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## Factors affecting the elicitation of vocal responses from coyotes *Canis latrans*

Tyler R. Petroelje, Jerrold L. Belant & Dean E. Beyer, Jr.

Long-distance vocalizations by canids play an important role in communication among individuals, and researchers have elicited these vocalizations to estimate canid occurrence and relative abundance. We evaluated the efficacy of broadcasted coyote *Canis latrans* group-yip calls and gray wolf *C. lupus* lone howls to elicit vocal responses from 18 GPS-collared coyotes on 144 occasions in Michigan's Upper Peninsula during August-September 2009 and June-September 2010-2011. We evaluated coyote responses to each call type using mixed-effects logistic regression models with time (month), residency status (resident or transient), presence in wolf territory, sex, distance, movement and call type as fixed effects hypothesized to influence coyote vocal response rates. The individual coyote and year were included as random effects. Overall, call type, sex and presence of wolf territory did not affect coyote response rates; however, coyotes did not respond to wolf calls broadcasted at distances of > 2.0 km. Resident coyotes were three times more likely to respond than transients and the greatest overall response rates occurred in August. We conclude that eliciting coyote vocalizations where wolves are present will not bias responses, and we recommend eliciting coyote vocalizations using recorded coyote group-yip howls during July-September to estimate the species' presence or density.

*Key words:* call type, *Canis latrans*, *Canis lupus*, coyote, gray wolf, howling, Michigan, vocalization

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Canids use long-distance vocalizations for individual identification, for communication among pack members and for establishing territory boundaries between packs (Joslin 1967, Theberge & Falls 1967, Mitchell et al. 2006). Researchers have studied canid vocalizations since the 1970s to examine aspects of behavioural ecology (Laundré 1981, Harrington & Mech 1982, Walsh & Inglis 1989) and communication (McCarley 1975, Wenger & Cringan 1978, Lehner 1982, Okoniewski & Chambers 1984, Mitchell et al. 2006). In addition, wildlife managers have broadcasted coyote *Canis latrans* vocalizations to attract and remove problem coyotes (Lehner 1976, Coolahan 1990, Mitchell 2004). Other uses of broadcast stimuli to elicit vocal responses include

an estimation of canid densities by dividing the number of individuals or packs responding by the area surveyed (Fuller & Sampson 1988, Dunbar & Giordano 2002) and to monitor the status of recolonizing gray wolves *C. lupus* (Gaines et al. 1995).

Broadcast stimuli used to elicit canid vocal responses include sirens (Wenger & Cringan 1978, Pyrah 1984), human-simulated howling (Okoniewski & Chambers 1984, Fuller & Sampson 1988) and recordings of species-specific vocalizations (Lehner 1982, Mitchell et al. 2006). Human-simulated howling can be as effective as recorded howls for eliciting vocal responses from wolves (Joslin 1967); however, comparative work is not available for coyotes. A

disadvantage of human-simulated howling for many applications (e.g. monitoring the status of canid populations) is variability in duration, frequency and intensity of stimuli. Consequently, Lehner (1976) suggested using recorded broadcasts to standardize the trials for eliciting responses.

Canid vocal responses include barks, group howls and group-yip howls for coyotes (Lehner 1982) and lone howls and chorus howls for wolves (Harrington & Mech 1982, Gazzola et al. 2002). The group-yip howl appears to be the most effective for eliciting calls from coyotes (Lehner 1982). Harrington & Mech (1982) recommended the use of individual wolf howls that alternated between 'flat' (single-sustained frequency) and 'breaking' (variable frequency) howls to reduce the variation in the response rate by packs of different sizes.

Using a single-species broadcasted call to detect multiple species would be useful if the call did not inhibit the response rate of any species. Non-vocal types of communication (e.g. urine-marking) may serve similar purposes (e.g. territory announcement) across canid species (e.g. wolves, coyotes and red foxes *Vulpes vulpes*) including interspecific communication (Harrington 1981). Few studies have assessed the efficacy of eliciting vocalizations of a canid using a sympatric canid species vocalization. Gaines et al. (1995) reported a greater response rate from coyotes (9.9%) than from wolves (0.1%) using a human-simulated wolf howl, though this difference was likely due to low wolf density and not greater interspecific responsiveness from coyotes. By using collared individuals, one can estimate the true response rates of coyotes to different call types.

Residency, sex and geographic location of coyotes may affect response rate. Resident coyotes often howl to define territorial boundaries, whereas transients may display risk-avoidance behaviour by not vocalizing or approaching a broadcasted call (Mitchell 2004). The sex of resident coyotes may affect vocal response behaviour; in a captive study of four coyote pairs, males vocalized more than females (Mitchell 2004); however, there is little information on free-ranging populations. Also, the regional variation of breeding and dispersal behaviour may affect peak times for elicitation. In the northeastern United States (U.S.), the greatest responsiveness occurred from late-summer to early-fall before dispersal (i.e. during September-November; Okoniewski & Chambers 1984) when territory announcement may be important. In the western and southwestern U.S., pair formation and breeding (February-March) as

well as late-summer and early-winter (August and November) were the periods of greater responsiveness (Laundré 1981, Walsh & Inglis 1989), whereas the months of the greatest responsiveness for the Midwest have not been reported.

Identifying factors that influence vocal responses from coyotes may improve the utility of howl surveys as a technique to estimate abundance where coyotes and wolves are sympatric. We quantified vocal response rates of coyotes to two species-specific (one coyote, one wolf), broadcasted vocalizations and assessed the importance of factors that may influence these responses. We hypothesized that response rates would increase from June-September, would be greater for residents and males and that both call types would elicit responses equally due to intraspecific and interspecific communication, as coyotes and wolves are sympatric in Michigan's Upper Peninsula.

## Material and methods

### Study area

We conducted our study in portions of Delta and Menominee counties in Michigan's Upper Peninsula (45.6°N, 87.4°E) encompassing about 870 km<sup>2</sup>. Limestone bedrock, ground moraine, cedar swamps, northern hardwood forests and coastal marshes characterized the study area (Albert 1995). Land ownership consisted of private (74%) and public (26%) lands, including the Escanaba River State Forest. Predominant land covers included 29% lowland deciduous (e.g. green ash *Fraxinus pennsylvanica*, speckled alder *Alnus incana*), 17% upland deciduous (e.g. sugar maple *Acer saccharum*, quaking aspen *Populus tremuloides*), 14% lowland conifer (e.g. black spruce *Picea mariana*, balsam fir *Abies balsamea*) forests and 17% agriculture (e.g. row crops, hay fields and pastures; Michigan Center for Geographic Information 2002). Elevations ranged from 177 to 296 m. The western portion of the study area contained more agriculture and a rolling landscape. Temperatures ranged from average highs of 24.2°C during July to average lows of 7.4°C during September. Rainfall during June-September of 2009-2011 averaged 17.69 cm (Escanaba, MI airport; Automated Surface Observation System, National Weather Service 2011).

### Data collection and analysis

We captured coyotes and wolves during May-July 2009-2011 using #3 padded foot-hold traps (Oneida

Victor, Cleveland, Ohio, USA) and MB-750 four-coil foothold traps (Minnesota Brand, Pennock, Minnesota, USA), respectively. Also, during March 2011, we captured coyotes using neck cable restraints (Etter & Belant 2011). We anaesthetized the coyotes and wolves using a ketamine (4 mg/kg and 10 mg/kg, respectively) and xylazine (2 mg/kg) mixture (Kreeger 2007). We administered yohimbine (0.15 mg/kg) as a reversal for xylazine before we released the animals at their capture sites (Kreeger 2007). Prior to release, we sexed, weighed, applied ear tags (Rototags, Nasco Farm Supply, Fort Atkinson, Wisconsin, USA) and inserted a passive integrated transponder tag (Avid, Norco, California, USA) subcutaneously between the scapulae of all individuals. We injected each coyote and wolf with oxytetracycline (0.074 ml/kg) or penicillin (0.074 ml/kg) as an antibiotic. We fitted the coyotes and wolves with a global positioning system (GPS) collar with a very high frequency (VHF) transmitter (Model GPS7000SU, Lotek Wireless, Newmarket, Ontario, Canada). We programmed the GPS collars to acquire and store locations every 15 minutes. We flew in an aircraft 1-2 times weekly to upload the collar location data, using ultra-high-frequency communication and a handheld command unit (Lotek Wireless Inc., Newmarket, Ontario, Canada). The Mississippi State University Institutional Animal Care and Use Committee approved all capture and handling procedures (protocol 09-004).

We tested two species-specific calls (one coyote, one wolf) to identify the call type most likely to elicit coyote responses, as well as factors that may affect the response rate of individuals to each call type (e.g. residency, sex and month; Laundré 1981, Okoniewski & Chambers 1984, Mitchell et al. 2006 and presence in known wolf territory). We elicited vocalizations during August-September 2009 and June-September 2010-2011 from dusk until 3:00 a.m. (Harrington & Mech 1982, Okoniewski & Chambers 1984). We located collared coyotes monthly using a VHF receiver and a 3-element yagi antenna and exposed them to one of the calls at random for the first howling trial. We relocated and attempted to vocally elicit collared coyotes up to four times monthly, alternating the call type to limit the possibility of habituation (Wenger & Cringan 1978).

We used a FX3 game-caller (FoxPro, Lewiston, Pennsylvania, USA) to broadcast coyote and wolf calls. Using only the front speaker to minimize distortion, we oriented the game-caller vertically

about 2.2 m above the ground to broadcast omnidirectionally. We broadcasted calls at 105dB, which is similar to the volume of coyote vocalizations (Mitchell et al. 2006). We elicited vocalizations when wind speed was < 12 km/hour (Kestrel 1000 weather metre; Nielsen-Kellerman, Boothwyn, Pennsylvania, USA) and when there was no precipitation, as these conditions can inhibit responses or the identification of responses (Harrington & Mech 1982). We broadcasted coyote group-yip howls (duration of 20 seconds) or five lone-wolf howls, alternating between flat and breaking (5-7 seconds each), followed by a 90-second listening period. We repeated this process three times. We attempted to record coyote vocal responses using a Sennheiser MKH 70 shotgun microphone (Sennheiser Electronic, Wennebostel, Germany) attached to a laptop computer through a two-channel analog-audio-to-digital-audio mixer (US-144mkII; Tascam, Montebello, California, USA). We used Audacity® audio recording software (version 1.3.12; Audacity Team 2011) to record digitized vocalizations at a 24-bit/96 kHz sampling rate. We classified the recorded coyote responses as a bark, bark-howl, lone howl, group howl or group-yip howl (Lehner 1978) and whether responses were from individual coyotes or groups ( $\geq 2$  coyotes). We recorded each telemetered coyote detected as moving or stationary (Okoniewski & Chambers 1984) using two 15 (minutes) GPS locations, obtained from collars, immediately preceding each howling trial. We recorded the coyote response behaviour (i.e. approaching, retreating or stationary) to each broadcast by using two (15 minutes) GPS locations, obtained from collars, immediately following each howling trial.

We considered coyotes residents if their seasonal range (May-September) did not overlap the ranges of other coyotes as seen in transient individuals (Kamler & Gipson 2000). We used seasonal ranges of GPS-collared wolves to determine when collared coyotes were in known wolf territories during a broadcasted trial. We calculated seasonal ranges for coyotes and wolves using a 95% fixed-kernel-density estimate with an *ad hoc* smoothing parameter, using package *adehabitatHR* (version 0.3.3) in Program R (version 2.13.1, R Foundation for Statistical Computing, Vienna, Austria; available at <http://www.r-project.org>).

Researchers have detected coyote responses to broadcasted calls from up to 2 km in a habitat similar to our study area (Wolfe 1974). To assess the audible distance of elicited calls and identify if a collared

individual was responding, we estimated the distances of collared coyote responses by comparing their GPS-collar locations with the broadcast locations nearest to the time of the elicited response, or broadcasted call if no response was observed, using ArcGIS® (version 10.0; ESRI, Redlands, California, USA). We compared the bearing from the broadcast location to the GPS-collar location (obtained using ArcGIS) to the bearing obtained with the directional antenna. We assumed the response was from a different individual if these bearings differed by  $> 5^\circ$ .

We used mixed-effects logistic regression models (LOGIT) to estimate which factors influenced coyote responses to broadcasted vocalizations (R package lme4, version 0.999375-42). The response variable was elicited coyote vocalizations per trial (i.e. response or no response) and explanatory variables included month, presence of collared coyotes within known wolf territory, call type broadcasted (coyote group-yip or wolf howl), sex and residency status (resident or transient) of collared individuals. We used an independent LOGIT which included distance, call type, coyote movement preceding each broadcast and coyote response behaviour following broadcasts as explanatory variables, as only 91 of 144 observations included associated GPS data. We included the year and the individual coyote as random

effects and calculated standard error (SE) and the upper and lower 95% confidence interval for each estimated parameter for each model. We used a least-square-differences multiple range test to discern differences in response rates across months, and a power analysis test (R package pwr, version 1.1.1) to verify the adequate power of our inferences. Statistical power was sufficient for the analyses conducted and statistical significance was set at  $\alpha = 0.05$ .

## Results

From 2009 to 2011, we captured and collared 25 coyotes, of which 18 (11 male and seven female) were located and exposed to broadcasted howls. We captured and collared eight wolves to determine wolf territories (during June-September) within the study area that ranged from 38 to 837 km<sup>2</sup> in size. Overall, we exposed the 18 coyotes to a coyote group-yip call 12, 14, 28 and 23 times from June to September, respectively, and a lone-wolf call 14, 11, 20 and 22 times from June to September, respectively. The coyote response rate was greater ( $P < 0.05$ ) in August than in June; however, response rates during July and September were neither greater than those in June ( $P > 0.05$ ) nor less than those in August ( $P >$

Table 1. Estimated parameter effects on coyote vocal response to broadcasted coyote and gray wolf calls during August-September 2009 and June-September 2010-2011, in the Upper Peninsula of Michigan, USA.

Parameter <sup>a</sup>	Estimate	95% Confidence Interval		z-value	P
		Lower	Upper		
MONTH (July) <sup>b</sup>	2.05	-0.24	4.34	1.76	0.079
MONTH (August) <sup>b</sup>	2.38	0.25	4.51	2.19	0.029
MONTH (September) <sup>b</sup>	2.06	-0.08	4.19	1.89	0.059
CALLTYPE (Wolf lone howl) <sup>b</sup>	-0.11	-0.94	0.72	-0.26	0.794
GENDER (Female) <sup>b</sup>	-0.50	-1.49	0.49	-0.98	0.325
RESID (Resident) <sup>b</sup>	1.55	0.00	3.11	1.96	0.050
WOLF TERRITORY (In) <sup>b</sup>	0.15	-2.09	2.39	0.13	0.896
WOLF TERRITORY (In) × RESID (Resident) <sup>b</sup>	-1.30	-4.48	1.89	-0.80	0.425
DISTANCE <sup>c</sup>	-0.71	-1.59	0.17	-1.58	0.115
CALLTYPE (Wolf lone howl) <sup>c</sup>	1.41	-1.43	4.26	0.97	0.330
MOVING (Yes) <sup>c</sup>	0.30	-1.18	1.78	0.40	0.691
MOVERESP (Toward) <sup>c</sup>	-0.12	-2.03	1.79	-0.12	0.903
MOVERESP (Away) <sup>c</sup>	0.99	-0.80	2.78	1.09	0.277
DISTANCE × CALLTYPE (Wolf lone howl) <sup>c</sup>	-2.61	-5.99	0.77	-1.52	0.130
CALLTYPE (Wolf lone howl) × MOVERESP (Toward) <sup>c</sup>	3.30	0.03	6.57	1.98	0.048
CALLTYPE (Wolf lone howl) × MOVERESP (Away) <sup>c</sup>	-1.73	-4.98	1.52	-1.05	0.296

<sup>a</sup> Reference categories include month = MONTH (June), residency status = RESID (transient), call type = CALLTYPE (coyote group yip), gender = GENDER (Male) and wolf territory = WOLF TERRITORY (Out), movement = MOVING (No), movement after broadcast = MOVERESP (Neither direction).

<sup>b</sup> Estimated with 144 observations and 37 responses.

<sup>c</sup> Estimated with 91 observations and 21 responses.

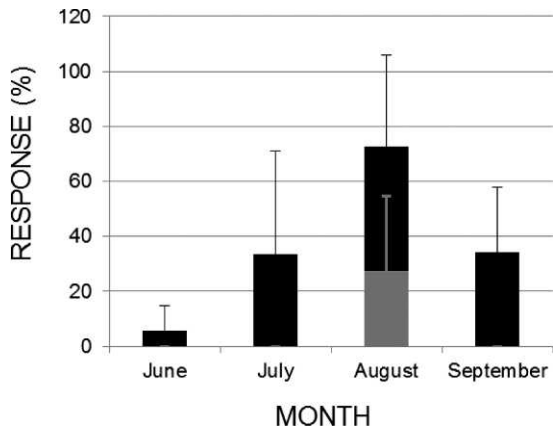


Figure 1. Resident (■) and transient (■) coyote response rates to broadcasted coyote and gray wolf calls (with standard deviation shown), during August-September 2009 and June-September 2010-2011, in the Upper Peninsula of Michigan, USA.

0.05). Responses were elicited at 37 of 144 howling trials (response rate=25.7%) and included one bark, 14 bark-howls, two lone howls, three group howls and 17 group-yip howls. Group responses occurred at 53% and 55% of male and female trials, respectively. Coyote activity level (i.e. moving or stationary) at the time of broadcast did not influence vocal response from individuals ( $P = 0.691$ ,  $SE = 0.757$ ).

Male and female response rates were similar (Table 1). Resident ( $N = 13$ ) and transient ( $N = 5$ ) coyotes had average seasonal ranges of  $16 \text{ km}^2$  ( $SD = 5.7 \text{ km}^2$ ) and  $183 \text{ km}^2$  ( $SD = 70.7 \text{ km}^2$ ), respectively. Resident coyotes (31%) responded three times more frequently than transient individuals (10%); transients vocalized only during August (Fig. 1). We noted that wolves responded during three broadcasted lone-wolf call howling trials, twice followed by non-target coyote response. Broadcasted calls in ( $N = 25$ ) and out ( $N = 119$ ) of known wolf territories elicited similar coyote response rates ( $P = 0.896$ ,  $SE = 1.143$ ); there was no interaction between resident coyote response rates in and outside of known wolf territories.

Calls were broadcasted at distances of 0.24-4.69 km ( $\bar{x} = 1.32 \text{ km}$ ,  $N = 91$ ) and elicited responses were detected at distances of 0.26-2.85 km ( $\bar{x} = 0.94 \text{ km}$ ,  $N = 21$ ). We found no correlation (positive or negative) between the response rate of coyotes and distance, and there was no interaction between the call type and the distance of response (see Table 1). Coyotes responded similarly to both types of broadcasted calls at distances  $< 2.0 \text{ km}$  (Fig. 2), and only one response was elicited with a coyote group-yip howl at a distance  $> 2.0 \text{ km}$ . Coyotes were more likely

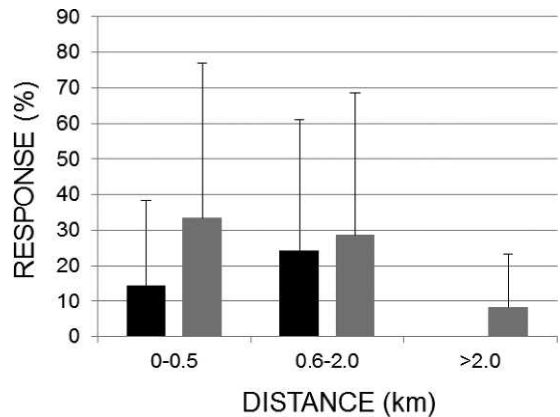


Figure 2. Proportion of coyote responses to broadcasted coyote (■) and wolf (■) calls (with standard deviation shown), during August-September 2009 and June-September 2010-2011, in the Upper Peninsula of Michigan, USA.

to respond ( $P = 0.048$ ,  $SE = 1.670$ ) when they moved toward broadcasts of a lone-wolf howl as compared to responding when stationary and a coyote group-yip howl was played.

## Discussion

Vocal response by coyotes to broadcasted calls was greatest from residents, in or outside of wolf territories, during August, and was not influenced by call type. We expected a greater response rate in August-September because long-distance vocalizing becomes more important as pups mature and pack members become more spatially dispersed (Harrington & Mech 1979). The low responsiveness of resident individuals during June (5.6%) was similar to the findings by Laundré (1981) and Gaines et al. (1995), who also reported fewer responses in June than in August. When pups are young (i.e. June) long-distance vocalizations may not be necessary, or may pose a higher risk to young at den sites. Individual variation and repeated trials on the same individuals may also affect responsiveness across months. Although we attempted to minimize the potential for habituation by alternating calls and limiting repeated trials, we exposed individuals to the same calls, which could have caused habituation (Wenger & Cringan 1978) and potentially reduced response rates in later months. Thus, our reported response rates may be conservative.

Apparent male and female response rates were similar; however, for resident collared males and females it was unknown to which group individuals

were actually responding; 48.6% of the responses were group responses and either member of the pair could have initiated the responses. Similar to Gese & Ruff (1998), we were unable to determine if a conspecific group member was present and initiated responses; however, Mitchell (2004) identified that captive paired females were more likely to respond after a male initiated a response which may have influenced the response rates of free-ranging females if they followed the same pattern.

We observed a lesser response rate for transient coyotes, which may be due to risk-avoidance behaviour toward territorial coyotes or lack of territory to defend (Harrington & Mech 1979, Gese & Ruff 1998). Assuming an equal capture probability, transients comprised 28% of our sample population, similar to Gese et al. (1988) who reported that 22% of the coyotes were transient. When conducting broadcast-elicitation surveys, residents are more likely to respond, but additional individuals likely exist in the population as non-responding transients, and wildlife managers should adjust the estimates of abundance to include them. If we consider 25% of the population to be transient and their response rate to be  $\frac{1}{3}$  of residents, it may be appropriate to inflate the survey estimates by 16.7%.

Howling appears to serve similar purposes (e.g. territory maintenance) for wolves and coyotes (Theberge & Falls 1967, Gese & Ruff 1998) and the observed equal response rate of coyotes to both calls at distances of  $< 2.0$  km, and within or outside of known wolf territories, suggests that coyotes may perceive lone-wolf vocalizations as a non-threatening interspecific communication. Coyotes would likely reduce vocalizations or would move away from broadcasts if the coyotes perceived wolf calls as a predation risk. Our observations of coyotes moving toward lone-wolf broadcasts after responding suggests that these individuals did not perceive lone-wolf call broadcasts as a high risk at the distances observed. Given our results of similar coyote response rates to broadcasted coyote and wolf vocalizations, a lone-wolf howl may be an effective technique to estimate the presence or abundance of both species simultaneously.

Distance from broadcasted calls to coyotes may influence vocal response rates. We observed coyotes (collared and non-collared) approach us, without vocalizing, on five occasions after broadcasting. Broadcasting calls close to coyotes using a coyote group-yip or lone-wolf call may limit vocal responses due to vocalizations being a high risk factor when in

close proximity to a conspecific or wolf, or long-distance vocalizations may not be necessary when individuals are close. We heard coyote responses to broadcasted vocalizations from distances similar to those observed by Fuller & Sampson (1988). By sampling locations  $\geq 4.0$  km apart, double-counting individuals during a survey would be unlikely. Most calls were elicited at 0.5-2.0 km (86%), and although coyotes likely hear calls at farther distances (Lehner 1982), the likelihood of hearing a response from  $> 2.0$  km appears low, especially in densely forested habitat.

It is important to identify factors that influence, or are associated with, response rates to improve the precision of surveys, and reduce the number of surveys to confirm the presence or absence of coyotes when response is low. Because transient coyotes may represent a substantial proportion of the population, abundance estimates based on broadcast elicitation should account for differences in response rates by resident and transient individuals. We recommend using recorded coyote vocalizations to elicit coyote responses as the associated equipment is of low cost and is easy to transport, and recordings provide consistent and high-quality broadcasts. We recommend conducting surveys for coyotes in the Upper Peninsula of Michigan during July-September and sampling locations  $\geq 4.0$  km apart to increase the response rates and decrease the probability of double-counting individuals for more precise estimates of abundance or density. We conclude that coyote surveys conducted in areas of sympatric wolves will not be biased by low response, as coyotes did not reduce their vocal response rates within known wolf territories.

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## References

- Albert, D.A. 1995: Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working classification. U. S. Forest Service. - Northern Prairie Wildlife

- Research Center, Jamestown, North Dakota, USA, 250 pp.
- Audacity Team 2011: Free software distributed under the terms of the GNU General Public License. - Available at: <http://audacity.sourceforge.net> (Last accessed in July 2009).
- Coolahan, C. 1990: The use of dogs and calls to take coyotes around dens and resting areas. - *Proceedings of the Vertebrate Pest Conference* 14: 260-262.
- Dunbar, M.R. & Giordano, M.R. 2002: Abundance and condition indices of coyotes on Hart Mountain National Antelope Refuge, Oregon. - *Western North American Naturalist* 62: 341-347.
- Etter, D.R. & Belant, J.L. 2011: Evaluation of 2 cable restraints with minimum loop stops to capture coyotes. - *Wildlife Society Bulletin* 35: 403-408.
- Fuller, T.K. & Sampson, B.A. 1988: Evaluation of a simulated howling survey for wolves. - *Journal of Wildlife Management* 52: 60-63.
- Gazzola, A., Avanzinelli, E., Mauri, L., Scandura, M. & Apollonio, M. 2002: Temporal changes of howling in south European wolf packs. - *Italian Journal of Zoology* 69: 157-161.
- Gaines, W.L., Neale, G.K. & Naney, R.H. 1995: Response of coyotes and gray wolves to simulated howling in north-central Washington. - *Northwest Science* 69: 217-222.
- Gese, E.M., Rongstad, O.J. & Mytton, W.R. 1988: Home range and habitat use of coyotes in southeastern Colorado. - *Journal of Wildlife Management* 52: 640-646.
- Gese, E.M. & Ruff, R.L. 1998: Howling by coyotes (*Canis latrans*): variation among social classes, seasons, and pack sizes. - *Canadian Journal of Zoology* 76: 1037-1043.
- Harrington, F.H. 1981: Urine-marking and caching behavior in the wolf. - *Behavior* 76: 280-288.
- Harrington, F.H. & Mech, L.D. 1979: Wolf howling and its role in territory maintenance. - *Behavior* 68: 207-249
- Harrington, F.H. & Mech, L.D. 1982: An analysis of howling response parameters useful for wolf pack censusing. - *Journal of Wildlife Management* 46: 686-693.
- Joslin, P.W.B. 1967: Movements and home sites of timber wolves in Algonquin Park. - *American Zoology* 7: 279-288.
- Kamler, J.F. & Gipson, P.S. 2000: Space and habitat use by resident and transient coyotes. - *Canadian Journal of Zoology* 78: 2106-2111.
- Kreeger, T.J. 2007: Handbook of wildlife chemical immobilization. 3rd edition. - Wildlife Pharmaceuticals, Fort Collins, Colorado, USA, 417 pp.
- Laundré, J.W. 1981: Temporal variation in coyote vocalization rates. - *Journal of Wildlife Management* 45: 767-769.
- Lehner, P.N. 1976: Coyote behavior: implications for management. - *Wildlife Society Bulletin* 4: 120-126.
- Lehner, P.N. 1978: Coyote vocalizations: A lexicon and comparisons with other canids. - *Animal Behaviour* 26: 712-722.
- Lehner, P.N. 1982: Differential vocal response of coyotes to "group howl" and "group yip-howl" playbacks. - *Journal of Mammalogy* 63: 675-679.
- Linhart, S.B. & Knowlton, F.F. 1967: Determining age of coyotes by tooth cementum layers. - *Journal of Wildlife Management* 62: 362-365.
- McCarley, H. 1975: Long-distance vocalizations of coyotes (*Canis latrans*). - *Journal of Mammalogy* 56: 847-856.
- Michigan Center for Geographic Information 2002: Department of Information Technologies. Land cover and use for Delta and Menominee Counties, Michigan 1992. - Available at: <http://www.mcgi.state.mi.us/mgdl/?rel=ext&action=cext> (Last accessed in February 2010).
- Michigan State Climatology Office 2011: Climate normals and extremes by month. Escanaba station 2626. - Available at: [http://climate.geo.msu.edu/Stations/2626/1981-2010 monthly summary.pdf](http://climate.geo.msu.edu/Stations/2626/1981-2010%20monthly%20summary.pdf) (Last accessed in October 2011).
- Mitchell, B.R. 2004: Coyote vocal communication and its application to the selective management of problem individuals. - PhD thesis, University of California, Berkeley, USA, 212 pp.
- Mitchell, B.R., Makagon, M.M., Jaeger, M.M. & Barrett, R. 2006: Information content of coyote barks and howls. - *Bioacoustics: The International Journal of Animal Sound and its Recording* 15: 289-314.
- National Weather Service 2011: Automated Surface Observation System, KESC. - Available at: <http://www.nws.noaa.gov/asos/> (Last accessed in January 2012).
- Okoniewski, J.C. & Chambers, R.E. 1984: Coyote vocal response to an electronic siren and human howling. - *Journal of Wildlife Management* 48: 217-222.
- Pyrach, D. 1984: Social distribution and population estimates of coyotes in north-central Montana. - *Journal of Wildlife Management* 48: 679-690.
- Theberge, J.B. & Falls, J.B. 1967: Howling as a means of communication in timber wolves. - *American Zoology* 7: 331-338.
- Walsh, P.B. & Inglis, J.M. 1989: Seasonal and diel rate of spontaneous vocalization in coyotes in south Texas. - *Journal of Mammalogy* 70: 169-171.
- Wenger, C.R. & Cringan, A.T. 1978: Siren-elicited coyote vocalizations: an evaluation of a census technique. - *Wildlife Society Bulletin* 6: 73-76.
- Wolfe, G.J. 1974: Siren-elicited howling response as a coyote census technique. - M. Sc. thesis, Colorado State University, Fort Collins, USA, 206 pp.