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Original Article

Efficacy of Acoustic Triangulation for Gray Wolves

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ABSTRACT Acoustic triangulation is a unique, relatively noninvasive monitoring approach that can inform our understanding of a species' distribution in time and space. Acoustic triangulation relies on standard triangulation techniques to determine the location of an acoustic event. Howl surveys are frequently used to survey wolves (*Canis lupus*) and other canids. We evaluated the efficacy of acoustic triangulation for estimating the location of wolves. We measured precision and accuracy of acoustic triangulation using an experimental mock howl survey and field data collected with wild wolves in northern Wisconsin, USA (2014–2018). Precision of acoustic triangulation was similar to triangulation with ground-based radiotelemetry for both pooled data and individual wolves at specific times, although the 2 techniques did not result in similar predicted locations. Distance from the howl source was the most consistently significant factor influencing the efficacy of acoustic triangulation. Error ellipse size was 33 times smaller at distances <1 km. Wind speed also reduced the accuracy of acoustic triangulation for mock howl surveys. Precision for modified howl surveys with wild wolves improved with the number of bearings. We estimated a mean bearing error of 13.2° (±2.1, 95% CI) for single bearings and a maximum distance of 1.76 km (range = 0.96–1.76 km; $\bar{x} = 1.41$ km) detection for audible anthropogenic howls. Such information can be applied to howl survey data to generate more fine-scale location information for wolf-pack home sites. Acoustic triangulation of wolves can provide high-quality location information in areas where wolves are not monitored with radiocollars. © 2020 The Wildlife Society.

KEY WORDS *Canis latrans*, *Canis lupus*, coyote, home sites, howl survey, noninvasive monitoring techniques, rendezvous sites, telemetry, wildlife management, wolf.

Species management requires population-level information derived from population monitoring efforts (Lyons et al. 2008). Species conservation is often plagued by decisions based on limited or incomplete population-level information (Berg et al. 2017). Population-level information, such as the distribution of a species or characteristics of breeding habitat for that species, are fundamental to sound conservation strategies. However, in reality, species monitoring is an exercise in cost–benefit decision-making within a given set of real-world constraints (e.g., time, funding, personnel, access to technology, or political will). Thus, techniques that enhance the quality or quantity of data generated, or reduce the costs associated with monitoring, can benefit conservation efforts and improve scientific access to data (Berg 2016, Berg et al. 2017).

Species monitoring efforts often exploit unique life-history characteristics of a species to gain insight into population-level metrics. Some species are highly elusive, cryptic, or difficult to access, thus challenging monitoring efforts. Many species of birds, amphibians, mammals, and invertebrates produce vocalizations that can be useful for monitoring. Acoustic monitoring is a relatively noninvasive monitoring method that is becoming more common in the conservation sciences.

For decades, scientists have used passive surveys (listen for a set period of time) and playback or callback surveys (elicit a response following a human-generated vocalization mimicking a species' natural vocalization or other auditory cue) to monitor species, especially birds and amphibians (Mendez-Carvajal 2012, Leblond et al. 2017, Stiffler et al. 2018). More recently, however, scientists are beginning to use stationary or mobile acoustic monitoring systems technology to monitor

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for wildlife. Acoustic monitoring is a proven, versatile technique. For example, researchers have used acoustic monitoring to evaluate site biodiversity (Aide et al. 2017), species presence (O'Farrell and Gannon 1999, Lefebvre and Poulin 2003, Krofel 2009), range of vocalizations for a species (Pedos et al. 2002), niche partitioning (Jachowski et al. 2014), habitat use (Bassi et al. 2015), group composition and status (Bassi et al. 2015, Palacios et al. 2016), and abundance (Thompson et al. 2010).

For a species like wolves (*Canis lupus*), scientists use howl surveys (i.e., callback surveys) to elicit responses, thus exploiting vocalizations associated with territory maintenance to monitor the species (Harrington and Mech 1982, Fuller and Sampson 1988). Howl surveys can be used to evaluate breeding status (Harrington and Mech 1982, Bassi et al. 2015, Palacios et al. 2017), habitat use (Krofel 2009, Kenaga et al. 2013, Bassi et al. 2015), canid behavior (Leblond et al. 2017), and, when merged with other data, site occupancy (Ausband et al. 2014). Howling is typically conducted from midsummer to early autumn to limit disturbance to den sites (Harrington and Mech 1982, Frame et al. 2007, Wiedenhoeft 2014, Sazatornil et al. 2016). Standard howl surveys for wolf monitoring typically result in a single location (location where elicited howl was heard), single bearing (direction from which the elicited howl was heard), and an estimated distance from howling wolves (Wiedenhoeft 2014).

Acoustic triangulation is a technique used to determine the location of a sonic event. Stoner (1994) and Mendez-Carvajal (2012) used acoustic triangulation to evaluate the population densities of howler monkeys (*Alouatta* spp.) in Costa Rica and Panama, respectively. Lefebvre and Poulin (2003) demonstrated the feasibility of acoustic triangulation for determining booming locations of great bitterns (*Botaurus stellaris*) in the field. Like radiotelemetry or global positioning systems technology, acoustic triangulation estimates the location of the source of a signal (i.e., sound) based on multiple, directional observations made from multiple locations.

Adapting standardized howl surveys to incorporate acoustic triangulation may be a noninvasive way to obtain supplemental distribution data for wolves or similar species, such as coyotes (*C. latrans*). Acoustic triangulation could also help researchers and conservationists identify home sites for wolf packs that are not being monitored with other technologies (e.g., telemetry). We evaluated the efficacy of acoustic triangulation for estimating the location of wolves. We evaluated the precision and accuracy of acoustic triangulation using an experimental mock howl survey and then field-tested the method with wild wolves. We also evaluated the error associated with single bearings and maximum distance of detection for audible anthropogenic howls to produce an error polygon using single-point, single-bearing howl surveys. We expected that distance, wind speed, characteristics of howl responses, and number of bearings would influence the efficacy of acoustic triangulation.

STUDY AREA

We implemented experimental mock howl surveys and modified field howl surveys in wolf range within Bayfield and Ashland counties of northern Wisconsin, USA (range = 46.95300°N, −90.86248°W to 45.82279°N, −91.00995°W; Fig. 1). Both counties were >80% forest land and >40% public lands in the core of wolf habitat in Wisconsin (Mladenoff et al. 2009). Wolves returned to Wisconsin in the mid-1970s after being extirpated in the 1950s (Wydeven et al. 2009). At the time of this study (winter 2018) minimum count of wolves for Wisconsin was 905–944 wolves in the state, with 40% of wolves in the northwestern Wisconsin zone that includes these 2 counties (Wiedenhoeft et al. 2018*a, b*). Other canids within the study area were coyotes, red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), and domestic dogs (*C. familiaris*).

Wolf range in Wisconsin contained temperate forests interspersed with wetlands, water bodies, agricultural lands, and open areas (Mladenoff et al. 1997). Bayfield and Ashland counties, located on the southern edge of Lake Superior, consisted of rolling glacial outwash plains with many small lakes, wetlands, and bogs. The area was located along a transitional zone between boreal forest and northern temperate forests (northern mesic and pine forests, pine barrens, and conifer swamps; Curtis 1959). Mean annual monthly temperatures for the years of the study (2014–2018) ranged from −20.9° C in winter to 27.2° C in summer with seasonal mean annual precipitation of 916.9 mm for Ashland, Wisconsin (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, accessed 14 Apr 2020).

Wisconsin Department of Natural Resources (WDNR) monitored the Wisconsin wolf population since 1979, and wolf monitoring relied on territorial mapping techniques informed by winter track surveys and telemetry monitoring (Wydeven et al. 2009). Howl surveys were used by the WDNR to evaluate the breeding status of wolf packs (Wydeven et al. 2009, Wiedenhoeft 2014).

METHODS

We tested the efficacy of acoustic triangulation for estimating the location of wolves detected through howl surveys. First, we evaluated the precision and accuracy of acoustic triangulation using an experimental mock howl survey from September 2017 through February 2018. Second, to compare acoustic triangulation with other similar monitoring techniques, we compared the precision of, and distance between, predicted locations for radiotelemetry and acoustic triangulation using pooled and individual data (i.e., individual wolves at a specific time). Third, we examined factors influencing the precision of acoustic triangulation with data from wild wolves (i.e., modified howl survey). Finally, we evaluated the error associated with single bearings and maximum distance of detection for audible anthropogenic howls to produce an error polygon using single-point, single-bearing howl surveys.

Data Collection

Mock howl survey.—To evaluate the accuracy (i.e., difference between predicted and real locations) and precision (i.e., size of error ellipse) of acoustic triangulation for wolves, we

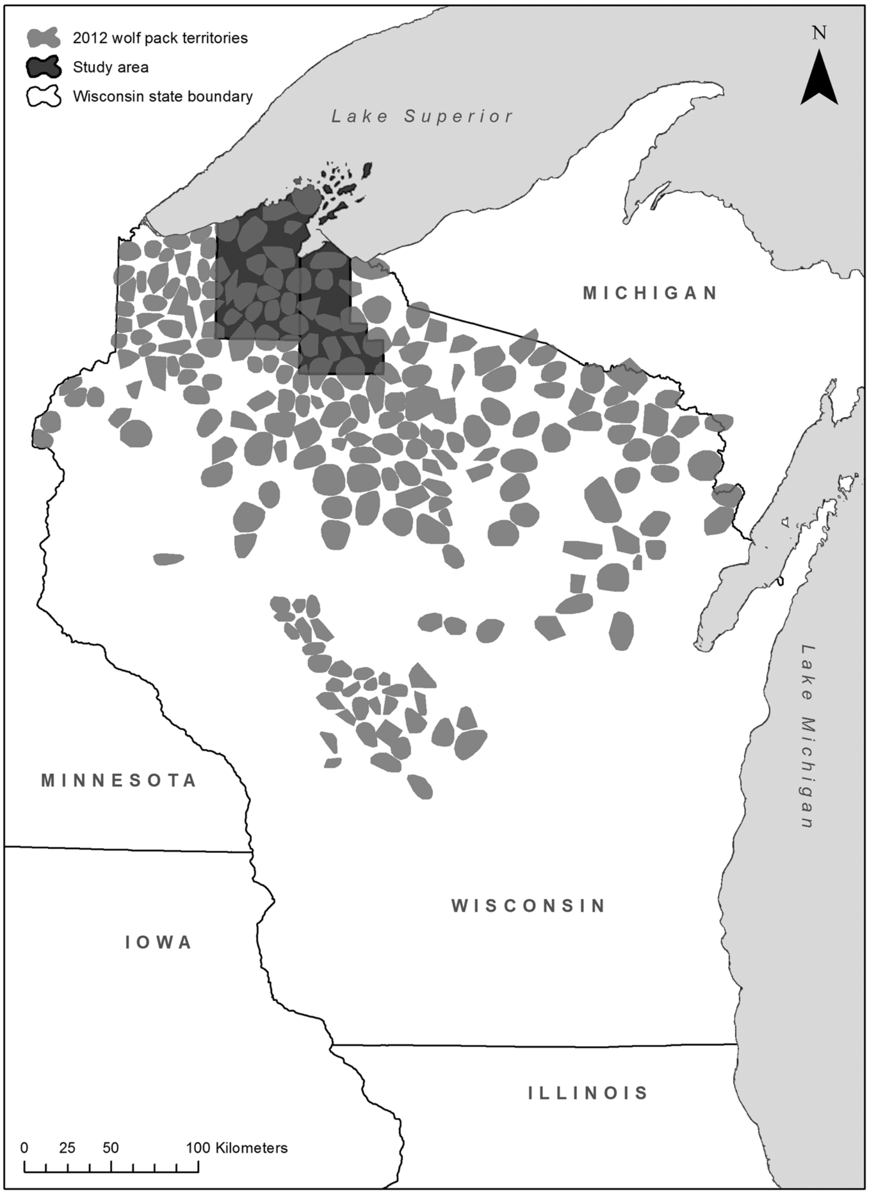

Figure 1. Wolf pack territories in Wisconsin, USA, as delineated by the Wisconsin Department of Natural Resources, relative to our study area.

implemented anthropogenic, or "mock," howl surveys. Mock howl surveys are designed to simulate a howl survey in the field with wild wolves, but instead of wolves howling in response, humans respond with simulated wolf howls (Passilongo et al. 2015). To perform a mock howl survey, we split into 2 groups of individuals, 'listeners' and 'howlers.' 'Listeners' represented a group of field technicians implementing a howl survey and 'howlers' represented a lone or pack of wolves responding to simulated howls generated by 'listeners.' We implemented mock howl surveys during the day so field staff could easily move around the landscape. We selected for areas with limited anthropogenic noise (e.g., vehicle traffic) that would not typically occur during actual howl surveys. We recorded the date, general location, habitat type, topography, wind speeds (low, <8 km/hr; medium, 8–16 km/hr; high, >16 km/hr), and ambient noise for each location. We conducted mock howl surveys with 3–4 individuals (listeners) spaced 50–100 m apart and oriented along an approximate west–east or north–south orientated line roughly 200 m in length—each with a global positioning system (GPS) unit, a baseplate bearing compass with 2-degree graduation precision, 2-way radio for communication, and data sheet (Lefebvre and Poulin 2003). At least 3 additional individuals (howlers) with a GPS unit and data sheet would move to random locations in the forest adjacent to the line of listeners. After confirming howlers were ready via hand-held radio, a listener would initiate the mock acoustic survey. The center listener initiated a series of 3 howls alternating breaking and flat howls done at full volume (~87 decibels at 10 m, roughly equivalent to a wolf howl; Filibeck et al. 1982, Harrington and Mech 1982, Passilongo et al. 2015). Prior to responding, howlers randomly selected a 'response type': 3 individuals howling together, 2 individuals together, 1 individual alone, or 2 types of split howls. Split howls consisted of either one or 2 individuals together followed immediately by one individual at another location. Howlers also randomly selected a time to response: immediately, 30 seconds after, 60 seconds after, 120 seconds after, or spontaneously without notifying or waiting for the listeners to elicit a response. We expected that the variation in response options would better represent variation in responses from wild wolves. Howlers recorded the time of their howl, GPS coordinates, howl type, and time to response. Upon hearing a howl response, the listeners would record the time, GPS coordinates, a compass bearing of the response, number of howlers heard, and an estimated distance from the howl. Listeners were instructed to slowly rotate and tilt their head while listening to generate a more accurate bearing; a similar strategy to that of a hunting barn owl (*Tyto alba*; Payne 1971). Once howlers completed a specific howl series, they moved to a new location and repeated the above process. We instructed howlers to attempt to surprise listeners in terms of their location of each subsequent response, increase the uncertainty of where the next howl may originate from, and better represent conditions observed during typical howl surveys.

To better understand the maximum distance of detection for audible anthropogenic howls under typical field conditions, we used mock howl trials where 2 individuals remained stationary while 2 other individuals traveled down a road, assuring no visual contact, and howling at approximately 100-m intervals. We made sure the winds were classified as low (<8 km/hr) because that is what is typically done in the field by WDNR and other agency staff (Wiedenhoeft 2014). Both groups howled at each other until all individuals could no longer detect audible howls. The maximum distance for audible howl detection under these circumstances represented the maximum distance of audible howl detection.

Radiotelemetry.—We used wolf telemetry data collected by Erik R. Olson (ERO) and students from his Wolf Ecology or Wildlife Techniques courses at Northland College between May 2015 and October 2017. They used directional Yagi antennae and very-high-frequency (VHF) receivers (Communications Specialists, Inc., Orange, CA, USA) to locate radiocollared wolves within our study area (Wydeven et al. 2009). Once a collared wolf was detected, ERO would establish groups of 2–3 students spaced 100–200 m apart along a road. If VHF signal was weak, the groups would shift along the road systematically, until the signal improved. Groups would record GPS locations, compass bearings based on radiotelemetry, and time of day; every 2–5 minutes until monitoring ceased. ERO encouraged groups to take frequent bearings to improve the accuracy and precision of the triangulation. If wolves or coyotes howled spontaneously during the telemetry survey, each group would record a compass bearing, time of howl, and estimated number of individuals howling.

Modified howl surveys.—We used data collected by ERO's undergraduate classes from May 2015 to October 2017, on 8 different wolf packs within our study area. Modified howl surveys were conducted along predetermined routes, between a half-hour before sunset and 0100 (Harrington and Mech 1982). We followed a modified version of the WDNR howl survey protocol (Wiedenhoeft 2014), which is based on the recommendations of Harrington and Mech (1982). We stood quietly and listened for 30–60 seconds before the main group initiated 5 quiet howls alternating between "breaking" and "flat" howls in a sequence and then waited 90 seconds for a response (Harrington and Mech 1982). If a response was heard, we determined and recorded the species responding, an estimate of the number of adults and pups, bearing(s) of the howl(s), the time of response, and our coordinates using a GPS. To facilitate acoustic triangulation, we exited the vehicle, split up into groups, and spread out along the road. The main group (group howling) generally stayed within approximately 50 m of the vehicle and other individuals or groups spread out along the road forming an approximately 200-m line. We allowed groups to haphazardly spread themselves along the road. When the number of observers was too few, we instead moved to multiple nearby locations after the initial response (~400 m apart) and attempted to obtain additional bearings for the same responding animals. If there was >1 group or species responding, we took multiple bearings to clearly distinguish between different groups. If there was no response, we initiated 5 loud alternating "flat" and "breaking" howls (Harrington and Mech 1982). We waited 90 seconds for a response. If no response was detected, we initiated a second set of loud howls. This was continued at 1.5–2.5-km intervals until the route was completed or weather conditions forced the observers to stop the howl survey early.

Field personnel were trained how to differentiate between coyote, wolf, and wolf pup howls and exposed to multiple examples in the field. Typically one experienced individual was present during each howl survey to help confirm the identity of the howl.

Statistical Analysis

We entered all howl and radiotelemetry data into Radio Tracker, a Microsoft Excel spreadsheet developed by J. Cary (in 2000) at the University of Wisconsin—Madison for monitoring wildlife via radiotelemetry. We used Radio Tracker to generate predicted locations, an estimated error ellipse (m^2), and plots visualizing the data based on the GPS locations and bearings collected by the observers. Similar to standard radiotelemetry practices, we used visualization plots and the timing of bearings to ensure accuracy of triangulations and filter bearings perceived as outliers (e.g., pointing in the opposite direction of the rest of the bearings; Bassi et al. 2015).

Mock howl surveys.—We only considered acoustic triangulations with ≥3 bearings for the mock howl analyses. First, we used a logistic regression to examine factors influencing the success of generating an error ellipse <90 km^2 in Radio Tracker using the following variables: distance (m), time to response, whether the howl was a split howl or not, the number of individuals howling, whether it was a chorus howl or not, and wind speed (Fig. 2). We then examined the effect each of these covariates had on the accuracy (i.e., distance between predicted and actual location) and precision (i.e., size of error ellipses) of acoustic

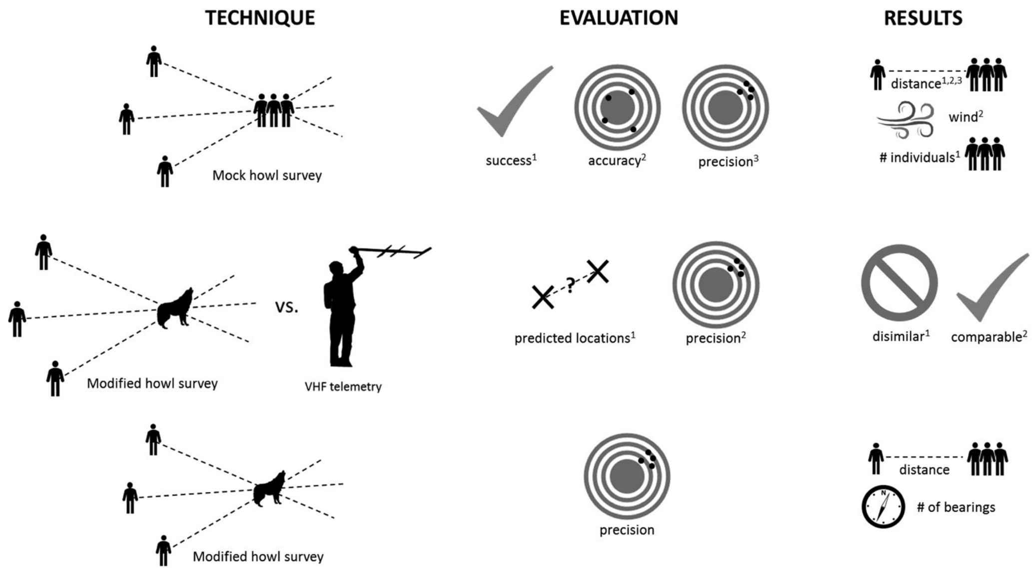

Figure 2. Graphical description of the techniques used, types of evaluations considered, and general results of tests regarding efficacy of acoustic triangulation for wild canids in northern Wisconsin, USA (2014–2018). We evaluated whether or not we could successfully predict a location using acoustic triangulation from mock howl surveys. We also evaluated the accuracy (bullseye figure depicts a technique that is accurate, but not precise) and precision (bullseye figure depicts a technique that is precise, but not accurate) of acoustic triangulation using mock howl surveys conducted with wild wolves and found that distance between observer and the source of the sound, wind speed, and number of individuals howling were significant factors. We examined the distance between predicted locations from acoustic triangulation to that of radiotelemetry triangulation, which were found to be statistically different from one another. We also compared the precision of the 2 techniques and found that they were statistically comparable. We tested the precision of acoustic triangulation on wild canids and found that distance from the observer and the number of bearings were significant. (Superscript numbers identify results for specific evaluations via mock howl survey technique).

triangulation (Fig. 2). For accuracy (i.e., distance between predicted and actual locations), we used simple linear regression analysis to examine the effect of distance (m) from source of howl. We also used a 2-way analysis of variance (ANOVA) to evaluate the effects of wind speed, number of individuals howling, whether it was a split howl or not, and time to response. To evaluate factors influencing the precision of acoustic triangulation (i.e., size of error ellipse), we used simple linear regression to examine the effects of distance (m). Again, we used a 2-way ANOVA to examine the effects of wind speed, number of individuals howling, whether it was a split howl or not, and time to response.

Comparison of radiotelemetry and acoustic triangulation.—We evaluated the effectiveness of acoustic triangulation for wild canids (wolves and coyotes). We compared the precision (i.e., size of error ellipses) of radiotelemetry with the precision of acoustic triangulation (Fig. 2). We used a *t*-test to compare the precision (i.e., size of error ellipses) between radiotelemetry and acoustic telemetry for the pooled data collected throughout the entire sampling period. Next, we compared the precision (i.e., size of error ellipses) and accuracy (i.e., distance between predicted location from acoustic triangulation and predicted location from radiotelemetry) for individual wolves at specific times. We used a paired *t*-test to compare the precision (i.e., size of error ellipses) of radiotelemetry with acoustic telemetry for individual data because radiotelemetry and acoustic triangulations were paired for an individual wolf at a specific time. To compare the predicted locations between the 2 techniques, we examined whether the 95% confidence intervals (CIs) for the average distance between a predicted location using radiotelemetry and a predicted location from acoustic triangulation overlapped zero.

Modified howl surveys.—We evaluated the efficacy of acoustic triangulation for wild wolves and coyotes (Fig. 2). We used a simple linear regression to test for effects of distance (m) and the number of bearings on precision (i.e., size of error ellipses). We used a 2-way ANOVA to compare the precision of split howls with nonsplit howls, chorus to nonchorus howls, and effects of wind speed on the size of the error ellipse.

Single-bearing error analysis.—We evaluated the error associated with single bearings and maximum distance of detection for audible anthropogenic howls to produce an error polygon using single-point, single-bearing howl surveys. Such information can be retroactively applied to historical howl survey data or used in future howl surveys to generate more fine-scale location information for wolf pack den and rendezvous sites with limited additional monitoring costs. We used the distance formula derived from the Pythagorean Theorem to determine the distance between the actual and predicted point and then the distance between the actual and predicted points and observer location. Using the law of cosine, we then calculated the angle of error between the bearing and an accurate bearing. Using our mock howl trials to determine the maximum distance of audible howl detection and our bearing error, we then were able to prescribe an error polygon for bearings. We also evaluated the effects of wind speed, distance from the observer to the actual location, number of individuals howling, whether it was a split howl or not, and time to response on bearing error using simple linear regression and 2-way ANOVA.

We completed all statistical analyses in Program R 3.4.2 (R Core Team 2017), with $\alpha = 0.05$. We used the *NCstats* package in R 3.4.2 to evaluate outliers, test assumptions, and transform variables.

RESULTS

Mock Howl Survey

Mock howl surveys were implemented 7 times resulting in 88 triangulations. Distance between observer and howl location ($P = 0.003$) and the number of individuals howling ($P = 0.03$) were the only covariates that influenced our ability to estimate a location and generate an error ellipse (Table 1, Fig. 3).

Distance between the observer and howl location ($P < 0.001$, coefficient = 1.6) affected the accuracy of acoustic triangulation (i.e., distance between predicted and actual location; Fig. 4). Wind speed also had an effect on the accuracy of acoustic triangulation ($P < 0.001$, coefficient = 4.6). We did not detect a relationship between the number of individuals howling ($P = 0.50$, coefficient = 4.03), split howl or not ($P = 0.78$, coefficient = 0.09), or time to response ($P = 0.78$, coefficient = 3.8) and distance between the predicted and actual location (i.e., accuracy).

Distance between observer and howl location ($P < 0.001$, coefficient = 1.81) affected the precision of acoustic triangulation (i.e., error ellipse size; Fig. 4). We did not detect a relationship between wind speed ($P = 0.19$, coefficient = 8.3), number of individuals howling ($P = 0.51$, coefficient = 7.7), split howl or not ($P = 0.66$, coefficient = 8.2), or time to response ($P = 0.90$, coefficient = 7.5) and precision (i.e., error ellipse size).

Comparison of Radiotelemetry and Acoustic Triangulation

When we pooled the entire data set of 208 telemetry triangulations and 56 acoustic triangulations for wild canids ($n = 264$) we found no difference in precision between the 2 techniques ($P = 0.27$, coefficient = −0.58). We then compared the precision of radiotelemetry triangulations for individual wolves at specific times with the precision of acoustic telemetry for those same wolves at the same time ($n = 44$). The precision of the 2 techniques were not different ($P = 0.40$, coefficient = −0.43), indicating that acoustic triangulation had similar precision (i.e., produced similar sized error ellipses) as radiotelemetry. For the same subset of individual wolves at specific times ($n = 44$), the 95% CIs for average distance between predicted locations from the 2 separate techniques did not overlap zero ($\bar{x} = 838.6$ m ± 344, 95% CI), indicating that the 2 techniques did not produce similar predicted locations on average.

Table 1. Logistic regression results for the effects of distance, split howls, number of individuals, chorus howls, time to response, and wind speed on the ability to generate an error ellipse <90 km^2, based on mock howl surveys conducted in northern Wisconsin, USA (2014–2018).

Variable	Coefficient	P	SE
Distance to observer	−0.00276	0.003	0.0009
Split vs. nonsplit	0.4914	0.63	0.4914
No. of individuals	0.6885	0.03	0.3215
Chorus vs. nonchorus	0.6539	0.20	0.5134
Time to response	0.1072	0.57	0.1890
Wind speed (km/hr)	−0.06561	0.67	0.1541

Modified Howl Survey

We used 56 acoustic triangulations of wild wolves ($n = 42$), coyotes ($n = 8$), and dogs or undetermined canids ($n = 6$) during modified howl surveys to evaluate factors influencing the precision of acoustic triangulation under typical field conditions. Similar to mock howls, the distance between the observer and the predicted location of the wild canid affected the precision of acoustic triangulation ($P < 0.001$, coefficient = 1.58; Fig. 5). However, precision of acoustic triangulation was consistently smaller at distances <1 km (Fig. 5); distances ≥1 km had error ellipse sizes roughly 33 times larger on average ($P < 0.001$). Number of bearings used in triangulation also significantly ($P = 0.035$, coefficient = −0.46) influenced precision (i.e., error ellipse size; Fig. 5). We found no effect of wind speed ($P = 0.50$, coefficient = 0.11), split howls ($P = 0.54$, coefficient = 10.3), or chorus howls ($P = 0.12$, coefficient = 10.9) in regards to error ellipse size for acoustic triangulation with wild wolves and coyotes.

Single-Bearing Error Analysis

Using data collected through our mock howl surveys, we were able to evaluate our bearing error from 226 separate bearings. We calculated a median bearing error of 8.74°; meaning that for any bearing used for triangulation there is a 17.5° error polygon around the bearing (Fig. 3b). The bearing error data had 95% CIs of 63.6°. The mean bearing error was 13.2° (±2.1°, 95% CIs for the mean; SD = 16.3). Of the 226 bearings, 17 of them had a bearing error of >30°, representing only 7.5% of the successful bearings. We also determined a maximum distance of audible howl detection of 1.76 km (0.96–1.76 km; $\bar{x}$ = 1.41 km; $n = 7$).

Bearing error increased with high winds (>8 km/hr; $P = 0.011$, coefficient = 2.3) and with increasing distance between the observer and the howl ($P = 0.001$, coefficient = 0.35). Number of individuals howling ($P = 0.47$, coefficient = 2.1), split howl or not ($P = 0.81$, coefficient = 2.2), and time to response ($P = 0.09$, coefficient = 2.3) did not affect the bearing error (i.e., accuracy).

DISCUSSION

We evaluated the efficacy of acoustic triangulation in a relatively controlled setting. Our results suggest that acoustic triangulation is an accurate, precise, and effective noninvasive monitoring technique for determining location information of howling wolves and coyotes. Precision of acoustic triangulation is comparable to that of VHF radiotelemetry triangulation. Radiotelemetry is a useful tool for intensely monitoring and researching wolves, but is much

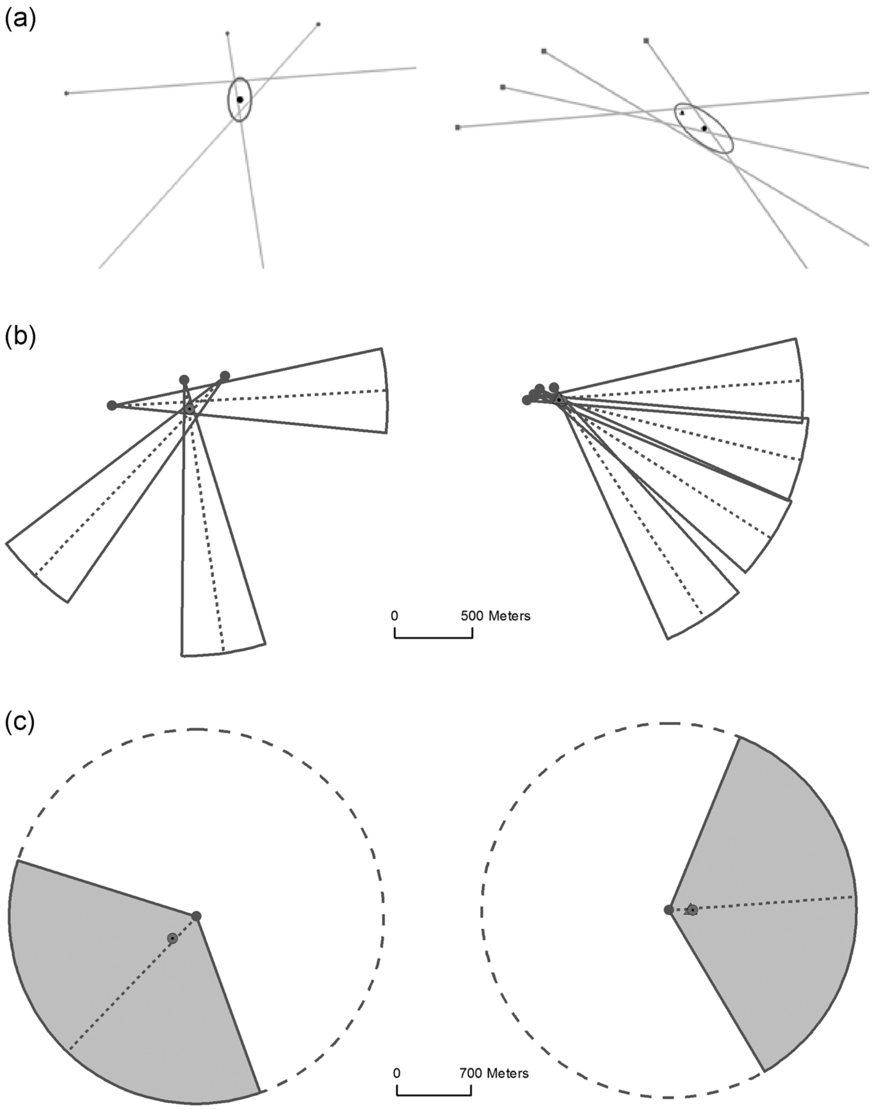

Figure 3. Acoustic triangulation for wild wolves in the field (left figures) and for mock howl surveys (right figures) conducted in northern Wisconsin, USA (2014–2018) from a) Radio Tracker Excel spreadsheet triangulation tool developed by J. Cary at University of Wisconsin-Madison, b) triangulation using multiple bearings with median bearing error of 8.74° to generate an error polygon for each, and c) single bearings ±63.6° (95% CI for data set). All buffers for polygons are based on a maximum audible detection distance of 1.76 km. Black dots are estimated locations, triangles are actual locations, and shaded areas are error polygons.

more invasive (requiring capturing and handling) and costly. Acoustic triangulation is relatively less invasive and can be easily incorporated into existing monitoring strategies to provide additional location information. Acoustic triangulation can be incorporated within existing monitoring techniques (i.e., howl surveys, radiotelemetry) to generate supplemental location information, especially for individuals not being monitored via other technologies.

Acoustic monitoring can be especially helpful for locating rendezvous sites, which will allow researchers to better understand and protect these home sites (Joslin 1967, Harrington and Mech 1982, Bassi et al. 2015, Sazatornil et al. 2016). Generally, such howl surveys will not be as successful in locating den sites used in early spring when response rate by wolves is low (Joslin 1967, Harrington and Mech 1982) and spontaneous howling by adult wolves is at its annual low (McIntyre et al. 2017). The Wisconsin DNR also recommends against howling during the denning period because of low response rates and potential disturbance of wolves at dens (Wiedenhoeft 2014).

We found that distance affected accuracy, precision, and effectiveness of acoustic triangulation. With increasing distance, the ability to triangulate a position and the accuracy and precision of that position information decreased. Lefebvre and Poulin (2003) also found that distance had a negative effect on the ability to adequately triangulate a booming great bittern. Lefebvre and Poulin (2003) concluded that for increased precision, distance between a booming great bittern and the observer should be <200 m. Our data suggest that acoustic triangulation for howling wolves is most precise at distances <1 km from the source. However, acoustic triangulation produced estimated locations with acceptable (i.e., <5,000 m^2) precision for some howls with distances ≥1 km. The maximum distance

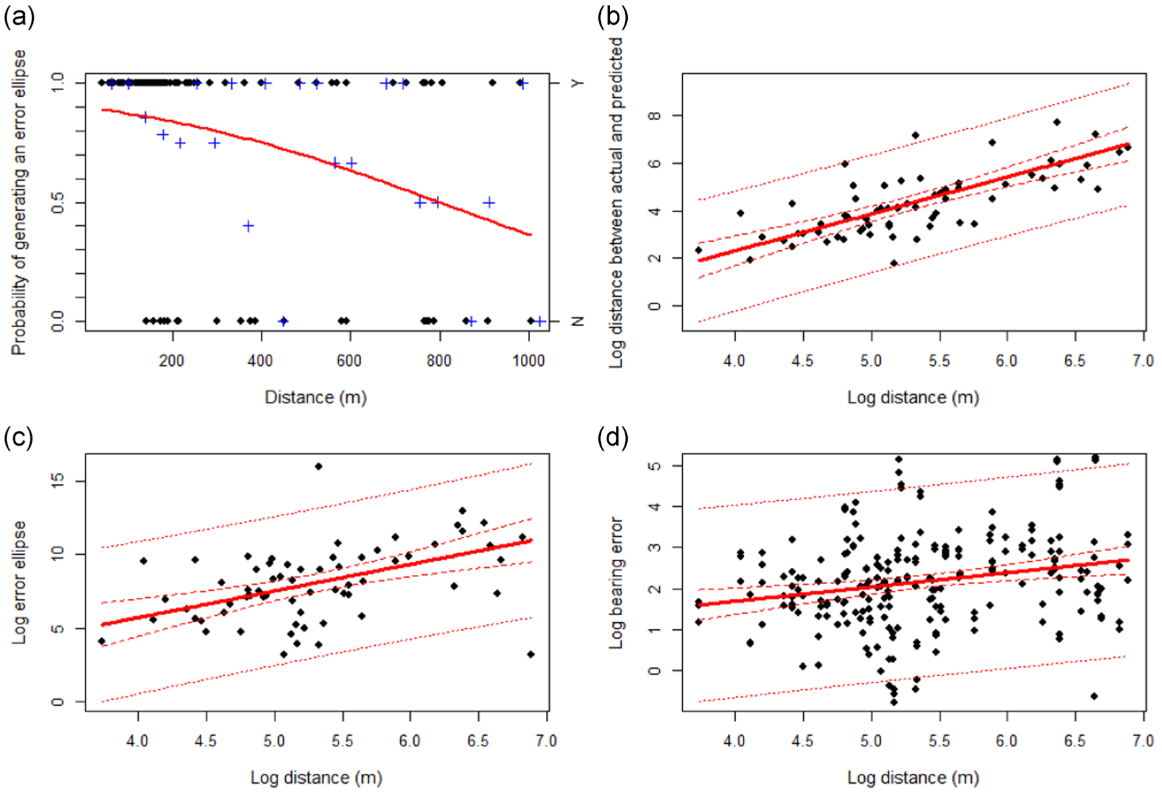

Figure 4. Effect of distance between observer and origin of howl during mock howl surveys conducted in northern Wisconsin, USA, (2014–2018) on a) ability to generate an error ellipse using acoustic triangulation ($P < 0.001$), b) accuracy of acoustic triangulation (i.e., distance between actual and predicted location; $P < 0.001$), c) precision of acoustic triangulation (i.e., error ellipse size; $P = 0.001$), and d) bearing error ($P = 0.004$) for mock howl surveys. Black dots are howls observed during mock howl surveys, blue crosses are predicted points, red line are fit lines based on logistic regression (a) and simple linear regression (b–d), red dashed lines are 95% confidence intervals for best fit line, and red dotted lines are 95% confidence intervals for data points.

of audible anthropogenic howl detection was approximately 1.8 km under optimum conditions. Thus, we recommend that acoustic triangulation be attempted even at distances ≥1 km, but probably not beyond 1.8 km in forested environments with flat to rolling topography. The optimal distance for acoustic triangulation is likely to differ among species based on the characteristics and context of their vocalizations. We believe our findings are most applicable to wild canids, especially gray wolves and coyotes.

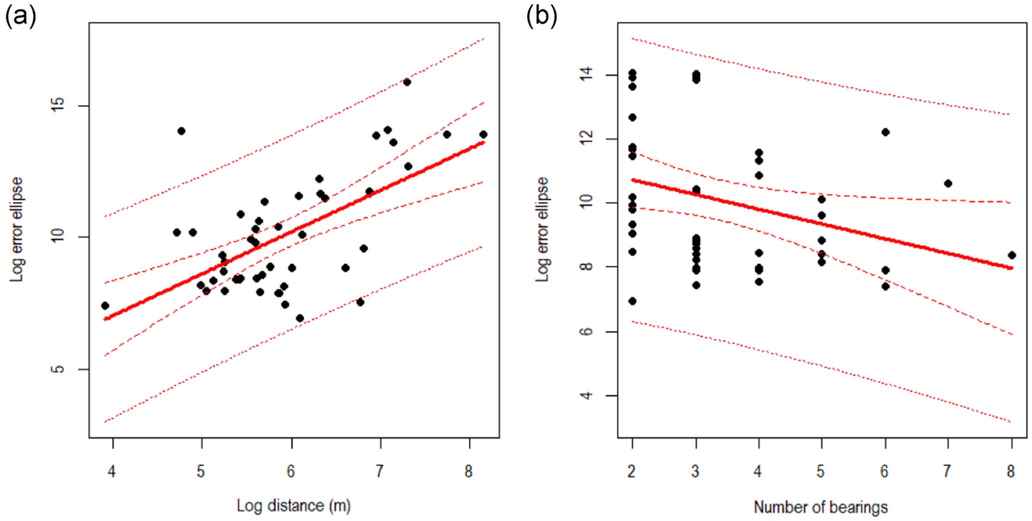

Figure 5. Effects of a) distance between observer and origin of howl ($P < 0.001$) and b) number of bearings ($P = 0.035$) on the precision (i.e., error ellipse size) of acoustic triangulations from modified howl surveys with wild wolves in northern Wisconsin, USA (2014–2018). Black dots are howls observed during howl surveys, red lines are fit line based on simple linear regression, red dashed lines are 95% confidence intervals for best fit line, and red dotted lines are 95% confidence intervals for data points.

Beyond distance, few other factors affected the accuracy or precision of acoustic triangulation. Wind speed has been shown to be an important factor influencing the ability to elicit a howl response (Joslin 1967, Harrington and Mech 1982) and the accuracy of acoustic triangulation (Lefebvre and Poulin 2003). Wind speed had negative effects on the accuracy of acoustic triangulation for our mock howl surveys and our single bearing error. Based on our data, wind speed did not appear to affect the precision of acoustic triangulation, but our data for this test did not span a wide range of wind speeds (0.00–12.87 km/h) because, for howl surveys with wild wolves, we generally selected days with low wind speeds to minimize the effect of wind. Based on our findings and recommendations of Harrington and Mech (1982) and Lefebvre and Poulin (2003), we recommend avoiding high wind (e.g., >12 km/hr) for acoustic triangulation.

Lefebvre and Poulin (2003) found that the occurrence of "poor booms" (i.e., bittern vocalizations that were shorter, anomalous, or unstructured) negatively affected their ability to accurately locate booming great bitterns using acoustic triangulation. Based on our experiences with wild wolves in the field, we expected split howls, lone wolf howls, spontaneous howls, howl responses after long waits, or movements by wolves to lead to less accurate and precise triangulations. Yet, none of these factors were significant predictors of acoustic triangulation efficacy. We did observe that as the number of individuals responding increased, so too did our ability to triangulate a location during mock howl surveys. We have observed howl responses that are less clustered (i.e., pack members spread-out over a larger area). We suggest that researchers attempting to use acoustic triangulation for wolves and other canids be sure to take detailed notes on different characteristics of the howl response (e.g., clustered, spread-out over larger area, split howls).

Lefebvre and Poulin (2003) also found that the number of bearings can affect the precision of acoustic triangulation. We detected a similar effect for acoustic triangulation of wild wolves and coyotes.

We observed a mean bearing error of 13.2° (SD = 16.3) for acoustic triangulation, compared with mean bearing errors of 2.0–8.5° reported by Lefebvre and Poulin (2003). We speculate that a lack of familiarity with a compass, diversity of compass types, variation in declination adjustment, or the presence of metallic objects nearby influenced some of these bearings; thus, our bearing errors likely are greater than what we would expect from trained professionals doing this repeatedly. Thus, we would expect the bearing error of more experienced professionals to be lower than what we report, especially at shorter distances (e.g., Lefebvre and Poulin 2003). Additionally, our bearing errors likely are liberal, which is important because it suggests this technique can be implemented effectively with limited training and that the accuracy and precision of the technique likely is even greater when implemented by more experienced individuals. Using our bearing error and our maximum distance of audible howl detection, others can then generate error polygons for each bearing associated with howl surveys, providing a more refined estimate of wolf or coyote location information even with only 1 or 2 bearings.

We estimated a maximum distance of audible anthropogenic howl detection of 1.76 km and an average up to 1.4 km (0.96–1.76 km; *n* = 7) based on our field tests using simulated howls in ideal conditions. During modified howl surveys with wild wolves, our predicted maximum distance between wolves and the observer was 1.4 km, and error ellipse size increased substantially at distances >1 km. Although on open Arctic tundra, humans can potentially hear wolves as far as 16 km away (Henshaw and Stephenson 1974), in forested environments maximum detection distance is 5–6 km, but normal human hearing is generally ≤3.2 km (Joslin 1967, Harrington and Mech 1982). Fuller and Sampson (1988) conducted howl surveys in Minnesota, USA, near Harrington and Mech's (1982) study area and detected wolf howls up to 2.5 km from wolves, but 88% of responses were from ≤2.0 km. Similarly, in forested habitat, Nowak et al. (2007) found a maximum detection distance of 1.2 km. In Idaho, USA, Ausband et al. (2011) using a broadcast system playing wolf howls, were able to detect howls on average up to 1.6 km in forest and 3.2 km in open meadows. Suter et al. (2016) were able to detect wolves reliably at 3 km using stationary acoustic monitoring devices. Our maximum distance of howl detection was similar to Fuller and Sampson (1988), Ausband et al. (2011), and Nowak et al. (2007) in forested environments. These findings suggest that environment, context, weather, and individual variation likely are important determinants of the maximum detection distance of a wolf howl. It appears that more heavily vegetated, relatively level terrain has a lower maximum detection distance than areas with slightly greater variation in topography or less dense vegetation. Howl surveys in flat to rolling, forested landscapes should generally be conducted at 1.6–3.2-km intervals to avoid missing animals between stops (e.g., Harrington and Mech 1982).

Based on our findings, we are able to make an assumption that the margin of error from our study can be applied to a single bearing taken on any landscape to find a predicted location of an individual that is more refined than a simple buffer around the location of the observer with an unknown buffer distance. By simply applying a measure of bearing error with a known maximum distance of audible howl detection, researchers can generate an error polygon that likely contains the howling wolf(ves). For example, an error polygon generated using the 95% CI of the bearing error data and a maximum distance of 1.76 km should encompass 95% of detected howls, and represent a much smaller area than a simple buffer. Use of multiple bearings can further refine the area of these polygons and generate an estimated location via acoustic triangulation.

We recommend additional research on the efficacy of acoustic triangulation for wolves focusing on the use of stationary acoustic monitoring devices or use of GPS collars. Blumstein et al. (2011) indicate that researchers are already beginning to explore ways of implementing acoustic telemetry using acoustic microphone arrays for studying a variety of wildlife. Ausband et al. (2011) and Suter et al. (2016) have demonstrated the use of acoustic monitoring devices for detecting adult and pup wolves in summer. Such automated devices may reduce risk of disturbance.

MANAGEMENT IMPLICATIONS

Howl surveys, in Wisconsin, are used as an index of pup production and indicators of summer home site locations. Should management agencies desire more specific locations of home site use, acoustic triangulation can be a useful tool. Currently, howl surveys in Wisconsin are conducted by one observer and observers typically only collect a single bearing and an estimated distance for wolf howls (Wiedenhoeft 2014). We recommend that agencies implementing standard howl surveys consider modifying those surveys to support acoustic triangulation. This can be done in 2 relatively cost-effective ways: 1) if multiple trained individuals (i.e., trained volunteers) are available, surveys can be done similar to our modified surveys as described in the methods; or 2) if only 1–2 people are conducting a survey, triangulation might be accomplished by implementing multiple (2–4) additional howl stops within a short distance (0.3–1 km) of a response. These 2 modifications require only subtle changes to howl survey protocol and can be done at minimal additional cost. However, intensively monitoring a wolf pack may disturb wolves; potentially altering response rates or risk abandonment of home sites (Frame et al. 2007, Sazatornil et al. 2016). Efforts should be made to avoid oversampling wolf packs when pups are very young (late spring and early summer). Yet, specific location information may allow managers to better understand wolf distribution, protect home sites, or estimate the rate of movement between home sites. Thus, when the need to more carefully document home site use outweighs potential risk of disturbing wolves, more intense acoustic triangulation could be incorporated into wolf howl surveys. Acoustic triangulation can be a useful tool for wildlife managers and researchers studying vocal, yet cryptic species.

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LITERATURE CITED

Aide, M. T., A. Hernandez-Serna, M. Campos-Cerqueira, O. Acevedo-Charry, and J. L. Diechmann. 2017. Species richness (of insects) drives the use of acoustic space in the tropics. Remote Sensing of Tropical Forest Biodiversity 9:1096.

Ausband, D. E., R. N. Lindsey, E. M. Glenn, M. S. Mitchell, P. Zager, D. A. W. Miller, L. P. Waits, B. B. Ackerman, and C. M. Mack. 2014. Monitoring gray wolf populations using multiple survey methods. Journal of Wildlife Management 78:335–346.

Ausband, D. E., J. Skrivseth, and M. S. Mitchell. 2011. An automated device for provoking and capturing wildlife calls. Wildlife Society Bulletin 35:498–503.

Bassi, E., S. G. Willis, D. Passilongo, L. Mattioli, and M. Apolloini. 2015. Predicting the spatial distribution of the wolf (*Canis lupus*) breeding areas in a mountainous region of central Italy. PLoS ONE 10:e0124698.

Berg, S. S. 2016. Supplementary data for modeling and conservation of wildlife populations in managed landscapes: a trade-off between effort and results. Dissertation, University of Minnesota—Twin Cities, Minneapolis, USA.

Berg, S. S., J. D. Erb, J. R. Fieberg, and J. D. Forester. 2017. Utility of radio-telemetry data for improving statistical population reconstruction. Wildlife Society Bulletin 81:535–544.

Blumstein, D. T., D. J. Mennill, P. Clemins, L. Girod, K. Yao, G. Patricelli, J. L. Deppe, A. H. Krakauer, C. Clark, K. A. Cortopassi, S. F. Hanser, B. McCowan, A. M. Ali, and A. N. G. Kirschel. 2011. Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. Journal of Applied Ecology 48:758–767.

Curtis, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison, USA.

Filibeck, U., M. Nicoli, P. Rossi, and G. Boscagli. 1982. Detection by frequency analyzer of individual wolves howling in a chorus: a preliminary report. Italian Journal of Zoology 49:151–154.

Frame, P. F., H. D. Cuff, and D. S. Hik. 2007. Response of wolves to experimental disturbance at home sites. Journal of Wildlife Management 71:316–320.

Fuller, T. K., and B. A. Sampson. 1988. Evaluation of a simulated howling survey for wolves. Journal of Wildlife Management 52:60–63.

Harrington, F. H., and L. D. Mech. 1982. An analysis of howling response parameters useful for wolf pack census. Journal of Wildlife Management 46:686–693.

Henshaw, R. E., and R. O. Stephenson. 1974. Homing in the gray wolf (*Canis lupus*). Journal of Mammalogy 55:234–237.

Jachowski, D. S., C. A. Dobony, L. S. Coleman, W. M. Ford, E. R. Britzike, and J. L. Rodrigue. 2014. Disease and community structure: white-nose syndrome alters spatial and temporal niche partitioning in sympatric bat species. Diversity and Distributions 20:1002–1015.

Joslin, P. W. B. 1967. Movements and home sites of timber wolves in Algonquin Park. American Zoologist 7:279–288.

Kenaga, B., R. A. Krebs, and W. B. Clapham. 2013. Coyote land use inside and outside urban parks. American Midland Naturalist 170:298–310.

Krofel, M. 2009. Confirmed presence of territorial groups of golden jackals (*Canis aureus*) in Slovenia. Natura Slovenia 11:65–68.

Leblond, M., C. Dussault, and M. H. St-Laurent. 2017. Space use by gray wolves (*Canis lupus*) in response to simulated howling: a case study and a call for further investigation. Canadian Journal of Zoology 95:221–226.

Lefebvre, G., and B. Poulin. 2003. Accuracy of bittern location by acoustic triangulation. Journal of Field Ornithology 74:305–311.

Lyons, J. E., M. C. Runge, H. P. Laskowski, and W. L. Kendall. 2008. Monitoring in the context of structured decision-making and adaptive management. Journal of Wildlife Management 72:1683–1692.

McIntyre, R., J. B. Theberge, M. T. Theberge, and D. W. Smith. 2017. Behavioral and ecological implications of seasonal variation in the frequency of daytime howling by Yellowstone wolves. Journal of Mammalogy 98:827–834.

Mendez-Carvajal, P. 2012. Population study of Cobia howler monkeys (*Alouatta coibensis coibensis*) and Cobia capuchin monkeys (*Cebus capucinus imitator*), Cobia Island National Park, Republic of Panama. Journal of Primatology 1:104.

Mladenoff, D. J., M. K. Clayton, S. D. Pratt, T. A. Sickley, and A. P. Wydeven. 2009. Change in occupied wolf habitat in the northern Great Lakes region. Pages 119–138 *in* A. P. Wydeven, T. R. Van Deelen, and E. J. Heske, editors. Recovery of gray wolves in the Great Lakes Region of the United States: an endangered species success story. Springer, New York, New York, USA.

Mladenoff, D. J., R. G. Haight, T. A. Sickley, and A. P. Wydeven. 1997. Causes and implication of species restoration in altered ecosystems. Bioscience 47:21–31.

Nowak, S., W. Jedrezejewski, K. Schmidt, J. Theuerkauf, R. Myslajek, and B. Jedrzejewska. 2007. Howling activity of free-ranging wolves (*Canis lupus*) in the Bialowieza Primeval Forest and the Western Beskidy Mountains (Poland). Journal of Ethology 25:231–237.

O'Farrell, J. O., and W. L. Gannon. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. Journal of Mammalogy 80:24–30.

Palacios, V., E. Font, E. J. Garcia, L. Svensson, L. Llaneza, J. Frank, and J. V. Lopez-Bao. 2017. Reliability of human estimates of the presence of pups and the number of wolves vocalizing in chorus howls: implications for decision making process. European Journal of Wildlife Research 63:59.

Palacios, V., J. V. Lopez-Bao, C. Fernandez, and E. Font. 2016. Decoding group vocalizations: the acoustic energy distribution of chorus howls is useful to determine wolf reproduction. PLoS ONE 11:e0153858.

Passilongo, D., L. Mattioli, E. Bassi, L. Szabo, and M. Apollonio. 2015. Visualizing sound: counting wolves by using a spectral view of the chorus howling. Frontiers in Zoology 12:22.

Payne, R. S. 1971. Acoustic location of prey by barn owls (*Tyto alba*). Journal of Experimental Biology 54:535–573.

Pedos, J., V. M. F. da Silva, and M. R. Rossi-Santos. 2002. Vocalizations of Amazon River dolphins, *Inia geoffrensis*: insights into the evolutionary origins of delphinid whistles. Ethology 108:601–612.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/. Accessed 14 Apr 2020.

Sazatornil, V., A. Rodríguez, M. Klaczek, M. Ahmadi, F. Álvares, S. Athur, J. C. Blanco, B. L. Borg, D. Cuff, Y. Cortés, E. J. García, E. Geffen, B. Habib, Y. Iliopoulos, M. Kaboli, M. Krofel, L. Llaneza, F. Marucco, J. K. Oakleaf, D. K. Person, H. Potočnik, N. Ražen, H. Rio-Maior, H. Sand, D. Unger, P. Wabakken, and J. V. López-Bao. 2016. The role of human-related risk in breeding site selection by wolves. Biological Conservation 201:103–110.

Stiffler, L. L., J. T. Anderson, and T. E. Katzner. 2018. Evaluating autonomous acoustic triangulation surveying techniques for rails in tidal marshes. Wildlife Society Bulletin 42:78–83.

Stoner, K. E. 1994. Population density of the mantled howler monkey (*Alouatta palliata*) at La Selva Biological Reserve, Costa Rica: a new technique to analyze census data. Biotropica 26:332–340.

Suter, S. M., M. Giordano, S. Nietlispach, M. Apollonio, and D. Passilongo. 2016. Non-invasive acoustic detection of wolves. Bioacoustics 26:237–248.

Thompson, M. E., S. J. Shwager, K. B. Payne, and A. K. Turkalo. 2010. Acoustic estimation of wildlife abundance: methodology for vocal mammals in forested habitats. African Journal of Ecology 48:654–661.

Wiedenhoeft, J. E. 2014. Howl surveys for wolves in Wisconsin. Wisconsin Department of Natural Resources, Park Falls, USA.

Wiedenhoeft, J. E., D. M. MacFarland, N. S. Libal, and J. Bruner. 2018*a*. Wisconsin gray wolf monitoring report 15 April 2016 through 14 April 2017. Bureau of Wildlife Management, Wisconsin Department of Natural Resources, Madison, USA.

Wiedenhoeft, J. E., S. Walter, N. S. Libal, and M. Erick-Pilch. 2018*b*. Wisconsin gray wolf monitoring report 15 April 2017 through 14 April 2018. Bureau of Wildlife Management, Wisconsin Department of Natural Resources, Madison, USA.

Wydeven, A. P., J. E. Wiedenhoeft, R. N. Schultz, R. P. Thiel, R. L. Jurewicz, B. E. Kohn, and T. R. Van Deelen. 2009. History, population growth, and management of wolves in Wisconsin. Pages 87–105 *in* A. P. Wydeven, T. R. Van Deelen, and E. J. Heske, editors. Recovery of gray wolves in the Great Lakes Region of the United States: an endangered species success story. Springer, New York, New York, USA.

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