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Tools and Technology

Testing a New Passive Acoustic Recording Unit to Monitor Wolves

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ABSTRACT As part of a broader trial of noninvasive methods to research wild wolves (*Canis lupus*) in Minnesota, USA, we explored whether wolves could be remotely monitored using a new, inexpensive, remotely deployable, noninvasive, passive acoustic recording device, the AudioMoth. We tested the efficacy of AudioMoths in detecting wolf howls and factors influencing detection by placing them at set distances from a captive wolf pack and compared those recordings with real-time, on-site howling data between 22 May and 17 June 2019. We identified 1,531 vocalizations grouped into 428 vocal events (236 solo howl series and 192 chorus howls). The on-site AudioMoth correctly recorded 100% of chorus and solo howls that were also documented in real-time. The remote array detected 49.5% of chorus and 11.9% of solo howls ($\geq$1 unit detected the event). The closest remote AudioMoth (0.54 km, 0.33 mi) detected 37% of choruses and 8.9% of solo howls. Chorus howls (9.4%) were detected at the farthest unit (3.2 km, 2.0 mi). Favorable wind (carrying source howls to the remote units) and calm (no wind) conditions increased detectability and detection distance of chorus howls. Temperature was inversely related to detection. Given the detection distances we observed, AudioMoths are probably useful in studying specific sites during periods when wolves move less frequently (e.g., during late spring and summer at homesites or potentially during winter at kill sites of very large prey). AudioMoths would also be useful in a passive sampling array (e.g., occupancy studies), especially when used in concert with other methods such as camera-trapping. Additional research should be conducted in areas with different environmental variables (e.g., wind, temperature, habitat, topography) to determine performance under varying conditions and also when fitted with a parabolic dish. © 2020 The Wildlife Society.

KEY WORDS acoustic monitoring, AudioMoth, *Canis lupus*, detection, grey wolf, howl, noninvasive, remote.

Population studies of elusive large carnivores, such as gray wolves (*Canis lupus*), often entail live-capture, radio-collaring, and subsequent aerial tracking (Phillips and Smith 1996, Mech et al. 1998, Mech 2009). This method is especially useful in obtaining information such as winter pack counts, territory size, den and mortality locations, causes of death, predation sites and rates, dispersal, pack formation, etc. (Phillips and Smith 1996, Mech et al. 1998, Mech 2009). In densely forested areas, such as the Superior National Forest (SNF) in northeastern Minnesota, USA, where helicopter darting of wolves is typically not an option, wolves have been captured for radiocollaring via foot-hold trapping since the late 1960s (Mech 2009). However, injuries of varying degree occur with foot-hold trapping as well as captures of nontarget species (Frame and Meier 2007). Consequently non-invasive methods (such as scat or hair genetic surveys and camera-trapping; Galaverni et al. 2012) are preferred (Long et al. 2012).

Monitoring wild wolves via relatively noninvasive howl surveys has long been practiced (Joslin 1967, Harrington and Mech 1982, Fuller and Sampson 1988, Thiel et al. 2009). Such surveys consist of a biologist howling and waiting for a response from wild wolves (Joslin 1967, Harrington and Mech 1982, Fuller and Sampson 1988). This technique is generally not suitable for obtaining precise counts of wolves within a pack (Harrington 1975;

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Harrington and Mech 1979, 1982), but is useful for detecting successful reproduction (presence of pups; Palacios et al. 2016) and for locating packs in relatively small areas (Harrington and Mech 1982, Fuller and Sampson 1988).

Gable et al. (2018) recently demonstrated that wild wolf summer homesites could be reliably monitored by understanding how frequently and how far wolves move homesites, and by incorporating observer error when triangulating wolf howls (see also O'Gara et al. 2020). Advances have also been made in the remote monitoring of wild wolves via acoustic units. Howlboxes (self-contained, automated, simulated-howl broadcasting and recording devices; Ausband et al. 2009, 2011) have been successfully used to remotely monitor summer wolf rendezvous sites and confirm reproduction through the detection of pup howls (Ausband et al. 2009, 2011). Howlboxes were less effective in detecting wolves during winter (likely because of the greater mobility of wolves during that season). Nevertheless, researchers concluded Howlboxes may be useful to aid in snow-tracking by attracting wolves in areas with overlapping pack territories (Brennan et al. 2013). Differences in the arrival times of howls at various remote recording devices were used to determine the locations of wolves in Yellowstone National Park (Kershenbaum et al. 2019). Researchers in Italy used SM3 SongMeters (Wildlife Acoustics, Inc., Maynard, MA, USA) to detect wild wolves (Suter et al. 2016). Others in France trialed a passive acoustic microphone array suitable for monitoring large-scale wolves recolonization dynamics using the same device with synthetic sounds (not real-time wild wolf howls; Papin et al. 2018). In northern Alberta, Canada, researchers compared detectability and occupancy estimates of wolves from remote camera traps with those from autonomous recording units (ARUs) and found ARUs were comparable to camera traps even though the ARUs only operated for 3% of the time the cameras were active (Garland et al. 2020).

Furthermore, advances in the analysis of wolf howls have yielded additional insights into the complexity of howls. Analyses of wolf howls have shown that wolves display individual variation in howl characteristics (e.g., fundamental frequency; Tooze et al. 1990); individual wild eastern grey wolves (*C. l. lycaon*) can be identified (Root-Gutteridge et al. 2014); and wolves may recognize one another by their distinct howls (Palacios et al. 2007, 2015). The complexity and distinctiveness of wolf howls and our increasing ability to record and analyze them suggests that wolf howls may be used to identify and precisely count the number of wolves within a wild pack (Root-Gutteridge et al. 2014, Rocha et al. 2015, Palacios et al. 2016).

As part of a broader trial of noninvasive methods to research wild wolves in the SNF, we were interested in whether wolves could be remotely monitored *in situ* using an ARU, specifically, the AudioMoth (Hill et al. 2018, 2019)—newly available, inexpensive, and remotely deployable. We were interested in AudioMoths as recording devices because they are much cheaper (<US$100/device) and more mobile (approximately the size of a deck of playing cards) than other ARUs (e.g., Howlboxes, SongMeters [Wildlife Acoustics, Inc.]), resulting in the potential to deploy a greater number of units simultaneously in the field (Hill et al. 2018, 2019). AudioMoths have been used to monitor species such as the New Forest cicada (*Cicadetta montana*) and events such as gunshots (potentially related to poaching) in a tropical forest in Belize (Hill et al. 2018). To our knowledge, no publications exist regarding use in studying wolves. We tested their efficacy in detecting wolf howls and identified factors that influence detection by placing AudioMoths at set distances from captive wolves situated near the SNF, where the ages, sexes, and demographic statuses of the wolves were known and where real-time howling data could be checked against the AudioMoth-generated audiofiles.

STUDY AREA

Source howls originated from socialized, captive wolves housed at the International Wolf Center (IWC) in Ely, Minnesota (Fig. 1). Wolf management at the IWC was authorized under the U.S. Department of Agriculture Animal and Plant Health Inspection Service Exhibit Permit number 41-C-0077. Animal handling protocol, including noninvasive research procedures, was under the guidelines of the Animal Welfare Act and detailed in the IWC's Wolf Care manual.

The captive wolves included 6 males and 1 female ranging in age from 3 to 15 years. Four wolves were housed in the main outdoor exhibit enclosure (approx. 5,735 m^2) and 3 other wolves were maintained in an immediately adjacent, off-exhibit, outdoor habitat enclosure (approx. 678 m^2). Surrounding the enclosure perimeter was a thick plasticized-fabric border that reached to the top of the fencing to minimize stress for the wolves and outside-enclosure interactions with other animals. The enclosure area was situated near the top of a hill and included a slope up toward where we remotely deployed AudioMoths (Fig. 1). Some areas in the enclosure sloped gently downhill away from the remote recorders, so some of our results may reflect variations in conditions that field researchers may also encounter. We presumed that in field situations where the source howl is elevated relative to the remote recorders, detection distance should be greater (all else being equal) when compared with our results.

We deployed AudioMoths in the Superior National Forest, Minnesota, USA (48°N, 92°W; see Nelson and Mech 1981 for a detailed description) within 3.2 km (2.0 mi) of the IWC (Fig. 1). Elevations ranged from 325 m to 700 m above sea level and included swamps, uneven upland, and rocky ridges (Mech 2009). Vegetation was mostly conifers (e.g., jack pine [*Pinus banksiana*], white pine [*P. strobus*], red pine [*P. resinosa*], black spruce [*Picea mariana*], white spruce [*P. glauca*], balsam fir [*Abies balsamea*], white cedar [*Thuja occidentalis*], and tamarack [*Larix laricina*]) in the forest overstory and was interspersed with white birch (*Betula papyrifera*) and quaking aspen (*Populus tremuloides*) as a result of logging and fires

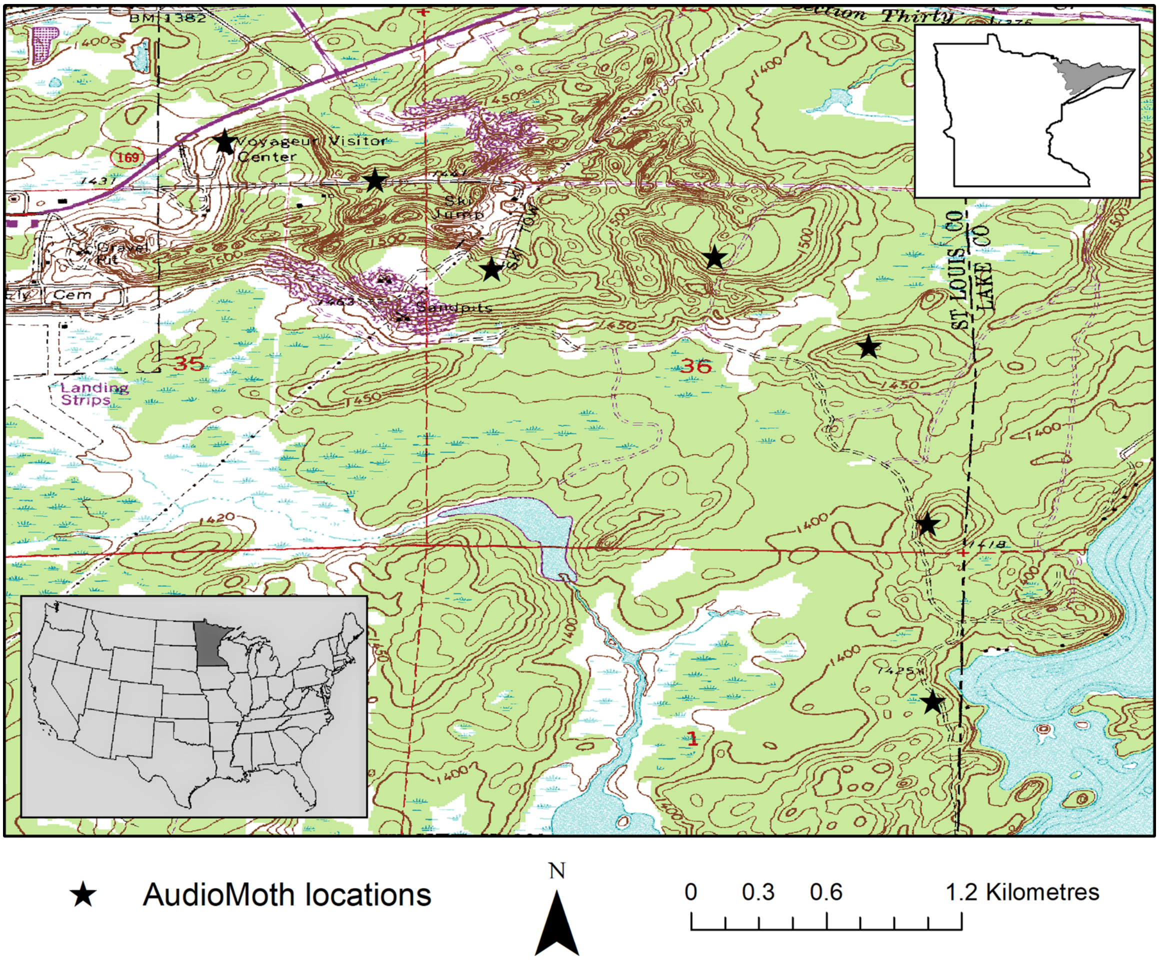

Figure 1. Locations of AudioMoths (black stars) at the International Wolf Center, Ely, Minnesota, USA (labeled Voyageur Visitor Center on the map), and remotely deployed during 22 May–17 June 2019 in the Superior National Forest, Minnesota. Insets depict the location of Minnesota, USA (lower left) and the northeast region of Minnesota (upper right) where our study area was located.

(Mech 2009; see Heinselman 1993 for a detailed description). Temperatures in late May–mid-June 2019 (during the period we recorded howls) ranged from −1° C to 30° C, and average 24-hour temperatures were generally between 7° C and 15° C.

METHODS

We deployed 7 AudioMoths (version 1.1.0) from 22 May to 17 June 2019. We used the AudioMoth Configuration App to set the sample rate to 8 kHz, gain at highest level, sleep duration at 0 seconds, and recording duration at 3,600 seconds. These settings allowed round-the-clock recording, resulting in hourly files sized up to 55 MB each, totaling approximately 1,318 MB/day. We also enabled LED, low-battery cutoff, and battery-level indication. Under these conditions, battery usage each day was predicted to be 252 milliamp hours, indicating that the 3 lithium batteries in each AudioMoth should last 14 days.

We placed one AudioMoth immediately near the captive wolf enclosures facing the center of the enclosure area. This device was at a distance of 0 km (≤100 m relative to the farthest location a captive wolf could be howling within the enclosure) from the source howls. We placed 6 additional AudioMoths at approximately 536-m (0.33-mi) intervals out to a distance of 3.2 km (2.0 mi). Land access limitations dictated that we deploy the AudioMoths in an ESE direction from the IWC (Fig. 1). We selected elevated areas at each deployment distance. We oriented AudioMoths with their microphones facing the IWC and fixed them to tree trunks at approximately 1.5–2 m above ground. To protect the AudioMoths from moisture, we sealed them inside a Ziploc© (S. C. Johnson & Son, Inc., Racine, WI, USA) baggie and used removable zip ties to hold the bagged AudioMoth to the tree (Fig. 2; Hill et al. 2018). After our study, waterproof cases for AudioMoths became available (https://www.openacousticdevices.info/case, accessed on 6 Jun 2020).

To test the efficacy of AudioMoth detection of wolf howls when distance is 0 km, staff and volunteers at the IWC documented in real-time when they heard a captive wolf or wolves howling and the general wind and weather conditions at the time. These observations were bounded by staff presence, occurring from roughly 0700 hours to 1730 hours daily. When possible, howls were also verified by surveillance video. We compared a sample (6 randomly chosen days) of these real-time notes with the audiofiles

Figure 2. AudioMoth deployed in the Superior National Forest, Minnesota, USA, during 22 May–17 June 2019.

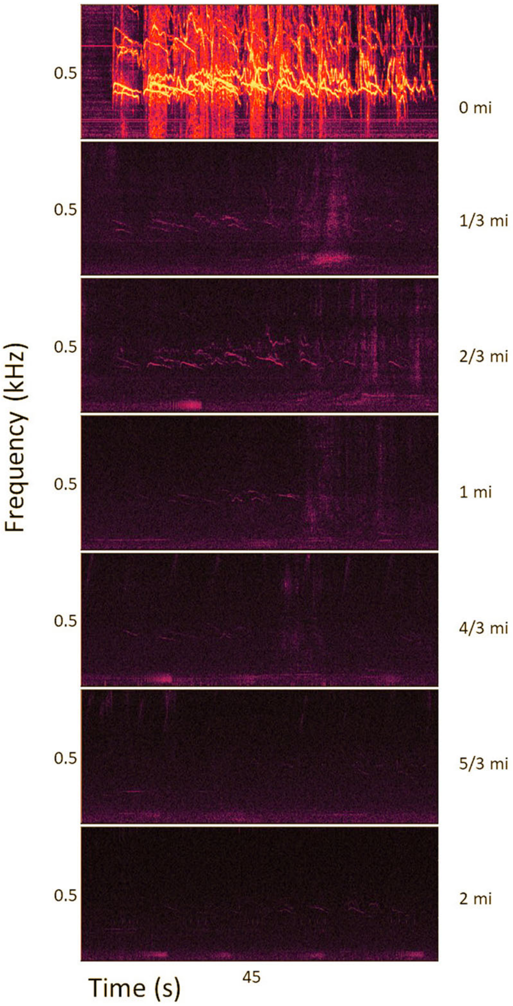

Figure 3. Spectrograms generated in Adobe Audition CS6 (Adobe Systems, San Jose, CA, USA) of a chorus howl recorded by AudioMoths detected on 30 May 2019 at specified distances (0, 1/3, 2/3, 1, 4/3, 5/3, 2 mi = 0.54, 1.07, 1.61, 2.15, 2.68, and 3.21 km, respectively) from the source howl at the International Wolf Center, Ely, Minnesota, USA. Winds were favorable (from the northwest, categorized as west per our methods), wind speed was 4.8 km/hour (3.0 mi/hr) and the temperature was 5.6° C (42° F).

from the AudioMoth deployed at the IWC to assess the ability of AudioMoths to detect solo and chorus howls in the immediate area of wolves.

We used Kaleidoscope Pro 5.1.9 g (Wildlife Acoustics 2017) to select audiofiles that contained wolf vocalizations from the IWC AudioMoth (signal detection parameters: frequency range = 300–1,000 Hz, length of detection = 3–20 sec, maximum inter-syllable gap = 1 sec). We then examined the selected audiofiles to audibly identify wolf vocalizations that included howls emitted by one individual (solo) and choruses (>1 individual vocalizing simultaneously). We grouped vocalizations into vocal events based on the silence interval between 2 consecutive vocalizations. We grouped all consecutive vocalizations with silence intervals <60 seconds as one event. This included solo howl series (one to several howls emitted by one individual) and chorus howls (events that also could include solo howls when the silence interval between the vocalizations was <60 sec). To compare detection of the vocal events recorded by the IWC AudioMoth with those at the remotely deployed AudioMoths, we visually inspected the audiofile spectrograms (Fig. 3) and audibly confirmed vocalizations in Adobe Audition CS6 (Adobe Systems, San Jose, CA, USA) and Audacity 2.3.2 (https://www.audacityteam.org/, accessed 4 Aug 2020).

Weather data for 22 May–17 June 2019 were gathered by the KELO automated station (Ely, MN), http://www.wunderground.com/history/ (accessed 1 Nov 2019). We used hourly weather data (the highest temporal resolution available) to approximate the weather conditions (wind direction, wind speed, temperature, and humidity) when source howls were emitted. Wind direction in our models is relative to the approximate line of AudioMoths heading east–southeast away from the IWC (i.e., wind direction is not relative to the actual map direction the winds came from). We shifted the wind direction in our analysis so we could more easily identify the importance of wind direction relative to the AudioMoths (vs. relative to a map). Thus, west wind in our analysis refers to winds that actually came from west–northwest relative to a map. We included in our models the variable wind condition with 3 categories: calm wind (i.e., no wind), winds that came from the west relative to the line of remote AudioMoths (likely favorable wind), and winds from other directions.

Wind speed has been reported to affect the reply rate of wild wolves (Harrington and Mech 1982) and howl surveys are preferably done when wind speeds are minimal (Gable et al. 2018). Thus, we assessed wind speed as a continuous covariate potentially affecting detectability. We also speculated that wind blowing source howls toward AudioMoths would increase detectability, whereas wind blowing source howls away would decrease detectability. Additionally, we hypothesized that increased distance to the source howl and hourly temperature would decrease detectability (Wiley and Richards 1978). Further, we hypothesized that increased humidity (moist air; Wiley and Richards 1978), longer howls, and chorus howls (more than one wolf) would increase detectability.

We used generalized linear models (GLM) with the binomial family to assess variables (weather variables, time of day, and type of howl) hypothesized to affect detectability of wolf vocal events at the closest remote AudioMoth (0.54 km, 0.33 mi). Similarly, we used GLM with the Poisson family to assess whether these variables affected the detection distance (the farthest AudioMoth that detected the howl out of the 6 remotely deployed). We only allowed variables that were not correlated ($|r| < 0.50$) to be assessed at the same time in the GLM and assessed leverage and Cook's Distance (values <0.2 indicated acceptable influence) to examine the effects of potential outliers on the outcome of the regression. We considered statistical tests significant at $\alpha = 0.05$. We conducted all statistics in Program R version 3.1.3 (R Core Team 2015).

Time of day is often correlated with temperature and humidity (Wiley and Richards 1978). In our experiment, we also considered it a potential influence on howling rates because of the IWC wolf viewing hours and staff interaction with wolves. We measured whether wolves howled more when the IWC was open versus closed. If the wolves howled more when the IWC was open (during typically warmer daytime weather conditions), or if they howled facing the exhibit viewing windows (away from the remotely deployed AudioMoths) more frequently during the day, we hypothesized that could reduce detectability.

RESULTS

We identified 1,531 vocalizations during the 25 24-hour periods and 2 partial days (days AudioMoths were deployed and retrieved from the field). We grouped these into 428 vocal events: 236 solo howl series and 192 chorus howls.

All solo and chorus howls recorded by IWC staff and volunteers on a randomly selected 6-day sample were successfully recorded by the IWC AudioMoth. Relative to the AudioMoth at the IWC, 49.5% of choruses and 11.9% of solo howls were detected by the remote array (vocalization detected by ≥1 remote AudioMoth). The closest remote AudioMoth (0.54 km, 0.33 mi) detected 37.0% of choruses and 8.9% of solo howls relative to the detections on the IWC AudioMoth, while the farthest (3.2 km, 2.0 mi) detected none of the solo howls and 9.4% of choruses (Table 1).

Initial analyses indicated wind speed ($\bar{x} = 6.6$ km/hr or 4.1 mi/hr, range = 0–29 km/hr or 0–18 mi/hr) was not influential and including it as a variable decreased the coefficient of determination (R^2), so we excluded it from additional models. We also determined that temperature and time of day were correlated (Spearman's rank correlation, $r = 0.60$, $P \leq 0.001$), so only temperature was allowed to remain in the models because we were most interested in factors affecting sound transfer across distance to the AudioMoths. We also removed humidity from the models because this variable was not influential and was inversely correlated to temperature (Pearson's correlation, $r = -0.70$, $P \leq 0.001$). Additionally, preliminary models indicated that the type of howl (solo or chorus) was the most influential variable affecting detectability (≥1 remote AudioMoth detecting the event; β estimate = −2.64, $P \leq 0.001$) and the number of remote AudioMoths that detected the event (e.g., approximate proxy for distance detected; β estimate = −2.14, $P \leq 0.001$). Therefore, we conducted further analyses grouped by the type of howl (solos and choruses) to more readily examine the mechanisms relating to successful AudioMoth detection of vocal events.

Wind condition and temperature were significant factors affecting chorus howl detectability at the closest AudioMoth and distance of detection (Table 2). Highest detection rates (≥1 recorder detected the chorus) were achieved with favorable winds carrying the source howl to the detectors and in calm (no wind) conditions (Fig. 4A,B). For solo howls, temperature and duration of the vocal event were significant factors affecting detectability at the closest AudioMoth and detection distance (Table 3). The few solo howls detected by ≥1 remote AudioMoth were those emitted under calm (no wind) conditions or with winds from the west (Fig. 4B). More choruses and solo howls were detected when the IWC was closed than open (Fig. 4C,D), but the period when the IWC was closed was also generally correlated with lower

Table 1. Proportion of chorus ($n = 192$) and solo ($n = 236$) howls from captive wolves detected at remotely deployed AudioMoths based on distance from the International Wolf Center, Minnesota, USA, 22 May–17 June 2019.

	Chorus howls		Solo howls	
AudioMoth	**Detected %**	**Undetected %**	**Detected %**	**Undetected %**
0.54 km (0.33 mi)	37.0	63.0	8.9	91.1
1.07 km (0.67 mi)	28.1	71.9	5.0	95.0
1.61 km (1.00 mi)	30.7	69.3	3.4	96.6
2.15 km (1.33 mi)	23.4	76.6	3.0	97.0
2.68 km (1.67 mi)	16.1	83.9	1.3	98.7
3.21 km (1.99 mi)	9.4	90.6	0.0	100.0

Table 2. Parameters and significant ($P \leq 0.05$) fixed effects in the generalized linear models of chorus howl detectability ($R^2 = 0.21$) and detection distance ($R^2 = 0.29$) at the International Wolf Center, Minnesota, USA, 22 May–17 June 2019.

	Detectability at closest AudioMoth				Detection distance			
Factor	**Estimate**	**SE**	***z***	***P*-value**	**Estimate**	**SE**	***z***	***P*-value**
Intercept	3.523	1.008	3.494	≤0.001	2.295	0.406	5.656	≤0.001
WC: favorable west wind[a]	1.044	0.452	2.308	0.02	0.379	0.181	2.088	0.038
WC: wind from other directions[a]	−0.679	0.45	−1.51	0.131	−1.036	0.262	−3.953	≤0.001
Temperature	−0.078	0.02	−3.915	≤0.001	−0.031	0.008	−3.766	≤0.001
Duration	−0.002	0.002	−0.691	0.49	−0.0003	0.001	−0.258	0.797

[a] Wind conditions (WC) were calm wind, favorable west wind, and wind from other directions.

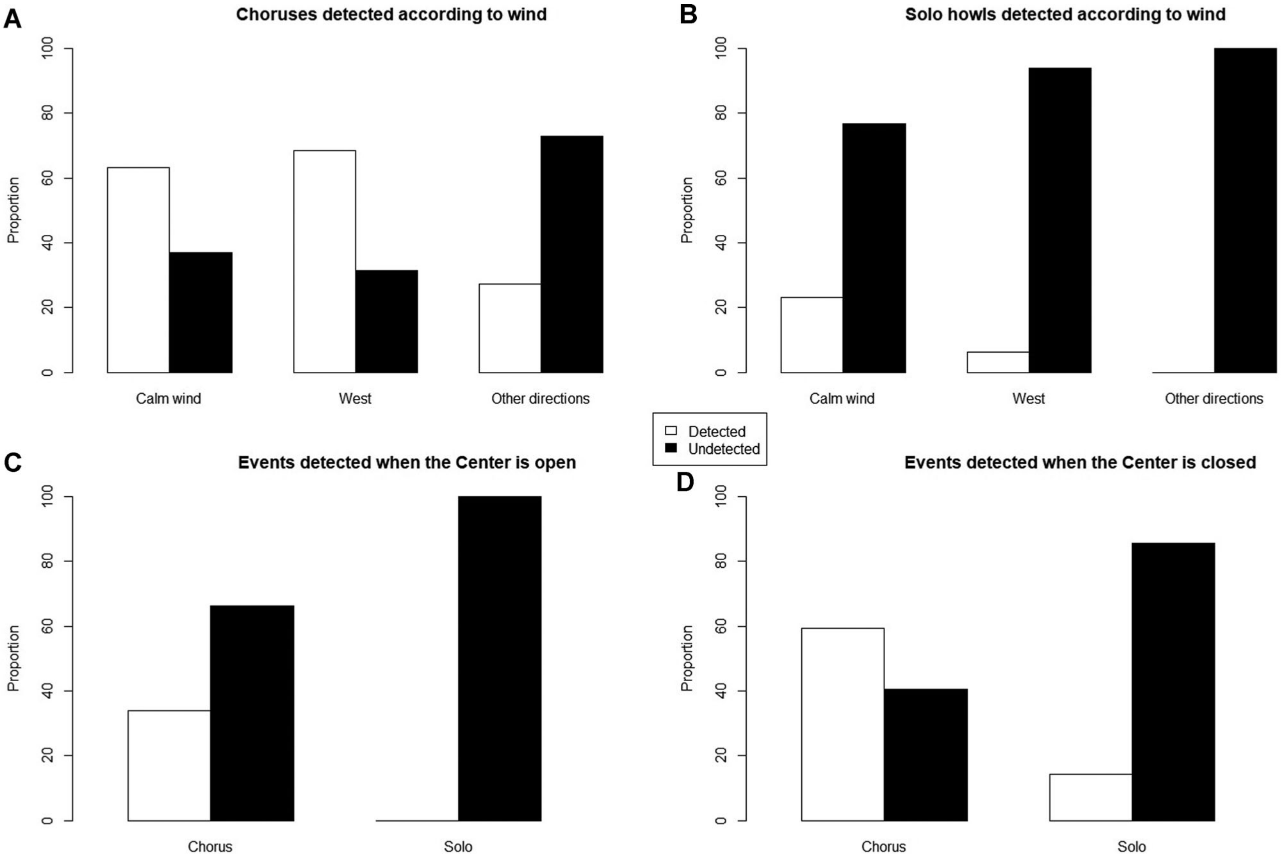

Figure 4. A) Chorus howls detected according to wind presence and direction by the remote array (≥1 remote AudioMoth detected the event) in the Superior National Forest, Minnesota, USA, during 22 May–17 June 2019. Wind conditions for chorus howls were calm ($n = 57$), winds from the west ($n = 54$), and winds from other directions ($n = 81$). B) Solo howls detected according to wind presence and direction by the remote array (≥1 remote AudioMoth detected the event) in the Superior National Forest, Minnesota, during 22 May–17 June 2019. Wind conditions for solo howls were calm ($n = 104$), winds from the west ($n = 65$), winds from other directions ($n = 67$). C, D) Proportion of chorus and solo howls from captive wolves detected by the remote array (≥1 remote AudioMoth detected the event) relative to the International Wolf Center, Minnesota, being open (Fig. 4C; chorus [$n = 74$] and solo howls [$n = 40$]) or closed (Fig. 4D; chorus [$n = 118$] and solo howls [$n = 196$]), 22 May–17 June 2019.

Table 3. Parameters and significant ($P \leq 0.05$) fixed effects in the generalized linear models of solo howl detectability ($R^2 = 0.31$) and detection distance ($R^2 = 0.42$) at the International Wolf Center, Minnesota, USA, 22 May–17 June 2019.

	Detectability at closest AudioMoth				Detection distance			
Factor	**Estimate**	**SE**	***z***	***P*-value**	**Estimate**	**SE**	***z***	***P*-value**
(Intercept)	4.761	1.572	3.028	0.002	3.982	0.651	6.118	≤0.001
WC: favorable west wind[a]	−0.13	0.787	−0.162	0.872	−0.282	0.348	−0.812	0.417
WC: wind from other directions[a]	−16.79	1947	−0.009	0.993	−16.668	994	−0.017	0.987
Temperature	−0.19	0.047	−4.001	≤0.001	−0.14	0.019	−7.196	≤0.001
Duration	0.011	0.003	3.259	0.001	0.008	0.001	6.456	≤0.001

[a] Wind conditions (WC) were calm wind, favorable west wind, and wind from other directions (Note: quasi-complete separation in the response variable occurred with the wind from other directions category as no solo howls were detected).

daily temperatures (a variable that was significant in our GLMs analyses). Temperature was inversely related to detection (i.e., decreased temperature related to increased detection).

DISCUSSION

The AudioMoth close to the vocalization source (<100 m) was 100% successful in detecting both solo and chorus howls. Half of the choruses were detected by the remote array (vocalization detected by ≥1 AudioMoth). The nearest AudioMoth in the array (0.54 km, 0.33 mi) detected 8.9% of solo and 37% of chorus howls—but note that some vocalizations missed by this unit were detected by the next farther unit. Some choruses (9.4%) were even detected at our most remote AudioMoth (3.2 km, 2.0 mi), which is farther than the mean distance wolf howls could be heard by humans (2 km, 74 trials) in Minnesota (Fuller and Sampson 1988). Using SM3 SongMeter devices, Suter et al. (2016) detected human-simulated howling harmonics on a spectrogram to a distance of >3 km, with traces of the howls visible on a spectrogram at 4.6 km. The potential to increase detection distance by fitting a parabolic dish around an AudioMoth is being evaluated by nocturnal-bird migration researchers (https://nocmig.com/audiomoth; accessed 25 Mar 2020). Presumably, any detection distance increase would be directional with a potential reduction in detection from the opposite direction. Directionality would be ideal if surveying a known location (e.g., a rendezvous site), but less desirable in a broader survey.

We suspect that because our first remote AudioMoth (0.54 km, 0.33 mi) was situated near a gravel road (increased background noise), some choruses were not detected on that device although they were captured on the next farther AudioMoth at 1.1 km (0.7 mi). This result demonstrates the importance of situating the AudioMoths to minimize other possible sounds in the area. Studies in more ideal field conditions than the varying topography in our study area and upsloping landscape at the IWC may find greater detection rates at distance than we did. Unfortunately, mainly as a result of land access issues, we were unable to deploy multiple AudioMoths at similar distances at different locations from the IWC. Thus, we are not able to provide information on expected variability in detection rates at a given distance (i.e., our sample size at each distance = 1).

In addition to distance from the source, wind direction was also important to detection of chorus howls. To minimize detectability issues with distance and wind, ARUs should be arranged to surround reliable wolf locations (e.g., homesite, kill site, etc.) and placed as close as possible to the source howls but at a distance that does not disturb the wolves and cause them to alter their current or future behavior (e.g., such as relocating or using different travel paths). Ideally, some ARUs should also be spread wider to achieve greater coverage to detect wolves as they make small movements around homesites and kill sites.

Temperature inversely affected detection, as expected, given the mechanics of sound transfer (Wiley and Richards 1978). Higher temperatures were negatively correlated with humidity, and dry air absorbs more sound (increases sound attenuation) than moist air (Wiley and Richards 1978). Temperature's significance in the models could also be in part due to its correlation with time of day (when the IWC was open or closed) and wind speed (generally peaks midday when temperature is higher as well).

Although not a specific objective of our study, we confirmed that wild wolves including pups are detectable by AudioMoths at the configuration settings we used. At our most distant AudioMoth (which happened to be situated in part of a wild wolf pack's territory), wild wolf chorus howls including pups (based on their higher pitched vocalizations; Palacios et al. 2016) were opportunistically recorded.

Similar to other studies that use ARUs, a primary challenge was data storage and transfer. Continuous 24-hour audiofiles over >25 days required us to use external hard drives to store, back up, and share data. Another logistical constraint was the batteries had to be replaced every 14 days (when set to record continuously). This can be limiting if AudioMoths are at remote locations or if there are many simultaneously deployed. Further, whenever batteries are replaced, the AudioMoth must be reprogrammed. Thus, the researcher must either bring into the field a separate preprogrammed AudioMoth (with fresh batteries) to swap out, or a laptop, etc. to reprogram the previously deployed AudioMoth when replacing batteries. Although an external battery can be attached to the AudioMoth (after modification) to extend battery life (Hill et al. 2019; section 5.3), that could significantly alter the ease of remote field deployments of multiple units.

Given the minor challenges encountered, we conclude that AudioMoths are useful for monitoring wolves at specific sites and also for wider surveys. Based on the detection distances we observed (deployed without parabolic dishes), monitoring specific sites will be most effective during periods when wolves move less frequently (e.g., during late spring and summer). AudioMoths may be used near homesites to confirm reproduction and document pup persistence (Palacios et al. 2016), even if the exact location of the homesite is not known. Rigorous individual identification of wild wolves by their vocalizations is very complex (Palacios et al. 2007, Root-Gutteridge et al. 2014), and not all wolves are always present at homesites; therefore, it will likely still prove challenging to obtain precise pack counts, at least in the foreseeable future. Nevertheless, AudioMoths are a reasonable alternative to determine an estimated pack size at homesites, when scats for genetics either cannot be collected because of land access restrictions or because the precise location of the homesite is unknown, when the genetic sample size will be insufficient on account of rapid scat degradation in certain environments (Stenglein et al. [2011] reported that 50 noninvasive genetic samples from rendezvous site areas detected 65–100% of pack members, 100 samples detected 90–100%, and 150 samples detected 100%), or when the budget does not allow for analyzing sufficient scats.

AudioMoths can record continuously and do not rely on responses to simulated howling, so researchers also can examine natural howling rates (and changes over time) at homesites. Wolves sometimes reuse homesites from prior years, therefore, it may be possible to deploy AudioMoths at multiple homesites so data are more seamless when wolves move homesites, which can be fairly frequent (Gable et al. 2018). If AudioMoths are used to comparatively assess howling rates, pack size should be accounted for because chorus howls were detected more often than solo howls and chorus howls would presumably be more likely in a larger pack (at least to an extent). Furthermore, when comparing howling rates among studies, environmental factors of each study area must be considered because detectability will most likely differ among sites (e.g., topography, habitat, temperature, wind regimes; Wiley and Richards 1978).

Increased mobility of wolf packs when not using spring and summer homesites means that opportunistic monitoring of specific sites during winter may be most effective at kill sites of large prey where wolves spend more time. Batteries sometimes lose charge more rapidly in cold temperatures, so we tested one AudioMoth (using the same settings) deployed during 5–18 February 2020 when ambient temperatures reached a maximum of −1.1° C (30° F) and minimum of −34° C (−29° F). The unit did not exhibit any battery issues and the correct number of files were recorded.

Some chorus howls were detected by AudioMoths as far away as 3.2 km (2.0 mi), so AudioMoths could be used any time of the year to monitor multiple packs simultaneously in a wider sampling array (Papin et al. 2018). Similar to other ARUs, AudioMoths would be effective in occupancy studies, especially if used in concert with other noninvasive tools such as camera-trapping (Harrington and Mech 1982, Garland et al. 2020). Our detectability findings are directly relevant to occupancy studies in distinguishing between nondetection and absence of wild wolves (i.e., probability of detection). For additional details regarding survey designs for terrestrial acoustic monitoring, we refer readers to Sugai et al. (2019). We suggest additional research be conducted in areas of different environmental variables (e.g., wind, temperature, habitat, topography; Wiley and Richards 1978) to determine the AudioMoth's performance under varying conditions and also when fitted with a parabolic dish.

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LITERATURE CITED

Ausband, D. E., M. S. Mitchell, A. Mynsberge, C. M. Mack, J. Stenglein, and L. Waits. 2009. Developing wolf population monitoring techniques: a cooperative research effort between University of Montana, Nez Perce Tribe, University of Idaho, Idaho Department of Fish and Game, Montana Fish, Wildlife and Parks, and U.S. Fish and Wildlife Service. Final Report. University of Montana, Missoula, USA.

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.

Brennan, A., P. C. Cross, D. E. Ausband, A. Barbknecht, and S. Creel. 2013. Testing automated howling devices in a wintertime wolf survey. Wildlife Society Bulletin 37:389–393.

Frame, P. F., and T. J. Meier. 2007. Field-assessed injury to wolves captured in rubber-padded traps. Journal of Wildlife Management 71:2074–2076.

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

Gable, T. D., S. K. Windels, and J. K. Bump. 2018. Finding wolf homesites: improving the efficacy of howl surveys to study wolves. PeerJ 6:e5629.

Galaverni, M., D. Palumbo, E. Fabbri, R. Caniglia, C. Greco, and E. Randi. 2012. Monitoring wolves (*Canis lupus*) by non-invasive genetics and camera trapping: a small-scale pilot study. European Journal of Wildlife Research 58:47–58.

Garland, L. A., A. Crosby, R. Hedley, S. Boutin, and E. M. Bayne. 2020. Acoustic vs photographic monitoring of wolves: a methodological comparison of two passive monitoring techniques. Canadian Journal of Zoology 98:219–228.

Harrington, F. H. 1975. Response parameters of elicited wolf howling. Dissertation, State University of New York, Stony Brook, USA.

Harrington, F. H., and L. D. Mech. 1979. Wolf howling and its role in territory maintenance. Behaviour 68:207–249.

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

Heinselman, M. 1993. The Boundary Waters wilderness ecosystem. University of Minnesota Press, Minneapolis, USA.

Hill, A. P., P. Prince, E. P. Covarrubias, C. P. Doncaster, J. L. Snaddon, and A. Rogers. 2018. AudioMoth: evaluation of a smart open acoustic device for monitoring biodiversity and the environment. Methods in Ecology and Evolution 9:1199–1211.

Hill, A. P., P. Prince, J. L. Snaddon, C. P. Doncaster, and A. Rogers. 2019. AudioMoth: a low-cost acoustic device for monitoring biodiversity and the environment. HardwareX 6:e00073.

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

Kershenbaum, A., J. L. Owens, and S. Waller. 2019. Tracking cryptic animals using acoustic multilateration: a system for long-range wolf detection. Journal of the Acoustical Society of American 145:1619–1628.

Long, R. A., P. MacKay, J. Ray, and W. Zielinski, editors. 2012. Noninvasive survey methods for carnivores. Island Press, Washington, D.C., USA.

Mech, L. D. 2009. Long-term research on wolves in the Superior National Forest. Pages 15–34 *in* A. P. Wydeven, T. R. VanDeelen, and E. J. Heske, editors. Recovery of gray wolf in the Great Lakes Region of the United States: an endangered species success story. Springer, New York, New York, USA.

Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis, USA.

Nelson, M. E., and L. D. Mech. 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildlife Monographs 77.

O'Gara, J. R., C. A. Wieder, E. C. Mallinger, A. N. Simon, A. P. Wydeven, and E. R. Olson. 2020. Efficacy of acoustic triangulation for gray wolves. Wildlife Society Bulletin 44:351–361. https://doi.org/10.1002/wsb.1089

Palacios, V., E. Font, and R. Márquez. 2007. Iberian wolf howls: acoustic structure, individual variation, and a comparison with North American populations. Journal of Mammalogy 88:606–613.

Palacios, V., E. Font, R. Márquez, and P. Carazo. 2015. Recognition of familiarity on the basis of howls: a playback experiment in a captive group of wolves. Behaviour 152:593–614.

Palacios, V., J. V. López-Bao, L. Llaneza, and C. Fernández. 2016. Decoding group vocalizations: the acoustic energy distribution of chorus howls is useful to determine wolf reproduction. PLoS ONE 11(5):e0153858.

Papin, M., J. Pichenot, F. Guérold, and E. Germain. 2018. Acoustic localization at large scales: a promising method for grey wolf monitoring. Frontiers in Zoology 15:1–10.

Phillips, M. K., and D. W. Smith. 1996. The wolves of Yellowstone. Voyageur Press, Stillwater, Minnesota, USA.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Accessed 1 Nov 2019.

Rocha, L. H. S., L. S. Ferreira, B. C. Paula, F. H. G. Rodrigues, and R. S. Sousa-Lima. 2015. An evaluation of manual and automated methods for detecting sounds of maned wolves (*Chrysocyon brachyurus* Illiger 1815). Bioacoustics 24:185–198.

Root-Gutteridge, H., M. Bencsik, M. Chebli, L. K. Gentle, C. Terrell-Nield, A. Bourit, and R. W. Yarnell. 2014. Identifying individual wild Eastern grey wolves (*Canis lupus lycaon*) using fundamental frequency and amplitude of howls. Bioacoustics 23(1):55–66.

Stenglein, J. L., L. P. Waits, D. E. Ausband, P. Zager, and C. M. Mack. 2011. Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. Journal of Mammalogy 92:784–795.

Sugai, L. S. M., C. Desjonquères, T. S. F. Silva, and D. Llusia. 2019. A roadmap for survey designs in terrestrial acoustic monitoring. Remote Sensing in Ecology and Conservation Nov 13:1–16.

Suter, S. M., M. Giordano, S. Nietlispach, M. Apollonio, and D. Passilongo. 2016. Non-invasive acoustic detection of wolves. Bioacoustics 26(3):1–12.

Thiel, R. P., W. Hall, Jr., E. Heilhecker, and A. P. Wydeven. 2009. A disjunct gray wolf population in Central Wisconsin. Pages 107–117 *in* A. P. Wydeven, T. R. VanDeelen, and E. J. Heske, editors. Recovery of gray wolf in the Great Lakes Region of the United States: an endangered species success story. Springer, New York, New York, USA.

Tooze, Z. J., F. H. Harrington, and J. C. Fentress. 1990. Individually distinct vocalizations in timber wolves, *Canis lupus*. Animal Behaviour 40:723–730.

Wildlife Acoustics. 2017. Kaleidoscope analysis software. https://www.wildlifeacoustics.com/products/kaleidoscope-pro. Accessed 4 Aug 2020.

Wiley, R. H., and D. G. Richards. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behavioral Ecology and Sociobiology 3:69–94.

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