RESEARCH ARTICLE

Development of snake-directed antipredator behavior by wild white-faced capuchin monkeys: III. the signaling properties of alarm-call tonality

Richard G. Coss[1,2] (iD) | Cailey Cavanaugh[1] | Whitney Brennan[2]

[1] Department of Psychology, University of California, Davis, California

[2] Graduate Group in Animal Behavior, University of California, Davis, California

Correspondence
Richard Coss, Department of Psychology, University of California, Davis, One Shields Ave Davis, CA, 95616.
Email: rgcoss@ucdavis.edu

In many primates, the acoustic properties of alarm calls can provide information on the level of perceived predatory threat as well as influence the antipredator behavior of nearby conspecifics. The present study examined the harmonics-to-noise ratio (tonality of spectral structure) of alarm calls emitted by white-faced capuchin monkeys (*Cebus capucinus*) in trees directed at photographic models of a boa constrictor, neotropical rattlesnake, scorpion eater snake, and white snake-shaped control presented on the ground. The average and peak harmonics-to-noise ratios of initial alarm calls by infants, juveniles, and adults and those of nearby second callers were analyzed using PRAAT software. Averaged for age class, the peak harmonics-to-noise ratio of alarm calls directed at the boa constrictor model, characterizing a primary capuchin predator, was reliably higher than the peak harmonics-to-noise ratio of alarm calls directed at the harmless scorpion eater model. This effect was influenced by the higher harmonics-to-noise ratio of infant alarm calls and it disconfirmed our prediction, based on primate vocalization research, that snake perception would increase arousal and alarm-call noisiness. Levels of call tonality did not distinguish the boa and rattlesnake or rattlesnake and scorpion eater models for any age class. Higher alarm-call tonality appeared contagious to nearby perceivers, with focal alarm calling influencing the level of tonality of the first calls of second callers. Together, these findings suggest that the higher peak harmonics-to-noise ratio of capuchin alarm calling directed at snakes is contagious and possibly conveys information about the level of perceived predatory threat.

KEYWORDS
age comparison, alarm-call tonality, antipredator behavior, *Cebus capucinus*, snake-species discrimination

1 | INTRODUCTION

Alarm calling is a particularly nuanced facet of both animal communication and antipredator behavior and can serve two main purposes. It can simultaneously inform nearby conspecifics that a predator is nearby and dissuade predators, particularly ambush predators, from pursuing calling individuals (Tilson & Norton, 1981; Zuberbühler, Jenny, & Bshary, 1999). The latter function is adaptive to both parties, as the predator avoids wasting energy on an unsuccessful ambush, while the prey survives. Such an effect would not apply to ambush snake predators in which hearing is limited to frequencies lower than that typically emitted by alarm calls (Young, 1997, 2003).

Calling can also direct conspecific behavior, either signaling a need to escape or else recruiting conspecifics for other types of antipredator behavior (Fichtel & Hammerschmidt, 2003).

In some species, alarm calls provoke adaptive behavior similar to the behavior elicited by the threat that prompted the call. These types of calls are known as "functionally referential" calls (Evans, 1997; Fischer & Hammerschmidt, 2001; Price et al., 2015), as they appear to "refer" to a specific type of predator or its hunting capabilities. For example, in black-fronted titi monkeys (*Callicebus nigrifrons*), an alarm call given in response to an aerial predator elicits conspecific movement towards undergrowth where raptors cannot reach them, while acoustically different calls at ground-bound predators (such as large cats) elicit movement into trees (Cäsar, Byrne, Hoppitt, Young, & Zuberbühler, 2012). Even in species without specifically "referential" calls, alarm calls can differ acoustically depending on the level of threat perceived by the caller (Owren & Rendall, 1997).

The capability to produce and respond to such referential calls requires a species to have developed fairly sophisticated socio-cognitive skills (for review, see Fischer & Price, 2017). Recognizing a threat as a specific type, and likewise recognizing specific types of alarm calls that attract attention and initiate defensive behavior, requires categorization of the dangerous context (Berthet, Neumann, Mesbahi, Cäsar, & Zuberbühler, 2018). With categorization, an animal selectively makes some (usually adaptive) distinctions while ignoring others (Russ, Lee, & Cohen, 2007). For example, an animal may distinguish another species as a "predator" and "ground-bound" while not distinguishing the exact species of predator. Many species of primates, for example, employ categorization to identify conspecific callers (either individually or by broader categories such as age or sex) and different types of calls, including alarm calls (Russ et al., 2007).

As alarm calling tends to be inherently costly to the calling individual (either due to increased risk of their own predation or energy spent calling in safe situations, such as when out of reach of a snake), one would expect calling to be affected by the social context of the situation. Indeed, the call rates of wild vervet monkeys (*Chlorocebus pygerythrus*) differ depending on the identity of their listeners; females with nearby kin alarm call at higher rates than those without (Cheney & Seyfarth, 1985). In a related finding, male Thomas langurs (*Presbytis thomasi*) do not alarm call after seeing a tiger if there are no other langurs around to hear them, even though they do engage in other antipredator strategies, such as energetic escape patterns (Wich & Sterck, 2003). This indicates that many alarm calls are produced specifically for conspecific recruitment rather than predator dissuasion, and that many primates are able to distinguish between situations in which alarm calling is beneficial to them and situations when it is not.

Another facet of alarm calls is how the acoustical properties of these calls reflect the caller's excitability that could potentially influence listener behavior. One distinctive property of alarm calls is the harmonics-to-noise ratio (HNR, dB) representing the degree of periodicity in the acoustic spectrum. Harmonic (tonal) components exhibit regularity in vocal-fold vibrations whereas irregular vibrations produce nonharmonic (atonal or noisy) energy in the acoustic spectrum (see discussion in Qi & Hillman, 1997; Riede, Hanspeter, Hammersch-

midt, Brunnberg, & Tembrock, 2001). Alarm calls with higher tonality possess continuous stacks of distinctive fundamental frequencies and harmonics over the main course of the calls with no abrupt frequency changes. In spectrograms, different levels of noise in alarm-calls can range from subharmonics between the harmonics to chaotic broad-band energy obscuring the stacked harmonic structure. Noisier alarm calls can indicate a caller's higher level of physiological arousal and motivational state in relation to a perceived threat (see Briefer, 2012; Manser, 2001, 2010). As argued by Scherer (1986, 2003), elevated physiological arousal can augment exhalation during alarm calling, producing aperiodic motion of the vocal folds and turbulent airflow through the glottis producing sounds with nonlinear properties. It is this turbulence that generates chaotic noise in the acoustic spectrum (see Fitch, Neubauer, & Herzel, 2002; Wilden, Herzel, Peters, & Tembrock, 1998). Such a burst of exhalation during call onset is modulated by the midbrain periaqueductal gray (PAG) and bordering reticular formation that contain neurons regulating vocalization and respiration (Larson, 1991; Jürgens, 2009). Based on neurophysiological evidence from squirrel monkeys (*Saimiri sciureus*), a tonic increase in neuronal activity in neocortex is transmitted to the PAG via limbic structures, such as the amygdala and bed nucleus of the stria terminalis, that modulate the emotional component of threat appraisal that influences alarm calling (Düsterhöft, Haüsler, & Jürgens, 2004; Jürgens, 1982). As the crucial relay station triggering alarm calling, the PAG sends descending projections to the ventrolateral pontine vocalization area regulating vocal-pattern generation (Hannig & Jürgens, 2006; Siebert & Jürgens, 2003). Bonnet macaques (*Macaca radiata*), for example, do not have distinct alarm calls based on predator type; rather, the harmonics-to-noise ratio of their calls decreases (and call noisiness increases) with their assessment of greater potential danger. A model leopard detected at a safe distance engenders a more harmonic alarm call than a model leopard appearing dangerously close (Coss, McCowan, & Ramakrishnan, 2007). Higher physiological arousal yielding noisy vocalizations can reflect unpleasant emotional states, such as anger and fear (Dujardin & Jürgens, 2006; Fichtel, Hammerschmidt, & Jürgens, 2001; Jürgens, 1979) as characterized by squirrel monkey aversion to electrophysiological self stimulation. As such, the emotions expressed by fearful vocalizations might be contagious to nearby listeners (see Owren & Rendall, 2001).

While the aforementioned process of physiological arousal involves higher levels of neocortical involvement, subcortical struc-tures at a lower level of perceptual organization might play an important role in alarm-call emissions. In mammals, the superior colliculus projects directly to the PAG and can affect physiological arousal by its indirect projection to the amygdala via the pulvinar (Gruber-Dujardin, 2010). Although its perceptual capability is relatively course (low spatial frequency), the superior colliculus does exhibit fast, automatic snake-recognition capability in infant and adult capuchins (Maior et al., 2011), a property useful for initiating rapid evasive behavior during surprise encounters with snakes (see Le et al., 2014; Tamietto & de Gelder, 2010; Vitale, Visalberghi, & De Lillo, 1990). Direct projection of the superior colliculus to the PAG might foster the emission of alarm calls that supersedes arousal modulation of call

noisiness via the colliculo-pulvinar-amygdala pathway to the PAG. Although speculative in this context, Blumstein and Chi (2012) were surprised to find that marmots (*Marmota flaviventris*) experiencing greater physiological arousal emitted alarm calls with lower noise than predicted by the literature. They argue (p. 191) that: "highly aroused animals produce piercing alarm calls that are probably the product of selection to have an immediate strong response in receivers."

White-faced capuchin monkeys (*Cebus capucinus*), the subject of this study, have multiple types of alarm calls. They have two general classes of alarm calls: one class that includes calls given in response to aerial predators, other monkeys, and approaching humans, and another given in response to any other type of terrestrial threat, such as snakes (cf. Digweed, Fedigan, & Rendall, 2005; Fichtel, Perry, & Gros-Louis, 2005; Gros-Louis et al., 2008). The calls within the latter category were previously determined to be too similar in structure under different circumstances (e.g., snake vs. caiman threat) to be truly functionally referential, and were hypothesized to be more general in nature (Fichtel et al., 2005). However, Meno, Coss, and Perry (2013a), who studied snake-directed calls by white-faced capuchins, determined that the rate of alarm calls directed at photographic models of a boa constrictor (*Boa constrictor*) and neotropical rattlesnake (*Crotalus durissus*) that prey on capuchins was reliably higher than calls directed at a similarly sized white snake-like model (control) or model scorpion eater (*Stenorrhina freminvillei*), a snake that does not prey on capuchins. Corrected herein, the scorpion eater snake model was originally misidentified by Meno et al. (2013a, 2013b) as a Central American indigo snake (*Drymarchon melanurus*, Harry Greene, personal communication 2014). According to Greene, this error does not disconfirm capuchin ability to differentiate dangerous from nondangerous snakes.

It is important to note here that infant capuchin monkeys are able to recognize and alarm call at dangerous snakes, an adaptation most likely driven by the greater susceptibility of infants than adults to snake predation (Meno, 2012; Meno et al., 2013a). However, young monkeys also have higher rates of "false alarms" at nondangerous animals than do adults (Perry et al., 2003). This implies that some facets of alarm calling at snakes are learned, either from individual experience or via social learning. Capuchins across age groups also alarm call at higher rates when alone than when in a group, and capuchins that alarm at higher rates are more likely to recruit conspecifics (Meno, Coss, & Perry, 2013b). Recruitment may also play a role in social learning; an infant calling at a nondangerous animal that fails to recruit adults may learn that this species is not considered a threat. That said, Meno et al. (2013b) did not discover any statistically significant impact of the age of the caller on the recruitment of conspecifics.

1.1 | Experimental questions and predictions

This study's objective was to expand on the work of Meno et al. (2013a, 2013b) using digital analyses to determine if more subtle acoustic properties of capuchin snake-directed alarm calls conveyed information about the threat level of the snake species that elicited them. Specifically, we analyzed the harmonics-to-noise ratio (tonality of spectral structure) of alarm calls, as this acoustic feature has been previously linked to arousal levels in other animals (including many primates, i.e., Fichtel et al., 2001). In particular, Digweed et al. (2005) examined the alarm-call tonality of white-faced capuchins during natural encounters with snakes, birds, and terrestrial predators. The alarm calls elicited by birds and terrestrial mammals were reliably noisier than snake-directed alarm calls that were still noisier than tonal. Based on evidence from Meno et al. (2013a) that the boa constrictor and rattlesnake models engendered higher rates of alarm calling than the scorpion eater model, presumably the result of elevated arousal, we predicted that the boa and the rattlesnake would engender noisier alarm calls with lower harmonics-to-noise ratios than alarm calls engendered by the harmless scorpion eater. We were also interested in whether the ability to recognize and respond to different snake species, as possibly indicated by the harmonics-to-noise ratio of alarm calls that they elicited, changed as capuchins matured.

Another facet of our interest was whether the acoustic properties of alarm calls directed at snakes signaled their level of dangerousness. For example, when white-faced capuchins are separated from their groups, these lost individuals emit loud long-distant calls with acoustic cues to caller identity. These "lost calls" are selectively answered when they are emitted by individuals of higher social rank (Digweed, Fedigan, & Rendall, 2007). Because these lost calls were highly variable in tonality, it seemed reasonable to expect that the tonality of focal alarm calls in our study might influence the alarm calls of nearby troop members as an audience effect (see Owren, Amossi, & Rendall, 2010; Pollick, Gouzoules, & de Waal, 2005). To address this question, we conducted exploratory analyses of the social impacts of these alarm calls, and whether the harmonics-to-noise ratios of focal callers influenced the harmonics-to-noise ratios of the calls of nearby conspecifics. By examining more closely the acoustic differences between calls and whether capuchins responded to them, we hoped to shed more light on the cognitive development of these monkeys, as well as their social behavior.

2 | METHODS

2.1 | Study site and subjects

The fieldwork for this study was conducted in the Lomas Barbudal Biological Reserve in Costa Rica, over the course of three seasons: June-July 2007, January-June 2009, and January-May 2010. Greater detail of the field methods and description of capuchin monkeys appears in Meno et al. (2013a, 2013b). The subjects for this study consisted of six groups of white-faced capuchin monkeys, with group sizes ranging from 6 to 32 individuals. Individuals were divided into three age groups: infants (2 months to 2 years of age), juveniles (between 2 and 5 years of age) and adults (over 5 years of age). Due to the requirement that focal animals be independent of the group, nonmobile infants (younger than 2 months of age) were not used as focal animals. Each individual monitored during the experiment was given a name and identified based on facial markings. All experiments were approved by the UC Davis Animal Care and Use Committee and were in accordance with both the laws of Costa Rica and the ASP ethical guidelines.

2.2 | Acquisition of alarm call recordings

In each trial, focal animals were presented with a photographic model of one of four snakes: A) boa constrictor (dangerous); B) neotropical rattlesnake (dangerous); C) scorpion eater snake (nondangerous); and D) a white snake-shaped "novel" control (Figure 1). All models were approximately the same size. One dangerous and one nondangerous model were presented to each group per day. Models were hidden under a fabric cover that matched the ground coloration (green or brown), and revealed when the focal animal (Figure 2), but no other nearby animals, would see them immediately. Focal animals were selected based on their relative proximity to both the model and relative distance away from other conspecifics. The focal animal was videorecorded using a Panasonic digital video camera (Panasonic model PV-DV601D, Panasonic Corporation of America) with audio input recorded on two tracks in 16 bit (48 kHz) sampling frequency. Alarm calls were recorded digitally with an Audio Technica ATR55 (Audio-Technica U.S., Inc., Stow, OH) cardioid condenser shotgun microphone (70–18,000 Hz) until either the focal monkey left the area of the model or 5 min had elapsed. During video recording, assistants would vocally indicate all instances of alarm calling (and other alarm calling behavior not addressed by this study) from both the focal animal and any nearby conspecifics. Each caller would be identified by name. Field recordings were uploaded to iMovie software on a Macintosh computer and edited into 30-s to 5-min clips sorted by the name and age group of the focal animal.

2.3 | Digital analysis of alarm calls

Not all video recordings contained alarm calls; in those that did, the first alarm calls with low background noise from wind, insects, birds, and announcing humans were exported to a QuickTime video player on a Macintosh computer, and then saved as a wav audio file. This file was then opened by Audacity (version 2.0.6, audacity.sourceforge.net), a recording and sound-editing program. In Audacity, individual

FIGURE 1 Photographic models presented on the ground to capuchins. (a) coiled boa constrictor, (b) coiled neotropical rattlesnake, (c) coiled scorpion eater snake, and (d) novel control (white foam-core underside of coiled rattlesnake)

FIGURE 2 Video still frame of Carrot, an adult female white-faced capuchin, alarm calling at a model boa constrictor detected well ahead of her group

calls could be cropped at the call beginning and ending and then exported for analysis of "periodicity-harmonicity" by the acoustic analysis program PRAAT version 5.2.17, www.praat.org (see Boersma, 1993 for computational method and Yumoto & Gould, 1982 for discussion of vocal noise). The resulting mean and peak harmonics-to-noise ratios were recorded and organized by the age of caller (since the harmonic structure of a monkeys call was expected to change with age) and type of snake that elicited the call.

2.4 | Analyses of snake models and social effects

Since many individuals called at more than one snake model, but not at all four models, pairwise comparisons of models which elicited alarm calls with low background noise were examined to achieve the largest sample sizes using one-factor between subjects (age class), one-factor within subjects (models) repeated measures analyses of variance (ANOVAs). Tests of simple effects compared the age classes for each snake and model differences for each age class. Linear and quadratic trend analyses examined age-related changes for each model, the sources of which were examined further by post hoc pairwise model comparisons. Both average and peak HNR (dB) were examined.

In analyses of social effects, we examined only the peak HNR (dB) of alarm calls. For all age classes combined and for specific age classes, linear regression analyses examined whether the peak HNR (dB) of the focal caller's initial alarm call predicted the peak HNR (dB) of the first alarm call of an identified second caller and its latency of emission. A second social property of interest was whether hearing second callers altered the subsequent alarm calls of focals. To assess focal-caller consistency, we used regression analysis to examine a predictive association of the focal's first alarm call after snake detection and its first alarm call after hearing the second caller.

3 | RESULTS

The number of individuals emitting clear alarm calls for pairwise comparisons of snake models appears in Table 1. We did not compare

TABLE 1 Number of the same individuals alarm calling at two snake models

Age class	Scorpion eater Boa constrictor	Scorpion eater Rattlesnake	Rattlesnake Boa constrictor
Adult	6	9	8
Juvenile	10	11	11
Infant	6	10	6
TOTAL	22	30	25

capuchin sex due to small sample sizes. In all pairwise comparisons of snake models, Levine's test revealed that the variances of mean and peak HNR (dB) were statistically homogeneous.

3.1 | Mean alarm-call HNR (dB) and snake recognition

For all pairwise comparisons of snake models, none of the main effects for age class and snakes and their interactions achieved statistical significance ($\alpha = 0.05$). One main effect, averaged for age class, that approached statistical significance, $F(1,27) = 3.831$, $p = 0.061$, was the higher tonality while viewing the rattlesnake model compared with the scorpion eater model.

3.2 | Peak alarm-call HNR (dB) and snake recognition

Averaged for the boa and scorpion eater models, the three age classes (6 infants, 10 juveniles, and 6 adults) did not differ appreciably in the peak HNR (dB) of their alarm calls ($p = 0.83$). Nevertheless, when each snake model was examined separately to compare age class in a test of simple effect, the boa model engendered similarly elevated HNRs (dB) for all age classes unlike the scorpion eater model (see Figure 3) that engendered an age-related rise and fall of the peak HNR (dB) that yielded a statistically significant quadratic trend, $F(1,19) = 4.396$, $p = 0.05$. A post hoc comparison of this rise in peak HNR (dB) showed that juveniles viewing the scorpion eater model had reliably higher call tonality, $F(1,19) = 5.065$, $p = 0.036$, than infants with a large standardized effect size (Cohen's $d = 1.0$).

The main effect comparing the boa and scorpion eater models, averaged for age class, was significant, with the boa engendering a peak HNR (dB) of alarm calls that was significantly higher than the peak HNR (dB) of alarm calls directed at the scorpion eater, $F(2,19) = 10.019$, $p = 0.005$. This finding does not support our prediction, based on vocalization research on other primates, that the boa would engender greater physiological arousal leading to the emission of noisier alarm calls. For each age class, the source for this model difference was revealed by a test of simple effect. Infant alarm calls directed at the boa model exhibited a significantly higher peak HNR (dB) than alarm calls directed at the scorpion eater model, $F(1,19) = 7.706$, $p = 0.012$. The standardized effect size for mean difference was large (Cohen's $d = 0.90$), suggesting that the more harmonic properties of infant alarm calls during boa recognition might have important communicative properties to nearby perceivers.
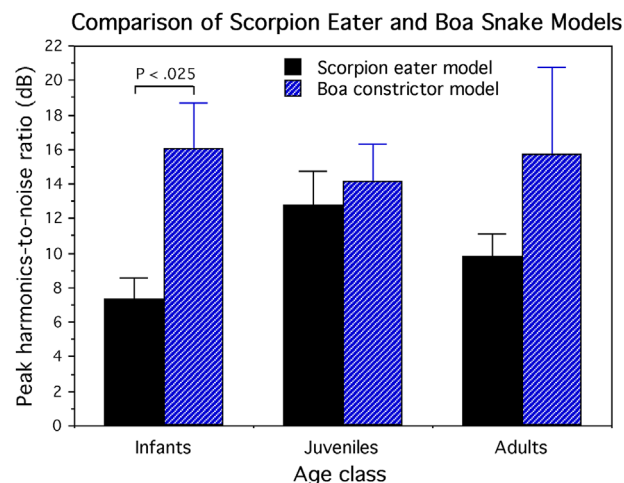
FIGURE 3 Peak harmonic-to-noise ratios (dB) of alarm calls across age classes directed at scorpion eater and boa constrictor snake models. Mean and standard error values are shown. Note that 0 dB indicates an equal amount of noise and periodicity in the acoustic signal. Averaged for age class, the boa elicited alarm calls with reliably higher alarm-call tonality ($p < 0.005$) than the scorpion eater, an effect most pronounced in infant capuchins

Though juveniles did not have a significantly different peak HNR (dB) for the boa and scorpion eater models ($p = 0.573$), the increased tonality of adult calls directed at the boa compared with the scorpion eater approached statistical significance (simple effect: $F(1,19) = 3.549$, $p = 0.075$). The effect size for this mean difference in peak HNR (dB) for adults was also large (Cohen's $d = 1.1$).

Pairwise comparisons of the other snake models in separate ANOVAs did not reveal significant differences in the peak HNR (dB) of alarm calls averaged for age class or snake models. The white novel snake model did not engender alarm calling in a sufficient number of infants and adults for comparing age class and models using one-factor between subjects, one-factor within subjects ANOVAs. However, enough juveniles alarm called at the novel model, allowing pairwise comparisons of this model with the other snake models using one-factor repeated measures ANOVAs. None of the comparisons of the novel model with other snake models yielded significant differences in the peak HNR (dB) of juvenile calls.

## 3.3 | Social effects of peak alarm-call HNR (dB)

For the three photographic snake models and age classes combined, 46 focal monkeys (14 infants, 22 juveniles, 10 adults) emitted their first alarm calls in situations in which second callers were identified (13 infants, 11 juveniles, 22 adults) and their initial calls were followed by focal individuals emitting another alarm call. Linear regression analysis of repeated focal alarm calls revealed a reliable consistency in the tonal properties of their first alarm calls and their next calls after hearing second callers, $r = 0.344$, $F(1,44) = 5.890$, $p = 0.019$.

Since some monkeys approached focal callers during their early emissions of alarm calls, there was the possibility that second callers had already detected the snake models prior to hearing focal callers. To

examine a possible bias from early snake-model detection affecting our interpretation of alarm-call contagion, we used a two-factor ANOVA to compare the peak HNR (dB) of second callers for snake-model presentations and age class. None of the main effects for snake-model presentations and age were significant (presentations: $p = 0.926$), indicating that variation in the tonality of second callers was uninfluenced by the different presentation contexts. As such, we proceeded to examine alarm-call contagion by employing linear regression to examine the statistical association of the peak HNR (dB) of focal individuals' first clear alarm calls and the peak HNR (dB) of the first clear alarm calls of identified second callers.

Regression analysis revealed that these unique focal- and second-caller dyads were associated reliably, $r = 0.306$, $F (1,44) = 4.537$, $p = 0.039$ (Figure 4). Infant focals were found to be the major source of this statistically significant association, as evinced by their reliable correlation coefficient, $r = 0.693$, $F (1,12) = 11.108$, $p < 0.01$ (Figure 5) followed by the contribution of 22 juvenile focals, $r = 0.349$, $p = 0.111$. Conversely, the strength of the positive correlation of all age classes was suppressed by the negative correlation of the peak HNR (dB) of 10 adult focals and the peak HNR (dB) of second callers, $r = -0.352$, $p = 0.318$. Further analysis revealed that this negative correlation coefficient of adult focals differed reliably from the aforementioned positive correlation coefficient of 14 infant focals, $z = 2.162$, $p < 0.05$ two tailed. Regression analysis of the peak HNR (dB) of all focal alarm calls predicting the latency (sec) of all first calls of second callers in these 46 unique dyads showed a positive tread approaching statistical significance, $r = 0.256$, $p = 0.086$. The average latency of the second caller's first call was 16.5 s.

There was also suggestive evidence that focals from all age classes were attentive to the alarm-call tonality of nearby monkeys. The average latency of the focal caller's next call after hearing the second caller was 13.3 s, with the peak HNR (dB) of the second caller's first call predicting the latency of emission of the following call by the focal monkey at a nearly significant level, $r (44) = 0.281$, $p = 0.059$.
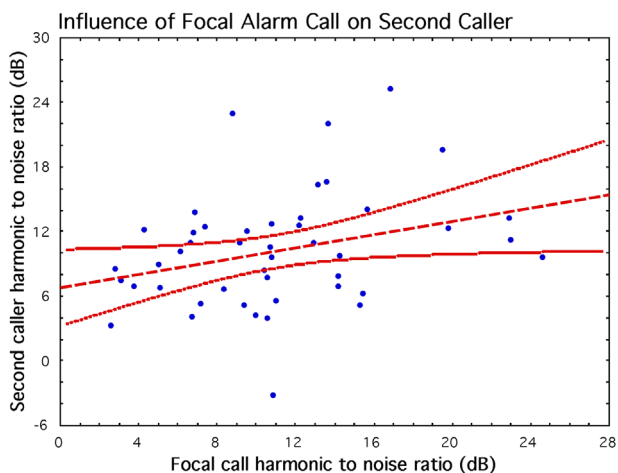
FIGURE 4 Association of the peak HNR (dB) of initial focal alarm calls from all age classes directed at snake models and the peak HNR (dB) of the first alarm calls of second callers from all age classes (95% confidence intervals are shown)
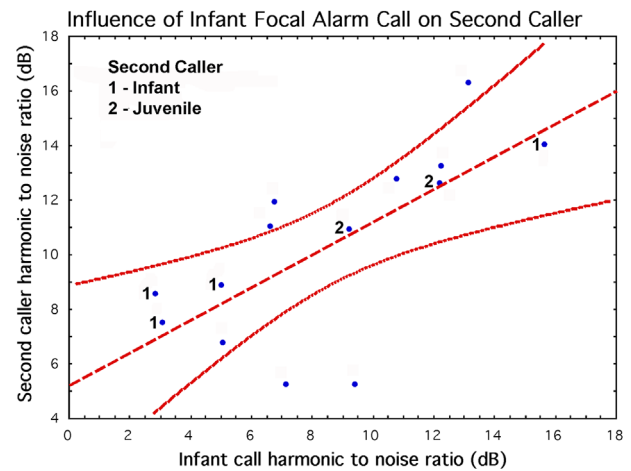
FIGURE 5 Association of the peak HNR (dB) of initial alarm calls of focal infants directed at snake models and the peak HNR (dB) of the first alarm calls of second callers from all age classes (95% confidence intervals are shown). The majority of second callers were adults

4 | DISCUSSION

In the first part of this study, we examined the relationship among the mean and peak harmonics-to-noise ratio of a white-faced capuchin alarm call, the age of the monkey, and the type of snake that elicited the call. Based on Meno and colleagues prior study (2013a), we knew that rates of alarm calling were higher during presentations of capuchin snake predators, the boa constrictor and neotropical rattlesnake models, compared with the rate of alarm calling directed at the harmless scorpion eater model. Due to this finding and the literature on arousal and call noisiness (Coss et al., 2007; Fichtel et al., 2001; Fitch et al., 2002), we predicted that both the boa and the rattlesnake models would engender noisier alarm calls with lower mean and peak HNRs (dB) than alarm calls evoked by the scorpion eater model. This hypothesis was disconfirmed by the comparison of the boa and scorpion eater models, characterizing the two snakes that differed the most in level of dangerousness. Averaged for age class, the peak HNR (dB) of alarm calls directed at the boa constrictor model was reliably higher than the peak HNR (dB) of alarm calls directed at the scorpion eater model. This effect was influenced by the lower peak HNR (dB) of infant alarm calls to the scorpion eater model (Figure 3). Levels of call tonality did not distinguish the boa and rattlesnake or rattlesnake and scorpion eater models for any age class.

Relevant to the issue of whether learning promoted snake-species discrimination, the perceptual discrimination of the boa and scorpion eater snakes based on call tonality was most pronounced in infants, with adults exhibiting nearly reliable snake-species discrimination. While recognized as a snake by infants, the uncertainty of threat posed by the scorpion eater might have increased their cognitive-processing load (for humans, see Öhman, 2005), elevating arousal, and noisier alarm-call production. Unlike infants that apparently perceived the scorpion eater with more uncertainty and higher arousal, the higher, more equivalent call tonality of juvenile alarm calls directed at both the

boa and scorpion eater argues for the process of perceptual generalization in which all snakes are perceived as dangerous. With respect to this assumption of snake generalization by juveniles, Meno et al. (2013a) reported that adults showed a decline in their visual monitoring of the scorpion eater model that is similar to their decline in alarm-call tonality reported herein. Such a decline in both level of vigilance and call tonality between juveniles and adults might reflect the role of experience with repeated observations of nondangerous snakes (for age-related changes in bonnet macaques, see Ramakrishnan, Coss, Schank, Dharawat, & Kim, 2005). Conversely, recognition of the boa model by less experienced infants, despite the inference of higher arousal based on their prolonged visual monitoring of this snake (Meno et al., 2013a), could indicate an adaptive bypassing of arousal circuits via the direct projection of the superior colliculus to the PAG that modulates alarm-call exhalation and resultant aperiodicity of vocal-fold motion.

Although capuchins directed their alarm calls at the snake models, irrespective of the ability of real snakes to actually hear them effectively (Young, 1997, 2003), it is reasonable to consider that capuchins of all ages recognized the boa rapidly and unambiguously and thus emitted more harmonic alarm calls as clear signals to alert nearby capuchin perceivers of the potential threat. Moreover, the snake-directed tonal calls examined herein exhibited the highest energy at frequencies (Figure 6) within the "forest window" of 1,585–2,500 Hz for the best propagation of pure tones in low-forest canopies reported by Morton (1975). These tonal calls also exhibited acoustic properties consistent with Morton's argument that natural selection shapes the acoustic properties of signals so they propagate most effectively in the environment in which they are emitted. This is especially evident for the tonelike calls of birds living in low forest canopies (Marten & Marler, 1977; Morton, 1975). Another possible attribute of more tonal snake-directed alarm calls is that they might
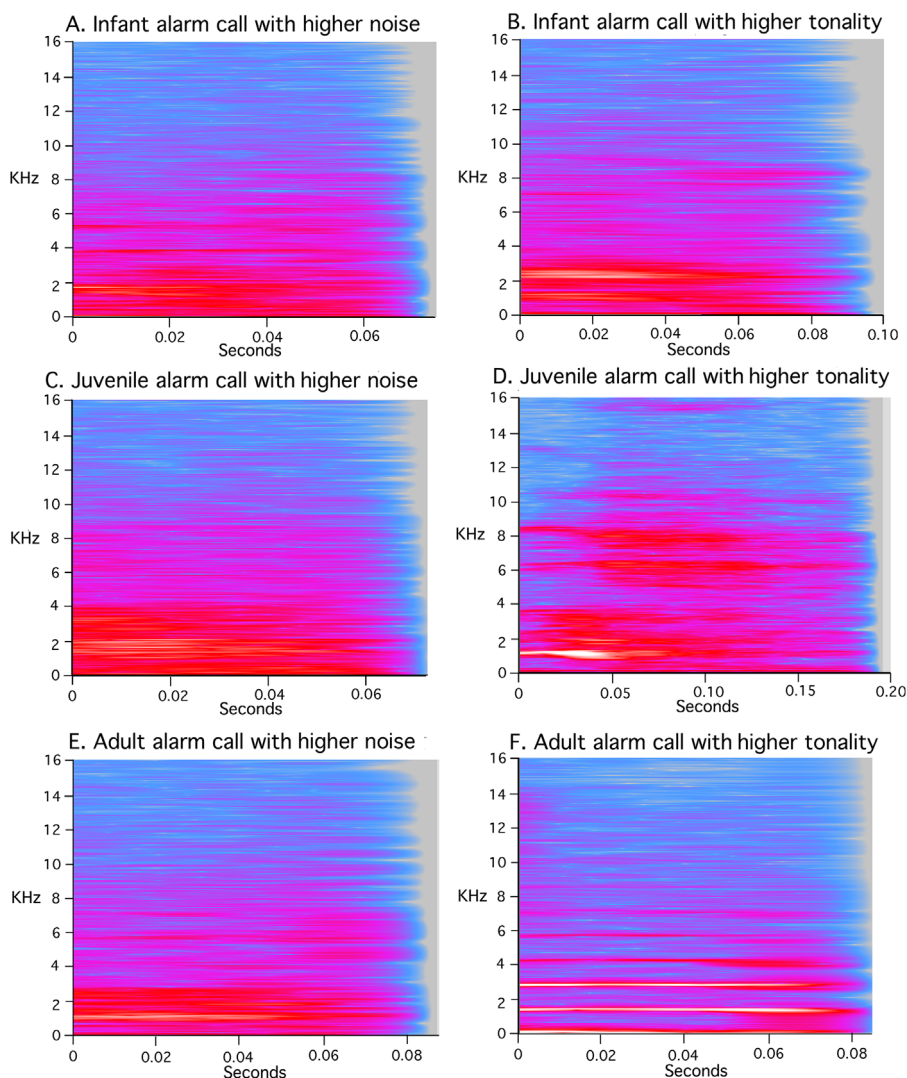
FIGURE 6 Spectrograms of infant, juvenile, and adult alarm calls exhibiting higher peak noise or tonality (2048 point FFT). Note that calls with higher tonality exhibit more distinctive parallel bands or harmonic stacks whereas noisier calls exhibit more subharmonics between the harmonics that obscure the harmonic stacks

reduce perceiver habituation and maintain troop vigilance, a phenomenon documented by Karp, Manser, Wiley, & Townsend, 2014 using playbacks on meerkats (*Suricata suricatta*).

The process of predator recognition by prey entails an implicit understanding of the spatial relationship of the perceiver and the predator's hunting capability. The boa is particularly relevant to capuchins because it is an arboreal snake and, unlike the terrestrial neotropical rattlesnake, can seize and constrict monkeys in trees and on the ground. In support of this perspective, the neotropical rattlesnake did not elicit calls with reliably higher call tonality than the scorpion eater even though it is an opportunistic predator of capuchins encountered on the ground (Meno et al., 2013a). Again, the higher peak HNR (dB) of the alarm calls directed at the most dangerous snake, the boa constrictor, could characterize immediate predator recognition and intentional signaling of the predatory threat to nearby conspecifics.

There may be several reasons that peak HNR (dB) is a better indicator of call harmonic structure than the mean HNR (dB). While the lower mean HNR (dB) indicating noisier alarm calls is a good indicator of physiological arousal in some primates, capuchin alarm calls are much briefer; for example, they can be half to one-fourth the duration of typical bonnet macaque alarm calls (Coss et al., 2007). Considering how the PRAAT harmonics-to-noise analysis program slices the entire alarm call into multiple segments for forward cross-correlational analysis (Boersma, 1993), the greatest sound energy in the frequency spectrum of capuchin alarm calls is most apparent in the earliest portion of the calls. This finding is consistent with the snake-directed alarm calls recorded by Digweed et al. (2005) during natural snake encounters. As such, averaging all the segments of the entire call includes this diminution of call energy (Figure 6).

One possible explanation for snake-species discrimination by capuchins is related to how other mammalian species recognize predators innately, notably primates capitalizing on salient recognition cues of partially visible predators, such as the rosettes on the pelage of leopards (cf. Coss and Ramakrishnan, 2000; Schel, Tranquilli, & Zuberbühler, 2009) or repetitive scale patterns of snakes by ground squirrels (Coss, 1991). Wombolt and Caine (2016) have shown that repetitive crosshatch and stars patterns engraved on snake-shaped clay models enhance their provocative appearance to captive common marmosets (*Callithrix jacchus*). Isbell and Etting (2017) report a similar finding for wild vervet monkeys. If similar perceptual abilities exist in capuchins, it may be that capuchins can innately recognize and alarm at the distinctive scale pattern of boa constrictors partially concealed by bushes and leaf litter. Field observations of capuchins alarm calling vigorously at boa constrictors under leaves with only small segments of their scales exposed support this interpretation (Susan Perry, personal communication 2014). Another example indicative of snake-species discrimination is evidence that wild capuchins (*Sapajus libidinosus*) in Brazil hunt and consume nonthreatening snakes while avoiding dangerous boas and venomous snakes (Falótico et al., 2018). The lack of repetitive blotches or diamonds on the scales of the scorpion eater (Figure 1) would eliminate one distinguishing snake-recognition cue.

The second facet of this study was determining for all age classes if the level of tonality of the initial calls of focal callers predicted the level of tonality of the first alarm calls of nearby monkeys. We determined that the level of peak HNR (dB) of focal callers, notably infants, influenced the peak HNR (dB) of the first calls of second callers, with higher call tonality prompting higher call tonality in second callers. While the higher tonality of second callers might simply reflect the contagious properties of unanticipated alarm calls with high levels of tonality, the greater influence of the initial alarm calls of focal infants suggests that second callers, predominantly adults (Figure 5), might be assessing levels of infant endangerment. Nevertheless, this positive correlation of focal and second callers provides support to our argument that call tonality has communicative properties.

In light of our findings, one might also expect that the higher tonality of the initial focal alarm calls at snakes would engender a greater urgency for nearby monkeys to respond quickly. In a similar fashion, focals viewing the snake model might respond more quickly with another alarm call after hearing more harmonic alarm calls from second callers. The level of peak HNR (dB) of focal callers was positively correlated with the latencies of alarm calls emitted by second-callers, as was the level of peak HNR (dB) of second callers on the latencies of the next focal alarm calls, but these associations only approached statistical significance. There are varying circumstances that could assuage the urgency to emit alarm calls after hearing nearby alarm calls. Second callers are not likely waiting until they can see the snake for themselves, as capuchins tend to forage in dense tree cover and often respond to alarms they can hear without seeing what elicited them (Meno et al., 2013b). These neighboring monkeys may be waiting stochastically to assess the situation further by moving closer for group antipredator mobbing displays, which would impact call latency differently depending on the type of threat. Further study of capuchin antipredator behavior will shed light on the dynamics of alarm calling and any audience effects modulating reciprocal calling.

ORCID

Richard G. Coss http://orcid.org/0000-0002-7981-8862

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