Exploring the Adaptive Significance of Five Types of Puma (*Puma concolor*) Vocalizations

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Communication is a central component of animal behaviour, yet communicative behaviours are poorly studied due to their complexity and varied functions. Pumas (*Puma concolor*) are wide-ranging, solitary felids that primarily use indirect cues (e.g., scent marking) for communication. Because these cryptic carnivores are rarely observed directly, little is known about their vocalizations in the wild. We recorded a variety of Puma vocalizations among females and family groups using motion-triggered video cameras and then attempted to understand the function of each vocalization. We found two categories of vocalizations: 1) attention-attracting (caterwauling and mewing), and 2) calls (contact, agitated, and alarm). Vocalizations to attract attention ranged across broad frequencies. Contact, agitated, and alarm calls are narrow-frequency vocalizations that varied in intensity and were used to communicate with nearby conspecifics. Vocal communication entails risk, and while some Puma vocalizations may provide benefits that outweigh their risk, others are structured to limit detection and risk. These observations highlight the importance of the structure of vocalizations used during different behaviours to understand their adaptive significance.

Key Words: Alarm call; communication; family groups; *Puma concolor*; vocalizations; remote camera

Introduction

Communication to convey information between individuals or groups is a central component of animal behaviour (Davies *et al*. 2012). All behavioural interactions between individuals, from courtship and mate selection to territorial defense, are conducted through signals or displays (Bradbury and Vehrencamp 1998; Davies *et al*. 2012). Felid species, being primarily solitary, conduct most of their communication using a variety of indirect signals (Seidensticker *et al*. 1973; Smith *et al*. 1989; Peters and Tonkin-Leyhausen 1999; Logan and Sweanor 2001; Allen *et al.* 2016), including visual, olfactory, auditory, and tactile cues (Bailey 1974; Verberne and Leyhausen 1976; Logan and Sweanor 2010). Such communicative behaviours require study, especially for cryptic species, due to their complexity and varied functions (Bradbury and Vehrencamp 1998; Davies *et al*. 2012). By better understanding acoustic communications, we can shed light on the evolutionary basis of these calls as well as provide a more complete picture of animal behaviour.

Pumas, *Puma concolor* (Linnaeus, 1771) are large, solitary felids that range widely across North and South America. Intraspecific communication between Pumas is dominated by indirect cues via scent marking, with the most common form being scraping (Logan and Sweanor 2001; Allen *et al*. 2014, 2015). Vocal communication is generally limited to family groups (i.e., between mothers and kittens) and to mating pairs (Rabb 1959; Currier 1983; Logan and Sweanor 2001). Male and female Pumas have different life histories with males occupying much larger home ranges and more frequently creating scent marks (Logan and Sweanor 2001; Allen *et al*. 2014, 2015), and only female Pumas exhibiting parental care (Logan and Sweanor 2001). Females give birth to 1–4 kittens in each litter and raise them for 12–24 months before the kittens disperse (Logan and Sweanor 2001). Vocalizations may be an important aspect of communication between adult females and their young prior to dispersal.

Due to the difficulty of observing wild Pumas, there is little known about their vocalizations, and most information on their vocalizations has been based on captive animals (e.g., Rabb 1959; Potter 2002). However, captivity often alters an animal's behaviours or creates new ones (Mallapur and Chellam 2002; Quirke *et al*. 2012), making it important to collect observations of Puma vocalizations in the wild. Logan and Sweanor (2001) described observing several different types of vocalizations by wild Pumas but, due to the limitations of field observations, they were not always able to visually identify both the sender and receiver of the communications and their associated body language. Other researchers have tested Puma reactions to recorded vocalizations (Macarrao *et al*. 2012) or described Puma vocalizations during a hunt (Smallwood 1993), but these

instances were either not recorded or were responses to unnatural situations. Recent advances in the technology of motion-triggered video cameras now enable researchers to remotely record intimate behaviours in Pumas and other cryptic species (e.g., Macarrao *et al*. 2012; Allen and Taylor 2013). Thus, although vocalizations have been observed in the wild by researchers, we can now use motion-triggered cameras with sound recording capabilities to document Puma communications under natural conditions.

The structure of Puma vocalizations likely reflects adaptations to their specific function and behaviour. For example, vocal exchanges between females and kittens potentially attract the attentions of male Pumas and other large predators that are a major source of mortality for Puma kittens (Logan and Sweanor 2001). Thus, acoustic characteristics of each of these vocalizations have likely been optimized through natural selection to communicate most effectively at different distances (short-, medium-, and long-range) while minimizing exposure to predation risks (Peters and Tonkin-Leyhausen 1999). In this study, we compared and categorized five different types of Puma vocalizations to better understand how these acoustic communications contribute to and illuminate different behaviours.

Study Area

We studied Pumas living in a 1700 km^2 area of the Santa Cruz Mountains of California (36°58'26.82"N, 122°1'50.87"W). Pumas live throughout in this region and are not hunted, although much of their mortality is nevertheless due to anthropogenic causes (e.g., killed for livestock depredations or by vehicle collisions; C. C. W., unpublished data). The Pacific Ocean, cities of San Francisco and San Jose, and Highway 101 bound the western, northern, and eastern edges of the study area, respectively. The study area has a Mediterranean climate with the majority of rainfall occurring from November to April. Elevations range across a gradient from sea level to 1155 m (Wilmers *et al*. 2013).

Methods

As part of a larger study on Puma ecology we captured 42 Pumas from 2010–2013 (see Wilmers *et al*. 2013 and Allen *et al*. 2014 for study overview and Puma capture information). We monitored the Pumas using Global Positioning System (GPS)-telemetry collars (Model GPS Plus 1D, Vectronics Aerospace, Berlin, Germany) and opportunistically deployed motion-triggered video cameras with microphones (Bushnell TrophyCam IR 6 mp, Overland Park, Kansas, USA) at sites of interest. These sites included community scrapes (n = 45, scent marking locations regularly used by Pumas e.g., Allen *et al*. 2014), a nursery (n = 1), and baiting sites (n = not recorded) where we placed road-killed deer carcasses. We located these sites (except for baiting sites) using GPS information collected by the collars we placed on the wild Pumas. At each location, we placed one motion-triggered video camera, set to record 60 s of audio and video each time motion was detected with a 1 s delay before triggering again.

Studies of wild felid vocalizations have limited sample sizes due to the elusive nature of the research subjects (Peters and Tonkin-Leyhausen 1999), but the frequency and harmonics of vocalizations are generally stereotypical having been selected for over many generations (Peters and Peters 2010). In addition, although we placed numerous cameras at sites, we were not prioritizing acoustic data and thus our recordings were of variable quality and distances from the signal producer. Therefore, instead of reporting mean results from multiple recordings of similar behaviours, we used the videos with the highest quality sound recording to ensure the integrity of the recording and accurate characterizations of vocalizations. For each recording, we used the package Seewave (Sueur *et al*. 2008) in the program R (R Development Core Team 2013) to create spectrograms and measure the structure of the vocalization, including the dominant frequency, frequency range, and duration (defined as the duration for one vocalization, not the series).

Results

Attention-attracting vocalizations

On 17 May 2013, a camera we placed at a community scrape recorded an uncollared female Puma caterwauling (Video S1). The female Puma made a series of caterwauls for 14 s. The caterwauling vocalization was loud, long, and covered a large frequency range. It ranged from 0.1–5.0 kHz and had the longest duration of all vocalizations (caterwauling call = 1.9 s; Figure 1).

A camera set at the site of a nursery of Puma female 23F (Video S2) captured 23F interacting with three neonatal kittens on 23 May 2012. The kittens do not vocalize in a prior video before their mother's return and do not make any vocalizations when their mother arrives at the nursery, possibly because they are sleeping. While nursing, the kittens do not initially vocalize but then begin mewing as they shift their nursing positions. The mewing by kittens had the largest frequency range of all Puma vocalizations (2.1–14.7 kHz, duration = 0.4 s; Figure 2), over twice as large as those of caterwauling, but the vocalizations were much shorter in duration.

Call vocalizations

We placed many cameras at community scrape sites, which were regularly used for communication by Pumas. On 31 August 2012, one of these cameras recorded a female Puma walking through the community scrape with her kittens (Video S3). The group leaves the area covered by the camera and 11 s later the mother Puma begins giving a high whistling call. After 23 s, a third straggling kitten is then seen walking past the camera to catch up with the rest of the family group. The structure of the contact call exhibits a sweeping

frequency pattern (i.e., progressing from one frequency to another and then back to the original again), with the dominant frequency near the top of their range. The contact call ranged from 2.2–4.5 kHz (duration = 0.4 s; Figure 3), with a dominant frequency of 4.3 kHz.

At a camera set at another community scrape site on 6 September 2013, we recorded a young kitten (5–7 months old) alone investigating the site (Video S4). The mother was not visible when the kitten began to give an agitated call and no response from any of its family members was recorded. The call ranged from 0.4–4.1 kHz (duration = 0.5 s; Figure 4).

On 25 January 2012, we recorded the alarm call of 33M, a 13-month-old un-collared male kitten of 19F, when he was trapped by a foot-hold snare. We set a camera and a foot-hold snare at this location in an attempt to video a recapture of collared female 19F near one of her kill sites (Video S5). 33M triggered the foot-hold snare instead of his mother. He was visibly startled immediately upon capture, and he vocalized a series of short whistles 15 s later. His mother was in the immediate vicinity based on her GPS location data. The alarm call of 33M had a large range, from 0.9–5.2 kHz (duration = 0.3 s; Figure 5), with the dominant frequency of 2.9 in the middle of the range.

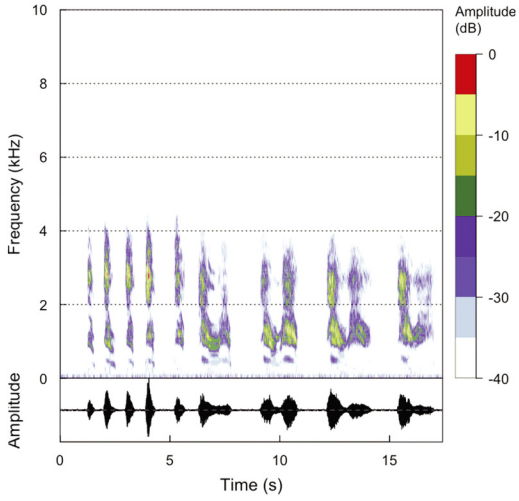

Figure 1. A spectrogram of a Puma (*Puma concolor*) caterwauling (from Video S1).

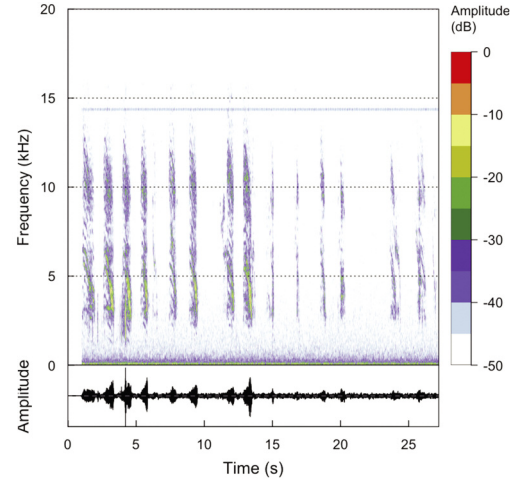

Figure 2. A spectrogram of a Puma (*Puma concolor*) mewing (from Video S2).

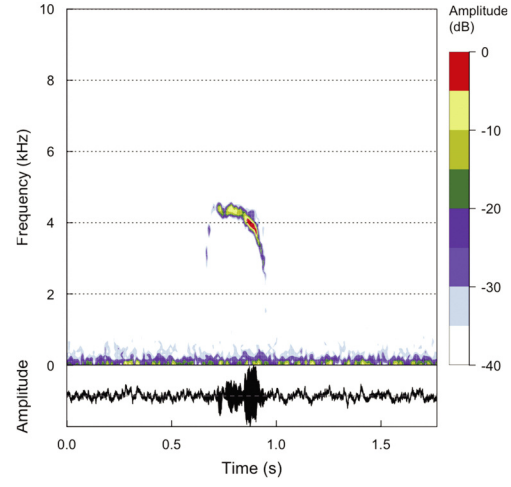

FIGURE 3. A spectrogram of a Puma (*Puma concolor*) contact call (from Video S3).

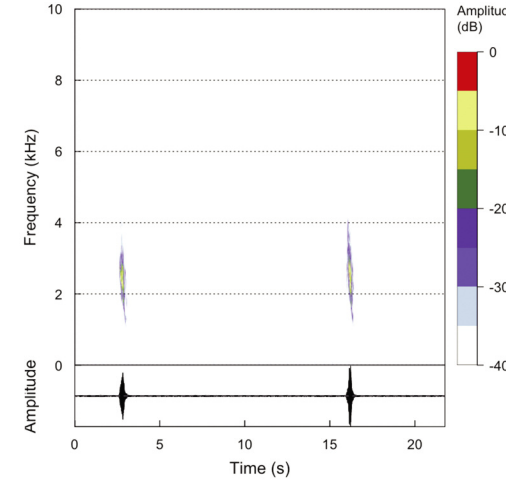

FIGURE 4. A spectrogram of a Puma (*Puma concolor*) agitated call (from Video S4).

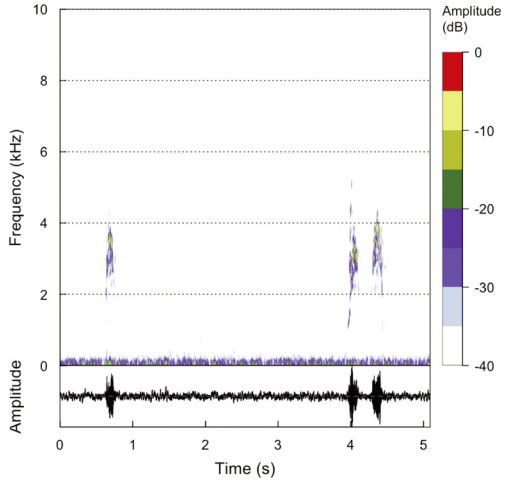

FIGURE 5. A spectrogram of a Puma (*Puma concolor*) alarm call (from Video S5).

Discussion

These are among the first published recordings of vocalizations from wild Pumas, and provide new insight into the structure and possible adaptive significance of Puma vocalizations. Vocal communication entails risk, as it can attract the attention of predators or competitors and increase the risk of injury or mortality for both the sender and receiver of communications (Hughes *et al*. 2012). Our findings suggest that our recorded vocalizations fall into two types: 1) vocalizations that are used to attract attention of conspecifics with little regard to cost, and 2) contact and alarm calls which are short calls that vary in intensity and are used to communicate with nearby conspecifics.

Vocalizations designed to attract attention (caterwauling and mewing) were characterized by broad frequencies and modulations, or changes in frequency (Vencl 1977; Redondo and deReyna 1988), and caterwauling was characterized by long durations. Caterwauling is presumed to be used to attract mates from a distance (Logan and Sweanor 2001) and is primarily used by females (Logan and Sweanor 2001; Allen *et al*. 2014). The range of frequencies used likely enables the vocalizations to carry long distances to attract all possible mates in the vicinity. Similarly, mewing is a vocalization aimed at gaining attention, despite the danger clearly posed to young animals. An experiment conducted with ground-nesting birds found that begging increased predation risk, which suggests that the immediate reward of food greatly outweighs any observed risks (Haskell 1994). Young animals in a single litter or brood compete with each other, and the more insistent individuals often obtain more nutrition (e.g., Redondo and De Reyna 1988), allowing them to be larger and out-compete other individuals, and increase their chances of survival. The direct benefits of attracting a mate or caregiver apparently outweigh any potential risks posed by predators.

Contact calls are vocalizations that are theoretically used for communication while limiting danger, and are characterized by pure tones and high pitches that are difficult to localize and attenuate over short distances (Vencl 1977). This allows for immediate communication, but limits the ability of predators to easily locate the sender or receiver of vocalizations. It is the nature of Puma family groups to travel large distances, and they appear to use vocalizations to stay together. After kittens reach three months of age, they are capable of traveling distances greater than1 km to kill sites with their mothers, and regularly accompany their mothers after they reach six months of age (Logan and Sweanor 2001). With multiple kittens there are always opportunities for one to lag behind or stray while in transit that could increase their risk of injury or mortality. Therefore, contact and alarm call vocalizations between family groups could serve to reduce this risk. Puma vocalizations may be structured to limit detection risk from larger predators (e.g., Gray Wolves (*Canis lupus*), bears (*Ursus* sp.), humans) while allowing close-range communications.

Agitated and alarm calls were superficially similar to contact calls in that they were short but they contrasted in that they incorporated broad frequencies and were harsher. Similar patterns, in which calls signifying higher urgency and danger tend to be noisier and harsher, have been found in other species as diverse as Baboons (*Papio cynocephalus ursinus*) and Mongoose (*Suricata suricatta*; Seyfarth and Cheney 2003). The broader frequencies likely made the sender more immediately locatable than contact calls (Redondo and De Reyna 1988), but the increased risk of these calls might be acceptable because these calls were produced in response to a perceived immediate threat or danger. For example, defensive calls by birds and small mammals may recruit conspecifics to help mob a predator (Vencl 1977; Maier *et al*. 1983), and defensive calls by Puma kittens may serve a similar function by eliciting protective behaviour by their mother.

The structure of Puma vocalizations informs our understanding of their adaptive significance. Pumas are large mammals capable of producing deep and guttural calls; that they instead sometimes use birdlike calls to communicate likely reflects the adaptive significance of those call structures. Although the volume, or amplitude, of calls is also an important factor to consider, we could not compare absolute amplitudes because calls were recorded at different distances from the microphones. The use of vocalizations by Pumas demonstrates that acoustic communications may provide benefits that outweigh their risks and highlights the importance of the structure of vocalizations used during different behaviours. Based on our video recordings that support and enhance the field observations of Smallwood (1993) and Logan and Sweanor (2001), Pumas vocally commu-

nicate in numerous circumstances, including at nurseries, to maintain contact between family groups while travelling or in distress, and when trying to locate mates. The use of motion-triggered video cameras with sound-recording capabilities can create new avenues of scientific research, including cataloguing the full range of Puma vocalizations, understanding intraspecific communication for breeding, intra-familial behaviours exhibited at nurseries, and interspecific interactions including predation and competition.

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SUPPLEMENTARY MATERIAL:

VIDEO S1. A video of a female Puma (*Puma concolor*) caterwauling. https://youtu.be/U3o3x6T-bmI
VIDEO S2. A video of Puma (*Puma concolor*) kittens mewing at their nursery. https://youtu.be/rv6KzyQ7BeA
VIDEO S3. A video of a Puma (*Puma concolor*) giving a contact call. https://youtu.be/seXH_kqM_KM
VIDEO S4. A video of a Puma (*Puma concolor*) giving an agitated call. https://youtu.be/fCadngkBreA
VIDEO S5. A video of a Puma (*Puma concolor*) giving an alarm call. https://youtu.be/uToKCSQJa8M