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Predator Avoidance Behaviour in the Buffy-headed Marmoset, *Callithrix flaviceps*

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ABSTRACT. The predator avoidance behaviour of a free-ranging group of buffy-headed marmosets, *Callithrix flaviceps*, was recorded in detail during the course of a long-term study of behavioural ecology at the Fazenda Montes Claros, southeastern Brazil. Four distinct patterns of predator avoidance behaviour, each with specific vocalisations, were recognised and are described here. The selection and use of sleeping sites by the study group are also described. An analysis of the records indicates that these small monkeys are generally most vulnerable to predation by aerial raptors. Variations in the frequency of alarm calls also indicate that the marmosets tend to be more vigilant at higher levels in the forest and when the leaf cover is less extensive. The implications of group size and social structure for both the evolution and the efficacy of the anti-predator behaviour of marmosets are also discussed.

Key Words: Callitrichids; *Callithrix flaviceps*; Behaviour; Predator avoidance.

INTRODUCTION

With average adult body weights ranging from 119 g to 710 g (MITTERMEIER et al., 1988), the marmosets and tamarins of the family Callitrichidae are vulnerable to a wide range of potential predators, and it appears that predation pressure has had a fundamental influence on most aspects of the behavioural evolution of these small, cryptic monkeys, including their vocalisations and habitat preferences (SUSSMAN & KINZEY, 1984). In spite of such adaptations, the tamarins *Saguinus fuscicollis* and *Saguinus imperator* were found to suffer the highest estimated rates of predation in a recent survey of the data available for 20 primate species (CHENEY & WRANGHAM, 1987). The available data appear to indicate that many other callitrichid species suffer similarly high rates of predation, although with one exception, successful attacks by predators have only been recorded for *Saguinus*. While this is undoubtedly a result of the comparatively large body of data available for this genus, there may be systematic differences in the vulnerability of the different callitrichid genera to predation.

Identified predators of callitrichids include hawks (*Micrastur ruficollis*: IZAWA, 1978; *Micrastur semitorquatus*: ALONSO & LANGGUTH, 1989; *Spizaetus ornatus*: DAWSON, 1976; GOLDIZEN, 1987; *Spizaetus tyrannus*: DAWSON, 1976), ocelots (*Felis pardalis*: GOLDIZEN, 1987), and anacondas (*Eunectes murinus*: HEYMANN, 1987), and a tayra, *Eira barbara*, has been observed carrying a dead tamarin in its mouth (MOYNIHAN, 1970). In addition to a variety of snakes and birds of prey, a number of other potential predators have been observed eliciting typical avoidance responses in callitrichids, including tufted capuchins, *Cebus apella* (HLADIK & HLADIK, 1969; NEYMAN, 1978; POOK & POOK, 1982; SOINI, 1988), raccoons, *Procyon cancrivorus* (Ferrari, 1988), and coatimundis, *Nasua nasua* (Rylands, 1982), along with birds such as vultures (Cathartidae) and toucans (*Ramphastos* spp.).

Despite these reports, and the apparent importance of predation pressure for callitrichid evolution, only very general accounts of anti-predator behaviour are available for most species (but see Caine, 1984, 1986, 1987; Bartecki & Heymann, 1987; Caine & Marra, 1988). In this paper, detailed descriptions of the patterns of predator avoidance behaviour of the buffy-headed marmoset, *Callithrix flaviceps*, are presented and the records of these patterns collected during a long-term field study are analysed. In addition to characterising patterns of behaviour which appear to be common to most marmosets, if not all callitrichid species, the results of this study also provide some insights into the relative vulnerability of these primates to predators of different types, and in different habitats. The importance of group size and structure for predator avoidance are also discussed.

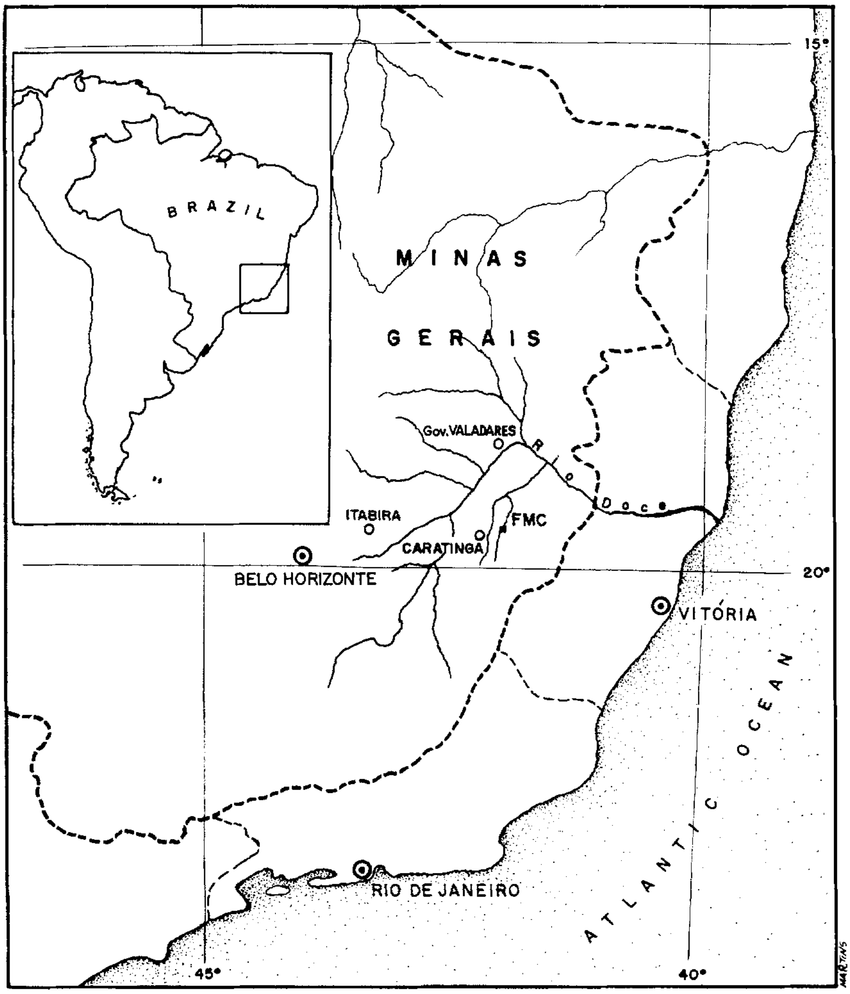

Fig. 1. Map showing the location of the study site at the Fazenda Montes Claros (FMC) in south-eastern Brazil.

STUDY SITE AND METHODS

The data presented here were collected during a long-term study of the behaviour and ecology of *C. flaviceps* (Ferrari, 1988) carried out between December 1984 and October 1986 at the privately-owned reserve on the Fazenda Montes Claros, a remnant of the Atlantic Coast Forest in the municipality of Caratinga, Minas Gerais, southeastern Brazil (see Fig. 1). The 880 ha of the reserve encompass both relatively undisturbed and secondary forest habitats along with areas of scrub and bracken.

The main focus of the study was an habituated group containing between 11 and 15 individuals whose behaviour, including activity levels and ranging patterns, were recorded in detail using scan sampling (Altmann, 1974). Specific features of the group's behaviour, including vocal oı behavioural reactions to potential predators, were recorded in "all events" fashion. These records include events occurring during scan samples. As extremely close contact was maintained with the study group during scan sampling and as such behaviour invariably involves a vocal component, it seems likely that most, if not all events, would normally be recorded during observation periods and that these records represent a realistic estimate of the frequency with which such events occur.

The *C. flaviceps* study included the collection of data on plant phenology, based on the monthly observation of 1,302 marked trees in eight 25×25 m quadrats selected at random within the study group's home range. Leaf cover, measured as a percentage of the total crown volume of all marked trees in selected quadrats, was also monitored on a monthly basis (see Ferrari, 1988).

Descriptions of the characteristic patterns of behaviour, including vocalisations, associated with the avoidance of different types of predator are presented. The frequencies with which the different patterns were recorded during the 96 full observation days (i.e. when the group was followed from one day's sleeping site to the next) carried out during the ten months between November 1985 and August 1986 are also analysed.

RESULTS

While extremely attentive to their surroundings at all times, members of the *C. flaviceps* study group rarely exhibited the "visual scanning" behaviour reported for *Saguinus labiatus* (Caine, 1984), and usually only in response to disturbances, alarm calls or during the approach to a sleeping site (see below). Ferrari (1988) suggests that the typical "scan-and-pounce" foraging behaviour of these marmosets effectively combines the capture of prey with anti-predator vigilance. This may have important implications for the time-minimising foraging strategy of these small primates, given that others, such as *Cebus olivaceus*, may devote a significant proportion of their daily activity budget to scanning for predators (de Ruiter, 1986).

C. flaviceps exhibits two basic patterns of behaviour when reacting to potential predators of different types. Whereas the characteristic response to an aerial raptor is an "avoidance" pattern, the marmosets typically "mob" terrestrial predators. Both patterns have two distinct modes: a high-intensity response to an immediate danger and a low-intensity or "monitoring" type of behaviour which stimulates a general state of alertness in the group. The response also varies in accordance with both the type of predator and the context of the encounter. The intensity of the response to relatively harmless birds such as parrots or caciques, for example, often depends on the height at which they pass over the group. When such birds fly rapidly overhead at low levels, the marmosets frequently react decisively, although at other times these birds will normally only stimulate a "monitoring" response. The patterns, the contexts in which they are exhibited, and the frequencies with which they were recorded during the *C. flaviceps* study are described in detail below. The use of sleeping sites by the study group is also described.

Pattern 1a: Low-intensity Response to Potential Aerial Predators

Because of their ability to swoop down silently without alerting group members, aerial predators appear to represent the greatest danger to callitrichids, a danger which is reflected in both the number of reported captures by raptors and the vigilance behaviour of the primates themselves. Almost any object passing overhead will stimulate some response. *C. flaviceps* study group members would even react with alarm to large dead leaves, such as those of *Cecropia* spp. (Moraceae), falling from above. In both this and the majority of other cases of potential danger from aerial predators, the marmosets responded with the low-intensity, monitoring pattern of behaviour (Table 1).

The basic characteristic of this pattern is the [see] alarm call (STEVENSON & RYLANDS, 1988), a short, soft whistle normally given with the mouth closed. As a monitoring call, the [see] alerts other group members, which may often look upwards to scan for signs of danger (Fig. 2) and respond with similar calls, but does not usually stimulate any marked reaction in the group as a whole. Individual marmosets, especially the younger animals, will sometimes react with avoidance behaviour and freezing as in Pattern 1b, however, especially when finding themselves in relatively exposed positions in the upper canopy. The frequency of these alarm calls, which were recorded on average just over 11 times each day during the study, that is more than once per hour of activity, reflects the generally vigilant nature of the group.

Pattern 1b: High-intensity Response to Potential Aerial Predators

While most birds stimulate a low-intensity response when flying directly overhead, the marmosets appear to be able to recognise the characteristic flight profile of falconiforms, to which they normally react with a very different, "rapid avoidance" pattern of behaviour. The alarm call is a [seep], a much louder, more intense whistle given with the mouth half open (STEVENSON & RYLANDS, 1988). Other group members will also sometimes give [seeps] in response to this call, while immediately taking cover and freezing (remaining completely motionless). In taking cover at relatively low levels in the forest, the marmosets normally move to the underside of the supporting branch with a rapid lateral movement. When active

Table 1. Frequencies of predator avoidance behaviour patterns of different types recorded during the *Callithrix flaviceps* study.

	No. of events recorded		
Avoidance pattern	Total	Per observation day	Per hour of observation
Response to aerial predators			
1a. Low-intensity	1087	11.32	1.16
1b. High-intensity	33	0.34	0.04
Response to terrestrial predators			
2a. Low-intensity	47	0.49	0.05
2b. High-intensity	15	0.16	0.02

Fig. 2. "*Paxo*," a sub-adult male *C. flaviceps*, scanning for raptors in response to an alarm call.

at relatively high levels, especially in exposed tree crowns, they instinctively move downwards before freezing. On a number of occasions, *C. flaviceps* were observed leaping 10 m or more straight down into the dense vegetation of the lower canopy from the relatively bare, open crowns of *Anadenanthera peregrina* (Leguminosae: Mim.), which was a major source of gum for the study group. The freezing response seems to be instinctive, being a standard reaction to alarm calls in young marmosets almost as soon as they are able to move independently, i.e. at between 4 and 6 weeks of age.

In other situations, however, the marmosets did not react with alarm to the presence of birds of prey. On one occasion, an adult member of the study group was observed approaching to investigate an American kestrel (*Falco sparverius*) which had perched on a branch near the group. Similar behaviour has been recorded for *Saguinus oedipus* (NEYMAN, 1978), although RYLANDS (1982) reports that *Callithrix humeralifer* would mob forest hawks, such as *Micrastur*, when encountered sitting in the crowns of trees.

C. flaviceps also tolerated the presence of kites, *Ictinia plumbea* and *Leptodon cayanensis*, which were frequently observed in the vicinity of the study group during the early wet season months of October, November, and December, when large numbers of mature cicadas were emerging from their nymphal casts. Both kite species formed temporary associations with marmoset groups, systematically capturing the cicadas put to flight by the disturbance caused by their foraging activities (FERRARI, in press). Similar associations with raptors, in particular the double-toothed kite (*Harpagus bidentatus*), have been recorded for both *Cebus* and *Saimiri* (FONTAINE, 1980; TERBORGH, 1983; BOINSKI & SCOTT, 1988). While the marmosets would sometimes react with loud alarm calls when the kites flew low overhead, they generally ignored their presence during these periods.

The typical "rapid avoidance" pattern is not restricted solely to birds of prey, however. Almost any type of medium- to large-bodied bird (or bat) may stimulate this more intense reaction by appearing suddenly, either by passing overhead at a very low level or by flying out from a tree-top, often when disturbed by the marmosets themselves. In this context, the alarm calls and avoidance behaviour can be seen as a basic response to any immediate or potential danger appearing above the group. Such dangers are not necessarily airborne—a *C. humeralifer* group was observed responding in exactly this way to a tayra which appeared overhead in the crown of a tree (A. B. RYLANDS, pers. comm.), even though these marmosets normally mobbed this terrestrial predator as in Pattern 2b, below. *C. flaviceps* would also sometimes give [seep] alarm calls in response to the sudden appearance of large animals such as humans or domestic cattle in the open fields adjacent to their home range.

In general, this pattern of avoidance behaviour was observed relatively rarely during the *C. flaviceps* study, being recorded less than once per day, on average (see Table 1). The relative lack of records corresponds with the apparent frequency with which the group was threatened by the danger of an aerial attack. In contrast with the situation facing *Saguinus fuscicollis* in the Manu National Park, Peru, where "predation attempts by raptors occur about once per week per group" (GOLDIZEN, 1987), in fact, no obvious attack on the *C. flaviceps* group by an aerial predator was recorded in well over 1,500 contact hr. Whether this contrast corresponds with a significant difference in the numbers of raptors at the two sites is not clear, although it seems unlikely that the absence of attacks on the *C. flaviceps* group is due to a lack of potential predators. On the contrary, at least five different falconiform species are known to exist at Montes Claros and raptors were seen frequently within the home range of the study group, often within a short distance of the marmosets.

Pattern 2a: Low-intensity Response to Potential Terrestrial Predators

According to the behavioural record, the *C. flaviceps* study group appeared to encounter terrestrial predators far less frequently than potential raptors (Table 1). Rather than avoiding this type of predator, the marmosets usually approach en masse in order to mob the animal. Vocalisations are again an important, integral part of this type of behaviour. As for Pattern 1, in fact, the characteristic alarm calls were often the only component of this pattern recorded, especially in low-intensity encounters. The vocalisations associated with this type of predator avoidance behaviour are not only more varied than those which characterise the other three patterns, but also slightly less specific, being commonly heard in mildly alarming situations such as inter-group encounters.

The vocalisations which characterise this behaviour pattern are of a much lower frequency than the relatively high-pitched whistles given in response to aerial predators. Two of the calls, the [twitter] and the [tsak] are, however, made up of [seep]-like elements (STEVENSON & RYLANDS, 1988), normally given in a continuous, repeated sequence. The [tsak] is a more intense call than the [twitter] and, while normally given in combination with each other, the [tsak] is more commonly heard in an anti-predator context. The sequence of these calls is also frequently punctuated by the much lower frequency short calls [cough] and [ek]. Depending on the context, these calls may be given either by just one or two group members or by the group as a whole, particularly during the mobbing of snakes.

These vocalisations may be provoked by almost any relatively harmless terrestrial animal, such as rabbit-like tapitis (*Sylvilagus brasiliensis*) or teid lizards, and can again be seen as a form of "monitoring" behaviour. In this context, just one or a few of the marmosets will usually give the calls while visually monitoring the presence of the animal and there is very little reaction in other group members.

While again basically a monitoring pattern, the presence of a snake stimulates a very different type of behaviour. The whole group will approach, often to within 1 m, to watch the snake intently while giving relatively quiet alarm vocalisations. Similar snake-mobbing behaviour has been reported for *S. fuscicollis* (BARTECKI & HEYMANN, 1987). The marmosets were visibly nervous during such encounters and would rush rapidly away from the snake, usually upwards, at the slightest disturbance, a majority of which were caused by unexpected movements of the marmosets themselves. The *C. flaviceps* group would normally "mob" the snake in this way for between 5 and 15 min before continuing with its normal activities. While such encounters were recorded relatively rarely, it is interesting to note that the youngest marmosets invariably moved much closer to the snake than other group members and it seems that the young marmoset may learn to recognise this type of predator in the context of such encounters.

Pattern 2b: High-intensity Response to Potential Terrestrial Predators

The most obvious, and striking component of this pattern is again the characteristic alarm vocalisation. As for Pattern 2a, the basic element of the mobbing call is a repeated [tsak-tsak], although in this context the call is very much louder, given rapidly with the mouth wide open. In accordance with its function, which is to drive the predator away, this call might be best described as "piercingly" loud.

In encounters with terrestrial predators such as tayras, *E. barbara*, the whole group approaches to mob the animal, giving continuous loud [tsak] calls. On one occasion, the *C. flaviceps* group was observed mobbing a tayra, which it encountered in a dense tree crown at 12 m above the ground. The majority of the group members moved into the tree while giving the characteristic mobbing vocalisations. After approximately 10 min, the tayra came down to the ground and moved rapidly away, although the loud [tsak] calls continued sporadically for around 20 min after it had moved out of sight. In contrast with the mobbing of snakes, the youngest group members appeared to avoid contact with the predator. One 4-month-old infant, visibly disturbed, remained some 15 m from the tree in which the tayra was located throughout the mobbing incident.

On another occasion, the group members directed loud mobbing calls at a raccoon, *P. cancrivorus*, which appeared on the ground at the edge of the forest. Rather than being driven away, however, the raccoon appeared to be relatively unperturbed by the intensity of the calls, moving in the direction of the group and even climbing up into the trees. While the circumstances were very different from those which characterised their encounter with the tayra, it appears that the marmosets were actually avoiding the raccoon, rather than approaching to mob it.

Loud mobbing calls were also sometimes given, less systematically, by one or two group members in response to sudden movements either on the ground or low down in the forest.

Such disturbances would frequently cause the marmosets to rush upwards instinctively, much as they rush downwards in response to aerial predators.

USE OF SLEEPING SITES

In addition to the more direct patterns described above, the choice and use of sleeping sites by marmosets appear to be fundamental components of their anti-predator behaviour (MOYNIHAN, 1976; COIMBRA-FILHO, 1978; NEYMAN, 1978; DAWSON, 1979; LINDSAY, 1979; TERBORGH, 1983; CAINE, 1987). The sleep-trees utilised by the *C. flaviceps* study group varied in height from around 8 to more than 20 m and were typically both densely overgrown with climbers and relatively isolated from the surrounding vegetation. The latter characteristic presumably increases the probability of detecting the approach of a terrestrial predator. When retiring, the group members usually huddle together in a large ball which may serve to confuse possible predators by taking on the appearance of either a much larger animal or even a termite nest (DAWSON, 1979).

The number of different trees used by a marmoset group appears to vary systematically with both home range size and, presumably, the availability of suitable sites within that range. A *Callithrix jacchus* group occupying a range of 0.5 ha utilised the same sleeping site each night on 30 different occasions (STEVENSON & RYLANDS, 1988), while a second *C. jacchus* group had 15 different sleep-trees within its 4.98-ha home range (ALONSO & LANGGUTH, 1989). During a three-month study, a *Callithrix penicillata* group occupying a 10-ha range used 14 sites and the *C. humeralifer* study group utilised 46 sites within its 28-ha home range (STEVENSON & RYLANDS, 1988). Similarly, the *C. flaviceps* study group, which had a home range of 35.5 ha, was observed using 49 different sleep-trees. In addition to using a large number of different sites, the group normally never returned to a tree in which it had roosted during the previous night—in fact, it returned to a sleeping site on only one occasion in more than 150 full observation days.

This variation in the use of sleeping sites is reflected in the group's behaviour prior to retirement. While the marmosets invariably exhibit vigilance behaviour similar to that recorded for other callitrichids and approach the sleeping site with a characteristic silent, "creeping" style of locomotion, the type of route followed by the group differed considerably from one afternoon to the next. There are three basic types of approaches: (1) The direct approach: The group travels directly, and often rapidly, towards the sleep-tree, often from a late afternoon resting bout. (2) The "roundabout" approach: The group follows a highly variable, indirect path to the sleep-tree, frequently doubling-back on its route a number of times. Locomotion is typically slower than in the direct approach, with frequent halts during which the marmosets vigilantly scan the forest. (3) The "decoy" approach: Similar to the roundabout approach, except that the marmosets make use of "decoy" sleep-trees into which they ascend in the normal fashion, but descend again after a short period of time, varying between less than 1 min and more than 20 min. The *C. flaviceps* group visited six decoy trees at the end of one afternoon, before settling on a seventh. A. B. RYLANDS (pers. comm.) reports a similar pattern of behaviour for *C. humeralifer*.

As for the choice of sleeping site, the study group almost invariably followed a different type of approach, or variations on the same pattern, on consecutive afternoons. In addition, "sentinels," animals which remain behind to scan for predators while the group settles into the sleep-tree (see WOLTERS, 1978; LINDSAY, 1979; TERBORGH, 1983; CAINE, 1987), were often, but not invariably, deployed.

The descent from the sleep-tree in the morning varies very little from one day to the next, however. Once awake, the marmosets move rapidly away from the sleeping site before starting on their foraging activities.

The timing of both retirement and the descent from the sleep-tree in the morning also seems to be a functional component of the anti-predator behaviour of these animals. In addition to a degree of variation, like that in their approach to the sleep-tree, from one day to the next marmosets (and tamarins) both retire early and arise late, especially when compared with other small-bodied insectivorous platyrrhines such as *Saimiri* and *Cebus*. The *Callithrix flaviceps* group normally retired between 1 and 2 hr prior to dusk, and sometimes even earlier, while the descent from the sleep-tree normally begins between 10 and 30 min after full light.

Consistent with the time-minimising foraging strategy of these primates (FERRARI, 1988), the shortening of the daily activity period does not just maximise the time spent at rest, the most cryptic of activities, each day, but appears to further reduce the risk of both detection and capture by predators. In retiring well before dusk, the group guarantees an adequate period of daylight during which it can move to an alternative sleeping site if disturbed by a predator. Once they settle down for the night, however, the marmosets experience a condition of torpor during which body temperature may fall by as much as 4°C from daytime levels (MORRISON & SIMÕES, 1962; HETHERINGTON, 1978) and alertness is greatly reduced. The ability of marmosets to "hibernate" on a day-to-day basis in this way appears to make an important contribution to their time-minimising strategy by reducing energetic demands and, in turn, foraging requirements. It also seems likely that the animals will require a certain amount of time to come out of this state of torpor in the morning, especially if activity is triggered by the onset of daylight, and that they would be reluctant to abandon the relative safety of the sleep-tree until fully alert.

VARIATIONS IN THE FREQUENCY OF ANTI-PREDATOR BEHAVIOUR PATTERNS

While the frequency of anti-predator behaviour will obviously vary in accordance with the rate at which potential predators are encountered, other factors may be important. Predator detection rates may be higher in larger groups than in smaller ones (VAN SCHAIK et al., 1983), for example, while there is some evidence that primates are more likely to give alarm calls in the presence of close kin (CHENEY & SEYFARTH, 1985; CHENEY & WRANGHAM, 1987). These factors are not easily evaluated in the present study, however, given both that the size and composition of the study group were relatively stable and that the individual initiating anti-predator behaviour was only very rarely identified with any certainty. A detailed analysis of the records indicates, however, that the vigilance of the *C. flaviceps* group did fluctuate in relation to variables such as the availability of cover and activity levels.

For the analysis of seasonal differences, the records can be divided into a wet season (November to March) and a dry season (April to August) sample, each covering a total of 48 observation days. To allow for differences in the daily activity period, which averaged 10 hr 20 min during the wet season sample but only 9 hr 16 min in the dry season, the records are best compared as rates per hundred observation hours (Table 2).

Differences in the size and composition of the study group between the two sample periods were negligible, being less than one individual for any age/sex category. The group averaged 13.42 independent members per observation day during the wet season sample and 12.98

Table 2. Seasonal differences in the frequencies of predator avoidance behaviour patterns recorded during the *Callithrix flaviceps* study.

	Total number of records per pattern per observation day[1]			
Month/season	1a	1b	2a	2b
November	4.5	0.2	0.4	0.2
December	2.5	0.3	0.6	0.3
January	3.7	0.1	0.4	0.1
February	5.2	0.3	0.4	0.1
March	9.7	0.7	0.6	0.3
April	15.8	0.6	0.8	0.1
May	12.5	0.4	0.8	0.0
June	23.4	0.6	0.4	0.1
July	18.4	0.2	0.3	0.1
August	19.6	0.1	0.5	0.0
Wet season	5.2	0.3	0.4	0.3
(November to March)	(50.60)	(2.62)	(4.03)	(2.42)
Dry season	17.4	0.4	0.6	0.1
(April to August)	(187.87)	(4.49)	(6.07)	(0.67)

[1] Values in parentheses show the number of records collected per hundred hours of observation.

during that of the dry season, while the mean number of immatures in the group was 4.42 and 4.83, respectively. Similarly, there were four adult males in the group throughout the study period, while the mean number of adult females fell from 5 during the wet season to 4.15 during the dry. The available evidence also indicates a high degree of relatedness between all group members (FERRARI, 1988), while there were no immigrations during either sample period.

Other things being equal, then, it would seem reasonable to expect these behaviour patterns to have been recorded at relatively similar rates during the two sample periods. Despite the small number of records collected, this does appear to be the case for both the terrestrial predator and the high-intensity raptor patterns (Patterns 1b, 2a, and 2b, see Table 2). There is a major contrast in the number of records of the low-intensity raptor pattern, 1a, collected during the two samples, however. There is an almost fourfold increase in the number of records collected per hundred observation hours, from 50.60 during the wet season to 187.87 during the dry. While it seems likely that fluctuations in the rates of the other three patterns reflect the actual frequency of encounters with potential predators, which were rare overall, the marked and systematic increase in Pattern 1a appears to indicate that *C. flaviceps* group members were more than three times more vigilant, or more aware of the possibility of an aerial attack, during the dry season than they were during the wet season.

While the factors determining such an increase in this type of vigilance are not easily identified, there is little evidence to suggest that it was directly related to changes in the size or composition of the study group. Given that predation pressure may have had an important influence on the evolution of the typical callitrichid preference for low levels in the dense vegetation of disturbed forest habitats (SUSSMAN & KINZEY, 1984), it seems reasonable to assume that prevailing habitat conditions will have some influence on such behaviour. While there were no significant seasonal differences in the activity levels of the *C. flaviceps* study group, which spent two-thirds of its time at or below 5 m, the semi-deciduous secondary forest encompassed by its home range exhibited marked seasonal fluctuations in leaf cover (FERRARI, 1988). In general, leaf cover varied in accordance with rainfall levels and exhibited a sharp decline towards the end of the dry season (Fig. 3).

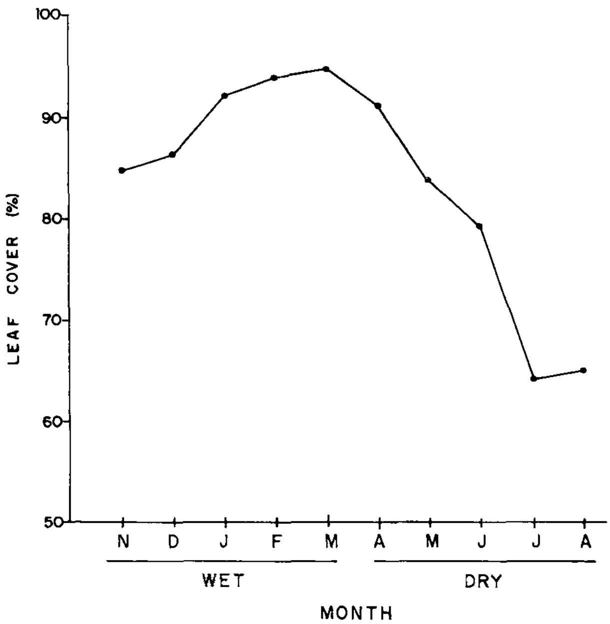

Fig. 3. Monthly variation in the leaf cover recorded in phenology quadrats between November 1985 and August 1986. Values are percentages of the total crown volume of all marked trees in the selected quadrats.

Table 3. Spearman rank correlation coefficients for comparisons of the daily rates of predator avoidance behaviour patterns exhibited by the *C. flaviceps* study group each month (November to August) with the percentage of leaf cover recorded in the phenology quadrats at the study site.

Pattern	r_s	p	N
1a	−0.576	<0.05	10
1b	0.506	>0.05	10
2a	0.454	>0.05	10
2b	0.529	>0.05	10

A comparison of the daily rates of Pattern 1a recorded each month with leaf cover, according to monthly measures recorded in the phenology quadrats at the study site, reveals a significant negative correlation (Table 3). This appears to support the hypothesis that the availability of leaf cover had some influence on the monitoring or vigilance behaviour of the study group in terms of the possibility of an aerial attack. In contrast, the remaining three behaviour patterns exhibit weak positive correlations with leaf cover, a trend which is probably far from meaningful, given the small numbers of records involved and the large proportion of tied scores. If anything, these results re-emphasize the idea that the frequency of this behaviour is predominantly related to predator encounter rates.

In addition to seasonal fluctuations, anti-predator behaviour was recorded at widely differing rates at different times of day (Table 4). All four patterns tended to be recorded more frequently during the early part of the day, and relatively rarely towards the end. If it is assumed that the rates of the three rarest patterns (1b, 2a, & 2b) are again closely related to those of predator encounters, it may be significant that the marmosets themselves tend to

Table 4. Frequencies of predator avoidance behaviour patterns recorded at different times of day during the *C. flaviceps* study.

Time	Mean activity level (m)	Mean number of events recorded per hour per pattern			
		1a	1b	2a	2b
06:00–06:55	7.56	1.51	0.06	0.09	0.03
07:00–07:55	6.58	1.50	0.06	0.06	0.01
08:00–08:55	5.46	1.77	0.05	0.08	0.01
09:00–09:55	4.84	1.58	0.10	0.02	0.03
10:00–10:55	4.19	1.26	0.03	0.03	0.07
11:00–11:55	4.02	1.03	0.01	0.04	0.02
12:00–12:55	3.92	1.13	0.02	0.02	0.00
13:00–13:55	3.98	0.81	0.00	0.06	0.02
14:00–14:55	3.35	0.72	0.01	0.03	0.00
15:00–15:55	3.94	0.31	0.00	0.02	0.00

Given the inconsistency of the study group's activity both prior to 06:00 and after 16:00, values for these periods are omitted from the present analysis. The mean values for activity levels are calculated from scan sample records.

Table 5. Spearman rank correlation coefficients for comparisons of the daily variation in the exhibition of predator avoidance behaviour patterns by the *C. flaviceps* study group with activity levels.

Pattern	r_s	p	N
1a	0.806	<0.01	10
1b	0.739	<0.05	10
2a	0.618	<0.05	10
2b	0.539	<0.05	10

spend more time at rest as the day progresses, frequently indulging in long "siesta" periods of resting and socialising after mid-day, when ambient temperatures are at their highest (FERRARI, 1988). Similar activity patterns have been recorded for both *Brachyteles arachnoides* (STRIER, 1987) and *Alouatta fusca* (MENDES, 1985) at Montes Claros, and it seems likely that many other diurnal birds and mammals, including predators, will also tend to be less active during the early afternoon, further reducing the likelihood of encounters with the marmosets.

Assuming that the frequency of the low-intensity raptor pattern, 1a, may be partly related to factors other than predator encounter rates, on the other hand, it is interesting to note that the group was generally active at lower levels in the forest as the day progressed (Table 4). While the frequency of all four anti-predator behaviour patterns correlated significantly with mean activity levels (Table 5), as might be expected, only Pattern 1a was significant at the 1% probability level. While this evidence is far from conclusive, it does suggest that the marmosets were normally more vigilant at higher levels in the forest, where they would be more exposed to the possibility of an aerial attack, and further supports the hypothesis that predation pressure has had an important influence on the evolution of callitrichid habitat preferences.

DISCUSSION

While no attacks on the study group were recorded, the present study of *C. flaviceps* indicates that predation has exerted strong selection pressure on a number of aspects of the behaviour of this species, as it appears to have done for most other callitrichids. In common with other species (POLA & SNOWDON, 1975; RYLANDS, 1982; CLEVELAND & SNOWDON, 1982; MASATAKA, 1983; BARTECKI & HEYMANN, 1987), both the alarm calls and the avoidance behaviour of *C. flaviceps* are highly predator-specific. The degree of vigilance and systematic behaviour patterns associated with the use of sleeping sites were also similar to those recorded for other species (MOYNIHAN, 1976; NEYMAN, 1978; DAWSON, 1979; LINDSAY, 1979; TERBORGH, 1983; CAINE, 1987) and again appear to have evolved in response to the vulnerability of these small primates to a wide range of predators.

The analysis of both seasonal and diurnal variation in the rates at which anti-predator behaviour patterns were recorded also indicates that the marmosets were significantly more vigilant, in particular towards aerial predators, both at higher levels in the forest and during periods when leaf cover was scarcest. This appears to support the hypothesis that predation pressure has been fundamental to the evolution of the preference of this and most other callitrichid species for the dense vegetation of the lower levels of disturbed and secondary forest habitats (SUSSMAN & KINZEY, 1984).

Other, more general aspects of the study raise some interesting questions with regard to variables such as group size and social structure. As reported above, no obvious attacks were observed during more than 1,500 contact hours with the *C. flaviceps* study group and no animals disappeared in the 18-month period between May 1985 and October 1986. This contrasts considerably with the situation of *S. fuscicollis* and *S. imperator* at Manu in Peru (GOLDIZEN, 1987; CHENEY & WRANGHAM, 1987), where attacks occur regularly and predation rates are high. While studies of other *Saguinus* species encompass shorter periods of observation, the relatively numerous records of predation (DAWSON, 1976; IZAWA, 1978; HEYMANN, 1987) indicate that they may suffer comparably high predation rates. GARBER (1988) reports, however, a lack of either predation or attacks on a large mixed troop of *Saguinus mystax* and *S. fuscicollis* during the course of a 12-month study.

The only comparable study of a *Callithrix* species is that of *C. humeralifer* at Aripuanã, western Brazil (RYLANDS, 1982). While this site is far more similar to Manu, in terms of habitat type and, presumably, the abundance of predators, than to Montes Claros, the composition of the *C. humeralifer* study group, which contained between 10 and 15 members, remained virtually unchanged over a similar study period. An adult female group member did disappear during the study, but predation was not confirmed. In addition, while RYLANDS records a variety of encounters with potential predators, he does not indicate any exceptional frequency of attacks such as that reported for *S. fuscicollis* at Manu (GOLDIZEN, 1987). The only confirmed report of predation on a marmoset is for *C. jacchus* (ALONSO & LANGGUTH, 1989).

Taken as a whole, the available evidence suggests that *Callithrix* and *Saguinus* may differ in their vulnerability to predation. While the two genera are broadly similar to each other in characteristics such as body size and dietary preferences, a variety of other factors, including habitat type and predator abundance, would obviously have some influence on such a contrast. It is nevertheless possible that differences in their vulnerability are at least partly linked to systematic differences in group size and structure. In general, tamarin groups are much smaller and less stable than those of marmosets, and migrations of solitary animals between groups are far more frequent (FERRARI & LOPES FERRARI, 1989).

Given that predator detection rates may be higher in larger groups (VAN SCHAIK et al., 1983), the predator avoidance behaviour of marmoset groups, which average just under ten individuals, may generally be far more effective than that of tamarin groups, which average just over five members. The long-term stability and cohesiveness of these marmoset groups may also contribute to the efficacy of their anti-predator behaviour, especially if closely related individuals are more likely to cooperate in such activities than unrelated animals (CHENEY & SEYFARTH, 1985; CHENEY & WRANGHAM, 1987). Eventually, however, the benefits of large group size, in terms of predator detection, may be outweighed by a reduction in the effectiveness of the cryptic anti-predator behaviour typically employed by callitrichids (CLUTTON-BROCK & HARVEY, 1977; TERBORGH, 1983). Predation pressure may thus be a factor restricting the maximum size of callitrichid groups to around 15 individuals.

Ultimately, the systematic analysis of the influence of such factors on the evolution of anti-predator behaviour in the callitrichids will require far more information, not just on variables such as predation rates and the frequency of alarm calls, but also on the abundance of predators and the availability of cover in different habitats.

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REFERENCES

ALTMANN, J., 1974. Observational study of behavior: sampling methods. *Behaviour*, 49: 227–265.

ALONSO, C. & A. LANGGUTH, 1989. Ecologia e Comportamento de *Callithrix jacchus* (Primates: Callitrichidae) numa ilha de Floresta Atlântica. *Rev. Nordestina Biol.*, 6: 105–137.

BARTECKI, U. & E. W. HEYMANN, 1987. Field observation of snake-mobbing in a group of saddle-back tamarins, *Saguinus fuscicollis nigrifrons*. *Folia Primatol.*, 48: 199–202.

BOINSKI, S. & P. E. SCOTT, 1988. Association of birds with monkeys in Costa Rica. *Biotropica*, 20: 136–143.

CAINE, N. G., 1984. Visual scanning by tamarins: a description of the behavior and tests of two derived hypotheses. *Folia Primatol.*, 43: 59–67.

———, 1986. Visual monitoring of threatening objects by captive tamarins (*Saguinus labiatus*). *Amer. J. Primatol.*, 10: 1–8.

———, 1987. Vigilance, vocalizations and cryptic behavior at retirement in captive groups of red-bellied tamarins (*Saguinus labiatus*). *Amer. J. Primatol.*, 12: 241–250.

——— & S. L. MARRA, 1988. Vigilance and social organization in two species of primates. *Anim. Behav.*, 36: 897–904.

CHENEY, D. L. & R. M. SEYFARTH, 1985. Vervet monkey alarm calls: manipulation through shared information? *Behaviour*, 94: 150–166.

——— & R. W. WRANGHAM, 1987. Predation. In: *Primate Societies*, B. B. SMUTS, D. L. CHENEY, R. M. SEYFARTH, R. W. WRANGHAM, & T. T. STRUHSAKER (eds.), Univ. of Chicago Press, London, pp. 227–239.

CLEVELAND, J. & C. T. SNOWDON, 1982. The complex vocal repertoire of the adult cotton-top tamarin (*Saguinus oedipus oedipus*). *Z. Tierpsychol.*, 58: 231–270.

CLUTTON-BROCK, T. H. & P. H. HARVEY, 1977. Primate ecology and social organization. *J. Zool. Soc. London*, 183: 1–39.

COIMBRA-FILHO, A. F., 1978. Natural shelters of *Leontopithecus rosalia* and some ecological implications. In: *The Biology and Conservation of the Callitrichidae*, D. G. KLEIMAN (ed.), Smithsonian Institution Press, Washington, D.C., pp. 79–89.

DAWSON, G. A., 1976. Behavioral ecology of the Panamanian tamarin, *Saguinus oedipus*. Unpubl. Ph.D. dissertation, Michigan State Univ., East Lansing.

———, 1979. The use of time and space by the Panamanian tamarin *Saguinus oedipus*. *Folia Primatol.*, 31: 253–284.

FERRARI, S. F., 1988. The behaviour and ecology of the buffy-headed marmoset, *Callithrix flaviceps* (O. THOMAS, 1903). Unpubl. Ph.D. thesis, Univ. College London.

———, in press. A foraging association between two kite species (*Ictinea plumbea* and *Leptodon cayanensis*) and buffy-headed marmosets (*Callithrix flaviceps*) in southeastern Brazil. *Condor.*

——— & M. A. LOPES FERRARI, 1989. A re-evaluation of the social organisation of the Callitrichidae, with reference to the ecological differences between genera. *Folia Primatol.*, 52: 132–147.

FONTAINE, R., 1980. Observations of the foraging association of double-toothed kites and white-faced capuchin monkeys. *Auk*, 97: 94–98.

GARBER, P. A., 1988. Diet, foraging patterns, and resource defense in a mixed species troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. *Behaviour*, 105: 18–34.

GOLDIZEN, A. W., 1987. Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behav. Ecol. Sociobiol.*, 20: 99–109.

HETHERINGTON, C. M., 1978. Circadian oscillations of body temperature in marmosets, *Callithrix jacchus*. *Lab. Anim.*, 12: 107–108.

HEYMANN, E. W., 1987. A field observation of predation on a moustached tamarin (*Saguinus mystax*) by an anaconda. *Int. J. Primatol.*, 8: 193–195.

HLADIK, A. & C. M. HLADIK, 1969. Rapports trophiques entre végétation et primates dans la forêt de Barro Colorado (Panama). *Terre et Vie*, 23: 25–117.

IZAWA, K., 1978. A field study of the ecology and behavior of the black-mantle tamarin (*Saguinus nigricollis*). *Primates*, 19: 241–274.

LINDSAY, N. B. D., 1979. A report on the field study of Geoffroy's tamarin *Saguinus oedipus geoffroyi*. *Dodo. J. Jersey Wildl. Preserv. Trust*, 16: 27–51.

MASATAKA, N., 1983. Categorical responses to natural and synthesized alarm calls in Goeldi's monkeys (*Callimico goeldii*). *Primates*, 24: 40–51.

MENDES, S. L., 1985. Uso de espaço, padrões de atividades diárias e organizações de *Alouatta fusca* (Primates, Cebidae) em Caratinga, MG. Unpubl. M. Sc. thesis, Univ. of Brasília.

MITTERMEIER, R. A., A. B. RYLANDS, A. F. COIMBRA-FILHO, & G. A. BOUCHARDET OA FONSECA, 1988. *Ecology and Behavior of Neotropical Primates, Vol. 2*, World Wildlife Fund, Washington, D.C.

MORRISON, P. & J. SIMÕES, JR., 1962. Body temperature in two Brazilian primates. *Bol. Fac. Fil., Ciên. Letr. Univ. S. Paulo* 261 (*Zoologia no. 24*): 167–178.

MOYNIHAN, M., 1970. Some behavioral patterns of Platyrrhine monkeys. II. *Saguinus geoffroyi* and some other tamarins. *Smiths. Contr. Zool.*, 28.

———, 1976. *The New World Primates*. Princeton Univ. Press, Princeton, New Jersey.

NEYMAN, P. F., 1978. Aspects of the ecology and social organization of free-ranging cotton-top tamarins *Saguinus oedipus* and the conservation status of the species. In: *The Biology and Conservation of the Callitrichidae*, D. G. KLEIMAN (ed.), Smithsonian Institution Press, Washington, D.C., pp. 39–71.

POLA, Y. V. & C. T. SNOWDON, 1975. The vocalizations of pygmy marmosets (*Cebuella pygmaea*). *Anim. Behav.*, 23: 826–842.

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

DE RUITER, J. R., 1986. The influence of group size on predator scanning and foraging behaviour of wedgecapped capuchin monkeys (*Cebus olivaceus*). *Behaviour*, 98: 240–258.

RYLANDS, A. B., 1982. The behaviour and ecology of three species of marmosets and tamarins (Callitrichidae, Primates) in Brazil. Unpubl. Ph.D. thesis, Univ. of Cambridge.

VAN SCHAIK, C. P., M. A. VAN NOORDWIJK, R. J. DE BOER, & I. DEN TONKELAAR, 1983. The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behav. Ecol. Sociobiol.*, 13: 173–181.

SOINI, P., 1988. The pygmy marmosets, genus *Cebuella*. In: *Ecology and Behavior of Neotropical Primates, Vol. 2*, R. A. MITTERMEIER, A. B. RYLANDS, A. F. COIMBRA-FILHO, & G. A. BOUCHARDET DA FONSECA (eds.), World Wildlife Fund, Washington, D.C.

STEVENSON, M. F. & A. B. RYLANDS, 1988. The marmoset monkeys, genus *Callithrix*. In: *Ecology and Behavior of Neotropical Primates, Vol. 2*, R. A. MITTERMEIER, A. B. RYLANDS, A. F. COIMBRA-FILHO, & G. A. BOUCHARDET DA FONSECA (eds.), World Wildlife Fund, Washington, D.C.

STRIER, K. B., 1987. Activity budgets of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). *Amer. J. Primatol.*, 13: 385–395.

SUSSMAN, R. W. & W. G. KINZEY, 1984. The ecological role of the Callitrichidae: A review. *Amer. J. Phys. Anthropol.*, 64: 419–449.

TERBORGH, J., 1983. *Five New World Primates: a Study in Comparative Ecology*. Princeton Univ. Press, Princeton, New Jersey.

WOLTERS, H. J., 1978. Some aspects of role taking behaviour in captive family groups of the cotton-top tamarin (*Saguinus oedipus oedipus*). In: *Biology and Behaviour of Marmosets*, H. ROTHE, H. J. WOLTERS, & J. P. HEARN (eds.), Eigenverlag, Göttingen, FRG, pp. 259–278.

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