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Road traffic noise modifies behaviour of a keystone species

Graeme Shannon [a,*], Lisa M. Angeloni [b], George Wittemyer [a], Kurt M. Fristrup [c], Kevin R. Crooks [a]

[a] Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO, U.S.A.
[b] Department of Biology, Colorado State University, Fort Collins, CO, U.S.A.
[c] National Park Service, Natural Sounds and Night Skies Division, Fort Collins, CO, U.S.A.

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Prey species have to balance their foraging and vigilance behaviour in order to maximize nutritional and energetic intake while avoiding predation. Anthropogenic noise, a ubiquitous form of human disturbance, has the potential to influence antipredator behaviour through its effects on predator detection and perceived risk. Noise might increase perceived risk as predicted by the risk disturbance hypothesis, reduce risk by providing protection from disturbance-sensitive predators, or have no effect on antipredator behaviour if animals are tolerant of nonlethal forms of human disturbance. Road traffic is a pervasive source of anthropogenic noise, but few studies have experimentally isolated the effects of road noise on behaviour. Using systematic playback experiments, we investigated the influence of traffic noise on foraging and vigilance in a keystone species in North American prairie systems, the prairie dog, *Cynomys ludovicianus*. Exposure to road traffic noise significantly lowered aboveground activity, reduced foraging and increased vigilance, as predicted by the risk disturbance hypothesis. These effects were prevalent irrespective of temperature, a strong influence on such behaviours, and they were consistent across the 3-month study period, providing no evidence of habituation. Our results provide the first experimental investigation of the potential costs of this ubiquitous disturbance in a free-ranging mammal, demonstrating that road noise can alter key survival behaviours of this ecologically pivotal species. These findings highlight that the presence of animals in a location is no guarantee of population and ecological integrity, while also underlining the potential synergistic impacts of noise on a species that has already experienced severe declines across its historic range due to human disturbance. Globally, roadways have profound impacts on biodiversity, and quantifying the behavioural and fitness costs associated with different forms of disturbance such as noise is crucial for mitigation.

Animals need to optimize their behavioural time budgets to maximize reproductive success and survival. One of the primary mechanisms by which such optimization occurs in prey species is by temporally and spatially adjusting foraging behaviour to meet energetic and nutritional demands while minimizing predation risk (Brown & Kotler, 2004; Verdolin, 2006). Diverse behavioural strategies and morphological adaptations evolved across taxa in response to the selection pressure of predation risk (Abrams, 2000). Predator–prey interactions are also dependent upon a number of external (e.g. environmental conditions, food quality, competition) and internal (e.g. physiological state, hunger, growth) factors, which also change over time and space (Lima & Dill, 1990). There is considerable interest in how human disturbance interacts with the complex relationships between foraging and vigilance among predators and prey alike, and the implications of such disturbance on fitness and reproductive success (Beale & Monaghan, 2004; Frid & Dill, 2002).

Anthropogenic noise presents a pervasive source of human disturbance that has the potential to influence antipredator behaviour through its effects on predator detection and perceived risk. For example, noise can distract prey and take attention away from predator detection (Chan, Giraldo-Perez, Smith, & Blumstein, 2010), it can mask or inhibit the perception of predator sounds and conspecific alarm calls (Barber, Crooks, & Fristrup, 2010), and it can alter perceived predation risk and thus investment in antipredator behaviour (Quinn, Whittingham, Butler, & Cresswell, 2006). Different hypotheses make contrasting predictions for how noise, and human disturbance more generally, might affect perceived predation risk. For example, the risk disturbance hypothesis predicts that noise and other forms of anthropogenic disturbance will elicit antipredator behaviour, such as vigilance, that takes time and

* Correspondence: G. Shannon, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523, U.S.A.
E-mail address: graeme.shannon@colostate.edu (G. Shannon).

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energy from foraging and other fitness enhancing activities (Frid & Dill, 2002). Alternatively, human noise may have no effect on antipredator behaviour if animals are tolerant of nonlethal forms of human disturbance or if they have habituated over time to repeated exposures without negative consequence (Bejder, Samuels, Whitehead, Finn, & Allen, 2009). A third possibility is that prey species may use human activity and noise as a refuge from disturbance-sensitive predators (Berger, 2007; Francis, Ortega, & Cruz, 2009), such as ungulate species in Grand Teton National Park, Wyoming, U.S.A., which show reduced vigilance and increased foraging behaviour near busy roadways (Brown et al., 2012; Shannon, Cordes, Hardy, Angeloni, & Crooks, 2014).

One of the most ubiquitous sources of anthropogenic noise is road traffic, which has the potential to disturb animals hundreds of metres from roadways, making its biological effects of considerable interest to scientists and conservation practitioners (Barber et al., 2010). Indeed, roads are one of the most spatially extensive alterations of the landscape, with more than 80% of the contiguous U.S. within 1 km of a road (Riitters & Wickham, 2003). Correlation studies suggest that noise alters animal behaviour and reduces species richness, abundance and reproductive success (Arévalo & Newhard, 2011; Goodwin & Shriver, 2011; Halfwerk, Holleman, Lessells, & Slabbekoorn, 2011; Parris & Schneider, 2009). However, it is difficult to distinguish the effects of road noise from other forms of disturbance including habitat fragmentation, direct mortality, chemical pollution and reduced foraging opportunities (Summers, Cunnington, & Fahrig, 2011). Experimental playbacks that manipulate sound levels in the field have proved effective in controlling for the effects of confounding variables, with playback studies documenting reductions in sage grouse, *Centrocercus urophasianus*, lek attendance (Blickley, Blackwood, & Patricelli, 2012) and reductions in stopover habitat use by migratory songbirds (McClure, Ware, Carlisle, Kaltenecker, & Barber, 2013). These results, combined with studies of biological responses to quiet versus noisy gas compressor stations (Bayne, Habib, & Boutin, 2008; Francis, Kleist, Ortega, & Cruz, 2012; Francis et al., 2009), offer evidence that noise alone can degrade ecological function. However, our understanding of the mechanisms by which road noise negatively impacts animals requires greater investigation.

Anthropogenic noise research has been taxonomically biased towards birds, with only limited coverage of other taxa and behaviours outside of vocal communication (Shannon et al., n.d.). Moreover, studies that have experimentally explored the effects of transport noise (terrestrial and aquatic) on critical behaviours such as foraging and vigilance have been primarily investigated in laboratory settings (Schaub, Ostwald, & Siemers, 2008; Siemers & Schaub, 2011; Voellmy et al., 2014; Wale et al., 2013b; but see Bracciali, Campobello, Giacoma, & Sarà, 2012; Chan et al., 2010). We conducted a series of playback experiments to explore the effects of road traffic noise on the surface behaviour of prairie dogs, *Cynomys ludovicianus*, in their natural grassland habitat, representing the first exploration of the potential costs of this ubiquitous disturbance in a free-ranging mammal. Prairie dogs are social, live in high densities, rely on vocal communication and have defined antipredator behavioural responses (Hoogland, 1995; Slobodchikoff, Kiriazis, Fischer, & Creef, 1991) that are modified by human disturbance (Adams, Lengas, & Bekoff, 1987; Magle & Angeloni, 2011; Magle, Zhu, & Crooks, 2005; Pauli & Buskirk, 2007), and therefore present several advantages for anthropogenic noise research. Furthermore, as a politically controversial animal and keystone species within prairie and steppe ecosystems in North America, the behaviour and ecology of the prairie dog in the face of human disturbance is of broad interest (Kotliar, 2000; Miller et al., 2007; Soulé, Estes, Miller, & Honnold, 2005). This study aimed to determine whether surface activity, foraging and vigilance are altered in the presence of controlled broadcasts of road noise. Based on the risk disturbance hypothesis, we predicted that prairie dogs exposed to road noise would show reduced surface activity, while those remaining aboveground would invest more in vigilance and less in foraging.

METHODS

Study Site

The experiments were conducted on two prairie dog colonies located at the United States Department of Agriculture – Agricultural Research Service (USDA-ARS) Central Plains Experimental Range (CPER), 40 km northeast of Fort Collins, Colorado. The terrain is characterized by flat to gently undulating grass plains and receives a mean annual precipitation of 340 mm (Augustine & Derner, 2012). The colonies were comparable in size (~10 ha) and located 5 km apart in similar grassland habitat. The distance to the nearest road was 1.5 km, and human disturbance was minimal due to restricted access (predominantly limited to research scientists and land managers). A 200 m^2 observation area was demarcated at each site, with the centre of the colony forming the midpoint. Natural features were used to delineate the boundaries of the observation area.

Noise Stimulus

Road noise was recorded along Interstate 25, 16 km south of Fort Collins (1500–1600 hours Mountain Daylight Time, 20 March 2013). A calibrated sound level meter (Larson-Davis 831) was connected to a digital audio recorder (Roland R05) and positioned 14 m from the centre of the northbound lanes. The audio recording used the wav format and a 44 kHz sampling rate, while sound intensity was measured across one-third octave bands using the A-weighted filter. The Leq over the recording period was 77 dBA (re. 20 μPa: see Supplementary Fig. S1) at a distance of 14 m from the northbound carriageway, and traffic volume was approximately 5600 vehicles/h (Colorado Department of Transportation).

Playback Procedure

Twenty experiments were conducted from 21 May to 14 August 2013 (10 at each colony). The experiments included a 1 h exposure to traffic noise and a 1 h control period with presentation sequence alternating across experiments. A 25 min ‘relaxation time’ was initiated prior to each experiment and between treatment and control periods (Pauli & Buskirk, 2007; Powell, Robel, Kemp, & Nellis, 1994). At the start of the relaxation time, a single experienced observer (G.S.) entered a camouflaged observation hide (Ameristep portable hunting blind) that was located about 30 m outside the periphery of the colony; the hide provided a complete view of the colony while concealing the observer from the prairie dogs. Two minutes before the treatment period, road noise was broadcast 115 m from the centre of the colony and 15 m in front of the observation hide (Community R-5-94Z speaker and Bazooka MBT801 bass tube), with sound levels incrementally raised until they reached authentic calibrated levels (77 dBA Leq at 10 m) 30 s before the first observation. Sound levels were recorded over a period of 2.5 min using a calibrated sound level meter (Larson-Davis 831). The received levels at the centre of the colony measured 48–58 dBA Leq at 115 m (mean = 52 dBA Leq) during exposure to traffic noise, while natural ambient levels measured before and after the experiment were 26–38 dBA Leq (mean = 32 dBA Leq).

The behaviour of all aboveground animals was scanned every 5 min during the treatment and control periods (26 observations