The effects of wind turbines on antipredator behavior in California ground squirrels (*Spermophilus beecheyi*)

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ABSTRACT

Electricity-generating wind turbines are an attractive energy source because they are renewable and produce no emissions. However, they have at least two potentially damaging ecological effects. Their rotating blades are hazardous to raptors which occasionally fly into them. And wind turbines are very noisy when active, a feature that may interfere with the lives of animals beneath them. We studied California ground squirrels (*Spermophilus beecheyi*) in the Altamont Pass Wind Resource Area of Northern California. These squirrels emit vocalizations that alert others to the presence of a predator, and so may be forced to compensate for turbine noise by modifying antipredator behavior. We compared the antipredator behavior of squirrels at two sites, one close to and the other far from turbines, and under two conditions, during baseline and playback of conspecific alarm calls. We generated composite two variables using principle components analysis, one representing vigilance and one representing another cautionary antipredator tactic, for further statistical comparisons. Animals at the Turbine site exhibited elevated levels of vigilance and showed increased caution demonstrated in part, by returning to the area near their burrows during alarm calling. We conclude that this site difference is probably caused by the disparity in turbine noise, since predator abundance, group size, and vegetation type and density were similar for the two sites. Though population level impacts of these behavioral differences remain to be explored, our results indicate that behavioral impacts of turbines on wildlife should be considered during future turbine development.

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1. Introduction

Animals can be important gauges of ecological disturbances (Sullivan and Sullivan, 2001). Under modified conditions, the demographics, dynamics, and phenology of populations can be measured to determine how different environmental perturbations affect species (Miller and Mullette, 1985; Wilson et al., 1997; Blaustein et al., 2001; Beebee, 2002; Waser and Ayers, 2003). Data from these studies can then be used to make recommendations for mitigation (Thiollay, 1989; Price et al., 1994; Carey and Johnson, 1995; Wilson et al., 1997; Sullivan and Sullivan, 2001) and to measure the efficacy of such mitigation attempts (Miller and Mullette, 1985; Peach et al., 1999).

Installations of electricity-generating wind turbines, or windfarms, create an ecological disturbance that affects both

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resident and transient animals moving through these farms. In the Altamont Pass Wind Resource Area (APWRA) in Northern California, over 7000 wind turbines have been installed since the early 1980s (Davidson, 1998) with close to 4700 still in operation in 2002 (Nakafuji et al., 2002). Some impacts of these windmills are already well documented. Raptors are killed by turbines after flying into rapidly rotating turbine blades. During 1994 for example, 348 raptor fatalities were reported in the APWRA of which 35 were golden eagles (Alameda County, 1998). Decision-makers have identified this as a potential problem and have attempted to mitigate such impacts in the redevelopment of windfarms in the Altamont Pass (Alameda County, 1998).

Though mortality studies and population measurements certainly identify ecological disturbances posed by windfarms, behavioral studies can provide additional sensitive measures of the effects of anthropogenic habitat-modifications on animals (for examples, see Witherington, 1997; Eadie et al., 1998; Pettifor et al., 2000; Rabin et al., 2003; Slabbekoorn and Peet, 2003; Brumm, 2004; Foote et al., 2004; McDonald and St Clair, 2004; Sun and Narins, 2005). Animals living beneath strings of turbines or on hillsides close to turbine installations may be affected by this acoustically challenging environment. For resident wildlife using sound to communicate, high-amplitude noise produced by turbines may interfere with the detection of acoustic signals, a phenomenon known as acoustic "masking" (Patterson and Green, 1978). If turbines create new challenges for resident animals, individuals may modify their behavior to cope. Such a behavioral shift would be indicative of ecological disturbance.

2. Rationale

In this paper we use California ground squirrel (*Spermophilus beecheyi*) antipredator behavior in the APWRA as one gauge of the ecological disturbances caused by electricity-generating wind turbines and the high-amplitude noise they emit during operation. California ground squirrels are an ideal species with which to explore these potential impacts both because *S. beecheyi* is abundant and because California ground squirrels prefer the kind of open grassland habitat in which APWRA turbines have been installed. Ground squirrels are highly vocal in a variety of contexts and depend on acoustic communication to avoid predation (Owings and Hennessy, 1984; Hanson and Coss, 2001). Any interference with communication due to turbine noise has the potential to pose a significant challenge to individual survival. If squirrels have difficulty hearing the antipredator calls of others because of the masking effects of turbine noise, they may detect predators less quickly and so experience higher predation risk. In response, squirrels might change their visual scanning behavior, feeding behavior, and amount of time spent near or in safe refuge through both developmental and evolutionary processes. We will explore how behavior differs between a turbine and a control site during baseline conditions and during playback of ground squirrel alarm vocalizations. We will also assess group size and predator densities at the two sites as potential confounding factors since antipredator

behavior can vary as a function of these two factors (Lima and Dill, 1990).

3. Materials and methods

3.1. Location and study site

The Altamont Pass Wind Resource Area (APWRA) in Northern California spans over 160 km^2. Approximately 3500 of the turbines currently installed in the APWRA (56% of all turbines installed in this area) are 100 kW Kenetech Windpower, Inc. turbines. The production of wind-generated electricity is seasonal with almost 70% of the annual output being produced in the Spring and Summer quarters (Nakafuji et al., 2002). California ground squirrels are most active during this period of the year.

Research for this experiment was conducted at the approximately 7500 hectare Los Vaqueros Watershed in the APWRA. The watershed consists primarily of oak-savanna habitat with rolling hills and grassland. The height of grasses and other vegetation is kept low by cattle ranching. Squirrels were studied at two field sites. The first, the Turbine site, is located on a hillside immediately adjacent to a string of 6 turbines (lat: 37°48.02′N; long: 121°43.25′W) with strings of wind turbines installed on the surrounding hillsides, as well. All turbines are 100 kW Kenetech turbines. Turbine activity was variable but peaked in the morning. All observations were conducted among the abundant ground squirrel burrows adjacent to the turbines. The Control site is 2.7 km from the Turbine site and is located in an area where turbines are absent (lat: 37°46.64′N; long: 121°43.80′W). Hills bordering the Control site act as a barrier to turbine noise emitted in the surrounding area. As a result, turbine noise was negligible (see below). Grasses and scattered shrubs at each site were cut prior to trials to aid in visibility and to maintain similar patterns of signal degradation and attenuation when alarm calls were broadcast.

3.2. Acoustic characterization of ambient noise at sites

Sound pressure levels were measured at each site using a Bruel and Kjaer 2209 sound-pressure level meter set at Impulse-Hold (flat/linear response) with UA-0237 windscreen. Twenty readings were taken, each separated by at least 1 min. Each measurement was taken ∼0.25 m above the substrate for a period of 5 s. At the Control site, one set of readings was taken. At the Turbine site, two sets were taken, one while turbines were active and one while turbines were inactive. The time average decibel level (L_p) was then calculated for each set with the 20 documented readings.

Recordings of ambient noise at each site were also made at ground level near ground squirrel burrows using an AKG SE5E-10 microphone with omnidirectional capsule (CE2) enclosed in a Rycote windscreen and windsock. Ambient noise at the Turbine site was recorded once when all turbines surrounding the site were active and again when no turbines were active. Recordings were made on the dedicated audio track of a VHS tape using a JVC BR-S405U VHS video cassette

recorder with audio set to Hi-Fi. To produce spectrograms and power spectra, recordings were played from a Panasonic AG-7350 video cassette recorder, digitized via a Sony DVMC-DA2 Media Converter (16 bit, 48 kHz sampling frequency), and saved as uncompressed digital WAVE files using BIAS Peak DV (Berkeley Integrated Audio Software, Inc.). Cool Edit Pro 2.0 (Syntrillium, Inc.) was then used to generate spectrograms and power spectra (sampling rate of 48 kHz; 1024-Point FFT Spectrum with Hamming Filter).

3.3. Characterization and analysis of predator abundance

In order to characterize the predator abundance at each site, normative data on S. beecheyi predators were collected during a subset of 10-min experimental trials occurring between July 15 and August 26, 2002. During each trial, the presence of raptors and of predatory mammals (coyotes, badgers, and bobcats) was recorded. A two-tailed Fisher's exact test evaluated differences in predator abundances between the two sites. Because these 10-min experimental trials were short, little opportunity was provided to observe predators. As a result, we also analyzed predator abundances from a previous field season where normative data on predators was collected during 30-min samples. These data were collected at the same two sites between August 13 and September 6, 2001 and were also analyzed using a two-tailed Fisher's exact test.

3.4. Playback stimuli used in playback experiments

Alarm call series were elicited and recorded from ground squirrels in the field during or immediately after exposure to a domestic dog, simulating a canid predator, between August 20 and September 6, 2001. From these series, 5 min playbacks were created that started with a chatter, a call typically given in response to mammalian predators (Owings and Virginia, 1978) and progressed into repetitive calls (chats) known to maintain elevated vigilance (Owings and Hennessy, 1984; Owings et al., 1986; Loughry and McDonough, 1988). Eight different series from squirrels of different age and sex classes were used. Four of these series, referred to hereafter as Turbine-Call-Series, were obtained from 4 different squirrels at two turbine sites during periods of moderate to high turbine activity. Another 4 call series were obtained from 4 different squirrels at a nonturbine site and will be referred to as Nonturbine-Call-Series. Filtering and noise reduction was performed using Cool Edit Pro 2.0 (Syntrillium, Inc.) to remove ambient noise from playbacks while preserving the ground squirrel acoustic signal (see Fig. 1). For additional details on call recording, digitization, and processing, see Rabin (2005).
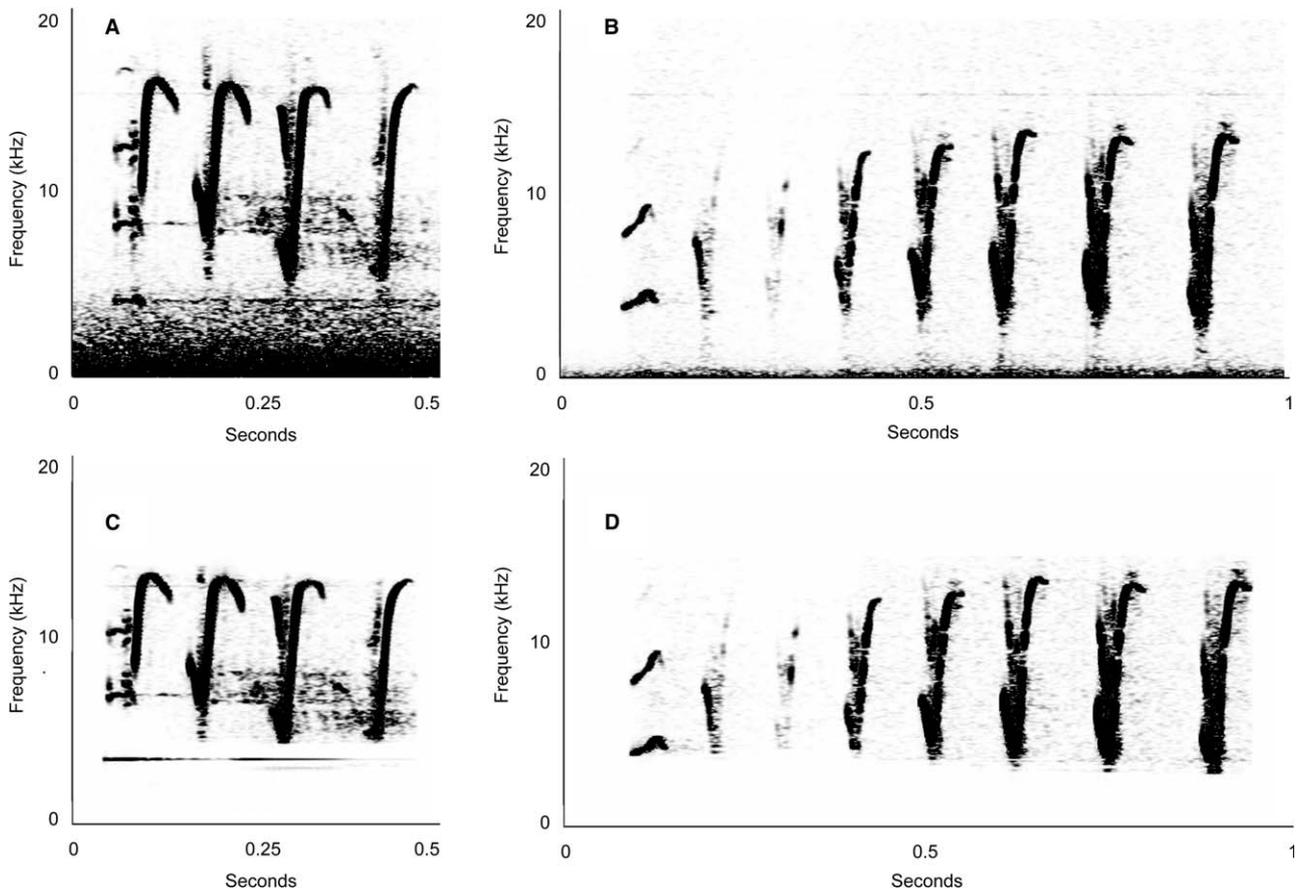

Fig. 1 – Spectrograms of initial chatters in two playback call series: (A) Chatter from a Turbine-Call-Series playback; (B) Chatter from a Nonturbine-Call-Series playback; (C) Chatter in spectrogram A after noise reduction and bandpass filtering and (D) Chatter in spectrogram B after noise reduction and bandpass filtering. Spectrograms were produced using a 512-point FFT with Hamming Filter.

To ensure that calls remained provocative after noise filtering, behavioral responses to playbacks were compared with baseline behavior, as described below, to explore for appropriate antipredator responses to playbacks. Because alarm calls reliably elicit antipredator responses in squirrels (Loughry and McDonough, 1988; Loughry and McDonough, 1989; Hanson and Coss, 2001) a lack of such responses at both the Control and Turbine sites would indicate that the calls were not appropriate for use.

3.5. Playback experiment

Prior to the experiment, 8 adults (2 males and 6 females) and 34 juveniles (17 males and 17 females) from the Turbine site were live trapped, tranquilized, aged ("juvenile" or "adult"), sexed, and dye marked for individual identification as were 7 adults (4 males and 3 females) and 45 juveniles (17 males and 28 females) from the Control site (methods described in Rabin, 2005). Data were collected between July 15 and August 26, 2002 with the first trial beginning 3 days after the last tranquilization.

Focal squirrels were followed for 10 min, beginning with a 5-min baseline sample and ending with a 5-min playback sample. Samples were identical except that during playback samples, a 5-min alarm call series was broadcast. Though turbine activity at the Turbine site was variable, samples were always taken there when at least some of the turbines were active. Squirrels were videotaped from an observer's blind at a distance of 40–60 m. Videotaping allowed for behavioral coding in the lab using continuous focal animal sampling (Altmann, 1974). The percent of time spent in each of the following behaviors was recorded: Head Up, Head Down, Post, Feed, At Burrow, and In Burrow (see Table 1). Instantaneous focal animal samples (Altmann, 1974) were also taken every 30 s from a subset of squirrels to count the number of squirrels within 3 m of the focal squirrel. Instantaneous data from each squirrel were then averaged to obtain clustering data, a measure used in the past as a surrogate for group size (Metcalfe, 1984b; Metcalfe, 1984a; Blumstein et al., 2001). An actual measure of group size could not be made because squirrels did not consistently forage together as a group.

During playbacks, alarm calls were broadcast at ground level from a speaker array made up of four Motorola piezoelectric tweeters driven in pairs by two amplifier channels. Call series were played from compact disc using a battery powered Sony CD Compact Player, model D-231 attached to a Coustic MP 380 (125 W/channel) amplifier. Gain was set such that the amplitude of the initial chatter in each series was 105 dB SPL at 0.25 m from the speaker array (measured by a Bruel & Kjaer model 2209 SPL meter set at peak amplitude with linear weighting). Trials were separated by at least 1 hour.

Trials were only initiated on squirrels that were within the borders of a 25 m² baited area located 40 m from the speaker array. Prior to the start of trials each day, this area was baited with 600 g of oats to attract squirrels. In between successive trials on the same day, oats were replenished with an additional sprinkling of 300 g. Trials began no less than 30 min after baiting, to allow animals to resume natural patterns of behavior.

Two variants of the experimental design were performed, one in which focal squirrels were played a Nonturbine-Call-Series during playback. In the other, a Turbine-Call-Series was broadcast. Squirrels served as focal animals in each variant no more than once, though not all squirrels were focal animals in both variants. We alternated between playing Turbine-Call-Series and Nonturbine-Call-Series on successive trials to prevent order effects.

3.6. Playback experiment statistical analysis

Because many of the coded behaviors are correlated, we attempted to reduce the analyzed behaviors (Head Up, Head Down, Post, Feed, and At Burrow) into a subset of composite variables indicative of antipredator behavior. To accomplish this, a single principle components analysis (PCA) was performed that included all samples (for baseline and playback as well as for Nonturbine-Call-Series and Turbine-Call Series samples). The behavioral measures, "Average number of squirrels within 3 m" and "In Burrow" were excluded and analyzed separately. We excluded "In Burrow" from the PCA because our primary interest in performing the PCA was to create composite variables indicative of antipredator behavior occurring outside of the burrow. The PCA was generated without rotation and all components with eigenvalues greater than 1 were extracted. Available component scores for individual squirrels could thus be analyzed for comparisons of site, baseline vs. playback conditions, and age class.

Table 1 – Definitions of coded behaviors	
Behavior	Definition
Head Up	Animal stands or sits with head oriented so that the animal's eyes are above the horizontal axis of its body. The animal's front feet may or may not be off the ground. However, the axis of the body remains horizontal or diagonal relative to the ground. Animal's body axis is not vertically oriented.
Head Down	Animal stands or sits with head either touching the ground or oriented toward the ground. Animal's eyes are below the horizontal axis of its body.
Post	Animal sits on hind limbs. Body axis is rotated upwards and oriented vertically. Back is not bent and is perpendicular to the substrate.
Feed	Animal chews on food, manipulates food with mouth, or brings food to the mouth with front paws.
At Burrow	Animal is in view and located within 12 in. of burrow entrance.
In Burrow	Animal is out of view and located inside its burrow.

Unless stated otherwise, type III weighted repeated measures ANOVAs with sample (baseline vs. playback) as the repeated measure and with site (Turbine vs. Control) and age (adult vs. juvenile) as fixed effects were then performed on each principle component (PC) using the generated individual component scores. Analyses were performed separately for Nonturbine-Call-Series and Turbine-Call-Series trials because not all squirrels were sampled in both variants of trials (only 13 out of 32 squirrels were focal animals in both variants). As a result, the two trial series could not be considered a repeated measure.

A weighted ANOVA was used to cope with inherent between-site heteroscedasticity in the data (Neter et al., 1985). Weighted least squares weights were generated by first running the ANOVA without weighting and then using the inverse of the variance of the error term $(1/\sigma_i^2)$ at each site as the weight for squirrels at that site. "Average number of squirrels within 3 m" was also analyzed using a Type III repeated measures ANOVA with site as a fixed effect. However, age class was not included as a factor because small sample sizes forced us to pool adults and juveniles. Weighting was unnecessary because there was no violation of the assumption of homogeneity of variance. For the behavior "In Burrow", two-tailed Mann–Whitney U Tests were performed with site (Turbine vs. Control) as a grouping variable.

4. Results and interpretation

4.1. *Acoustic characterization of site noise*

The average decibel level for ambient noise at the Control site was substantially lower than at the Turbine site during turbine activity (79.8 dB vs. 110.2 dB, ranges = 70–88 dB and 93–118 dB SPL respectively). Representative spectrograms and power spectra for ambient noise at the sites are presented in Fig. 2. When turbines are active, the Turbine site has a complex spectral signature with high amplitude noise extending as high as ∼6–8 kHz. The "swooshing" sound of the sweeping windmill blades are identified on the spectrogram in Fig. 2A by arrows. The ambient noise spectrum at the Control site
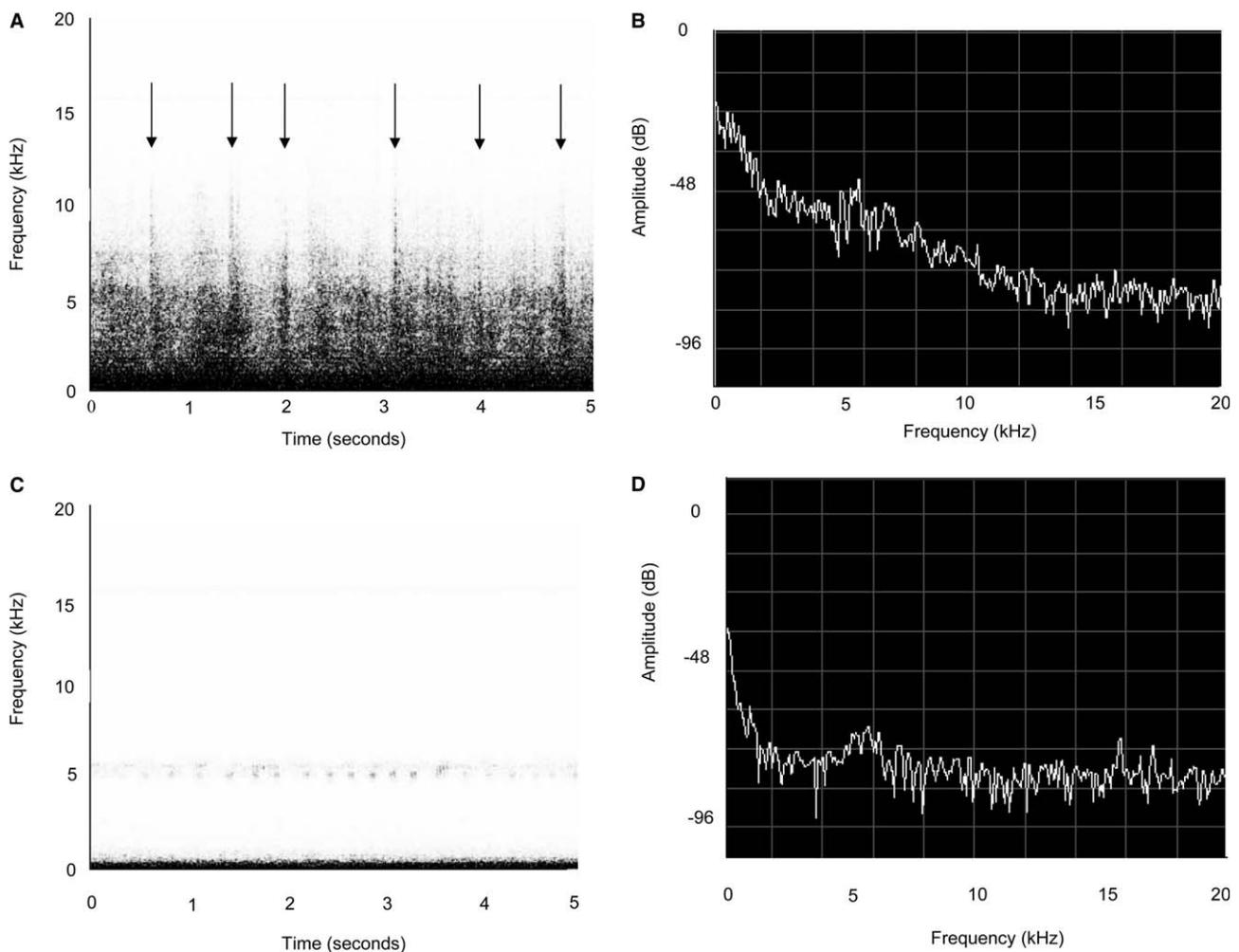

Fig. 2 – Spectrograms and power spectra of ambient noise at Turbine and Control sites: (A) Turbine site ambient noise. Arrows mark the spectral signatures of the turbine blades 'swooshing' as they rotate. (B) Power spectrum of the ambient noise shown in A. (C) Control site ambient noise and (D) Power spectrum of the ambient noise shown in C. Spectrograms and power spectra were produced using 1024-point FFT with Hamming filter. Power spectra were produced by averaging the five second recordings shown in the spectrograms.

is much simpler with noise produced mostly at very low frequencies by wind. Crickets were abundant at the Control site with chirping occurring repetitively at ~5 kHz. When turbines were not in operation at the Turbine site, ambient noise was very similar to that at the Control site both in terms of decibel level (75.8 dB, range = 63.5–83.5 dB) and frequency characteristics. Though a separate spectrogram and power spectrum are not presented here for the Turbine site during turbine inactivity, both look very similar to those in Figs. 2C and D.

4.2. Principle components analysis

Twenty-four Nonturbine-Call-Series trials ($n = 6$ adults; 18 juveniles) and 21 Turbine-Call Series trials ($n = 4$ adults; 17 juveniles) were used to generate the PCA. Both the baseline sample and the playback sample from each trial were used in the PCA, for a total of 90 samples. Two PCs were extracted from the PCA (see Table 2). PC 1 explained 64.1% of the variance and can be interpreted as a measure of vigilance. The different individual behaviors loaded on this PC in a general order of increasing alertness (e.g. Posting is more vigilant than Head Up and Head Down is less alert than any other behavior). As a result, we have named PC 1, "ALERTNESS". PC 2 explained 21.2% of the variance and was indicative of a different tactic that involved staying in close proximity to refuge, and to a lesser extent posting. PC 2 was less a composite score indicative of vigilance and more a score that expressed a squirrel's return to the area near its burrow (see PC 2 scores in Table 2). Therefore, we have named PC 2, "PROXIMITY TO SHELTER."

4.3. Behavioral responses during trials

Levene's tests on component scores of individual squirrels for ALERTNESS and PROXIMITY TO SHELTER determined that in some cases, the variance was not homogeneous across sites. As a result, weighted ANOVAs were performed using site weights that were generated separately for Nonturbine-Call-Series and Turbine-Call-Series trials. Nonturbine-Call-Series trials and Turbine-Call-Series trials were thus analyzed separately in different weighted ANOVAs.

4.3.1. Test of call-series effectiveness
Through statistical analysis of the repeated measure (baseline vs. playback), we were able to assess whether or not the two types of playbacks (Nonturbine or Turbine) were evocative.

In fact, the two types of playbacks did differ in their ability to evoke an antipredator reaction. Squirrels responded to Nonturbine-Call-Series, but not to Turbine-Call-Series. Squirrels responded to Nonturbine-Call-Series (see Fig. 3) by significantly increasing ALERTNESS during playback ($F_{[1,20]} = 21.353$; $p < 0.001$). PROXIMITY TO SHELTER scores changed differentially at the two sites, increasing at the Turbine site on playback but decreasing at the Control site (interaction between site and the repeated measure; $F_{[1,20]} = 9.238$; $p = 0.006$; see Fig. 4). Because behavioral shifts occurred during playback for both PCs, we can conclude that the Nonturbine-Call-Series were behaviorally provocative. In contrast, playbacks of the
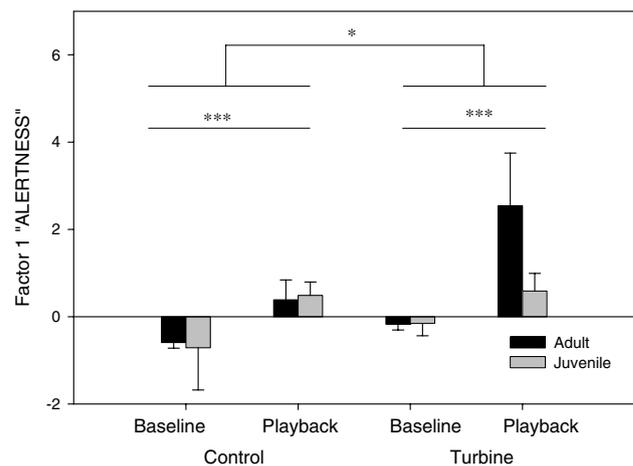

Fig. 3 – Mean (and SE) of PC 1 "ALERTNESS" scores for trials. Asterisks indicate significant differences in the repeated measure and site. The difference in values between baseline and playback is highly statistically significant (***) (weighted repeated measures ANOVA, $p < 0.001$). Values are also significantly higher (*) at the Turbine site than at the Control site (weighted repeated measures ANOVA, $p < 0.05$).
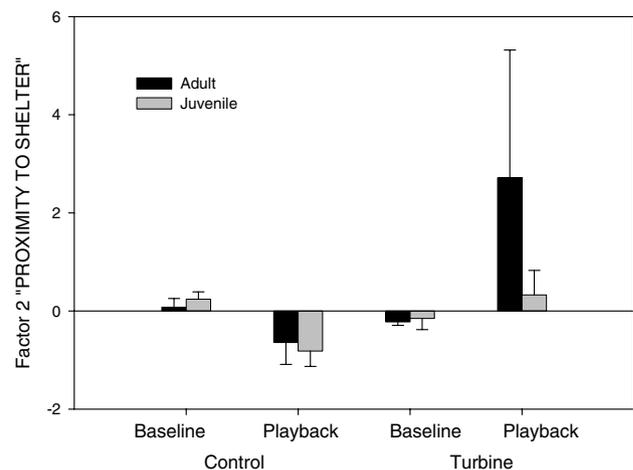

Fig. 4 – Mean (and SE) of PC 2 "PROXIMITY TO SHELTER" scores for trials. Squirrels at the Turbine site increased PROXIMITY TO SHELTER during playbacks. At the Control site, the opposite pattern emerged (interaction between site and the repeated measure, $F_{[1,20]} = 9.238$; $p = 0.006$).

Table 2 – Summary of principle component loadings for the two extracted principle components		
Behavior	"ALERTNESS" PC 1	"PROXIMITY TO SHELTER" PC 2
Posting	0.761	0.477
Head Up	0.730	−0.621
At Burrow	0.564	0.638
Feed	−0.910	0.148
Head Down	−0.973	0.138
Eigenvalue	3.024	1.060
Percent of variance	64.1	21.2

Turbine-Call-Series did not elicit a response from squirrels for either ALERTNESS ($F_{[1,17]} = 2.899$; $p = 0.107$) or for PROXIMITY TO SHELTER ($F_{[1,17]} = 0.203$; $p = 0.658$).

There are a variety of reasons that Turbine-Call-Series may have been ineffective. Although Rabin et al. (2003) reported that the noise reduction feature in Cool Edit Pro can be utilized with minimal signal loss in quantitative acoustic analyses, the high noise-to-signal ratios in the Turbine-Call-Series may have exceeded the noise reduction capabilities of this software. To our ears, Turbine-Call-Series remnant noise (See Fig. 1C) was associated with a slightly artificial quality after noise reduction. Nevertheless, we needed to assess how provocative these calls were through playbacks, an assay in which the squirrels proved to be unresponsive. On the other hand, the low noise content in the Nonturbine-Call-Series may have been in the range in which this noise-reduction feature is effective. Second, recordings taken at turbine sites may have been degraded at the time of recording because high amplitude turbine noise forced us to significantly reduce the gain of our recorder. A third possibility is that squirrels at turbine sites emitted inherently less provocative calls. A systematic analysis of the acoustic properties of these calls could certainly test for that possibility but such an analysis is beyond the scope of this study.

Since squirrels at neither site appeared to recognize Turbine-Call-Series as alarm calls, we reasoned that data obtained during these trials were not relevant to our primary goal of exploring differences in antipredator behavior during baseline and playback. As a result, we have removed those trials from our analyses below. All subsequent analyses will report only on data obtained during Nonturbine-Call-Series trials and will hereafter be referred to simply as 'Playback trials'.

4.3.2. Site differences in antipredator behavior

Adults and juveniles did not differ in ALERTNESS ($F_{[1,20]} = 1.811$; $p = 0.193$; Fig. 3) or in PROXIMITY TO SHELTER ($F_{[1,20]} = 2.007$; $p = 0.172$; Fig. 4) in playback trials. Similarly, there are no significant interactions between age and baseline/playback or between age and location ($p > 0.10$).

Squirrels at the Turbine site showed higher levels of ALERTNESS overall than squirrels at the Control site (main site effects during trials; $F_{[1,20]} = 4.938$; $p = 0.038$; Fig. 3). This statistical difference in the main effect reflects the average of both the baseline and playback samples. The same trend is evident for baseline and playback conditions separately, but the weighted simple effects only approached significance (baseline and playback, respectively: $F_{[1,20]} = 2.803$; $p = 0.110$; $F_{[1,20]} = 3.477$; $p = 0.077$). The lack of any significant differences in simple effects is likely due to the high amount of behavioral variation among squirrels, variation that could be accounted for in the repeated-measures ANOVA but not in the simple effects design.

For PC 2, squirrels at the Turbine site increased their PROXIMITY TO SHELTER during playbacks whereas values at the Control site decreased (interaction between site and the repeated measure, $F_{[1,20]} = 9.238$; $p = 0.006$; Fig. 4).

The percent of time spent In Burrow did not differ significantly between sites for either baseline ($U_{[12,12]} = 60.0$; $p = 0.149$) or for playback ($U_{[12,12]} = 53.0$; $p = 0.241$).

4.4. Group size

Group size data were collected from a subset of 14 focal squirrels during trials ($n = 5$ Control; 9 Turbine). Squirrels reduced clustering significantly during playback (see Fig. 5) when compared with baseline ($F_{[1,12]} = 8.048$; $p = 0.015$). This change in clustering was the result of squirrels scattering during playback. However, there were no differences in clustering between the two sites ($F_{[1,12]} = 0.598$; $p = 0.454$) nor was there an interaction between site and the repeated measure ($F_{[1,12]} = 0.622$; $p = 0.446$).

4.5. Characterization of predator abundance

During 10-min trials in 2002, normative data were collected during 14 samples taken from the Control site and 17 from the Turbine site. Though differences are not statistically significant (two tailed Fisher's exact test, $p = 0.452$), raptors were present at the Control site during 7.1% of trials and were never observed at the Turbine site during data collection (see Fig. 6). Consistent with this trend, aerial predators were observed significantly more frequently during 2001 at the Control site ($n = 23$ thirty-minute trials at each site; two tailed Fisher's exact test, $p < 0.0001$). Raptors were present at the Control site during 52.1% of trials but were never observed at the Turbine site during this time (Fig. 6). Mammalian predators were not observed while collecting quantitative data in 2001 or in 2002 (Fig. 6) though they were observed at other times. At the Turbine site a resident badger, whose large burrow was located near the colony, was observed on one occasion. At the Control site, coyotes were frequently seen when predator data were not being collected.
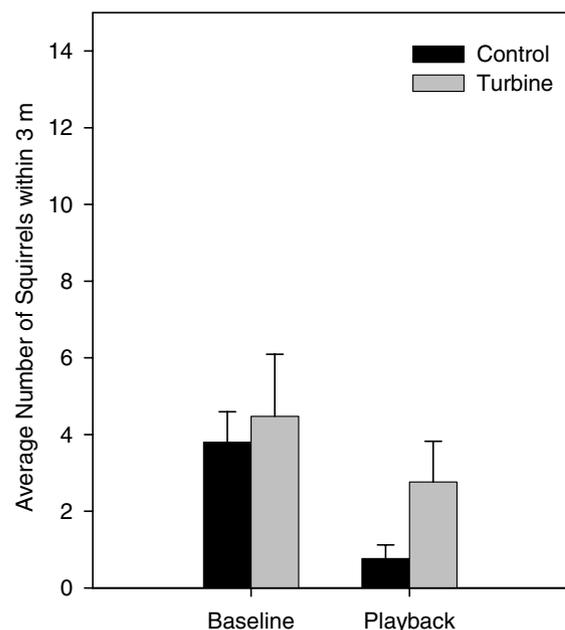

Fig. 5 – Mean (and SE) for the measurement "Average number of squirrels within 3 m of the focal squirrel." Squirrels clustered less during playback than during baseline samples (Repeated Measures ANOVA, $p < 0.05$). Site differences were not statistically significant.
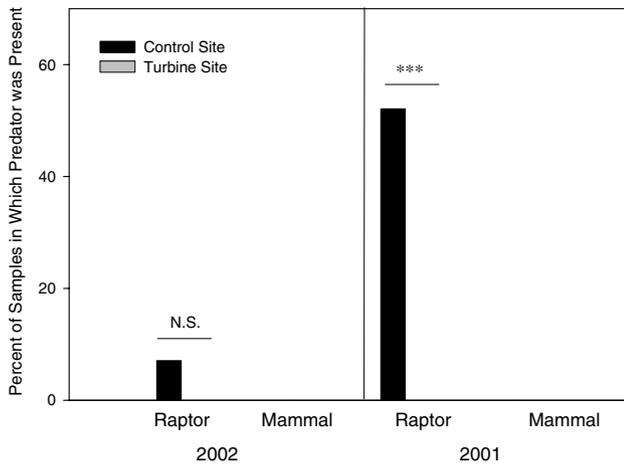
Fig. 6 – Predator abundances at each site during samples collected in 2002 and 2001. No mammals were observed during data collection in 2002 or 2001. In 2001, there were significantly more raptors (***) at the Control site than at the Turbine site (two tailed Fisher's exact test, $p < 0.001$). In 2002, difference in raptor abundance were not statistically significant (N.S.) (two tailed Fisher's exact test, $p > 0.1$).

5. General discussion

5.1. Effects of turbines on california ground squirrel behavior

The expectation that turbine noise would affect the behavior of squirrels was confirmed by behavioral differences between Turbine and Control sites (See Table 3). Three general differences emerged in our study. The first is that noise at the Turbine site, when turbines were active, was much higher in amplitude than at the Control site. The second general result is that, regardless of site, squirrels increased their vigilance in playback samples when compared with baseline (as indicated by the ALERTNESS composite variable, Table 3). However, squirrels at the Turbine site were more vigilant than squirrels at the Control site overall (Fig. 3, Table 3). Elevated Turbine site ALERTNESS occurring prior to playback suggests that site differences in ALERTNESS did not arise simply because broadcast call series were novel at the Turbine site. The third result is that squirrels at the Turbine site had a greater tendency to return to the area immediately around their burrows and post during playbacks (as indicated by the PROXIMITY TO BURROW composite variable). Squirrels at the Control site actually reduced their PROXIMITY TO BURROW during these

same playbacks (Fig. 4, Table 3). At the Turbine site, a return to the burrow area concomitant with posting allowed animals to manage predation risk in a second fashion by providing more immediate access to refuge. The utilization of both responses at the Turbine site, as well as the higher level of overall ALERTNESS at that site, indicates that Turbine squirrels perceived themselves to be under higher risk than Control squirrels.

It is possible that factors other than noise were responsible for these behavioral differences (e.g. site differences in vegetation type and density, predator abundance, group size, and distance from refuge; see Lima and Dill, 1990 for review of those factors' effects on antipredator behavior). But, those factors probably did not drive site differences for the following reasons: (1) Vegetation type and density were kept similar at both sites by cattle grazing and the removal of tall vegetation by the investigators. (2) During trials at both sites, the distance from focal squirrels to shelter was similar since trials were only initiated on squirrels within a baited area located close to resident ground squirrel burrows. (3) Raptor abundance did not differ between sites and may have even been lower at the turbine site (see Fig. 6). And any heightened levels of vigilance associated with the presence of a badger at the Turbine site were likely balanced at the Control site by repeated encounters with coyotes. (4) Though animals did cluster less during playback than during baseline conditions as a result of scattering to refuge, there were no apparent clustering differences between sites (see Fig. 5, Table 3).

Some other unique factor or combination of factors is likely driving the higher overall ALERTNESS values at the Turbine site and the increased use of PROXIMITY TO BURROW during playback. Our data support the assertion that the turbine installations and their associated noise are one of these factors. California ground squirrels are preyed on by a number of predators (Fitch, 1948) and use acoustic communication to reduce predation. When predators approach *S. beecheyi* colonies, squirrels call using a variety of antipredator vocalizations (Owings and Virginia, 1978; Owings and Hennessy, 1984) and respond to these vocalizations by increasing their levels of vigilance, returning to their burrows, or both (Leger and Owings, 1978; Leger et al., 1979; Loughry and McDonough, 1988; Loughry and McDonough, 1989; Hanson and Coss, 2001). However in a noisy environment, signals are more difficult to detect when the frequency of the signal and noise overlap, or when the amplitude of the noise source is high relative to signal intensity (Patterson and Green, 1978). During turbine activity,

Table 3 – Significant behavioral differences[a]				
Variable	Baseline vs. Playback		Turbine vs. Control site	
	F value	P value	F value	P value
ALERTNESS	21.353	<0.001	4.938	0.038
PROXIMITY TO SHELTER	Repeated measure/site interaction, $F = 9.238$; $p = 0.006$			
Group size/clustering	8.048	0.015	0.598	0.454

a Only trials conducted using Nonturbine-Call-Series as playbacks are included because Turbine-Call-Series were not effective in provoking behavioral responses. See text for further explanation.

ambient noise levels at our Turbine site averaged 110.2 dB but reached as high as 118.0 dB SPL. Much of this noise was produced in the spectral band between 100 Hz and 6 kHz (see Fig. 2). Though components of California ground squirrel calls do extend above this spectral band (Fig. 1), the lower frequency components of the calls overlapped with turbine noise. And because the higher-frequency components of calls attenuate more rapidly with distance, it is the lower-frequency components that are most likely to be important for long-range communication. Thus, there is great potential for noise at turbine sites to interfere with the detection and assessment of alarm calls. In turbine environments, animals have shifted their antipredator tactics to utilize the visual modality more as seen by increased levels of ALERTNESS and PROXIMITY TO SHELTER. In doing so, squirrels appeared to attempt to compensate for acoustic masking as a result of turbine noise. One confounding factor could not be controlled for, the low frequency noise associated directly with greater winds at the Turbine site. However acoustic interference from wind noise would be highly unlikely as the frequency of wind noise is well below ground squirrel acoustic sensitivity (Henry and Coss, unpublished data).

It may seem surprising that animals at the Turbine site reacted strongly to playbacks. If alarm signals are completely masked, we would expect to see no behavioral reaction to playbacks when broadcast with simultaneous turbine noise, since noise would prevent animals from hearing calls. Instead, we see that levels of ALERTNESS and PROXIMITY TO SHELTER are both higher at the Turbine site on playback than at the Control site. A number of non-mutually exclusive hypotheses might account for this pattern. First, noise at the Turbine site might not completely mask emitted alarm calls. This would allow squirrels to hear some components of the broadcast calls though the quality of the calls may be degraded and call perception altered. In this case, turbine squirrels may be less effective at extracting subtle information from calls, and may instead use a simple rule of thumb, to be more alert and seek refuge under noisy conditions. Second, animals likely listen, as well as watch for the approach of an incoming predator after detecting an alarm call. Predators quickly approaching on the ground will make noise as their footfalls disturb loose substrate. But during turbine activity, animals may be unable to detect these low-amplitude sounds, warranting an increase in visual vigilance. Finally, animals at the Turbine site may have suffered some degree of hearing loss due to chronic exposure to high-amplitude noise. On hearing salient antipredator signals, those animals would be forced to compensate with visual scanning or a return to refuge. Each of these hypotheses requires further investigation.

Time spent In Burrow did not differ either between baseline and playback samples or between sites. These results follow Leger and Owings (1978), Owings and Leger (1980), and Owings et al. (1986) which suggest that alarm calling or the presence of distant predators does not often drive squirrels underground. Though California ground squirrels are likely to flee inside their burrow after close encounters with a predator (e.g. Hanson and Coss, 1997), hearing alarm calls alone does not appear to induce this behavior.

5.2.   *Implications for other species of wildlife*

Turbine-related impacts on S. *beecheyi* might indirectly affect other species of concern that depend on ground squirrels as a resource. For example, S. *beecheyi* makes up over 25% of the diet of golden eagles (Carnie, 1954). And burrowing owls, red legged frogs, and California tiger salamanders rely on California ground squirrel burrows for shelter (Bente, 1938; Rowe et al., 1986; Jennings and Hayes, 1994; Loredo et al., 1996). Any movement of ground squirrel populations away from turbine installations could also negatively impact these other species. Our study suggests that ground squirrels may be able to cope with turbines and their associated acoustic noise through behavioral modifications in a predatory context. Additional research in non-predator/prey contexts should further test this assertion.

The fact that California ground squirrels appear to be able to adjust their behavior appropriately to cope with the presence of turbines is not surprising since S. *beecheyi* has demonstrated its ability to live in a variety of habitats under a variety of anthropogenic modifications (Marsh, 1998). However, for species of special concern that may be more sensitive to habitat change, studies along these same lines will help to identify the potentially adverse effects of turbines on other wildlife.

The findings presented here are not intended to suggest that turbine development be stopped. Wind-generated power should continue to be considered as an attractive alternative energy source due to its ability to produce energy without emissions. However, as engineers and turbine installers continue to develop new windmills and install new windfarms, consideration should be made towards reducing any impacts that turbines have on California's wildlife.

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