

Prey-capture benefits in a mixed-species group of Amazonian tamarins, *Saguinus fuscicollis* and *S. mystax*

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Summary. Tamarins of the genus *Saguinus* feed on a wide range of arthropods and small vertebrates, which compose a critical component of their diet. This paper examines the foraging patterns and capture success of the Avila-Pires saddle-back (*S. fuscicollis avilapirensi*) and the red-capped moustached tamarin (*S. mystax pileatus*) in very stable mixed-species groups, and whether and how any foraging benefits for either species resulted from their association. Moustached tamarins actively searched for prey items which were mainly well exposed on the midstorey foliage. Saddle-back tamarins, on the other hand, foraged at lower heights, largely by manipulating a variety of microhabitats potentially concealing embedded prey. The foraging activity of the numerically dominant and larger-bodied moustached tamarins often resulted in prey items escaping to lower substrates, usually the forest leaf-litter. The “beating effect” of this species substantially facilitated captures of large, mobile prey items by saddle-backs, which were highly adept at locating and retrieving flushed prey. It is estimated that, while saddle-backs obtained 66–73% of their prey biomass from flushed items, this proportion was substantially lower (2–9%) for moustached tamarins. Commensal insectivory appears to involve a highly asymmetric benefit to saddle-backs, and a low cost to moustached tamarins, which partly explains the stability of mixed-species groups.

Introduction

Interspecific associations are a widespread phenomenon in several vertebrate taxa including primates (Struhsaker 1981; Terborgh 1983), ungulates (Leuthold 1977), birds (Munn and Terborgh 1979; Wiley 1980), and fish (Alevi-

zon 1976). The ecological advantages promoting the evolution and maintenance of stable mixed-species groups may be similar to those of monospecific social groups, and are usually viewed in terms of benefits derived from increased predator-avoidance, increased foraging efficiency, or both (e.g. Terborgh 1990).

In primates, stable interspecific associations are primarily restricted to two of the most diverse genera: guenons (*Cercopithecus* spp.) in Africa (Cords 1987; Gautier-Hion 1988) and tamarins (*Saguinus* spp.) in South America (Terborgh 1983; Garber 1988). Opportunities for associations arose within these species-groups following their high rates of speciation, which resulted in the co-occurrence of congeners throughout their geographical ranges (HersHKovitz 1977; Kingdon 1988). Competition theory predicts that, under resource-limited conditions, associated heterospecifics (which potentially encounter equal units of the same resources at equal rates) should segregate ecologically to a certain extent, or else their long-term coexistence could be threatened by competitive exclusion (e.g. May 1974). Yet patterns of resource use by each species in mixed-species groups cannot be too divergent because costs of forming and maintaining their association would become prohibitive. Overlap in resource use then provides room for potentially intricate interspecific interactions ranging from mutually beneficial, to commensal, to competitive. The level of stability of an association, given its initial changes of occurring at all, may then reflect a balanced trade-off between these interactions.

In this paper I examine the very stable interspecific associations between two small-bodied insectivorous primate species occurring in a central Amazonian forest site: the Avila-Pires saddle-back tamarin (*Saguinus fuscicollis avilapirensi*) and the red-capped moustached tamarin (*S. mystax pileatus*). I describe the animal component of tamarins' diet, the characteristics of their prey items, and the techniques they used to search, capture, and handle prey. I emphasise ecological differences between these two species, as dictated by parameters intimately related to prey acquisition. The costs and benefits of

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foraging in mixed-species groups are then examined in terms of how each species affected the other's prey capture success. Finally, these results are compared to those of other studies of mixed-species associations in primates.

Methods

Study site and animals. This study was carried out in the upper Urucu river, Amazonas, Brazil (4° 50' 52" S, 65° 16' 05" W), from February 1988 to September 1989. Observations were restricted to a 900-ha plot of undisturbed, non-hunted, unflooded (*terra firme*) forest located 4 km inland from the river, which was accessible mainly by helicopters. High forest accounted for 93% of the study plot, and consisted of tall, undisturbed forest on undulating terrains, 53–71 m above sea level. The rest of the plot included two low-lying habitat types – creekside forest and palm swamps – which ran along a black-water perennial forest stream. Annual rainfall in this area averaged 3256 ± 589 mm ($n=2$ years). A detailed description of the plant community and habitat types in the study area is presented elsewhere (Peres 1991).

Animals and behavioural sampling. Mixed-species groups of tamarins in the Urucu consisted of 5.5 ± 0.5 ($n=6$) saddle-backs (adult body weight = 394 ± 42 g, $n=17$), and 8.6 ± 0.7 ($n=6$) moustached tamarins (adult body weight = 523 ± 70 g, $n=6$). With the help of four field assistants, I observed eight mixed-species groups of *Saguinus* during 170 days spread over a 2-week period in each of 14 consecutive months. One of these groups, which ranged in size from five to eight saddle-backs and eight to ten moustached tamarins, was observed systematically for 731 h over 138 days in 13 consecutive months, following a 3-month period of intensive habituation. Here I consider primarily data collected when tamarins searched, pursued, captured, and ingested animal prey items whilst both species remained together. Such mixed-species associations are defined as any context in which at least one member of each species was within 50 m of the other.

Prey foraging effort and success were measured using scan and focal-animal sampling. Instantaneous scan samples (Altmann 1974) were obtained every 10 min throughout the day from all visible animals of both species in the group. This resulted in a total of 12923 and 16039 scans for saddle-back and moustached tamarins, respectively. During scans, the foraging pattern, the type, size and height of searched substrates were determined whenever possible. In the case of successful captures, I noted the taxon, size, and substrate of the prey item, as well as the prey capture technique used. Tamarins' prey items were assigned to one of four colour categories and variations therein: (i) dark (brown, grey, mottled brownish grey); (ii) yellow; (iii) green; and (iv) red-and-green. In addition, mobile prey items were distinguished from sedentary ones if the latter were inherently unable to escape from predators (e.g. dragonfly larvae in a bromeliad). However, most prey types were mobile (e.g. adult orthopterans), and thus capable of fleeing an approaching tamarin. Prey characteristics were left "undetermined" whenever an animal was handling an item following an unobserved capture.

Foraging focals are defined as focal-animal samples (Altmann 1974) during foraging activities. These were obtained independently of 10-min scans: the two forms of sampling were not conducted on the same days. Because the distinction between foraging and other activities was often ambiguous, focal foragers were only sampled if they were obviously searching for prey. Focal-sample periods were timed with a stop-watch, and consisted of any length of time between the beginning of the observation and the point at which the animal captured a prey item, discontinued foraging and switched to another activity, or became invisible to the observer. Samples aborted within less than 30 s were disregarded. Subjects of foraging focals were rotated within each species of tamarins at any given day, and I strived for a balanced between-species

sampling effort throughout the study. Foraging focals lasted on average 167 ± 103 s ($n=96$) for saddle-backs and 162 ± 101 s ($n=110$) for moustached tamarins. For each focal forager I recorded (i) the number, mode and context of prey captures, and (ii) the size, type, and substrate of the prey. Prey capture success, defined as the number of captures per unit of foraging time, was also calculated. This measure of foraging success was considered more accurate for between-species comparisons than that derived from instantaneous scan samples because it involved no assumptions of sampling homogeneity.

The effect of neighbouring foragers on an animal's probability of capturing prey was examined in terms of whether or not the prey item had been observed to be flushed by a group-member before it was captured, and the proximity and species-identity of its nearest neighbour. Two broad categories of prey pursuit were thus distinguished: (i) active foraging, when animals located and captured prey unaided by group-members; and (ii) passive foraging, when animals appeared to be scanning, mostly multi-directionally, for prey flushed by other group-members. Flights of potential prey items during sampling, rather than being spontaneous, appeared to be caused by tamarins' movements and foraging activity.

Data on intragroup spacing was only noted when the forager was within a horizontal distance of 10 m from its nearest neighbour. This cut-off point was based on escape responses of tamarins' prey, which was assessed independently by experimental "flushing trials" conducted early in the study with katydids – the tamarins' most frequently taken prey-items (Peres 1991). During these trials, katydids found up to 4 m in the vegetation were disturbed by gently shaking their substrates with a 1.5-m stick. The vertical and horizontal distance between their take-off and landing points were then estimated.

Prey size. Because highly chitinous and sclerotized body parts of large insects (e.g. wings, legs) were always discarded by tamarins, it was often possible to use such retrieved appendages to estimate prey size by actual measurements. Based on observations of handling manoeuvres and of prey items themselves, four classes of prey size were defined early in the study: (i) small – had a longest dimension of up to 10 mm, and tamarins transferred them to their mouths at once, leaving no external traces of the prey to the observer other than chewing; (ii) medium – ranged from 10 to 24 mm, and were handled for several seconds before the entire item was transferred to the mouth and chewed; (iii) large – ranged from 25 to 44 mm, and were hand-held during feeding for up to 1 min before ingestion had been completed; and (iv) very large – ranged from 45 to 110 mm, and involved up to 12 min of handling, often causing its capturer to lag behind the rest of the group, particularly if food-sharing had not taken place.

Prey biomass. The relationship between linear dimensions and the biomass of prey was assessed by measuring and weighing live, whole Orthoptera taken from an indoor colony of African locusts (*Schistocerca gregaria*, Acrididae) in the Department of Zoology, Cambridge University. This species was chosen because its body plan is very similar to that of katydids. The standard body length and weights of 15 individuals in each of four size classes – 2nd, 3rd, 4th instar, and fully-grown adults – were measured using a calliper and a Metler PM480 digital balance, accurate to the nearest milligram. These growth stages approximated the estimated lengths of tamarins' small, medium, large, and very large prey items, respectively, and were thus likely to give realistic estimates of prey weights. The median point of each of these size classes was used to predict their average weights based on a non-linear regression between locust length and weight with a determination coefficient of 0.98. These mean weights were then applied to capture frequencies to estimate biomass of prey harvested by each tamarin species.

Foraging overlap. The degree of foraging overlap between tamarin species was calculated using the Petraitis' (1979) general overlap index (GO), which is given by, $GO = e^E$, where $E = \sum_i \sum_j [n_{ij}(\ln c_j)]$

$-\ln p_{ij})/T$, where n_{ij} is the total number of cases in which each resource class (j) was used by each tamarin species (i); p_{ij} is the proportion of cases in which each resource j was used by each species (i); c_j is the combined proportion of cases in which both species used each resource class; and $T = \sum_{j=1}^r (t_j)$, where t_j are the

tallied totals for each resource class. This index measures the likelihood that the resource utilization curve of either tamarin species (i) was drawn from a "common" utilization curve, and can be tested using the V statistic, which follows a chi-square distribution (Petraitis 1985). Resource availability at the study site was not independently quantified – a common pitfall in measures of niche overlap based entirely on resource use (Hurlbert 1978). This problem is partly overcome by the highly stable and coordinated associations between the two tamarin species: tamarins tended to search for prey simultaneously and near one another, and interspecific interference competition over prey items was negligible. Differences in the above parameters were thus not related to differences in prey availability for each species. For this analysis, therefore, data on prey captures obtained from monospecific groups were excluded.

Statistical analysis. All statistical tests are two-tailed unless stated otherwise. Categorical data were analysed using log-likelihood ratio tests (G -tests), except where empty cells required the use of chisquare tests. G -tests follow Sokal and Rohlf (1981), and non-parametric statistics Siegel (1956). Two-sample Kolmogorov-Smirnov tests are referred to as "K-S".

Results

Stability of associations

On 97.6% of all observation days ($n=170$) the observed groups consisted of both tamarin species for as long as the observer remained with the group. Of 138 days on which the main group of tamarins was observed, group members of each species drifted apart and moved independently of one another during only 2 days (1.4%). This equated to only 12.5 h (1.7% of 731 observation hours) of monospecific life for the main group during the entire study. In the remaining 136 days (98.6%), individual saddle-backs and moustached tamarins spent the entire observation period together, usually within 25 m of one another. Because tamarins of each species used separate sleeping sites, usually within 50 m of one another (45.9 ± 22.6 m, $n=82$ nights), the mixed-species group fragmented over 5.1 ± 2.3 min ($n=76$; range = 1–9 min) before retiring to an overnight shelter in the late afternoon, and coalesced again early in the next morning over 3.2 ± 1.4 min ($n=62$; range = 0.5–8 min) after leaving their shelters. These periods in monospecific groups accounted for only 1.5% of tamarins' activity periods which on average lasted for 9 h 12 min ($n=62$ days).

Rallying long-calls early in the morning appeared to be the primary long-distance signals promoting interspecific group coalescence. The first long-calls and counter-calls in a day were produced by adults of either species. The species in a mixed group that initiates calling on any given day – presumably to elicit vocal responses from heterospecifics – may be associated with a greater willingness to maintain the association (e.g. Gautier-Hion and Gautier 1974). Saddle-back and moustached tamarins respectively initiated rallying calls prior to

group coalescence on 56.3% and 43.7% of 48 days in which the species identity of the first caller was determined. This difference was not significantly greater than that expected by chance ($\chi^2=0.75$, 1 *df*, $P=0.39$), which suggests that the initial choices of maintaining a monospecific or a heterospecific group on any given day were symmetric between the two species.

The frequency of these interspecific associations obviously did not result by chance. However, this was tested against Waser's (1982) "perfect gas model", in which primate groups are said to behave like molecules in a two-dimensional ideal gas with velocities following a Maxwell-Boltzmann distribution, except that they pass through each other without colliding. Given data on tamarins' mean group velocity (1.991 km/day), group density (1.24 groups/km²), mean group radius of each species (10 m), and that the criterion distance for association was 50 m (Peres 1991), this model provides an expected rate of 0.488 interspecific encounters per day. The observed rate of 136 encounters in 138 days (0.986) was, therefore, considerably greater.

In addition, the expected duration of associations for the main group derived from Waser's (1984, 1987) equation was 34 min/day, which is far less than the observed average of 544 min/day. The two species thus appeared to seek out one another and remain associated, rather than to independently converge upon resources held in common.

Foraging segregation

During scans, a total of 213 and 635 prey captures were observed for saddle-back and moustached tamarins, respectively. Tamarins foraged for prey items throughout most of their activity period, though the two species diverged substantially in certain characteristics of their prey, prey capture techniques, substrates searched and context of prey capture.

Taxa and substrates of prey. Both tamarin species relied heavily on tettigoniid orthopterans, such as bush katydids (Phaneropterinae) and sylvan katydids (Pseudophyllinae), accounting for 68–82% of their non-plant feeding records. A variety of other forms of arthropods and small vertebrates, such as *Anolis* lizards, were taken less frequently. The taxonomic order of prey consumed by tamarins did not diverge significantly ($GO=0.945$, $V=18.7$, 15 *df*, $P>0.2$) mainly because orthopterans were very prominent in both species' diet.

The substrates from which these items were taken, however, differed substantially between the two species ($GO=0.628$, 13 *df*, $V=185.9$, $P<0.001$). Of 208 prey items of saddle-backs with a known origin, 31% were removed from within a variety of natural shelters coexisting prey, such as woody crevices, knotholes, notches in other rigid substrates, aerial leaf-litter, curled dead leaves, and the underside of tree bark (hereafter, "blind microhabitats"). Another 32% of this species' prey items were captured from the soil leaf litter, usually after they had taken cover. Of 580 items taken by moustached ta-

Table 1. Size of prey items captured by each *Saguinus* species

Prey size	<i>S. fuscicollis</i>		<i>S. mystax</i>		Both species	
	Freq.	%	Freq.	%	Freq.	%
Small (< 10 mm)	27	18.9	207	42.0	234	36.8
Medium (10–24 mm)	39	27.3	199	40.4	238	37.4
Large (25–44 mm)	49	34.3	70	14.2	119	18.7
Very large (> 45 mm)	28	19.6	17	3.4	45	7.1
No. of items of known size	143	100	493	100	636	100

marins, 94% were either mobile on, or attached to, foliage. This resulted in a significant association between whether or not a prey item was embedded within a substrate and the tamarin species which captured it ($G = 124.9$, 1 *df*, $P < 0.001$).

Prey size. Size of prey items captured by tamarins ranged from 2 mm, such as young spiders taken during raids on spider colonies, to large-bodied and robust (≤ 11 -cm long) carnivorous species of pseudophylline katydids (e.g. *Steirodon* sp.), which could be shared by as many as four conspecifics for as long as 12 min. Although both tamarin species were capable of handling the same range of prey, there were obvious differences in the size frequencies of prey items taken, which resulted in a low interspecific overlap ($GO = 0.921$, 3 *df*, $V = 32.7$, $P < 0.001$). Most prey captured by saddle-backs were large (34%), whereas those of moustached tamarins were mostly small (42%; Table 1), which resulted in a significant difference between the distribution of each species' prey size ($G = 77.3$, 3 *df*, $P < 0.001$).

Prey mobility. Many prey items captured by tamarins were unable to divert predation, their survival depending entirely on avoiding being discovered and the quality of their shelters. In contrast, other prey species relied heavily on behavioural and chromatic crypsis to avoid capture. Whilst inert or "frozen" postures appeared to minimize their chances of being detected, they often undertook sudden escape responses, such as free-falls, power dives, or flights to another substrate, if encountered by tamarins at close quarters. Following 16% of the experimental flushing trials ($n = 25$), katydids, particularly large-bodied species, dropped or jumped directly to the soil leaf-litter without using their wings. The other 84% of the trials resulted in katydids jumping to a lower foliage substrate, but unfolding their wings in the process, within a horizontal distance of 8 m. In 76% of the trials, the negative vertical displacement between take-off and landing points was greater than the horizontal distance covered. These data support (i) other observations on several species of large orthopterans, which tend to lose height when escaping foraging manoeuvres by tamarins, and (ii) studies of wing kinematics of other saltatorial insects, such as mantids and bush crickets, which tend to drop to lower substrates after induced take-offs (Brackenbury 1991).

Table 2. Relationship between mobility and size of prey items captured by tamarins during scan samples

Prey mobility	Prey size	Percentage of captures		
		<i>S. fuscicollis</i>	<i>S. mystax</i>	Both species
Sedentary prey	Small	17.9	20.8	20.1
	Medium	20.0	10.3	12.4
	Large	6.4	1.9	2.9
	Very large	4.3	0.4	1.2
	Total stationary	48.6	33.4	36.6
Mobile prey	Small	2.1	12.6	10.4
	Medium	7.1	35.8	29.7
	Large	28.6	15.0	17.9
	Very large	13.6	3.1	5.4
	Total mobile	51.4	66.5	63.4
No. of items of known size		140	514	654

The two tamarin species differed in the number of mobile and sedentary prey items they captured (χ^2 with Yates' correction = 8.4, 1 *df*, $P = 0.004$). Saddle-backs captured a similar number of mobile (55.2%) and sedentary prey (44.8%, $n = 201$), whereas mobile prey were more common in the diet of moustached tamarins (66.9%, $n = 610$). There was also a significant association between prey mobility and prey size for both tamarin species (saddle-back: $G = 56.8$, 3 *df*, $P < 0.001$; moustached tamarin: $G = 100.6$, 3 *df*, $P < 0.001$; Table 2). A substantial proportion of saddle-backs' prey (42%) was large to very large and mobile, most of which were flushed from above by a foraging moustached tamarin. Other captures consisted largely of small to medium-sized sedentary prey concealed within blind microhabitats. On the other hand, most items captured by moustached tamarins were either small and attached to foliage (21%), or medium and mobile (36%).

Prey colour. Items captured by moustached tamarins were largely green, or red-and-green (Table 3), whereas those captured by saddle-backs were mostly brown or grey. This resulted in a significant difference between the colour of prey taken by the two species ($G = 89.8$, 3 *df*, $P < 0.001$), which tended to match the background

Table 3. Colour of prey items taken by each tamarin species

Prey colour	<i>S. fuscicollis</i>		<i>S. mystax</i>		Both species	
	Freq.	%	Freq.	%	Freq.	%
Dark (brown or grey)	87	70.2	37	20.6	124	40.8
Green	25	20.2	129	71.7	154	50.7
Yellow	5	4.0	10	5.6	15	4.9
Red and green	7	5.6	4	2.2	11	3.6
No. of items of known colour	124	100	180	100	304	100

colour of their substrates. Whilst moustached tamarins took mainly green prey items well-exposed on live foliage, saddle-backs took mainly dark items embedded within blind microhabitats allowing little light through to them, or exposed on dark, or lichen-covered substrated (e.g. tree trunks).

Modes and contexts of prey capture. The two species of tamarins segregated widely by method of prey capture ($GO=0.768$, 3 *df*, $V=105.5$, $P<0.001$), and the ways they searched, detected, and approached prey items. Saddle-backs captured 55.3% ($n=123$) of their prey by active foraging (Table 4). These unaided searches were mainly manipulative, and directed at blind microhabitats likely to conceal small to medium-sized prey items, such as day-roosting cockroaches and certain pseudophylline and copiphorine katydids.

Moustached tamarins almost always foraged as active foliage gleaners. This prey-capture technique involved visual searches and rapid foraging manoeuvres aimed at prey items undisturbed on the foliage. Their relentless searches were carried out nearly stationarily for short intervals, and by scanning the terminal twigs and foliage at 3 m above ground or higher. Once detected, an item was either attacked immediately, or stalked stealthily. "Stalks" consisted of slow approaches suddenly terminated within striking distance by forward lunges, abrupt pounces, swipes, or snatches. In other cases, this species used long-distance pounces, usually directed to items at a lower height even if the substrate was too flimsy to support the impact. Not surprisingly, the frequency of observed free-falls of foraging moustached tamarins ($n=22$) throughout the study was over 3 times greater than that of saddle-backs ($n=7$).

Flushing of prey was caused almost exclusively by moustached tamarins as they worked their way through the midstorey. Arthropods, whether or not they had been detected, often escaped from their original foliage position to other lower substrates. Flushed prey then became vulnerable to neighbouring foragers by becoming readily detectable during movement, more accessible at their landing point, or both. Captures of leaf-roosting orthopterans by saddle-backs almost always involved the pur-

suit of such prey, which they were highly successful at retrieving: 44.7% ($n=123$) of their prey was obtained in this manner (Table 4). In rare cases, a foraging moustached tamarin captured prey flushed by itself (1.2%, $n=505$), or prey flushed by conspecifics (4.2%). In 848 captures observed during scans, never did a moustached tamarin retrieve prey flushed by a saddle-back, and only twice were saddle-backs seen flushing prey of any kind.

Piracy by the larger-bodied, dominant moustached tamarins of prey items seized by saddle-backs was never observed. In rare cases, however, moustached tamarins appeared to benefit from foraging with saddle-backs by exploiting the latter's ability to detect flushed prey. This occurred because large orthopterans flushed to the ground became difficult to locate as they quickly retreated underneath the leaf-litter. Having followed the insect's trajectory, a saddle-back descended on a vertical tree-trunk to within 1 m above ground and searched the immediate area where the insect had landed. The ensuing search, both above and beneath the litter, then often led to a capture. However, a saddle-back close to a large morsel became vulnerable to displacements by a moustached tamarin, which were occasionally able to find and retrieve such large prey items. The moustached tamarin was thus able to kleptoparasitise the greater ability of saddle-backs to locate prey flushed to the ground.

Foraging height. The two species of tamarins differed significantly in the vertical distribution of their prey captures (K-S, $z=6.9$, $P<0.001$; Fig. 1). Moustached tamarins harvested 73% of their prey between 5 and 15 m, and had a mean capture height of 10.1 ± 5.2 m ($n=625$). By contrast, saddle-back tamarins foraged for prey at lower strata, capturing 75% of their prey up to 6 m above ground, and with a mean capture height of 4.7 ± 5.5 m ($n=210$). This is clearly related to differences in heights occupied by the two species during all activities (saddle-backs: 11.0 ± 9.5 , $n=7817$; moustached tamarins: 14.1 ± 8.6 m, $n=10133$; K-S, $z=26.4$, $P<0.001$).

This divergence in vertical space can be partly explained by the foraging method used by each species. Height of prey captures by either species for those prey items which presented an escape response differed from

Table 4. Methods and contexts of prey-captures by each tamarin species

Mode and context of capture	<i>S. fuscicollis</i>		<i>S. mystax</i>		Both species	
	Freq.	%	Freq.	%	Freq.	%
Unaided captures						
Pounce or snatch	4	3.3	301	59.6	305	48.6
Manipulative manoeuvre	64	52.0	177	35.0	241	38.4
Aided captures						
Flushed by others	55	44.7	21	4.2	76	12.1
Self-flushed	0	0.0	6	1.2	6	1.0
No. of captures of known contexts	123	100	505	100	628	100

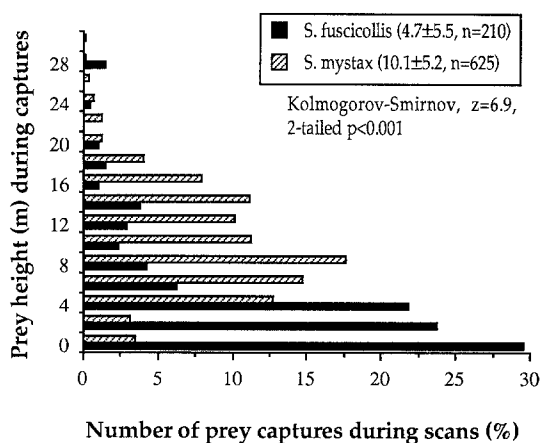


Fig. 1. Height of prey captures for each tamarin species

those which did not (K-S, $z = 1.7$, $P = 0.006$). Sedentary prey were captured by saddle-backs, almost always manipulatively, at an average height of 5.8 ± 4.4 m ($n = 83$), whereas mobile prey were captured considerably lower, at 2.5 ± 3.5 m ($n = 110$). On the other hand, moustached tamarins captured sedentary and mobile prey at almost identical heights of 9.8 ± 4.9 ($n = 183$) and 9.9 ± 5.3 m ($n = 383$), respectively. This difference was significant for saddle-back (K-S, $z = 3.3$, $P < 0.001$), but not for moustached tamarins (K-S, $z = 0.7$, $P = 0.64$), largely because the mobile prey caught by saddle-backs had usually been flushed from the midstorey, losing height in the process.

Rate and biomass of prey harvest

Capture rates were remarkably similar between tamarin species, averaging 0.127 and 0.120 captures/min for saddle-back and moustached tamarins, respectively (Table 5). The two species thus required a similar average of 7 min 52 s and 8 min 20 s of foraging effort to obtain an individual prey item of any size. However, because saddle-backs captured a greater number of larger items, their biomass harvest rate (0.041 g/min) was considerably higher than that of moustached tamarins (0.028 g/min), even though the former species converted fewer capture attempts into successful captures.

Flushed prey were usually large to very large items (Table 2; Fig. 2a), and represented 73.3% of the prey biomass harvested by saddlebacks ($n = 92.7$ g in 143 captures; Fig. 2b). By contrast, only 1.7% of the prey biomass harvested by moustached tamarins ($n = 131.6$ g in

Table 5. Foraging patterns, capture rates, and biomass of prey harvested by tamarin species as determined by focal samples

Foraging parameter	<i>S. fuscicollis</i>	<i>S. mystax</i>
Capture attempts (%)		
Closed microhabitats	81.2	16.4
Prey attached to foliage	0.0	35.8
Mobile prey on foliage	5.8	46.3
Flushed prey	13.0	1.5
No. of attempts	69	67
Successful captures (%)		
Small prey	44.1	44.4
Medium prey	26.5	38.9
Large prey	23.5	11.1
Very large prey	5.9	5.6
No. of captures	34	36
No. of flushed prey captured (%)	26.5	2.8
Capture rate (captures/min)	0.127	0.120
Capture effort (attempts/min)	0.257	0.224
Capture success (captures/attempt)	0.493	0.537
Biomass of flushed prey harvested (%)	65.5	9.3
Total biomass of prey harvested (g)	11.03	8.47
Biomass harvest rate (g/min)	0.041	0.028
Number of foraging focals	96	110
Focal observation time (min, s)	268' 36"	299' 41"

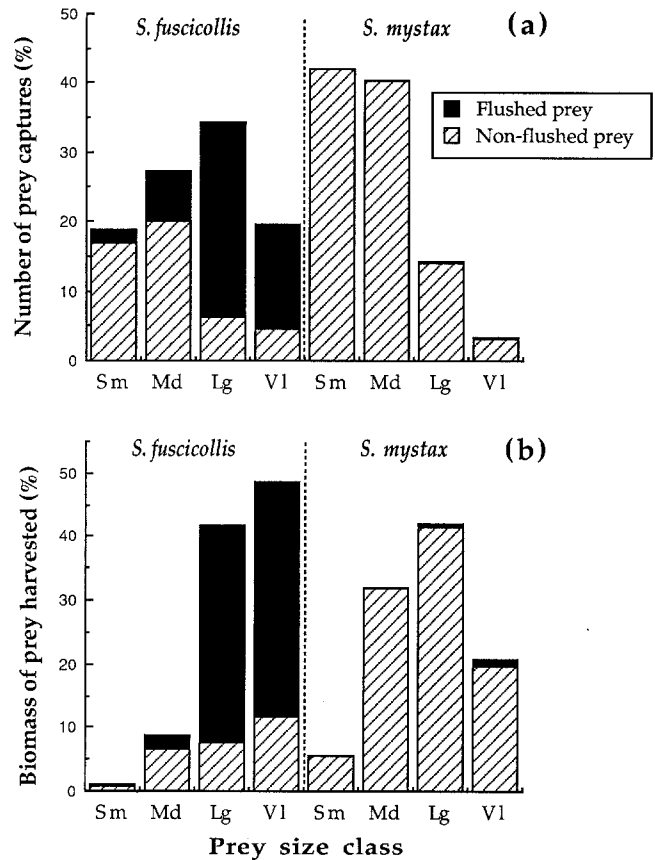


Fig. 2a, b. Percentage of prey harvested by each tamarin species, expressed in terms of **a** frequency, and **b** biomass of prey items in 4 size classes. *Black* and *hatched bars* represent the proportions of prey captures in each size class which had, or had not been flushed, respectively. Calculations are based on 143 captures by saddle-back and 493 captures by moustached tamarins in which prey size could be estimated

493 captures) was obtained from flushed items with the aid of group members of either species. Commensal prey captures by passive foragers exploiting the other species' beating effect was thus largely a one-way benefit generated by moustached tamarins and accrued by saddle-backs ($G = 119.6$, 1 *df*, $P < 0.001$). Moreover, the total *per capita* intake of prey biomass of saddle-backs was slightly greater than that of moustached tamarins, because members of the former species tended to catch larger prey items. For instance, correcting for the amount of time individuals of each species were observed, single saddle-back and moustached tamarins harvested on average 16.9 and 15.0 g of prey throughout the study, respectively.

Intragroup spacing during captures

Distance to a nearest neighbour at the time of captures by either tamarin species was shorter for mobile than for sedentary prey items (K-S, $z = 1.9$, $P = 0.001$; Fig. 3). For such non-flushable items, proximity to a nearest neighbour could neither enhance nor hinder its capture success. By contrast, mobile prey may become more conspicuous to neighbours as prey escape a short distance

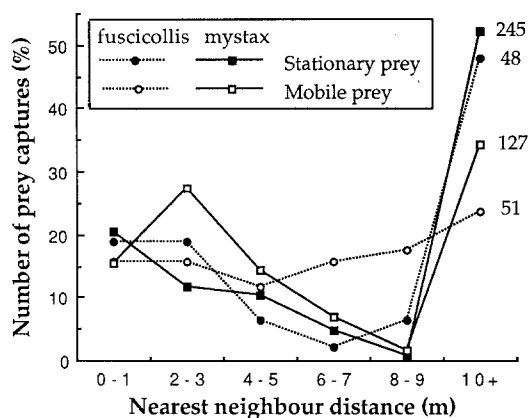


Fig. 3. Distance to nearest neighbours at the time of prey captures by individuals of each tamarin species, for stationary and mobile prey. Numbers indicate sample sizes

at the approach of a forager. The variation of nearest-neighbour distances was similar between tamarin species for captures of sedentary prey (Fig. 3). Saddle-backs, however, captured fewer mobile prey than moustached tamarins at distances of 10 m or farther from a nearest neighbour, presumably because distance from a potential flusher affected capture probability. The distribution of nearest-neighbour distances between captures of mobile and sedentary prey thus differed for saddle-backs ($K-S, z = 1.4, P < 0.05$), but not for moustached tamarins ($K-S, z = 1.2, P = 0.11$). This further supports the idea that the group's collective "beating effect" had significant consequences only for the foraging behaviour of that species whose capture success was boosted by the other's flushing activity.

Discussion

Animal prey represents the highest-quality dietary component of wild callitrichids, even though plant material makes up most of their diet (Yoneda 1981; Soini 1982; Terborgh 1983; Ferrari 1988; Rylands 1990; Peres 1989, 1991). Foraging callitrichids tend to adopt either (i) a manipulative-search pattern, targeted on sedentary prey items which can be removed from relatively discrete microhabitats, or (ii) a visual-search and pounce pattern, targeted on mobile prey fully exposed on foliage. Whether a given species forages manipulatively or visually should be related to its body size, other morphological adaptations, and the availability of prey types and prey substrates in its habitat. For instance, in the largest-bodied callitrichids – lion tamarins *Leontopithecus* (c. 650 g) – pouncing may have become impossible because violent motion of flexible, terminal substrates (branches) would reduce the efficiency of captures by stealth (Peres 1986). This may have reinforced morphological specializations to deal with sedentary prey. Lion tamarins' long, slender fingers, for instance, enable them to extract deeply embedded items, such as tree frogs (*Hyla* spp.) hiding in bromeliads and other common microhabitats (Peres 1989).

Mobile folivorous insects are highly abundant, because their substrates and potential food sources occur

at very high biomass densities. Tettigoniid orthopterans made up a very large proportion of tamarins' non-vegetative diet, reflecting the very high katydid diversity and productivity in neotropical forests (Beier 1962; Nickle 1988; Janson and Emmons 1990; Belwood in press). This group of nocturnal insects faces a wide suite of acoustically-oriented leaf-gleaning predators by night (e.g. phyllostomid bats: Belwood and Morris 1987), and visually-oriented ones while they roost during the day (e.g. birds: Willis and Oniki 1978; Gradwohl and Greenberg 1984; Remsen and Parker 1984; Munn 1985; primates: Terborgh 1983; this study).

The abundance of katydid and other prey taken by *Saguinus* was not sampled along the forest vertical gradient. Herbivorous orthopterans would be expected to track their foraging substrates, primarily young terminal foliage. Prey items such as leaf-roosting katydids should then be most common in the midstorey, less common in the upper canopy, and least common in the low understorey, if prey density correlates with foliage density (J. Malcolm, unpubl. data). This distribution need not be the same for prey embedded in natural shelters, which would be expected to conform with the stratification of woody and dead plant materials, which appear to be more abundant at lower heights (cf. Gradwohl and Greenberg 1984; Remsen and Parker 1984). Moreover, because many prey capable of actively evading predators drop to low substrates (often the soil leaf-litter) when exposed to predation threats, foraging heights of predators searching for either undisturbed or disturbed prey should also diverge accordingly.

The pursuit of mobile prey forced saddle-backs but not moustached tamarins to forage lower in the forest, which can be partly explained by (i) the former species' ability to retrieve flushed prey, and (ii) the latter species' ability to operate as leaf-gleaners, capturing and flushing mobile prey directly from the midstorey foliage. Searching for and capturing prey flushed to lower heights thus appeared to reinforce the use of the understorey for saddle-backs. Capture heights of sedentary prey – which suffer no interference of flushing activity – also differed between tamarin species along with the vertical stratification of microhabitats they searched: the rigid substrates preferred by saddle-backs (e.g. basal tree-trunks) were always lower than, say, the terminal twigs used by moustached tamarins.

Interspecific divergence in prey substrates searched and capture methods should be most strongly demarcated in mixed-species groups because resource use by associated species usually overlaps in both space and time. This appears to be the case in other mixed-species primate groups, where partitioning of substrates searched conforms to prey capture method (Yoneda 1984; Terborgh 1983; Cords 1987; Gautier-Hion 1988). Of five primate species studied by Terborgh (1983), for instance, overlap in foraging substrates was lowest between two tamarin species foraging in mixed-species groups. This form of resource partitioning is even more refined in foraging parties of avian insectivores, particularly in the highly species-rich flocks of Neotropical forests (Munn and Terborgh 1979; Wiley 1980). These flocks usually

consist of some 20, and as many as 40, species foraging together, most of which pursue arthropods of one kind or another (Munn 1985; Munn and Terborgh 1979; Peres and Whittaker 1991). Opportunities for evolution of intricate interspecific interactions, such as deceptive alarm calls followed by piracy of prey items (Munn 1986), are considerable because the temporal stability of these groups and their individual membership are very high.

It has been proposed (but not tested) that a species' flushing activity may enhance the foraging success of another in polyspecific primate groups both in the New (e.g. Klein and Klein 1973) and Old World (Gartlan and Struhsaker 1972; Gautier-Hion and Gautier 1974; Rudran 1978). More recently, however, this possibility has been almost entirely dismissed or ignored (Struhsaker 1981; Terborgh 1983; Oates and Whitesides 1990). Previous studies of mixed-species groups of tamarins have emphasised interspecific divergences in foraging height, substrates searched, and capture techniques during active foraging (Pook and Pook 1982; Terborgh 1983; Yoneda 1984), but failed to document any direct advantages related to prey capture success. Terborgh (1983) states that prey foraging benefits should work for birds but not for monkeys because "once startled they [large mobile prey] can easily bound or fly away". While birds are best at intercepting prey in mid-air – a feat largely impossible for non-volant mammals – saddle-backs were adept at locating the landing point of prey items on the forest floor and retrieving them. It is thus clearly demonstrated that a large proportion of the prey captures of at least some group members were facilitated by heterospecifics. However, because tamarin species very rarely foraged apart from one another – forming one of the most stable mixed-species associations documented to date – it was not feasible to test whether their foraging success would indeed have been lower in monospecific groups.

In the Urucu, saddle-backs were not the only commensal beneficiary of the beating effect caused by moustached tamarins. Several species of avian insectivores also joined tamarin groups to enjoy facilitated captures of disturbed or disclosed prey. Although double-toothed kites *Harpagus bidentatus* were the most regular followers of tamarins, this role was also played by red-billed ground cuckoos *Neomorphus pucheranii*, white-browed hawks *Leucopternis kuhli*, red-necked woodpeckers *Campyphilus rubricolis*, and occasionally plain-brown woodcreepers *Dendrocincla fuliginosa*, white-fronted nunbirds *Monasa morphoeus*, and great jacamars *Jacamerops aurea* (Peres and Whittaker 1991; unpubl. data). General benefits of joining monkey groups for certain bird species have been shown at a number of other forest sites (Gautier-Hion and Gautier 1974; Fontaine 1980; Terborgh 1983; Boinski and Scott 1988; Peres and Whittaker 1991). Similarly, both multi-species flocks of understory avian insectivores (Willis and Oniki 1978; Peres, unpubl. data), and monospecific groups of three marmoset species (Rylands et al. 1989) are known to associate with army ants to take advantage of flushed prey, in this case primarily leaf-litter arthropods.

There was a strong between-species asymmetry in the

net foraging benefits derived from the presence of heterospecifics. Individual moustached tamarins almost always foraged autonomously for mobile prey, thus gaining little from nearby saddle-backs. Individuals of this latter species, on the other hand, more than doubled their prey yield by foraging passively alongside moustached tamarins and capturing prey items flushed by this species. This energetically conservative pursuit of flushed insects accounted for most of the prey biomass harvested by saddle-backs, representing a very strong incentive for this species to associate with moustached tamarins. The retrieval of flushed prey by saddle-backs appeared to incur little or no costs to moustached tamarins, because prey items diving for cover became largely inaccessible both to the flusher and its conspecifics.

Munn (1986) also reports that certain core members of polyspecific bird flocks in the forest canopy and understory rely on insect-flushing abilities of other species for $\geq 85\%$ of their food. These species' roles in the flock are, however, the reverse of those of tamarins, in that the beneficiary species act as key sentinels, often warning the flock of approaching bird-eating raptors, whereas in tamarins the species providing flushed prey is also responsible for most of the group's vigilance effort against avian predators (Peres in press).

Given that foraging benefits are strongly biased towards one of the two tamarin species, what then accounts for the efforts invested by the other in consistently maintaining their association? The answer probably lies in the realm of other adaptive advantages of mixed-species group living, which for tamarins include joint territorial defence of a large, congruent home range, and division of labour in locating plant-food patches and detecting different forms of predation threats held in common (Peres 1991). Should we be able to integrate these disparate fitness components into a common, measurable currency of natural selection (e.g. lifetime reproductive success), we may still find an asymmetric pay-off favouring saddle-backs. Mixed-species groups, however, should evolve and remain stable so long as the ensuing benefits are greater than the costs for each species independently, given the ever-present alternative of monospecific life.

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