

Variable specificity in the anti-predator vocalizations and behaviour of the white-faced capuchin, *Cebus capucinus*

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Summary

Much research in animal communication is aimed at understanding the functional design features of animal vocal signals. Our detailed analyses of the vocalizations and behavioural responses elicited in white-faced capuchins by predators and other disturbances point to two call variants that differ modestly in their acoustic structure and that are accompanied by functionally distinct behavioural responses. The first variant is given exclusively to avian predators and is almost invariably accompanied by the monkey's immediate descent from the treetops where it is most vulnerable; therefore, we label this call variant the 'aerial predator alarm'. The second variant, that differs only slightly but noticeably from the first, is given to a wide range of snakes and mammals, including a range of species that represent no predatory threat to the monkeys. This second call is also associated with more variable responses from calling monkeys, from delayed retreat from the source of disturbance, to active approach, inspection, and sometimes mobbing of the animal involved. We therefore label this variant more generally as an 'alerting call'. Although some other primate species show a more diverse system of anti-predator calls, and the capuchins themselves may yet be found to produce a greater variety of calls, a system of two call variants with varying degrees of predator specificity and behavioural response is not uncommon among primates and appears functionally appropriate for capuchins. The basic structure of the alerting call allows conspecific listeners to localize the caller and the source of disturbance readily, thereby allowing listeners to approach and assist in mobbing in cases where the disturbance warrants it, or to avoid the area in cases where the disturbance is identified as a predatory threat. Conversely, the aerial predator alarm is inherently less localizable and therefore conveys the

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presence of a predator to conspecific listeners nearby while allowing the signaler itself to remain relatively inconspicuous.

Keywords: vocalizations, alarm call, alerting call, *Cebus*.

Introduction

Much research in animal communication is aimed at understanding the potential adaptive function of vocal signals and the underlying proximate mechanisms that guide both their production in callers and their interpretation by listeners. Vocalizations given in response to encountering predators have been a particular focus of research because these vocalizations mediate events with high adaptive significance and because they are also associated with relatively discrete and unambiguous eliciting stimuli (specific types of predator) and typically precipitate dramatic behavioural responses that are readily observed by researchers. This combination of factors facilitates research into the function of these vocalizations as well as the proximate mechanisms through which the animals themselves perceive, categorize, and interpret elements of the world around them (Cheney & Seyfarth, 1990; Owings, 1994).

Research on many different species has revealed important variation both in the diversity of anti-predator vocalizations that are produced and in the functional behavioural responses that accompany them. For example, seminal work by Marler (1955) identified two structurally and functionally distinct types of call that small birds produce when encountering larger raptorial predators. One variant is given to flying raptors that represent an immediate threat. This call, often called a 'seet', is generally a high-frequency, tonal signal with gradual onsets and offsets that is audible to conspecific listeners nearby but is otherwise difficult to localize in space. This combination of features allows the caller to announce the presence of a threatening predator to conspecifics without drawing additional attention to itself. Accordingly, this type of call is also associated with cryptic behaviour such as immediate flight and hiding, or freezing. A second call variant is given to perched raptors that represent no immediate threat but could become a threat if they remain in the area. This call, sometimes also referred to as the 'chink' or 'chert' call, is generally a short, broad-band (or noisy) signal with abrupt onsets and offsets, which makes it comparatively easy to localize. Notably, this

call type is associated with active recruitment of others to the location of the disturbance followed by collective mobbing of the perched predator.

Subsequent research on primates has revealed even greater diversification in the structure of anti-predator vocalizations in some species as well as in the functional behavioural responses associated with each call variant. For example, early work on vervet monkeys documented at least three different call variants given to three different classes of predator that prey on the monkeys — large snakes, such as the python; large raptors, such as the martial eagle; and large cats, most notably the leopard (Struhsaker, 1967; Seyfarth et al., 1980). Because each call variant appears to pick out a different type of predator quite specifically and to precipitate a different escape response that is functionally appropriate to each type, the anti-predator calls of vervet monkeys have been proposed to represent, or refer to, the different predators in a way that is at least crudely similar to our own human words for these animals. Additional research has documented similar referential properties in the anti-predator calls of several other primate species, as well as some non-primate mammals and birds (Gyger et al., 1987; Slobodchikoff et al., 1991; Evans et al., 1993; Zuberbühler, 2000).

At the same time, research on other primates and other mammals suggests that acoustically distinct anti-predator calls do not always represent the different predators per se but can instead signal differences in the relative threat or danger associated with them, or in the urgency of response that is required (Masataka, 1983; Le Roux et al., 2001; Randall & Rogovin, 2002). For example, California ground squirrels (*Spermophilus beecheyi*) generally produce 'whistle' alarm calls when they encounter large raptors (e.g., various species of eagle or hawk) and 'chatter' alarm calls when they encounter terrestrial predators, such as the coyote (Owings & Virginia, 1978; Owings & Leger, 1980). Although production of these two call variants often correlates closely with this categorical difference between aerial and terrestrial predators, careful research has shown that it actually tracks the imminence of the danger involved — and thus also the urgency of the response that is required — in specific encounters with either predator type (Owings & Hennessy, 1984).

Taken together, this body of work has highlighted the variety of possible patterns of call diversification and functional behavioural responses to predators that might exist across taxa, sparking productive theorizing about

the relative importance to each of these dimensions of the range of predatory threats encountered by a particular species and the range of possible escape options that are available to it (e.g., Macedonia & Evans, 1993). More recently, researchers have considered the additional possibility that conspecific listeners might not be the only targets of anti-predator calls, and that some of them might instead be directed at the predators themselves as part of an attempt to repel them, or otherwise communicate to them that they have been discovered and that their probability of a successful hunt is therefore minimal (e.g., Owings & Hennessy, 1984; Zuberbühler et al., 1999; Shelley & Blumstein, 2005). This focus has also underscored the important influence that listener sensory and perceptual systems might have in affecting the structural design of anti-predator vocalizations based on the broader realization that certain signal features might be inherently more detectable to receivers, more memorable to them, or otherwise more influential in capturing and channeling their attention and responsiveness (Marler, 1955; Guilford & Dawkins, 1991; McConnell, 1991; Endler, 1992; Fernald, 1992; Endler & Basolo, 1998; Ryan, 1998). These various insights have been integrated into more general frameworks that attempt to account for the functional design of these and other types of signals (Endler, 1992; Owings & Morton, 1997, 1998; Owren & Rendall, 1997, 2001; Ryan, 1998).

In this paper, we report research on the anti-predator vocalizations and associated behavioural responses of the white-faced capuchin, a group-living neotropical primate. There has been little systematic research on the anti-predator vocalizations and behaviour of New World monkeys generally; however, they represent an especially productive focus for comparative research on anti-predator call diversification and function because they are taxonomically distinct from, but behaviourally quite similar to, the monkeys of the Old World (e.g., vervets, macaques, and baboons) for which systematic research has documented structurally and functionally distinct anti-predator calls (Seyfarth et al., 1980; Fischer, 1998; Fischer et al., 2001). Capuchins make an especially promising focus here because they are similar in many respects to Old World vervet monkeys. Both are small-bodied primates and both are semi-arboreal and semi-terrestrial. As a result, they are both exposed to a wide range of possible raptors, snakes, and mammalian predators, and they inhabit a three-dimensional environment that affords a variety of potential escape options, which are two of the most important factors proposed to influence the diversification of anti-predator vocalizations and responses (Macedonia & Evans, 1993). Indeed, a handful of previous studies

have suggested that capuchins might use distinct alarm calls for different types of predators including snakes, large cats, and raptors (Oppenheimer, 1968; Norris, 1990; Di Bitetti, 2001; Fichtel et al., 2005). However, the degree of call diversification and the functional pressures that have influenced it remain unclear.

Methods

Study site and species

Research was conducted in Santa Rosa National Park, which is a 108 km² park located in the larger Area de Conservacion Guanacaste approximately 35 km northwest of Liberia, Guanacaste, Costa Rica (Fedigan & Jack, 2004). There are two distinct seasons in this area, a dry season that runs from mid-December through late May with little or no rainfall, and a rainy season from June through late November with mean rainfall of approximately 1473 mm (Janzen, 1983).

This study was carried out on two habituated groups of white-faced capuchins that are part of a long-term study by Dr. L.M. Fedigan. One group, named Cerco de Piedra (CP), had 18 members and consisted of two adult males, one sub-adult male, five adult females, seven juveniles and three infants. The other group, named Los Valles (LV), had 18 members and consisted of three adult and two sub-adult males, five adult females, six juveniles and two infants. In this study, we focused on the behaviour and vocalizations of adults (\geq six years of age) in both groups to avoid potential age confounds in the structure and usage of vocalizations that can sometimes occur (e.g., Seyfarth & Cheney, 1986).

Behavioural observations and vocalization recording

Behavioural and vocal data were collected by S.M.D. from May to July 2002 and from January to June 2003 using the sequence sample method (Lehner, 1996). A sequence began when loud vocalizations made by the capuchins were heard, or when a potential predator was spotted, and continued until vocalizations by the focal animal had ceased for 10 minutes. During this time, all vocalizations were recorded and several associated behaviours exhibited by the caller were scored continuously. Vocalizations were recorded on Maxwell XII-S metal tapes using a Sony WM-D6C recorder and a Sennheiser

ME66 directional microphone. Recordings were then digitized to a Macintosh iBook computer with 16-bit accuracy at a sampling rate of 44.1 kHz.

Vocalization sample

In total, we recorded 113 bouts of calling from adult individuals. Some individuals contributed disproportionately to the recordings database, and some recordings contained considerable background noise associated with the monkeys' activity in response to predators that prohibited detailed acoustic analyses of them. After screening for both factors, we retained for subsequent acoustic analyses a total of 57 bouts of calling, representing 227 individual vocalizations that represented the highest possible recording quality and the best possible balance of individuals. This sample comprised calling bouts from 36 separate encounters with predators or other sources of disturbance. Of these, 11 encounters were associated with birds, 16 encounters were associated with snakes, and nine encounters were associated with terrestrial mammals. Table 1 provides additional details of the number of individuals contributing vocalizations in each predator category, as well as the number of bouts they contributed and the number of individual vocalizations that this represented.

Acoustic analysis

To test the potential specificity of vocalizations produced to each class of predator, our analysis of call recordings proceeded in two steps. First, we undertook detailed spectrographic analyses of the structure of recorded calls using the PRAAT[®] acoustic analysis software (Version 4.1.9). Our acoustic analysis focused on the structure of individual vocalizations. For each vocalization, we measured a standard set of temporal and spectral features. In the temporal domain, we measured the duration of each call from its waveform representation, and we used two measures of the intensity trajectory of each call to characterize the relative smoothness or abruptness of its onset. Here, we used the intensity contour display in PRAAT to measure signal intensity from call onset to the point of maximum intensity both as an absolute value (in seconds) and as a proportion of call duration.

We characterized the spectral structure of each vocalization using several variables. First, we made a qualitative assessment of the relative harshness or tonality of each call using a 5-point scale where: 1 = noisy, 2 = primarily

Table 1. Details of vocalization sample.

Predator category	Individual callers	Number of call bouts for each predator category	Total number of calls for each predator category
Bird/Terrestrial/Snake	Limp*	3/2/2	4/9/7
Bird/Terrestrial/Snake	K-Lee	1/1/1	1/6/7
Bird/Terrestrial/Snake	Timone	2/1/2	5/3/8
Bird/Terrestrial/Snake	Pumba	1/1/2	1/4/14
Bird/Terrestrial/Snake	Salsa	1/1/2	3/2/8
Bird/Terrestrial/Snake	Fiesty	1/1/3	3/6/9
Bird/Snake	Dos Leches	1/1	2/7
Bird/Snake	Nyla	1/4	2/16
Terrestrial/Snake	Picante*	1/1	6/2
Terrestrial/Snake	Rafiki*	2/4	11/11
Terrestrial/Snake	Nose*	3/2	14/10
Terrestrial	Trickle*	1	6
Snake	Chili	2	10
Snake	Alien	1	7
Snake	Tobasco	1	7
Snake	Seria	3	9
Snake	Blanquita	1	7
Bird Total	8	11	21
Terrestrial Total	10	14	67
Snake Total	16	32	139

* Individuals that contributed calls in response to encountering a tayra.

noise with minor tonal components, 3 = obvious tonal components, 4 = more tonality than noise, 5 = tonal, no noise. We supplemented this approach by using Linear Predictive Coding (LPC) to identify a set of spectral peaks in each call. LPC is a spectral smoothing technique used routinely in the analysis of human speech to identify broad spectral peaks that represent the resonances of the vocal tract (Markel & Gray, 1976). However, there is nothing conceptually specific about the application of LPC to speech sounds, or to vocal tract resonances. Rather, it can be used more generally to identify spectral peaks in a variety of acoustic signals, and it is particularly useful in the analysis of signals whose noisy structure otherwise precludes extraction of specific frequency measurements (Owren & Bernacki, 1997). Thus, we used LPC here to identify peaks in the often noisy frequency spectrum of the calls capuchins produced in response to predators without making any assumption that the peaks necessarily reflected the resonance properties of

the vocal tract. It is possible, for example, that the spectral peaks identified reflect the action of the laryngeal source instead.

We used autocorrelation-based LPC to identify the frequency of major spectral peaks in each call. The LPC analysis was based on a 256-point fast-Fourier-transform (FFT) taken from the midpoint of each call using 40 coefficients and full pre-emphasis starting at 50 Hz. We used a large number of coefficients in this analysis because our high sampling rate (44.1 kHz) produced a very large bandwidth for the signals (20 kHz) and there were a number of minor peaks in the high-frequency end of this range. Therefore, in order to accurately fit the 3-4 major spectral peaks occurring in the frequency range below 10 kHz, which is the range that is most likely to be salient to the monkeys, it was necessary to increase the order of the LPC analysis.

We then tested for consistent differences in the vocalizations given to different predator classes in two ways. First, we used univariate Analysis of Variance (ANOVA) to test for significant differences in each acoustic feature considered separately. Second, we used multivariate discriminant function analysis (DFA) to test for consistent differences in the structure of calls produced to different classes of predators when all acoustic features were considered simultaneously. The latter is a more comprehensive test of overall structural differentiation in the calls.

Behavioural analysis

To evaluate differences in the monkeys' behavioural responses to the various classes of predators, we used the Pearson Chi-square statistic to test for significant associations between particular predator types and the specific patterns of response they elicited from the monkeys.

Results

General vocal responses to predators and other disturbances

Adult capuchins produced vocalizations when they encountered a variety of different species. Many of these species were known or potential predators of capuchins, or closely related neotropical primates, but some of them were unlikely to prey on the monkeys. For example, the monkeys vocalized in response to a variety of snakes, including the poisonous rattlesnake (*Crotalus*

durissus) and constrictor species (e.g., *Boa constrictor*), which are known to prey upon capuchins (Chapman, 1986). They also gave calls to a variety of terrestrial mammals. One of these, the tayra (*Eira barbara*), is a carnivorous mustelid that is widely considered a predatory threat to capuchins, since it has been seen to chase them (Hernandez & Cooper, 1976) and to take other mammalian prey the size of immature capuchins (Presley, 2000). It is also a confirmed predator on other neotropical monkeys (Galef et al., 1976). However, several non-threatening terrestrial mammals also elicited calling from the capuchins, such as raccoons (*Procyon lotor*), coatis (*Nasua narcia*), and peccaries (*Tayassu tajacu*).

The capuchins called in response to several bird species as well, including turkey vultures (*Cathartes aura*), roadside hawks (*Buteo magnirostri*), and laughing falcons (*Herpetotheres cachinnans*). The latter two species are small raptors (40-50 cm) that may occasionally threaten young capuchins but probably do not represent a serious threat to adults. Similarly, although vultures are large birds that resemble larger raptors that do threaten capuchins and other neotropical monkeys (e.g., the harpy eagle, *Harpia harpyja*; Rettig, 1978); they too are unlikely to actually prey on the capuchins. However, vocalizations produced in response to these species were always given to birds that were flying above the monkeys rather than perched, and in most cases the bird was rapidly diving or swooping down. Therefore, it is possible that the monkeys did not always get an adequate opportunity to accurately identify these birds before responding.

Behavioural responses to predators

We observed several different types of response from calling monkeys that had encountered a predator. In the case of birds spotted overhead, the monkeys would typically scan the sky above them and move quickly down the tree that they were in. They generally responded the same way when they heard calls given by others to potential bird predators. In contrast, when they encountered a snake or terrestrial mammal predator, they typically moved up off the ground or higher in a tree. In response to hearing calls given to snakes or terrestrial mammals, most individuals would first scan the area and then move up in the trees. However, their responses were not as rapid as when they actually encountered either type of predator. In many cases, monkeys encountering a snake or terrestrial predator would actively mob it, by

moving towards it, dropping objects (e.g., branches) on it, and occasionally making physical contact with it, all while giving repeated vocalizations.

Mobbing occurred on 33 occasions, all during encounters with either snakes or terrestrial mammals. The mobbing response varied across individuals. Males were more frequent mobbers than females, participating in 29 of 33 mobbing encounters. In contrast, females participated in only 4 of 33 mobbing encounters ($\chi^2 = 37.84$, $df = 1$, $p < 0.001$).

We tested the association between these behavioural responses by the monkeys and the types of predator encountered using chi-square tests. In this analysis, we used 82 events for which the predator was positively identified and we focused only on the behaviour of the calling animal. There was a significant association between the type of predator encountered and the behavioural response of the caller ($\chi^2 = 26.596$, $df = 2$, $p < 0.001$). Individuals who called to birds generally moved down the tree towards the ground (14 of 19 events) rather than up off the ground into the trees. Conversely, individuals who called to snakes almost invariably moved up off the ground (40 of 44 events). Finally, individuals who called to terrestrial mammals showed mixed responses, often moving down the tree they were in (12 of 19 events) but sometimes moving up the tree instead (7 of 19 events).

Structural differences in anti-predator vocalizations

Vocalizations produced by capuchins in response to birds were generally harsh to our ear (i.e., had a noisy spectral structure), and they were typically given only in a single burst of one or two calls. Vocalizations produced in response to snakes and terrestrial mammals were similarly noisy in structure (Figure 1). However, individual calls given in these contexts were noticeably shorter in duration and seemed to have a more abrupt onset giving them a more plosive, or bark-like, quality. They were also typically given in protracted bouts of repeated calling.

Univariate analysis of variance

To more systematically evaluate potential structural differences in the individual vocalizations produced by the capuchins, we grouped the calls into three different categories according to fundamental differences in the class of animal that elicited the calls: birds, snakes, and terrestrial mammals. We then used univariate ANOVA to test for significant differences in each of

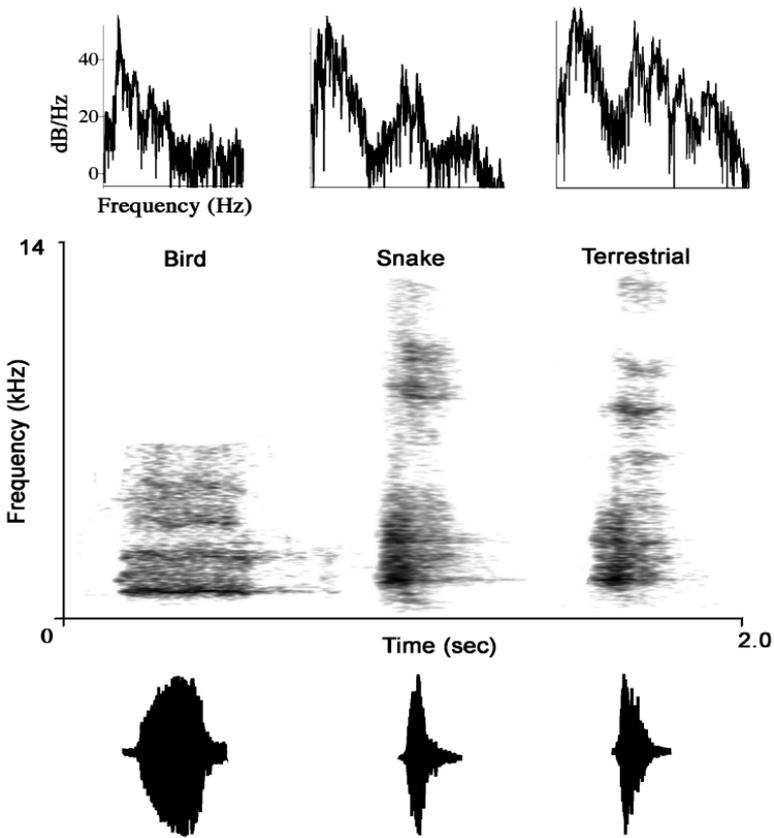


Figure 1. Waveforms, spectrograms, and frequency spectra (FFT) for vocalizations produced by white-faced capuchins to bird, snake, and terrestrial threats. All three calls show a similar broad-band structure, but the call to birds is longer than the other two and slightly more tonal. It also has a more gradual intensity onset evident in the more gently sloped envelope of its air-pressure waveform.

the acoustic features measured across these three predator categories. This analysis confirmed the basic difference in call duration between calls given to birds and those given to either snakes or terrestrial mammals. Post-hoc analyses indicated that the mean duration of calls to birds (0.296 s) was significantly longer than the mean duration of calls given to either snakes or terrestrial mammals (0.128 s and 0.131 s, respectively), while the mean duration of calls given to the latter two predator classes did not differ (Table 2).

ANOVA analysis also confirmed our impression that alarm calls to snakes and terrestrial mammals had more abrupt onsets than those given to birds whether call onset was measured in absolute temporal terms or as a percent-

Table 2. Acoustic features of capuchin alarm calls, their mean values (\pm SD), and statistics from univariate Analysis of Variance¹⁾ and Discriminant Function Analysis²⁾.

Acoustic feature	ANOVA				
	Bird	Snake	Terrestrial	F-value; p-value	DFA
Call duration (s)	0.296 (0.07) A	0.132 (0.02) B	0.132 (0.02) B	258.1; <0.001	*
Onset abruptness (s)	0.131 (0.02) A	0.024 (0.005) B	0.023 (0.004) B	1485.5; <0.001	*
Onset abruptness (% of duration)	47.7 (18.0) A	18.6 (5.66) B	18.3 (4.11) B	168.7; <0.001	
LPC Peak 1:					
Frequency (Hz)	1043.4 (158)	1159.4 (142)	1134.9 (236)	3.9; 0.02	
Bandwidth (Hz)	152.3 (119)	138.9 (215)	83.8 (125)	3.2; 0.03	
LPC Peak 2:					
Frequency (Hz)	1855.6 (361)	2025.1 (\pm 1231)	1855.7 (826)	2.8; 0.05	
Bandwidth (Hz)	857.6 (789) A	374.5 (474) B	472.3 (386) B	9.0; <0.001	
LPC Peak 3:					
Frequency (Hz)	2239.6 (1424)	2645.0 (1577)	2330.5 (1614)	3.1; 0.03	
Bandwidth (Hz)	581.2 (489.6) A	96.2 (107.4) B	187.9 (263.1) B	11.2; <0.001	
Call Tonality	1.38 (0.49) A	2.07 (0.94) B	1.45 (0.50) A	17.1; <0.001	

¹⁾ Letters A and B indicate the predator categories between which the acoustic differences in call features were statistically significant in post-hoc analyses using Tukey's HSD.

²⁾ Asterisks (*) indicate acoustic features with canonical weights greater than 0.5 on discriminant function 1.

age of overall call duration (Table 2). Thus, the peak intensity of calls given to birds was reached at 0.131 s, or about the midpoint of these calls (47.7% of call duration), while the peak intensity of calls given to snakes and to terrestrial mammals occurred significantly earlier in these calls at 0.025 s and 0.024 s, respectively (or 18.6% and 18.3% of call duration). The timing of the peak intensity did not differ between calls given to snakes and terrestrial mammals.

Some of the spectral features of vocalizations showed the same pattern of differences. Thus, the bandwidth of the second LPC peak differed significantly between calls given to birds and those given to both snakes and

terrestrial mammals but not between the latter two categories (Table 2). The bandwidth of the third LPC peak showed the same pattern of differences. Our qualitative measure of call tonality also differed significantly between predator categories, but the pattern was different for this feature. Calls given to birds and terrestrial mammals were both significantly harsher (or less tonal) in structure than those given to snakes, but there was no significant difference in the harshness of calls given to birds or terrestrial mammals (Table 2). The remaining spectral features did not show significant differences between predator categories at an alpha level of 0.01.

Discriminant function analysis

This analysis considered all acoustic features of the vocalizations simultaneously and searched for the combination of features that would best discriminate between calls that had been elicited by the different classes of predator (birds, snakes, and terrestrial mammals). The overall Wilks' Lambda that resulted from this analysis was 0.05. Wilks' Lambda is a multivariate statistic that can vary from 0.0 to 1.0, with the former indicating complete differentiation between the calls elicited by different predator classes and the latter indicating no differentiation in the calls elicited by different predator classes. The statistical significance of a given value of Wilks' Lambda can also be evaluated using the chi-square approximation. In this case, the observed Wilks' Lambda (0.05) indicates considerable differentiation in the structure of calls given to the three different predator classes, and it was also statistically significant when tested using the chi-square approximation ($\chi^2 = 656.86$; $p < 0.001$).

This significant differentiation was captured primarily only in the first discriminant function that separated calls given to birds from those given to either snakes or terrestrial mammals. This first discriminant function was associated with the original acoustic features of call duration and call abruptness (Table 2). The eigenvalue associated with this function was 15.74. The eigenvalue associated with a particular discriminant function summarizes the ratio of between- to within-group variance in the multivariate dimension, and, like Wilks' Lambda, is another useful measure of the degree of differentiation between groups. An eigenvalue of 1.0 indicates that the variation between groups and within groups is the same. Values greater than one indicate that the variation between groups is greater than it is within them,

and values less than one indicate that the variation is greater within groups than between them. In this case, then, the eigenvalue for the first discriminant function (15.74) indicates that the variation in structure between calls given to birds and those given to the combination of snakes and terrestrial mammals was much greater than was the variation within the two functional groupings combined.

In contrast, the eigenvalue associated with the second discriminant function that attempted to separate calls given to snakes from those given to terrestrial mammals was only 0.21 indicating that the variation within the snake and terrestrial mammal classes was greater than was the variation between them. The Wilks' Lambda statistic associated with this second discriminant function was 0.826. This value is statistically significant using the chi-square approximation ($\chi^2 = 41.86$; $p < 0.001$); however, its absolute magnitude confirms the relatively weak discrimination of calls given to these two predator classes by comparison to those given to birds. This asymmetry in the relative distinctiveness of calls given to birds versus those given to snakes and terrestrial mammals is illustrated in Figure 2.

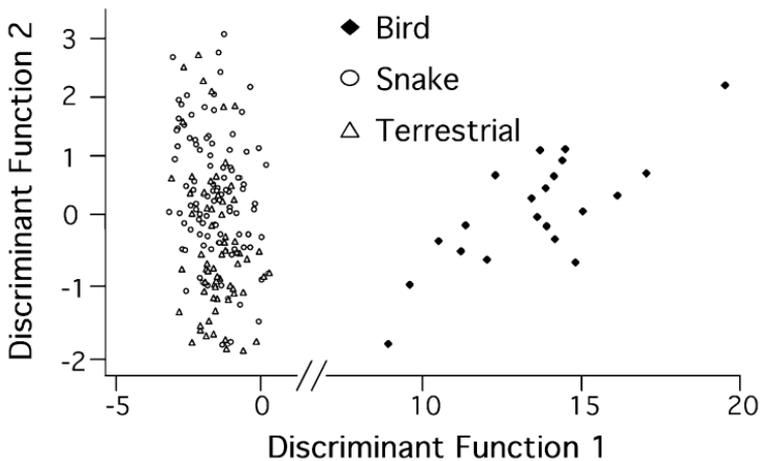


Figure 2. Scatterplot based on the values of each vocalization given to a bird, snake, or terrestrial mammal on the first two functions from discriminant function analysis. The separation between calls to birds and those given to snakes and terrestrial mammals is obvious, and occurs primarily along the first discriminant function. In contrast, there is almost complete overlap in the distributions of calls given to snakes and terrestrial mammals on both discriminant functions, accounting for the modest classification success of calls elicited by these two predator types.

Table 3. Results of discriminant function classification of vocalizations given to birds, snakes, and terrestrial mammals.

Predator type	Predicted bird	Predicted snake	Predicted terrestrial	Total
Bird	21	0	0	21
Snake	0	92	47	139
Terrestrial	0	15	52	67
Total correct:				165/227

These result patterns are born out in more practical terms by the results of the discriminant function classification of the individual calls (Table 3). Using the discriminant functions to classify each of the calls in the sample, a total of 165 of the 227 calls (72.7%) could be correctly assigned to the predator type that elicited them. However, there was considerable variation in the classification success across the different predator types. Fully 100% of the calls given to birds were correctly categorized, whereas only 66.2% and 77.6% of the calls given to snakes and terrestrial mammals, respectively, were correctly classified. Additionally, misclassified snake and terrestrial mammal calls were attributed only to one or the other of these two categories and never to the bird category.

We conducted a second discriminant analysis, identical to the first, except that we limited the cases of calls given to terrestrial mammals to only those given in encounters with tayras. We undertook this modification because we felt that the cases in which calls were given to non-predatory mammals might be confounding the analysis and blurring possible distinctions between the calls given to snakes and terrestrial predators. After eliminating calls given to non-predatory mammals, the remaining sample of calls given to terrestrial predators consisted of 33 calls produced by five different individuals in four separate encounters with a tayra (Table 4).

The results of this discriminant analysis were similar to those of the original analysis. Once again, the overall Wilks' Lambda (0.043) indicated significant differentiation across the three predator classes ($\chi^2 = 581.75$; $p < 0.001$), with a large eigenvalue for the first discriminant function (17.24) separating calls given to birds from those given to snakes and terrestrial mammals. However, there was evidence this time of greater discrimination between the calls given to snakes and those given specifically to tayras. The

Table 4. Results of discriminant function classification of vocalizations given to birds, snakes, and tayras.

Predator type	Predicted bird	Predicted snake	Predicted tayra	Total
Bird	21	0	0	21
Snake	0	103	36	139
Tayra	0	4	29	33
Total correct:				153/193

eigenvalue for the second discriminant function separating these two predator classes (0.262) was somewhat higher than it was in the original analysis, and it was also associated with a smaller value of Wilks' Lambda (0.793, $\chi^2 = 43.10$; $p < 0.01$). Discriminant function classification of the calls was also slightly better. Here again, all of the calls given to birds were correctly assigned, but successful classification of the calls given to snakes and to tayras improved to 74.1% and 87.9%, respectively.

Part of this improvement might reflect the smaller number of individuals contributing calls to the tayra category ($N = 5$) in this analysis by comparison to the number contributing calls to the broader terrestrial category in the original analysis ($N = 10$). This difference in sample size would necessarily affect the amount of individual variation in the calls that interacted with potential variation in the calls according to predator type in the two analyses, which could contribute to better sorting of tayra calls in the second analysis due simply to a reduction in the confounding individual variation in these calls.

Discussion

Variably specific anti-predator vocalizations and behaviour in capuchins

White-faced capuchins at Santa Rosa, Costa Rica produced loud vocalizations in response to a variety of birds, snakes, and mammals. Many of the species eliciting calls from the monkeys were known or likely predators of the monkeys (e.g., the tayra and the boa constrictor) but others were not. For example, the capuchins vocalized when they spotted turkey vultures or small falcons, even though neither type of bird is likely to prey on the monkeys. However, in every case, the birds were flying rapidly above the monkeys,

sometimes diving or swooping down nearby. Therefore, the capuchins might not have had time to fully identify the birds before responding, and, as a result, might have treated these species as raptorial predators that they otherwise resemble both in general form and in flight pattern.

At the same time, the monkeys also vocalized when they encountered several non-threatening mammals including raccoons, peccaries, and coatis. None of these species is known to prey on capuchins or other monkey species of similar size — indeed, capuchins are known to prey on coati pups (Perry & Rose, 1994). Nor do any of these species particularly resemble other mammalian predators that the capuchins face such as tayras, ocelots, or jaguars. Therefore, although it is possible that the capuchins sometimes confused a raccoon, peccary, or coati with a predatory species, this seems unlikely to account for the several instances of calling that we observed to these non-threatening species. Instead, it seems more likely that these species are significant to the capuchins in other ways. Raccoons and coatis are both opportunistic omnivores, like the capuchins themselves, feeding on a wide range of foods including fruits, insects, snails, small reptiles, and birds' eggs. The peccary is also omnivorous, feeding on a variety of foods encountered along the ground including insects, woody vegetation, and fruit, particularly that which has fallen, or been discarded, during the course of the capuchins' own arboreal foraging. Therefore, it is possible that these other species are particularly salient to capuchins either as food competitors, or, in the case of coatis, as potential prey.

Thus, although encounters with potential bird predators invariably induced immediate movement by the capuchins down out of the trees, their responses to the snakes and other terrestrial mammals to which they vocalized were more varied. At times, the capuchins actively avoided the latter species after first confirming their presence. However, at other times, they actively approached such species to further inspect or mob them. Mobbing may be functional not only as an attempt to repel some kinds of predator but also as an attempt to irritate and repel potential food competitors.

These patterns and interpretations are also consistent with previous descriptions of variable specificity in the anti-predator vocalizations and behavioural responses of white-faced and other capuchin species (Oppenheimer, 1968; Fichtel et al., 2005). For example, Oppenheimer (1968) and Di Bitetti (2001) both reported that capuchins gave alarm calls not only to a predictable

set of avian and mammalian predators but also to a number of patently non-predatory species including tapir, agouti, armadillos, coati, collared peccary, and even brocket deer. Additionally, Fichtel et al. (2005), studying white-faced capuchins at Lomas Barbudal, Costa Rica, found that the calls given by the monkeys to snakes and terrestrial predators were also used during highly aggressive interactions with conspecifics. In both contexts, the monkeys appeared highly aroused and combined assertive, aggressive postures and behaviours with a tendency both to approach and to withdraw.

This pattern of mixed behavioural responses to predators and other disturbances is mirrored in the results of our detailed analysis of the acoustic structure of the calls given in these contexts. Thus, the calls given to birds, snakes, and terrestrial mammals were broadly similar in being relatively short, broad-band (noisy) calls. Discriminant function analysis consistently differentiated calls given to birds from those given to either snakes or terrestrial mammals, but it revealed far less differentiation in the calls given to the latter two predator categories. There was some evidence that calls given specifically to the tayra, an established mammalian predator, might vary structurally from those given to snakes. However, it is also possible that this result was due to the small sample of individuals contributing calls to the tayra category by comparison to the bird and snake categories. Therefore, additional research, including systematic playback experimentation, is needed to test the potential distinctiveness of the calls given to snakes versus tayras.

Overall, then, the capuchins produced relatively distinctive vocalizations to bird predators and exhibited relatively distinct escape responses to them as well. In contrast, their calls to snakes and mammals were comparatively non-distinct and their responses to both of these predator types were mixed. Taken together, these patterns point to a system of variably specific anti-predator vocalizations and responses in these capuchins. One call, that we label the 'aerial predator alarm', picks out aerial predators relatively specifically and induces a quite specific escape response. The other call, that we label more generally as an 'alerting call', applies far more broadly to a range of predatory and non-predatory species and induces a more diffuse response that involves first identifying the source of disturbance and only then either retreating from it, or approaching it to inspect and potentially mob the animal involved.

This kind of system is not uncommon among primates. For example, white sifakas (*Propithecus verreauxi verreauxi*) and redfronted lemurs (*Eulemur fulvus rufus*) both produce two variants of anti-predator call (Fichtel & Kappeler, 2002). Like capuchins, one is used specifically for birds and consistently elicits the same behavioural response, while the other is given in response to a variety of terrestrial predators but is also used in a range of other situations that are characterized by high arousal (Fichtel & Kappeler, 2002). Similarly, Barbary macaques (*Macaca sylvanus*) are reported to produce several distinctive anti-predator barks in response to dogs, snakes, and humans. However, the calls elicit variable responses that are not uniformly linked to the predator encountered, but appear instead to vary depending upon additional contextual details associated with specific encounters (Fischer & Hammerschmidt, 2001).

Why only two variants of anti-predator call?

It is possible that white-faced capuchins produce more than two variants of anti-predator call. Indeed, the wedge-capped capuchin (*Cebus olivaceus*) is reported to produce at least three distinct calls to snakes, terrestrial mammals, and aerial threats (Norris, 1990), and, in first describing the vocal repertoire of the white-faced capuchin, Oppenheimer (1968) proposed that it too produced three distinct call variants. However, in contrast, Di Bitetti (2001) described only two variants of anti-predator call for the tufted capuchin (*C. apella*), one that was given to aerial predators and one that was given to ground predators. Similarly, Fichtel et al. (2005) reported only two call variants for white-faced capuchins at Lomas Barbudal, both of which agree well with those identified in our study. Nevertheless, it is possible that white-faced capuchins might display one or more additional call variants to large mammalian predators (e.g., puma, jaguar, coyote) that are present at Santa Rosa and other locations but that were not encountered by the monkeys during our study.

Notwithstanding this possibility, the variably specific two-call system observed in white-faced capuchins appears functionally appropriate. To begin with, recent theorists have stressed that the diversity of anti-predator calls in any given species varies less with the diversity of predators per se and more with the diversity of response strategies that are appropriate to them (Macedonia & Evans, 1993). For example, vervet monkeys are semi-terrestrial,

semi-arboreal animals inhabiting a complicated three-dimensional environment that offers a relatively wide range of escape options (e.g., up into trees, down out of trees, under bushes) and the monkeys have developed a corresponding diversity of anti-predator calls. In contrast, ground squirrels inherently have fewer response options for the threats they experience from raptors and terrestrial mammals, retreating ultimately to the safety of their underground burrow being their primary escape response. The salient issue for them for these two types of threat (their responses to snakes are different, Hennessy et al., 1981) becomes the urgency with which they should retreat. As a result, they have developed a two-call system ('whistle' versus 'chatter') for these two predatory threats that prescribes either sustained vigilance or immediate flight (Owings & Hennessy, 1984). The same argument has been applied to the two-call system of some lemur species that are almost entirely arboreal and therefore similarly limited in their range of escape options (Macedonia, 1990).

White-faced capuchins, like vervet monkeys, are semi-terrestrial and semi-arboreal and so, in principle, have a correspondingly diverse range of escape options. Like vervet monkeys, white-faced capuchins are also subject to a range of aerial predators for which an unambiguous escape response is appropriate (rapid descent from the treetops). However, unlike vervet monkeys, many of the mammalian predators that threaten white-faced capuchins (e.g., tayra, ocelot, marguay, jaguarundi) have almost equal capabilities in the trees as on the ground. The response appropriate to such predators may therefore vary depending on both the monkeys' and the predator's positions. Furthermore, because many of these predators are also relatively small-bodied, one option available to white-faced capuchins (but not to vervet monkeys) is active defense, via group approach and mobbing. Hence, the capuchins appear to have developed one call variant for avian predators that is associated with an unambiguous escape response and a second call variant that elicits a more variable response depending on the type of disturbance involved, where it is located, and where the monkeys themselves currently are.

Furthermore, the calls themselves appear well designed for such responses. Both call types are moderately loud but short, broad-band signals which make them maximally audible to other capuchins over short distances against the diffuse background noise of the forest. However, the aerial predator alarm is more protracted than is the call given to snakes and terrestrial

mammals, giving it a less bark-like plosive quality (Figure 1). It is also typically given only singly. Both properties should, in principle, reduce the localizability of the aerial predator alarm giving it a more ventriloquial quality than the call given to snakes and mammals (Marler, 1955). Although the anti-predator calls of primates have not typically been discussed in terms of their relative localizability, such ventriloquial properties are common in the anti-predator calls of a wide variety of other taxa in response to bird predators whose predatory style favors an immediate escape response without attracting additional specific attention to the caller (Marler, 1955; reviewed in Bradbury & Vehrencamp, 1998). For instance, research on Australian honeyeaters, Sebright chickens, common chickens, and small passerine birds has established that even small changes in call structure, especially to the intensity of the introduction of the call, can make individuals less detectable to predators (Wood et al., 2000; Jones & Hill, 2001; Bayly & Evans, 2003). There is also evidence from research on the golden marmot (*Marmota flaviventris*) that callers can make themselves less conspicuous to potential aerial predators by simply reducing the number of 'whistle' calls they produce in a calling bout (Blumstein & Armitage, 1997). Similarly, the capuchins' aerial alarm call appears well designed to capture the attention of conspecifics nearby and induce their rapid descent from the trees, but to do so without dramatically increasing the caller's own susceptibility to predation through increased localization by the bird predator.

In contrast, the more general alerting call given to snakes and mammals is shorter and more plosive (abrupt-onset), giving it a conspicuously bark-like quality. It is also typically given repeatedly in protracted bouts of calling. In combination, its broad-band structure, plosive onset, and repeated nature make it easy to localize (Marler, 1955; Bradbury & Vehrencamp, 1998). These subtle variations in call structure also appear functionally appropriate, as the typical response accompanying these calls and the predatory or non-predatory species associated with them was to localize the source of the calling and then to respond either by fleeing, or by approaching, inspecting, and sometimes mobbing the animal involved. These same acoustic features (short, abrupt-onset, broad-band calls given repeatedly) also characterize mobbing calls used by a wide array of bird species to recruit others to the location of a predator in order to attack or repel it (Marler, 1955). Thus, the call given by white-faced capuchins to snakes and a range of terrestrial mammal species appears to announce the location of some disturbance and

thus in some cases to facilitate recruitment of others to the location to assist in mobbing.

Based on these results and those of related studies (e.g., Di Bitteti, 2001; Fichtel et al., 2005), we tentatively conclude that the white-faced capuchins at Santa Rosa, Costa Rica, produce two variants of vocalization in response to predators and other disturbances. The two variants represent subtle modifications on a common structural design that involves a short, broad-band spectral structure. The modifications involve either increasing or decreasing both the duration and harshness of the call, and smoothing or punctuating its intensity onset, in addition to calling either in short bouts of only a single call or in protracted bouts of multiple calls. These subtle structural modifications, in principle, have the effect of reducing or promoting the localizability of the caller and thus also the source of the disturbance, and this in turn appears well suited to the mix of avian and terrestrial disturbances encountered by the monkeys for which cryptic escape versus active approach and mobbing responses are functionally appropriate.

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