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# Influence of human footprint and sensory disturbances on night-time space use of an owl

C. A. Scobie[1,3,*], E. M. Bayne[1], T. I. Wellicome[1,2]

[1]Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada
[2]Canadian Wildlife Service, Environment Canada, 9250 49 Street NW, Edmonton, Alberta T6B 1K5, Canada
[3]*Present address:* Royal Alberta Museum, 12845 102 Avenue, Edmonton, Alberta T5N 0M6, Canada

ABSTRACT: Artificial sensory disturbances (sound and light) can extend far beyond the physical footprint of human development. Nocturnal predators such as owls may be influenced by artificial sound and light, as they depend on aural and visual cues when hunting. Owl nocturnal movements may also be altered by physical changes to the landscape, as these can affect prey availability. The burrowing owl population in Canada has declined by 90% and was classified as endangered in 1995. We tracked adult male burrowing owls *Athene cunicularia* with GPS dataloggers, and used resource selection models to examine their night-time movement patterns in relation to human infrastructure and associated artificial light and sound. The amount of sound and light from compressor stations, oil wells, traffic, towns and buildings was calculated for each owl and random location. We found that owl night-time space use was better predicted by distance to infrastructure on the landscape than by intensity of sensory disturbance. Burrowing owls did not show a pronounced avoidance of artificial sound. Infrastructure best predicts owl space use, perhaps because associated changes to vegetation alter prey abundance and availability. While human infrastructure most influenced owl nocturnal space use, the extent to which ecosystems are impacted by artificial sound and light is becoming clearer and needs to be considered when assessing the total effect of human development on species.

KEY WORDS: Sensory disturbance · Human development · Light · Sound · Resource selection · Burrowing owl · *Athene cunicularia*

## INTRODUCTION

The greatest threat to native species from human development is habitat loss (Brooks et al. 2002, Fischer & Lindenmayer 2007). However, an increasing body of evidence suggests that habitat degradation caused by anthropogenic sensory disturbances (e.g. noise and light) often exacerbates the direct effects of habitat loss by degrading the quality of the remaining habitat (Francis & Barber 2013). Sensory disturbances affect a wide range of taxa (Longcore & Rich 2004, Francis & Barber 2013) and can alter a variety of breeding and foraging behaviours (Brumm 2004, Titulaer et al. 2012). In extreme cases, sensory disturbance has resulted in animals completely avoiding otherwise suitable habitat (Rotics et al. 2011, Blickley et al. 2012). Thus, if the impacts of sensory disturbances are not quantified, the cumulative area impacted by human developments may be underestimated.

It is challenging to separate the behavioural effects caused by the physical changes in vegetation structure and composition resulting from human development (hereafter, 'footprint') from those caused by sensory disturbances (hereafter, 'disturbance'). Studies evaluating the effects of noise on terrestrial wildlife typically have compared animal abundance or behaviour in the vicinity of quiet versus noisy roads, or

*Corresponding author: corey.scobie@gov.ab.ca



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close to versus far from noisy roads. With such study designs, it is difficult to separate the effects of footprint from disturbance (Delgado et al. 2008, Summers et al. 2011), especially for wide-ranging species whose home ranges are influenced by multiple sensory disturbances. In these situations, it is difficult to use a noisy versus quiet or bright versus dark dichotomy when conducting analyses. Nonetheless, understanding how wide-ranging species, such as predators, react to disturbance is essential because they rely heavily on visual and auditory cues to detect and capture prey.

Sound emanating from anthropogenic sources has the potential to affect both predators and their prey. While travelling, prey may disturb vegetation, causing it to rustle, and rustling vegetation typically creates sound in frequencies above 1.6 kHz (Miller 1978, Schomer & Beck 2010). Many predators rely on sound in these high frequencies to detect, locate and capture small mammals (Payne 1971, Knudsen & Konishi 1979, Singheiser et al. 2010). Mice select routes to minimize visibility and production of sound in these frequencies (Barnum et al. 1992) and in some situations travel on quieter substrates (Roche et al. 1999). Consequently, predators that use acoustic cues may avoid hunting in noisy areas if such noise affects their ability to detect the specific sounds made by moving prey (Hübner & Wiegrebe 2003, Goerlitz et al. 2008, Siemers & Schaub 2011). When noisier areas are not avoided, predators that rely on acoustic cues for hunting are less successful in capturing prey than when hunting in quieter areas (Schaub et al. 2008). Importantly, high frequency sounds travel shorter distances from the source than low frequency sounds (see ISO 1993), so the potential impact of anthropogenic sound on hunting may depend on which frequencies of sound are emitted.

Artificial light can affect circadian rhythms of animals at all times of the day, but the greatest impacts are typically on species that are active at night (Longcore & Rich 2006, Gaston et al. 2013). The impact of artificial light on predators in particular is unclear. Nocturnal predators, such as owls, rely on both sight and sound when hunting (Dice 1945, Kaufman 1974), requiring a minimum level of light and acoustic cues to detect prey. Accordingly, most owls are more active (Penteriani et al. 2011, Frye & Jageman 2012) and bring more prey back to their young (Poulin & Todd 2006, Zárybnická et al. 2012), during crepuscular periods. Therefore, artificial light could actually benefit owls if it extends the period of time that they can see prey at night. Conversely, although light increases the detectability of prey, it could be detrimental if prey availability decreases because prey remain closer to cover when it is brighter (Lockard & Owings 1974, Kaufman & Kaufman 1982, Clarke 1983, Wolfe & Tan Summerlin 1989, Kotler et al. 1991, Daly et al. 1992). With increased illumination, prey move and forage less (Abramsky et al. 2004, Bird et al. 2004, Rotics et al. 2011), likely in response to increased predation risk (Clarke 1983, Kotler et al. 1991), so predators may need to search larger areas to find the same amount of prey under such conditions (Rockhill et al. 2013).

The effects of anthropogenic activities on predators that are hunting are often studied by tracking individuals as they travel through a landscape. However, few studies have attempted to separate the relative importance of footprint versus disturbance on predatory behaviour. Those studies that have attempted to do this (Chubbs et al. 1993, Jiang et al. 2010, Neumann et al. 2013) have typically been confounded because they rely on coarse categories of sensory disturbances (high versus low) rather than directly measuring the magnitude of sensory disturbances. Given the strong overlap in space and time of multiple disturbances in the 'disturbance landscape' for a wide-ranging predator, more precise measurement is needed to evaluate how disturbance levels alter predator behaviour.

Detailed measures of sensory disturbances are needed to evaluate the response of predator space use to artificial light and sound. Both light and sound are types of energy that move as waves through the air and decay as a function of distance. However, modelling only the distance to the nearest sound or light source will not accurately reflect resulting sound and light levels because of their differing physical properties and attenuations. Also, when sound or light from 2 sources spatially and temporally overlap, there is an increase in magnitude because of an additive effect, which is not captured by distance to source alone. Light waves are much smaller than sound waves, making them less susceptible to attenuation. Environmental conditions (wind, humidity, temperature, atmospheric pressure) and ground surface have a large effect on the propagation of sound waves, but those factors do not affect light as it travels from a source. The intensity of sound and light emanating from human structures can be quite diverse, resulting in a landscape with spatially and temporally varying sound and light levels. This is the first study to consider these factors and develop detailed measures of light and sound in an effort to examine space use of a nocturnal predator in relation to artificial sensory disturbances.

To study the influence of both light and sound on the space use of a predator that relies on both auditory and ocular cues while hunting, nocturnal movement patterns must be quantified. Burrowing owls occur throughout North and South America and the IUCN lists the entire population (≥15 subspecies) as Least Concern due to its large range (BirdLife International 2012). The Western burrowing owl *Athene cunicularia hypugaea* in Canada was classified as endangered in 1995 (Wellicome & Haug 1995), where it has declined by 90 %, resulting in less than 800 breeding pairs (Environment Canada 2012). Portions of Canada's grasslands have been developed significantly, forcing burrowing owls to live in landscapes with varying levels of anthropogenic light and sound. Burrowing owls capture the majority of their prey during twilight (Poulin & Todd 2006); however, they do not have asymmetrical ears (Volman & Konishi 1990) to help them effectively locate prey by sound, so they cannot capture prey in very low light conditions like owls that do have asymmetrical ears (Dice 1945). Thus, burrowing owls rely on both hearing and sight to detect prey. If owl movement patterns are influenced by artificial light and sound, that influence will be most pronounced during twilight hours when owls are moving most and the largest number of prey are brought back to the nest (Poulin & Todd 2006).

To examine the night-time movement patterns of a predator in relation to human infrastructure and associated artificial light and sound, we tracked the nocturnal foraging of adult male burrowing owls wearing GPS dataloggers under 2 temporal periods (twilight and night). If owl nocturnal space use is influenced most by sensory disturbance associated with human development, then models containing only those variables will fit best. If the best models contain variables relating to the footprint, then owls are likely more affected by the physical landscape changes that result from human development. If these disturbances are sufficient to alter hunting behaviour, we predict that male owls will be most influenced by sensory disturbances during twilight hours and will select areas with lower sound levels in high sound frequencies and lower levels of artificial light to enable effective detection of prey in areas where prey availability is greatest.

## MATERIALS AND METHODS

Between 2007 and 2010, we monitored 521 burrowing owl nesting attempts within the dry mixed-grass ecoregion of southern Alberta and Saskatchewan, Canada, where cattle ranching and annual crop production are the primary land uses. Petroleum development also occurs throughout the study area in Alberta and in localized areas in Saskatchewan. Within the burrowing owl range in Alberta and Saskatchewan (~177 000 km$^2$), there are over 190 000 gas wells, 160 000 oil wells (IHS Energy 2011c), 1600 compressor stations and other petroleum facilities that pro-

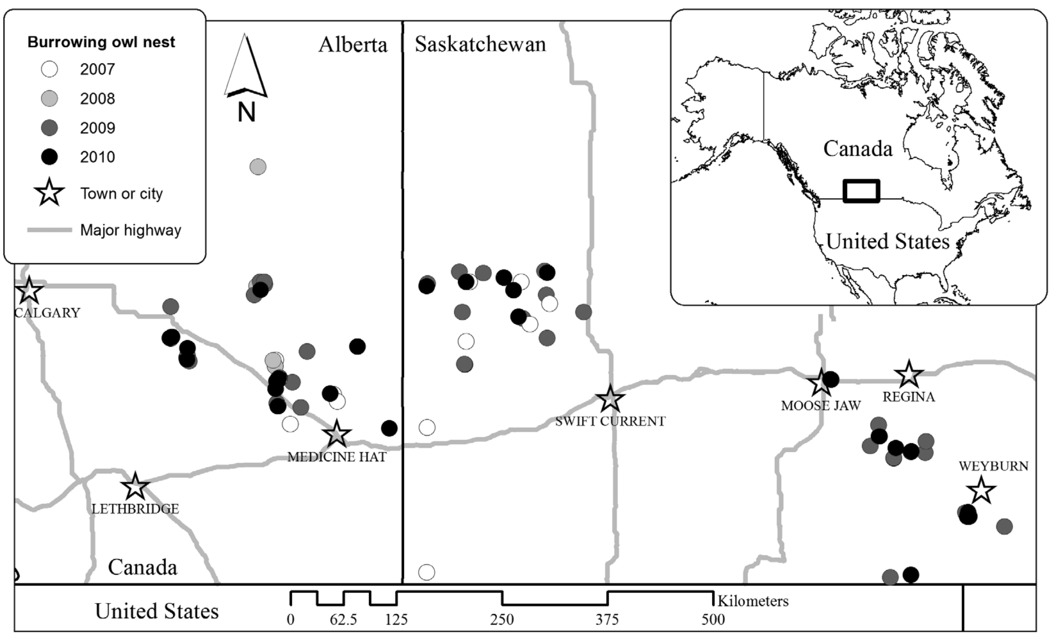


Fig. 1. Locations of burrowing owl *Athene cunicularia* nests from which each adult male was tracked with a GPS datalogger

duce sound (IHS Energy 2011a), over 20 000 km of paved roads (IHS Energy 2011b) and approximately 500 000 people that live in 24 urban areas (Statistics Canada 2012). Less than 30 % of the grasslands in Alberta, Saskatchewan and Manitoba remain uncultivated (Gauthier & Wiken 2003).

At a subset of the burrowing owl nesting attempts monitored, 84 adult males were tracked with GPS dataloggers (Fig. 1). Nests were located in early May using call play-back surveys, and were visited once per week throughout the breeding season (see Fisher et al. 2015 for additional details). After the female finished laying, and before juveniles fledged, each adult male owl was captured with either a 1-way walk-in (Winchell 1999) or bow-net trap (Bloom 1987). During these stages in nesting, the male delivers over 80 % of the prey to the nest (Poulin & Todd 2006) and thus travels more and farther from the nest than the female. Therefore, tracking the male will give us the greatest ability to detect whether landscape features or sensory disturbances influence where owls spend their time while hunting. Each trap had 1 of the following lures: (1) a dead mouse, (2) a speaker playing a burrowing owl primary call, (3) a decoy burrowing owl, or (4) some combination of these 3 lures. A 7 g GPS datalogger (TechnoSmArt, Guidonia Montecelio) was attached to each owl, using Teflon ribbon in a backpack-style configuration. Teflon was secured to the datalogger with light-weight packing tape containing a tear-proof fibreglass cross-weave. Males were returned to their nest burrows for release after dataloggers were attached. The dataloggers were upgraded by the manufacturer each year, resulting in varying options and program schedules over time. Dataloggers were programmed to turn on and take locations every 2 s (2009 and 2010), every 15 min (2007, 2009, 2010), or every hour (2008). The following data were stored in the internal memory within the GPS datalogger: latitude, longitude, speed, altitude, dilution of precision, Greenwich Mean Time and date. To retrieve the data, each owl was re-trapped after approximately 12 d, by which time its GPS datalogger battery had been depleted. Owl locations with dilution of precision >1.5, speed >64 km $h^{-1}$, and altitude ≤20 m below and ≥80 m above the elevation of the owl's nest were excluded. One location every 15 min (2007, 2009, 2010), or else 1 location every hour (2008), was selected for these analyses. The accuracy of the GPS dataloggers was tested by measuring the distance between locations from a stationary GPS datalogger placed on a fence post for 3 d and the stationary datalogger's location as determined with the averaging function in a hand-held GPS unit. All data were collected by trained field staff in possession of valid animal care approval, federal and provincial research permits and bird banding licenses (permit number 10796).

Burrowing owl GPS datalogger locations were used to examine owl foraging areas and movement patterns. For each owl, we delineated the average hourly step length (distance between successive owl locations) area of the 100 % minimum convex polygon and for each night tracked using ArcMap 10.1 (ESRI) and Geospatial Modelling Environment (Beyer 2012). Average step length and distance to nest were calculated for each owl for each hour of the night. Each year, land-cover surrounding the nest of each tracked owl was documented by driving the roads around the nest and recording the land-cover types on aerial photographs. These aerial photographs were digitized in a GIS environment onto SPOT5 imagery (2006 coverage). Land-cover types (permanent cover [native and tame grassland], annual crop, riparian area [sparse vegetation and seasonally dry], road, water bodies [standing water all year], buildings [residential and agricultural buildings], shrubs and trees) were all included in statistical models, with permanent cover being the reference category.

We included in our analyses owl locations taken between nautical twilight start and end, to ensure that we used only locations from nocturnal foraging activities (Poulin & Todd 2006). Owl prey delivery rates vary considerably between the twilight and night period (Poulin & Todd 2006), so locations in these 2 periods were analysed separately. All locations between sunset and sunrise were categorized as night locations, and all remaining locations that occurred between night and nautical twilight start and night and nautical twilight end were categorized as twilight locations. Sun position times were determined from the National Research Council Canada website (www.nrc-cnrc.gc.ca/eng/services/sunrise/advanced.html) using the coordinates of the nests.

Prior to analyses, all data were evaluated for co-linearity among covariates. When co-linearity was detected, the variable with the highest variation inflation factor (VIF) was removed and the VIF was then recalculated for each variable. This was repeated until all VIFs were <3 (Quinn & Keough 2002).

'Available' area was defined as a radius around the nest equal to the maximum distance that an individual owl travelled during the period it was tracked (Glenn et al. 2004). Using this area as available allows an examination of the factors that influenced where owls placed their foraging areas in relation to their nest burrows. This is the best way to detect avoidance of areas near the nest. For each owl location, 5 random locations were generated within the available area. Land-cover, sound, light (2009 Defense Meteorological Satellite Program average light images [Data collected by the US Air Force Weather Agency and processed by NOAA's National Centers for Environmental Information; http://ngdc.noaa.gov/eog/dmsp/downloadV4composites.html), and distance to nest burrow, nearest compressor station, oil well, paved road, building and town were determined for each owl datalogger location and each random location. The Defense Meteorological Satellite Program average stable light images for 2009 were used to determine the amount of artificial light at each owl and random location. These images are based on data collected by the US Air Force Weather Agency and Processed by the National Oceanic and Atmospheric Administration National Geophysical Data Center (now the National Centers for Environmental Information). Pixels in the image were given values of 0 if they contained ephemeral light or no light, whereas cities, towns and other sites with persistent light contained values ranging from 1 to 63, depending on the intensity of light in that pixel. Distances to the nearest compressor station, paved road and oil well were limited to features that were within a radius equal to the available area plus 5 km. Features within these spatial limits were used because that area includes all of the sound sources used to calculate the sound pressure level at each datalogger and random location. Also, it is possible that light from features outside the available area extend into the available area, so we wanted to ensure that these light sources were included in the footprint models. The model for each owl contained all covariates with VIFs $<3$.

We used resource selection functions (RSFs) to examine owl space use in relation to human infrastructure and in relation to the light and sound emanating from this infrastructure. To understand if the sensory disturbance or the footprint of human development most strongly influenced owl night-time movements, 3 models (baseline, disturbance and footprint) were compared for both nocturnal periods (twilight and night). The baseline model contained land cover and distance to the nest burrow. The disturbance model contained land cover, distance to nest burrow, light, and sound. The footprint model contained land cover, distance to nest burrow, and the nearest distance to each feature from which either sound or light emanates (compressor station, oil well, paved road, town and human building). Distance to each of these landscape features was used because sound emanates from compressor stations, oil wells and high traffic-volume roads and light emanates from compressor stations, cars driving on paved roads and towns and buildings (e.g. farm yards, agricultural buildings, etc.). Sound and light levels are not perfectly correlated with distance to sound and light sources because each source has different levels of light and sound that are subject to differing sources of attenuation, and sound and light can combine to produce areas with higher disturbance levels.

The 3 models (baseline, disturbance and footprint) were compared only for owls with exposure to artificial light or sound in the disturbance model and if all 3 models converged. A generalized linear model with a binomial error and logit link was used to analyse the data for each owl. Random locations were given one-fifth the weight of the datalogger locations of used points when computing statistical significance (see Aldridge & Boyce 2007). A 2-step approach was employed, whereby the coefficients and standard errors from the model for each owl were used to calculate the inverse variance weighted mean (Nielsen et al. 2009), standard error, $z$-value and p-value for each covariate. A generalized linear mixed model (with each owl as the random variable) was also used to determine owl selection within the available area. Models with the lowest Akaike's information criterion (AIC; Burnham & Anderson 2002) were identified as the best fitting models. The negative regression coefficients are presented for distance variables so that the response of the owl (selected versus avoided) matched the signs (positive versus negative) of the coefficients for the other variables.

## Sound

The number of decibels above that which can be detected by an owl was determined for each one-third octave band for each owl and random location. Following the protocol outlined in ISO 8297 (ISO 1994), sound was measured with a handheld Brüel & Kjær Type 2250 sound level meter at all compressor stations within the available area plus 5 km. Sound from individual oil wells does not vary significantly, so following ISO 3746 (ISO 2010), sound was measured at a subset of each type of sound-producing oil well (pump jacks and screw pumps). The equivalent continuous ($LZ_{eq}$) sound power level was then calculated for each one-third octave band between 0.5 and 10 kHz for each sound source, using the calculations provided in each corresponding standard. The average sound power level of all oil wells for each one-

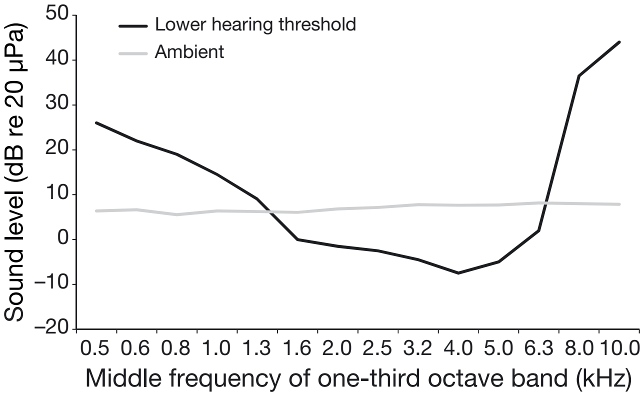


Fig. 2. Lower hearing threshold of eastern screech owls *Megascops asio* (adapted from Brittan-Powell et al. 2005) and ambient sound level for each one-third octave band from 0.5 to 10 kHz. Owls can hear sounds that are louder than ambient sound or are above their lower hearing threshold

third octave band was used when modelling sound propagation from each oil well. During each day of sound data collection in the field, ambient sound ($L_{eq}$(1 min)) was measured at locations at least 5 km away from sound-producing structures. All of our ambient sound measurements were taken during the day, so the lowest sound pressure level of all ambient sound measurements for each one-third octave band was used as the night-time ambient sound pressure level (Fig. 2). The sound level meter was calibrated with a Brüel & Kjær sound level calibrator type 4231 at the beginning of each day prior to the collection of sound measurements.

Traffic data were collected from 15 roads that ran near owl nests in our study. Pneumatic tube traffic counters (MetroCount; MC5600 Series Roadside Unit) were deployed on 9 roads, traffic data for 4 roads were provided by the Saskatchewan Ministry of Highways and Infrastructure, and data for 2 roads were provided by the Alberta Ministry of Transportation. The pneumatic tube traffic counters recorded the date, time, speed and class of each vehicle that passed. Data provided by the provinces contained average hourly traffic volume, speed and proportion of heavy vehicles for each day. All data were collected for dates during the summer within 1 yr of the owl being tracked. Individual vehicle hits recorded on the traffic counters were used to calculate average traffic volume, speed, and percent heavy vehicles for each hour the owls were tracked (sunset to sunrise). Vehicles were considered heavy if they were in the fourth weight class or greater according to the Federal Highway Administration (2013).

Average hourly continuous energy equivalent sound power level of traffic (herein average traffic sound) was calculated for roads within the available area plus 5 km. Hourly traffic volume, speed and proportion of heavy vehicles were used to calculate energy equivalent sound level for each hour ($L_{eq}$(1 h)) for each road (using Besnard et al. 2009). Only roads with at least 20 vehicles $h^{-1}$, for at least 1 h during the nocturnal period, were included. Traffic volumes <20 vehicles $h^{-1}$ produce infrequent sensory disturbance and would not likely affect owl movement patterns at a scale detectable by the frequency of our owl locations. For the same reason, average traffic sound was used instead of the instantaneous sound from the loudest vehicle ($L_{eq}$(max)) that passed each hour.

Sound propagation and attenuation, from sound sources to each owl and random location, were calculated using the international standards ISO 9613-1 (ISO 1993) and 9613-2 (ISO 1996). Sound was modelled from each compressor station and each road with ≥20 vehicles $h^{-1}$, and from the nearest 10 oil wells, to each owl location and each random location. For calculating the attenuation of sound due to atmospheric interference, 5 random locations were randomly matched with 1 owl location by assigning the same above-ground height, date and time as was recorded at the corresponding owl location. Characteristics of the tallest hill (Natural Resources Canada 2000) blocking the line of sight between the sound source and receiver (owl or random location) were used to calculate attenuation from screening. Hourly temperature, humidity and atmospheric pressure from the nearest Environment Canada weather station (http://climate.weather.gc.ca/index_e.html#access) were used to calculate the atmospheric attenuation coefficient for each owl and random location. ArcMap 10.1 (ESRI) was used to extract all other cartographical variables needed for attenuation calculations. The sound pressure levels from all sources were then added together for each owl and random location.

### Owl detection of sound

To adjust differences in hearing sensitivities, the minimum sound level that an animal can detect in each frequency can be extracted from lower hearing threshold audiograms and be used in sound detection calculations to better reflect how a species perceives sound (Pater et al. 2009). A burrowing owl audiogram was not available, but they have symmetrical ears and hunt similar prey to that of eastern screech owls *Megascops asio*, so the auditory brainstem response for the latter species (Brittan-Powell et al. 2005) was converted to a behavioural lower hearing threshold by subtracting 30 dB from the sound pressure level in each one-third octave band (Brittan-Powell et al. 2002).

Sound from the source(s) was detectable at the receiver location (owl or random location) if the sound pressure level was above ambient sound levels when ambient sound was above the lower hearing threshold (Fig. 2). If ambient sound was below the lower hearing threshold, then sound was detectable if the sound pressure level from the source(s) was greater than the lower hearing threshold. These criteria were then used to calculate the number of decibels that could be detected at the receiver location for each one-third octave band. A value of 0 was assigned if no sound could be detected.

Eastern screech owls hear best in the 4 kHz one-third octave band (Brittan-Powell et al. 2005), but have similar abilities to detect sounds between 1.6 and 6.3 kHz when masking from ambient sounds is also considered (Fig. 2). The sound levels were highly correlated for all frequencies, so the frequency with the highest VIF was selected. The one-third octave band with the highest VIF was 2.5 kHz.

The distance from which burrowing owls can still detect sound from each source (i.e. the listening area; see Barber et al. 2010) in each one-third octave band from 0.5 to 10 kHz was calculated. The average sound power level of each sound source (Fig. 3) and the formulae from international standards 9613-1 (ISO 1993) and 9613-2 (ISO 1996) were used to calculate sound propagation and attenuation under the average nighttime environmental conditions experienced by owls while they were being tracked. The calculations assumed no barriers, and that there was grassland between sound source and receiver, and that wind speed was negligible. Owl detection of sound was determined using the same criteria outlined above.

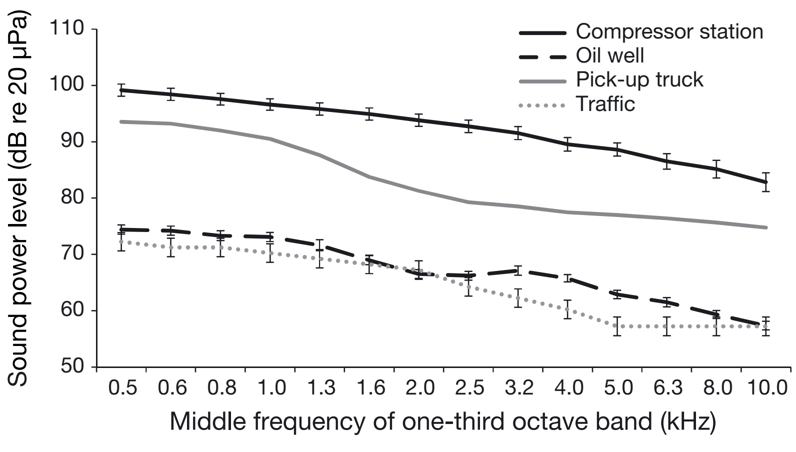


Fig. 3. Average sound power level of 38 compressor stations, 44 oil wells (35 pump jacks and 9 screw pumps combined), average hourly continuous energy equivalent sound power level of traffic ($L_{eq}$(1 h)) on 14 roads and the average maximum instantaneous sound power level ($L_{max}$) of a half-tonne pick-up truck travelling 97 km h$^{-1}$ on a gravel road for each one-third octave band from 0.5 to 10 kHz. Error bars are 95% confidence intervals

### Home range size

We also used linear regression to examine the relationship between the total area within each owl's nocturnal home range and the area within the home range that was exposed to artificial light and sound in the 2.5 kHz one-third octave band. Prior to analysis, light and sound were log-transformed because they each contained outliers, and we also modelled these variables as categorical variables (present in home-range = 1, absent = 0). All models contained the number of nights tracked as a covariate, and we used AIC to select the form of the sensory disturbance variable that best fit the data.

## RESULTS

We tracked 84 male owls for an average (±SE, unless otherwise noted) of 3.7 ± 0.33 nights (range: 1–10) per owl. All owls were tracked between 17 May and 19 July. From these owls, we acquired a total of 8760 locations, with an average of 104 ± 9.7 locations (7–332) per owl. The GPS dataloggers were successful in obtaining fixes 96% of the time (74–100%). Locations from the stationary test-datalogger were an average of 4.3 ± 2.9 m (SD) from the test location, with a dilution of precision ≤1.5. While owls were being tracked, average hourly humidity was 76.5 ± 5.11%, temperature was 11.7 ± 1.31°C, atmospheric pressure was 93.1 ± 0.32 kPa, and wind speed was 3.3 ± 0.64 km h$^{-1}$.

Owl step length and 100% minimum convex polygon were smaller in the first full night after datalogger attachment than in the remaining tracking nights, so owl locations from the first full night were excluded from the analyses. This left 6196 locations from 63 owls, over an average of 4.7 ± 0.38 nights, with an average of 98 ± 10.92 locations per owl.

We measured sound at 38 compressor stations and 44 oil wells (35 pump jacks and 9 screw pumps), and took 21 ambient sound measurements. Sound

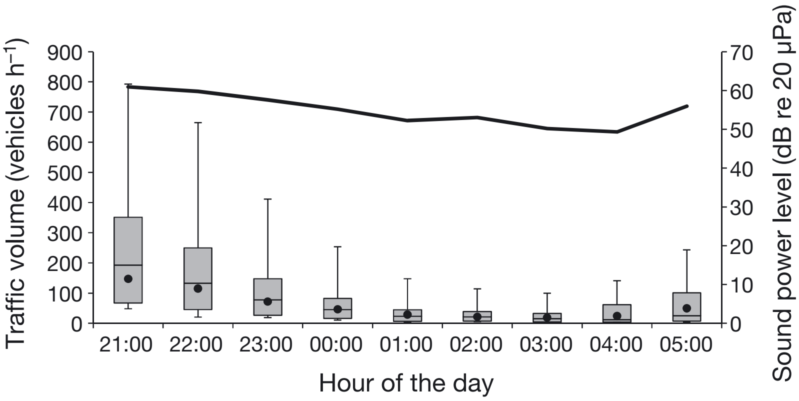


Fig. 4. Hourly traffic volume (box plots) and average hourly continuous energy equivalent sound power level (solid line) of traffic (in 2.5 kHz one-third octave band) on 14 paved roads near burrowing owl *Athene cunicularia* nests where owls were tracked with GPS dataloggers. Upper limit of a box plot is the third quartile; middle line is the median; lower limit of the box is the first quartile; whiskers represent minimum and maximum values, and the black dot is the average

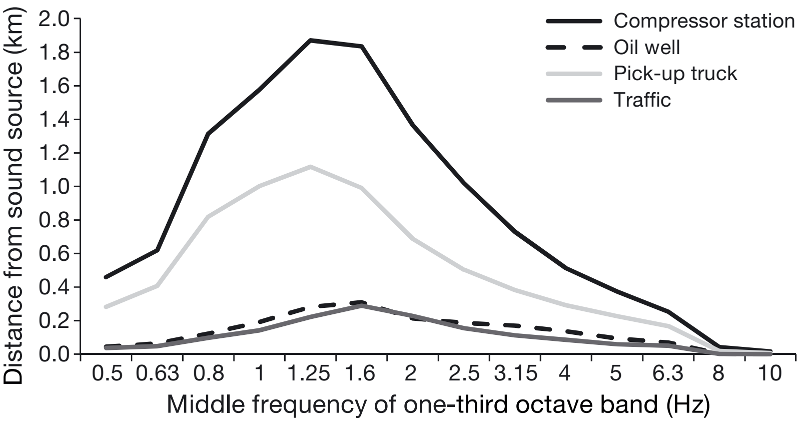


Fig. 5. Distance at which a burrowing owl *Athene cunicularia* can detect each of 4 sound sources in the 2.5 kHz one-third octave bands. Sound levels used in the calculations were the average sound power levels of compressor stations and oil wells. For traffic, the average continuous energy equivalent sound power levels were calculated across all hours for traffic for each road, and then averaged for all roads. The sound level used for the pick-up truck calculations was the average instantaneous sound power level of a half tonne pick-up truck travelling at 97 km $h^{-1}$ on a gravel road. Calculations assume that there are no barriers between source and receiver (owl) and that wind is negligible

power levels for all sound sources were greatest in the lower frequencies (Fig. 3). On average, there were 2 compressor stations (0–11) and 31 oil wells (0–346) within the burrowing owl available area.

Average traffic sound was calculated for 14 paved roads that passed near the nest burrows of 29 owls tracked with dataloggers. The average hourly vehicle speed was 96.9 km $h^{-1}$ (91–100 km $h^{-1}$), average hourly proportion of heavy vehicles was 0.21 (0.15–0.38), and average hourly traffic volume was 58.0 vehicles $h^{-1}$ (range of averages: 19.0–146.8; Fig. 4). These roads were, on average, 4.58 km (0.04–10.12 km) from a nest. The average sound power level on these roads in the 2.5 kHz one-third octave band was 64.24 dB (55.6–72.9 dB). Compared to the sound power levels of oil wells and compressor stations, average traffic sound was low, especially in the high sound frequencies, primarily because of low traffic volumes (<100 vehicles $h^{-1}$ for all hours except 21:00 and 22:00 h, Fig. 4). The average speed of vehicles travelling at night was 97 km $h^{-1}$. The maximum sound power level ($L_{eq}$(max)) of a pickup truck travelling at 97 km $h^{-1}$ is 79.3 dB in the 2.5 kHz one-third octave band.

Owls are likely able to detect sound in the 2.5 kHz one-third octave band up to 1020, 187, 156 and 504 m from compressor stations, oil wells, traffic and a passing pickup truck driving at 97 km $h^{-1}$, respectively, but they can hear sound in the 1.25 or 1.6 kHz one-third octave band from all of these sources the farthest (Fig. 5). This is because owls hear best in higher frequencies (i.e. 4 kHz), but sound in high frequencies are affected more by atmospheric attenuation, and therefore do not travel far from the source. The sound levels produced by these sources are also greater in the low frequencies (Fig. 3), and owl hearing ability declines dramatically in frequencies lower than 1.25 kHz (Fig. 2).

On average, 3.2 ± 0.01% (0–26.7%) of the home range contained sound audible to owls in the 2.5 kHz one-third octave band and 19.4 ± 0.03% (0–100%) contained artificial light. We found no significant relationship between owl home-range sizes and amount of artificial light or sound in the 2.5 kHz one-third octave band.

During both night-time and twilight, the footprint RSF models were better predictors of resource selection than the disturbance or baseline models (Fig. 6). The footprint model was also better for the generalized linear mixed models (GLMMs) (Table 1). Models containing sensory disturbance variables were the best models during the twilight hours for 39% of owls (Fig. 6).

The inverse variance weighted (IVW) mean and GLMM RSF coefficients indicate that owls were weakly attracted to areas with higher sound levels in

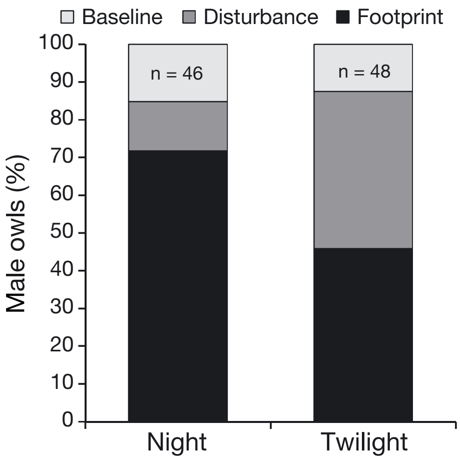


Fig. 6. Percent of burrowing owls *Athene cunicularia* with the baseline, disturbance or footprint model as the best resource selection function (RSF) model. The baseline model contained land cover and distance to the nest burrow; the disturbance model contained land cover, distance to nest burrow, light and sound; and the footprint model contained land cover, distance to nest burrow and the nearest distance to each feature from which either sound or light emanates (compressor station, oil well, paved road, town, building). During both night and twilight, the footprint models were the best predictors of selection

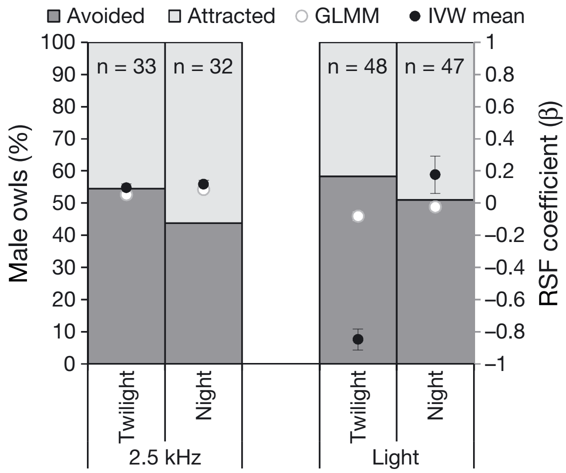


Fig. 7. Percent of male burrowing owls *Athene cunicularia* attracted to ($\beta > 0$) or avoiding ($\beta < 0$) sound (2.5 kHz) and light and the inverse variance weighted (IVW) mean and generalized linear mixed model (GLMM) resource selection function (RSF) coefficients (β). Bars are related to the left *y*-axis; circles and error bars are related to the right *y*-axis. Error bars are 95 % confidence intervals

the 2.5 kHz one-third octave band, but only about half of the owls had a positive RSF coefficient (Fig. 7). Although there is only about a 15 % difference between the number of owls avoiding sound during night versus twilight, more owls were avoiding higher audible sound during twilight hours (Fig. 7). At night, 18 owls showed selection for areas with higher sound levels (Fig. 7), but only 7 showed statistically significant attraction ($p < 0.05$). Each of these 7 owls was also significantly attracted to at least 1 of the sound-producing structures in the footprint models. In addition, the footprint model was the best fitting for 5 of those 7 owls. During twilight hours, 15 owls showed selection for areas with higher sound levels (Fig. 7), but only 5 significantly so. Four of these 5 owls were significantly attracted to at least 1 sound-producing structure, and the footprint model fit best for all 5.

Table 1. Comparison of burrowing owl *Athene cunicularia* generalized linear mixed models (GLMM) resource selection functions (RSF) using Akaike's information criterion (AIC). Baseline model contained land cover and distance to the nest burrow; disturbance model contained land cover, distance to nest burrow, light and sound; footprint model contained land cover, distance to nest burrow and the nearest distance to each feature from which either sound or light emanates (compressor station, oil well, paved road, town, building). *k* is the number of parameters in the model

| Model | *k* | AIC | ΔAIC |
|---|---|---|---|
| **Twilight** | | | |
| Footprint | 14 | 29386 | 0 |
| Disturbance | 12 | 29818 | 433 |
| Baseline | 9 | 30052 | 667 |
| **Night** | | | |
| Footprint | 14 | 27945 | 0 |
| Disturbance | 12 | 28964 | 1018 |
| Baseline | 9 | 29529 | 1584 |

Significance between RSF coefficients in the IVW mean and GLMM models for light differed from each other, but followed a similar trend where there were smaller values (increased avoidance) during twilight hours and larger values (increased selection) during night-time hours (Fig. 7).

There was less agreement between the IVW means and GLMM RSF coefficients for distance to nearest facility and oil well, although most owls are attracted to these features during both twilight and night-time (Fig. 8). Though not always significant, the IVW mean RSF coefficients showed more attraction to these features during the night than during twilight hours (Fig. 8). All RSF coefficients showed that owls were significantly attracted to paved roads in both time periods (Fig. 8).

## DISCUSSION

Owl night-time space use was better predicted by distance to infrastructure on the landscape than by degree of sensory disturbance. The best model for

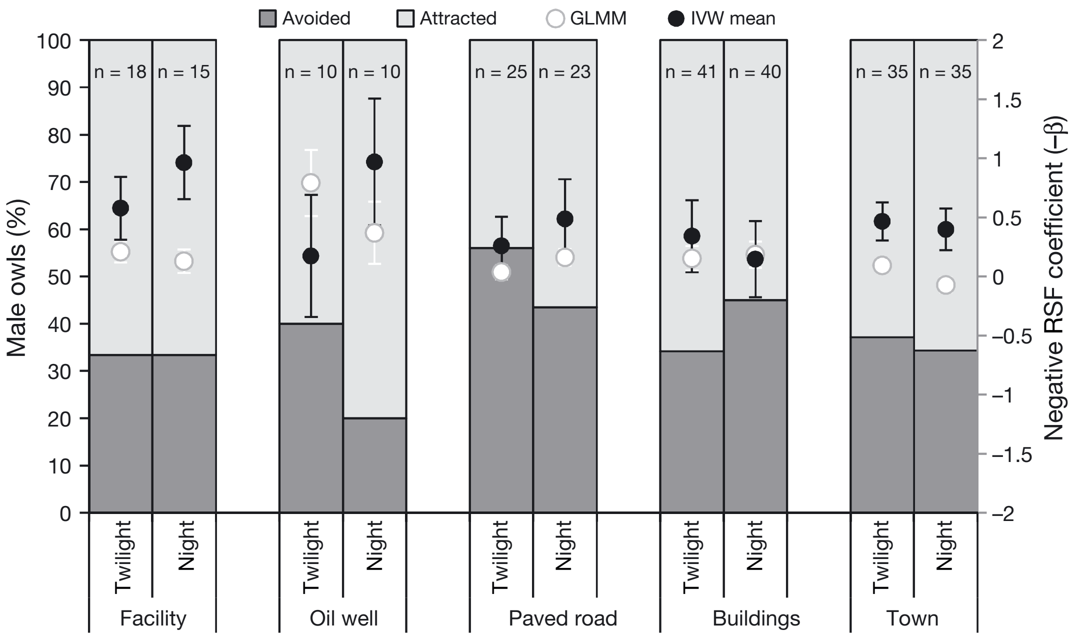


Fig. 8. Percent of male burrowing owls *Athene cunicularia* attracted to (−β > 0) or avoiding (−β < 0) compressor stations, oil wells, paved roads, buildings and towns and the inverse variance weighted (IVW) mean and generalized linear mixed model (GLMM) resource selection function (RSF) coefficients (−β). This figure shows variables that were the distance to the nearest feature, so the negative of the RSF coefficient is presented such that the direction of the sign (positive vs. negative) corresponds to owl response to the feature (attracted vs. avoided). Bars are related to the left *y*-axis; circles and error bars are related to the right *y*-axis. Error bars are 95 % confidence intervals

the majority of owls, and mixed effect models, contained distance to nearest human structures, and not variables related to the sound and light that these human structures emit. This differed from our predictions that owl nocturnal space use would be most influenced by anthropogenic sound and light levels. Owls rely on auditory and visual cues when hunting at night, but our analysis indicates that their nighttime movement patterns were better predicted by changes to the physical landscape than by sensory disturbances. The construction of buildings, roads, compressor stations and oil wells on the landscape changes land-cover type, vegetation height and density, presence of perches and amount of edge habitat. These alterations to the landscape could affect prey abundance, prey availability, perch availability and predation risk. It is likely a combination of these landscape changes that is influencing owl nocturnal space use.

We suggest that the greatest influence on owl nocturnal space use from alterations to land cover resulted from changes to prey habitats and populations. Small mammals depend on vegetation for cover and food, without which their populations cannot persist. Although artificial sound and light can influence prey abundance and availability (Francis et al. 2011, Gaston et al. 2013), changes to the vegetation from construction of human features on the landscape probably has a much larger impact on prey populations than noise or light (Andrén 1994, Sauvajot et al. 1998, Mortelliti et al. 2009). Most roads in the Canadian grasslands follow the 1 mile (~1.6 km) section lines originally laid out by the Dominion Land Survey of Canada in the late 1800s. Agricultural and industrial access roads reach deep inside those square-mile sections, leaving little of the landscape that is <400 m from the nearest road and, therefore, almost all land is influenced by proximity to this human footprint. Construction of any road removes vegetation and typically changes adjacent vegetation type and height, resulting in widespread changes to grassland vegetation alongside roads and across the landscape (e.g. Wellicome et al. 2014). Ditches are associated with many roads, and vegetation grows taller and more dense in ditches because of greater local moisture levels, thus supporting greater small mammal populations (Poulin 2003). Direct removal and alteration of vegetation has a greater effect on small mammal populations, and thus space use of burrowing owls while hunting, than do effects from sensory disturbance.

If burrowing owl nocturnal space use was influenced by artificial sound, it would most likely be high frequency sounds, because they have the greatest potential to mask sounds made by prey (Miller 1978, Schomer & Beck 2010). Sound in the 2.5 kHz one-third octave band could only be potentially detected by owls within 3.2% of the home range, and sound in frequencies above 2.5 kHz could be heard in smaller percentages of their home range. During dawn and dusk, the majority (slightly more than half) of the owls avoided areas with greater sound levels in high frequencies, but selection coefficients indicated that some individuals were attracted to these areas. Even if owls had shown strong avoidance of sounds in high frequencies, the impact to their foraging areas would have been negligible because the amount of area where owls could hear high frequency sounds was small.

The small number of owls that showed strong (significant) attraction to areas with higher sound levels were more influenced by distance to the infrastructure producing the sound. The sound modelling we conducted is very accurate and gives the ability to detect subtle impacts to owl nocturnal space use, but due to the nature of sound propagation and attenuation, there still remains a correlation between distance to sound-producing structures and sound levels. This correlation may explain why half of the owls showed selection for areas with higher sound levels, as the structures themselves may have had some attribute (i.e. perches) that owls selected. Alternatively, it is possible that burrowing owls rely more on visual detection of prey when hunting in areas with greater sound levels and are able to exploit prey that are less able to hear predators, thereby increasing owl hunting efficiency. It is more likely that owls are attracted to other characteristics, particular to the developments that are producing these sounds, rather than the higher sound levels. There are a number of features other than sound associated with sound sources that are more likely to be attracting owls. There are typically other structures near the sound sources (e.g. fences) that do not produce sound that could be used as perches, which are important features for burrowing owls (Sissons 2003, Scobie et al. 2014). In addition, gravel roads are constructed to access oil wells and compressor stations, many of which have ditches that likely have high abundances of small mammals (Adams & Geis 1983, Sabino-Marques & Mira 2011, Ruiz-Capillas et al. 2013).

Sound in the middle frequencies (1.25 and 1.6 kHz) can be heard by burrowing owls farthest from the source, compared to either higher or lower frequencies. Anthropogenic sound in mid to low frequencies may not significantly affect an owl's ability to detect prey, but could affect its ability to attract a mate or effectively communicate warnings to mates or young. The primary song of the male burrowing owl that is used in pair formation and territory defense is comprised mostly of sound in low frequencies, ≤1.3 kHz (Martin 1973). Warning calls given by adult burrowing owls also consist mostly of low frequency sounds, not exceeding 2.5 kHz except when the highest degree of threat is being communicated (Martin 1973).

There is weak evidence that owls are influenced by artificial sound and light while foraging at night, but those effects are small when compared to the influence of physical changes to the landscape. Changes to prey abundance and/or availability and corresponding owl nocturnal space use likely explain why owls were most influenced by landscape changes from human development rather than by the sensory disturbances associated with human developments. Although owl nocturnal space use was least influenced by sensory disturbances, these effects should be considered, together with the effects from physical landscape changes, when determining effective habitat loss or degradation from development. While habitat loss is the greatest threat to terrestrial species (Wilcove et al. 1998, Sala et al. 2000), the extent to which ecosystems are impacted by artificial sound and light is becoming more clear (Francis & Barber 2013, Gaston et al. 2013) and needs to be considered when assessing the total effect of human development on species.

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