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Wildlife is exposed to increasing anthropogenic disturbances related to shale oil and gas extraction in response to rising worldwide demands. As these disturbances increase in intensity and occurrence across the landscape, understanding their impacts is essential for management. On Anticosti Island (Québec, Canada), we equipped six white-tailed deer *Odocoileus virginianus* with GPS collars taking hourly locations. We then designed a playback experiment by simulating constant drilling noise emitted by generators to which half of the collared deer were exposed for a three-week period. Deer tolerated noise levels up to 70 dB(C). However, the number of locations recorded in areas where the noise was above 70 dB(C) was on average 73% (SE ± 18%) lower than before the disturbance, which suggests that deer experienced fine scale functional habitat loss. This loss of habitat occurred up to 200 m from the noise source. The size of home ranges and movement rates did not appear to be affected by the noise disturbance. In addition, during the experiment, deer were able to relocate in areas of their home range where food availability was similar to that of sites used before the disturbance. These results show that drilling noise can affect the habitat use of white-tailed deer. However, future research is needed to better understand the cumulative impacts of shale mining on large mammals, as this study isolated only one of the many disturbances present near mining sites and for a limited period.

Disturbances, whether natural or anthropogenic, may cause detrimental behavioural or physiological responses in wildlife. Much attention has been given to the effects of anthropogenic disturbances on wildlife (Stankowich 2008, Sodhi et al. 2009). Liddle (1997) categorised disturbances into three large classes. The first is the interruption of placidity in which the animal senses human presence. The second type is interference in which the animal's habitat is modified and the third is molestation, defined by physical contact with the animal. The drastic rise in anthropogenic disturbances of the first and second types during the last decades is worrying as they may ultimately affect the overall energy budgets and fitness of disturbed animals (Pyke et al. 1977, Liddle 1997, Laurance 2010). Of these disturbances, anthropogenic acoustic stimuli, otherwise known as noise pollution, have become particularly pervasive worldwide (Slabbekoorn and Ripmeester 2008, Kight and Swaddle 2011, Slabbekoorn 2013).

Many studies have reported concerns about the possible effects of noise pollution on the integrity and quality of ecosystems in natural areas (Barber et al. 2011, Pijanowski et al. 2011). Despite the non-lethal nature of most anthropogenic sounds, acoustic stimuli can induce response behaviours such as increased alertness, avoidance and flight (Rabin et al. 2006, Stankowich 2008, Shannon et al. 2014, Padié et al. 2015, Simpson et al. 2015). These anti-predator behaviours have evolved to reduce the predation risk perceived by prey species in response to stimuli (Frid and Dill 2002). Yet these behaviours also incur a cost when exhibited in response to non-lethal stimuli such as compressor noises around a well pad, for example, because they can affect overall energy budgets (Pyke et al. 1977, Bradshaw et al. 1997).

In light of the impacts that noise may have on wildlife, measuring the behavioural responses to noise exposure is a first step in determining the full impact of anthropogenic noise pollution on wildlife. Particular attention should be paid to activity sectors, such as resource extraction, that have the potential of causing large scale increases in anthropogenic noise disturbances in natural areas.

Resource extraction such as shale oil and gas is an eminent threat to natural soundscapes for a number of reasons. Primary energy consumption is on the rise worldwide (British Petroleum 2014), and previously unexploitable gas and oil reserves from unconventional reservoirs such as shale are now producing at a profitable rate as a result of efficient technologies such as horizontal drilling and hydraulic

fracturing (Passey et al. 2010, Malakoff 2014). Wells in unconventional reservoirs must be 'fracked' multiple times to prolong production while high demands have also caused a proliferation in the number of wells drilled (Howarth et al. 2011). Consequently, the intensity and occurrence of anthropogenic disturbances associated with these types of energy developments are likely to increase across the landscape.

Several studies have already reported the negative effects of anthropogenic disturbances associated with fossil fuel exploration and exploitation on wildlife. One of these effects is habitat loss, which alone is the single most important impact of anthropogenic disturbances today (Barnosky et al. 2011). Habitat loss may be direct when the physical components of a habitat are destroyed, but may also be indirect when anthropogenic stimuli decrease the quality of a habitat thereby eliciting an avoidance response. Two studies have shown that areas of high use by mule deer *Odocoileus hemionus* and elk *Cervus canadensis* prior to development of natural gas fields became avoided during development, indicating indirect in addition to direct habitat loss (Sawyer et al. 2006, Buchanan et al. 2014). In caribou *Rangifer tarandus*, the noise from simulated petroleum exploration increased movement rate, thereby increasing energy expenditure (Bradshaw et al. 1997). Additionally, predator–prey relationships in birds have been modified around loud well pads with compressors and greater sage grouse *Centrocercus urophasianus* males were found in lower abundances at lek sites exposed to chronic and intermittent noise disturbances associated with natural gas production than elsewhere (Francis et al. 2009, Blickely et al. 2012). The underlying stimulus responsible for these behavioural changes is thought to be anthropogenic noise, a growing pervasive pollutant whose extent and intensity have grown in recent decades (Slabbekoorn and Ripmeester 2008, Barber et al. 2009, Slabbekoorn 2010).

Our study aimed at quantifying the effects of noise associated with oil exploration on the habitat use of a large mammal, the white-tailed deer *Odocoileus virginianus*. We used a noise playback approach to mimic the noises produced by exploration activities and isolate the effects of noise disturbances from other confounding factors related to energy development such as vegetation change by road edges, moving vehicles and pollution. To our knowledge, our study is the first to quantify the effects of noise amplitude associated with drilling rigs on the behaviour of a wild ungulate. Our objective was to assess the changes in habitat use of white-tailed deer in response to constant acoustic stimuli associated with the generators used to power the drill rigs. We hypothesised that white-tailed deer would exhibit anti-predator responses to noise disturbances (Frid and Dill 2002). Therefore, we predicted that 1) deer would respond to disturbance by avoiding high intensity noise, thereby increasing the size of their home ranges and that 2) deer exposed to noise would increase their movement rates during the disturbance. In addition, we predicted that 3) individuals exposed to noise from a simulated drilling rig would have reduced access to food resources during the noise simulation based on the assumption that their home range prior to the disturbance was located in the best available habitat i.e.

where the amount of food resources was highest (Massé and Côté 2009).

Study area

The study was conducted on Anticosti Island (7943 km²) in the Gulf of St-Lawrence, Québec, Canada (49°28′N, 63°00′W). Anticosti is home to an abundant white-tailed deer population (>20 deer km^{-2}), introduced in 1896 (Rochette and Gingras 2007). Originally the boreal forests of Anticosti were dominated by balsam fir *Abies balsamea* – white birch *Betula papyrifera* stands, but long term over-browsing has favoured the regeneration of white spruce *Picea glauca* and black spruce *P. mariana* stands (Potvin et al. 2003). In addition, the composition and structure of both the shrub and herbaceous layers have also been greatly modified by over-browsing (Potvin et al. 2000, 2003, Côté et al. 2008). The landscape is now a mosaic of peatlands, clearcuts and forest stands (Potvin et al. 2003). In recent years, liquid and gaseous hydrocarbons have been discovered in the Macasty Shale formation that covers most of the Island (Chi et al. 2010, Lavoie and Thériault 2012). Studies are currently underway to determine whether these resources can be profitably extracted with reasonable impacts on the environment and the quality of deer hunting which is an important social activity for the local population and the main economical activity on the island.

Methods

Deer captures

We captured six female white-tailed deer in mid-June 2013 by net-gunning from a helicopter in the western portion of the Island. The deer were equipped with GPS Iridium collars with built-in automatic drop-offs (Vectronics, Germany). Location fixes were attempted every hour during the nine-week period. The minimum number of locations collected for an individual was 1284. We therefore randomly selected 1284 locations for the five other individuals to ensure all individuals were equally represented in the analyses. We captured three deer within 1 km of the playback sites (experimental individuals) and three others at more than 1 km of the playback sites for controls. The average minimal distance between a control individual and the playback site was 1026 ± 3.8 m (SE). All capture and handling procedures were approved by the Animal Welfare Committee of Université Laval and of the Ministère des Forêts, de la Faune et des Parcs du Québec.

Study design and noise playback experiment

We used a playback experiment to mimic the noise of oil exploration activities. In August 2012 we recorded the noise produced by a drilling rig and its generators in Gaspésie, Québec, similar to those that will be used on Anticosti. We placed a lightweight condenser shotgun microphone (NTG2, RØDE Microphones) and a digital audio recorder (H4n, Zoom) at a distance that was as far from the drilling rig as possible without interference from the trees and topography

(~ 55 m). We specifically selected the microphone because of its ability to capture all sound frequencies between 20 and 20 000 Hz. These frequencies overlap the range of frequencies white-tailed deer are most sensitive to (4000–8000 Hz) and cover most of their detectable spectrum (0.25–30 000 Hz) (D'Angelo et al. 2007). We recorded the noise for four 1 h-periods over the course of a two-day period when wind speed was below 4 on the Beaufort wind scale (Supplementary material Appendix 1). We edited the audio recordings by sampling segments that were typical of the baseline noise emitted by oil exploration activities. Therefore, we excluded noises such as voices, trucks and horns. The final recording was 30 min (Supplementary material Appendix 2). The audio editing was performed using Audacity 2.0.1. (2012), (< http://audacity.sourceforge.net/ >, accessed September 2012).

We used a hand-held sound pressure level (SPL) meter (Caselle-246) to measure the ambient noise levels at varying distances of the Gaspésie drilling rig along four transects that were separated by 90° angles. We calibrated the SPL meters using the CEL-120 Acoustic Calibrator.

Based on these measurements, we used the mean amplitude sound level measured 15 m away from the drilling rig in Gaspésie to adjust the volume of the speakers on Anticosti, so that the noise levels were equivalent at equal distances (88 ± 0.4 dB(C) (SE)).

The playback experiment on Anticosti took place at two different sites simultaneously. We collected deer locations before the playback and we positioned the speakers in two locations that maximised the sound coverage of the home ranges belonging to the experimental individuals. This design was chosen to ensure experimental individuals fully received the noise treatment, given the small sample size. The first site was located at the border of the home range of one deer and the second site was close to the home ranges of the other two experimental deer (Fig. 1).

On the 30 September 2013, we set up two bi-amp two-way powered speakers (Yamaha MSR400) in the first location projecting the sound at 180° toward the first individual's home range; the four other speakers were installed at the second site to project the sound at 360°. Each site was powered by a 2000 watt Honda inverter generator whose size and therefore noise was not comparable to an actual drilling rig generator. Both sites were visited daily within an hour of each other to refuel the generators. The study was divided into three periods of three weeks each: before [9 Sept – 29 Sept], during [30 Sept – 21 Oct] and after [21 Oct – 11 Nov] the playback. The playback was only interrupted 5 min daily to refuel the generators and 20 min once a week to change the generator oil. A random location near the center of the home range of each control individual was chosen and visited daily to account for the disturbance associated with the experimenter while refueling the generators. We selected and tested the speakers with the help of a sound technician based on their capacity to reproduce the appropriate sound frequencies (50–20 000 Hz) and their ability to produce the necessary sound amplitude without distortion (88 ± 0.4 dB(C)).

During the second week of the playback, 16 transects located around the two playback sites were sampled with SPL meters to record the noise amplitude. The transects were separated by 45° (Fig. 2). Beginning at the source, the first six sound measurements along a given transect were taken every 15 m. Subsequent sound measurements were taken every 30 m until 15 measurements were taken or until the background sound level (40 dB(C)) was reached. Each measurement was taken for one minute. If another noise was heard or the wind reached more than 3 on the Beaufort wind scale, the measurement was discarded and was retaken as soon as conditions were favorable. Sound measurements were quantified using the Leq and were taken in C weighting so as not to filter the lower frequencies emitted by the drilling rig noise (Krausman et al. 2004).

Vegetation sampling

We determined the core area (70% fixed kernel) used by marked individuals for each of the three test periods (before, during and after noise playbacks). From these areas, we randomly selected a minimum of 18 deer fixes per period to sample the available food resources, before, during and after the playbacks. At each of these locations, we sampled
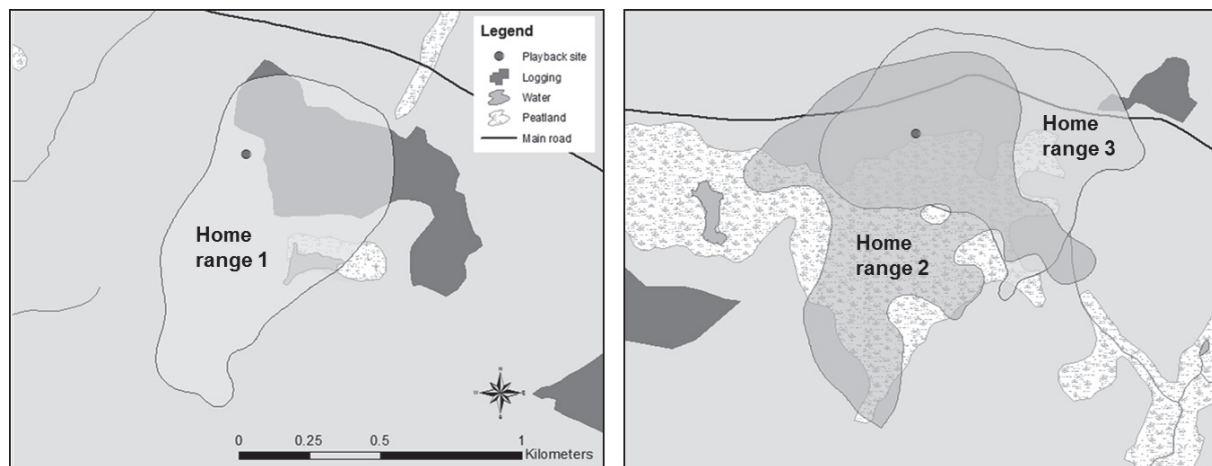

Figure 1. Position of speakers (gray dot) used to play the simulated drilling noise in relation to the 99% home range of the three experimental deer during the nine weeks of the study period.
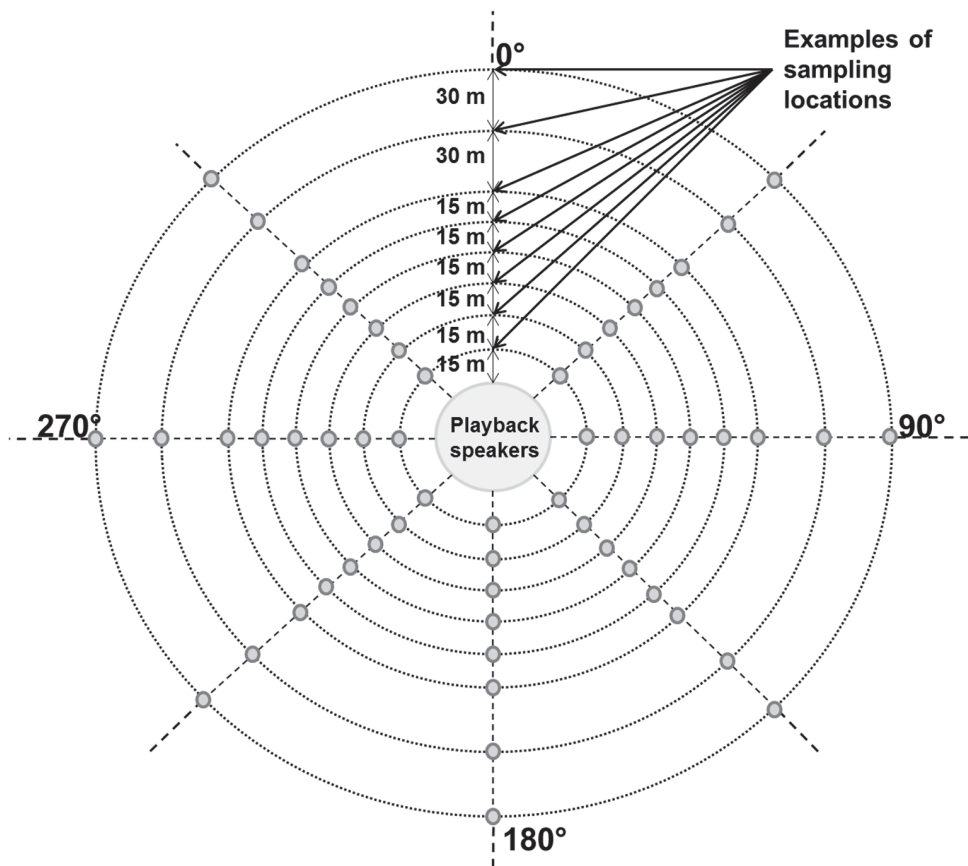
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Figure 2. Sampling design used to measure the simulated drilling noise around a playback site. The first six sampling locations along a transect were separated by 15 m, while subsequent locations were separated by 30 m.

vegetation in three 4-m² circular plots. These three plots were randomly assigned a distance of 5, 10 or 15 m around the actual fix. The first plot was always oriented north (0°), the second at 120° and the third at 240° from the fix (Fig. 3). We visually estimated the percentage cover for the herbaceous layer using 1% classes between 0% and 10%, 5% classes between 10% and 30%, and 10% classes from 30% to 100%. We focused on herbaceous plants because they are at the basis of the summer–autumn diet of deer on Anticosti (Massé and Côté 2009).

Data analysis

Home range estimation, movement rate and probability of habitat use
To test the effect of noise on the home-range size and hourly movement rate of deer we used a set of linear mixed-effect candidate models (lme4 package in R; <www.r-project. org>). We estimated the size of each deer's home range using the Brownian bridge technique (adehabitatHR package in R). This allowed us to consider the path used by individuals between successive locations as opposed to a standard kernel method (Bullard 1991). We obtained movement rates by calculating the distance between two successive locations and dividing it by the time elapsed between the two. The dependent variable was the size of the home range or the movement rate, and the independent variables were Type (control or experimental individuals) and Period

(before, during or after the playbacks). We also included the identity of deer as a random term in every model. We used Akaike's information criterion corrected for small sample size to rank and select the best candidate model (Burnham and Anderson 2002). The most parsimonious model was chosen when competing models had a delta AICc < 2 (Arnold 2010). We used a posteriori comparisons of least square means (lsmeans: lsmeans package in R) to investigate significant effects. In addition, the mean distance between the noise simulation and every deer location was computed for the three experimental individuals and each period of the study.

Sound and vegetation models
We estimated the noise amplitude around both playback sites using the 'gstat' package in R. We created a sound amplitude raster map using interpolation through ordinary kriging (Supplementary material Appendix 3). We preferred a kriging approach to a mathematical sound model because it inherently takes into account variables such as topography and vegetation that act as noise obstacles between the playback and the sound pressure meter (Cressie 1988). We obtained a single static map representing sound levels experienced by deer around the playback sites under average weather conditions. We then reclassified the raster values into seven decibel categories as follows: 40 dB = background sound level, 45 dB = sound level > 40 and < 50 dB, 55 dB = sound level ≥ 50 and < 60 dB, … 90 dB = sound level
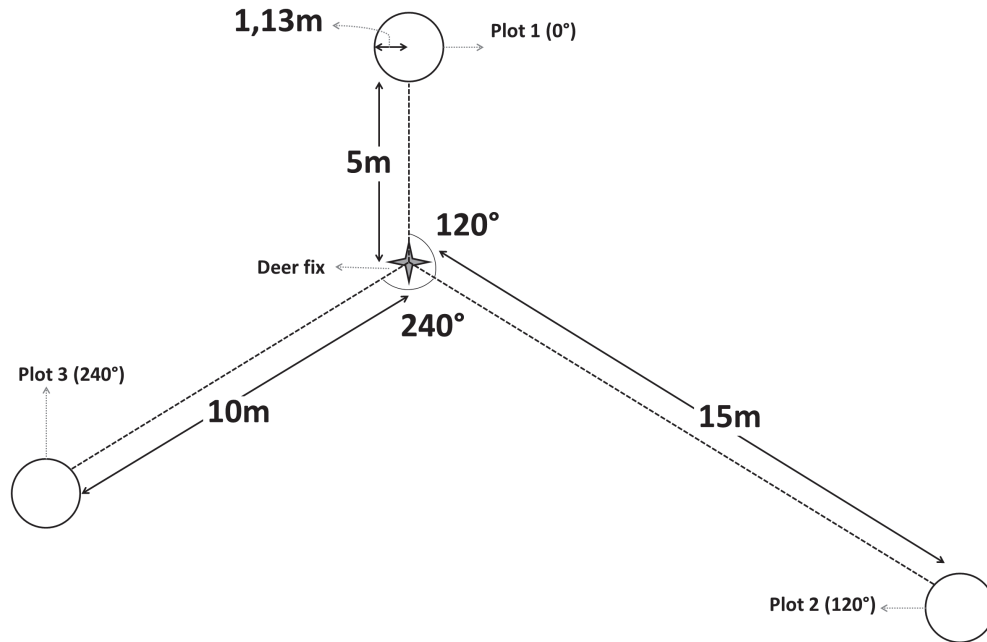
Figure 3. Sampling design used to estimate the percentage cover of herbaceous plants at the randomly selected white-tailed deer fixes. The position of the three subplots was determined by randomly assigning a distance from the plot center to three pre-determined directions (0°, 120°, 240°).

≥ 90 dB. To verify whether avoidance by deer occurred above a certain sound amplitude level, we totalled the number of experimental deer locations in each of the seven amplitude categories (sound zones), for each period (before, during and after) and performed a G-test to determine if the frequency of locations in the different amplitude sound zones differed between the three periods. We pooled the number of locations for the three experimental individuals in each sound zone for each period.

We calculated the mean percentage cover of herbaceous plants in the three plots at each sampling point. We used a mixed-effect model to assess the effect of noise on the availability of food resources at the sampled locations. We used least-square means (lsmeans; lsmeans package in R) to assess whether the percentage cover of the herbaceous layer differed between control and experimental individuals for each period.

Results

Home range size and movement rate

Home range size did not depend on the interaction between study period (before, during and after the playback) and type of deer (control versus experimental) (Table 1). The null model received the most support (Table 1), indicating that the playbacks did not affect home range size.

The most parsimonious model explaining movement rate only included the Period suggesting that the playback experiment did not influence movement rate (Table 1).

Table 1. Model selection for analyses testing the influence of noise playback simulation on the home range size, movement rate and availability of food resources of white-tailed deer on Anticosti Island, Quebec, Canada. Independent variables were deer Type (experimental vs control) and Period (before, during and after the playback experiment).

| Dependent variable	Model	LL	AICc	Δ AICc	AICcWt	K
Home range size	Null (1|ID_deer)	−25.02	57.76	0	0.63	3
	Deer type	−24.15	59.38	1.62	0.28	4
	Period	−23.51	62.02	4.27	0.07	5
	Period + Deer type	−22.59	64.82	7.06	0	6
	Period × Deer type	−21.89	75.78	18.03	0	8
Movement rate	Period	2787.73	−5565.45	0	0.66	5
	Period + Deer type	2787.74	−5563.46	1.98	0.25	6
	Period × Deer type	2788.79	−5561.56	3.89	0.09	8
	Null (1|ID_deer)	2726.52	−5447.04	118.41	0	3
	Deer type	2726.53	−5445.05	120.4	0	4
Food resource availability	Period × Deer type	205.12	−393.8	0	0.75	8
	Period + Deer type	201.73	−391.21	2.59	0.21	6
	Period	199.21	−388.25	5.55	0.05	5
	Deer type	189.51	−370.89	22.9	0	4
	Null (1|ID_deer)	187.04	−368.01	25.78	0	3
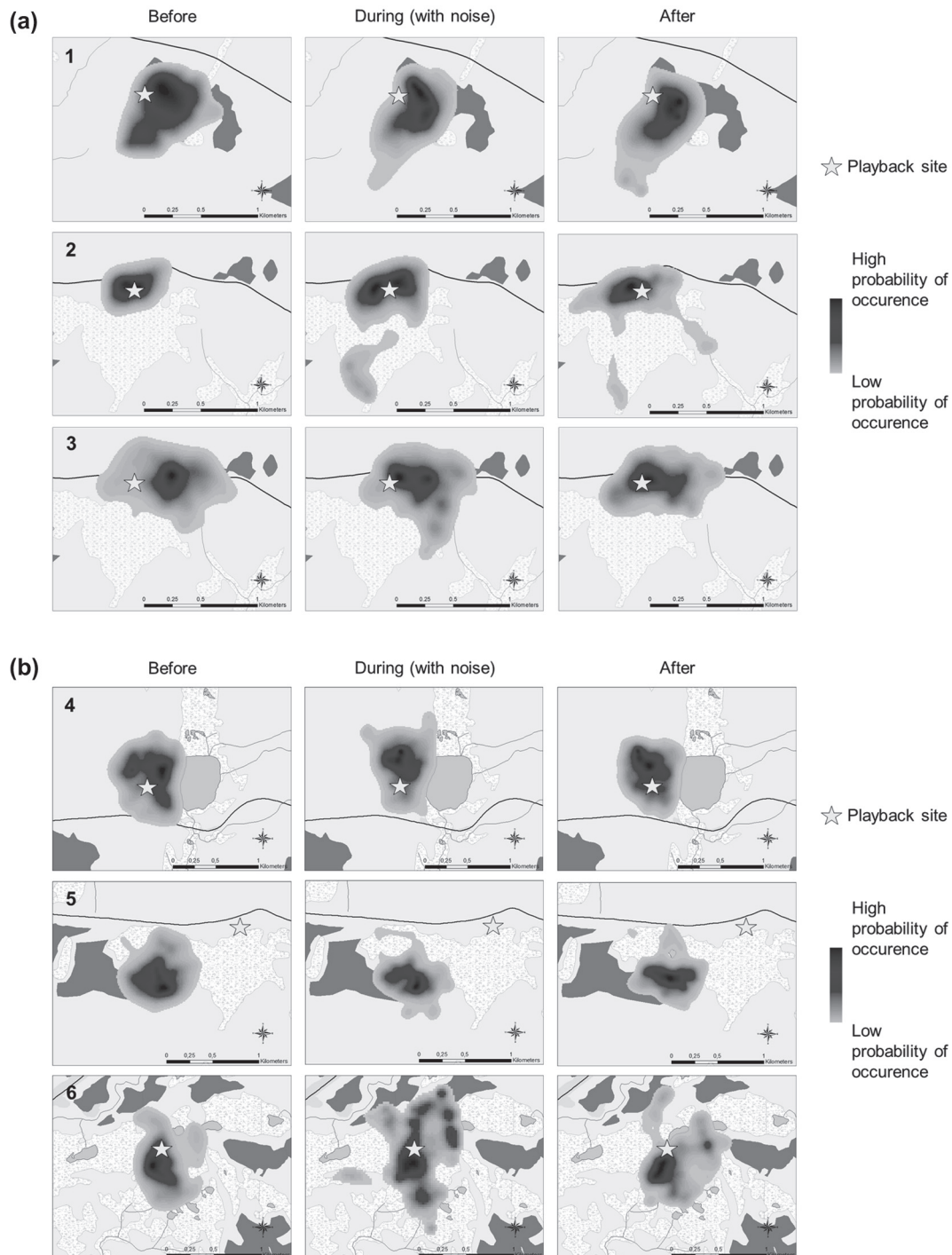
Figure 4. The probability distribution grids (based on Brownian bridge kernels) of three experimental white-tailed deer exposed to simulated drilling noise (a) and estimated playback site (no noise) for the three control deer (b) on Anticosti Island, Québec, Canada, before, during and after the sound simulation.

Mean distance of deer to the playback site and probability of use

Deer remained on average at a distance of 279 ± 5 m (SE) from the source of noise during the playback. Avoidance of noise simulations is evidenced by the changes in the probability distributions around the playback site (Fig. 4). The first and second deer clearly avoided the playback site during the noise simulation. The third individual

was the furthest overall from the playback site before the experiment began and appeared to approach the playback site, yet remained at a similar distance from the noise than the other deer (right).

Sound zones

The frequency distribution of deer locations in the different sound zones changed in relation to the period ($G = 104.9$,
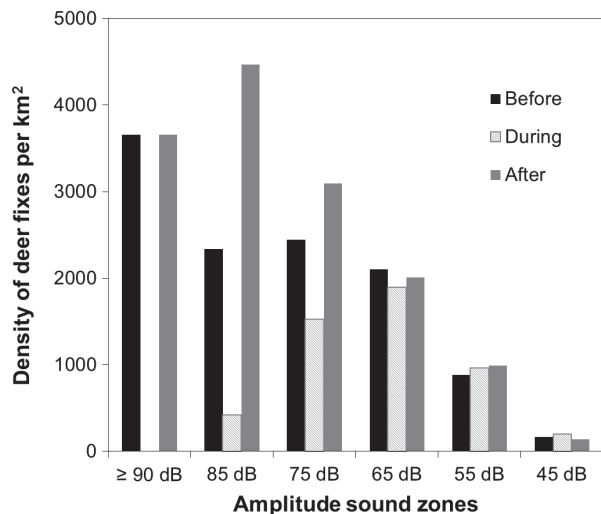
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Figure 5. Comparison of the density (fixes km⁻²) of experimental white-tailed deer locations recorded inside each amplitude sound zone before, during and after a drilling sound simulation. The density of locations in a lower amplitude zone does not take into account the density of locations in the higher amplitude zones.

p < 0.001) (Fig. 5). During the playbacks, we respectively observed lower and higher frequencies of deer locations in the loud and in the quieter sound zones. More specifically, the number of deer locations inside the 90 dB, 85 dB and 75 dB zones was on average 73% lower during the playbacks than before and after. In the 45 dB zone, the pattern was reversed, with a higher number of locations during the playbacks than before and after. The number of locations in the 65 and 55 dB zones was similar in all periods.

Resource use

The percentage of herbaceous plant cover differed between periods and treatment groups. The model including the interaction between Period and deer Type received the most support (Table 1, 2). A higher percentage of herbaceous cover was observed in the experimental plots than in the control plots during the noise simulation (DF = 40.53, t ratio = –3.3, p = 0.002).

Table 2. Parameter estimates and confidence intervals for the top vegetation model testing the influence of noise playback simulation on the availability of food resources for white-tailed deer on Anticosti Island, Quebec, Canada. The model included a significant interaction between the two independent variables; deer Type (experimental vs control) and Period (before, during and after the playback experiment).

Parameter	β	Confidence interval
Before		
control	0.166	[0.125–0.206]
experimental	0.176	[0.119–0.233]
During		
control	0.189	[0.140–0.238]
experimental	0.291	[0.222–0.359]
After		
control	0.227	[0.178–0.276]
experimental	0.278	[0.210–0.346]

Discussion

We used an experimental approach favouring the isolation of one of the many disturbances surrounding shale exploration as a first step in examining the behavioural response of a large mammal to anthropogenic disturbances associated with shale oil and gas exploration. Our study considered the constant noise emitted from a drilling rig, but did not consider other disturbances such as moving vehicles that occur around oil or gas development. Contrary to our predictions, neither the home range nor the movement rate increased in response to the noise disturbance. However, white-tailed deer did experience a fine scale habitat loss when above a threshold of 70 dB(C).

The size of the home range was not affected by the study period and deer type (experimental or control), contrary to our prediction. The size of a home range can depend on several factors such as food supply, visibility (cover), or the presence of offspring (Tufto et al. 1996). Roe deer, for example, adjust their home range to make a compromise between food availability and cover, which reduces predation risk (Tufto et al. 1996). Likewise, the same compromise between forage and cover has been observed on Anticosti Island despite the absence of natural predators (Massé and Côté 2009), suggesting that both factors are probably more important than noise disturbances at lower sound amplitudes. Furthermore, our study was conducted on an abundant white-tailed deer population (Rochette and Gingras 2007). Winter survival of deer living at high densities is strongly dependent on pre-winter body mass and weather conditions (Gaillard et al. 1996, Taillon et al. 2006). We conducted our study during the fall season when the quality and quantity of food resources are decreasing gradually. Hence, the size of the home range was most likely governed by the availability of food resources to accumulate winter body reserves than the playback. Moreover, in high density contexts, white-tailed deer show high philopatry to their home ranges, in both summer and winter (Lesage et al. 2000). Given the small size of the home ranges and the high philopatry observed it is possible that philopatry minimised the avoidance response and that the deer response to the noise disturbances would have been higher in a lower density setting.

Experimental individuals did not increase their movement rate during the noise simulation. The decision of an animal to flee a predator depends mainly on the speed and direction of the predator as well as the distance at which the prey detects the predator (Stankowich and Coss 2006). During the course of this experiment, the simulated noise disturbance, which could have been perceived initially as a predation risk (Frid and Dill 2002), remained in the same location emitting constant and repetitive noise, creating favourable conditions for habituation to occur. However, habituation over such a short period is unlikely which suggests that the lack of response reflects more a tolerance behaviour to the non-lethal stimuli than actual habituation (Weisenberger et al. 1996, Bejder et al. 2009).

In addition, the decreasing movement rate observed during the course of the study was most likely due to behavioural changes in response to seasonal changes in the environment. White-tailed deer exhibit behavioural and metabolic changes to favour energy conservation as resources get scarcer and

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temperatures get colder (Moen 1978). Given that the study was conducted from late September to the beginning of November when days are rapidly shortening and temperatures are approaching winter temperatures, the deer most likely exhibited decreasing movement rates in response to these seasonal temperature changes to reduce their energy expenditure (Moen 1976).

However, despite the disturbance being limited only to constant noise emitted mainly from well-pad generators, we observed a zone of avoidance by white-tailed deer where noise amplitudes reached 70 dB(C) or more. The decision of an animal to avoid a portion of its habitat can depend on several factors such as the quality of its habitat as well as the distance, quality and availability of alternate sites (Gill et al. 2001). An avoidance response such as the one we observed suggests that constant noise disturbances indirectly decreased the quality of the habitat perceived by the animal which led to a functional habitat loss at a fine scale in areas where noise amplitudes were sufficiently high. The avoidance zone was relatively small (50 ~ 200 m) and deer did not incur a relocation cost because the availability of food resources was not affected.

The sample size was limited to only six individuals because of the difficulty of capturing deer around the two playback sites. The main shortcoming of a small sample size is the difficulty of detecting the effect of a treatment. Small sample sizes may lead to an increase in type II errors, meaning the possibility of not detecting the effect of a treatment when in fact the treatment has an effect (Freiman et al. 1978). In experiments where interindividual variability is large, this phenomenon can be greatly exacerbated. Therefore results should be interpreted with caution.

In addition, the noise disturbances we used were punctual in space and time, yet real mining activities produce larger scale disturbances over longer periods. In mule deer, elk and pronghorn, the development of gas fields have caused indirect and direct habitat loss (Sawyer et al. 2006, Beckmann et al. 2012, Buchanan et al. 2014). In addition, the extent of the avoidance in all three cases was much larger than the one observed here and appeared to increase over time. Other sources of disturbance present in these studies, such as vehicle traffic along roads and human presence, are known to cause avoidance in ungulates and likely explain the difference in the extent of avoidance we observed (Ciuti et al. 2012, Neumann et al. 2013). Cumulative effects, defined by Sorensen et al. (2008) as the sum of incremental effects on wildlife resulting from the combined influence of anthropogenic and/or natural disturbances, may explain why multiple disturbances caused a greater avoidance response than the one we detected. Nevertheless, constant noise disturbances around energy development sites are sufficient to initiate a spatial change in the habitat use of white-tailed deer, in a short period of time and at a small spatial scale.

The type of noise disturbance may also be an important factor in determining the extent to which anthropogenic activities affect the habitat use of wildlife (Francis and Barber 2013). The sounds emitted from the generators used around well pads produce constant noise disturbances, yet other acoustic stimuli occur around drilling sites. In a similar playback experiment, Blickely et al. (2012) demonstrated that intermittent noise caused by the vehicles circulating to and from a drilling site had a much greater impact on the attendance of male sage grouse at leks than the constant noise of the compressors. Therefore, we consider our results conservative as they only consider the constant noises associated with the generators and do not include the full range of anthropogenic noise disturbances that may be emitted around a drilling site.

Despite the avoidance observed in response to loud drilling noise (>70 dB) experimental deer did not experience a reduction in the available amount of forage contrary to our predictions. In fact, the slight avoidance observed resulted in an increase in the percentage cover of herbaceous plants available in their home range. This suggests that food resources in mid-autumn were still readily available allowing experimental deer to find alternate food patches. It could also highlight the importance of food availability to deer during the study period, during which benefits could overcome the potential costs associated with drilling noise in the context of high density. We might have observed another outcome from this tradeoff during other periods of the year or in other systems where food availability is less limiting.

Behavioural responses can incur energetic costs due to relocation and vigilance and are therefore the first step in evaluating the impact of anthropogenic disturbances (Reimers et al. 2003). However, anthropogenic acoustic stimuli may also disrupt fundamental biological processes that behavioural responses may or may not reflect (Kight and Swaddle 2011). In domestic pigs *Sus scofa* (German landrace), exposure to chronic noise resulted in changes to the hypothalamic–pituitary-adrenal axis, responsible for maintaining homeostasis, as well as inducing a state of chronic stress (Kanitz et al. 2005). In certain wildlife species, chronic stress has been inversely related to immune response, survival, recruitment and body mass index (Saino et al. 2003, Blas et al. 2007, Cabezas et al. 2007). Thus, anthropogenic noise disturbances may potentially affect fitness even if behavioural responses are not detectable. We suggest that further research should attempt to determine whether individuals can tolerate anthropogenic disturbances by evaluating reactions to noise over longer time periods, as well as physiological and energetic costs affecting survival and reproduction (Reimers et al. 2003). The concentration of stress hormones, heart and respiration rates or distance and length of flight events could be useful indicators to measure energetic and physiological costs (Gabrielsen and Smith 1995, Bradshaw et al. 1997, Creel et al. 2002).

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Supplementary material (available online as Appendix wlb-00225 at <www.wildlifebiology.org/appendix/wlb-00225>). Appendix 1–3.