

# Space use by gray wolves (*Canis lupus*) in response to simulated howling: a case study and a call for further investigation

Mathieu Leblond, Christian Dussault, and Martin-Hugues St-Laurent

**Abstract:** Simulated wolf howling sessions are a popular ecotourism activity, but no exhaustive evaluation has been made on their potential impacts on wolf ecology. We evaluated the effects of simulated wolf howling sessions on the space use of gray wolves (*Canis lupus* L., 1758) in the Montmorency Forest (Quebec, Canada). Although we equipped 22 individuals with GPS collars from 2005 to 2008, only four wolves could potentially hear our 20 simulated howls (July to October 2008). We used power analyses to select two spatiotemporal scales of analysis with sufficient location data to investigate wolf reactions. We evaluated the distance and orientation of wolf movements relative to howling stations, their movement rates, and their mean distance to other collared pack members, which we used as an index of pack cohesion. We found that wolves approached howling stations (at both scales) and were closer to other pack members (at broad scale only) after simulated howls. The reactions of wolves were of relatively low magnitude, and we conclude that simulated howling sessions were unlikely to have strong negative impacts on the movement patterns of wolves. We encourage future studies to evaluate the effects of simulated howling on the activity levels and fine-scale space use by wolves.

**Key words:** animal communication, *Canis lupus*, ecotourism, gray wolf, satellite telemetry.

**Résumé :** Bien que les sessions d'appels aux loups réalisées dans le cadre d'activités écotouristiques soient populaires, aucune évaluation exhaustive de leurs impacts sur l'écologie du loup n'a été faite à ce jour. Nous avons évalué l'utilisation de l'espace du loup gris (*Canis lupus* L., 1758) en réponse à des appels simulés dans la Forêt Montmorency (Québec, Canada). Bien que nous ayons muni 22 individus de colliers GPS entre 2005 et 2008, seulement quatre loups ont vraisemblablement pu entendre nos 20 appels simulés (juillet à octobre 2008). Nous avons utilisé des analyses de puissance afin de cerner deux échelles spatiotemporelles d'analyse ayant suffisamment de localisations télémétriques pour évaluer les réactions de ces loups. Nous avons ensuite mesuré la distance et l'orientation des loups par rapport aux stations d'appel, leurs taux de déplacement, ainsi que leur distance moyenne par rapport à d'autres membres de la meute, que nous avons utilisé comme un indice de la cohésion de la meute. Nous avons observé que les loups s'approchaient des stations d'appel (aux deux échelles) et étaient plus près des autres membres de leur meute (à grande échelle seulement) à la suite d'un appel simulé. Ces réactions étaient toutefois de faible ampleur et nous concluons que nos appels simulés n'ont probablement pas eu d'impact négatif sur les patrons de déplacement des loups. Nous encourageons davantage d'études sur les effets des appels simulés sur les niveaux d'activité et l'utilisation de l'espace à fine échelle des loups.

**Mots-clés :** communication animale, *Canis lupus*, écotourisme, loup gris, télémétrie satellitaire.

## Introduction

During the last century, the general attitude toward gray wolves (*Canis lupus* L., 1758) has evolved from universal hatred to relative tolerance, sympathy, and even admiration (Kellert 1985; Musiani and Paquet 2004; Mech 2012). Successful reintroductions, like the restoration of wolves in the Greater Yellowstone Ecosystem (USA), have raised public awareness about the crucial role played by wolves as apex predators (Phillips et al. 2010; Woodroffe and Redpath 2015). This change in perception has led to the increasing popularity of wolf howling sessions, an ecotourism activity during which naturalists imitate wolf howls in the hope that wild wolves will respond. A prime example is found in the Algonquin National Park, Ontario, Canada, where more than 10 000 people participate in wolf howling sessions each year (<http://www.algonquinpark.on.ca/>). Simulated howlings have also been used to facilitate detection of wild canids for observation, data acquisition, capture, or culling

(Alcorn 1946; Robbins and McCreery 2003), and to assess the abundance of wolves and coyotes (*Canis latrans* Say, 1823) over broad areas (Crête and Messier 1987; Fuller and Sampson 1988; Hansen et al. 2015).

Howling may be used by territorial wolves to reveal their presence to competing packs, which could serve to reduce agonistic encounters with conspecifics (Harrington and Mech 1979; Mech and Boitani 2003). Harrington and Mech (1979) observed that wolves reacted to human imitations of wolf howls cautiously or agonistically, suggesting that they considered them to be real howls from alien wolves. They also found that wolves rarely retreated (15% of the time) or approached (2%) the source of a simulated howl. Harrington (1986) later corroborated these results using howling playbacks and showed that wolves approached howls on only 5% of occasions. More recently, Manseau et al. (2003) observed that wolf packs could show increased activity at the den 24 h after a howling

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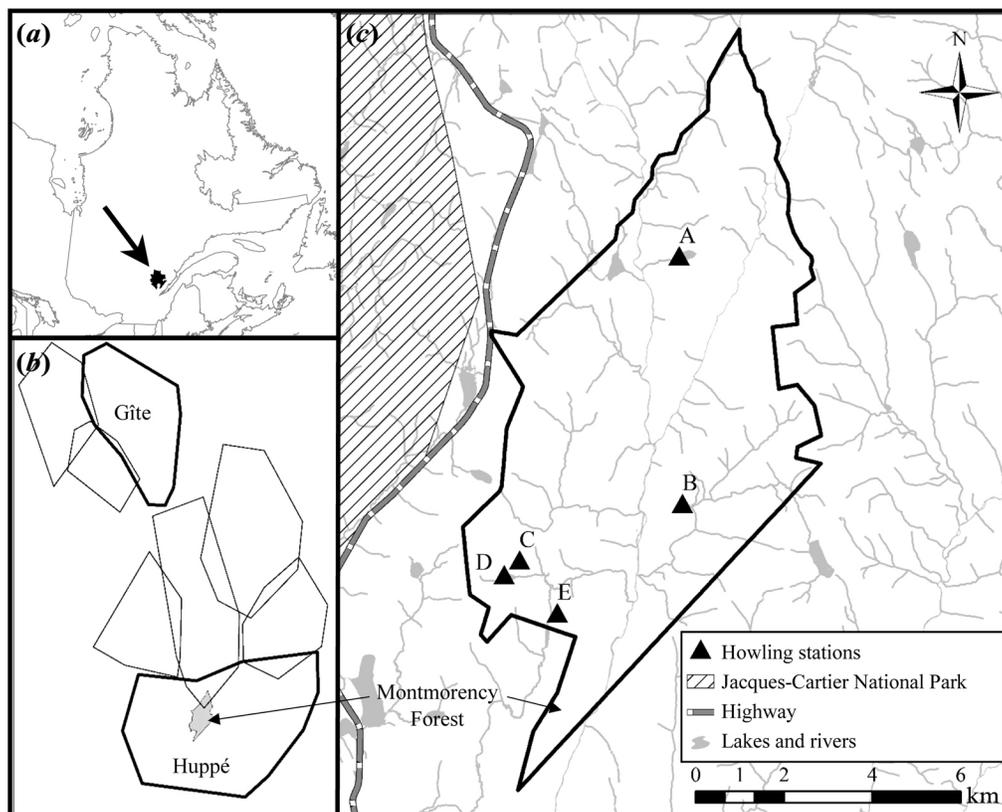
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**Fig. 1.** (a) Location of the Laurentides Wildlife Reserve in Quebec, Canada, where the Montmorency Forest is located. (b) Location and approximate boundaries of eight known gray wolf (*Canis lupus*) packs in the area, as determined using 100% minimum convex polygons around locations of GPS-collared wolves; wolves analysed in this study belonged to one of the two packs indicated by the thick black polygons (one wolf from the northernmost “Gîte” pack was probably transient and entered our study area). (c) Study area showing the five howling stations (A–E) where 20 wolf howling sessions occurred between July and October 2008 (for details see Supplementary Table S1).<sup>1</sup>



stimulation, although this reaction was variable among packs. Therefore, the few studies that assessed behavioral reactions of wolves to simulated howling (other than vocalizations) showed that they increased their presence at rendezvous sites (sensu Joslin 1967) after howling sessions (Manseau et al. 2003), frequently retreated when they did not reply, and never habituated to simulated howls (Harrington and Mech 1979). One might expect that recurring howling stimulations over prolonged or critical periods could alter the movements and activity levels of wolves and influence other aspects of their daily activities. Assessing the impacts of simulated howling on wolf ecology would help to adequately manage simulated howlings conducted in the context of ecotourism (Duffus and Dearden 1990).

Our objective was to compare the space use of GPS-collared wolves before and after simulated howling sessions in the Montmorency Forest (Quebec, Canada). Based on observations by Harrington and Mech (1979), we predicted that wolves would react to simulated howling by avoiding the source of the stimulus (the “retreat” hypothesis; Harrington 1986). Alternatively, we predicted that wolves could equally go towards the source of the vocalization if they believed that an intruder had entered their territory. Under the “opposition” hypothesis, we predicted that wolves would approach the source of the stimulus to identify and eventually to chase this potential intruder (Dekker 1985). We tested these hypotheses by measuring changes in the distance and orientation of wolf movements relative to howling stations. We also evaluated the mean movement rates of wolves, which we used as an index

of activity level (Whittington et al. 2004). We predicted that the movement rates of wolves would increase following simulated howls (Harrington and Mech 1979). Finally, we predicted that simulated howling would increase pack cohesion by inciting pack members to regroup (Manseau et al. 2003), which we evaluated using the mean distance separating collared pack members before and after simulated howls.

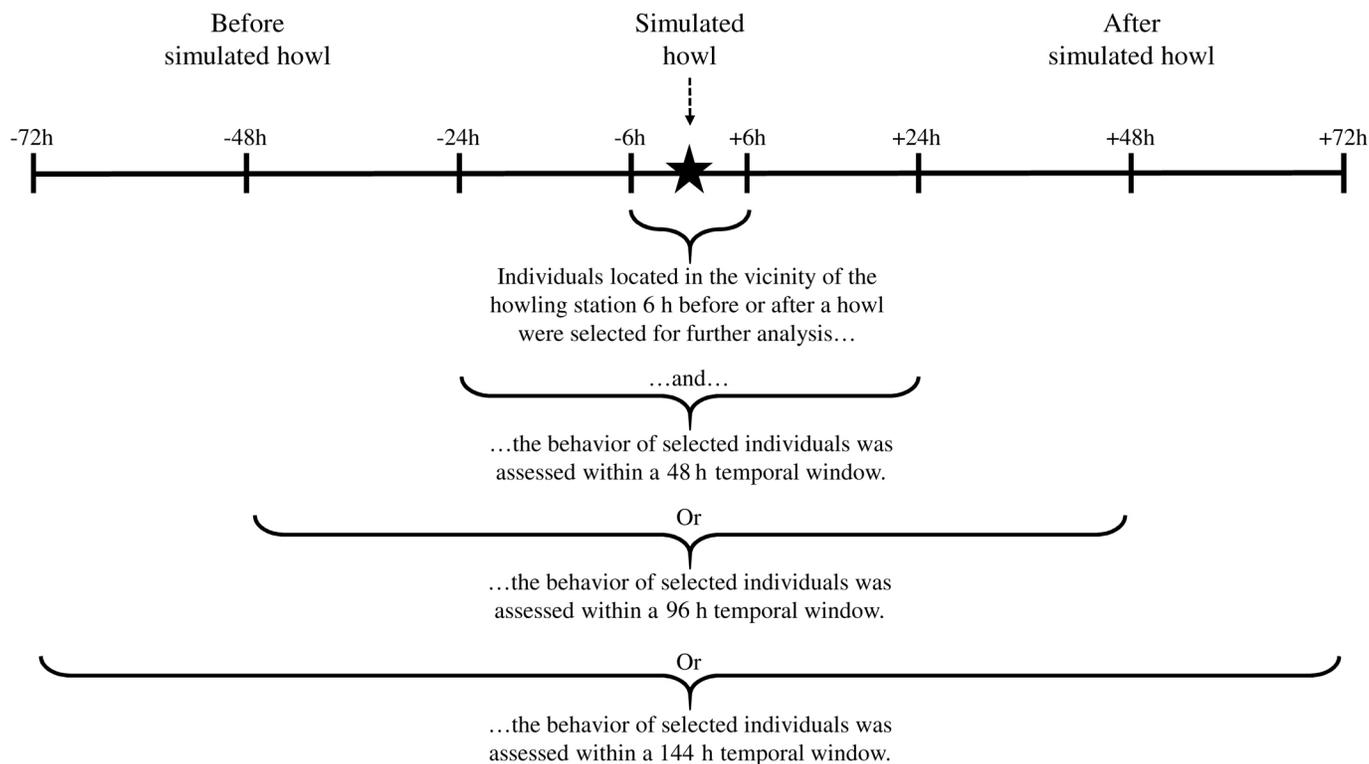
## Materials and methods

### Study area

Simulated howling sessions took place in the Montmorency Forest, a 66 km<sup>2</sup> area dedicated to teaching and research located within the Laurentides Wildlife Reserve, Quebec, Canada (Figs. 1a–1c). Based on the most recent aerial survey (1998; Ministère des Forêts, de la Faune et des Parcs du Québec (hereafter MFPP, unpublished report), gray wolf density in the Laurentides Wildlife Reserve was estimated at approximately 0.4 individual/100 km<sup>2</sup>. Moose (*Alces americanus* (Clinton, 1822)) occurred in the area at a density of 41 individuals/100 km<sup>2</sup> (MFPP, unpublished report). Boreal caribou (*Rangifer tarandus caribou* (Gmelin, 1788); a small population of approximately 75–80 individuals) and black bear (*Ursus americanus* Pallas, 1780) were also present in the region. The area was characterized by a mixture of coniferous and mixed forest stands, including stands dominated by balsam fir (*Abies balsamea* (L.) Mill.) and black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.). Mean maximal and minimal daily temperatures were, respectively,

<sup>1</sup>Supplementary Tables S1 and S2 are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2016-0191>.

**Fig. 2.** Schematic representation of the temporal windows used to select individuals composing the data set and to study the space use and movements of GPS-collared gray wolves (*Canis lupus*) in response to simulated howling in the Montmorency Forest (Quebec, Canada) in 2008.



-6.9 and -19.8 °C in January, and 20.2 and 8.6 °C in July (<http://climate.weather.gc.ca/>).

### Wolf capture and telemetry

From 2005 to 2008, we captured 22 gray wolves belonging to eight packs across the Laurentides Wildlife Reserve. We fitted individuals with GPS telemetry collars (models 3300SW (Lotek Engineering Inc., Newmarket, Ontario, Canada) or TGW-4580 (Telonics Inc., Mesa, Arizona, USA)) programmed to acquire location fixes every 4 h year-round. We captured wolves either by darting or net-gunning from a helicopter in winter (Potvin and Breton 1988) or foot-hold trapping during late summer. All capture and handling procedures were approved by the Animal Welfare Committees of the Université du Québec à Rimouski (certificate No. CPA-27-07-53-R2) and MFPP (certificate No. CPA-07-00-02), based on the guidelines of the Canadian Council on Animal Care.

We started collaring wolves in 2005, i.e., 3 years before the onset of simulated howling sessions, as part of a larger research project (see Lesmerises et al. 2012). However, a lot of the collared wolves were killed by trappers, and individuals were monitored for  $322 \pm 164$  days (mean  $\pm$  SD). Moreover, some wolves were captured far from the Montmorency Forest, whereas others moved away from the study area in the years prior to the study. Despite our sampling efforts, only four wolves from two packs were still present in the vicinity of the howling stations ( $\leq 10$  km) when simulations occurred (two males and one female from the local “Huppé” pack and one transient male from the northern “Gîte” pack; see Fig. 1b).

### Howling sessions

Twenty simulated howling sessions occurred from 23 July to 26 October 2008 at five locations (stations A–E) in the Montmorency Forest (see Fig. 1c and Supplementary Table S1<sup>1</sup>). During these sessions, one or two experienced male naturalists performed one to four live imitations of a solitary wolf ( $n = 16$  occurrences) or wolf pair ( $n = 4$  occurrences) to elicit wolf responses. Naturalists were either alone or accompanied by a small group of

ecotourists (group size =  $2.6 \pm 2.6$ , mean  $\pm$  SD). Howling sessions occurred between the hours of 1800 and 2200, lasted between 15 and 90 min, and were spaced 2–10 days apart ( $5.3 \pm 2.1$  days, mean  $\pm$  SD; Supplementary Table S1<sup>1</sup>). Naturalists took note of the prevailing meteorological conditions, including lunar phase, cloud cover ( $32.5\% \pm 35.4\%$ , mean  $\pm$  SD), temperature ( $6.4 \pm 6.4$  °C, mean  $\pm$  SD), and wind velocity ( $6.9 \pm 10.2$  km/h, mean  $\pm$  SD) during each session (Supplementary Table S1<sup>1</sup>).

### Spatiotemporal scales of analysis

We evaluated the reactions of collared wolves to simulated howling by studying their space use before and after howling sessions. We restricted our data set to include individuals most susceptible to hear simulated howls (i.e., within hearing range of a typical howl; see below), and at periods directly preceding and following howls. Because published information regarding the maximum distance at which wolves can hear howls in forested landscapes is inconsistent and ranges between 1.6 km (Pimlott and Joslin 1968) and 10.8 km (Harrington and Mech 1979), we generated four data sets using locations found in circles of 1.5, 2.5, 5.0, and 10.0 km radii centered on the howling stations (hereafter perceptual ranges). We then identified all wolves that were within range of the simulated howls  $\leq 6$  h before or after howls, and retained these wolves for further analyses. Once wolves were identified, we subsampled each wolf data set to only retain locations recorded 24, 48, and 72 h before and after simulated howls (hereafter 48, 96, and 144 h temporal windows; see Fig. 2) to investigate potential behavioral changes. Typically, 48, 96, and 144 h temporal windows, respectively, included 12, 24, and 36 wolf locations distributed equally before and after howls.

We performed a power analysis using the pwr package (Champely 2015) in R version 3.1.1 (R Core Team 2014) to determine the finest spatiotemporal scale at which sample size was sufficient to meet our study objectives. In other words, we aimed to obtain the “best” trade-off between the size of the perceptual range  $\times$  temporal

**Table 1.** Perceptual range  $\times$  temporal window combinations used to study behavioral reactions of GPS-collared gray wolves (*Canis lupus*) before and after simulated howls in the Montmorency Forest (Quebec, Canada) in 2008.

Temporal window (h)	Perceptual range							
	1.5 km		2.5 km		5.0 km		10.0 km	
	No. of locations before simulated howls	No. of locations after simulated howls	No. of locations before simulated howls	No. of locations after simulated howls	No. of locations before simulated howls	No. of locations after simulated howls	No. of locations before simulated howls	No. of locations after simulated howls
48	10	10	14	14	35	39	<b>91</b>	<b>91</b>
96	21	20	35	29	<b>82</b>	<b>90</b>	<b>191</b>	<b>192</b>
144	31	28	60	45	<b>134</b>	<b>143</b>	<b>289</b>	<b>297</b>

Note: The no. of locations sufficient to detect medium-sized to large effects ( $d \geq 0.5$ ) at  $P \leq 0.05$  are shown in boldface type. Sufficient sample sizes were determined using a power analysis with a type II error probability of 0.80.

window (as small as possible) and sample size (as large as possible). We used values of 0.05 for significance level (type I error), 0.80 for power (type II error), and because our sample size was relatively small for all perceptual range  $\times$  temporal window combinations, we evaluated our capacity to detect medium-sized to large effects ( $d \geq 0.50$ ; Cohen 1988). Following power analyses, we retained two data sets for further analyses: (1) the smallest perceptual range  $\times$  temporal window with sufficient sample size (the “best” trade-off), and (2) the largest sample size, which also represented the largest spatiotemporal scale. For parsimony, we did not retain other combinations with sufficient power because they were comprised between these two spatiotemporal scales.

### Behavioral reactions of wolves

In each of the retained perceptual range  $\times$  temporal window combinations, we evaluated the mean distances (m) and mean orientations of wolf movements ( $^\circ$ ) relative to howling stations, the mean movement rates (m/h) between wolf locations (used as indices of activity levels; Whittington et al. 2004), and the mean distances separating collared pack members (used as indices of pack cohesion; Manseau et al. 2003) before and after simulated howls. We calculated movement metrics using ArcGIS version 10.2 (ESRI Inc., Redlands, California, USA), Geospatial Modelling Environment (Beyer 2012), and the adehabitatLT package (Calenge 2006) in R. Small sample sizes precluded us from pairing before–after data based on wolf identity. We thus compared pooled values of each behavioral metric before and after simulated howls using Welch two-sample  $t$  tests. We interpreted statistically significant differences after vs. before simulated howls as changes in the broad-scale movement patterns of wolves in response to howls.

### Results

Despite relatively good prevailing meteorological conditions during the 20 howling sessions (Supplementary Table S1),<sup>1</sup> wolves only replied to one simulated howl, for a response rate of 5%. The power analysis revealed that the 5 km perceptual range at 96 h was sufficient to detect medium-sized to large effects at  $P \leq 0.05$  ( $n > 63.8$  locations/group; Table 1). We also used the 10 km perceptual range at 144 h, which allowed detection of smaller effects ( $d = 0.23$ ) but at a broader spatiotemporal scale. The smallest perceptual ranges (i.e., 1.5 and 2.5 km) could not be analysed due to insufficient sample size.

In accordance with the “opposition” hypothesis, wolves moved closer to howling stations after simulated howls. This was perceptible at both fine scale ( $12\,993.3 \pm 1\,058.1$  m before vs.  $9\,479.5 \pm 519.9$  m after) and broad scale ( $13\,176.0 \pm 472.5$  m before vs.  $11\,254.0 \pm 372.8$  m after; Table 2). Although wolves moved closer to the source of the howls, their movement steps seemed to be oriented away from the stations after simulated howls at the broader perceptual range  $\times$  temporal window ( $77.1^\circ \pm 3.1^\circ$  before vs.  $89.2^\circ \pm 3.0^\circ$  after; Table 2). Wolves did not modify their mean movement rates following simulated howls ( $P \geq 0.3$ ; see Table 2), but they

were closer to other pack members at the 10 km and 144 h scale ( $9\,441.5 \pm 223.1$  m before vs.  $6\,767.4 \pm 223.9$  m after).

### Discussion

The first description of behavioral reactions of canids to simulated howling was provided by Alcorn (1946), who used vocal imitations and sirens to lure and hunt coyotes. Since then, at least 43 studies have reported extensive to anecdotal results on elicited (i.e., provoked using a simulated howl) and spontaneous howlings from wild wolves and coyotes (see Supplementary Table S2).<sup>1</sup> The vast majority of these studies have focused on the response rates (i.e., no. of replies/no. of elicitations) of canids, whereas other aspects of their ecology (e.g., movements, pack cohesion) have been largely ignored (but see Manseau et al. 2003). Our study aimed at assessing the influence of simulated howling on the space use of wild wolves in the context of ecotourism activities. Although we deployed substantial efforts to capture and monitor 22 wolves over 3 years, our ensuing data set was quite modest: ultimately, only 4 collared wolves were still present in the study area when we conducted our simulated howling sessions. Based on our power analysis, we identified two usable data sets, and although statistically significant results at the broader scale of analysis (i.e., 10 km at 144 h) were not always significant at the finer scale (i.e., 5 km at 96 h), they were always of the same magnitude and direction. Therefore, we discuss both scales simultaneously.

Wolves in the Montmorency Forest responded to 5% of simulated howls, a response rate that was low but comparable with other studies in eastern Canada (Crête and Messier 1987) and the USA (Fuller and Sampson 1988). Past research has revealed that wolves and coyotes reply to approximately 25% of elicitations, on average, but their response rates may range from 0.1% to 56.8% (Supplementary Table S2).<sup>1</sup> Harrington and Mech (1979) found that nonresponding wolves (often lone wolves or wolves from small packs) retreated 34% of the time after hearing simulated howls. These authors, along with Harrington (1986), found that wild wolves in Minnesota rarely approached human howlers and were more inclined to stand their ground. Contrastingly, we showed that wolves in the Montmorency Forest moved closer to howling stations after simulated howls, suggesting that they may have wanted to identify the source of these unknown howls (i.e., the “opposition” hypothesis). However, wolves in our study area remained several kilometres away from howling stations (i.e., from 13.0 km before howls to 9.5 km after howls, on average), whereas Harrington and Mech (1979) and Harrington (1986) howled at <100 to 900 m from wolves. It is therefore probable that wolves reacted differently in our study because of the large distance separating them from the source of the stimuli.

Howls made a few hundred metres away from wolves may represent a direct intrusion within a wolf’s territory and may suggest to nearby wolves that an agonistic encounter is imminent (Harrington and Mech 1979). In this context, wolves may choose to

**Table 2.** Space use of GPS-collared gray wolves (*Canis lupus*) before and after simulated howls in the Montmorency Forest (Quebec, Canada) in 2008.

Perceptual range × temporal window	Wolf behavior	Before simulated howls	After simulated howls	t	df	P
		(mean ± SE)	(mean ± SE)			
5 km at 96 h (fine scale)	Mean distance to the station (m)	12 993.3 ± 1 058.1	9 479.5 ± 519.9	2.98	118.6	<0.01
	Mean orientation relative to the station (°)	75.3 ± 5.7	87.7 ± 6.0	-1.41	151.0	0.16
	Mean movement rate (m/h)	448.1 ± 87.1	458.7 ± 68.6	-0.09	139.9	0.93
	Mean distance to pack members (m)	6 360.2 ± 466.9	5 348.9 ± 380.2	1.68	160.0	0.09
10 km at 144 h (broad scale)	Mean distance to the station (m)	13 176.0 ± 472.5	11 254.0 ± 372.8	3.19	550.6	<0.01
	Mean orientation relative to the station (°)	77.1 ± 3.1	89.2 ± 3.0	-2.69	543.8	0.01
	Mean movement rate (m/h)	496.3 ± 44.4	431.2 ± 38.1	1.08	531.1	0.28
	Mean distance to pack members (m)	9 441.5 ± 223.1	6 767.4 ± 223.9	8.46	583.9	<0.01

**Note:** We compared the behavioral reactions of wolves before and after howls at two scales (see the section Spatiotemporal scales of analysis and Table 1) using Welch two-sample *t* tests.

stand their ground or retreat (Harrington and Mech 1979). Howls made from several kilometres away, on the other hand, may be attributed to distant neighboring packs and may be interpreted as a lesser threat. Wolves may approach the source of these distant howls to better discriminate their characteristics (e.g., duration, harmonics; Palacios et al. 2007; Root-Gutteridge et al. 2014) and possibly try to identify the howlers (Tooze et al. 1990; Palacios et al. 2015). They may also move nearer to the source of howls to reduce attenuation or distortion of sounds (Richards and Wiley 1980) and better assess the distance separating them from potential intruders (Naguib and Wiley 2001). The increased angle relative to howling stations observed in our study suggests that wolves may have approached the source of vocalizations cautiously from the flank, and not directly. This behavior could be linked to olfactory detection (Peters and Mech 1975), although additional data on wind direction would be necessary to test this hypothesis.

We found that wolves decreased their mean distance to other collared pack members following simulated howls; however, individuals remained >6.8 km away from each other, on average, and we could not demonstrate that wolves regrouped at rendezvous sites following howls. At this scale, pack cohesion probably remained comparable with what it was before simulated howls. Manseau et al. (2003) evaluated fine-scale pack cohesion in wolves and found that more adults remained at the den and at rendezvous sites following simulated howls, possibly to increase protection of pups. Howling sessions in our study area occurred from late July to late October, when young wolves are mobile and packs move among rendezvous and kill sites (Mech and Boitani 2003). It is possible that wolves came closer together following an alien howl to communicate vocally with dispersed members of the pack (Harrington and Mech 1979). Alternatively, the apparent grouping of wolves could have been an artificial consequence of wolves approaching a fixed point in space (i.e., the source of the stimulus).

### Management and research perspectives: a call for further investigation

We found that wolves were closer to howling stations and to other pack members following simulated howls. These behavioral reactions were of relatively low magnitude and, on the long term, should not have detrimental impacts on wolves, unless these movements generated significant energy expenditure. We emphasize, however, that the wolves in our study area were ranging relatively far from howling stations and that their behavioral reactions were difficult to measure and were restricted to relatively broad spatiotemporal scales. It is possible that wolves reacted to simulated howls at a much finer scale than what we measured in this study, i.e., at rendezvous sites or in the first few minutes after a howl. Such behavioral reactions were impossible to measure with remote telemetry and would have required direct observation of wolves. It is also possible that simulated howls generated impacts at other biological scales, i.e., by increasing the physiological stress responses of wolves (Creel et al. 2002).

We recommend that future evaluations of simulated wolf howling be made on a large number of simulations across broad areas. Howling stations should be spread across as many wolf territories as possible to allow assessment of interpack variability (Manseau et al. 2003). Different parameters of wolf howling sessions, such as their frequency, duration, and type (e.g., solitary vs. pack howl), should also be evaluated using replicate designs. We encourage researchers to study various aspects of wolf behavior (e.g., activity levels, space use) in addition to their vocal responses. Likewise, more data would be necessary to study changes in habitat selection and in the frequency of social interactions among packs. For example, wolves may modify the size, shape, or location of their territory following simulated howls if they believed howls were performed by the leader of a larger competing pack (Harrington and Mech 1979). Satellite telemetry with a high relocation frequency could be used to detect these otherwise silent reactions.

Simulated howling sessions, when performed in or near protected areas, could potentially limit the availability of suitable habitat for wolves if they believed it to be functionally unavailable (i.e., occupied by other wolves). Until more is known about the impacts of wolf howling sessions, naturalists and park managers should consider the territorial behavior of wolves when promoting this ecotourism activity. Avoiding repeated howling at the same location could be a good way to favor the establishment of wolf packs in protected areas.

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