RESEARCH ARTICLE

Environmental and social factors influencing wolf (*Canis lupus*) howling behavior

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Abstract

Animals communicate in a variety of ways and calls are used for a number of important behaviors. Temperature, wind, time of day, and human activities can affect animals' use of calls, particularly over long distances. Effects of group size on the use of calls can be particularly influential in territorial social carnivores. Where gray wolves (*Canis lupus*) are hunted by humans, for example, howling may make it easier for hunters to locate individuals and ultimately increase mortality. We hypothesized that a suite of factors would affect wolves' responses to simulated howling. Specifically, we predicted that howling behavior would increase with (a) group size, (b) pup age, and (c) during crepuscular time periods and howling behavior would decrease (a) where wolves were harvested and (b) when it was hot or windy. Contrary to our prediction, larger groups did not respond as quickly to simulated wolf howls as smaller groups did and minimum and maximum daily temperatures were not good predictors of wolf howling response rates. Individuals in small litters of pups may have responded more quickly to howls than those in large litters because they are eager to seek safety from and have socialization with adults returning from foraging bouts. Although harvest did not appear to affect vocal communication by wolves, group size, pup age, time of day, wind, and number of howls emitted greatly affected wolves' behavior and responses during howling surveys. Howling responses did not change because of harvest; response rates from wolves were nearly identical with (2.2%) and without (2.3%) harvest. The year-round benefits of long-distance vocal communication may outweigh the costs of increased mortality arising from howling during harvest season.

KEYWORDS

acoustic signal, *Canis lupus*, communication, gray wolves, harvest practices, howling, social groups

1 | INTRODUCTION

Animals communicate in a variety of ways and calls can be used over long distances for a number of important behaviors including breeding, rearing young, predator avoidance, and territory defense (Bolt, 2013; Feighny, Williamson, & Clarke, 2006; Harrington & Mech, 1978; Santema & Clutton Brock, 2013). For some species, long-distance calling is used to advertise size and dominance of males, convey group size to neighboring groups, and indicate an area is occupied by a group, particularly when such an area contains high-quality resources (Bolt et al., 2019; Delgado, 2006; Sekulic, 1982; Van Belle, Estrada, & Garber, 2013). Such calling has been shown to function as "honest advertisement" of competitive abilities (Clutton-Brock & Albon, 1979). Indeed, studies have shown that calling is a key

behavior in mate defense (Bolt, 2013; Wich & Nunn, 2002). At relatively close distances, calls emitted by both young and parents (Altmann, 1951) are commonly used to facilitate feeding bouts and safe travel when young are exposed to heightened predation risk (Ridley, 2016). Calls can also be used to gather and coordinate group members during cooperative hunting (Nowak et al., 2007).

In group-living species, the propensity for vocal communication may also depend on group size and perceived risk (Abbey-Lee, Kaiser, Mouchet, & Dingemanse, 2016; Harrington & Mech, 1978; Llaneza, Ordiz, Palacios, & Uzal Fernandez, 2005; Nowak et al., 2007). Some species benefit from large group size during conflicts with conspecifics (Cassidy, MacNulty, Stahler, Smith, & Mech, 2015), and advertising large group size through vocalizations may be beneficial to avoiding unnecessary conflict. Human activities can also adversely affect animals' use of sound to communicate effectively. For example, sound from seismic oil and gas exploration in the ocean can disrupt breeding activities in humpback whales (*Megaptera novaeangliae*; Cerchio, Strindberg, Collins, Bennett, & Rosenbaum, 2014*)*. The threat of predation in particular can decrease animals' use of vocal communication (Abbey-Lee et al., 2016); humans routinely use calls to attract and harvest animals (Bassi, Willis, Passilongo, Mattioli, & Apollonio, 2015; Walsh, White, & Freddy, 1991). For example, hunters commonly howl and use predator calls to attract gray wolves (*Canis lupus*; Linnaeus) for harvest in Idaho, USA (IDFG, 2017). Large males that use calls to locate and defend mates are often (Feighny et al., 2006) desired by humans for harvest. If animals communicate less frequently because of harvest risk, other activities such as locating and provisioning young could be affected as well.

Environmental factors can also affect the use and efficacy of sound for vocal communication. Howler monkeys (*Alouatta pigra*), for example, have been shown to call more in the morning when conditions are optimal for sound to travel unattenuated over long distances (Van Belle et al., 2013). Howling by gray wolves can also vary with environmental conditions such as season and reproductive activity, time of day, wind conditions, and even the presence of rain or fog (Gazzola, Avanzinelli, Lorenza, Scandura, & Apollonio, 2002; Harrington & Mech, 1978; McIntyre, Theberge, Theberge, & Smith, 2017). Wolves have been shown to howl more frequently during the breeding season, but howl less after giving birth when pups are vulnerable to predation (Harrington & Mech, 1978; McIntyre et al., 2017). Additionally, increased temperatures associated with time of day can negatively affect wolf activity and associated howling behavior due to physiological intolerance (Gazzola et al., 2002; Nowak et al., 2007). Lastly, rain, fog, and wind could negatively influence the effectiveness of wolves use of vocal communication (Gazzola et al., 2002; Harrington & Mech, 1978).

Gray wolves in the Rocky Mountains of North America (i.e., Idaho, USA; Alberta, Canada) are a useful study species for examining environmental effects on an animal's use of vocal communication. Wolves generally live to 4–5 years of age and spend the first 2–3 years of their life within their natal group (i.e., pack; Fuller, Mech, & Cochrane, 2003). Wolves are capable of howling at just 3–4 weeks old (Harrington & Asa, 2003) and commonly use howling throughout their lives to coordinate activities among group members, announce the presence of predators, locate and provision young, and maintain and defend territories (Harrington & Asa, 2003; Harrington & Mech, 1978; McIntyre et al., 2017). Wolf populations reintroduced to the U.S. Rocky Mountains in 1995 (Bangs & Fritts, 1996) were monitored, in part, using howl surveys (Ausband et al., 2010). Additionally, howl surveys are used in many countries to locate wolves for collecting population monitoring and management data (Gable, Windels, & Bump, 2018; Gazzola et al., 2002; Jhala & Giles, 1991). However, few studies have used "blind" (i.e., no prior knowledge of wolf locations) surveys for wolves concurrent with sampling litter and group sizes independently over large areas.

Wolves were protected in the U.S. Rocky Mountains until public harvest (i.e., hunting and trapping) began in 2009 (Ausband, 2016). If wolves are subjected to increased mortality by responding to howls during the harvest season or perceive increased predation risk associated with communicating by calls (Abbey-Lee et al., 2016), they may howl less when their population is harvested. Individual wolves may learn to associate calling with the threat of harvest and alter their behavior accordingly. Alternatively, selection could favor wolves that call less, thereby affecting the evolution and persistence of such behavior. Lastly, if wolves reduce vocal communication due to humans, the howl surveys used by many around the world to monitor wolves may yield biased data leading to erroneous inferences about management effects and abundance.

We investigated how environmental factors and group size influenced responses by wolves to howls simulated by humans and whether howling responses decreased after regulated public harvest began in Idaho in 2009. We hypothesized that a suite of factors would affect gray wolf (*Canis lupus*) responses to simulated howling. Specifically, we predicted that howling behavior would increase with (a) group size, (b) pup age, and (c) during crepuscular time periods and howling behavior would decrease (a) where wolves were harvested and (b) when it was hot or windy. We compared results of howl surveys at >4,000 pup-rearing sites to group sizes derived from concurrent genetic sampling and to environmental factors recorded during surveys on 8 populations of wolves in Idaho (hunted after 2009) and Alberta (continuously hunted).

2 | METHODS

2.1 | Study areas

We conducted our work in eight study areas encompassing southwestern Alberta, Canada (2012–2014) and Idaho, USA (2007–2018). In Alberta, our 12,020 km² study area extended from the Canadian-United States border north to the Trans-Canada Highway but excluded Banff National Park (Figure 1a). Elevation ranged 429–3,560 m, annual temperatures ranged from −40°C in winter to 34°C in summer, and mean annual precipitation ranged 42–170 cm (Alberta Government, 2018). Mountain habitat was dominated by Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*),
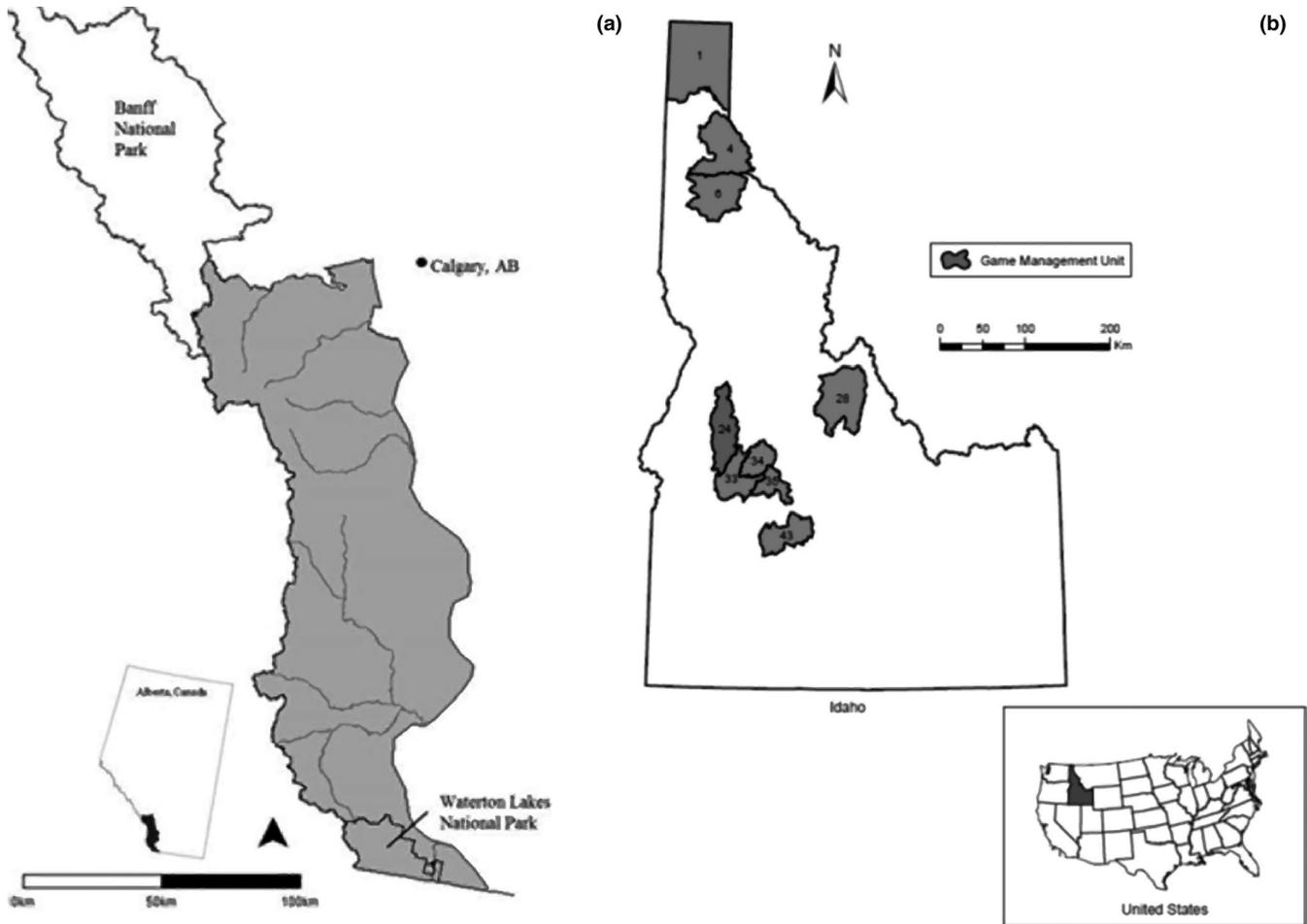
FIGURE 1 (a) Study area in Alberta, Canada, where howl surveys were conducted to determine wolf presence during summer (2012–2014). (b) Study areas in Idaho, USA where howl surveys were conducted to determine wolf presence during summer (2007–2018)

and spruce (*Picea engelmannii*) mixed forests that abruptly transitioned through aspen (*Populus tremuloides*) stands to fescue (*Festuca* spp.)-dominated grassland and agricultural land on the plains to the east (Desserud, Gates, Adams, & Revel, 2010; Natural Regions Committee, 2006). Wolves were harvested in all years of our study in Alberta, and the annual harvest rate in an adjacent studied population of wolves was 34% (Webb, Allen, & Merrill, 2011). Residents could hunt wolves without license year-round on private and leased lands (Alberta Government 2014a,2014b). Some counties offered bounties for wolves (Cardston County Council, 2012). Annual wolf harvest was concentrated primarily in November–March (Government of Alberta-Alberta Environment and Parks [AEP], unpublished data).

Seven study areas in Idaho were based on Game Management Unit boundaries (1, 4, 6, 24, 28, 33–35, and 43) and totaled an area of 23,657 km^2 (Figure 1b), although they were not all sampled simultaneously during the same years. Study areas were mountainous and dominated by a mix of ponderosa pine (*P. ponderosa*), lodgepole pine, and spruce forests and sagebrush (*Artemisia tridentata*) steppe. Annual precipitation ranged from 89–178 cm, and temperatures ranged from −34°C in winter to 38°C in summer (Western Regional Climate Center, 2009). Wolves were harvested in 2009 (beginning in

September after the pup-rearing season) and 2011–2018, but not in 2007, 2008, and 2010 (Ausband, 2016). Most wolf harvest occurred during September–March with a peak during the big-game rifle hunting season (September–November) and total harvest ranged 200–370 wolves annually (Ausband, 2016).

2.2 | Field methods

We surveyed for wolves during early June–mid-September at rendezvous sites predicted by a habitat suitability model (Ausband et al., 2010). The habitat model predicts the locations of wolf rendezvous sites using a combination of profile curvature, roughness, and normalized difference vegetation index (NDVI). We did not survey for wolves during the denning period or other times of the year. Rendezvous sites are used by wolf groups for several weeks at a time during the summer until early fall when pups are large enough to travel with adults on hunts (Packard, 2003) and groups typically use 3–5 sites/summer (Ausband et al., 2016). We surveyed high-quality rendezvous site habitat with >70% suitability comprising areas that held slow-moving or stagnant water throughout the dry summer months. We surveyed for wolves generally at dawn and

Area	Year	Before or after harvest	Sites surveyed (n)	Howl sets (n)	Responses (n)
Alberta	2012	After	411	1,774	3
Alberta	2013	After	301	1,100	9
Alberta	2014	After	319	1,230	20
Idaho	2007	Before	476	1,471	42
Idaho	2008	Before	471	1,485	11
Idaho	2009	Before	434	1,830	14
Idaho	2010	After	252	1,169	8
Idaho[a]	2012	After	74	357	NA
Idaho[a]	2013	After	122	400	NA
Idaho[a]	2014	After	139	513	NA
Idaho	2015	After	454	1,975	26
Idaho[a]	2016	After	142	574	NA
Idaho	2017	After	271	1,025	6
Idaho	2018	After	306	1,233	16

[a]Indicates year not used in calculations of response rate because sampling was not blind and used radiotelemetry knowledge during some surveys.

dusk although some sites were surveyed at other times depending on travel time and field logistics. At each site, one technician imitated a wolf howl by giving a series of five howls alternating between flat (constant pitch during howl except for start and end) and breaking (marked change in pitch during howl) howl types (Harrington & Mech, 1982). The technician would give three such howl series for a minimum of 15 individual howls emitted at each site. If wolves responded, technicians recorded the minimum number of adults and pups responding (group counts were made from subsequent genetic sampling; see below). Such minimum counts were made by listening for the chiming in of individuals at the onset of chorus howls. High frequency (i.e., >700 hz) howls short in duration were considered pups and lower frequency, and longer howls were considered adult wolves. Frequencies were not recorded and were estimated aurally by technicians. If no howling response was obtained, two technicians would survey the site for wolf sign for 30–45 min. Technicians were encouraged to give additional howls during surveys if they felt terrain or wind had diminished the effectiveness of the original howls. Technicians recorded any additional howl series (each with five howls) for up to six howl series for a maximum of 30 individuals howls emitted at each site. After howling, technicians defined wind conditions as low = no breeze or barely felt, moderate = trees and brush swaying, but periods of quiet, and high = difficult to hear, trees and brush continually swaying. Date and time of day were also recorded. Technicians were trained on wolf howling and survey protocols for 3 days prior to the start of each field season.

During 2007–2010, and 2015 in Idaho and 2012–2014 in Alberta, we surveyed for wolves using only potential rendezvous sites predicted by the habitat suitability model with no a priori knowledge of the location of potential rendezvous sites; we used data from those years to estimate wolf response rates to howling in association with harvest, group size, and differences in study area. During 2011–2014

and 2016–2018, we surveyed for wolves in Idaho using the habitat suitability model, but also had a priori knowledge of potential rendezvous sites from collared wolves. We combined data from these latter years with data from the previously listed years to further test for the effects of date, time, temperature, and wind conditions on successful howl surveys.

2.3 | Genetic methods

To estimate group size and verify wolf presence, we collected scats for genetic analyses at rendezvous sites of reproductively active wolf groups generally in July and August of each year. Technicians typically gathered 125–200 samples per group annually by collecting scats at activity centers (Joslin, 1967) of rendezvous sites and radiating out 500 m on trails from the center. Rarefaction analyses indicate most individuals in a group are detected after genotyping 50–60 samples (Stenglein, Waits, Ausband, Zager, & Mack, 2011). DNA analyses were performed at the University of Idaho's Laboratory for Ecological, Evolutionary and Conservation Genetics (Moscow, ID). Nine nuclear DNA microsatellite loci and sex identification primers were used to identify individuals and sex (Stansbury et al., 2014). Genotypes were generated at an additional nine microsatellite loci on the best sample for each unique individual (i.e., total = 18 loci) and for samples that differed at only one locus out of initial nine loci to verify matches or mismatches (Stenglein et al., 2011; Stansbury et al., 2014). Subsequent parentage analyses confirmed group membership of genotyped wolves (Ausband, Mitchell, Stansbury, Stenglein, & Waits, 2017). Further detailed methods and protocols can be found in Ausband et al., 2010, Stenglein, Waits, Ausband, Zager, & Mack, 2010, Stenglein et al., 2011, and Stansbury et al., 2014.

Annual harvest of wolves primarily occurred September–March, whereas howl surveys occurred the following June–August. Although any harvest mortality associated with howling occurred several months prior to our surveys, we assumed that the effects of harvest on howling lasted year-round. Surveys were conducted under animal use protocol 008-09MMMCWRU-031009 approved by the University of Montana IACUC.

2.4 | Data analysis methods

Howl response rates—We used a mixed effects logistic regression (did wolves respond, yes, no) to test for differences in howling responses of wolves by area (Alberta vs. Idaho) and whether the population was harvested in the previous year or not (Table 1). This model also included a random effect for year.

Analyses testing for the influence of group size would not converge using a mixed effects approach. Therefore, to test whether group size (i.e., number of adults and pups) influenced responses to howling, we removed study area and the random effect for year and used a logistic regression model. We also tested whether the number of pups or adults in the group affected howl responses by modeling howl responses as a function of the number of pups and adults separately. We performed analyses using package "lme4" in Program R (R Core Team, 2019; Supplemental S1).

Characteristics of successful howl surveys—After modeling differences in response rates, we examined the characteristics of only those howling surveys where we obtained responses (Table 2). We estimated pup age by assuming pups were born on 11 April each year (Trapp, 2004). We divided our sampling season into 2-week increments, calculated the proportion of positive responses per period, and used a two-proportion z-test to examine whether wolves were more likely to respond to howls as pups aged. We separated time into 4-hr increments corresponding to times we surveyed: 0500–0900, 0901–1300, 1301–1700, and 1701–2100. We had relatively large howl survey sample sizes and wanted to guard against spurious statistical significance; thus, we calculated the average proportion of sites surveyed during each time period for three randomly selected years, 2008, 2010, and 2015. Data from these 3 years provided a sufficient sample size (n = 1,195 sites) to determine whether wolves responded more during certain time periods compared to the proportion of surveys that were conducted in those respective time periods. For each time period, we used a two-tailed z-test for two proportions (De Veaux, Velleman, & Bock, 2005, pp. 436–438) to test whether the proportion of howl responses we received during a certain time period was different than the proportion of surveys we conducted during that time period.

Lastly, we used the maximum and minimum daily temperatures for nearby towns in our Idaho study areas in 2008 and 2015 (2010 climate data were only partially available) to compare temperatures observed during surveys with and without howl responses from wolves (www.usclimatedata.com/climate/idaho/united-states/3182; accessed 16 January 2019). Results showed similar

TABLE 2 Summary statistics for successful howling surveys for wolves in Alberta, Canada, and Idaho, USA, 2007–2018

Year	Group-year code	Time surveyed	No. of adults DNA	No. of pups DNA
2008	BV_08	0835–1301	16	4
2008	JM_08	0835–0945	10	6
2008	JM_08	0945–1415	10	6
2008	MB_08	1755–1830	11	5
2009	JM_09	0830–1020	11	3
2009	MB_09	0930–1015	14	6
2009	MB_09	0945–1330	14	6
2009	CC_09	0725–0800	7	4
2009	CC_09	0930–1630	7	4
2009	HJ_09	1525–1730	5	5
2010	HJ_10	0715–0820	7	4
2010	HJ_10	0630–0930	7	4
2010	DI_10	1000–1200	10	8
2010	CU_10	0830–0932	5	8
2010	CU_10	1630–1937	5	8
2012	WP_12	1830–2000	7	3
2012	LA_12	0800–1215	2	7
2012	BV_12	0910–1130	8	2
2012	CC_12	0600–1515	3	3
2012	SM_12	1615–2200	4	1
2012	JM_12	1200–1430	4	5
2012	JM_12	0700–1140	4	5
2012	MB_12	1800–2130	5	5
2012	MB_12	0650–1230	5	5
2012	HD_12	1932–2100	13	4
2012	CS_12	1915–2115	5	7
2012	WL_12	1750–2120	5	7
2013	SM_13	0617–1200	4	3
2013	TL_13	0540–0850	2	1
2013	TL_13	0600–1045	2	1
2013	WP_13	0720–1020	4	5
2013	WL_13	1121–1620	6	3
2013	BV_13	0740–1130	3	0
2013	HD_13	0800–1030	11	0
2013	TL_13	1745–1940	2	1
2014	JM_14	0623–1138	6	5
2014	OB_14	1031–1415	5	4
2014	MB_14	0930–1500	5	4
2014	SM_14	0707–0825	5	7
2014	SM_14	0930–1200	5	7
2014	SM_14	0725–1123	5	7
2014	WL_14	0718–1120	7	5
2014	HD_14	0750–7050	6	4

TABLE 2 (Continued)

Year	Group-year code	Time surveyed	No. of adults DNA	No. of pups DNA
2014	BC_14	0912–1237	2	2
2014	WP_14	1850–1920	2	0
2015	SW_15	0750–0858	4	4
2015	SW_15	0709–1111	4	4
2015	JM_15	1840–1900	6	3
2015	JM_15	1645–2130	6	3
2015	CB_15	0630–0900	4	4
2015	MB_15	2000–2100	2	5
2015	SM_15	0630–0715	11	5
2015	CB_15	1015–1630	4	4
2015	BV_15	1900–2100	5	4
2015	DC_15	0835–1630	2	4
2015	BB_15	1600–1900	9	7
2015	LC_15	0800–1130	2	6
2016	MB_16	0630–1000	6	5
2016	DC_16	1100–1600	4	4
2016	BV_16	0930–1130	6	3
2016	TL_16	0830–1200	2	5
2016	BB_16	0630–1030	10	4
2016	DQ_16	0700–1100	5	5
2016	DQ_16	0905–1030	5	5
2016	LC_16	1100–1400	6	4
2016	CB_16	0700–0750	5	0
2016	LC_16	0530–1130	6	4
2016	HD_16	0845–1500	8	5
2017	JM_17	0740–0925	9	0
2017	MB_17	1400–1800	7	6
2017	BW_17	0815–1530	2	4
2017	LC_17	0930–1230	6	6
2017	SM_17	0746–0831	2	6
2017	SM_17	0830–1330	2	6
2018	JM_18	0815–1115	4	0
2018	MB_18	0900–1435	8	4
2018	BV_18	0620–1220	9	4
2018	BB_18	0700–1400	2	7
2018	BV_18	1330–1800	9	4

temperatures with and without howls, and no statistical tests were conducted (see below). The three wind condition classes recorded by technicians during surveys were also summarized.

3 | RESULTS

We surveyed 4,172 predicted rendezvous sites where we conducted 16,136 howl series and emitted a total of 80,680 simulated wolf howls

(Supplemental S2). We detected no difference in response rates in populations with and without harvest (β = 0.39, SE = 0.34, p = .26) and response rates from wolves were generally low where wolves were harvested ($\bar{x}$ = 2.3%; SD = 0.01; n = 2,314 sites and 7,248 howl series) and where they were not harvested ($\bar{x}$ = 2.2%; SD = 0.009; n = 1,381 sites and 4,786 howl series). We found a weak negative trend toward lower howling response rates in Alberta compared to Idaho (1.7% vs. 2.5%; β = −0.66, SE = 0.38, p = .08). Mean group size (adults and pups) was 15.3 (SD = 3.9; range: 10–20) for 7 wolf groups when there was no harvest and 9.4 wolves (SD = 3.5; range: 2–18) for 56 wolf groups when there was harvest. Group size was negatively associated with the probability that wolves responded to the first howl series (β = −0.13, SE = 0.06, p = .03; Figure 2).

Response rates of wolves, including pups, were higher (0.07 vs. 0.03, Z = 2.99, p = .003) when pups were approximately 16–18 weeks old (late summer) than when they were younger. The majority (84%) of responses occurred during or immediately after the initial series of three simulated howls. Emitting a 4th howl series yielded an additional 11% of wolf responses (Figure 3). Morning surveys were the most productive with 56% of all responses occurring from 0500–0900 even though just 37% of surveys were conducted during that time (Z = 4.53, p < .0001). In fact, 82% of all responses were obtained by 1,300. By contrast, surveys at dusk were less productive; just 14% of all responses were obtained between 1701 and 2,100 even though 38% of surveys were conducted during that time (Z = −6.00, p < .0001). Supplemental howl series beyond the initial 3 were beneficial in the evening; 43% of responses occurring after 1–3 additional howl series were given were at dusk (Figure 4).

Daily minimum and maximum temperatures in Idaho were almost identical when wolves responded to howls ($\bar{x}$ min = 7.1°C, SD = 4.3; $\bar{x}$ min = 26.4°C, SD = 6.3; n = 46) and when they did not ($\bar{x}$ min = 7.8°C, SD = 4.4; $\bar{x}$ max = 27.1°C, SD = 4.9; n = 1,762). Although not always recorded, most howl responses were detected when wind conditions were deemed low (94.1%; n = 36) or moderate (5.9%; n = 36) with none heard when wind was high.

4 | DISCUSSION

Various factors such as group size, pup age, time of day, and wind conditions influenced wolves' behavioral responses to simulated howling, but the initiation of a harvest season did not appear to have lasting effects on wolves' use of calls outside of the harvest season. Contrary to our prediction, we found larger groups took longer to respond to simulated wolf howls than smaller groups. This finding contrasts with previous work which showed small groups of wolves were less likely to respond to howls, albeit from a limited sample size (Harrington & Mech, 1978). We note that our inference is limited to positive responses (i.e., groups that howled back), and smaller groups may have gone undetected more often than larger groups. It is commonly thought that wolves use calls, particularly near rendezvous sites, to reunite adults and pups for bouts of food provisioning. In addition to facilitating feeding bouts, individuals in small litters of

FIGURE 2 Modeled probability of response to first howl series emitted by technicians as a function of the number of wolves in Alberta, Canada (2012–2014), and Idaho, USA (2007–2018). Error bars represent the *SE*
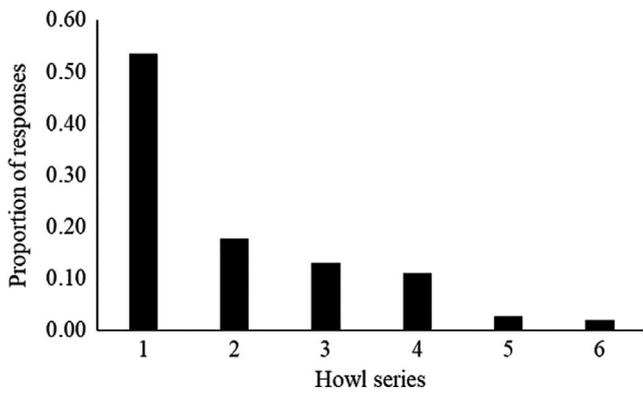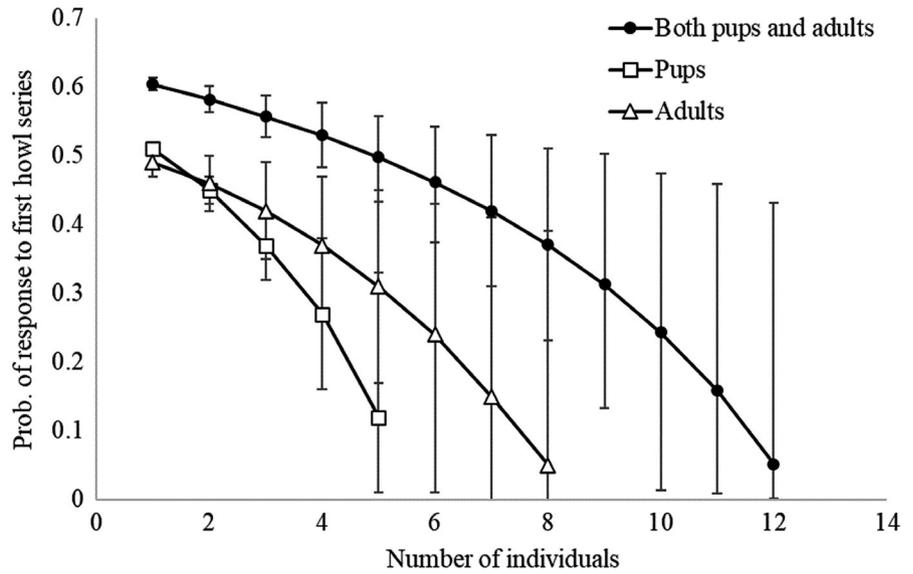

FIGURE 3 Proportion of wolf responses to 1–6 series of howls emitted by technicians where each series contained 5 individual howls, Alberta, Canada (2012–2014), and Idaho, USA (2007–2018)
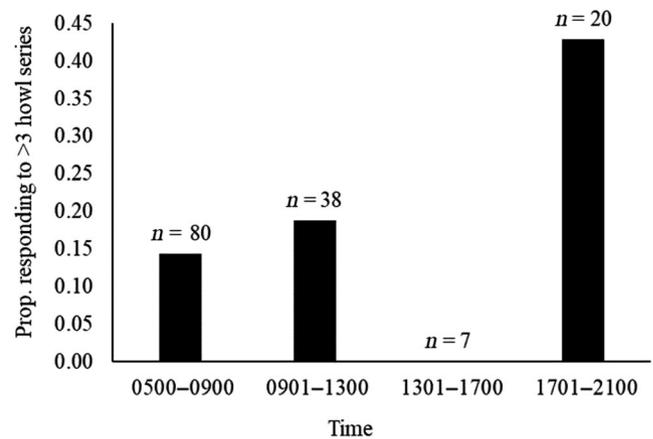

FIGURE 4 Time of day and proportion of wolf responses obtained when technicians emitted >3 howl series (5 individual howls in each series) in Alberta, Canada (2012–2014), and Idaho, USA (2007–2018). *n* = number of howl surveys

pups may have responded more quickly to howls than those in large litters because they are eager to seek safety from and have socialization with adults (Packard, 2003) returning from foraging bouts. Howling is largely used as intragroup communication during summer (McIntyre et al., 2017), and although we do not know why larger groups were more reticent to respond, it may be that individuals in large groups hear howls more frequently from group mates and are not as initially inclined to respond as wolves in smaller groups. We note that our genetic counts of group size could have included adults that were not present at the time of our survey. As a result, our inferences about the influence of number of adults on howling may be limited; relatively immobile pups, however, would likely all have been present when we surveyed and the influence of litter size on howling is presumed accurate.

We found that pups at 16–18 weeks old were more likely to respond to howls than younger pups. At 16–18 weeks, wolf pups in our study areas are the largest size they will be while still not traveling long distances with adults during foraging bouts (Packard, 2003). This time period also corresponds to when prey may be least vulnerable

to wolf predation and at the lowest biomass level in wolves' annual diet (Metz, Smith, Vucetich, Stahler, & Peterson, 2012). Thus, wolf pups at 16–18 weeks may be food stressed (Fuller et al., 2003) and more likely to respond via howls to what they perceive is an adult returning to the rendezvous site with food. Additionally, at 16–18 weeks, pups tend to move farther away from rendezvous site centers as they explore (Mills, Patterson, & Murray, 2008). Such pups may be more inclined to respond to howls simply because they are more distant from the rendezvous site center where an adult would be inclined to return with food.

Wolves responded to howls more during morning time periods. We posit this is likely due to two factors: (a) Adults are commonly returning to pup-rearing sites after foraging at night and group members, particularly pups, are eager to reunite with them, and (b) conditions in the morning are usually favorable for sounds to travel unattenuated in the environment (Van Belle et al., 2013). Wind also had effects on the likelihood of obtaining howl responses from

wolves, similar to other studies (Gazzola et al., 2002; Harrington & Mech, 1978). Moderate to high winds yielded few howl responses. Wind attenuated both the howls emitted and potential responses from wolves. We acknowledge that wolves may have responded but gone undetected, particularly during increased winds. Other environmental conditions such as rain or fog can also attenuate howls (Harrington & Mech, 1978), but we did not record such data when surveying.

If wolves are subjected to increased mortality by responding to howls during the harvest season, individual wolves could respond behaviorally by calling less and selection may even favor reduced use of vocal communication. Wolves, however, may not always respond audibly to howls, but instead approach the area where the howl came from to determine its source. In such instances, wolves may not be subjected to increased mortality because they are more likely to be undetected by humans. By contrast, selection can favor the continued use of calls (both call and respond) for communicating among group members during hunts, defending pups against predation, and maintaining territories. Such benefits of long-distance vocal communication may outweigh the costs of increased mortality arising from howling during hunting season. Despite mortality risks, both real (harvest) and perceived (our sampling at pup-rearing sites in summer), wolves continued to respond to howling over the course of our study.

While many studies have shown that calling is used in mate defense or for conveying an individual's size and relative dominance (Bolt, 2013; Bolt et al., 2019; Van Belle et al., 2013; Wich & Nunn, 2002), we suggest that these factors do not drive wolves' use of calling during the pup-rearing season. We posit that wolves call during the pup-rearing season for three primary reasons: (a) to reunite with pups after foraging, (b) to defend pups from predators, and (c) to congregate adult group members and facilitate coordination during foraging. If humans use howling to locate pup-rearing sites and harvest wolves, individual wolves may alter their behavior to call less frequently and selection may even begin to favor wolves that howl less during pup-rearing season. Idaho, USA, recently expanded harvest during the pup-rearing season (IDFG Game Commission, 2020), and long-term monitoring of wolf howling behavior in our study areas should provide insights about the potential behavioral effects of harvest on vocal communication in a social carnivore.

Response rates to howling in years with and without harvest were low (approx. 2.0%) compared to other studies that found markedly higher response rates (28.0%, Harrington & Mech, 1978; 13.0%, Gazzola et al., 2002; 39.0%, Nowak et al., 2007). However, none of the aforementioned studies used "blind" (i.e., no prior knowledge of wolf locations) surveys for wolves concurrent with genetic sampling for group and litter sizes over large areas. In comparison, we surveyed 4–6 sites/daily yielding an average of 1 group detected from howling every 8–12 workdays. Despite this low response rate, we were able to gather 155 responses due to the large number of surveys conducted. Howl surveys, and subsequent additional data collected during such surveys, can be useful for locating wolves in both harvested and unharvested populations (Jacobs & Ausband, 2018). Although three series of five howls each were previously recommended for howling surveys (Harrington & Mech, 1982), we suggest adding a 4th series to this protocol. Using four series of howls yielded 95% of wolf responses we observed. Additional howl series were also particularly useful when surveying at times of day when temperatures may still be high and wolves less likely to respond. Howl surveys are labor intensive, however, and their success relies on ideal environmental conditions and emitting ≥20 individual howls at each site to help ensure detection. We may have been able to obtain more wolf responses by howling at night when temperatures, and often wind, had diminished but we surveyed during the day for observer safety while working in mountainous country. Additionally, our surveys included sampling wolf scats after locating wolves and this was better accomplished during the day. Our inferences about wolf howling behavior are limited to daylight hours and do not necessarily encompass howling behavior at night.

CONFLICTS OF INTEREST
None.

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