RESPONSES OF COTTON-TOP TAMARINS *(SAGUINUS OEDIPUS)* TO FAECAL SCENTS OF PREDATORS AND NON-PREDATORS

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Abstract

The responses of 56 cotton-top tamarin monkeys (Saguinus oedipus) *to the faecal scent of predators and non-predators were recorded to determine if there was a differential response. Methylene chloride extracts were prepared from the faeces of suspected predators (margay and tayra) and non-predators (capybara and paca) known to co-exist with the tamarins in the wild. The faecal extracts were presented to the tamarins on wooden dowels in their enclosures. Untreated dowel and dowel treated with methylene chloride served as controls. The tamarins exhibited high anxiety responses to predator scent compared to non-predator scent which produced low anxiety responses. No sex differences were found but an age difference was apparent: younger individuals were more curious than their elders. The response pattern was observed in captive-born individuals and was not affected by whether or not their parents were wild-caught or captive-born. This indicates that the discrimination of predator and non-predator scents is innate. However, this should not be taken to mean that captive cotton-top tamarins should be re-introduced to the wild without prior predator avoidance training. The implication of this study for animal welfare is that in captive environments where both predator and prey species are kept, it is important that predators, and their faeces, are not situated where prey species can detect their presence through olfaction, because prey species may suffer continual levels of heightened anxiety with possible detrimental effects.*

Keywords: *animal welfare, Callitrichidae, cotton-top tamarins, faecal scents, predators*

Introduction

The hazards of predation are often considered to be one of the major ecological influences of group size in primates. Anti-predator behaviour differs widely and depends on a number of factors such as predator species and its hunting strategy, in addition to the size, strength and defensive abilities of prey and its temporal and spatial grouping (Cheney & Wrangham 1987). Some species of primates, such as baboons, *Papio cynocephalus,* use aggressive defence against predators (Altmann & Altmann 1970) while others, such as pottos, *Perodicticus potto*, have evolved tactics of vigilance and evasion (Charles-Dominique 1977).

There are few reports of successful predation of the marmoset and tamarin monkeys, Callitrichidae (Moynihan 1970, Hershkovitz 1977, Emmons 1987, Heymann 1987) because there have been relatively few field studies and detailed observations are often difficult where small monkeys live in dense forest. However, the paucity of data should not lead us to conclude that predation is rare. Even if it is, the predation risk may still play a part in moulding the behavioural strategies of the animals concerned. In view of their small size, callitrichids do seem to be potentially vulnerable to a wide range of predators, such as birds, reptiles and mammals (Hershkovitz 1977, Izawa 1978, Neyman 1978, Dawson 1979, Terborgh 1983, Emmons 1987, Heymann 1987, 1990, Buchanan-Smith 1990, Ferrari & Lopes Ferrari 1990). An estimation of predation rates indicates that over 15 per cent of saddle-back tamarin (*Saguinus fuscicollis)* and emperor tamarin (*S. imperator)* populations may be preyed upon each year, which puts them amongst the primates with the highest estimated predation rates (Cheney & Wrangham 1987). Such selection pressure has led to the evolution of behaviours in callitrichids which are thought to have anti-predatory significance, such as visual monitoring of threatening objects (Caine 1986), choice and use of sleeping sites (Dawson 1979, Ferrari & Lopes Ferrari 1990) and polyspecific associations (Terborgh 1983, Buchanan-Smith 1990).

Mobbing has been reported in some callitrichids (Buchanan-Smith 1990, Ferrari & Lopes Ferrari 1990). In the presence of tayras (*Eira barbara*), mixed species troops of red-bellied tamarin (*S. labiatus)* and saddle-back tamarin jointly mobbed the predators. On two separate occasions with different mixed species troops of tamarins, adults of both species approached and retreated from the two tayras. They alarm vocalized continually and did not leave the area until the tayras had left (Buchanan-Smith 1990). Similarly, buffy-headed marmosets (*Callithrix flaviceps*) are reported to approach terrestrial predators *en masse* in order to mob them (Ferrari & Lopez Ferrari 1990).

However, while in some cases mobbing may occur, it seems that many anti-predator strategies are predominantly adapted to avoiding rather than challenging predators. For instance, buffy-headed marmosets tend to be more vigilant at higher levels in the forest and when leaf cover is less extensive, which is likely to be related to the potential hazards of aerial predation (Ferrari & Lopes Ferrari 1990). A number of researchers have reported that callitrichids show typical avoidance responses to raccoons, *Procyon cancrivorus* (Ferrari 1988), coatimundis, *Nasua nasua* (Rylands 1982) and tufted capuchins, *Cebus apella* (Neyman 1978, Pook & Pook 1982, Soini 1988).

The responses of tamarins to predator-related objects and cues have been investigated in the laboratory. A recent study examined the responses of pairs of cotton-top tamarins (*S. oedipus*) to a live boa constrictor, a rat, leaves, artificial flowers, and an empty box (Hayes & Snowdon 1990). The results show that captive cotton-top tamarins do not demonstrate an alarm response which is specific to the boa constrictor, but that they may simply display fear of moving objects.

Caine and Weldon (1989) investigated the responses of the red-bellied tamarin to faecal odours of neo-tropical predators and non-predators. Olfaction is an important means of communication in callitrichids (Epple 1986) and the ability to detect the presence of predators through olfactory cues could have an important evolutionary advantage. Indeed, many prey species have been reported to elicit a fear response to predator smells (Stoddart 1982, Sullivan *et al* 1985a,b).

The study reported here extends that of Caine and Weldon (1989) using a different primate species, the cotton-top tamarin. Following Caine and Weldon's (1989) findings, we predicted that a) cotton-top tamarins would respond differentially to predator and non-predator scents; and b) there would be no difference between groups containing wild-caught individuals and groups which were all born in captivity, as previous experience with predator scents is unnecessary to elicit the response.

Methods

Subjects

The subjects were 56 cotton-top tamarins belonging to six nuclear families, each consisting of a single breeding male and female and their offspring (Table 1).

Table 1 **Details of tamarin group composition.**

		Family name					
	Sex	**Elsa**	**Genevieve**	**Jille**	**Roxanne**	**Delaware**	**Hopi**
Parent	*M*	1[a]	1	1	1[a]	1	1
	F	1[a]	1	1	1[a]	1	1
Adult	*M*	3	2	0	2	1	2
	F	2	4	0	1	5	2
Subadult	*M*	0	0	0	0	2	1
	F	2	1	0	1	0	0
Juvenile	*M*	2	0	1	1	0	2
	F	0	1	1	1	0	0
Infant	*M*	[2][b]	1	0	0	0	0
	F		0	0	2	1	0
No independent group members		11	11	4	10	11	9

[a] wild-caught

[ ][b] not independent group members, sex unknown

Family sizes ranged from 4-11 individuals - infants which were not moving independently were excluded. The groups resembled wild groups in both size and age-sex composition (Price & McGrew 1990). The parents of two of the families (Roxanne's and Elsa's) were wild-born but imported before the UK ratified the Convention on International Trade in Endangered Species (CITES) in 1976. All other monkeys were captive-born. Age classes followed Cleveland and Snowdon (1984) and were calculated from the start of the study on 1 July 1990. The tamarins were identified by coloured disks on necklaces or by the presence or absence of picric acid (a yellow dye) on the crests of young monkeys.

Housing

All the family groups lived in the Primate Unit of the Department of Psychology, University of Stirling. Four of the groups (Roxanne's, Elsa's, Genevieve's and Delaware's) each occupied a home room (mean dimensions 3.45m x 3.54m x 2.91m high). The other two groups (Jille's and Hopi's) lived in two-cage units (each unit was 1.19m x 1.68m x 1.97m high) in a colony room. The groups were kept in visual and tactile isolation, but could hear and smell each other. Natural light entered the rooms at all times, and additional lighting came from fluorescent strip lights operated by automatic time switches, which allowed the seasonal changes found in the species' natural environment to be simulated. Temperature was maintained between 20-25°C and relative humidity was kept between 40-60 per cent. Each enclosure had a wide variety of natural branches and other furnishings including nest boxes, and a layer of wood shavings covered the floor. The tamarins were fed a mixed diet of commercially prepared and fresh food. Price and McGrew (1990) provide further details of housing and diet.

It is important to note that rodents were not present in the Primate Unit at Stirling University, nor were the tamarins fed with young mice. Hence, any response to rodent odour is not likely to be related to familiarity or exposure to similar scents.

Procedure

Fresh faecal samples were obtained from animals in zoological gardens, and were kept frozen until extraction. The two predator species used were margay *(Felis wiedi)* and tayra (*Eira barbara;* Mustelidae). Both these species are forest dwellers and excellent climbers of trees (Walker 1983, Macdonald 1984). The margay is a carnivore and the tayra an omnivore. The two non-predator species used were paca *(Agouti paca)* and capybara *(Hydrochaeris hydrochaeris)*, both of which are herbivorous rodents.

Using the technique reported by Caine and Weldon (1989) faecal extract solutions were prepared by rinsing the faeces with HPLC grade methylene chloride (CH_2Cl_2); 20ml per 10g of faecal material. The slurry was filtered under vacuum and the resulting solution kept in an air-tight container. Hence the faecal extracts presented to the tamarins were not at any stage evaporated which would have removed the volatile chemicals.

Wooden dowels (0.5cm x 60cm) were used as the medium for presentation of the scents. Untreated dowels and dowels treated with methylene chloride alone served as controls for each group. Treated dowels had 3ml of the solution under test pipetted on to them. This amount was chosen since it covered the dowel adequately. The dowel was left to air dry for five minutes before being introduced to the tamarins' enclosure. The dowel was affixed to the wire mesh at the front of the enclosure, at a height of 1 metre. The position of the dowel was kept constant between presentations, and as far as possible between groups. The location of the dowel had two advantages. Firstly, the tamarins had to face the observer when investigating the dowel and hence their identification by colour of tag on their necklace was easy. Secondly, the dowel's location was rarely otherwise visited by the tamarins, so that when they did, it was likely to be in order to investigate the dowel.

Before each observation session, the observers sat outside the tamarin enclosure for five minutes to allow the tamarins to adjust to their presence. At the end of this time, a technician entered the tamarin enclosure and attached the dowel as quickly as possible and with the least possible fuss. Data collection started as soon as the technician had left the enclosure and the responses of the tamarins to the dowel were recorded continuously for the next 30 minutes. The dowel was removed from the enclosure when data collection was finished.

The scents were presented at the same time of day within groups to provide consistency between presentations. No testing was done just before or after feeding. At least one day elapsed between presentations for each group. Each group was tested four times, first with untreated wooden dowel, second with wooden dowel treated with 3ml methylene chloride, and the third and fourth presentations were either with 3ml of predator scent or with 3ml of non-predator scent. Three of the groups received the predator scent third and the non-predator scent fourth, and the other three groups had the order of the predator and non-predator scents reversed (Table 2). The two controls were presented first in order to reduce the effects of novel visual cues and the novelty of the presence of methylene chloride. Each time a dowel was used for a test it was discarded, ie a fresh dowel was used for each test for each group.

The observers practised blind testing to remove experimenter bias, so that they were not aware whether the predator or non-predator scent was being presented.

Focal object observation was employed: the observers watched the dowel and recorded the individual identity and behaviour of each monkey approaching and interacting with the dowel. An extended initial pilot study using three of the groups (Jille's, Genevieve's and Elsa's), indicated which behavioural measures were most appropriate to record. The behavioural measures were chosen to separate curious and anxious responses to the scent (Table 3). The *'bite/touch', 'headcock stare'* and *'sniff'* responses were considered curiosity related behaviours. While performing these behaviours, the tamarins showed no intention to avoid the dowel, indeed in some instances they were recorded as engaging in object play with it. The *'approach dowel and withdraw'* and *'sniff and run'* measures were classed as anxiety responses; the tamarins were extremely alert and immediately left the vicinity of the dowel. The frequency of these behaviours, and the identity of the monkeys performing them, were recorded on to checksheets.

The observers were DAA and CWR. The average inter-observer reliability (Martin & Bateson 1986), calculated using the Pearson product moment correlation coefficient, was 0.95.

Table 2 Order of presentation of dowells.

Group	Presentation 1	Presentation 2	Presentation 3	Presentation 4
Elsa's *Genevieve's* *Jille's*	Untreated dowel	Dowel treated with methylene chloride	Capybara (non-predator)	Tayra (predator)
Roxanne's *Delaware's* *Hopi's*	Untreated dowel	Dowel treated with methylene chloride	Margay (predator)	Paca (non-predator)

Table 3 Definitions of behavioural measures.

Behavioural measure	Definition	Behavioural category
Bite/touch	Manipulation of the dowel with hands or mouth	Curious
Headcock stare	Cocking of head from side to side while looking at the dowel (after Menzel 1980)	Curious
Sniff	As in colloquial use, tamarin sniffed the dowel, and did not immediately retreat	Curious
Approach dowel and withdraw	Tamarin approached to within 1m of dowel, with apparent intent of investigating it, but withdrew before investigating it	Anxious
Sniff and run	Brief sniff of dowel followed by immediate and rapid retreat	Anxious

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The data were analysed using the ALICE computer package specialized for analysis of variance. Individual scores for each behavioural measure and observational session were calculated. The dependent measures *'bite/touch'*, *'headcock stare'* and *'approach dowel and withdraw'* were subjected to a within-subjects design, with the variable 'Presentation' having four levels (experimental Presentations 1-4, see Table 2). The *'sniff and run'* and *'sniff'* categories were seen as being the main indicators of anxiety and curiosity respectively, and a mixed design, three-way analysis of variance with parent type (wild or captive-born), sex and presentation as variables was carried out. When a significant F ratio emerged, Neuman-Keuls post-hoc tests were conducted to identify the source of the effect (Winer 1962). Significance levels were set at $P<0.05$ unless otherwise stated.

Results

There were qualitative differences in the tamarins' responses to the dowel between presentations. When exposed to the predator scented dowel, the tamarins would approach the dowel and then immediately and rapidly retreat, occasionally sniffing it briefly before they retreated. The tamarins' investigations in control presentations and non-predator scent presentations typically involved biting, headcocking and sniffing without immediate retreat. Tamarins carrying a new-born infant did not approach the dowel but on several occasions passed the infant to another and then immediately moved to inspect the dowel. It appeared that the carrying of infants constrained adults' investigation of the dowel.

The tamarins performed significantly more *'bite/touch'* behaviour [$F(3,56) = 10.86$, $P<0.001$] where the dowel was untreated (Condition 1) than in the other three conditions (Figure 1). This may have been a novelty effect, as the untreated dowel was the first condition. No significant effect was found for the *'headcock stare'* data (Figure 2).

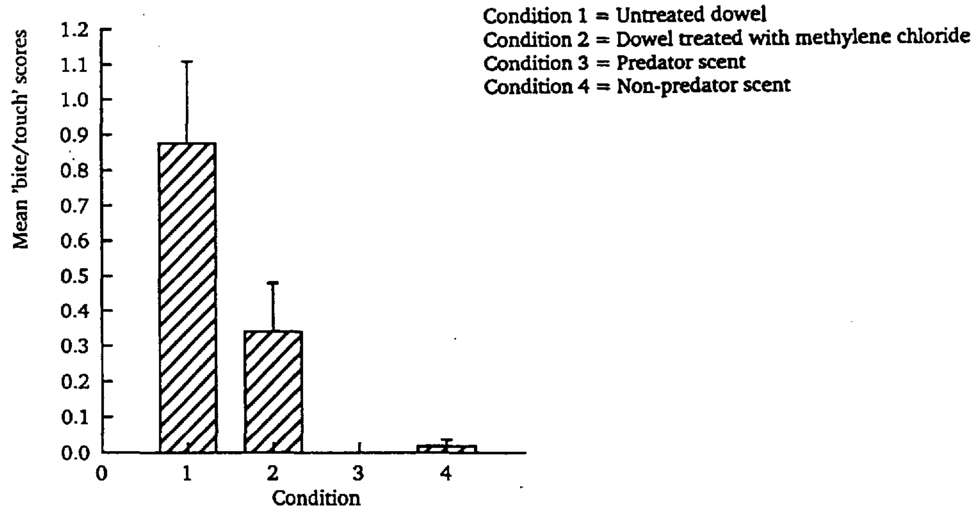

Figure 1 Mean individual scores (with standard error bars) for *'bite/touch'* behaviour across conditions.

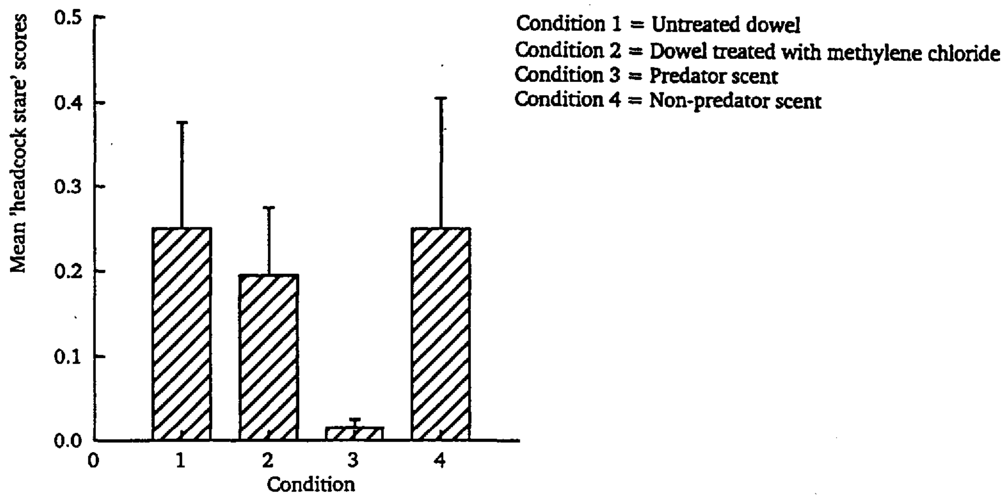

Figure 2 **Mean individual scores (with standard error bars) for *'headcock stare'* behaviour across conditions.**

The tamarins approached and withdrew from the dowel significantly more [F(3,165) = 4.81, $P<0.01$] in the predator condition than in all other conditions (Figure 3). A similar pattern was found for the other anxious behavioural category *'sniff and run'* [F(3,132) = 13.80, $P<0.001$] which occurred more in the predator condition than in all others (Figure 4). This behavioural measure was unaffected by the sex or type of parent.

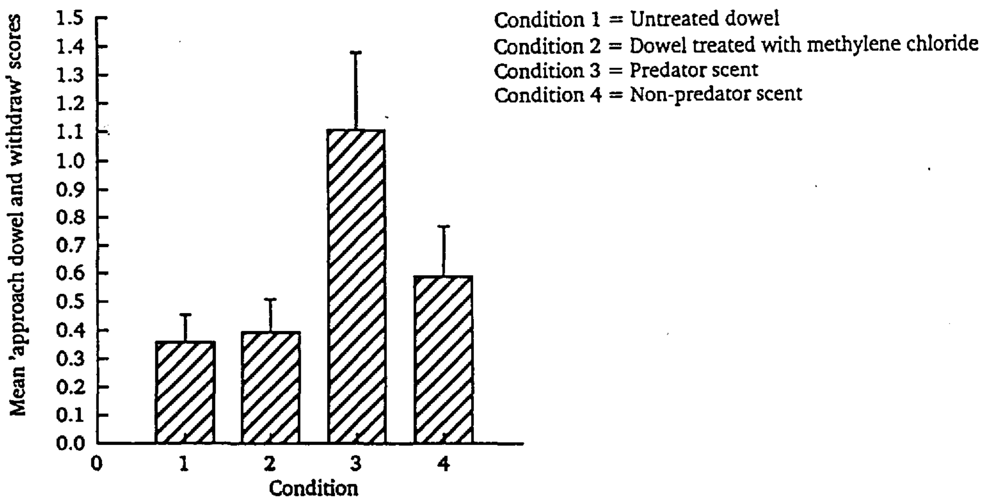

Figure 3 **Mean individual scores (with standard error bars) for *'approach dowel and withdraw'* behaviour across conditions.**

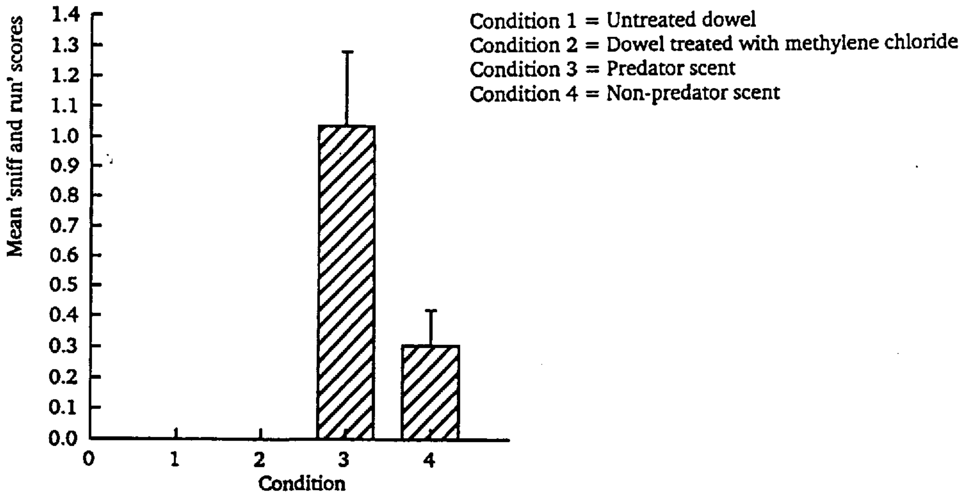

Figure 4 **Mean individual scores (with standard error bars) for *'sniff and run'* behaviour across conditions.**

The *'sniff'* data provided the reverse pattern to the *'sniff and run'* data [F(3,132) = 2.68, $P<0.05$]. The tamarins sniffed the dowel without retreating, more in the non-predator condition than in the other conditions (Figure 5). No significant effect of sex or parent type was found for this behavioural measure.

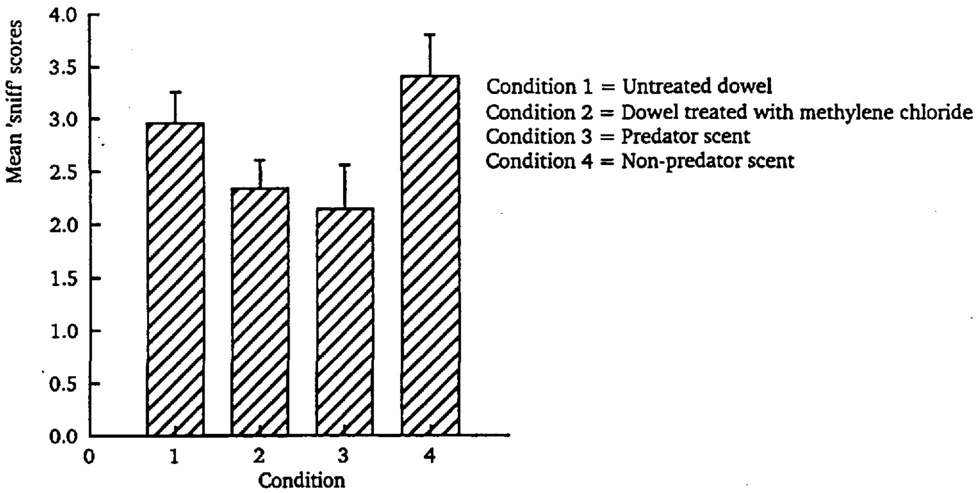

Figure 5 **Mean individual scores (with standard error bars) for *'sniff'* behaviour across conditions.**

As each behavioural measure was judged to be either anxious or curious in nature, it was possible to create general indices of anxious and curious responses. This was done by summing individual scores for the predator and non-predator conditions in the *'bite/touch', 'headcock stare'* and *'sniff'* categories and adding these totals to form an index of curiosity. Similarly, an index of anxiety was calculated using the *'approach dowel and withdraw'* and *'sniff and run'* results. These indices indicate that low anxiety investigation occurred in the non-predator condition. Contrasted with this there was relatively high anxiety related behaviour recorded in the predator condition (Figure 6). While the index for curiosity was higher in the non-predator condition than the predator condition, the difference is not as marked as for the anxiety index.

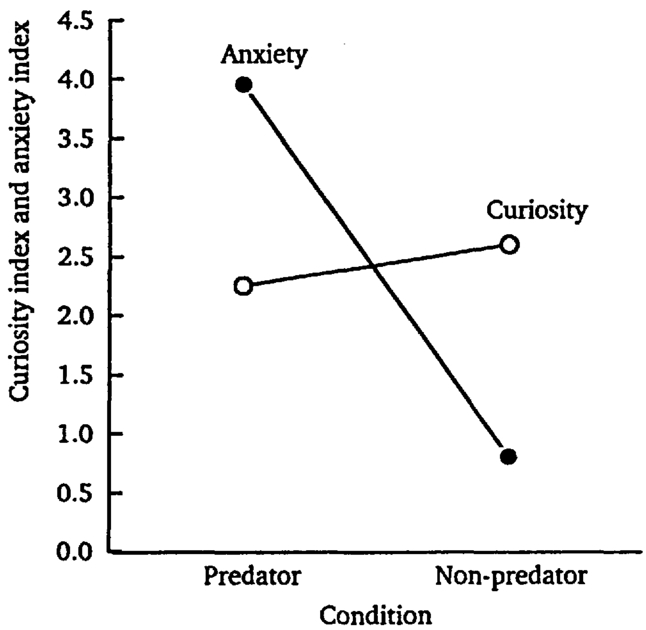

Figure 6 **Graph to illustrate the relationship between curiosity and anxiety in response to predator and non-predator scents.**

The data were further analysed by calculating a curiosity and an anxiety index for each individual tamarin, by combining the condition scores for these behavioural categories. The relationship of group size to these indices were investigated using the Pearson product moment correlation coefficient. No effect for group size was found for either the curious or anxious index. A similar correlation was performed for age (in absolute terms rather than in age categories) and this produced a significant negative correlation with curiosity [$r(54)$ = -0.4480] but no significant value was obtained with anxiety related responses.

Discussion

It is important for tamarins to avoid predators if they are to survive the reportedly high predation attempts (Hershkovitz 1977, Izawa 1978, Neyman 1978, Dawson 1979, Cheney & Wrangham 1987, Emmons 1987, Heymann 1987, 1990, Buchanan-Smith 1990, Ferrari & Lopes Ferrari 1990), and there could be an evolutionary advantage if the predator's presence could be identified and avoided by signs such as faecal deposits. If wild callitrichids are able to get forewarning of predator presence they may be more vigilant and avoid successful predation. These results suggest that this may occur. The overall findings of this experiment confirm our two main predictions. Firstly, the tamarins responded differentially to predator and non-predator scent. They showed high anxiety responses to predator scent and low anxiety responses to non-predator scent. Curiosity related behaviours were also slightly higher for the non-predator condition than the predator condition. Secondly, there was no significant difference between groups which had wild-caught parents and those with parents which had been born in captivity. Together, these findings suggest that the ability to discriminate predator scents from other scents is innate. This finding is in agreement with those of Caine and Weldon (1989) where red-bellied tamarins are reported to produce anxious behaviours in response to predator scents.

The tactile investigation reflected in the *'bite/touch'* data was observed most frequently in the first condition when the untreated dowel was initially presented. This indicates that these behaviours are directly concerned with the physical novelty of an object. In contrast, no significant differences were found for the *'headcock stare'* data. This finding was unexpected since this behaviour is considered to be related to unfamiliar visual stimuli (Menzel 1980) and we expected it to decrease as the tamarins became familiar with the dowel over the four conditions.

There was no effect of group size. Overall the individual tamarins in larger groups investigated the dowel about the same amount as those in smaller groups. This is in agreement with Caine's (1986) findings that the average number of vigilance checks per individual to novel objects by the red-bellied tamarin was stable between groups of different sizes. The adaptive significance of larger group size generally emphasizes the increased predator detection through an increase in the number of eyes and ears. The present findings indicate that individuals in larger groups have the benefit of more group members' active investigation of novel or threatening stimuli.

The present study found that younger group members were more likely to show curiosity towards the stimuli. Other studies which have looked at responses of primates to novel stimuli, have shown that younger animals are more likely to move towards and investigate novel objects (Menzel 1965, Bertrand 1969). However, Millar *et al* (1988) found that older offspring contacted novel objects sooner and for longer than parents and younger offspring. The apparent conflict between the results of Millar *et al* (1988) and those reported here may be explained by the fact that Millar *et al* did not make the distinction between curious and anxious responses. While they judged the objects which they presented to the callitrichids in their study to be non-threatening, it seems likely that initial presentations of these objects were threatening as the monkeys performed behaviours such as piloerection, tail-raised present and frowning to the objects. Millar *et al* reported that after repeated presentations of the objects the younger offspring spent longer investigating them. Had curious and anxious behaviours been separated, then a relationship between age and curiosity might have been found, in line with the present findings.

No sex differences were found, which is in agreement with other studies of the responses of callitrichid groups to novel objects (eg Millar *et al* 1988). Male and female tamarins are morphologically very similar and few behavioural sex differences have been reported that are not directly related to reproduction.

In any study which examines the responses of individuals in groups to novel stimuli, there is a possibility that observational learning affects group members' responses. That is, it is possible that group members are influenced by the first tamarin which approached the dowel, and they may respond in a similar fashion. The effect of observational learning was not investigated in the present study. If observational learning does occur, it is as likely to apply to wild groups of tamarins as to captive animals. It may be that the success of a female golden lion tamarin in one of the re-introduction projects (Beck cited in Hayes & Snowdon 1990) was the result of her pairing up with a wild male who served as a native guide for foraging and predator avoidance.

The findings of the present study need to be followed up. A number of interesting questions arise as to whether the responses of the tamarins would be different to predators which co-exist with the tamarins in the wild and those which do not co-exist with the tamarins. It may be that the responses are not specific, but rather the tamarins may respond anxiously to any carnivore faecal odour. Pilot data have been collected on the responses of the cotton-top tamarins to coatimundi faecal scent. The coatimundi is not known to prey on tamarins, however its diet does consist of both animal and vegetable material. The cotton-tops showed responses indicative of curiosity rather than anxiety to this faecal odour, which suggests that it may not be the carnivorous tendencies, but rather the predatory tendencies of the animals that correspond with the anxious response.

However, as they stand, the findings of this experiment do have two general practical implications. In the wild, the anxiety responses are likely to result in avoidance of the scent's location. This suggestion is supported by a range of field and semi-field studies on other species. Boonsta *et al* (1982) demonstrated that shrew odour depressed the trappability of voles, and a similar study showed reduced capture rates of short-tailed voles exposed to weasel odour (Stoddart 1982). It may be that the anxiety responses found in the laboratory resulted from the tamarins' inability to leave the area with the threatening scent. This prediction could be tested in captivity by giving the tamarins an alternative enclosure to flee to. In captive environments such as zoological gardens, where both predator and prey species are kept, it is important that predators and their faeces are not situated where prey species can detect their presence through olfaction. If this is not done, prey species may suffer continual levels of heightened anxiety with possible detrimental effects, such as impaired breeding or reduced life span. There is the possibility (unproven) that prey species in these sorts of situations may habituate to predator scent.

The second practical implication of these findings has some bearing on the conservation of the cotton-top tamarin. Habitat destruction and capture of wild cotton-top tamarins has led to their classification as an endangered species (International Union for Conservation of Nature and Natural Resources 1981), and re-introduction programmes of captive tamarins are one method of attempting to preserve species in the wild (Kleiman *et al* 1986). Price *et al* (1989) have assessed the competence of captive-bred cotton-top tamarins when faced with a naturalistic environment in the grounds of the Jersey Wildlife Preservation Trust. Work such as this can be complemented by studies in captivity, where research can ascertain what forms of behaviour needed for life in the wild are instinctive and which have to be learned. Our results indicate that the discrimination between non-predator and predator scent in this species is innate, although this should not be taken to mean that captive cotton-top tamarins should be re-introduced to the wild without any prior predator avoidance training.

Animal welfare implications

In captive environments such as zoological gardens, where both predator and prey species are kept, predators and their faeces should not be situated where prey species can detect their presence through olfaction. The findings also have implications for any re-introduction programmes of cotton-top tamarins to their natural environment and demonstrate that it is important to ascertain what forms of behaviour needed for life in the wild are instinctive, together with those which need inculcation before release. The present findings, however, should not be taken to mean that captive cotton-top tamarins should be re-introduced to the wild without prior predator avoidance training.

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References

Altmann S A and Altmann J 1970 *Baboon Ecology*. University of Chicago Press: Chicago

Bertrand M 1969 The behavioral repertoire of the stump-tailed macaque. *Bibliotheca Primatology 2:* 1-273

Boonsta R, Rodd F and Carlton D J 1982 Effect of *Blarina brevicauda* on trap response of *Microtus pennsylvanicus*. *Canadian Journal of Zoology 60:* 438-442

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

Caine N G 1986 Visual monitoring of threatening objects by captive tamarins *(Saguinus labiatus). American Journal of Primatology 10:* 1-8

Caine N G and Weldon P J 1989 Responses of red-bellied tamarins *(Saguinus labiatus)* to fecal scents of predatory and non-predatory neotropical mammals. *Biotropica 21:* 186-189

Charles-Dominique P 1977 *Ecology and Behaviour of Nocturnal Prosimians.* Duckworth: London

Cheney D L and Wrangham R W 1987 Predation. In Smuts B B, Cheney D L, Seyfarth R M, Wrangham R W and Struhsaker T T (eds) *Primate Societies* pp227-239. University of Chicago Press: Chicago

Cleveland J and Snowdon C T 1984 Social development during the first 20 weeks in the cotton-top tamarin (*Saguinus o. oedipus*). *Animal Behaviour 32:* 432-444

Dawson G A 1979 The use of time and space by the Panamanian tamarin *(Saguinus geoffroyi). Folia Primatologica 31:* 253-284

Emmons L H 1987 Comparative feeding ecology of felids in a neotropical rain forest. *Behavioral Ecology and Sociobiology 20:* 271-283

Epple G 1986 Communication by chemical signals. In Mitchell G and Erwin J (eds) *Comparative Primate Biology, Volume 2A: Behavior, Conservation and Ecology* pp 531-580. Liss Inc: New York

Ferrari S F 1988 *The behaviour and ecology of the buffy-headed marmoset,* Callithrix flaviceps *(O Thomas, 1903).* Unpublished PhD thesis, University College: London

Ferrari S F and Lopes Ferrari M A 1990 Predator avoidance behaviour in the buffy-headed marmoset, *Callithrix flaviceps. Primates 31:* 323-338

Hayes S L and Snowdon C T 1990 Predator recognition in cotton-top tamarins (*Saguinus oedipus*). *American Journal of Primatology 20:* 283-291

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

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

Heymann E W 1990 Reactions of wild tamarins *Saguinus mystax* and *Saguinus fuscicollis* to avian predators. *International Journal of Primatology 11:* 327-337

International Union for Conservation of Nature and Natural Resources 1981 *Red Data Book Vol 1 Mammalia.* Morges: Switzerland

Izawa K 1978 A field study of the ecology and behaviour of the black-mantled tamarin (*Saguinus nigricollis*). *Primates 19:* 241-274

Kleiman D G, Beck B B, Dietz J M, Dietz L A, Ballou J D and Coimbra-Filho A F 1986 Conservation program for the golden lion tamarin: captive research and management, ecological studies, education strategies, and reintroduction. In Benirschke K (ed) *Primates. The road to self-sustaining populations* pp959-979. Springer Verlag: New York

Macdonald D 1984 *The Encyclopaedia of Mammals*. Allen and Unwin: London

Martin P and Bateson P 1986 *Measuring Behaviour - an Introductory Guide*. Cambridge University Press: Cambridge

Menzel E W 1965 Responsiveness to objects in free ranging Japanese monkeys. *Behaviour 26:* 130-150

Menzel C R 1980 Headcocking and visual perception in primates. *Animal Behaviour 28:* 151-159

Millar S K, Evans S and Chamove A S 1988 Older offspring contact novel objects soonest in callitrichid families. *Biology of Behavior 13:* 82-96

Moynihan M 1970 Some behavior patterns of Platyrrhine monkeys, II, *Saguinus geoffroyi* and some other tamarins. *Smithsonian Contributions to Zoology 28:* 1-77

Neyman P F 1978 Aspects of the ecology and social organisation of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In Kleiman D G (ed) *The Biology and Conservation of the Callitrichidae* pp39-71. Smithsonian Institution Press: Washington D C

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

Price E and McGrew W C 1990 Cotton-top tamarins in a semi-naturalistic colony. *American Journal of Primatology 20:* 1-12

Price E C, Feistner A T C, Carroll B and Young J A 1989 Establishment of a free-ranging group of cotton-top tamarins, *Saguinus oedipus* at the Jersey Wildlife Preservation Trust. *Dodo, Journal of the Jersey Wildlife Preservation Trust 26:* 60-69

Rylands A B 1982 The behaviour and ecology of three species of marmosets and tamarins (Callitrichidae, Primates) in Brazil. *Unpublished PhD thesis, University of Cambridge*

Soini P 1988 The pygmy marmosets, genus *Cebuella*. In Mittermeier R A, Rylands AB, Coimbra-Filho A F and Bouchardet Da Fonseca G A (eds) *Ecology and behavior of neotropical primates, Volume 2* pp79-129. World Wildlife Fund: Washington D C

Stoddart D M 1982 Does trap odour influence estimation of population size of the short-tailed vole, *Microtus agrestis? Journal of Animal Ecology 51:* 375-386

Sullivan T P, Nordstrom L O and Sullivan D S 1985a Use of predator odors as repellants to reduce feeding damage by herbivores. I Snowshoe hares (*Lepus americanus*). *Journal of Chemical Ecology 11:* 903-920

Sullivan T P, Nordstom L O and Sullivan D S 1985b Use of predator odors as repellants to reduce feeding damage by herbivores. II Black-tailed deer (*Odocoileus hemionus columbianus*). *Journal of Chemical Ecology 11:* 921-935

Terborgh J 1983 *Five New World Primates: a Study of Comparative Ecology.* Princeton University Press: Princeton, New Jersey

Walker E P 1983 *Walker's Animals of the World.* The John Hopkins University Press: Baltimore

Winer B J 1962 *Statistical Principles in Experimental Design.* McGraw-Hill Book Co: New York