



Road traffic noise modifies behaviour of a keystone species



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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.

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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

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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, Cunningham, & 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 m² 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 Bazoooka 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

per experiment) by the observer. Seven categories of behaviour were distinguished based on previous prairie dog research, including foraging (cropping or chewing food while standing on all four feet), vigilant (either scanning with head raised and alert on all four legs, or posting with head alert and standing on two legs), socializing (playing, 'kissing' or grooming), resting, digging, aggression (fighting, chasing or fleeing) and moving (Hoogland, 1995; Magle & Angeloni, 2011; Pauli & Buskirk, 2007; Verdolin & Slobodchikoff, 2002). All behavioural observations were made using binoculars (Swarovski 8 × 42), while a digital voice recorder (Olympus VN-7200) was used to collect the data without having to interrupt a behavioural scan. Aggressive and digging behaviour accounted for less than 1% of the data set and were not explored further. Wind speed was averaged across the experiment, while hourly temperature data were downloaded from the Nunn weather station (National Oceanic and Atmospheric Administration), which is located within 5 km of both colonies. A minimum of 48 h separated repeat playbacks, with a maximum of two experiments per week at each colony. All experimental playback protocols complied with institutional regulations (Colorado State University: IACUC 13-4112A), and adhered to the ASAB/ABS guidelines for the treatment of animals in behavioural research and teaching.

Data Analysis

The data on foraging, vigilance and number of prairie dogs aboveground were analysed using the lme4 package in R (v.2.15.1; R Foundation for Statistical Computing, Vienna, Austria). Akaike's Information Criterion adjusted for small sample size (AICc) was used for model selection (Burnham & Anderson, 2002). The autocorrelation function (ACF) was used to explore potential autocorrelation between subsequent observations (Crawley, 2007), with the total number of prairie dogs and feeding behaviour demonstrating limited correlation (≤ 0.2). We therefore tested the fit of the global model with no autocorrelation structure against a model with a simple first-order autoregressive (corAR1()) and a moving average structure (corARMA). The corARMA structure returned the lowest AICc scores for the total number of prairie dogs and feeding behaviour response variables, while the analysis of alert behaviour generated similar AICc scores across all three models (see Supplementary Table S1). As a result, the corARMA structure was included in all subsequent models to account for potential autocorrelation and to maintain consistency across analyses. Survey number and colony ID were included as random factors in all models, allowing us to account for repeat playbacks to the same animals.

The response variables included (1) number of individuals counted, and bivariate data on (2) foraging and (3) vigilance (scored as 1 or 0). Twenty-two candidate models were generated a priori for each response variable based on several predictors: exposure (treatment versus control) to test for behavioural differences with and without road noise; temperature and wind speed, environmental variables that could influence aboveground activity; and observation number, Julian day and decimal time, to determine whether behavioural response changed temporally. These included a null model (intercept only), a model with only the exposure parameter, and 14 additive models, seven with the exposure parameter included and seven without (Table 1). The six models with interaction terms explored whether behavioural response to noise exposure changed over the duration of an individual experiment (observation number), throughout the day (decimal time) and over the course of the field season (Julian day) relative to the control period (Table 1). The treatment playbacks were analysed to explore whether variation in received sound level at the centre of the colony affected behaviour (same models as above with

Table 1

Structure of candidate models assessed for each of the three response variables

Candidate models
Null
Exposure
Exposure+Julian day+Decimal time
Exposure+Temperature
Exposure+Wind speed
Exposure+Temperature+Wind speed
Exposure+Temperature+Wind speed+Julian day+Decimal time
Exposure+Observation number
Exposure*Observation number
Exposure*Observation+Temperature+Wind speed+Julian day+Decimal time
Exposure*Julian day
Exposure*Julian day+Temperature+Wind speed+Decimal time
Exposure*Decimal time
Exposure*Decimal time+Temperature+Wind speed+Julian day
Exposure+Temperature+Wind speed+Julian day+Decimal time+Observation number
Julian day+Decimal time
Temperature
Wind speed
Temperature+Wind speed
Temperature+Wind speed+Julian day+Decimal time
Observation number
Temperature+Wind speed+Julian day+Decimal time+Observation number

Parameters in the interaction terms were also included in the model additively.

'received levels' replacing the 'exposure' parameter). The AICc-modavg package was used to extract AICc scores and model weights for candidate models of each response variable. Model averaging was conducted on the response-specific models accounting for at least 0.95 of the AICc weight to extract parameter β estimates and their 95% confidence intervals. The effect sizes were assessed by whether the 95% confidence intervals overlapped zero.

RESULTS

During traffic noise exposure, the number of prairie dogs aboveground declined by 21%, the proportion of individuals foraging was reduced by 18%, vigilance increased by 48%, while social and resting behaviour was halved (Fig. 1). Five top models were generated in the analysis of number of aboveground prairie dogs, with the top model accounting for 56% of the AICc weight (Table 2). Exposure was the key parameter and was featured in all of the top models (Table 2), with a reduction in aboveground numbers during traffic noise (Table 3, Fig. 2). Increasing ambient temperature resulted in consistently lower aboveground activity across the treatment and control periods (Table 3, Fig. 2a), while there was also a weak effect of increasing wind speed in reducing activity (Table 3). The exposure and time interaction revealed that fewer prairie dogs were present during treatment observations conducted later in the day compared with control periods (Table 3), concurring with the exposure and observation number interaction that demonstrated a slight, yet more sustained decline in activity during the treatment period (Fig. 2b).

Seven models accounted for all of the AICc weight in the foraging behaviour analysis (Table 2). As above, exposure was the key parameter in all of the top models (Table 2), with reduced foraging during the road noise playback, while increasing temperature led to lower foraging in both treatment and control periods (Table 3, Fig. 3a). Model selection generated eight top models for the vigilance analysis with the top three models accounting for 57% of the AICc weight (Table 2). Again, exposure was in all of the top models (Table 2), with vigilance increasing in the presence of noise (Table 3, Fig. 3b, c). Increasing ambient temperature also resulted in greater levels of vigilance during control and treatment periods (Fig. 3b). A negative interaction between exposure and observation

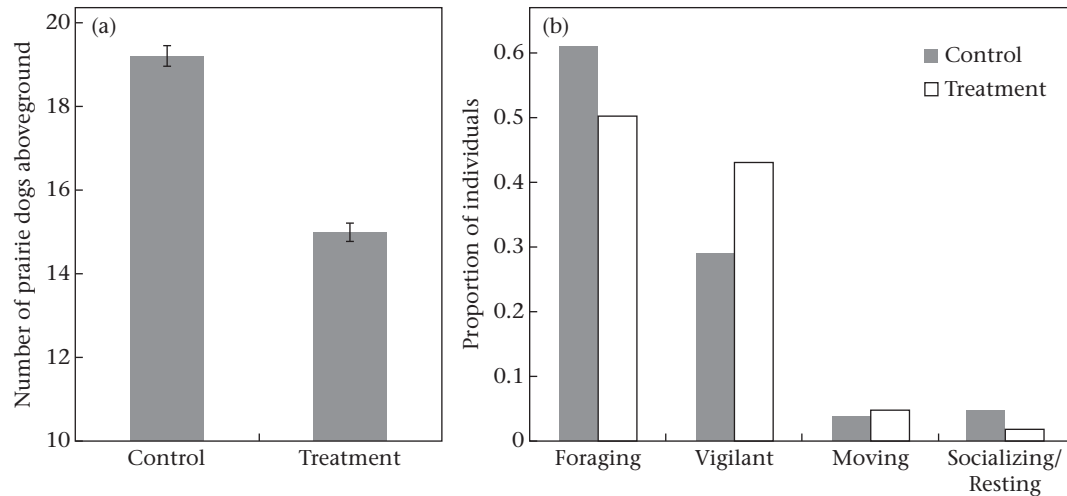


Figure 1. (a) The mean \pm SE number of prairie dogs aboveground and (b) the proportion of individuals engaged in key behaviours during the control and treatment periods.

number demonstrated that vigilance declined slightly as the treatment progressed (Fig. 3c). Variation in received noise levels at the centre of the colony during treatment periods did not affect behavioural responses (see Supplementary Table S2).

DISCUSSION

We provide the first experimental evidence that road traffic noise impacts the foraging and vigilance behaviour of a free-

ranging mammal. These behavioural responses, as well as declines in surface activity during the experimental exposure, are consistent with the risk disturbance hypothesis and indicate that traffic noise may be associated with increased perceived risk (Frid & Dill, 2002). Thus, we did not find that prairie dogs were tolerant of this nonlethal form of disturbance or that they perceived reduced risk during noisy periods because of predator shelter effects. Furthermore, there was no clear evidence of habituation, as behavioural responses were consistent over the course of the 3-month study. The analyses also revealed that temperature was a key covariate in explaining behavioural activity of prairie dogs. The reduction in the number of prairie dogs aboveground with increasing temperature is likely a thermoregulatory response, while decreased foraging and increased vigilance of those

Table 2
Top models accounting for ≥ 0.95 of the AICc weight for total number of aboveground prairie dogs, and foraging and vigilance behaviour

	K^*	$\Delta AICc$	AICc weight	Evidence ratio	Log likelihood
Total number					
Exp+Obs+Exp*Obs+Temp+Wind+Day+Time	10	0.00	0.56	1.00	-137.59
Exp+Time+Exp*Time+Temp+Wind+Day	9	1.75	0.23	2.43	-139.51
Exp+Temp+Wind+Day+Time+Obs	9	3.41	0.10	5.60	-140.34
Exp+Temp+Wind+Day+Time	8	4.84	0.05	11.20	-142.09
Exp+Day+Exp*Day+Temp+Wind+Time	9	5.04	0.04	14.00	-141.16
Foraging					
Exp+Temp	5	0.00	0.26	1.00	-196.26
Exp+Temp+Wind+Day+Time	8	0.62	0.19	1.37	-193.49
Exp+Temp+Wind+Day+Time+Obs	9	1.21	0.14	1.86	-192.75
Exp+Temp+Wind	6	1.26	0.14	1.86	-195.87
Exp+Obs+Exp*Obs+Temp+Wind+Day+Time	10	1.74	0.11	2.36	-191.97
Exp+Day+Exp*Day+Temp+Wind+Time	9	2.06	0.09	2.89	-193.17
Exp+Time+Exp*Time+Temp+Wind+Day	9	2.61	0.07	3.71	-193.45
Vigilant					
Exp+Day+Exp*Day+Temp+Wind+Time	9	0.00	0.22	1.00	-175.09
Exp+Temp	5	0.16	0.20	1.10	-179.29
Exp+Temp+Wind+Day+Time	8	0.80	0.15	1.47	-176.52
Exp+Temp+Wind	6	0.99	0.13	1.69	-178.68
Exp+Temp+Wind+Day+Time+Obs	9	1.42	0.11	2.00	-175.80
Exp+Obs+Exp*Obs+Temp+Wind+Day+Time	10	2.73	0.06	3.67	-175.41
Exp+Time+Exp*Time+Temp+Wind+Day	9	2.81	0.05	4.40	-176.49
Exp+Day+Time	6	3.81	0.03	7.33	-180.09

All models include survey number as a random effect and a moving average autocorrelation parameter.

* K is the parameter count for the model.

Table 3
The observed (β estimate \pm 95% CI) relationship between each response variable and the model-averaged parameters from the top models

	Parameter	β estimate	95% CI
Total number	Exposure	-0.27	-0.35, -0.19
	Temperature	-0.02	-0.03, -0.01
	Wind speed	-0.01	-0.02, 0.00
	Julian day	0.00	0.00, 0.00
	Time	-0.03	-0.07, 0.00
	Observation	-0.01	-0.01, 0.00
	Exposure*Julian day	0.00	0.00, 0.01
	Exposure*Time	-0.06	-0.11, -0.01
	Exposure*Observation	-0.01	-0.02, 0.00
Foraging	Exposure	-0.46	-0.55, -0.36
	Temperature	-0.03	-0.04, -0.01
	Wind speed	0.00	-0.01, 0.01
	Julian day	0.00	0.00, 0.00
	Time	0.01	-0.02, 0.05
	Observation	0.01	0.00, 0.02
	Exposure*Julian day	0.00	0.00, 0.00
	Exposure*Time	0.01	-0.05, 0.07
	Exposure*Observation	0.01	-0.01, 0.04
Vigilant	Exposure	0.60	0.51, 0.68
	Temperature	0.02	0.01, 0.03
	Wind speed	0.00	-0.01, 0.01
	Julian day	0.00	0.00, 0.00
	Time	0.03	-0.01, 0.06
	Observation	-0.01	-0.02, 0.00
	Exposure*Julian day	0.00	0.00, 0.01
	Exposure*Time	-0.01	-0.07, 0.05
	Exposure*Observation	-0.01	-0.03, 0.00

Bold text denotes β estimates with 95% CIs that did not overlap zero.

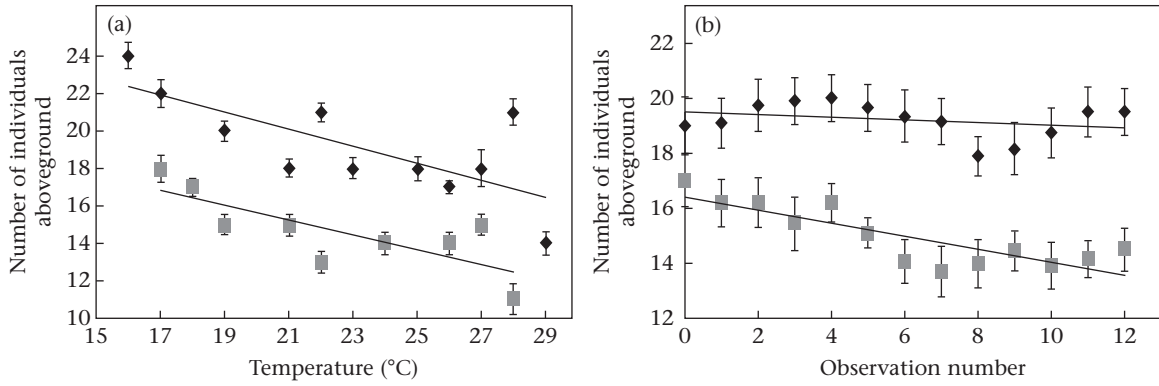


Figure 2. The number of aboveground prairie dogs during the noise treatment (grey square) and control (black diamond) as a function of (a) ambient temperature and (b) observation number.

remaining on the surface may result from smaller group sizes leading to greater risk of predation per individual (Hoogland, 1995; Verdolin & Slobodchikoff, 2002).

Our study provides novel information on the effects of noise and supports previous findings that prairie dogs commonly elevate alert behaviour and retreat below ground in response to predatory threats (Hoogland, 1995), including those induced by humans (Adams et al., 1987; Magle et al., 2005; Pauli & Buskirk, 2007). The observed changes in risk avoidance behaviours demonstrate the potential energetic costs associated with exposure to traffic noise in natural environments and are consistent with laboratory-based playback studies that have explored the effects of anthropogenic noise on other taxa in captive conditions (Quinn et al., 2006; Schaub et al., 2008; Siemers & Schaub 2011; Wale et al., 2013b). Our findings also concur with a previous field study that explored the effects of wind turbine noise on vigilance behaviour in

California ground squirrels, *Spermophilus beecheyi*, a related species that also occur in habitats modified by human activity (Rabin, Coss, & Owings, 2006). However in addition to shifts in vigilance, we have also now quantified the corresponding reduction in foraging behaviour while using a playback approach that specifically accounts for the effects of other potentially confounding variables (e.g. visual disturbance, chemical pollution, habitat loss). Of note, data were collected from only two prairie dog colonies; future study across additional sites would provide further inference regarding the generalizability of our findings.

Noise degrades habitat accessibility and may interact with other factors to threaten population persistence (Bayne et al., 2008; Francis et al., 2009), which has significant implications for this keystone species as well as more disturbance sensitive animals. While prairie dog colonies can persist in urban settings (Magle, Reyes, Zhu, & Crooks, 2010), our results demonstrate that traffic

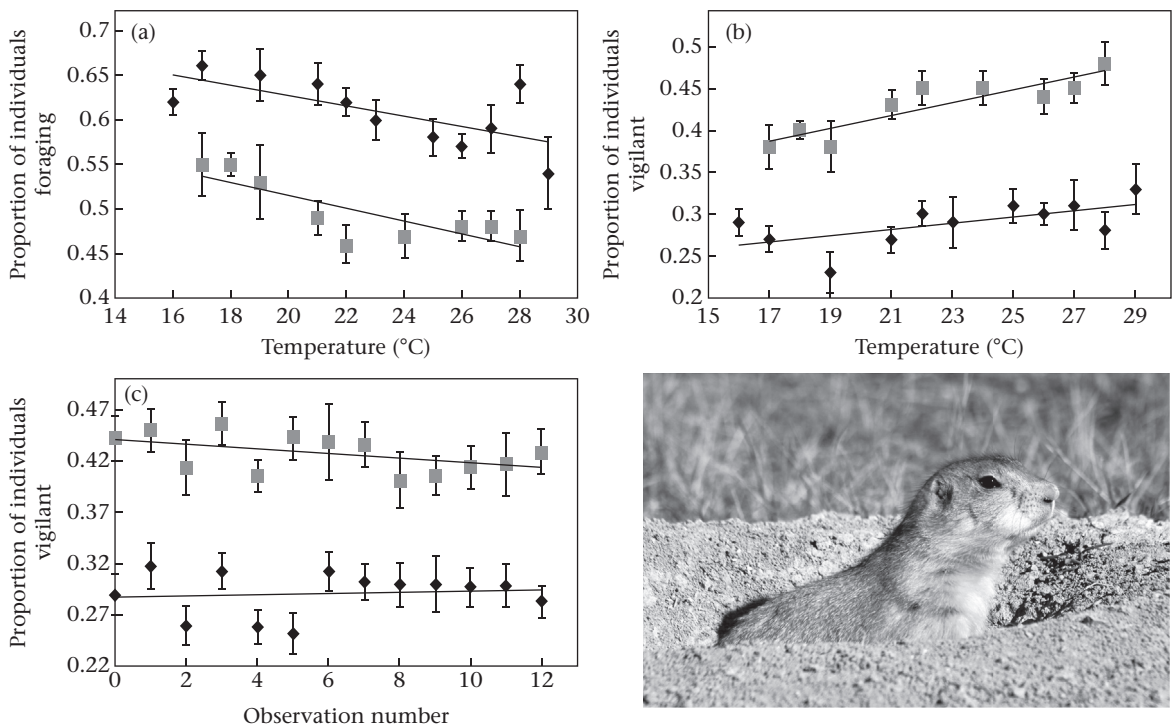


Figure 3. (a) The proportion of prairie dogs foraging during the noise treatment (grey square) and control (black diamond) as a function of ambient temperature. The proportion of prairie dogs vigilant as a function of (b) temperature and (c) observation number.

noise can drive significant changes in behaviour that could impact fitness through lost foraging opportunities (Frid & Dill, 2002). Pauli and Buskirk (2007) found that prairie dogs that survived exposure to a lethal form of anthropogenic disturbance (recreational shooting) showed reduced foraging and aboveground activity and increased alertness (the behavioural adjustments documented in our study), resulting in lowered body condition, elevated stress levels, reduced fitness and population-level impacts. Thus, the mere existence of a species at a site close to human activity or disturbance should not be interpreted as evidence of population and ecological integrity or lack of noise impacts in these settings (Francis & Barber, 2013).

Our results demonstrated marked shifts in critical behaviours of prairie dogs as a direct consequence of exposure to traffic noise. These effects may act synergistically with other anthropogenic disturbances to further impact vulnerable prairie dog populations. Importantly, extermination programmes, sylvatic plague and agricultural and urban development have already dramatically reduced prairie dog populations across a vast majority of their historic range (Miller, Ceballos, & Reading, 1994). Remaining populations commonly now occur in isolated pockets, and as a result, are much more susceptible to localized extinction (Magle et al., 2010; Wuerthner, 1997). Moreover, the loss of prairie dogs from grassland habitats has substantial negative impacts on ecosystem services (Martinez-Estévez, Balvanera, Pacheco, & Ceballos, 2013) and associated species diversity (Augustine & Baker, 2013). Similarly, altered behaviour of this highly interactive species (Kotliar, 2000; Miller et al., 2007; Soulé et al., 2005) may directly influence other organisms in the ecological community; for example, reduced surface activity may limit foraging opportunities for terrestrial and aerial predators. These potential community-level impacts of anthropogenic noise have received only limited research attention to date (but see Francis et al., 2012).

It is possible, however, that the behavioural changes we observed would decline with increasing experience if habituation or predator shelter effects require extended exposure to human disturbance, particularly as the colonies we studied were naïve to traffic noise prior to the experiments. In urban settings, prairie dogs tend to show reduced behavioural responses to anthropogenic disturbance compared to rural areas, suggesting they may behaviourally adapt to human stimuli over time (Adams et al., 1987; Magle & Angeloni 2011; Magle et al., 2005). However, prairie dogs do not consistently display patterns of habituation to repeated human disturbance (Magle et al., 2005). Our results did reveal that vigilance declined slightly during noise exposure, but this small effect was only observed within the course of an experiment. Overall, vigilance levels remained relatively constant among experiments, suggesting that prairie dogs did not readily habituate to the disruptive effects of noise. These findings have important implications for conservation management, particularly given that prairie dogs are generally considered a species that is adaptable and largely tolerant of nonlethal human disturbance. Nevertheless, further investigation is required to understand the longer-term responses to chronic noise exposure (e.g. Wale et al., 2013a).

Recently, Francis and Barber (2013) suggested that acute or infrequent noise results in responses akin to predation avoidance following the risk disturbance hypothesis (Frid & Dill, 2002), while chronic noise is more likely to impact sensory capabilities (e.g. masking crucial acoustic information). As our playback experiments involved broadcasting traffic noise for 1 h periods to naïve animals, our noise source likely lies on the continuum between acute and chronic. While the behavioural shifts observed during our study appear to reflect the increased stress and fear associated directly with the disturbance generated by traffic noise, further research is required to explore the contribution of acoustic masking

(Barber et al., 2010) and distraction (Chan et al., 2010), and how these underlying mechanisms interact. For example, prairie dogs rely on complex acoustic communication to transfer information on potential predators (Slobodchikoff et al., 1991), and human introduced noise may mask and reduce the communication space over which alarm signals are effective. Furthermore, responding directly to noise stimuli in the environment requires allocation of finite attention (Chan & Blumstein, 2011); the resulting distraction could potentially compromise the ability of prairie dogs to detect approaching predators.

The persistence of animal populations in fragmented habitats is a primary conservation concern (Wilcove et al., 1998), which is likely to be further compromised by exposure to heterotypic environmental stressors, such as anthropogenic noise (Francis & Barber, 2013). Globally, roadways are a major contributor to habitat fragmentation, due to traffic volume and the spatial extent of the road network (Benítez-López, Alkemade, & Verweij, 2010). Over the next 40 years, road travel is set to double worldwide, while an estimated 25 million lane-kilometres of roadways will be constructed during the same period (Dulac, 2013). The effects on biodiversity from this expansion are likely to be substantial (Benítez-López et al., 2010), and it is crucial that we are able to quantify the behavioural and fitness costs of different road-related disturbance factors, such as noise, in order to design and implement effective mitigation measures.

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Supplementary Material

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References

- Abrams, P. A. (2000). The evolution of predator–prey interactions: theory and evidence. *Annual Review of Ecology and Systematics*, 31, 79–105.
- Adams, R. A., Lengas, B. J., & Bekoff, M. (1987). Variations in avoidance responses to humans by black-tailed prairie dogs (*Cynomys ludovicianus*). *Journal of Mammalogy*, 68, 686–689.
- Arévalo, J. E. J., & Newhard, K. K. (2011). Traffic noise affects forest bird species in a protected tropical forest. *Revista de Biología Tropical*, 59, 969–980.
- Augustine, D. J., & Baker, B. W. (2013). Associations of grassland bird communities with black-tailed prairie dogs in the North American Great Plains. *Conservation Biology*, 27, 324–334.
- Augustine, D. J., & Derner, J. D. (2012). Disturbance regimes and mountain plover habitat in shortgrass steppe: large herbivore grazing does not substitute for prairie dog grazing or fire. *Journal of Wildlife Management*, 76, 721–728.
- Barber, J. R., Crooks, K. R., & Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution*, 25, 180–189.
- Bayne, E. M., Habib, L., & Boutin, S. (2008). Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. *Conservation Biology*, 22, 1186–1193.
- Beale, C. M., & Monaghan, P. (2004). Human disturbance: people as predation-free predators? *Journal of Applied Ecology*, 41, 335–343.
- Bejder, L., Samuels, A., Whitehead, H., Finn, H., & Allen, S. (2009). Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series*, 395, 177–185.

- Benítez-López, A., Alkemade, R., & Verweij, P. A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biological Conservation*, *143*, 1307–1316.
- Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, *3*, 620–623.
- Blickley, J. L., Blackwood, D., & Patricelli, G. L. (2012). Experimental Evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. *Conservation Biology*, *26*, 461–471.
- Bracciali, C., Campobello, D., Giacoma, C., & Sarà, G. (2012). Effects of nautical traffic and noise on foraging patterns of Mediterranean damselfish (*Chromis chromis*). *PLoS One*, *7*, e40582.
- Brown, C. L., Hardy, A. R., Barber, J. R., Fristrup, K. M., Crooks, K. R., & Angeloni, L. M. (2012). The effect of human activities and their associated noise on ungulate behavior. *PLoS One*, *7*, e40505.
- Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, *7*, 999–1014.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach*. Berlin, Germany: Springer.
- Chan, A. A. Y.-H., & Blumstein, D. T. (2011). Attention, noise, and implications for wildlife conservation and management. *Applied Animal Behaviour Science*, *131*, 1–7.
- Chan, A. A. Y.-H., Giraldo-Perez, P., Smith, S., & Blumstein, D. T. (2010). Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biology Letters*, *6*, 458–461.
- Crawley, M. J. (2007). *The R book*. Chichester, U.K.: J. Wiley.
- Dulac, J. (2013). *Global land transport infrastructure requirements*. Paris, France: International Energy Agency.
- Francis, C. D., & Barber, J. R. (2013). A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Frontiers in Ecology and the Environment*, *11*, 305–313.
- Francis, C. D., Kleist, N. J., Ortega, C. P., & Cruz, A. (2012). Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 2727–2735.
- Francis, C. D., Ortega, C. P., & Cruz, A. (2009). Noise pollution changes avian communities and species interactions. *Current Biology*, *19*, 1415–1419.
- Frid, A., & Dill, L. M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*, 11.
- Goodwin, S. E., & Shriver, W. G. (2011). Effects of traffic noise on occupancy patterns of forest birds. *Conservation Biology*, *25*, 406–411.
- Halfwerk, W., Holleman, L. J., Lessells, C. K., & Slabbekoorn, H. (2011). Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology*, *48*, 210–219.
- Hoogland, J. L. (1995). *The black-tailed prairie dog: Social life of a burrowing mammal*. Chicago, IL: University of Chicago Press.
- Kotliar, N. B. (2000). Application of the new keystone: species concept to prairie dogs: how well does it work? *Conservation Biology*, *14*, 1715–1721.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*, 619–640.
- Magle, S. B., & Angeloni, L. M. (2011). Effects of urbanization on the behaviour of a keystone species. *Behaviour*, *148*, 31–54.
- Magle, S. B., Reyes, P., Zhu, J., & Crooks, K. R. (2010). Extirpation, colonization, and habitat dynamics of a keystone species along an urban gradient. *Biological Conservation*, *143*, 2146–2155.
- Magle, S., Zhu, J., & Crooks, K. R. (2005). Behavioral responses to repeated human intrusion by black-tailed prairie dogs (*Cynomys ludovicianus*). *Journal of Mammalogy*, *86*, 524–530.
- Martinez-Estévez, L., Balvanera, P., Pacheco, J., & Ceballos, G. (2013). Prairie dog decline reduces the supply of ecosystem services and leads to desertification of semiarid grasslands. *PLoS One*, *8*, e75229.
- McClure, C. J. W., Ware, H. E., Carlisle, J., Kaltenecker, G., & Barber, J. R. (2013). An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20132290.
- Miller, B., Ceballos, G., & Reading, R. (1994). The prairie dog and biotic diversity. *Conservation Biology*, *8*, 677–681.
- Miller, B. J., Reading, R. P., Biggins, D. E., Detling, J. K., Forrest, S. C., Hoogland, J. L., et al. (2007). Prairie dogs: an ecological review and current biopolitics. *Journal of Wildlife Management*, *71*, 2801–2810.
- Parris, K. M., & Schneider, A. (2009). Impacts of traffic noise and traffic volume on birds of roadside habitats. *Ecology and Society*, *14*(1), 29. <http://www.ecologyandsociety.org/vol14/iss1/art29/>.
- Pauli, J. N., & Buskirk, S. W. (2007). Risk-disturbance overrides density dependence in a hunted colonial rodent, the black-tailed prairie dog *Cynomys ludovicianus*. *Journal of Applied Ecology*, *44*, 1219–1230.
- Powell, K. L., Robel, R. J., Kemp, K. E., & Nellis, M. D. (1994). Aboveground counts of black-tailed prairie dogs: temporal nature and relationship to burrow entrance density. *Journal of Wildlife Management*, *58*, 361–366.
- Quinn, J. L., Whittingham, M. J., Butler, S. J., & Cresswell, W. (2006). Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. *Journal of Avian Biology*, *37*, 601–608.
- Rabin, L. A., Coss, R. G., & Owings, D. H. (2006). The effects of wind turbines on antipredator behavior in California ground squirrels (*Spermophilus beecheyi*). *Biological Conservation*, *131*, 410–420.
- Riitters, K. H., & Wickham, J. D. (2003). How far to the nearest road? *Frontiers in Ecology and the Environment*, *1*, 125–129.
- Schaub, A., Ostwald, J., & Siemers, B. M. (2008). Foraging bats avoid noise. *Journal of Experimental Biology*, *211*, 3174–3180.
- Shannon, G., Cordes, L. S., Hardy, A. R., Angeloni, L. M., & Crooks, K. R. (2014). Behavioral responses associated with a human-mediated predator shelter. *PLoS One*, *9*, e94630.
- Shannon, G., McKenna, M.F., Angeloni, L.M., Lynch, E., Warner, K.A., Nelson, M.D., et al. (n.d.). A synthesis of two decades of research documenting the effects of noise on wildlife. Manuscript in preparation.
- Siemers, B. M., & Schaub, A. (2011). Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 1646–1652.
- Slobodchikoff, C. N., Kiriazis, J., Fischer, C., & Creef, E. (1991). Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. *Animal Behaviour*, *42*, 713–719.
- Soulé, M. E., Estes, J. A., Miller, B., & Honnold, D. L. (2005). Strongly interacting species: conservation policy, management, and ethics. *BioScience*, *55*, 168–176.
- Summers, P. D., Cunningham, G. M., & Fahrig, L. (2011). Are the negative effects of roads on breeding birds caused by traffic noise? *Journal of Applied Ecology*, *48*, 1527–1534.
- Verdolin, J. L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology*, *60*, 457–464.
- Verdolin, J. L., & Slobodchikoff, C. N. (2002). Vigilance and predation risk in Gunnison's prairie dogs (*Cynomys gunnisoni*). *Canadian Journal of Zoology*, *80*, 1197–1203.
- Voellmy, I. K., Purser, J., Flynn, D., Kennedy, P., Simpson, S. D., & Radford, A. N. (2014). Acoustic noise reduces foraging success in two sympatric fish species via different mechanisms. *Animal Behaviour*, *89*, 191–198.
- Wale, M. A., Simpson, S. D., & Radford, A. N. (2013a). Size-dependent physiological responses of shore crabs to single and repeated playback of ship noise. *Biology Letters*, *9*, 20121194.
- Wale, M. A., Simpson, S. D., & Radford, A. N. (2013b). Noise negatively affects foraging and antipredator behaviour in shore crabs. *Animal Behaviour*, *86*, 111–118.
- Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A., & Losos, E. (1998). Quantifying threats to imperiled species in the United States. *BioScience*, *48*, 607–615.
- Wuerthner, G. (1997). Viewpoint: the black-tailed prairie dog: headed for extinction? *Journal of Range Management*, *50*, 459–466.