


Eavesdropping in solitary large carnivores: Black bears advance and vocalize toward cougar playbacks

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Funding information

Natural Sciences and Engineering Research Council (NSERC)

Editor: L. Ebensperger

Abstract

Large carnivore behavioral responses to the cues of their competitors are rarely observed, but may mediate competition between these top predators. Playback experiments, currently limited to interactions involving group-living large carnivores, demonstrate that attending to cues indicative of the immediate presence of heterospecific competitors plays a substantial role in influencing competition among these species. Group-living species vocalize regularly to signal to one another, and competitors can readily “eavesdrop” on these acoustic cues. Solitary large carnivores also vocalize to conspecifics, but much less frequently, reducing the ease with which heterospecific competitors can eavesdrop. Eavesdropping could nonetheless play a substantive role in mediating competition among solitary large carnivores if the benefits of responding to the acoustic cues of heterospecific competitors (reducing risk or locating resources) are sufficiently large. Behavioral interactions between solitary large carnivore species are almost never observed, and there have been no experimental tests of their reactions to cues indicative of the immediate presence of other solitary large carnivores. We used an automated playback system to test the responses of a solitary large carnivore (black bear, *Ursus americanus*) to vocalizations of their similarly solitary competitor (cougar, *Puma concolor*), presenting both cougar and control vocalizations to free-living bears foraging along shorelines in British Columbia, Canada. Both mothers with cubs and solitary bears were significantly more likely to advance and vocalize toward cougar than control playbacks, mothers producing one or both of two distinct vocalizations and solitary bears producing just one. Cougars could either represent a potential risk to bears (particularly cubs), or a source of resources, as bears are known to regularly scavenge cougar kills. Our results are consistent with bears eavesdropping on cougars for both these reasons. As with group-living species, eavesdropping may be common among solitary large carnivores, and may be an important driver of competition between these species.

KEYWORDS

aggression, defensive behavior, interference competition, interspecific competition, playback experiment, scavenging

1 | INTRODUCTION

Interspecific competition between sympatric large carnivores can be a major determinant of habitat use, foraging ecology, and reproductive success in these species and plays an important role in structuring large carnivore guilds (Dröge, Creel, Becker, & M'soka, 2017; Durant, 2000a,b; Gorman, Mills, Raath, & Speakman, 1998; Lendrum et al., 2014). Thus, cues indicative of the immediate presence of competitors may be highly valuable sources of information, allowing carnivores to adjust their behavior to fine-scale changes in the level of threat or opportunity posed by competitors (Broekhuis, Cozzi, Valeix, McNutt, & Macdonald, 2013; Swanson, Arnold, Kosmala, Forester, & Packer, 2016; Webster, McNutt, & McComb, 2010). However, the mechanisms through which large carnivores acquire and use information on the immediate presence of heterospecific competitors remain largely unknown because most studies of large carnivore competition focus on the relatively coarse-scale overlap between species in space and time (Lendrum et al., 2014; Vanak et al., 2013). This is particularly true for solitary or cryptic large carnivore species, for whom direct behavioral interactions between heterospecific competitors are very rarely observed (Murphy, Felzien, Hornocker, & Ruth, 1998).

Much of our knowledge regarding competition between large carnivore species comes from African savannas, where coexistence between sympatric large carnivores has been shown to involve strong interference, including displacement, kleptoparasitism, and interspecific killing (Donadio & Buskirk, 2006; Durant, 2000a; Palomares & Caro, 1999; Périquet, Fritz, & Revilla, 2015). Nonetheless, shared dietary and/or habitat preferences often lead to fine-scale spatial overlap between competitor species. Thus, rather than avoiding competitors across broad spatial scales, a growing body of evidence suggests that interactions between African large carnivores are “reactive,” with individuals adjusting their behavior in response to the immediate presence of competitors (Broekhuis et al., 2013; Swanson et al., 2016). Cues of the immediate presence of a competitor may signal not only risk, but also the presence of resources, and competitors may in some instances react by approaching these cues. For instance, both lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) obtain a substantial portion of their diet in some areas by scavenging and/or kleptoparasitizing the other's kills, and both species often approach cues indicative of the other's presence (Watts, Blankenship, Dawes, & Holekamp, 2010; Webster et al., 2010), despite the fact that aggressive interactions between these species often result in injury or death (Périquet et al., 2015).

Reacting to the risks and opportunities presented by competitors over fine spatial scales requires information on their immediate presence, and social signals such as vocalizations may provide an important source of such information. “Eavesdropping” (i.e., exploiting signals intended for other individuals; Hughes, Kelley, & Banks, 2012; Magrath, Haff, Fallow, & Radford, 2015) on competitor vocalizations may therefore play a substantial role in mediating competition among sympatric large carnivores. Playback experiments indicate that eavesdropping on heterospecific competitor vocalizations is common among group-living African large carnivores (Durant, 2000a; Watts et al., 2010; Webster

et al., 2010), and the attraction of unwanted attention from scavengers may contribute substantially to competition between highly social species such as lions and hyenas (Périquet et al., 2015; Watts et al., 2010). Subordinate large carnivore species, including African wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*), also recognize lion and hyena vocalizations, and respond by avoiding these dominant competitors, which are a substantial source of mortality for both cheetahs and wild dogs (Durant, 2000a; Webster, McNutt, & McComb, 2012). Solitary large carnivores naturally vocalize much less frequently than group-living species, but where the benefits of eavesdropping are sufficiently large, competitors may nonetheless be expected to recognize and respond to the acoustic cues of solitary species. Just as in group-living species, these benefits may include both avoiding interactions with a potentially dangerous competitor (Durant, 2000a; Webster et al., 2012) and taking advantage of scavenging opportunities (Watts et al., 2010). Due to the logistical challenges involved, to date, there have been no experimental tests of the responses of solitary large carnivores to cues indicative of the immediate presence of heterospecific competitors. The role of eavesdropping in mediating competition among solitary large carnivores has thus remained unknown.

American black bears (*Ursus americanus*, hereafter “bears”) and cougars (*Puma concolor*) are solitary large carnivores that co-occur throughout large areas of western North America. Both species vocalize during intraspecific interactions (Allen, Wang, & Wilmers, 2016; Allen, Wittmer, & Wilmers, 2014; Beier, Choate, & Barrett, 1995; Herrero, 1983; Jordan, 1976; Logan & Sweanor, 2010), and although these vocalizations may be relatively infrequent, each species may benefit from recognizing and responding to acoustic cues indicative of the other's immediate presence. Each species poses some risk to the other. Bears weigh up to several times more than cougars (Reid, 2006) and are generally considered to be the dominant competitor (Allen, Elbroch, Wilmers, & Wittmer, 2014; Murphy et al., 1998), but cougars are known to occasionally kill cubs and juvenile bears (Allen, Elbroch, Wilmers, & Wittmer, 2015; LeCount, 1987). For bears, who regularly scavenge prey killed by cougars (Allen, Elbroch, et al., 2014; Murphy et al., 1998), cues of the immediate presence of a cougar may also signal the immediate presence of a resource. Recognizing and responding to cougar vocalizations may thus benefit bears by both reducing risk and providing access to resources, in the same way eavesdropping benefits group-living large carnivores. However, neither of these scenarios necessarily requires that bears recognize cougar vocalizations—mother bears, for example, are notoriously aggressive toward any perceived threat (Herrero, 1983), and it is possible that bears locate cougar kills haphazardly or respond solely to cues of the carcass itself (Krofel, Kos, & Jerina, 2012). Thus, competition between these species could occur largely in the absence of bears recognizing and demonstrating specific behavioral responses to the vocalizations of their competitor. Whether bears recognize and respond to cougar cues has to date remained unknown, in part because direct behavioral interactions between bears and cougars are almost never observed (Allen et al., 2015; Murphy et al., 1998).

To conclusively demonstrate that bears eavesdrop on cougar vocalizations requires experimentally testing their responses to cougar

and control (i.e., non-competitor) vocalizations (Hettena, Munoz, & Blumstein, 2014; Magrath et al., 2015). To better understand the behaviors that mediate competition between these solitary large carnivores, and whether responding to cues of the immediate presence of heterospecific competitors may play a role similar to that reported among group-living species, we used newly developed automated playback technology (Suraci et al., 2016) to experimentally test the reactions of bears to cougar vocalizations, recording previously unobserved responses of bears to cougar cues. Bears may respond by altering their movements and vocalizing themselves. Bears are known to vocalize during interactions with conspecifics (Herrero, 1983), and vocalization may be an important component of interactions with heterospecific competitors as well, potentially providing insights into the drivers of bear behavioral responses to competitor cues. For instance, bears frequently vocalize during aggressive interactions with conspecifics to both defend young and secure contested resources (Herrero, 1983), and may use similar signals during interactions with heterospecific competitors. Several previous studies have provided verbal descriptions of bear vocalizations (e.g., Herrero, 1983; Jordan, 1976), yet quantitative descriptions, based on the analysis of acoustic properties, are remarkably rare for vocalizations of any bear species (Pokrovskaya, 2013) and, to our knowledge, do not exist for vocalizations of American black bears. As a component of our experimental investigation into the behaviors that mediate competition between solitary large carnivores, we therefore additionally provide a quantitative analysis of the vocalizations produced by bears in response to cougar cues and discuss their potential functions in signaling to both dependent young and heterospecific competitors.

2 | MATERIALS AND METHODS

This study was conducted in Clayoquot Sound, on the remote central west coast of Vancouver Island, British Columbia, Canada, where large populations of bears and cougars coexist (Suraci, Clinchy, & Zanette, 2017; Suraci, Clinchy, Zanette, Currie, & Dill, 2014). We tested the behavioral responses of free-living bears using a fully automated playback system (Suraci et al., 2016), which, when triggered by a passing animal, broadcasts a playback from a custom-built speaker and video records the animal's response using a camera trap (in this case the Moultrie M-990i, Moultrie Products, LLC, USA), all in the absence of a researcher. Systems were set at shoreline sites just above the high tide line, directed toward the water to be triggered by bears foraging in the intertidal, and programmed to broadcast a 10-s playback, record a 90-s video, and record audio throughout the trial. Camera traps were set at the high tide line, and speakers were placed 3 m behind the camera trap. We compared bear responses to cougar vocalizations with their responses to the vocalizations of local pinnipeds (harbor seal [*Phoca vitulina*] and Steller sea lion [*Eumatopias jubatus*], hereafter "seals"), control sounds with which all bears in this coastal study population are likely to be familiar (Hansen, Searle, Szaniszló, & Munro, 2010; Suraci et al., 2017;). Similar playback experiments have been highly successful at testing the behavioral responses of

large carnivores to the sounds of their competitors (Durant, 2000b; Heinsohn & Packer, 1995; Webster et al., 2012). We prepared randomized playlists consisting of seven exemplars of each playback treatment (cougar or control), composed of a variety of different types of cougar and seal vocalizations, all of which were broadcast at a consistent volume of 80 dB at 1 m. Cougar playlists contained both aggressive (e.g., hissing, growling) and non-aggressive (e.g., caterwauling) vocalizations (Allen et al., 2016). The use of multiple exemplars is standard practice in playback experiments (Kroodsma, Byers, Goodale, Johnson, & Liu, 2001), enabling robust conclusions concerning responses to the "class" of sounds, as opposed to the specifics of a particular sound.

Bears and cougars overlap in their use of shoreline habitat in Clayoquot Sound and bears may thus be expected to be exposed to cougar vocalizations here. Previous research shows that both bears (Suraci et al., 2017) and cougars (Hansen et al., 2010) in Clayoquot Sound derive a substantial portion of their diet from marine resources, and we recorded images of cougars on multiple occasions on the same shoreline cameras used to film the bears' response to the playbacks. While cougar vocalizations are relatively rare compared to those of group-living large carnivores, cougars do communicate vocally with conspecifics, using a variety of call types (Allen et al., 2016). For instance, vocalizations are a common component of reproductive behavior for adult cougars of both sexes. Individuals caterwaul to advertise their reproductive status, with females doing so on c. 10% of visits to communal "scrapes" (Allen, Wittmer, et al., 2014), and both males and females regularly vocalize during multiday mating associations (Beier et al., 1995). Cougars also produce a range of distress vocalizations (Allen et al., 2016), and mothers and kittens are known to vocalize frequently throughout the up to 2-year period that kittens remain with their mother (Logan & Sweanor, 2010). Throughout western North America, cougars tend to breed between February and July, and produce litters between May and October (Logan & Sweanor, 2010). Thus, mating-related and mother-offspring vocalizations naturally occur during the spring and summer months, when our study took place (see below).

Trials ($n = 102$) were conducted between 25 May and 27 August 2015 at 10 shoreline sites, separated by an average (\pm SD) minimum distance of 2.4 (\pm 1.4) km. At each site, we obtained trials from one to three individual adult bears (identifiable from video by size, pelage, and the presence or absence of cubs; $n = 16$ individuals in total), with each individual being exposed to a given playback treatment an average of 3.5 times (range: one to nine exposures). Across all sites, we obtained trials from six individual females with cubs and ten solitary adult bears. The majority of individuals ($n = 10$) were exposed to both playback treatments. A single researcher (JPS), blind to playback treatment, scored videos of all trials, noting whether the bear (i) advanced toward the sound source and/or (ii) vocalized in response to the playback. We also noted instances of "evading" (i.e., quickly moving away) and "charging" (i.e., running toward a threatening stimulus), the latter being a highly aggressive display (Jordan, 1976). A second observer (DJR), also blind to playback treatment, visually scored spectrograms of the audio from each trial that was noted as containing a

bear vocalization during initial video scoring. Results presented below regarding the probability of bears vocalizing in response to playbacks therefore correspond to those trials that were agreed upon by both observers, scoring trials independently and using complementary methods.

As noted above, no quantitative description based on the analysis of acoustic properties exists concerning the vocalizations of the American black bear, according to a recent study (Pokrovskaya, 2013), and to our knowledge, this remains true; all that currently exists are verbal and onomatopoeic call descriptions (e.g., Jordan, 1976; Herrero, 1983). Indeed, according to this same study (Pokrovskaya, 2013), which quantified the vocal repertoire of the Asiatic black bear (*Ursus thibetanus*), the only other species of bear whose vocal repertoire has been comprehensively quantified is the giant panda (*Ailuropoda melanoleuca*). We accordingly used the same software (Avisoft SASLab Pro) and procedures to quantify our American black bear vocalizations that Pokrovskaya (2013) used to quantify Asiatic black bear vocalizations, which this author reported could be discriminated based on duration and frequency characteristics. Discriminating based on duration and frequency, we identified two distinct vocalizations produced by the bears in our experiment in response to the playbacks (Figure 1 and Table 1), a “very short, very low” vocalization (VSVL, Figure 1a) and a “short and low” vocalization (S&L, Figure 1b). To quantitatively characterize these two vocalizations, for each video of a playback trial containing a specific vocalization type (VSVL, $n = 26$; S&L, $n = 22$), we chose a single example of that vocalization (the one with the clearest spectrogram) and measured the duration; the peak frequency; and the lower (25%), middle (50%), and upper (75%) quartiles of the energy spectrum (Table 1); following Pokrovskaya (2013). The S&L vocalization exhibited two distinct frequency bands of high energy (Figure 1b), and we therefore report the peak frequency for each of these bands (Table 1).

Binary response variables describing the probability of bears advancing and vocalizing in response to playbacks were analyzed using binomial generalized mixed-effects models (GLMM), incorporating individual as a random effect to account for repeated measurements from individual bears, and accounting for temporal autocorrelation between consecutive trials where appropriate (see below). The presence or absence of cubs may have a strong effect on the reaction to playbacks, as mother bears are known to be highly aggressive toward anything perceived as a potential threat to their offspring (Herrero, 1983). Repeated exposures to playbacks may also affect bear responses through habituation. Accordingly, our GLMM analyses tested for the

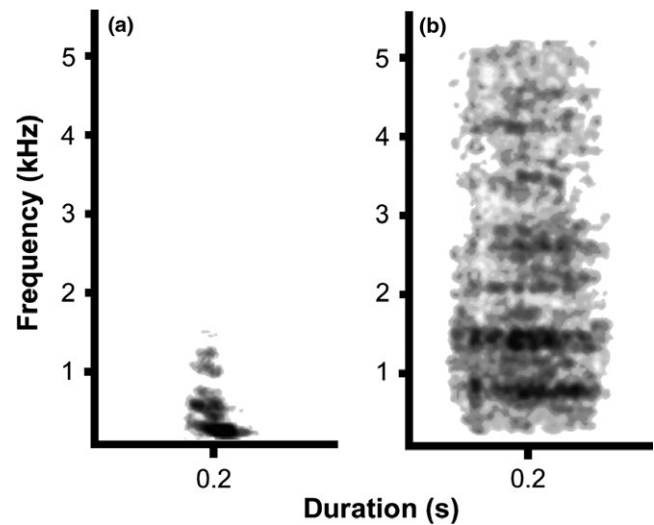


FIGURE 1 Spectrograms of the two distinct vocalizations produced by bears in response to the playbacks: (a) the very short, very low (VSVL) vocalization; and (b) the short and low (S&L) vocalization

	Very short, very low			Short and low		
	Mean	SD	Range	Mean	SD	Range
Duration	0.13	0.03	0.09–0.18	0.28	0.05	0.21–0.37
Principal peak frequency	0.16	0.02	0.11–0.19	0.77	0.12	0.49–0.94
Secondary peak frequency				1.54	0.32	1.12–2.20
Lower quartile of energy spectrum	0.15	0.01	0.11–0.18	0.60	0.19	0.31–0.97
Middle quartile of energy spectrum	0.16	0.01	0.13–0.19	0.91	0.25	0.45–1.36
Upper quartile of energy spectrum	0.18	0.02	0.15–0.21	1.71	0.62	0.98–3.05

TABLE 1 Duration (seconds) and frequency (kHz) characteristics of the very short, very low (VSVL; $N = 26$) and short and low (S&L; $N = 22$) vocalizations

Note that the VSVL vocalization exhibited a single peak frequency (Figure 1a) whereas the S&L vocalization exhibited a primary and secondary high-energy frequency band (Figure 1b).

main effects of playback treatment, exposure (i.e., whether a trial was an individual bear's first, second, etc., exposure to a given playback treatment), and the presence or absence of cubs; as well as all two-way interactions between these covariates. The VSVL vocalization, likely used for communication between mothers and cubs (see below), was produced almost exclusively by females with cubs present (93% of occurrences), and the analysis of the effect of playback treatment on the probability of producing the VSVL vocalization was therefore restricted to trials in which cubs were present.

To test for potential temporal autocorrelation between consecutive playbacks to the same bear, we first fit all binomial GLMM with a serial autocorrelation structure using the *glmmPQL* package in R (R Core Team, 2015). For all models, we used a first-order autoregressive correlation structure with time (in min since the start of the field season) as the position variable and observations grouped by individual (Pinheiro & Bates, 2000). This accounts for correlation between an individual bear's behavioral response in a given trial and its response in the immediately preceding trial (i.e., time lag = 1). Both the probability of advancing and the probability of producing the S&L vocalization showed evidence of temporal autocorrelation (autocorrelation parameter $\Phi = 0.92$ and 0.33 , respectively; Pinheiro & Bates, 2000). Thus, for these response variables, we present results from the GLMM with serial autocorrelation structure. Due to limited sample size for the probability of producing the VSVL vocalization (this analysis was restricted to trials from female bears with cubs only; see above), the GLMM with temporal autocorrelation structure failed to converge. These data were therefore refit with standard GLMM (using the *lme4* package in R). The residuals from this model were analyzed using an autocorrelation function (ACF) and showed no evidence of temporal autocorrelation. For all models, the significance of model terms was tested using Wald's chi-squared test (Bolker et al., 2009).

3 | RESULTS

All bears, whether mothers with cubs or solitary bears, were significantly more likely to advance toward cougar than control (seal) playbacks (Figure 2a; cougar, 75% of 56 trials; control, 39% of 46 trials; Wald's $\chi^2 = 6.20$, $df = 1$, $p = .013$). Mothers with cubs were significantly more likely to produce the VSVL vocalization in reaction to cougar playbacks, relative to controls (Figure 2b; cougar, 96% of 23 trials; control, 50% of six trials; Wald's $\chi^2 = 4.51$, $df = 1$, $p = .034$); and both mothers with cubs and solitary bears taken together were ten times more likely to produce the S&L vocalization in reaction to cougar playbacks, compared to controls (Figure 2c; cougar, 41% of 56 trials; control, 4% of 46 trials; Wald's $\chi^2 = 12.66$, $df = 1$, $p < .001$). The number of exposures did not significantly affect these responses, nor did the presence or absence of cubs significantly affect the likelihood of advancing or producing the S&L vocalization (all $p \geq .12$). Bears exhibited evasion—characterized by moving quickly away down the shoreline—in response to both cougar and seal playbacks in a small percentage of trials (cougar 7%, seal 4%). At the opposite extreme,

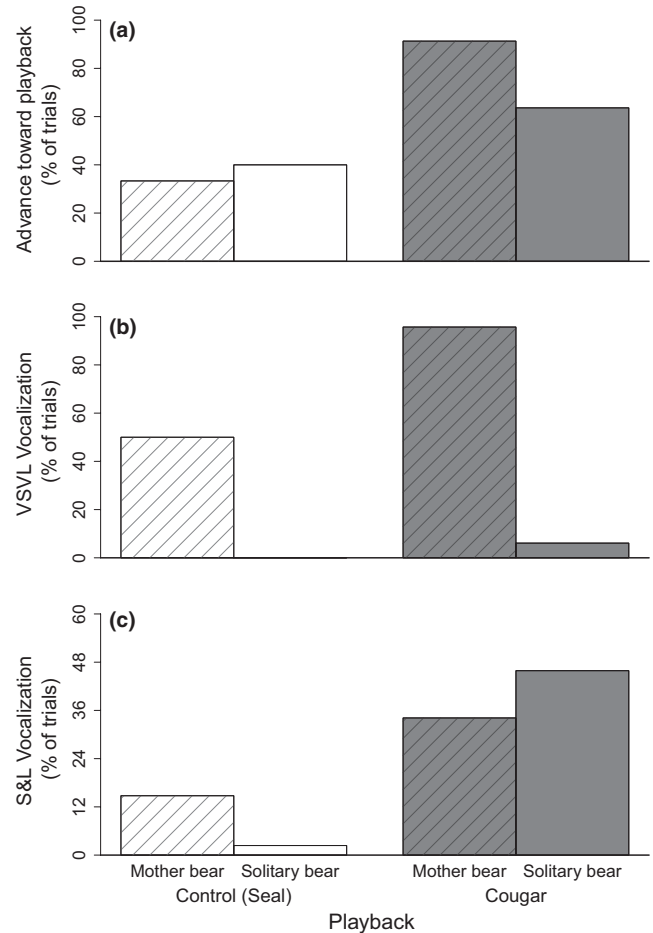


FIGURE 2 Percent of trials in which bears (a) advanced toward the sound source, (b) produced the very short, very low (VSVL) vocalization, and (c) produced the short and low (S&L) vocalization, in response to control (white bars) and cougar (gray bars) playbacks. The responses of both mother bears with cubs (hashed bars) and solitary bears (open bars) are shown

mothers with cubs charged the speaker in six trials, a highly aggressive reaction observed solely in response to cougars.

4 | DISCUSSION

In what is to our knowledge the first experimental test of eavesdropping in solitary large carnivores, we documented that black bears recognized and reacted to cues of the immediate presence of a competitor, clearly distinguishing cougar vocalizations from those of non-competitors. Bears were significantly more likely to advance (Figure 2a) and vocalize (Figure 2b,c) in reaction to cougar playbacks, relative to controls. The bears in our experiment produced two distinct vocalizations, and to the best of our knowledge, our analysis of these sounds (Figure 1, Table 1) additionally provides the first quantitative characterization of any American black bear vocalizations. The acoustic properties of the two vocalizations we identified overlap extensively with, and would thus appear to be analogous to, two vocalizations of Asiatic black bears identified by Pokrovskaya (2013),

our VSVL and S&L vocalizations corresponding, respectively, with what Pokrovskaya (2013) termed “grunts” and “snorts” (compare our Table 1 with Table 1 in Pokrovskaya, 2013). Pokrovskaya (2013) described a “grunt” as a short, low frequency tonal call, observing that this was consistent with verbal descriptions of calls used for communication between mothers and cubs in multiple bear species (including American black bears; see Jordan, 1976). A “snort” was described as a short unvoiced sound produced with the mouth closed, which Pokrovskaya (2013) noted was consistent with verbal descriptions of what other researchers have termed a “huff” (e.g., Herrero, 1983; Jordan, 1976), a vocalization typically produced when bears are anxious (Pokrovskaya, 2013), or as an aggressive signal (Herrero, 1983).

Studies on group-living African large carnivores indicate that the primary benefits of eavesdropping on heterospecific competitors include avoiding potential threats (Durant, 2000b; Webster et al., 2012) and identifying opportunities to exploit the competitor's resources (Périquet et al., 2015; Watts et al., 2010; Webster et al., 2010). Our results suggest that both of these factors may help explain the observed behavioral responses of bears to cougar vocalizations. Mother bears with cubs, well known to be highly aggressive toward perceived threats to their offspring (Herrero, 1983), advanced toward cougar playbacks in the great majority of trials (91%; Figure 2a), in some cases even aggressively charging the cougar playbacks, strongly indicating that mothers perceived cues of the immediate presence of a cougar as a threat to their cubs. This is corroborated by mothers with cubs producing the VSVL vocalization in reaction to cougar playbacks in the great majority of trials (96%; Figure 2b), this vocalization, as noted above, most likely being a contact call from mothers to their young (Pokrovskaya, 2013).

Solitary bears advanced toward cougar playbacks in the majority of trials (64%; Figure 2a) and produced the S&L vocalization in reaction to cougar playbacks in almost half of all trials (45%; Figure 2c). Whereas vocalizing by mothers with cubs (Figure 2b,c) may be a signal to their young, in the case of solitary bears with no cubs or other bears present, the signal (Figure 2c) is evidently directed toward the animal it is apparently advancing upon. As noted above, in comparison with Pokrovskaya's (2013) results, the S&L vocalization would appear to be associated with anxiousness or aggression.

Reaction to a perceived threat may not only explain the response of mother bears but may also partially explain the response of solitary bears to cougar playbacks. Defensive aggression in carnivores may occur in defense of the individual's offspring (as noted above), itself, or its food (Jordan, 1976; Penteriani et al., 2016). In the case of solitary bears, the risk cougars pose to adult bears (which are on average substantially larger than cubs; Reid, 2006) is likely low (Palomares & Caro, 1999). The threat to the bear's food supply may in contrast be considerable. Our research shows that bears in Clayoquot Sound spend a considerable portion of their time patrolling the shoreline, being recorded every third day on average on our camera traps (Suraci et al., 2017). Cougars here also evidently spend considerable time patrolling shorelines as almost half their diet (c. 45%) is composed of marine and aquatic prey (seal, otter, sea lions, mink; Hansen et al., 2010). As both bears and cougars here regularly hunt along shorelines, bears may be motivated to deter their competitor from this shared foraging ground.

Advancing and vocalizing in response to cougar vocalizations, particularly by solitary bears, may also be related to attempts to steal food by displacing cougars from carcasses. Bears may actively seek kleptoparasitism opportunities when they detect the immediate presence of a cougar, potentially contributing to the reportedly high levels of competition for cougar kills that occurs between these species (Murphy et al., 1998), and the high incidence of cougar displacement by bears (Allen, Elbroch, et al., 2014; Allen et al., 2015). Research in other habitats indicates that bears can potentially obtain a substantial proportion of their daily energetic requirements from scavenging/stealing cougar kills (Murphy et al., 1998). Large populations of bears and cougars co-occur in Clayoquot Sound (Suraci et al., 2014, 2017), and we suggest that bears here may benefit from eavesdropping on cougars in part because the immediate presence of a cougar may signal the immediate presence of a food source. Our study provides the necessary first step in testing this hypothesis by demonstrating: (i) the logistical feasibility of conducting eavesdropping experiments on solitary large carnivores; and (ii) that bears recognize and respond to cougar vocalizations. The next step to directly testing whether bears benefit from eavesdropping on cougars by gaining access to resources would be to conduct an experiment broadcasting playbacks at bait stations or food caches, to establish if bears more frequently find and eat those adjacent to speakers broadcasting cougar calls.

Our findings suggest that eavesdropping to reduce the threat posed by, or locate and secure resources from, heterospecific competitors may be common across large carnivore guilds, including those composed predominantly or entirely of solitary species. Eavesdropping on the vocalizations of group-living African large carnivores (e.g., lions and hyenas) by heterospecific competitors has been shown to mediate competition between these highly vocal species (Durant, 2000a,b; Watts et al., 2010; Webster et al., 2010, 2012), and our experimental results indicate that much the same may be true among solitary large carnivores. Despite the relatively lower rates of vocalization by solitary large carnivore species, the potential benefits of eavesdropping on heterospecific competitors may promote the recognition of acoustic cues among solitary large carnivores, much as it does among the more vocal group-living species. Interference and avoidance are thought to be major factors affecting the coexistence of sympatric large carnivores (Durant, 2000a; Gorman et al., 1998; Krofel et al., 2012; Périquet et al., 2015), yet, apart from the well-studied African systems described above, little is known about the behavioral mechanisms driving these interactions. Here, we provide experimental evidence that competition between solitary large carnivores may be mediated by eavesdropping on heterospecific vocalizations, and suggest that an increased focus on direct behavioral interactions may reveal that recognizing and reacting to cues indicative of the immediate presence of competitors is a major component of competition among top predators in general.

ACKNOWLEDGEMENTS

We thank the Tla-o-qui-aht First Nation and Parks Canada for access to field sites; L. Granger and P. Charlie for help in the field; and L. Dill for support. This study was conducted in compliance with the

guidelines of the Canadian Council on Animal Care and approved by the University of Victoria Animal Care and Use Committee, and conforms to the laws of Canada. Funding was provided by Natural Sciences and Engineering Research Council (NSERC) grants to L. Dill, MC, and LYZ; and an NSERC Industrial Postgraduate Scholarship to JPS.

REFERENCES

- Allen, M. L., Elbroch, L. M., Wilmers, C. C., & Wittmer, H. U. (2014). Trophic facilitation or limitation? comparative effects of pumas and black bears on the scavenger community. *PLoS One*, *9*(7), e102257.
- Allen, M. L., Elbroch, L. M., Wilmers, C. C., & Wittmer, H. U. (2015). The comparative effects of large carnivores on the acquisition of carrion by scavengers. *American Naturalist*, *185*(6), 822–833.
- Allen, M. L., Wang, Y., & Wilmers, C. C. (2016). Exploring the adaptive significance of five types of puma (*Puma concolor*) vocalizations. *The Canadian Field-Naturalist*, *130*(4), 289–294.
- Allen, M. L., Wittmer, H. U., & Wilmers, C. C. (2014). Puma communication behaviours: Understanding functional use and variation among sex and age classes. *Behaviour*, *151*(6), 819–840.
- Beier, P., Choate, D., & Barrett, R. H. (1995). Movement patterns of mountain lions during different behaviors. *Journal of Mammalogy*, *76*(4), 1056–1070.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135.
- Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J. W., & Macdonald, D. W. (2013). Risk avoidance in sympatric large carnivores: Reactive or predictive? *Journal of Animal Ecology*, *82*(5), 1098–1105. <https://doi.org/10.1111/1365-2656.12077>
- Donadio, E., & Buskirk, S. W. (2006). Diet, morphology, and interspecific killing in carnivora. *American Naturalist*, *167*(4), 524–536.
- Dröge, E., Creel, S., Becker, M. S., & M'soka, J. (2017). Spatial and temporal avoidance of risk within a large carnivore guild. *Ecology and Evolution*, *7*, 189–199.
- Durant, S. M. (2000a). Predator avoidance, breeding experience and reproductive success in endangered cheetahs, *Acinonyx Jubatus*. *Animal Behaviour*, *60*(1), 121–130.
- Durant, S. M. (2000b). Living with the enemy: Avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, *11*(6), 624–632.
- Gorman, M. L., Mills, M. G., Raath, J. P., & Speakman, J. R. (1998). High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature*, *391*(6666), 479–481.
- Hansen, B., Searle, R., Szaniszlo, W., & Munro, S. (2010). *Learning to live with large carnivores: Wildcoast project primer and guidelines*. Ottawa, ON, Canada: Parks Canada Agency.
- Heinsohn, R., & Packer, C. (1995). Complex cooperative strategies in group-territorial African lions. *Science*, *269*(5228), 1260–1262.
- Herrero, S. (1983). Social behaviour of black bears at a garbage dump in Jasper National Park. *Bears: Their Biology and Management*, *5*, 54–70.
- Hettena, A. M., Munoz, N., & Blumstein, D. T. (2014). Prey responses to predator's sounds: A review and empirical study. *Ethology*, *120*(5), 427–452.
- Hughes, N. K., Kelley, J. L., & Banks, P. B. (2012). Dangerous liaisons: The predation risks of receiving social signals. *Ecology Letters*, *15*(11), 1326–1339.
- Jordan, R. H. (1976). Threat behavior of the black bear (*Ursus americanus*). *Bears: Their Biology and Management*, *3*, 57–63.
- Krofel, M., Kos, I., & Jerina, K. (2012). The noble cats and the big bad scavengers: Effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology*, *66*(9), 1297–1304.
- Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S., & Liu, W.-C. (2001). Pseudoreplication in playback experiments, revisited a decade later. *Animal Behavior*, *61*, 1029–1033.
- LeCount, A. L. (1987). Causes of black bear cub mortality. *Bears: Their Biology and Management*, *7*, 75–82.
- Lendrum, P. E., Elbroch, L. M., Quigley, H., Thompson, D. J., Jimenez, M., & Craighead, D. (2014). Home range characteristics of a subordinate predator: Selection for refugia or hunt opportunity? *Journal of Zoology*, *294*(1), 58–66.
- Logan, K. A., & Sweaner, L. L. (2010). Behavior and social organization of a solitary carnivore. In M. G. Hornocker, & S. Negri (Eds.), *Cougar: Ecology and conservation* (pp. 118–137). Chicago: University of Chicago Press.
- Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: From mechanisms to consequences. *Biological Reviews*, *90*(2), 560–586.
- Murphy, K. M., Felzien, G. S., Hornocker, M. G., & Ruth, T. K. (1998). Encounter competition between bears and cougars: Some ecological implications. *Ursus*, *10*, 55–60.
- Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *American Naturalist*, *153*(5), 492–508.
- Penteriani, V., Delgado M. del M., Pinchera, F., Naves, J., Fernández-Gil, A., Kojala, I., ... López-Bao, J. V. (2016). Human behaviour can trigger large carnivore attacks in developed countries. *Scientific Reports*, *6*. doi: 10.1038/srep20552
- Périquet, S., Fritz, H., & Revilla, E. (2015). The Lion King and the Hyaena Queen: Large carnivore interactions and coexistence. *Biological Reviews*, *90*(4), 1197–1214.
- Pinheiro, J., & Bates, D. (2000). *Mixed-Effects Models in S and S-PLUS*. New York, USA: Springer.
- Pokrovskaya, L. (2013). Vocal repertoire of Asiatic Black Bear (*Ursus thibetanus*) cubs. *Bioacoustics*, *22*(3), 229–245.
- R Core Team. (2015). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reid, F. (2006). *A field guide to mammals of North America, North of Mexico*, 4th ed.. Boston, USA: Houghton Mifflin Harcourt.
- Suraci, J. P., Clinchy, M., Mugerwa, B., Delsey, M., Macdonald, D. W., Smith, J. A., ... Zanette, L. Y. (2016). A new Automated Behavioural Response system to integrate playback experiments into camera trap studies. *Methods in Ecology and Evolution*. <https://doi.org/10.1111/2041-210X.12711>
- Suraci, J. P., Clinchy, M., & Zanette, L. Y. (2017). Do large carnivores and mesocarnivores have redundant impacts on intertidal prey? *PLoS One*, *12*(1), e0170255.
- Suraci, J. P., Clinchy, M., Zanette, L. Y., Currie, C. M. A., & Dill, L. M. (2014). Mammalian mesopredators on islands directly impact both terrestrial and marine communities. *Oecologia*, *176*(4), 1087–1100.
- Swanson, A., Arnold, T., Kosmala, M., Forester, J., & Packer, C. (2016). In the absence of a “landscape of fear”: How lions, hyenas, and cheetahs coexist. *Ecology and Evolution*, *6*(23), 8534–8545.
- Vanak, A. T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S., & Slotow, R. (2013). Moving to stay in place: Behavioral mechanisms for coexistence of African large carnivores. *Ecology*, *94*(11), 2619–2631.
- Watts, H. E., Blankenship, L. M., Dawes, S. E., & Holekamp, K. E. (2010). Responses of spotted hyenas to lions reflect individual differences in behavior. *Ethology*, *116*(12), 1199–1209.
- Webster, H., McNutt, J. W., & McComb, K. (2010). Eavesdropping and risk assessment between lions, spotted hyenas and african wild dogs. *Ethology*, *116*(3), 233–239.
- Webster, H., McNutt, J. W., & McComb, K. (2012). African wild dogs as a fugitive species: Playback experiments investigate how wild dogs respond to their major competitors. *Ethology*, *118*(2), 147–156.

How to cite this article: Suraci JP, Clinchy M, Roberts DJ, Zanette LY. Eavesdropping in solitary large carnivores: Black bears advance and vocalize toward cougar playbacks. *Ethology*. 2017;00:1–7. <https://doi.org/10.1111/eth.12631>