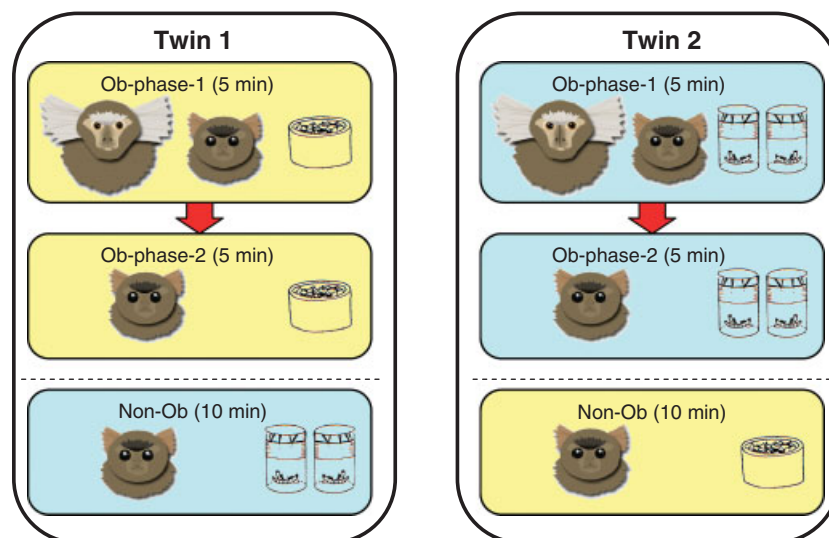


Fig. 1. Cross design—Observer and Non-Observer roles are allocated equally within twin pairs.

ANALYSIS

Behavioral Categories and Data Coding

Videos were analyzed frame-by-frame with Pinnacle Systems Studio 9 program. We measured the animals' *latency to approach* within 15 cm of the object, and the percentage of total time they spent *manipulating* it (defined as touching the object with hands or mouth). We also measured the percentage of total time they paid *attention*, defined as looking in the direction of an object without manipulating it. The approach latencies, manipulation- and attention percentages during *Ob-phase-1* were compared with those of *Ob-phase-2*, and with the first 5 min of the *Non-Ob*.

We rated touching an insect as *partial success* and killing it as *full success*. In embedded prey tasks, retrieving one mealworm counted as *partial success* and retrieving all worms counted as *full success*. Analyzing the number of trials observing and non-observing infants needed for partial and full successes involved pseudoreplication of the data ($N = 8$, calculated on four tasks, each of which was completed by two pairs of twins).

For *Ob-phase-1* we further noted the percentage of food that infants or juveniles obtained, and whether the food was passed from mother to offspring (*food sharing*) or picked up by the infant (*scrounging*). To compare success rates, manipulation- and attention percentage as well as approach latencies, we pooled the data of all four trials (11, 15, 19, and 23 weeks).

In the can opening trials (experimental and control conditions), we measured the time the mother took between opening a can and retrieving the first mealworm (*mealworm-retrieving-time*) and time not manipulating an opened can that still contained mealworms (*can left unattended*).

Statistics

As the behavioral data did not satisfy the conditions necessary for a parametric statistical model [Siegel & Castellan, 1988], we used nonparametric statistical analyses. In the result section, we present the median (1st quartile; 3rd quartile), when referring to approach latencies and the percentage of attention or manipulation. All tests were two tailed and α was set at 0.05, trends are reported for $0.1 > \alpha > 0.05$.

RESULTS

Attention, Approach Latency, and Manipulation Time

Infants showed significant differences in manipulation, attention, and approach in the three conditions of *Ob-phase-1*, *Ob-phase-2*, and *Non-Ob* (Table I). Infants manipulated longest in *Ob-phase-1*,

manipulated about half as long in *Ob-phase-2*, and showed nearly no manipulation at all during *Non-Ob*. (Friedman: $N = 4$, $df = 2$, $P = 0.05$, $Fr = 6.5$; Multiple comparisons: *Ob-phase-1* vs. *Ob-phase-2* $P > 0.05$; *Ob-phase-1* vs. *Non-Ob* $P < 0.05$; *Ob-phase-2* vs. *Non-Ob* $P > 0.05$). Attention percentages were highest in *Ob-phase-1*, intermediate in *Non-Ob* and lowest in *Ob-phase-2* (Friedman: $N = 4$, $df = 2$, $P = 0.05$, $Fr = 6.0$; Multiple comparisons: *Ob-phase-1* vs. *Ob-phase-2* $P < 0.05$; *Ob-phase-1* vs. *Non-Ob* $P > 0.05$; *Ob-phase-2* vs. *Non-Ob* $P > 0.05$). In *Ob-phase-1* infants approached soonest, whereas they approached very late or not at all in the *Non-Ob* condition. The *Ob-phase-2* was intermediate (Friedman: $N = 4$, $df = 2$, $P = 0.005$, $Fr = 8.0$; Multiple comparisons: *Ob-phase-1* vs. *Ob-phase-2* $P > 0.05$; *Ob-phase-1* vs. *Non-Ob* $P < 0.05$; *Ob-phase-2* vs. *Non-Ob* $P > 0.05$).

In contrast to the infants, the two juveniles showed the quickest approach and the longest manipulation during *Ob-phase-2*. During *Ob-phase-1*, juvenile manipulation was lowest, whereas infant manipulation was highest.

Success

Infant non-observers needed more trials (e.g. they were older) until achieving partial or full success compared with their observing twins (two-tailed signed test: $N = 8$, $P = 0.008$). The latter usually achieved partial success at the age of 15–19 weeks and full success at the age of 19 weeks. Non-observers never achieved full success (two-tailed signed test: $N = 8$, $P = 0.008$). Both juveniles were able to solve all tasks after three trials.

Development in Infant Manipulation

In *Ob-phase-1*, manipulation decreased significantly over time (Fig. 2A)(Friedman: $N = 4$, $df = 2$, $P = 0.0009$, $Fr = 11.1$; Dunn's multiple comparison test: first trial 67.56 (61.33, 69.60)% vs. third trial 32.81 (18.32, 45.74)%, $P < 0.05$), but increased significantly over time in *Ob-phase-2* with all infant observers showing a visible shift in manipulation time either at trial 2 or trial 3 when they were 15 or 19 weeks old (Fig. 2B)(Friedman: $N = 4$, $df = 2$, $P = 0.0062$, $Fr = 9.9$; Multiple comparisons: First trial 1.92 (0.50, 3.37)% vs. fourth trial 48.09 (45.77, 49.44)%, $P < 0.05$).

Manipulation time remained low in *Non-Ob* (Fig. 2C) (First trial: 0.28 (0.08, 2.45)%, last trial: 2.15 (1.35, 4.32) %; Friedman: $N = 4$, $df = 2$, $P = 0.53$, $Fr = 2.23$).

Behavior of the Mother in Embedded Prey Task

The mother showed differential behavior depending on the presence and the age of the infants.

TABLE I. Manipulation and Attention Percentages and Approach Latencies

	<i>Ob-phase-1</i>	<i>Ob-phase-2</i>	<i>Non-Ob</i>
<i>Infants (N = 4)</i>			
Manipulation %	44.38 (33.55, 51.65)	25.96 (24.72, 27.94)	2.90 (1.81, 4.63)
Attention %	31.94 (25.08, 40, 20)	14.14 (10.08, 17.03)	19.89 (17.94, 20, 82)
Approach latency in sec	19.29 (15.71, 22, 41)	51.57 (42, 58, 63.36)	124.35 (111.56, 159, 09)
<i>Juveniles (N = 2)</i>			
Manipulation %	26.52 (22.62, 30.41)	72.53 (63.44, 81.63)	59.07 (57.71, 60.43)
Attention %	43.75 (41.47, 46.03)	9.50 (7.94, 11.05)	16.17 (14.87, 17.46)
Approach latency in sec	14.15 (9.91, 18.38)	8.74 (5.84, 11.64)	29.35 (28, 64, 30.05)

Depicted are the medians, the first and the third quartile.

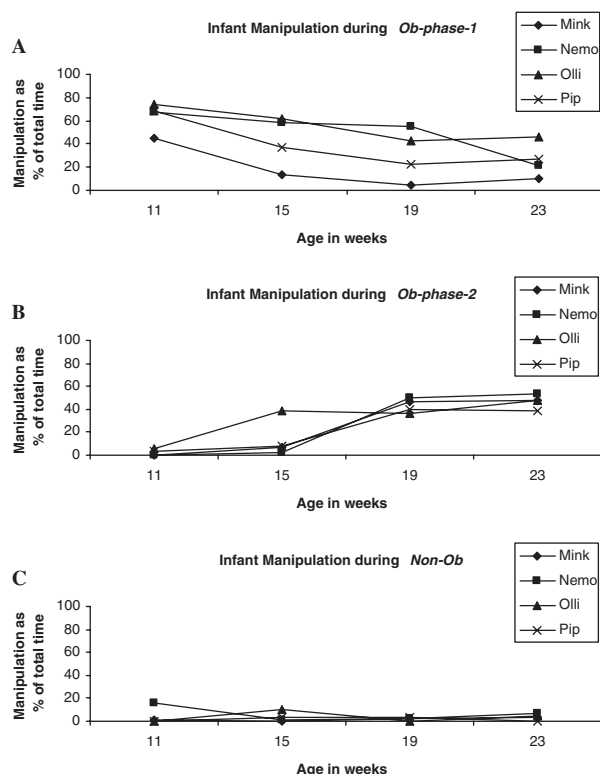


Fig. 2. Development of infant manipulation. Depicted are the manipulation percentages from 11 weeks (trial 1) to 23 weeks (trial 4).

In the presence of her 11–15-week-old infants, she always emitted food calls after opening a can if infants were not already manipulating it ($n = 7$ cans), but not if the infants were already manipulating the same or the other can ($n = 9$ cans) (Fisher's Exact test: $P = 0.0001$). The mother's food call always prompted the infants to instantly approach and manipulate the can. During trials with infants aged 19 and 23 weeks, the mother never emitted food calls ($n = 8$ cans), regardless of whether the infant manipulated a can ($n = 2$ cans). Similarly, no food calls were emitted when the mother was tested alone ($n = 8$ cans).

When infants were 11–15 weeks old, the mother left food-containing cans that she had opened unattended (e.g. she moved away from the cans and investigated the cage) for an average of 5.28 (0.0, 27.83) sec, whereas she hardly left cans unattended when tested with the two 19–23-week-old infants (average: 1.72 (0.0, 8.25) sec). In control trials without infants she never left the cans unattended before emptying them completely.

The mother also took longer between opening a can and retrieving the first mealworm in the presence of younger infants (17.36 (10.30, 24.20) than when alone (11.34 (9.86, 13.42) sec) and when in the presence of the older infants (9.52 (5.55, 13.23) sec). The difference in the delay between the older and younger infants was significant (Mann-Whitney- U : $n_1 = 16$; $n_2 = 8$, $U = 91.0$; $p = 0.047$).

Infants at 11–15 weeks obtained 9 out of 28 mealworms—two were given actively by the mother and seven were collected by infants from cans that the mother had opened and then abandoned. In trials with 19–23-week-old infants, all mealworms were eaten by the mother, who monopolized the prey and showed signs of aggression when infants approached it. We did not analyze the mother's behavior when present with the single observing juvenile.

DISCUSSION

Our study supports the view that social learning may be important for collecting information about food-related tasks in infant primates. Specifically, we found that although infants showed the quickest approach and the longest manipulation time when foraging *together* with the mother, juveniles did so *after* observing the mother. Moreover, the decrease in infant manipulation when foraging together with the mother between the 12th and the 24th week of life and the simultaneous increase in manipulation when alone but after observing the mother suggests that (1) age might limit the opportunities for close social contact with group members, necessitating the development of individual foraging strategies; and (2) social learning might be an important factor facilitating this development. Our finding that the mother changed her behavior from supporting her

young infants' foraging skills to basically preventing their access to the tasks and rewards as they grew older further supports the idea of a sensitive period during development when infants have the opportunity to learn what to eat and how to forage.

Social learning has been shown to be an important factor when infant primates are confronted with novel food items [Voelkl et al., 2006]. We found that observer infants were more explorative than non-observers when manipulating objects alone and also more successful in killing large prey. Previous studies provided evidence that the presence of family members is sufficient to reduce infant food neophobia [Vitale & Queyras, 1997; Voelkl et al., 2006; Yamamoto & Lopes, 2003], but that this effect is increased when infants see their parents manipulate the food item beforehand [Voelkl et al., 2006]. In our study proximity of the mother alone did not suffice to fully reduce infant neophobia. Infants that could observe the mother interacting with the object in *Ob-phase-1*, showed 15 times more manipulation in *Ob-phase-2* than non-observers, suggesting that the mothers' manipulation and feeding encouraged infants to manipulate. Infant observers needed fewer trials than non-observers to master the tasks, whereas juvenile observers and non-observers did not differ. Whether these results really reflect some kind of social learning as has been shown in adult marmosets [Bugnyar & Huber, 1997; Caldwell & Whiten, 2003; Voelkl & Huber, 2000, 2007] or whether the reduction in neophobia owing to the interaction of the mother with the specific objects is solely responsible requires further investigation.

Interestingly, we found a strong developmental change in infant behavior, supporting an earlier finding of increased attention during early infancy [Schiel & Huber, 2006]. Infants in our study showed the highest attention rates for the embedded prey task in their third and fourth month of life, the same time when free-living marmoset infants interest in the behavior of group members peaked [Schiel & Huber, 2006]. Furthermore, Schiel and Huber [2006] found that joint foraging and manipulation with the parents decreased at the age of four months. Accordingly, we found a strong increase in manipulation time in *Ob-phase-2* when the infants were 19 weeks old. Probably owing to this increase in individual manipulation, juveniles needed fewer trials than infants to solve the tasks, and observation of a model had no visible effect on their success.

Conceivably, 4-month-old infants are sufficiently skilled at foraging that extensive parental support is no longer necessary. Missler's [1992] proposal of postnatal stages in marmosets would support this hypothesis, as it predicts that infants master insect hunting when they are 16–20 weeks old. Infants in our study successfully caught and killed insects at 19 weeks, but only when they had observed the mother hunting the same insect species, suggesting that

observation of skilled group members aids infants in learning how to capture insects. However, the two juveniles in the same group were able to kill insects of both species independently of observation. Unfortunately, we cannot rule out the possibility that the juveniles had experience of capturing insects before the study. Further studies should address whether or not observation is necessary for learning how to kill large prey in marmosets.

Another interesting outcome of our study was the behavior of the mother, as although any conclusions must be made with caution owing to the small sample size ($n = 1$). Although the mother actively provisioned food to 11–15-week-old infants during the first two trials, she monopolized the food once the infants were older.

The mothers' behavior is consistent with anecdotal observations on wild lion tamarins [Rapaport & Ruiz-Miranda, 2002]. Tamarin parents were observed to hesitate upon finding prey embedded in the substrate. Instead of retrieving the prey they attracted infants with a food call, whereupon the infants retrieved and ate the prey. In our can-opening task, the mother emitted food calls in the presence of 11–15-week-old infants if the latter had not started to manipulate. Food calls led to an immediate approach, manipulation, and obtaining of mealworms by the infants. Interestingly, in contrast to the parents of 31–36-week-old lion tamarins in Rapaport and Ruiz-Miranda's study, the marmoset mother stopped emitting food calls when the infants were older than 15 weeks. Moreover, the marmoset mother removed obstructing paper to facilitate access to the embedded prey, whereas it is unclear whether the tamarin parents also prepared the substrate in a comparable way.

According to the criteria of Caro and Hauser [1992], parent-offspring behavior can be considered as teaching if (1) it occurs only in the presence of a naïve observer, (2) it is costly and does not provide any immediate benefit for the teacher, and (3) it facilitates knowledge acquisition or skill learning in the observer. All three criteria were met by the mother's behavior in the can-opening tasks. She opened cans without retrieving the enclosed prey, which is costly as it requires effort without immediate benefit. Infants were able to retrieve the prey because the mother waited after opening the can, often even leaving it unattended, and emitted food calls that attracted absent infants. All these behaviors ceased when infants grew older or when the mother was tested in the absence of infants. As observers were significantly more successful than non-observers, the criterion of learning facilitation is also met. Thus, keeping in mind that we only tested a single mother, our study suggests that marmosets might be a good species in which to study teaching behavior. Also, again with larger sample sizes further work should investigate whether mothers

change their behavior according to infants' age or prior experience.

This preliminary study on social learning of manipulative tasks in common marmoset infants suggest a possible sensitive period during infancy when both attention levels of infants toward group members and tolerance levels of close relatives toward the infants are high, promoting opportunities for infants to learn socially foraging tactics necessary for survival.

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