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INTRA- AND INTER-SPECIFIC SOCIAL LEARNING OF A NOVEL FOOD TASK IN TWO SPECIES OF TAMARIN

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ABSTRACT: Intra- and inter-specific social learning was investigated in two species of New World monkey, the saddle-backed tamarin (*Saguinus fuscicollis*) and the red-bellied tamarin (*S. labiatus*), which form stable and permanent mixed-species troops in the wild. We explored whether improved food acquisition, through social learning, is a potential advantage of mixed-species troop formation by allowing a pair of naive observers to watch a pair of trained demonstrators complete a novel foraging task. The aims of the study were (a) to determine if individuals succeeded at the task more quickly after having observed demonstrators, (b) to investigate whether speed of acquisition differed after observation of conspecific demonstrators as opposed to congeneric demonstrators, and (c) to compare performance between species. The number of trials taken by observers to succeed on the task was compared with that taken by naive demonstrators to succeed on the task initially. Individuals succeeded on the task more quickly if they had had the opportunity to watch demonstrators perform the task, regardless of whether the demonstrator was a conspecific or congeneric. There was no difference in performance between species. It is concluded that, for both species, the learning of a new foraging technique is facilitated by the presence of both conspecifics and congenerics and that the likely mechanism for this facilitation is a combination of stimulus enhancement and response facilitation. Social learning of this kind is discussed with respect its adaptive value in wild mixed-species tamarin troops.

Tamarins of the genus *Saguinus* are small bodied (300-550g: Hershkovitz, 1977), diurnal, arboreal, South American primates which feed primarily upon insects, ripe fruits, nectar, and plant exudates (Snowdon and Soini, 1988; Garber, 1993). Their social lives are characterised by high levels of co-operation, tolerance and adaptability (Caine, 1993). When travelling and foraging troop members move in a cohesive manner (e.g., Yoneda, 1984a; Goldizen, 1987 for *S. fuscicollis*; Garber, 1988a for *S. mystax*; Buchanan-Smith, 1989 for *S.*

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labiatus) and when palatable food is found, food calls are given which are thought to recruit troop mates to the vicinity of the caller (Caine *et al*., 1995 for *S. labiatus*). Tamarins also produce contact calls (Moody and Menzel, 1976 for *S. fuscicollis*; Caine and Stevens, 1990 for *S. labiatus*) which allow individuals to keep track of their troop mates, thereby maintaining cohesiveness within the troop, enabling movement in a co-ordinated manner and permitting co-operative ventures such as infant care and vigilance (Caine and Stevens, 1990). Furthermore, intra-troop aggression is rare (Goldizen, 1989; Buchanan-Smith, 1990 for *S. fuscicollis*; Coates and Poole, 1983 for *S. labiatus*) and, in comparison with squirrel monkeys (*Saimiri*), tamarins are reported to be tolerant of each other's presence at a newly discovered food source (Mayer *et al*., 1992 for *S. labiatus*).

Not only do tamarins co-operate intra-specifically, but also inter-specifically. *S. fuscicollis* forms stable and permanent mixed-species troops with three other species with which it is sympatric. These are *S. mystax* (Castro and Soini, 1977; Garber, 1988a,b; Heymann, 1990; Norconk, 1990; Peres, 1991, 1992a,b, 1993), *S. labiatus* (Yoneda, 1981; Pook & Pook, 1982; Buchanan-Smith, 1990; Hardie, 1998), and *S. imperator* (Terborgh, 1983). The most stable association is that between *S. fuscicollis* and *S. mystax*, that between *S. fuscicollis* and *S. labiatus* is intermediate, and *S. fuscicollis* and *S. imperator* associate the least (Heymann, 1997; Buchanan-Smith, in press). Associating species defend a shared home range in parallel against neighbouring mixed-species troops (e.g., Terborgh, 1983; Yoneda, 1984a; Garber, 1988b; Buchanan-Smith, 1990; Peres, 1991, 1992a) (each species directing its aggression towards its conspecific rival: Pook and Pook, 1982; Buchanan-Smith, 1990, 1991; Peres, 1992b) and co-ordinate their activity and movement to a remarkable degree, moving about the home range as a single cohesive unit (typically within 20-50m of each other: Buchanan-Smith, 1990; Heymann, 1990). Both species use vocal communication to maintain this intratroop cohesion (Castro and Soini, 1977; Pook and Pook, 1982; Norconk, 1990) and are known respond to each other's alarm calls (Buchanan-Smith, 1990 for *S. fuscicollis* and *S. labiatus*; Heymann, 1987; Peres, 1993 for *S. fuscicollis* and *S. mystax*; Terborgh, 1983; Windfelder, 1997 for *S. fuscicollis* and *S. imperator*). Participating species also exhibit high overlap in the percentage of plant species eaten (Terborgh, 1983; Garber, 1988a; Ramirez, 1989; Hardie, 1998). When feeding together at monopolisable food resources, however, the smaller *S. fuscicollis* is often either supplanted by its larger, dominant congeners (Terborgh, 1983; Heymann, 1990; Peres,

1991) or is forced to wait until its congeners have finished eating before it can gain access to the resource (Hardie, 1998).

Given such high levels of co-operation and cohesion within and between tamarin species, together with a tolerant nature towards others with food (at least intra-specifically), one might expect that social learning could play an important role in how these monkeys respond to food related challenges in both single- and mixed-species troops. It is generally accepted that there is a greater likelihood of social learning in tolerant species/societies exhibiting high levels of behavioural co-ordination (Cambefort, 1981; Coussi-Korbel and Fragaszy, 1995). For example, Weigl and Hanson (1980) suggest that the intra-specific tolerance shown by red-squirrels (*Tamiasciurus hudsonicus*) in deciduous areas may be especially conducive to observational learning and the efficient exploitation of diverse seasonal food resources.

We wished to investigate whether improved food acquisition, through social learning, could constitute a potential advantage of mixed-species troop formation. Although individual tamarins in mixed-species troops may accrue foraging benefits in a number of ways (for example, through increased insect capture rates: Klein and Klein, 1973; Pook and Pook, 1982; Peres, 1992a; or avoidance of previously used areas: Terborgh, 1983; Buchanan-Smith, 1990; Peres, 1992b), it is the hypothesis that species in mixed-species troops can increase their foraging efficiency by sharing or parasitising information regarding the location and nature of local food resources (Pook and Pook, 1982; Terborgh, 1983; Hardie, 1995; Peres, 1996) that lends itself most to tests in captivity. Tests with captive mixed-species troops of tamarins have proved useful in elucidating the costs and benefits of association. Hardie (1995) was able to show that *S. labiatus* is facilitated to approach objects placed low down in an enclosure after having observed *S. fuscicollis* approaching them. He suggests that *S. labiatus* may benefit in mixed-species troops from the increased responsiveness of *S. fuscicollis* in the lower part of their environment by allowing *S. fuscicollis* to expose itself to any potential danger first and/or by displacing it should the novel object prove beneficial.

The majority of laboratory studies of social learning phenomena have concentrated upon underlying mechanisms. Relatively few have focused on social influences on the transmission of learned behaviours in ways that inform us about the contributions of social learning to group-living animals (Laland *et al.*, 1993; Adams-Curtis and Fragaszy, 1995; Coussi-Korbel and Fragaszy, 1995). Moreover, with the exception of some ornithological studies, such as those by Krebs (1973) and Rubenstein *et al.* (1977), the majority of studies of social learning have examined learning within species. Here we present data on social learning of a novel food task both within and between-species.

METHOD

Study Animals

The study animals were taken from nine troops of *S. fuscicollis weddelli* and nine troops of *S. labiatus labiatus* housed in separate, adjacent, standard captive indoor/outdoor (2 x 1.75 x 1.5 m / 1.95 x 1.55 x 3.5 m) enclosures, off-exhibit from the public, at Belfast Zoological Gardens, N. Ireland, U.K. The monkeys were allowed free access between the indoor and outdoor areas, except when experimental protocol dictated otherwise. Indoor and outdoor areas were well furnished with a network of dead branches. In addition, the outdoor areas supported live shrubbery. The monkeys were fed once daily a mixed-diet of fresh-fruit and vegetables and primate pellets. Their diet also contained a protein element of either marmoset jelly, chicken, eggs or occasionally insects. Freshwater was provided daily. The monkeys' ages were similar across species and ranged from 1 year to 13 years at the time of testing. The mean age for *S. fuscicollis* was 4 years 7 months and for *S. labiatus* was 4 years 5 months. All individuals were captive-born.

The Foraging Task

The tamarins were required to learn how to obtain pieces of banana, a highly preferred food, suspended from the roofs of their enclosures by lengths of string. This task was considered to be a novel one for the tamarins, in that they had not previously been presented with food in this way and had no previous experience with this type of apparatus, but it is related to the foraging behaviour of the species in the wild. In their natural habitat, *Saguinus* take mainly small-sized or pod-like fruit resources which are situated on the terminal branches of the periphery of the tree crown (e.g., *Inga* spp., *Brosimum* spp., *Pourouma* spp.) or else hang down from moderate-sized branches (e.g., *Cecropia* spp.) (Garber, 1986, 1987, 1988a,b; Hardie, 1998 for *S. fuscicollis*; Yoneda, 1981, 1984b; Hardie, 1998 for *S. labiatus*). These terminal branches are not sturdy enough to support an upright stance (indeed, their thinness probably prohibits larger primate competitors from utilising these resources), so to reach the fruit the tamarins adopt a 'grasping' strategy whereby they hang upside down, suspended from the thin branches of the tree, usually by their legs only, but occasionally also using one of their arms, leaving the hands and mouth free for manipulation of the fruit (Hardie, 1998; Prescott, pers. obs.).

The behavioural components required to reach the food item in the experimental task were very similar to this grasping strategy. In order to obtain the food item, the monkeys had to climb up one of the enclosure sides to the roof, locomote by quadrapedal suspension across it, and upon reaching the string, pull it up with their hands whilst hanging bipedally (the length of the strings being longer than the length of an extended monkey hanging by his/her legs). These behavioural components were not assumed to be novel for the tamarins (bipedal hanging, lifting and pulling being part of the behavioural repertoire of all the study animals) but the specific sequence of these necessary to succeed on the task (in its totality) was.

Experimental Design

The basic experimental design followed that of Thorndike (1898) in which a demonstrator animal performs a task in front of an observer, the test then being whether the observer achieves some criterion of success on the task more quickly than when compared with a naïve animal who has not been allowed to observe a demonstrator.

The experiment was designed so that both species acted as demonstrators for their conspecifics and for their congeners, so that comparisons could be made both intra- and inter-specifically between demonstrators and observers. The experiment was designed in this way because it may be that one or both species learn from their congeners more quickly than they do from their own species, indicating an additional advantage of forming mixed-species troops over and above that due simply to an increase in troop size.

Such an experimental design also allows comparisons to be made between species in their rates of asocial learning (independent acquisition). If one of the demonstrator species, say *S. fuscicollis*, learns the task solution asocially more quickly than the other, then *S. labiatus* might benefit more from watching *S. fuscicollis* than they would from observing their conspecifics. This too would constitute an additional advantage to forming mixed-species troops for *S. labiatus*.

For the intra-specific condition, three male-female pairs of *S.*

fuscicollis performed as demonstrators for three male-female pairs of *S. fuscicollis*; and three male-female pairs of *S. labiatus* performed as demonstrators for three male-female pairs of *S. labiatus*. Intra-specific demonstrator and observer pairs were always related (usually parents and offspring) because it is not advisable to house unfamiliar, unrelated individuals of the same species next to each other. Due to the territoriality of tamarins, they may fight viciously (Prescott, pers. obs.). The pairs were normally maintained as family troops and separated only for testing. To avoid confounding effects of age, the number of pairs of parents or offspring acting as demonstrators and observers was counterbalanced.

For the inter-specific condition, three male-female pairs of *S. fuscicollis* performed as demonstrators for three male-female pairs of *S. labiatus*; and three male-female pairs of *S. labiatus* performed as demonstrators for three male-female pairs of *S. fuscicollis*. Interspecific demonstrator and observer pairs were normally maintained as mixed-species troops (and were therefore familiar with each other) and separated only for testing.

Testing was carried out between July and September, 1996, and between April and June, 1997. Species were tested in male-female pairs to minimise the stress of separation and to more closely resemble the social foraging environment of the wild. However, this meant that, in both the intra- and inter-specific conditions, the second monkey of each male-female pair to complete the task had had the opportunity to observe its pair-mate. Consequently, only the data for the first monkey of each pair to complete the task are used in the analysis. This means, also, that the data are not confounded by the possible presence of individuals who simply exploit the skills of others (in this case, steal the food from the successful individual) without learning those skills themselves, and as such block social learning and transmission (Giraldeau and Lefebvre, 1987; Fragaszy and Visalberghi, 1990; Beauchamp and Kacelnik, 1991).

Procedure

All tests were conducted before the tamarins' daily feed, to ensure they were motivated to obtain the food reward. The experimental procedure was as follows:

1. Two strings (50 cm in length) were suspended from the centre of the wire mesh roof of the outdoor portion of the enclosure of the male-

female pair to be tested, and each loaded with a piece of banana (2 cm in width), while the monkeys housed in all other cages were shut inside the indoor portions of their enclosures. The pair acting as demonstrators were then allowed to exit the indoor portion of their enclosure, after which the connecting door between the indoor and outdoor portions of the enclosure was closed. Recording started the moment the door was opened and continued for 30 minutes, or until both food items had been eaten, after which the strings were removed.

The pairs were presented with the task in this way, once per day, until both individuals had succeeded in obtaining the food at least twice. These animals were then considered to be 'trained demonstrators'. Data documenting their asocial learning of the task were termed 'naïve demonstrator data' and were later compared to that of observers.

2. Subsequent, daily trials involved shutting out the second pair (those in the role of observer), into the outdoor portion of an adjacent enclosure and allowing them to observe, through the mesh enclosure sides, the demonstrator-pair complete the task in a further three 30 minute trials. In each case, at least one of the demonstrators completed the task in each of the three trials.

3. Immediately following the third observed successful trial, the observers were presented with the task themselves in the outdoor portion of their own enclosure, with the adjacently housed demonstrators (and all other troops) shut indoors (to prevent 'interference' effects: see Zajonc, 1985; Zentall and Galef, 1988).

Recording Methods

Data were recorded directly onto a hand-held computer using THE OBSERVER 3.0 event recording program (Noldus, 1993). The time at which each individual approached within 15 cm of the string, touched the string, and obtained the food item were recorded.

Data Analysis

From the data collected, the latencies (in seconds) from exiting the indoor portion of the home enclosure to approach within 15 cm of the string, touch the string, and to obtain the food item, were determined for each individual in each trial. The latency for the first individual of each pair to obtain the food item on its first successful trial was added to the number of preceding unsuccessful 30 minute trials for that individual. This corrected, ‘true’, latency was used for analysis. Statistical comparisons between role (naïve demonstrator or observer), species, or condition (intra-specific or intra-specific) were made using non-parametric Mann-Whitney U-tests (with significance set at alpha < 0.05) because of sample-size limitations and deviations from normality.

RESULTS

Overall (pooling both species intra- and inter-specifically) observers, which had had the opportunity to observe completion of the task by trained demonstrators of either species, successfully obtained the food item significantly faster than those that had not observed (the naïve demonstrators) (z = - 3.32, $p < 0.01$; Figure 1).

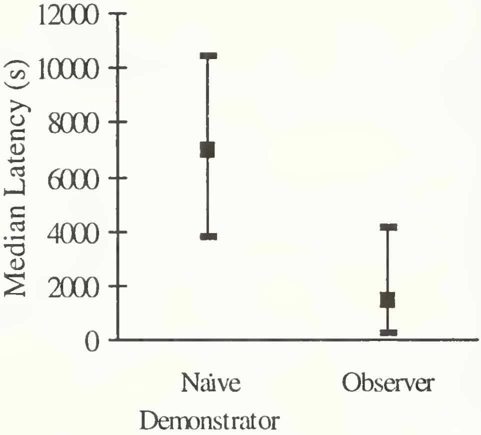

Figure 1. Median latencies (with interquartile ranges) to obtain food item for naive demonstrators and observers, pooling species intra- and inter-specifically.

Collapsing across species, but splitting the data according to intra- and inter-specific conditions, it is found that, for both the intra- and inter-specific conditions, observers were significantly faster to obtain the food item than were their respective naïve conspecific and congeneric demonstrators (z = - 2.31, $p < 0.05$, and z = - 2.02, $p < 0.05$; Figure 2).

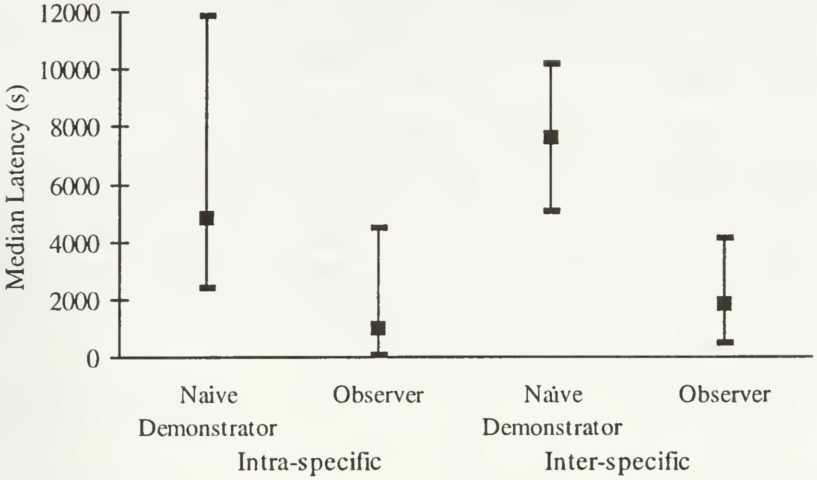

Figure 2. Median latencies (with interquartile ranges) to obtain food item for intra-specific and inter-specific naive demonstrators and observers.

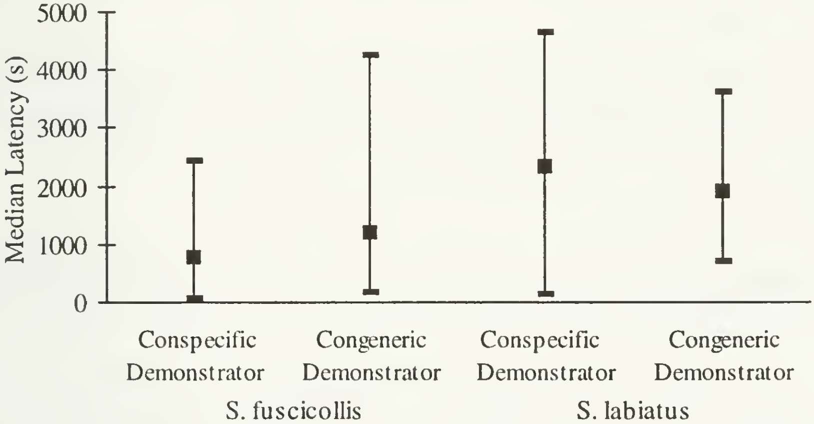

Figure 3. Median latencies (with interquartile ranges) to obtain food item for observer *S. fuscicollis* and *S. labiatus* after having observed conspecific or congeneric demonstrators.

No significant effect for demonstrator species was found. That is, for both *S. fuscicollis* ($z = - 0.96$, $p > 0.05$) and *S. labiatus* ($z = 0.00$, $p > 0.05$), the latencies to obtain the food item after observing conspecifc demonstrators did not differ from those after observing congeneric demonstrators. Nor was there a significant difference between the latency to obtain the food item by observer *S. fuscicollis* after having observed *S. labiatus* demonstrators and observer *S. labiatus* after having observed *S. fuscicollis* demonstrators (z = - 0.40, *p* > 0.05; Figure 3).

There was no significant difference between species in the rate of asocial learning by naïve demonstrators (z = - 0.12, *p* > 0.05). Collapsing intra- and inter-specific conditions, there was no significant difference between species in the rate of social learning by observers (z = - 0.06, *p* > 0.05; Figure 4). So, in addition to the absence of an effect for demonstrator species, species did not differ in their rates of learning either as naïve demonstrators or observers.

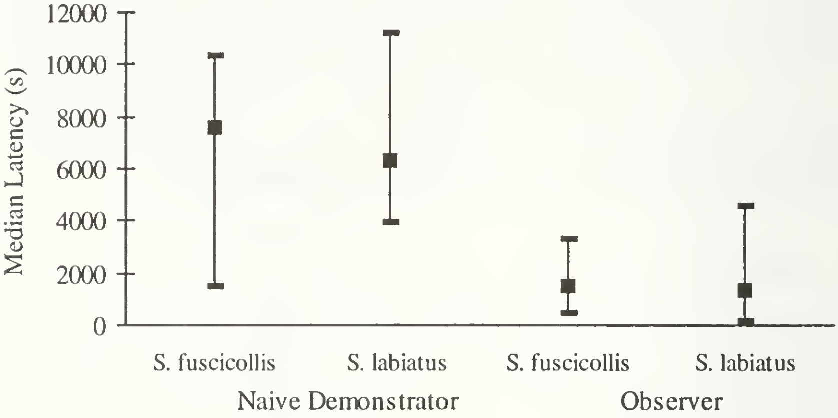

Figure 4. Median latencies (with interquartile ranges) to obtain food item for naive demonstrator and observer *S. fuscicollis* and *S. labiatus*.

In order to reach a deeper understanding of what aspects of the demonstrator's performance may have influenced the acquisition of the technique necessary to reach the food item, a more detailed analysis of the behaviour and interactions during the acquisition period is needed. By examining the relations between the latencies to approach and touch the string, and to obtain the food item, we can identify exactly which of these behavioural components is facilitated by observation of a demonstrator. For example, it may be that the tamarins are facilitated merely to approach and touch the apparatus, and hence learn simply that it is non-threatening, rather than learning how to complete the task once in proximity to the apparatus. Indeed, the latencies to approach

Table 1. Median latencies (seconds) to approach within 15 cm of apparatus. P-values refer to Mann-Whitney U-test. Bold indicates a significant result.

Variable 1	Variable 2		Z value
	Naive Demonstrators	Observers	
Pooling species intra- and inter-specifically	4507	767	z = -3.16, **p < 0.01**
Intra-specific condition	3844	945	z = -2.20, **p < 0.05**
Inter-specific condition	5570	567	z = -2.19, **p < 0.05**
	Conspecific demonstrators	Congeneric demonstrators	
S. fuscicollis observers	747	1301	z = -0.48, p > 0.05
S. labiatus observers	945	251	z = -0.64, p > 0.05
	S. fuscicollis	*S. labiatus*	
Naive demonstrators	5145	4488	z = -0.23, p > 0.05
Observers	915	573	z = -0.20, p > 0.05
Observers from congeneric demonstrators	1301	251	z = -0.58, p > 0.05

Table 2. Median latencies (seconds) to touch the apparatus. P-values refer to Mann-Whitney U-test. Bold indicates a significant result.

Variable 1	Variable 2		Z value
	Naive Demonstrators	Observers	
Pooling species intra- and inter-specifically	5368	769	z = -3.26, **p < 0.01**
Intra-specific condition	4641	978	z = -2.24, **p < 0.05**
Inter-specific condition	6009	623	z = -1.96, p > 0.05
	Conspecific demonstrators	Congeneric demonstrators	
S. fuscicollis observers	752	1303	z = -0.16, p > 0.05
S. labiatus observers	1021	361	z = -0.16, p > 0.05
	S. fuscicollis	*S. labiatus*	
Naive demonstrators	6026	4794	z = -0.17, p > 0.05
Observers	917	684	z = -0.29, p > 0.05
Observers from congeneric demonstrators	1303	361	z = -0.40, p > 0.05

within 15 cm of the apparatus (Table 1) and to touch the apparatus (Table 2) all followed a similar pattern to the latencies to obtain the food item, with the exception of an absence of a significant difference in the latency to touch the apparatus for inter-specific naïve demonstrators and observers (Table 2). To examine whether the tamarins actually learnt how to complete the task, the following inter-behaviour latencies were calculated: (a) the latency to approach within 15 cm of the apparatus was subtracted from that taken to touch the apparatus to give the approach-touch latency; (b) the latency to approach the apparatus was subtracted from the latency to obtain the food item to give the approach-obtain latency; and (c) the latency to touch the apparatus was subtracted from the latency to obtain the food item to give the touch-obtain latency.

It was found that, overall (pooling both species intra- and inter-specifically) observers were facilitated to obtain the food item once within proximity to the apparatus ($z = -2.26$, $p < 0.05$) and once having touched the apparatus ($z = -2.33$, $p < 0.05$). Latency to touch the apparatus once within proximity to it was not facilitated by observation ($z = -1.74$, $p > 0.05$; Figure 5).

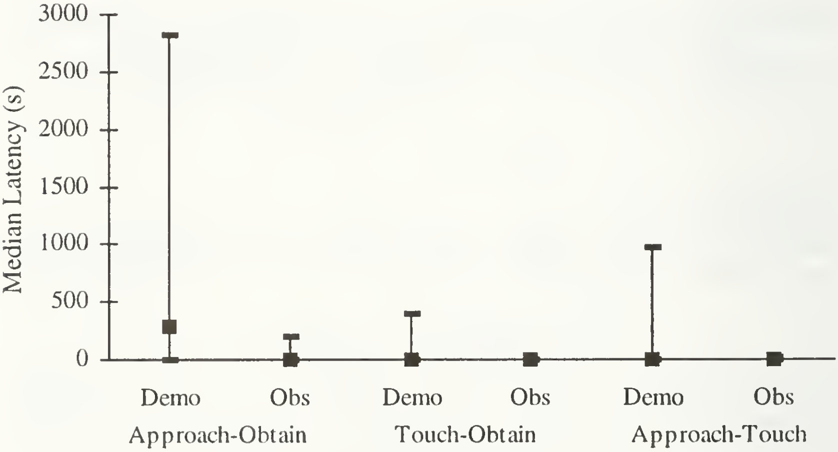

Figure 5. Median inter-behaviour latencies (between approach to obtain, touch to obtain and approach to touch) (with interquartile ranges) for naive demonstrators (demo) and observers (Obs), pooling intra- and inter-specifically.

DISCUSSION

The aim of this study was to investigate whether observation of an experienced conspecific or congener has any influence on the rate at which an individual tamarin learns how to access food in a novel food task. The opportunity to observe an experienced individual clearly did lead to faster successful completion of the task than did asocial learning. Such a facilitatory effect may have considerable adaptive value in wild tamarin troops, in that individuals can benefit by learning about their changing environment more quickly, through observation of experienced troop members, than by asocial learning alone. *Saguinus* inhabit tropical rain-forests. These are generally characterised by high species diversity but low species density (Milton, 1988) and thus it is probable that foraging individuals will come across potentially exploitable but novel food resources. In addition, each new generation is likely to come into contact with foods not previously encountered. If learning how to exploit these resources can be facilitated by observation, then social learning will be an adaptive strategy in enabling the rapid, effective and safe exploitation of the novel food resources, possibly at reduced energy cost and predation risk. Rapid exploitation of fruit resources requiring the grasping strategy may be important for *Saguinus* as they are especially vulnerable on the thin, terminal branches of tree crowns, particularly to their main predators, raptors (Peres, 1993). Provided species can learn from each other, association, through an increase in troop size, would increase the opportunity for information transfer between individuals accordingly. Social learning of this kind may be particularly important for the younger members of the troop who, in their naive immaturity, face a host of new environmental challenges for which the need to rapidly acquire the behavioural solutions necessary for survival may be particularly acute (Galef, 1976).

With regards to the adaptivity of mixed-species troops per se, neither species showed a significant difference in their latency to complete the task after having observed a conspecific demonstrator as opposed to a congeneric demonstrator. This is perhaps surprising given that, in all mixed-species troops studied to date, inter-specific social interactions are rare in comparison to intra-specific ones (Pook and Pook, 1982 for *S. fuscicollis* and *S. labiatus*; Norconk, 1986; Heymann, 1990 for *S. fuscicollis* and *S. mystax*). Those inter-specific interactions that do occur are most often agonistic and associated with the exploitation of monopolisable plant food resources. This lack of an effect for demonstrator species may simply be an indication of the considerable cohesion, integration and tolerance of tamarin mixed-species troops in the wild and in captivity. It is reported that more affiliative inter-specific interactions occur in captivity (e.g., grooming and social play: Heymann and Sicchar-Valdez, 1988; Heymann *et al.*, 1996; Hardie, 1997). Certainly both species of observer in this study spent brief but frequent periods of time intently observing their demonstrators behaviour at the apparatus, regardless of their species. Being able to learn from congeners as well as conspecifics may lead to an additional advantage to mixed-species troops over single-species troops, in that individuals can benefit from an increased knowledge base (i.e., the species-specific experience of their own species and that of their congeners). This possibility is important for tamarins given that, in all mixed-species troops studied thus far, there is vertical stratification between the associating species (with *S. fuscicollis* occupying a lower height than their congeners: Yoneda, 1981; Pook and Pook, 1982; Terborgh, 1983; Norconk, 1986; Buchanan-Smith, 1990) and thus the potential for differential knowledge regarding separate forest strata.

In this experiment, in addition to the absence of an effect for demonstrator species, there were no differences between species in their rates of learning, either as naive demonstrators or observers. Thus it cannot be concluded that mixed-species troops confer any additional advantage above that which would be accrued in monospecific troops of the same size. In any case, in the wild, large monospecific troops may be unattainable due to feeding competition and intra-sexual conflict between reproductive competitors (Buchanan-Smith and Hardie, 1997). Moreover, since there were no differences between the species in their rates of learning, and since *S. labiatus* having observed *S. fuscicollis* were no faster to complete the task than were *S. fuscicollis* after observing *S. labiatus*, the advantage accrued to each species from observing appears symmetrical.

Although we wished to concentrate upon the adaptive function of the monkeys' learning, in the context of mixed-species association, rather than the means by which it was achieved, we can speculate upon the mechanism at work. Identification of a mechanism is important in order to further our understanding of comparative primate intelligence. We are faced with the difficult task of sorting out a variety of processes occurring in social situations which can influence an observer's behaviour and lead to similar behaviours in the observer and observed. Our problem is thus one of exclusion of alternative mechanisms, an especially difficult problem given that there is no uniformly accepted classification of social learning mechanisms at present (e.g., Galef, 1988; Whiten and Ham, 1992; Heyes, 1993, 1994).

Since the observers did not have the opportunity to interact with the stimulus at the same time as the demonstrators, we can discard social facilitation (an indiscriminate increase in general activity as a result of observation: Zajonc, 1965) as a potential mechanism. Furthermore, in separating the demonstrator's apparatus from that of the observer by the use of duplicate cages we controlled for local enhancement, whereby the demonstrator's behaviour increases the probability that the observer will attend to the locale with which the demonstrator interacted (Thorpe, 1963). Instead, we need be concerned with four types of social learning, namely stimulus enhancement (Spence, 1937), imitation (Thorndike, 1898; Morgan 1900), goal emulation (Tomasello, 1990; Whiten and Ham, 1992), and response facilitation (Byrne, 1994).

For our purposes, stimulus enhancement refers to the demonstrator's behaviour increasing the probability that the observer will attend to/interact with stimuli of the same physical type as those with which the demonstrator interacted. Imitation refers to cases in which, as a result of observation, the observer acquires a novel behaviour from the repertoire of the demonstrator. Goal emulation refers to the observer duplicating the results of the demonstrator's behaviour (the goal) but not its methods. Response facilitation refers to the increased probability of the observer performing a particular behaviour (already in its repertoire) as a result of observing the demonstrator performing the same behaviour.

Since observers were facilitated to approach the apparatus, and to touch it once in proximity to it, one mechanism at work here appears to be stimulus enhancement, whereby the observer completes the task by simple trial and error learning but learns from the demonstrator to direct its appetitive actions towards the apparatus. However, since the categories of social learning are not mutually exclusive it is possible, in principle, that the demonstrator played several roles simultaneously. Thus the possibility remains that, through its behaviour at the string, the demonstrator increased the probability that the observer would interact with the apparatus (stimulus enhancement), and furthermore, may have acted as a model regarding the actions necessary to obtain the food item (imitation). Unfortunately, in recording simply the latency to perform the various behavioural components necessary to succeed on the task, we are ill-prepared to confirm the presence of imitation. As described by Whiten and Ham (1992) for the observer-demonstrator paradigm used here, "while speed of learning can be easily and objectively measured, it is insufficient to discriminate between stimulus enhancement and imitation" (p. 242). In order to distinguish explicitly between these two categories of social learning, one must use a 'two-action method' (Dawson and Foss, 1965), where there are two possible ways in which to complete the experimental task and one looks to see if the observers tend to complete the task using the method which their demonstrators used, in preference to the alternative method. Using this technique, Bugnyar and Huber (1997) have found common marmosets (*Callithrix jacchus*) able to imitate their conspecifics either pushing or pulling a pendulum door to open a wooden box (or at least 'mimic', excluding insight or any perception or understanding of how the copied behaviour is designed to bring about the goal). The task we are concerned with here could be completed successfully in one way only and so cannot provide evidence for imitation. Furthermore, because of an absence of data on differences in action pattern, we are also unable to draw any conclusions regards goal emulation.

With regard to our remaining mechanism, response facilitation, it is interesting to note that, although observers were facilitated to approach and to touch the string, they were also facilitated to complete the task once having done so. This suggests that they learned something about the actions necessary to succeed on the task and obtain the food item, apart from any intrinsic orienteering to the stimulus. So, in addition to having their attention and subsequent manipulations directed to the apparatus, the observers were also selectively enhanced to apply particular matching behaviours already in their repertoire (response facilitation) to solve the problem rapidly, giving the impression of imitation. Byrne (1995) writes that such a combination of stimulus enhancement and response facilitation is a powerful one, quite apart from the possibility of goal emulation.

We appear, then, to have an ecologically-orientated example of stimulus enhancement and response facilitation in two species of *Saguinus*. In past experiments, captive monkeys have often failed to show forms of social learning such as these (see Whiten and Ham, 1992: Table IV). The slow rate of learning described in previous captive studies may reflect irrelevance of the testing environment to the monkeys natural habitat, pronounced hierarchical differences among dyads, or may be a result of traditional fixed-trial procedures which allow only limited periods of interaction between individuals. In the field, where animals have the freedom to interact continuously, learning processes may be much more rapid (Galef, 1976).

Other reports of rapid learning exist for captive *Saguinus*. Hardie (1995) found that, after a single trial, troops of *S. fuscicollis* and *S. labiatus* respond differentially to objects paired with food and those not paired with food. Furthermore, this information could be retained for a period of at least 7 weeks and could be transferred between the species. Similar swift learning was again demonstrated in an eight-member family of *S. fuscicollis* (Menzel and Juno, 1982, 1984) who, on a single exposure to objects associated with food, increased their frequency of approach to those objects on the next trial. Such rapid learning in tamarins may reflect species-specific propensities for particular kinds of learning or learning capacity in relation to social structure (Goodall, 1973; Itani and Nishimura, 1973; Cambefort, 1981), social dynamics (Coussi-Korbel and Fragaszy, 1995), or to the distribution pattern of major food resources (Milton, 1988). For example, Coussi-Korbel and Fragaszy (1995) suggest that, squirrel monkeys (*Saimiri at al.*) would be less likely than tamarins to acquire information from one-another about the non-social environment, because, owing to competing attentional demands arising from a modest hierarchical organisation, they are less likely to focus their attention upon one-another for more than brief moments. This brings us back to the proposition that the transmission of information through ongoing behaviour will be greater in species exhibiting a high degree of tolerance and co-ordination in time and space. These are characteristics of both single and mixed-species tamarin troops.

Tamarins spend a great deal of their time foraging for food (*S. fuscicollis,* for example, are reported to spend around 60 % of their daily activity period foraging for plant food and insects: Soini, 1987; Terborgh, 1983). The identification and acquisition of food is likely to constitute one of their greatest environmental challenges. Foraging in a cohesive troop can, through social learning, convey important information about the availability, location, stimulus characteristics and method of acquisition of food to individual members. Mixed-species troop formation, by increasing troop size, is likely to facilitate the transfer of socially learned foraging information accordingly.

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REFERENCES

Adams-Curtis, L.E., & Fragaszy, D.M. (1995). Influence of a skilled model on the behaviour of conspecific observers in tufted capuchin monkeys (*Cebus apella*). *American Journal of Primatology, 37,* 65-71.

Beauchamp, G., & Kacelnik, A. (1991). Effects of the knowledge of partners on learning rates in zebra finches *Taeniopygia guttata. Animal Behaviour, 41,* 247-253.

Buchanan-Smith, H.M. (1989). The social organisation and mating system of the red bellied tamarins (*Saguinus labiatus labiatus*); Behavioural observations in captivity and in the wild. Unpublished Ph.D. thesis, University of Reading, Reading.

Buchanan-Smith, H.M. (1990). Polyspecific association of two tamarin species, *Saguinus labiatus* and *Saguinus fuscicollis*, in Bolivia. *American Journal of Primatology, 22,* 205-214.

Buchanan-Smith, H.M. (1991). Encounters between neighbouring groups of tamarins in northern Bolivia. *Primate Report, 31,* 95-99.

Buchanan-Smith, H.M. (1999). Tamarin polyspecific associations: Forest utilisation and stability of mixed-species groups. *Primates, 40,* 233-247.

Buchanan-Smith, H.M., & Hardie, S.M. (1997). Tamarin mixed-species groups: An evaluation of a combined captive and field approach. *Folia Primatologica, 68,* 272-286.

Bugnyar, T., & Huber, L. (1997). Push or pull: an experimental study on imitation in marmosets. Animal Behaviour, 54, 817-831.

Byrne, R.W. (1994). The evolution of intelligence. In P.J.B Slater & T.R. Halliday (Eds.), *Behaviour and Evolution* (pp. 223-265). Cambridge: Cambridge University Press.

Byrne, R.W. (1995). *The Thinking Ape: Evolutionary origins of intelligence.* Oxford: Oxford University Press.

Caine, N.G. (1993). Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: the role of predation pressures. In Rylands, A.B. (Ed.), *Marmosets and Tamarins: Systematics, behaviour, and ecology* (pp. 200-219) Oxford: Oxford University Press.

Caine, N.G., & Stevens, C. (1990). Evidence for a 'monitoring' call in captive red-bellied tamarins. *American Journal of Primatology, 22,* 251-262.

Caine, N.G., Addington, R.L., & Windfelder, T.L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour, 50,* 53-60.

Cambefort, J.P. (1981). Comparative study of culturally transmitted patterns of feeding habits in the Chacma baboon (*Papio ursinus*) and the vervet monkey (*Cercopithecus aethiops*). *Folia Primatologica, 36,* 243-263.

Castro, R., & Soini, P. (1977). Field studies on *Saguinus mystax* and other callitrichids Amazonian Peru. In D.G. Kleiman (Ed.), *Biology and Conservation of the Callitrichidae* (pp.73-78). Washington D.C.: Smithsonian Institution Press.

Coates, A., & Poole, T.B. (1983). The behaviour of the callitrichid monkey, *Saguinus labiatus*, in the laboratory. *International Journal of Primatology, 4,* 339-371.

Coussi-Korbel, S., & Fragaszy, D.M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour, 50,* 1441-1453.

Dawson, B.V., & Foss, B.M. (1965). Observational learning in budgerigars. *Animal Behaviour, 13,* 470-474.

Fragaszy, D.M., & Visalberghi, E. (1990). Social processes affecting the appearance of innovative behaviours in capuchin monkeys. *Folia Primatologica, 54,* 155-165.

Galef, B.G. (1976). Social transmission of acquired behavior: a discussion of tradition and social learning in vertebrates. In J.S. Rosenblatt, R.A. Hinde, E. Shaw & C. Beer (Eds.), *Advances in the Study of Behavior, Vol. 6.* (pp. 77-100). New York: Academic Press.

Galef, B.G. (1988). Imitation in animals: history, definition and interpretation of data from the psychological laboratory. In T.R. Zentall & B.G. Galef (Eds.), *Social Learning: Psychological and biological perspectives* (pp. 3-28). Hillsdale, New Jersey: Erlbaum.

Garber, P.A. (1986). The ecology of seed dispersal in two species of callitrichid primates (*Saguinus mystax* and *S. fuscicollis*). *American Journal of Primatology, 10,* 155-170.

Garber, P.A. (1987). Foraging strategies among living primates. *Annual Review of Anthropology, 16,* 339-364.

Garber, P.A. (1988a). Foraging decisions during nectar feeding by tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichidae, Primates) in Amazonian Peru. *Biotropica, 20,* 100-106.

Garber, P.A. (1988b). Diet, foraging patterns, and resource defense in a mixed species troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. *Behaviour, 105,* 18-34.

Garber, P.A. (1993). Seasonal patterns of diet and ranging in two species of tamarin monkeys: stability versus variability. *International Journal of Primatology, 14,* 145-166.

Giraldeau, L.A., & Lefebvre, L. (1987). Scrounging prevents cultural transmission of food-finding behaviour in pigeons. *Animal Behaviour, 35,* 387-394.

Goldizen, A.W. (1987). Tamarins and marmosets: communal care of offspring. In Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., & Struhsaker, T.T. (Eds.), *Primate Societies* (pp. 34-43). Chicago: University of Chicago Press.

Goldizen, A.W. (1989). Social relationships in a cooperatively polyandrous group of tamarins (*Saguinus fuscicollis*). *Behavioural Ecology and Sociobiology, 24,* 79-89.

Goodall, J. (1973). Cultural elements in a chimpanzee community. In W. Montagna (Ed.), *Precultural Primate Behavior: Symposium of the Fourth International Congress of Primatology* (pp. 144-184). Basel: Karger.

Hardie, S.M. (1995). The behaviour of mixed-species tamarin groups (*Saguinus labiatus* and *Saguinus fuscicollis*). Unpublished Ph.D. thesis, University of Stirling, Stirling.

Hardie, S.M. (1997). Exhibiting mixed-species groups of sympatric tamarins (*Saguinus* spp.) at Belfast Zoo. *International Zoo Yearbook, 35,* 261-266.

Hardie, S.M. (1998). Mixed-species tamarin groups (*Saguinus fuscicollis* and *Saguinus labiatus*) in northern Bolivia. *Primate Report, 50,* 39-62.

Hershkovitz, P. (1977). *Living New World Monkeys (Platyrrhini), Vol 1.* Chicago: University of Chicago Press.

Heymann, E.W. (1987). A field observation of predation on a moustached tamarin (*S. mystax*) by an anaconda. *International Journal of Primatology, 8,* 193-195.

Heymann, E.W. (1990). Interspecific relations in a mixed-species troop of moustached tamarins, *Saguinus mystax*, and saddle-back tamarins, *Saguinus fuscicollis* (Primates: Callitrichidae), at the Rio Blanco, Peruvian Amazonia. *American Journal of Primatology, 21,* 115-127.

Heymann, E.W. (1997). The relationship between body-size and mixed-species troops of tamarins (*Saguinus* spp.). *Folia Primatologica, 68,* 287-296.

Heymann, E.W., & Sicchar-Valdez, L.A. (1988). Interspecific social grooming in a mixed troop of tamarins, *S. mystax* and *S. fuscicollis* (Platyrrhini: Callitrichidae), in an outdoor enclosure. *Folia Primatologica, 50,* 221-225.

Heymann, E.W., Sicchar V., L.A., & Tapia, R.J. (1996). Experiences with mixed-species housing of tamarins, *S. fuscicollis* and *S. mystax* (Primates: Callitrichidae), in an outdoor enclosure. *Zoologischer Garten NF, 66,* 381-390.

Heyes, C.M. (1993). Imitation, culture and cognition. *Animal Behaviour, 46,* 999-1000.

Heyes, C.M. (1994). Social learning in animals: categories and mechanisms. *Biological Review, 69,* 207-231.

Itani, J., & Nishimura, A. (1973). The study of infra-human culture in Japan. In W. Montagna (Ed.), *Precultural Primate Behavior: Symposium of the Fourth International Congress of Primatology* (pp. 26-50). Basel: Karger.

Klein, L.L., & Klein, D.J. (1973). Observations of two types of Neotropical primate intertaxa associations. *American Journal of Physical Anthropology, 38,* 649-654.

Krebs, J.R. (1973). Social learning and the significance of mixed-species flocks of chickadees (*Parus* spp.). *Canadian Journal of Zoology, 51,* 1275-1288.

Laland, K.N., Richerson, P.J. & Boyd, R. (1993). Animal social learning: towards a new theoretical approach. In P.P.G. Bateson, P.H. Klopfer & N.S. Thompson (Eds.), *Perspectives in Ethology, Vol. 10* (pp. 249-277). New York: Plenum Press.

Mayer, K.E., Blum, C.A, & Caine, N.G. (1992). Comparative foraging styles of tamarins and squirrel monkeys. *American Journal of Primatology, 27,* 46. (Abstract).

Menzel, E.W., & Juno, C. (1982). Marmosets (*Saguinus fuscicollis*): Are learning sets learned? *Science, 217,* 750-752.

Menzel, E.W., & Juno, C. (1984). Are learning sets learned? Or: Perhaps no nature-nurture issue has any simple answer. *Animal Learning and Behaviour, 12,* 111-115.

Milton, K. (1988). Foraging behaviour and the evolution of primate intelligence. In R.W. Byrne & A. Whiten (Eds.), *Machiavellian Intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans* (pp. 285-305). Oxford: Oxford University Press.

Moody, M.F., & Menzel, E.W. (1976). Vocal communication in marmosets (*Saguinus fuscicollis*). *Folia Primatologica, 25,* 73-94.

Morgan, C.L. (1900). *Animal Behaviour.* London: Edward Arnold.

Noldus (1993). *The Observer: System for collection and analysis of observational data.* Wageningen, Netherlands: Noldus Information Technology b.v.

Norconk, M.A. (1986). Interactions between primate species in a neotropical forest: mixed species troops of *Saguinus mystax* and *S. fuscicollis* (Callitrichidae). Unpublished Ph.D. thesis, University of California, Los Angeles.

Norconk, M.A. (1990). Mechanisms promoting stability in mixed *Saguinus mystax* and *S. fuscicollis* troops. *American Journal of Primatology, 21,* 129-146.

Peres, C.A. (1991). Ecology of mixed species groups of tamarins in Amazonian terra firme forests. Unpublished Ph.D. thesis, University of Cambridge, Cambridge.

Peres, C.A. (1992a). Consequences of joint-territoriality in a mixed-species group of tamarin monkeys. *Behaviour, 123,* 220-246.

Peres, C.A. (1992b). Prey-capture benefits in a mixed-species group of Amazonian tamarins, *Saguinus fuscicollis* and *S. mystax. Behavioural Ecology and*

Sociobiology, 31, 339-347.

Peres, C.A. (1993). Anti-predator benefits in a mixed-species group of Amazonian tamarins. *Folia Primatologica, 61*, 61-76.

Peres, C.A. (1996). Food patch structure and plant resource partitioning in interspecific associations of Amazonian tamarins. *International Journal of Primatology, 17*, 695-723.

Pook, A.G., & Pook, G. (1982). Polyspecific association between *Saguinus fuscicollis*, *Saguinus labiatus*, *Callimico goeldii*, and other primates in north-western Bolivia. *Folia Primatologica, 38*, 196-216.

Ramirez, M. (1989). Feeding ecology and demography of the moustached tamarin, *Saguinus mystax*, in northeastern Peru. Unpublished Ph.D. thesis, City University of New York, New York.

Rubenstein, D.I., Barnett, R.J., Ridgley, R.S., & Klopfer, P.H. (1977). Adaptive advantages of mixed-species feeding flocks among seed-eating finches in Costa Rica. *Ibis, 119*, 10-21.

Snowdon, C.T., & Soini, P. (1988). The tamarins, genus *Saguinus*. In R.A. Mittermeier, A.B. Rylands, A. Coimbra-Filho, & G.A.B. Fonesca. (Eds.), *Ecology and Behavior of Neotropical Primates, Vol 2.* (pp. 223-298). Washington D.C: WWF.

Soini, P. (1987). Ecology of the saddle-back tamarin, *Saguinus fuscicollis illigeri* on the Rio Pacaya, northeastern Peru. *Folia Primatologica, 49*, 11-32.

Spence, K.W. (1937). Experimental studies of learning and higher mental processes in infra-human primates. *Psychological Bulletin, 34*, 806-850.

Terborgh, J. (1983). *Five New World Primates: A study in comparative ecology.* Princeton, New Jersey: Princeton University Press.

Thorndike, E.L. (1898). Animal intelligence: An experimental study of the associative process in animals. *Psychological Review Monograph, 2* (Suppl. 4), 1-109.

Thorpe, W.H. (1963). *Learning and Instinct in Animals.* London: Methuen.

Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signalling of chimpanzees? In S.T Parker & K.R.G. Gibson (Eds.), *"Language" and Intelligence in Monkeys and Apes: Comparative developmental perspectives* (pp. 274-311). Cambridge: Cambridge University Press.

Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. In P.J.B. Slater, J.S. Rosenblatt, C. Beer & M. Milinski (Eds.), *Advances in the Study of Behavior, Vol. 21* (pp. 239-283). New York: Academic Press.

Weigel, P.D., & Hanson, E.V. (1980). Observational learning and the feeding behavior of the red squirrel *Tamiasciurus hudsonicus*: the ontogeny of optimisation. *Ecology, 61*, 213-218.

Windfelder, T.L. (1997). Polyspecific association and inter-specific communication between two Neotropical primates: Saddle-back tamarins (*Saguinus fuscicollis*) and emperor tamarins (*Saguinus imperator*). Unpublished Ph.D. thesis, Duke University, Durham.

Yoneda, M. (1981). Ecological studies of *Saguinus fuscicollis* and *S. labiatus* with reference to habitat segregation and height preference. *Kyoto University Overseas Research Report of New World Monkeys, 2*, 43-50.

Yoneda, M. (1984a). Comparative studies on vertical separation, foraging behavior and travelling mode of saddle-backed tamarins (*Saguinus fuscicollis*) and red-chested moustached tamarins (*Saguinus labiatus*) in Northern Bolivia. *Primates, 25*, 414-422.

Yoneda, M. (1984b). Ecological study of the saddle backed tamarin (*Saguinus fuscicollis*) in northern Bolivia. *Primates, 25,* 1-12.

Zajonc, R.B. (1965). Social facilitation. *Science, 149*, 269-274.

Zentall, T.R., & Galef, B.G. (1988). *Social Learning*. Hillsdale, New Jersey: Erlbaum.