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Research article

Not afraid of the big bad wolf: calls from large predators do not silence mesopredators

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Large predators are known to shape the behavior and ecology of sympatric predators via conflict and competition, with mesopredators thought to avoid large predators, while dogs suppress predator activity and act as guardians of human property. However, interspecific communication between predators has not been well-explored and this assumption of avoidance may oversimplify the responses of the species involved. We explored the acoustic activity of three closely related sympatric canids: wolves *Canis lupus*, coyotes *Canis latrans*, and dogs *Canis familiaris*. These species have an unbalanced triangle of risk: coyotes, as mesopredators, are at risk from both apex-predator wolves and human-associated dogs, while wolves fear dogs, and dogs may fear wolves as apex predators or challenge them as intruders into human-allied spaces. We predicted that risk perception would dictate vocal response with wolves and dogs silencing coyotes as well as dogs silencing wolves. Dogs, in their protective role of guarding human property, would respond to both. Eleven passive acoustic monitoring devices were deployed across 13 nights in central Wisconsin, and we measured the responses of each species to naturally occurring heterospecific vocalizations. Against our expectation, silencing did not occur. Instead, coyotes were not silenced by either species: when hearing wolves, coyotes responded at greater than chance rates and when hearing dogs, coyotes did not produce fewer calls than chance rates. Similarly, wolves responded at above chance rates to coyotes and at chance rates when hearing dogs. Only the dogs followed our prediction and responded at above chance rates in response to both coyotes and wolves. Thus, instead of silencing their competitors, canid vocalizations elicit responses from them suggesting the existence of a complex heterospecific communication network.

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Keywords: *Canis familiaris*, *Canis latrans*, *Canis lupus*, eavesdropping, ecology of fear, interspecific communication

Introduction

Coexisting species need to minimize dangerous conflict and risk (Durant 1998, Haines 2006, Newsome and Ripple 2015b). Typically, the burden of resource partitioning, spatial distribution, and conflict avoidance falls on the species more at risk in interspecific interactions. It can, therefore, be predicted that where large predators and mesopredators share the same space, the mesopredators should broadly avoid detection by the large predators and pay attention to their signals to avoid negative interactions (Pangle and Holekamp 2010), but this is not always the case, as for lions *Panthera leo* (Comley et al. 2020). However, while there is evidence of spatial partitioning (Harmsen et al. 2009, Viota et al. 2012, Foster et al. 2013) and temporal partitioning (Arjo and Pletscher 1999, Shores et al. 2019) between large predators and mesopredators, evidence for this avoidance is not conclusive (Sévêque et al. 2021, Ferretti et al. 2023). Thus, it is not clear how well the ecology of fear, the total impact of predators on their prey which is clearly demonstrated for prey (Brown et al. 1999, Ripple and Beschta 2004), holds true for mesopredators (Wooster et al. 2021).

Communication is critical to social interactions, both within and between species (Bradbury and Vehrencamp 1998). While most studies focus on conspecific communication, there is growing interest in understanding how and why heterospecific communication moderates interspecific interactions (Rainey et al. 2004, Magrath et al. 2015, Nielsen et al. 2015, Apps et al. 2019). Heterospecific communication can be a deliberate transfer of information to an individual of another species, or incidental as when one species eavesdrops on the other (Lea et al. 2008, Foote et al. 2010, Banks et al. 2016). Eavesdropping, where information provided by a signaler that is perceived and potentially used by an unintended receiver, is considered one-way communication because no response is given by the listener. As acoustic signals are frequently effective at long ranges, they can be used to detect the presence of a species (Balakrishnan et al. 2014, Magrath et al. 2015). Thus, it could be expected that prey and mesopredators use large predator calls to locate potential dangers and coordinate their movements and behavior accordingly to avoid detection by predators, such as by remaining quiet when in audible range of a predator, and/or to gather information on scavenging opportunities. This type of heterospecific eavesdropping is well-documented for prey species (Lea et al. 2008, Trefry and Hik 2009, Fallow et al. 2013, Magrath et al. 2015, Westrip and Bell 2015), but its impact on mesopredator behavior is less well understood (Petroelje et al. 2013).

In contrast to eavesdropping, two-way communication requires the receiver to signal back (Magrath et al. 2015). Despite large predators' critical role in their ecosystem and their effect on sympatric mesopredators, their elusive and cryptic behavior inhibits direct observation making intraguild interference difficult to study (Wilson and Delahay 2001, Berger et al. 2008, Ritchie and Johnson 2009, Swanson et al. 2014, Newsome and Ripple 2015a). It is possible that mesopredators may choose to engage in two-way communication if there is a benefit to them, e.g. defensively signaling to a potential threat that the group is too large to be easy prey (Santema et al. 2019) or to mediate conflict between individuals from different species (Souriau et al. 2018). Furthermore, there is increasing evidence that predators communicate interspecifically through scent marking, with research supporting complex communication through chemical signals (Garvey et al. 2016, 2017, Allen et al. 2017, Apps et al. 2017, 2019, Edwards et al. 2022).

To explore interspecific communication between species that pose unequal threats to each other, we studied the vocal communication between three canid species: the grey wolf *Canis lupus*, coyote *Canis latrans* and domestic dog *Canis familiaris*. These species are closely related but ecologically and physically distinct, last sharing a common ancestor between 1.7 Mya (Zhao et al. 2016) and 2.6 Mya (Nyakatura and Bininda-Emonds 2012). Coyotes, dogs and wolves are all capable of successful hybridization, both historically and presently (Verardi et al. 2006, Bohling and Waits 2011). Each species is highly social and demonstrates complex social behavior (Bekoff and Wells 1986, Boitani and Ciucci 1995) even during interactions with other species (Switalski 2003, Alexander and Quinn 2011, Boydston et al. 2018).

Canids are a good model taxon for investigating interspecific communication as they are highly vocal and produce a range of long-distance calls (Feddersen-Petersen 2000). Wolf howls encode a wide range of information including individual identity (Theberge and Falls 1967, Tooze et al. 1990, Root-Gutteridge et al. 2014a, b), pack membership (Zaccaroni et al. 2012), and subspecies (Kershenbaum et al. 2016). While adult wolves rarely bark (Harrington and Mech 1978), dogs and coyotes produce barks, which encode information about the sex, identity, and, for dogs, breed of the sender (Yin and McCowan 2004, Chulkina et al. 2006, Mitchell et al. 2006, Molnár et al. 2009, Péter et al. 2014). Canid vocalizations in conspecific communication are used to maintain territories and contact between pack members with long-range howls (Harrington and Mech 1978, 1983, Watson et al. 2018). Little is known about heterospecific acoustic communication and eavesdropping, and although there is some evidence of coyotes responding to solo wolf howls at < 2 km, this is limited (Petroelje et al. 2013). A recent study of dogs' responses to wolf howls suggested that time since domestication had an impact on their behavior (Lehoczki et al. 2023). There are occasional anecdotes about positive dog-wolf interactions (Jans 2014, Landry et al. 2020) or the impact of wolves on coyotes (Prugh et al. 2023), but most research has focused on aggressive encounters (Kojola et al. 2004, Vanak and Gompper 2009, Gehring et al. 2010, Lescureux and Linnell 2014, Boydston et al. 2018).

However, the same animals can participate in different interactions at different times – from dogs' belligerent defense of sheep from wolf and coyote predation to wolves and dogs participating in play (Landry et al. 2020).

Agonistic interactions between wolves and coyotes are well-documented (Atwood and Gese 2008, Merkle et al. 2009, Prugh et al. 2023). While dogs are not typically apex predators, they can induce a 'landscape of fear' effect whereby wildlife avoid areas occupied by dogs (Laundré et al. 2001, Randall et al. 2006). For example, the sound of dogs barking has been shown to cause a trophic cascade and alter an entire food web (Suraci et al. 2016). Despite the risk of attack, dogs bark in response to perceived threats to fulfil their role as guardians of human property (Lescureux and Linnell 2014). For wolves and dogs, predator presence and human activity have been shown to suppress behavior of wolves and coyotes (Hebblewhite et al. 2005, Theuerkauf et al. 2007, Theuerkauf 2009, Davidson-Nelson and Gehring 2010, Young et al. 2019). For example, Indian wolves *C. l. pallipes* are known to produce fewer responses to elicitation howls when close to human habitation, presumably silenced by the threat of conflict with humans, though the role of dogs was not investigated (Sadhukhan et al. 2023).

In this study, we used passive acoustic monitoring (PAM) to explore whether wolves, coyotes and dogs in North America engage in active heterospecific communication or avoid the attention of potentially hostile species by reducing their own long-distance calling activity, whether barks or howls. PAM is a system of recording environmental sounds, typically with automated devices, to monitor species and ecosystems (Mellinger et al. 2007, Marques et al. 2013, Merchant et al. 2015, Sugai et al. 2019). We suggest there are three main scenarios under which these species interact vocally: canids hear other species but take no interest; canids hear other species and avoid responding vocally; or canids hear other species and respond vocally with long-distance, loud calls, by barking or howling. The response employed depends on the species and context, with choruses more likely if the responses are territorial, and therefore defensive (Harrington 1989), by advertising the number of individuals present. Based on wolves as apex predators and coyotes as mesopredators, we hypothesize that coyotes will be silenced by wolves and wolves will not be silenced by coyotes. We also hypothesize that dogs will act as surrogate apex predators, and potential markers of human presence, thus, dogs will silence both wolves and coyotes, but will increase their responses when they hear either species. As a final hypothesis, we posit that when coyotes respond to the apex predators, they will be more likely to produce chorus howls than solo howls, thus advertising their strength in numbers versus their vulnerable, lone status. If our hypotheses, which are based on the ecology of fear theory, are not supported, this would indicate more complex heterospecific communication between these canids, whereby information is intentionally exchanged across a social network.

Material and methods

Data collection

Eleven Wildlife Acoustics SM3 and SM4 autonomous recorders (Wildlife Acoustics, Concord, MA, USA) were deployed in Juneau County in Central Wisconsin, USA (Fig. 1) between 15 and 28 December 2019. In North America, wolves are typically vocally active from summer to the following spring, refraining from howling from spring to summer when pups are present and vulnerable (McIntyre et al. 2017). Recording devices were placed at locations dictated by the needs of a separate study, which imposed the requirement that acoustic events should be detectable on at least three devices for the purposes of multilateration (Smith et al. 2021). As such, devices were not placed along regular grid points or straight lines. However, multilateration was not used in the current study to ascertain the locations of calling individuals as no wolf howls were detected on three or more recorders (Smith et al. 2021). After

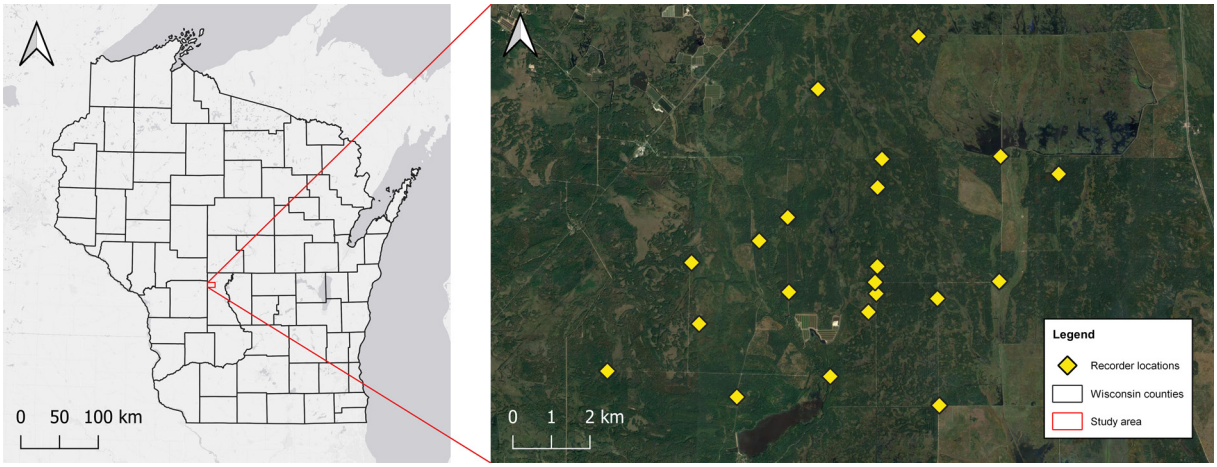

Figure 1. Location of the study site within central Wisconsin showing the deployment of the 11 acoustic recorders across 21 sites (yellow diamonds) in 2019. Maps produced in QGIS using Google Satellite and ESRI World Light Gray imagery.

the initial deployment and checking of audio files, some of the devices were moved to new sites nearer to those devices detecting wolf howls to ensure devices were located in the areas currently in use by wolves. Detectors were placed at a total of 21 sites over the study period (Fig. 1) where they were operational for between 1–12 nights (mean: six nights). Distances between devices changed due to devices being moved but the mean distance from one device to the next closest device was 1997 m (range: 459–3565 m). The mean distance between all devices, calculated in a pairwise manner, was 4364 m (range: 459–11 648 m). Recorders were programmed to collect audio data continuously at 16 kHz and were processed daily.

The topography of the area is flat with extensive wetlands interspersed with sandy, upland forests dominated by aspen *Populus grandidentata*, scrub oak *Quercus ellipsoidalis* and jack pine *Pinus banksiana*. Detailed land cover maps can be found in (Bru et al. 2023). Human and dog presence in the area is characterized by cranberry farms located near the center of the study area and a low-density settlement (< 8 people km^{-2}) located near the southern boundary of the study area (Wiedenhoeft et al. 2020). There are an estimated 37 wolf packs consisting of 137–143 individuals in the central forest region of Wisconsin (Wiedenhoeft et al. 2020). Our study area overlapped with the core territory of one known wolf pack (Mather East: estimated seven individuals and was likely in audible range of two additional packs, (Mather West: est. five individuals and Meadow Valley: est. six individuals (Wiedenhoeft et al. 2020). The number of coyotes and dogs in the area was unknown.

Recording devices were placed at locations dictated by the needs of a separate study, with the requirement that acoustic events should be detectable on at least three devices for the purposes of multilateration (Smith et al. 2021).

Data processing

In total, we recorded 3207 h of sound files over 13 nights from 11 recording devices. We analyzed only the recordings between 17:00 and 6:00 h, approximately 1788 h, as wolves and coyotes are more vocal during hours of darkness. Each recording file was scanned by a team member in Raven Pro 1.6 (Cornell Lab of Ornithology, Ithaca, NY, USA). A 2048 sample Hann window with 11.2 Hz bandwidth 3 dB filter, 50% overlap, with 1024 sample hop size was used to construct the spectrogram (Fig. 2). We marked canid vocalizations (howls, barks, howl-barks, yip-howls, etc.) using the Raven selection table feature, noting the species (wolf, coyote or dog) in the selection table. As marking of different sound files was carried out by seven different team members, we then extracted all marked detections, randomized their order, and returned them to team members to validate classifications. Train whistles, which occurred frequently in this study system, were also marked, and used as a control group because their onset was not influenced by canid vocalizations. Finally, all vocal events recorded on more than one device were manually checked to determine if they were likely to be the same event, e.g. whether a wolf chorus howl was recorded onto two different devices or if two different choruses were occurring at the same time. Therefore, potential pseudo-replication was corrected at the level of data processing, rather than at the level of data collection.

Temporal occurrence

Information from the marked sounds was assembled into a single SQL database (https://doi.org/10.5061/dryad.j9kd51ckc) and analyzed in MATLAB R2020a. Each call was time-stamped and the temporal distribution of calls for each species was calculated across the tested time period.

Bout analysis

Conspecific vocalizations were grouped into bouts, where a 'bout' was defined as a series of vocalizations by a particular species, separated by a time gap in which there were no vocalizations of that species. The length of the time gap between bouts was determined separately for each species by examining the histogram of inter-vocalization intervals, using the method described in Sibly et al. (1990). Our analysis of which species stimulated vocalizations of another was performed at the level of the bout, as once an individual or group of animals begins vocalizing, they typically continue for an extended period.

Heterospecific responses

We developed five hypotheses regarding the occurrence and nature of vocal interactions between the focal canid species.

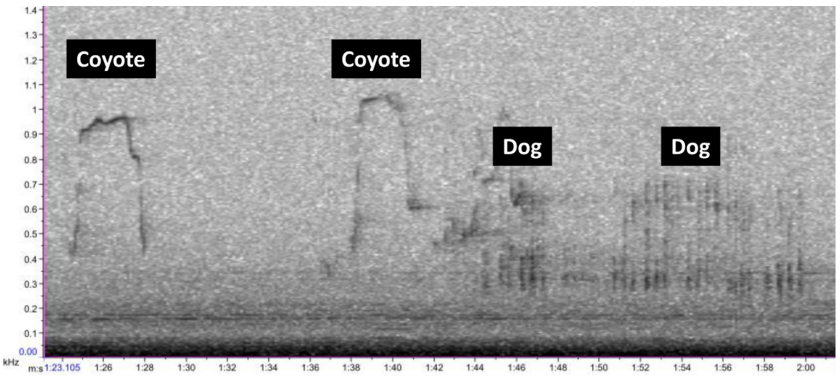

Figure 2. Example spectrogram showing coyote howls, followed by dog barks. Spectrogram produced in Raven Pro 1.5 with 2048 sample Hann window with 11.2 Hz bandwidth 3 dB filter, 50% overlap, and 1024 sample hop size.

These are summarized in Table 1, with a final hypothesis that coyotes would produce more chorus howls when responding as an advertisement of strength. We investigated these by analyzing whether acoustic stimuli (calls from wolves, coyotes, or dogs and a control abiotic sound of train whistles; hereafter referred to as the 'stimulus') affected the presence of absence of vocalizations of another species, hereafter referred to as the 'focal'. We summarize the predictions and tests in Table 1. There are three possible effects of hearing a stimulus (i.e. coyote, dog, or wolf call, or train whistle), all compared to chance: 1) silencing effect – the chance of vocalization falls, 2) ignoring effect – chance of vocalization unaffected and 3) eliciting effect – chance of vocalization increases.

We considered only those nights on which both the stimulus and the focal species appeared, as due to the highly mobile nature of the species and large home ranges (Gese et al. 1988, Forshner et al. 2004, Kittle et al. 2015, Margenau et al. 2023), one or both species may have been absent from the area on some nights. Although we could not test whether a vocalizing individual left the study area during the course of the night (so either the individual was no longer there to respond vocally, or had left the area in response to the stimulus), this is an unavoidable constraint of such a naturalistic study.

As we did not know which individual animal had vocalized, we grouped all conspecific vocalizations together, thus a bout by a coyote, dog, or wolf could be made by a single individual or many individuals. Thus, all analyses used a species-level response, and we could not compare results for responses across species to within species, i.e. we could not compare coyote–coyote bout interval to coyote–wolf, as we did not know whether a single or different coyotes were calling whereas all wolf responses must be from new individuals.

χ^2 exact test to compare event occurrence

To test the hypothesis that a focal bout was more or less likely to occur following a stimulus vocalization, we performed a χ^2 exact test. For this, we created 2 × 2 contingency tables for each focal-stimulus species pair. Rows indicated the focal species (absent/present, and columns indicated the stimulus species (absent/present). For simplicity, we divided the period between the first and last vocalization in each night into time slices of one-minute length and marked whether a focal or stimulus bout (or both) occurred in each of those slices. We then generated the following contingency table:

1) If neither species vocalized during a time slice, the absent–absent cell count was increased by one;
2) If only one species vocalized during a slice, the absent-present or present–absent count (depending on which species vocalized) was incremented;
3) If both species vocalized during a slice, we considered which vocalized first during that time slice.

i) If the stimulus species vocalized first, we considered this a potential case of stimulus generating a response and incremented the present–present cell count;
ii) If the focal species vocalized first, this was not a case of a stimulus generating a response, but as both species had vocalized nonetheless, we incremented both the present–absent and absent–present cell counts.

A χ^2 exact test was performed ($p < 0.05$), due to the non-independence of successive vocalizations, as these vocalizations tended to occur in bouts and, therefore, one vocalization would often be followed by multiple conspecifics. We then randomized the species labels of the bouts 10 000 times and repeated the contingency table construction and χ^2 test, comparing the χ^2 statistic for the randomized table to the statistic obtained from the true data.

χ^2 exact test to compare coyote responses as chorus or solos

For coyotes, we observed that two acoustic behaviors were common: either a single coyote howl was followed by other single howls (or none); or multiple coyotes chorus-howled simultaneously for an extended period. We defined a chorus howl as any coyote response longer than 16 s, based on visual inspection of the histogram of response lengths. As one suggested function of a chorus howl is the advertisement of a group's large size (Harrington 1989, Gaines et al. 1995), and thus might be more likely when in response to a perceived threat, we used a χ^2 test to determine whether an extended chorus howling bout was more or less likely following the three stimuli.

Table 1. Expected compared to observed number of vocalizations of the focal species in response to stimulus species. Exact test p-values compared to a null population where species identity was randomized. Values significant at < 0.05 are marked in bold. Values that went against predictions are marked in italics.

Stimulus	Focal	Expected	Observed	p	Predicted response	Observed response
Wolf	Dog	2.0	11.0	**0.033**	**Elicit**	**Elicit**
Wolf	Coyote	1.9	17.0	***< 0.001***	***Silence***	***Elicit***
Wolf	Train	2.5	6.0	0.732	Ignore	Ignore
Dog	Wolf	2.0	6.0	*0.473*	*Silence*	*Ignore*
Dog	Coyote	2.3	8.0	*0.341*	*Silence*	*Ignore*
Dog	Train	5.8	14.0	0.926	Ignore	Ignore
Coyote	Wolf	1.9	10.0	***0.012***	***Ignore***	***Elicit***
Coyote	Dog	2.3	33.0	**<0.001**	**Elicit**	**Elicit**
Coyote	Train	3.4	9.0	0.632	Ignore	Ignore
Train	Wolf	2.5	6.0	0.773	Ignore	Ignore
Train	Dog	5.8	19.0	0.660	Ignore	Ignore
Train	Coyote	3.4	5.0	0.964	Ignore	Ignore

Results

Bout analysis and temporal occurrence of calls

The inter-bout intervals were calculated as 45 s for wolves, 58 s for coyotes, 49 s for dogs, and 300 s for trains. The bout analysis resulted in a total count of 176 bouts from wolves, 202 from coyotes, 431 from dogs and 597 from trains.

The results of the temporal occurrence of each species' calls are presented in Fig. 3. While there was some variation in when the different species called, there was no time period when no calls were detected from each species.

Heterospecific interactions

Hypothesis 1: dogs will silence wolves and coyotes

Coyotes had a mean inter-bout interval of 246 s and wolves had a mean inter-bout interval of 190 s. As demonstrated by the χ^2 exact test (Table 1), in the 1-minute that featured dog vocalizations, neither coyotes (2.3 expected versus 8 observed, $p = 0.341$) nor wolves (2 versus 6, $p = 0.473$) showed different vocalization rates than chance, thus they were neither elicited to reply nor silenced by dogs.

Hypothesis 2: coyotes will be silenced by wolves

The χ^2 exact test (Table 1) showed that, instead of being silenced, coyotes vocalized ten times as often in response to wolves (1.9 expected versus 17 observed; $p < 0.001$). Thus, no silencing effect was found for coyotes hearing wolves.

Hypothesis 3: coyotes will produce more choruses in reply

Coyotes were not significantly more likely to produce chorus howls than solos, compared to chance distribution of both following any of the stimuli ($p > 0.05$).

Hypothesis 4: wolves will not respond to coyotes

The χ^2 exact test (Table 1) showed that wolves vocalized five times more often than expected in response to coyotes (1.9 expected versus 10 observed; $p = 0.012$).

Hypothesis 5: dogs will reply to both coyotes and wolves

Dogs had a mean inter-bout interval of 277 s in the absence of heterospecific stimuli. The dogs vocalized more in response to both coyotes and wolves (Table 1), producing 10 times as many responses to coyotes than expected (33 vs 2.3, $p < 0.001$), and five times as many responses to wolves (11 versus 2.0, $p = 0.033$).

Our predictions and results are summarized in Table 1 and Fig. 4. Only our prediction that dogs would respond to coyote calls by barking more than expected was upheld; our other predictions were not.

Discussion

We had predicted, under the ecology of fear theory, that dogs would silence wolves and coyotes and that wolves would silence coyotes, while dogs would not be silenced. However, we did not see a reduction in vocal activity by any focal species after hearing heterospecific vocalizations. Thus, vocal

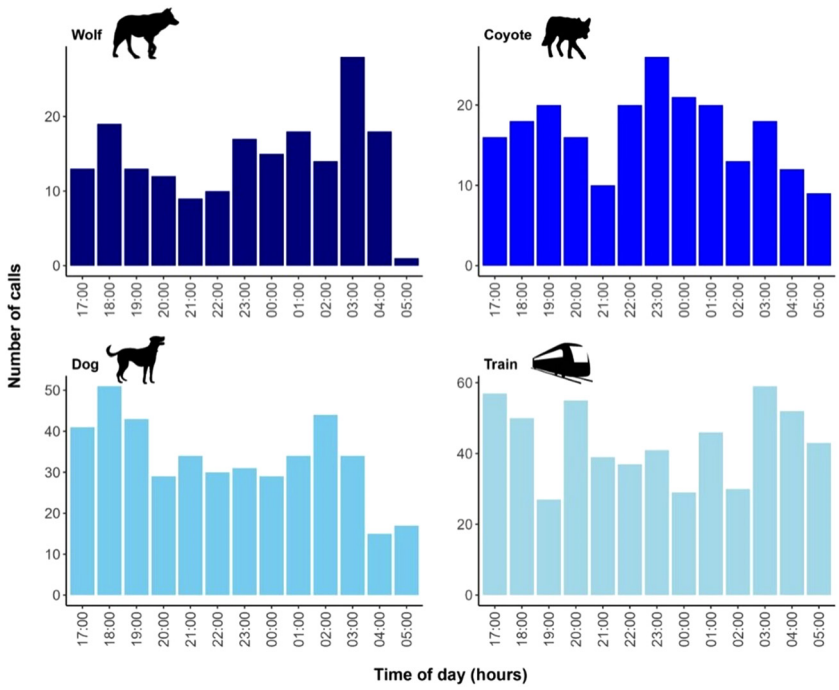

Figure 3. Temporal occurrence of calls shown by the number of calls (or train whistles) per hour each night for each of wolves, coyotes, dogs, and trains. The time under each bar is the start of the hour, e.g. the bar above 17:00 h is the number of calls between 17:00:00–17:59:59 h.

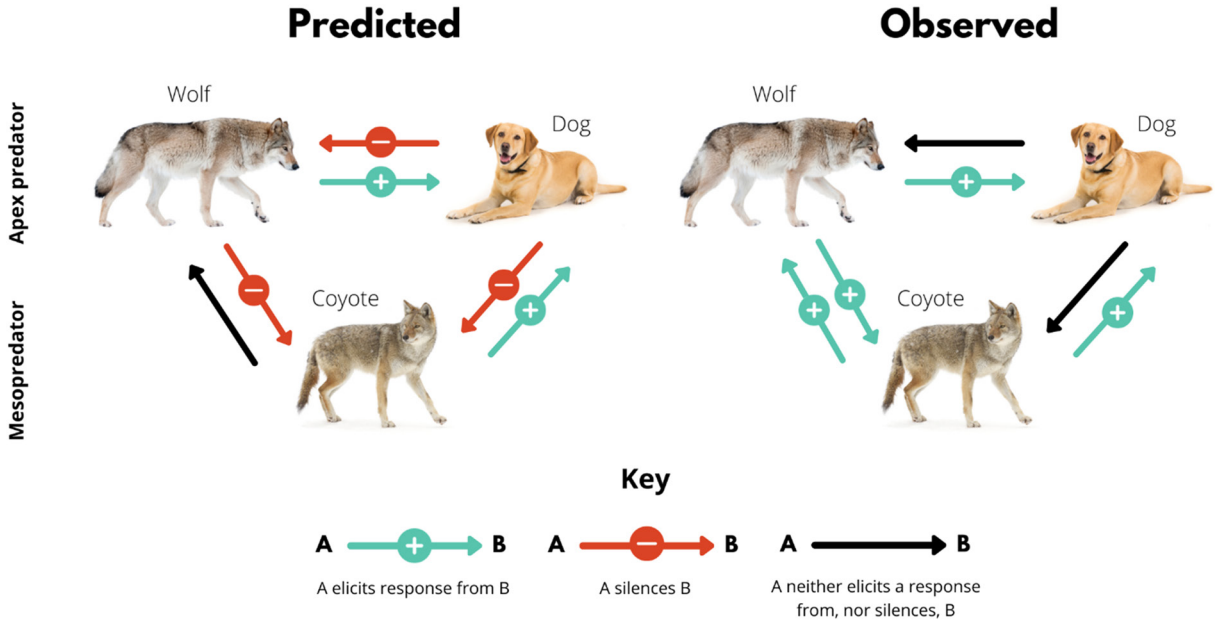

Figure 4. Summary of the predicted versus observed behavior. Arrow directions are to be read in the direction of the stimulus to the focal (i.e. the effect that the stimulus has on the focal). Based on the ecology of fear theory, the predictions were that coyotes and wolves would elicit vocal responses from dogs, green (+) arrows, while dogs would silence coyotes and wolves, as well as wolves silencing coyotes, red (−) arrows. Black arrows indicate no effect was predicted or had occurred. However, our results showed that coyotes elicited replies from both dogs and wolves at higher than chance rates, but responded only to wolves, and did not produce more choruses. Dogs responded to both coyotes and wolves, as predicted. Thus, no silencing effect was found. Images downloaded under a standard license from shutterstock.com and canva.com.

behavior was not driven by fear. Instead, coyotes responded to wolves and were not silenced by dogs. They also did not use more chorus howls following heterospecific calls. Thus, they seemingly advertised their presence when hearing large predators despite the presumed risk. Similarly, wolves were elicited to howl at higher than chance rates by coyote calls and at chance rates to dog calls. Again, we found no effect of dogs silencing the at-risk species. The results for dogs did uphold our hypotheses that they would be more vocal when responding to coyotes and wolves in their role as guardians or protectors of human property. We suggest that these three species are potentially engaged in a complex network of heterospecific communication.

Dogs, coyotes, and wolves occupy very distinct niches, with substantial opportunity for agonistic and competitive interactions, including exploitation and interference competition (Lescureux and Linnell 2014, Petroelje et al. 2021). Given the nocturnal activity of both wolves and coyotes, which limits visual signals in the study ecosystem, we proposed that one of the primary opportunities for interaction between these three species occurs via the acoustic medium, along with scent (Lescureux and Linnell 2014), and further hypothesized that heterospecific communication would be determined by threat risk and social roles. Dogs have been bred to use acoustic signals as part of their resource guarding, and thus would vocalize more readily in response to wolf and coyote vocalizations; the mesopredators, coyotes, would refrain from vocalizing in response to the large predators, wolves and dogs, as part of their general avoidance strategies (Shores et al. 2019, Prugh et al. 2023); and the large predator, wolves, would refrain from vocalizing in response to dogs, who pose a risk, but not to coyotes. However, most of our predictions were not supported by our data as no silencing effect was observed.

Further research could investigate the effects of volume, familiarity, call-type, and proximity on responses. Localization of the vocalizing animal using passive acoustic monitoring could assist with such an analysis, but this was not possible in this study as no wolf howls were recorded on three or more recorders (the minimum needed for acoustic multilateration) (Smith et al. 2021). Similarly, the wolves' increased vocalization rates in response to coyotes could be because they perceive them as territorial incursions. Their unchanged vocalization in response to dogs implies that the wolves are not attempting to hide their presence when they hear potentially aggressive vocalizations from domestic canids. Dog barks are known to convey emotional context (Yin and McCowan 2004, Molnár et al. 2009), but it is not known if they are linked to body size, though body size is encoded in dog growls (Faragó et al. 2010, Taylor et al. 2010). Our dataset was too small to allow conclusions to be drawn regarding the effect of call-type on response, but this would be another key area of future research. A recent study finding that more modern dog breeds respond less to howls than ancient breeds, and that genetic distance drove responsiveness (Lehoczki et al. 2023). However, we had no data on the sex, age, or breed of the dogs so these factors could not be explored further.

Overall, our results show complex acoustic interactions between three sympatric species. Despite the clear antagonism documented between coyotes and wolves (Berger and Gese 2007, Merkle et al. 2009, Benson and Patterson 2013, Lescureux and Linnell 2014), we found no evidence that any species reacted to a potential landscape of fear created by the others by refraining from vocalizing. In support of the complex interactions of dogs and wolves(Lescureux and Linnell 2014), we found that wolves did not reduce their calling when they heard dogs. However, a major caveat to our findings is that our sample size was relatively small, including between 1–3 wolf packs, and an unknown number of dogs from only two centers of dog habitation. Therefore, these results may not be broadly generalizable to other systems, in particular systems under different environmental conditions, or different levels of human activity (e.g. livestock farming). We also could not control for perceived volume at the location of the receiver, as both coyotes and wolves moved continuously through the territory, whereas we relied on fixed locations for recording devices.

Overall, we suggest that instead of creating a simple landscape of fear for mesopredators, where the species at greater risk is silenced by the activity of the large predators, predators may engage in a complex heterospecific communication network based on calls, similar to that of scent networks (Apps et al. 2019), or scavenging . The interrelationships between our focal species are known to be complex and multifaceted: wolves are influenced by human presence and activity, avoiding areas of higher human density (Whittington et al. 2005, Lesmerises et al. 2013), while also predating on dogs (Kojola et al. 2004, Butler et al. 2013, Lescureux and Linnell 2014). However, wolves' interactions with dogs are not well documented beyond predation events (Jans 2014, Lescureux and Linnell 2014) despite evidence of hybridization and thus, presumably non-agonistic, social interactions (Ciucci et al. 2003, Bohling and Waits 2011, Khosravi et al. 2015, Gómez-Sánchez et al. 2018). Similarly, while wolves represent interference competition and direct predation threats to coyotes (Switalski 2003, Merkle et al. 2009), wolves and coyotes can also reproduce (Way and Timm 2011), as can dogs (Kojola et al. 2004, Lescureux and Linnell 2014, Boydston et al. 2018). The mechanisms behind these very different outcomes are only poorly understood, and may be the result of complex interactions between many factors, including population sizes and distributions associated with resource selection (Olson et al. 2014, Tikkunen and Kojola 2019), contexts for interaction (Muhly and Musiani 2009, Butler et al. 2013, Olson et al. 2015, Boydston et al. 2018), season (Klauder et al. 2021), competitive pressures (Merkle et al. 2009, Levi and Wilmers 2012, Miller et al. 2012), and the demographics of the animals themselves (Kojola et al. 2016, Carricondo-Sanchez et al. 2020). As none of the recorded animals were tracked by other means, e.g. GPS collars or camera traps, we could not establish the distances between callers. However, distance between individuals may have been important to their response rate, as, for instance, very close proximity may still have exerted a silencing effect while greater distance may have increased confidence as direct conflict was less likely.

We have proposed that the animals may be engaging in a complex communication network. It is possible that the communication is as simple as advertisements of territorial defense, but this seems unlikely as the coyotes responded to wolf howls with solo responses as well as choruses. While numerical assessment has not been established in coyotes as it has been in lions (McComb et al. 1994), it is likely that they perceive the difference between a single wolf and entire pack and calculate the risk difference between them. It is unlikely that any of the signals were related to mating or reproduction as they were recorded in December, not February (Mech 2002, Carlson and Gese 2008). As our simplistic expectations that the adaptive advantage of communicating or not communicating is fear-based were not supported, the question remains, what advantage could animals obtain by responding in the way we have observed? It is possible that some poorly understood ecological factors in the relationships between the different species provide a purely selfish advantage to each individual, it is also possible that some mutualistic advantage is gained from interspecific communication in these closely related species, in which case further investigation is warranted to establish what messages might be being sent.

Our study demonstrates that passive acoustic monitoring is a powerful method to measure the direct interactions between spatially separate species, where long-range acoustic communication may form a vital part of heterospecific interaction. In contrast to expectations, the interspecific communication network of the three related species appears to be complex and multifactorial, rather than reflecting simple avoidance. Therefore, we suggest that assumptions underlying large predator and mesopredator interactions may need reassessment and that simple models of avoidance and partitioning may underestimate the complexity of their relationships.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j9kd51ckc (Root-Gutteridge et al. 2024).

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