

PHANTOM OCEAN, REAL IMPACT: NATURAL SURF SOUND EXPERIMENTS ALTER  
FORAGING ACTIVITY AND HABITAT USE ACROSS TAXA

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Sound Experiments Alter Foraging Activity and  
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## ABSTRACT

### Phantom Ocean, Real Impact: Natural Surf Sound Experiments Alter Foraging Activity and Habitat Use Across Taxa

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A growing body of research focuses on how background sounds shape and alter critical elements of animals' lives, such as foraging behavior, habitat use, and ecological interactions (Bradbury & Vehrencamp, 2011; Barber *et al.*, 2010; Kight & Swaddle, 2011; Shannon *et al.*, 2016). Much of this research has centered on the effects of anthropogenic noise (Dominoni *et al.*, 2020; Francis & Barber, 2013; Ortega, 2012; Swaddle *et al.*, 2015), but recent studies have also revealed that natural sound sources can influence animal behavior (Davidson *et al.*, 2017; Le *et al.*, 2019). Natural sounds, such as crashing surf, can create conditions where signaling and listening are difficult, but how this influences different species' ecological interactions are unknown.

To study the effects of crashing surf sound we experimentally introduced landscape-level acoustic playbacks where surf sound was not naturally present to create a "phantom ocean". Phantom ocean treatment sites were employed alongside higher frequency "shifted" treatment sites to test for frequency-dependent effects, "real ocean" sites where surf sound was endemic, and ambient control sites. The phantom and shifted treatments were played continuously during the spring and summer of 2017-2019. Within this acoustic experimental landscape we conducted multiple studies to test the effects of crashing surf sound on animal behavior, habitat use, and ecological interactions. Through an artificial caterpillar predation experiment modeled after Roslin *et al.* (2017), we found that when exposed to natural sound treatments the foraging activity of rodents and arthropods increased, while that of birds declined. A potential explanation for this pattern includes taxon-specific responses reflecting different perceived risk-reward trade-offs in natural sound conditions. To follow this up we performed occupancy modeling on data collected by camera traps set within our



system. We observed different responses among groups of species with different functional roles in the community for both detection ( $p$ ) and occupancy ( $\Psi$ ) probabilities.

Our combined results indicate different species and functional groups have unique foraging behavior and patch use responses to natural sounds, likely based on their ecological interactions. Specifically, Cricetid rodents are likely more active in areas exposed to natural sounds, possibly due to lower perceived predation risk because mesocarnivores are less active. Insectivorous birds are also likely less active under natural sounds conditions, although the frequency of the sound, and the body size and diet of the bird appear influential. Together these findings suggest that natural sounds shape not only individual behavioral adjustments, but also multi-trophic, community level interactions. Our results show that natural sounds are an important driver of ecological interactions, but much remains to be uncovered. The mechanisms by which natural sounds influence individuals, populations, and many other aspects of ecology remain unexplored and provide fertile ground for future inquiry.

Keywords: natural sounds, acoustic ecology, soundscape, perceived predation risk, rodents, birds, mesocarnivores, arthropods, occupancy models

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## CHAPTER 1

FORAGING BY THE PHANTOM OCEAN: EXPERIMENTAL SURF SOUND ALTERS PREDATION  
OF CATERPILLARS BY MULTIPLE TAXA

## 1. ABSTRACT

Animals rely on acoustic cues for many key behaviors including foraging and predator detection, and while a growing body of literature suggests that anthropogenic noise can interfere with these acoustic cues and lead to changes in behavior, physiology, and distributions, human activity is not the only source of sound in the landscape. Many natural sources, such as moving water, could create difficult conditions for signaling and listening as well. How these natural sounds alter ecological interactions is largely unknown. We used four natural sound treatments to test whether sounds from crashing surf influenced caterpillar predation by three taxa: rodents, birds, and arthropods. We used landscape level playbacks of unmodified crashing surf (phantom) and altered higher-frequency surf (shifted) compared to ambient sites set inland (control) and along the coast (real ocean). We deployed grids of plasticine clay caterpillars in each acoustic treatment for 72 hours and recorded bite impressions left by each predatory taxon. We found that foraging activity by rodents was higher under both introduced treatments (phantom and shifted) and real ocean conditions relative to control conditions. Foraging activity by birds was lower under the high-frequency shifted playback conditions relative to controls. More limited evidence suggested that foraging activity by arthropods was higher under phantom conditions compared to controls. Our results suggest that natural sounds can alter foraging activity and that they elicit taxon specific responses, likely in response to perceived predation risk, though the mechanisms remain uncertain. Natural sounds are likely an important ecological force that have been influencing animal



behaviors, populations, and communities for millennia, and research into the impact of natural sound will refine our understanding of the forces shaping ecological processes.

## 2. INTRODUCTION

Animals across the tree of life rely on the acoustic environment for foraging, communication, habitat assessment and many other critical behaviors (Bradbury & Vehrencamp, 2011). Only recently have we begun to understand how animal behaviors along with distributions, physiology, and community interactions are shaped by background sounds (Kight & Swaddle, 2011; Brumm and Slabbekoorn, 2005; Shannon *et al.*, 2016). The majority of this recent knowledge comes from studies focused on anthropogenic noise pollution (e.g., Barber *et al.*, 2010; Francis & Barber, 2013; Ortega, 2012; Patricelli & Blickley, 2006), which has been recognized as a conservation concern because it creates unnatural and novel acoustic conditions. However, each soundscape, which is the total collection of sounds from across the landscape (Pijanowski *et al.*, 2011), is comprised only in part of anthropogenic sound, with a myriad of natural sources present as well. Natural sounds can be found in all environments and are produced by many sources including moving water on coastlines, roaring rivers, wind-induced creaking branches, swishing grass, and chorusing animals. For example, there are over 1.6 million kilometers of marine coastlines worldwide (Pruett & Cimino, 2000), many of which could fundamentally alter acoustic characteristics throughout their adjacent terrestrial environments. Although all of these sources can elevate sound levels substantially (Bradbury & Vehrencamp, 2011), and the scope of influence is potentially vast, how and why natural acoustic conditions shape animal behaviors, distributions, and interactions have been largely ignored.

Natural sounds should have the same potential to affect animals as do anthropogenic sounds, but to our knowledge, there are very few studies involving the influence of natural sounds on animal behavior. One such study shows that treefrogs (Hylidae) prefer to call from louder areas near waterfalls whereas their gleaning bat predators (Phyllostomidae) prefer to hunt frogs calling in quieter areas (Tuttle & Ryan, 1982), suggesting natural sounds can shape predator-prey dynamics. Another study found that California ground squirrels (*Ottospermophilus beecheyi*), had increased vigilance and decreased movement when exposed to experimental river noise (Le *et al.*, 2019), indicating foraging and vigilance behavior can be shaped by natural sound as well. As these examples suggest, natural sounds likely play an under-appreciated role in shaping many ecological processes like predator-prey relationships and risk assessment. It is therefore crucial to our understanding of community dynamics that we study if and how natural sounds influence ecological interactions.

Every taxon perceives and experiences sound differently, in part due to different hearing sensitivities. For example, most songbirds hear best in the range of 2-3 kHz (Dooling, 2002) while many mice hear best around 16kHz (Masterton & Heffner, 1980). Thus, background sounds that could be audible for some species may be inaudible for others. Sensory stimuli, such as background sounds, that alter perceptions of risk can lead to a rebalancing in the trade-off between necessary survival behaviors like predator detection and foraging (i.e., foraging-vigilance trade-off). For example, exposure to anthropogenic noise causes a reduction in foraging activity and increase in vigilance in birds and rodents (Evans *et al.*, 2018; Quinn *et al.*, 2006; Shannon *et al.*, 2014; Ware *et*

*al.*, 2015). Changes to foraging behavior can restructure community processes because foraging is a direct link between trophic levels. These community level shifts have been documented in response to anthropogenic sound where altered foraging activity by birds and rodents led to increased pollination and decreased seed dispersal (Francis *et al.*, 2012). Therefore, like anthropogenic sound, it is likely that natural sounds shape community interactions and overall structure in similar ways.

Foraging activity of different functional or taxonomic groups has been used as a proxy to represent ecological interactions in general (Roslin *et al.*, 2017). Here we focus on the foraging activity of three insectivorous taxa (birds, rodents, and arthropods) to determine whether crashing surf, a natural sound source common along exposed coastlines, alters patterns of predation on insects. Using the approach outlined by Roslin *et al.*, (2017), we examined relative foraging activity via the bite impressions made by birds, rodents, and arthropods in artificial clay caterpillars when exposed to four different acoustic environments: two introduced experimentally and two endemically occurring. We introduced experimental playback of unmodified, natural-frequency crashing surf sound where it was not naturally occurring to create a “phantom” ocean and also introduced digitally-altered, higher-frequency, crashing surf sound to create a spectrally “shifted” ocean. The inclusion of the shifted surf stimulus provides, in addition to testing how elevated background sound levels influence behavior, the opportunity to compare how different frequency sounds influence animal behavior. We also had two treatments exposed only to the endemic, ambient sounds found there. We used sites situated inland where sounds generated from crashing surf were not present as

reference state “controls”, and “real ocean” sites situated along the coastline where crashing surf sound was produced by actual breaking waves. Using bite impressions left in plasticine clay caterpillars has been demonstrated to give accurate levels of predation (Tvardikova & Novotny, 2012), but only allows for assigning the identity of the animal that left the bite at the coarse taxonomic level of rodent, bird or arthropod (Low *et al.*, 2014).

Documented responses to anthropogenic noise guided our predictions regarding the potential direct effects of natural sounds on caterpillar predation. Previous work has documented avoidance of anthropogenic noise and decreased foraging rates of birds in noisy areas (Bayne *et al.*, 2008; Francis *et al.* 2009; Quinn *et al.* 2006; Ware *et al.* 2015) so we hypothesized that bird foraging activity would be impaired in natural sound conditions as it would interfere with passive acoustic surveillance. We expected the number of predation attempts by birds on caterpillars to be lower on phantom, shifted and real ocean sites compared to controls. Specifically, we also expected this decline in predation attempts to be stronger in response to the higher frequency shifted playback than the phantom or real ocean conditions because the higher frequency shifted treatment should have greater overlap with the smaller-bodied, insectivorous bird species’ most sensitive hearing range (Gleich *et al.*, 2005). Because rodents rely on acoustic surveillance for threat detection and loud conditions can mask acoustic predator cues that may lead to decreased foraging (Le *et al.*, 2019; Shannon *et al.*, 2014), we hypothesized that rodents also would have decreased foraging activity due to a loss in acoustic surveillance. We expected caterpillar predation attempts by rodents to

be fewer on phantom, shifted, and real ocean sites compared to controls, with a larger decline in predation attempts by rodents in high frequency conditions, due to the greater overlap with rodents' hearing sensitivities as well. The most likely arthropod predator on our sites, ants, are incapable of hearing far field sound (Hickling & Brown, 2000), thus we hypothesized arthropod foraging would not be affected by background sounds, and expected caterpillar predation attempts to be constant between all acoustic treatments. We alternatively hypothesized that natural sounds could have unforeseen indirect effects mediated by release from competition by one or more focal taxa. We predict that if predation attempts by birds decline in any treatment then rodents may compensatorily increase, or *vice versa*.

### 3. METHODS

#### Treatments

We conducted our artificial predation experiments during the summer (June-August) of 2017 and 2018 across Vandenberg Air Force Base, Santa Barbara County, California, (between 34°39'N and 34°46'N latitude and 120°36'W and 120°30'W longitude). We employed four different acoustic treatments: two experimentally manipulated treatments and two ambient conditions. Our experimental treatments were a landscape level playback of crashing surf ("phantom", [ $n = 5$  sites]), and a landscape level playback of digitally altered higher frequency crashing surf ("shifted", [ $n$

= 5 sites]). Our ambient conditions were an un-manipulated soundscape further inland where crashing surf was not audible (“control”, [n = 5 sites]), and an un-manipulated ambient soundscape situated along the coast where crashing surf sounds were present due to their proximity to real breaking waves (“real ocean”, [n = 4 sites]).



**Figure 1 | a.** Study area. Blue circles indicate **clusters**. Each cluster includes a phantom, shifted, and control site. Real ocean sounds sites are in two clusters of two. **Sites** are white points. **b.** Site Layout. A simplified view of each site (250m x 250m). Speakers represent location of treatment speakers or sham speakers. The squares are the caterpillar **grid** locations. Stars indicate the vegetation survey locations. The background gradient represents the sound level across the site. Not to scale. **c.** Arrangement of caterpillars within a **grid**. Each was 1m apart in five rows of four for a total area of 3m x 4m. **d.** Example of individual caterpillar deployment. Orientation and substrate varied.

To minimize environmental variation across site types, phantom, shifted, and control sites were grouped by geographic proximity into five clusters (Fig. 1a). Real ocean sites were not included with the other treatments in the clusters due to their constrained coastal locations (Fig. 1a). Each site was a 250m by 250m square with a random orientation on the landscape, with the exception of real ocean sites, which were oriented with the ocean along the “bottom” edge, (Fig. 1b). Phantom and shifted speaker towers were arranged 60m and 80m, respectively, from the site edge to maximize sound propagation throughout the entire area of each site. At ambient real ocean and control sites we set up speaker towers and sham speakers in the same locations to control for the presence of these objects.

By broadcasting ocean sounds with the same spectral properties as real breaking surf, the phantom treatment tests for the effects of ocean sounds without the other environmental factors that covary with proximity to the ocean (*e.g.*, sea spray, fog, pelagic birds). The shifted sites were included to test how the frequency of a sound stimulus may influence foraging activity apart from elevated sound levels. The control sites were not silent, but left unaltered, under the endemic acoustic conditions of the region, such as wind and singing birds. Real ocean sites were also unaltered acoustically, but were located at the coast so that crashing surf sounds from real breaking waves were present. The real ocean sites were included as a reference to compare how the foraging behavior along the coast aligned with the behavior under our experimental conditions. Sites were far enough apart that the acoustic treatment conditions at each

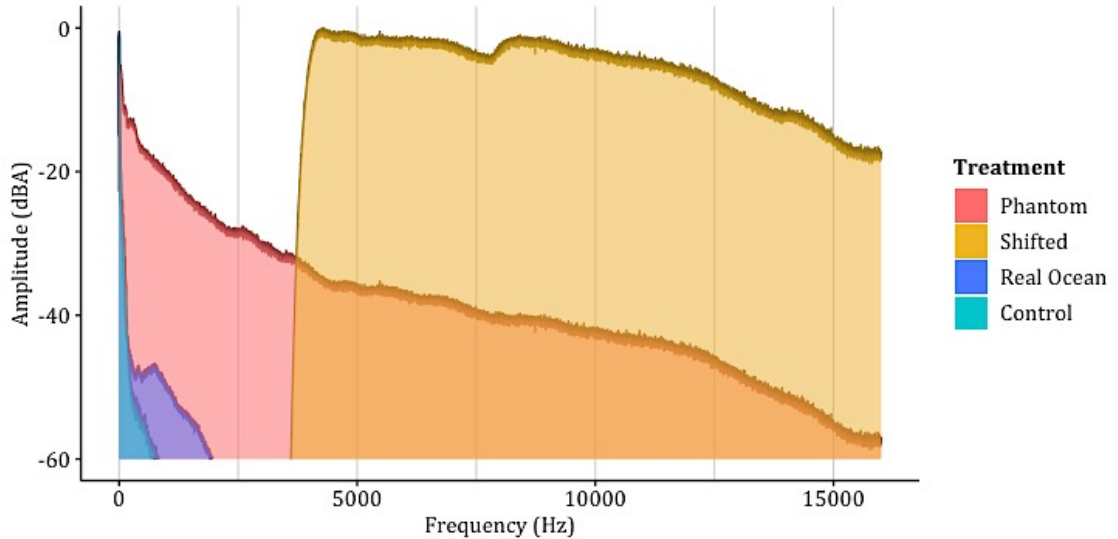


were independent. Treatment playbacks were started in early April and ran continuously through the end of the experiment in both 2017 and 2018.

### **Acoustic Playbacks**

Phantom ocean playbacks were generated using 45 minute files recorded on all four real ocean sites using R-05 recorders (Roland, USA; 48.0 kHz sampling rate, uncompressed WAV format) in a custom windscreen in late winter 2017. We sampled various sections of the recordings using Audacity (ver. 2.1.3, audacity.sourceforge.net) and amplified them to -2dB of the peak amplitude, resulting in a peak frequency of 4Hz (Fig. 2). We then clipped each 45-minute recording and stitched them together in random order to form a single four and half hour track with a seven second fade in / out and a five second crossfade to avoid clipping between files and when the track looped. The irregular four and a half hour track length prevented the tracks from syncing with the timing of other natural phenomena. For shifted ocean playbacks, we applied a 2 kHz high pass filter to the four and a half hour track and split the recordings using Audacity's Frequency Band Splitter into two bands: 2-14 kHz and 14-24 kHz. We then amplified the bands by 4 dB and 5 dB, respectively, prior to recombining them, for a peak frequency of 4.3 kHz (Fig. 2).

Both playbacks had the same natural rhythm and fluctuation in amplitude characteristic of crashing surf. We calibrated treatment speakers' sound levels with a



**Figure 2 |** Spectral plot of each acoustic treatment. Automated recording units cut off at 16kHz. Peak frequencies for each treatment were: Phantom: 4Hz; Shifted: 4300Hz; Real Ocean: 3Hz; Control: 6Hz.

two-minute A-weighted  $L_{eq}$  to  $75 \pm 1$  dB at 20m using a Larson-Davis 831 sound pressure meter (PCB Piezotronics, USA). All speakers were calibrated during a standardized section of the track. The treatments were broadcast across the landscape using omnidirectional speakers and Lepai model LP-2020TI (phantom) and PRV Audio model AD1200.1 (shifted) amplifiers. Sound files were played through Roland R-05 or R-09 digital players powered by 3.2V LiFeMnPO4 prismatic batteries (AA Portable Power Corp, USA). Each speaker was suspended from a tripod three meters above the ground (Fig. 3). Phantom ocean treatments used two large speakers consisting of four high compression horn drivers and a 46cm subwoofer (Octasound model-SP860A) with a speaker in the left and right towers. Due to shorter propagation distance of high frequency sound, the shifted treatment required three smaller speakers consisting of

four high compression horn drivers and a 25.5cm subwoofer (Octasound model-SP810A). As with control and real ocean sites, phantom sites included a third speaker tower with a sham speaker to control for the physical presence of the object. Speakers were powered by 2m x 1m solar panels (Suniva, USA, model-OPT285-60-4-100) with controllers (Midnight Solar, USA, model-The Kid) and AGM sealed batteries (Centennial, USA). Phantom sites used a single 12V battery (CB12-115) and shifted sites used two 6V batteries in series (CB6-224). Because solar panels can reflect polarized light that can attract animals (reviewed in Horváth *et al.*, 2009), we placed “sham panels” built from plywood painted with high-gloss black paint that reflected polarized light at each tower location lacking a real speaker/ panel combination. Sham panels were the same size and orientation as functional panels.

### **Artificial Caterpillar Deployment and Scoring**

We made artificial caterpillars (hereafter “caterpillars”) from green, odorless, non-toxic plasticine modeling clay (Van Aken Plastalina, USA), which does not dry or harden and remains soft and impressionable, allowing an animal that bites it to leave a mark. We made caterpillars following Roslin *et al.*, (2017):



**Figure 3** | Example treatment speaker.

2.5mm x 30mm to resemble a non-specific, general amalgamation of caterpillars. We carefully smoothed caterpillar forms to remove any wrinkles or scratches that could potentially be confused later with bite impressions, and each caterpillar was only used once. This method has been shown to give accurate estimates of predatory foraging activity (Sam *et al.*, 2015; Tvardikova & Novotny, 2012) which in our study is defined as the number of caterpillars in each deployment grid with predatory attempts that left bite marks, separated by predatory taxon. Our study design did not allow us to discriminate between changes in per capita foraging behavior or changes in the number of foraging individuals with no change in per capita foraging behavior, however both mechanisms result in the same effect on the caterpillar community.

In 2017 we set up three caterpillar grids on each site (Fig. 1b,c). Two were equidistant between the middle and side speaker towers on the right and left sides, respectively (35m from each tower). The third was along the center axis of the plot 100m from the middle tower. In 2018, we deployed only one grid per site, reusing locations used for the right or left side from the previous year.

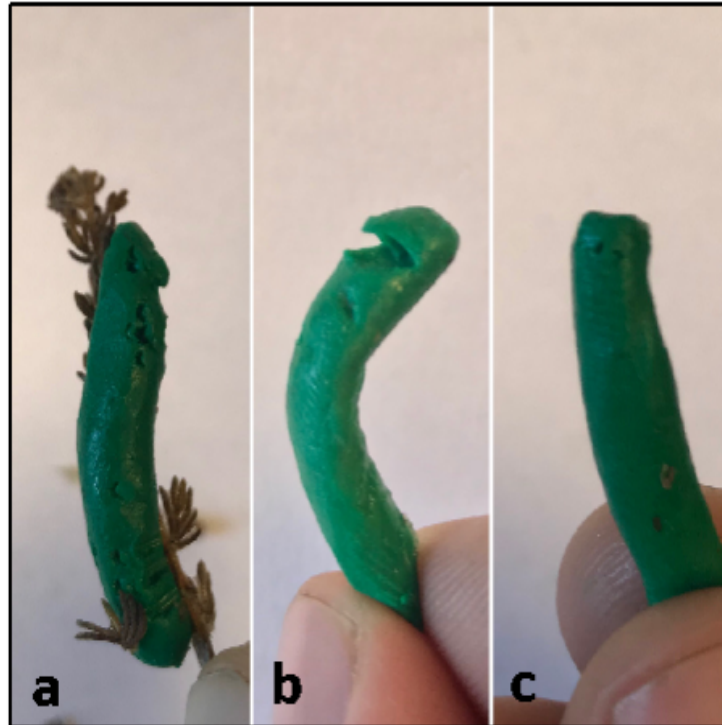
We deployed caterpillars in grids of twenty at one meter intervals, resulting in a three by four meter total grid area (Fig. 1c). All caterpillars were placed less than one meter above the ground and we chose placement locations using a hierarchy of ranked options related to vegetation structure: 1) a living shrub branch, 2) a dead shrub branch, 3) sturdy stalk of grass or forb and 4) bare ground (Fig. 1d). Horizontal positioning was preferred over vertical positioning and adaxial attachment was used when possible. Vegetation was never moved or manipulated for placement. We attached each

caterpillar to its location using cyanoacrylate glue. We added a unique ID written on a small piece of neutral brown masking tape located several centimeters away to track individual fate.

We deployed caterpillars for 72 hour intervals, with all grids within a cluster (geographical grouping of a set of phantom, shifted and control sites, or a pairing of real ocean sites, Fig. 1a) deployed on the same day. At 72 hours of exposure we returned to each grid and recorded each caterpillar's fate. Missing caterpillars were removed from subsequent analysis. For remaining caterpillars, we scored each into one of the following bite categories: no bite, rodent bite, bird bite, arthropod bite, or unknown bite. Two observers scored each caterpillar independently *in situ*. After the second scoring all caterpillars were collected and carefully returned to the lab in individual plastic containers. When observers scored a caterpillar differently (21.75% in 2017), the entire team (n=3) re-examined it in the lab and assigned a final score based on consensus. 2.25% of caterpillars were bit by more than one taxonomic group and because there was no way to identify which bite was left first, both were considered in our analyses. For example, for a caterpillar with a bite impression left by both a rodent and a bird, we assigned it a score of one for both mammal and bird but it remained only one in the combined taxa count.

We determined scoring visually based on the characteristic bite impressions left by different taxa's predation attempts following Roslin *et al.*, (2017) and Low *et al.*, (2014). Rodent bites were identified by clear impressions of individual teeth puncturing or scraping the clay (Fig. 4a). Bird bites were identified by a triangular piercing and

straight lines left by the bill (Fig. 4b), and arthropod bites were identified by sets of small round pinches in opposition made by mandibles (Fig. 4c).



**Figure 4** | Examples of bites by **A.** rodent **B.** bird **C.** arthropod.

Unknown bites were those where a caterpillar had obviously been manipulated by an animal, but due to excessive damage or ambiguous markings we were unable to sort it into a taxonomic category. Based on bite sizes and regional species composition (unpublished data), mammal bites likely reflected predation attempts by small rodents such as deer mice (*Peromyscus* spp.) or woodrats (*Neotoma* spp.), bird bites likely represented predation attempts by insectivorous gleaning passerines such as Bewick's wrens (*Thryomanes bewickii*), bushtits (*Psaltirparus minimus*) or wrentits (*Chamaea fasciata*) and arthropod bites likely reflected predation attempts primarily from ants

(Formicidae) although we can't rule out other predatory taxa like dragonflies (Odonata), or spiders (Araneae). There is mixed evidence regarding whether rodents are attracted to the smell of plasticine or not (Maier & Degraaf, 2001; Rangen *et al.*, 2000), but rodents do often nibble objects to gain olfactory cues (King, 1968); therefore, rodent bites may reflect investigation of the novel object as well as direct predation attempts. Regardless, bites reflect relative foraging activity across our experimental treatments.

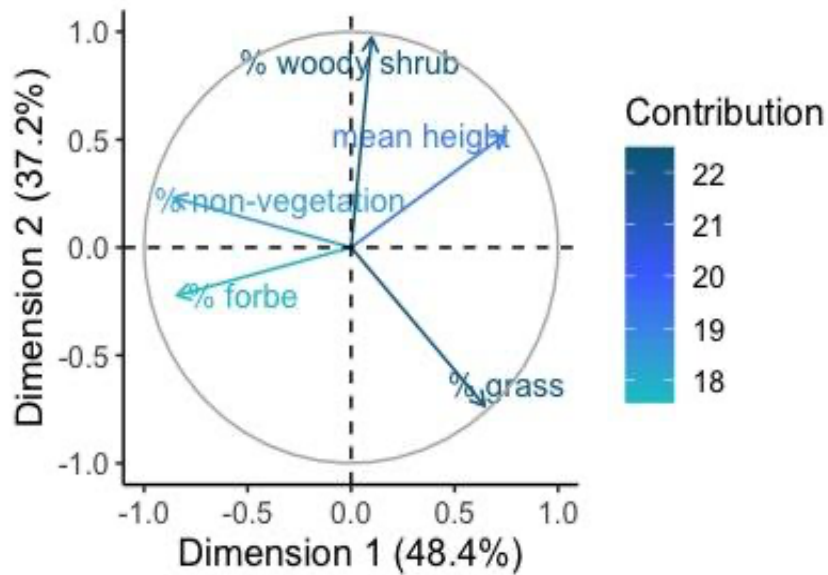
### **Environmental Variables**

We measured the sound level (2 minute, A-weighted  $L_{eq}$ ) at each caterpillar grid with a Larson Davis 831 on three separate occasions: at deployment, at collection, and 72 hours post-collection. Sound measurements were not taken when wind speed exceeded 15km/hr. We used the mean value from these measurements for subsequent analyses. To account for any differences in vegetation across sites, we conducted point intercept vegetation surveys at five standardized locations on each site (upper right, upper left, lower right, lower left and middle [stars in Fig. 1b]). At each survey location we set-up two 100m transect tapes perpendicular to each other, intersecting at the 50m mark over the standardized survey location in a random orientation. We recorded point intercept measurements every two meters for the height of the tallest plant where it intersected the vertical plane of the point, resulting in 99 points per survey. We recorded species when feasible and sorted plants into a broad morphological category (tree, woody shrub, soft shrub, forb, or grass). If there was no plant at a point it was

labeled bare ground. Dominant plants across the system were California sagebrush, (*Artemisia californica*), coyote brush, (*Baccharis pilularis*), mock heather, (*Ericameria ericoides*) and black sage, (*Salvia melifera*). Invasive iceplant, (*Carpobrotus edulis*) and African veldt grass (*Erhardta calycina*) were prevalent on many sites as well, sometimes forming monospecific patches.

Because of the high dimensionality of the vegetation data, we used principal component analysis (PCA) using the R packages psych (Revelle, 2018) and factoextra (Kassambara & Mundt, 2017) to reduce vegetation structural variation to the two principal components which explained the most variation. We used the principal components from the vegetation assessment points nearest each caterpillar grid to characterize local vegetation differences between grids. The environmental variables included in the PCA were average height of vegetation and proportion of woody shrubs, forbs, grasses and non-vegetation (*i.e.*, bare ground or rocks). Axis one (PC1) explained 48.4% of the variation and axis two (PC2) explained 37.2% for a cumulative variation of 83% (Fig. 5, Table 1). PC1 was characterized as a gradient from areas with shorter vegetation, more forbs and non-vegetated surfaces to areas with taller vegetation and more grass coverage. PC2 was characterized weakly by a gradient from areas with shorter vegetation with more grass coverage towards sites with taller vegetation and strongly associated with more woody shrub coverage.





**Figure 5 |** Principal component analysis vectors of mean vegetation structure. Color and length of line indicate strength of contribution for each variable. Dimension 1 explains 48.4% variation in vegetation structure and dimension 2 explains 37.2% of vegetation structure. Contribution is measured in percentage.

Because mammal and arthropod activity can be influenced by moonlight

(Johnson & De León, 2015; Orrock *et al.*, 2004; Klotz & Reid, 1993), we also obtained moon position and phase using the R packages *suncalc* (Thieurmel & Elmarhraoui, 2019) and *lunar* (Lazaridis, 2014). We calculated a “moon index” by multiplying the proportion of the moon’s surface illuminated each night by the number of hours the moon was above the horizon between dusk and dawn (Johnson & De León, 2015).

**Table 1** | Component loadings of PCA on vegetation structure.

	PC1	PC2
Mean height	0.90	0.19
% Woody shrub	0.47	0.84
% Forb	-0.85	0.14
% Grass	0.30	-0.89
% Non-vegetation	-0.68	0.56
SS loadings	2.30	1.87
Proportion variance	0.46	0.37
Cumulative variance	0.46	0.83

## Analyses

We constructed generalized linear mixed effect models (GLMMs) with Poisson error using the R package lme4 (Bates *et al.*, 2015) and treated each caterpillar grid as the unit of replication with the number of bites in each category as response variables. Unknown bites were included in the analysis of bites by all taxa combined only. Due to the hierarchical structure of our study design, we initially included grid nested within site nested within cluster as random intercepts. Preliminary analysis suggested that site had variance estimates near zero (i.e.,  $< 0.0001$ ), thus we removed it as a random effect (Bates *et al.* 2018) and retained grid nested with cluster for all models. We also included observer team as a random effect to account for any variation among observers. For fixed effects, we included: acoustic treatment (phantom, shifted, real ocean, control), mean sound level ( $L_{eqA}$ ), PC1, PC2, the interaction of PC1 and PC2, vegetation richness,

year, and moon index. Abbreviations and definitions for variables can be found in Table 2 and global models for each forager taxon can be found in Table 3.

**Table 2 |** Definitions and abbreviations for model variables used in analyses. Random effects variables are listed in gray.

<b>Term</b>	<b>Definition</b>
Tr	Acoustic treatment: P=phantom, S=shifted, O=real ocean, C=control
LEQ	Average $L_{eq}(A)$ in dB
PC1	Vegetation principal component 1 (see figure 5, table 1)
PC2	Vegetation principal component 2 (see figure 5, table 1)
Vg	Vegetation richness
Yr	Year 2018 relative to 2017
Moon	Moon index (% of lunar surface lit x duration moon was visible at night)
Cluster	Geographic cluster of sites containing P,S, and C sites, or O sites.
Side	Grid location within site (left, right, middle)
Observer	Individuals who scored each bite category.

Treatment was a categorical variable, with control (ambient sound away from the ocean) as the reference state. To achieve all possible pairwise comparisons, we changed treatment reference states and reran the model. Average sound level ( $L_{eq}$ ) was scaled to aid in model convergence for all models. It was also necessary to scale plant richness only in the bird models for convergence. Given the potential for multicollinearity between treatment and average sound level ( $L_{eqA}$ ), we used the “check\_collinearity” function in the performance package (Lüdecke *et al.*, 2019) and considered a variance inflation factor (VIF) > 10 as evidence for multicollinearity following Dormann *et al.* (2007). Only models of caterpillar predation by birds were

deemed problematic ( $VIF \leq 11.67$ ), thus for these models we used two global models: one with treatment and one with average sound level.

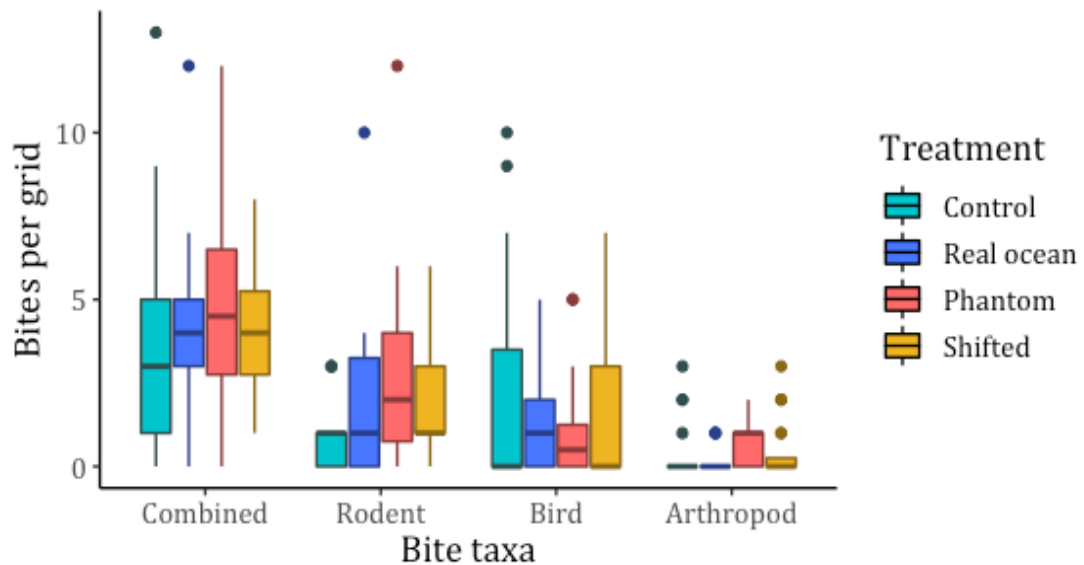
**Table 3 |** Global models for all taxonomic analyses. Random effects are applied to all models. See Table 2 for list of variables and their definitions.

Taxa	Global models
Combined	Scale(LEQ) + Tr + PC1 * PC2 + Vg + Moon + Yr
Rodents	Scale(LEQ) + Tr + PC1 * PC2 + Vg + Moon + Yr
Birds	Scale(LEQ) + PC1 * PC2 + scale(Vg) + Yr
Birds*	Tr + PC1 * PC2 + scale(Vg) + Yr
Arthropods	Scale(LEQ) + Tr + PC1 * PC2 + Vg + Moon + Yr
Random effects ( $\mu$ )	Cluster:Side + Observer

We used Akaike information criterion corrected for small sample sizes,  $AIC_c$  (Burnham & Anderson, 2002) from the dredge function in the MumIn package (Bartoń, 2019) to rank competing models for each predation response category (*i.e.*, combined, mammal, bird, arthropod). We considered models with  $\Delta AIC_c \leq 2$  of the top model as well supported and calculated model weights ( $w_i$ ) from among this set. We considered variables from well-supported models to have an effect or strong effect if the 85% or 95% confidence intervals (CI's) did not overlap zero, respectively (Arnold, 2010). We also performed a model using the same mixed effects structure to compare the mean  $L_{eqA}$  across treatments. All analyses were performed in RStudio ver. 1.0.153.

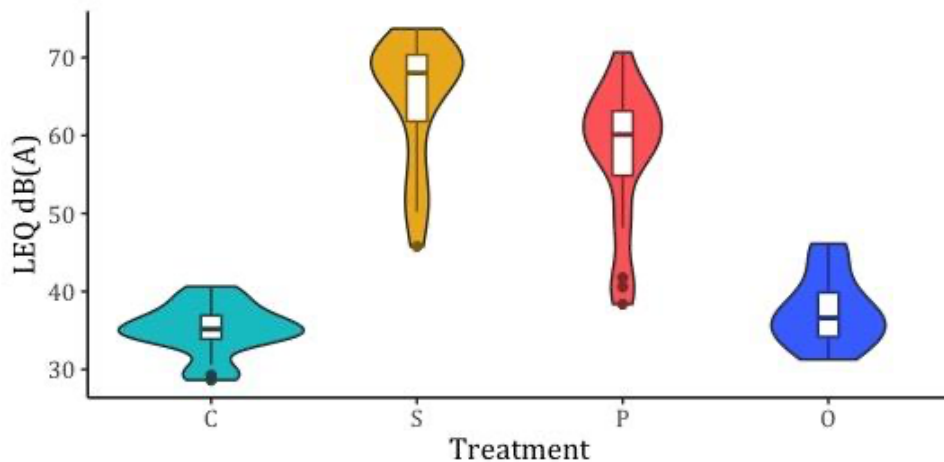
## 4. RESULTS

We deployed 1,520 individual clay caterpillars across 76 grids: 1,140 caterpillars across 57 grids in 2017 and 380 caterpillars across 19 grids in 2018. One grid was removed from analyses due to environmental data errors, resulting in a total of 75 grids. A total of 310 caterpillars were bit during exposure of which 145 were from rodents, 114 were from birds, 36 were from arthropods and 23 were unknown. The mean number of caterpillars present per grid at the end of the exposure period was  $19.87 \pm 0.05$  SE with a minimum of 18 of 20 present. The mean number of caterpillars bit per grid by all taxa was  $4.07 \pm 0.34$  SE,  $1.88 \pm 0.26$  SE by rodents,  $1.51 \pm 0.27$  SE by birds,  $0.48 \pm 0.09$  SE by arthropods and  $0.31 \pm 0.07$  SE were classified as unknown sources of predation (Fig. 6).



**Figure 6** | The number of caterpillars bit per grid by each taxon. Combined taxa values are the number of caterpillars bit by any taxon, and also includes bites of unknown origin. A single caterpillar bitten by multiple taxa is still only counted as one in the combined taxa.

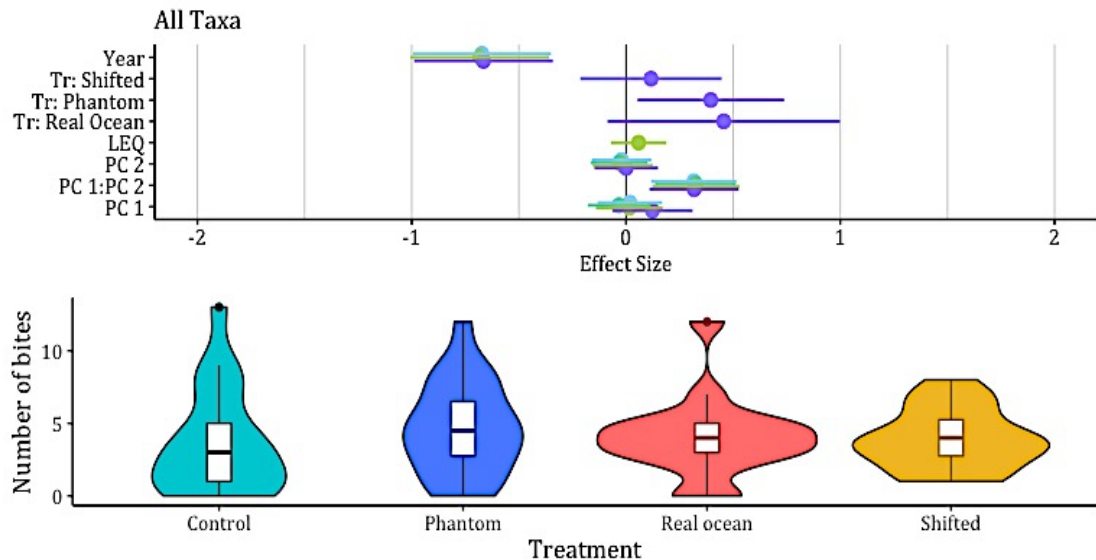
Sound levels across all grids ranged from 26.5 dB(A) to 74.7 dB(A), with a mean sound level of  $49.45 \pm 1.67$  SE dB(A). On control sites the mean LEQ was  $35.11 \pm 4.05$  SE dB(A), on phantom sites it was  $57.46 \pm 6.63$  SE dB(A), on shifted sites it was  $64.64 \pm 7.46$  SE dB(A), and on real ocean sites it was  $37.48 \pm 4.33$  SE dB(A) (Fig. 7). Phantom and shifted sites were louder than both control (ref. control,  $\beta_{\text{phantom}} = 22.19$ , 95%CI= 18.88, 25.50;  $\beta_{\text{shifted}} = 29.42$ , 95%CI= 26.09, 32.75) and real ocean sites (ref. real ocean,  $\beta_{\text{phantom}} = 19.30$ , 95%CI= 13.88, 24.71;  $\beta_{\text{shifted}} = 26.53$ , 95%CI= 21.11, 31.96). Shifted sites were also louder than phantom sites ( $\beta_{\text{shifted}} = 7.24$ , 95%CI= 3.99, 10.48). Real ocean sites did not differ in sound levels from control sites ( $\beta_{\text{real ocean}} = 2.89$ , 85%CI= -1.12, 6.90) at the time of the experiment, when ocean swells are at their mildest. The mean vegetation richness was  $11.82 \pm 0.38$  SE species.



**Figure 7** | Sound level measurements at caterpillar grids in each treatment: control (C), shifted ocean (S), phantom ocean (P) and real ocean (O). Three two-minute  $L_{eq}(A)$  measurements were taken at each grid 72 hours apart.

## Model Selection

All four well-supported models for predation by all taxa combined included a strong positive effect of the interaction between PC1 and PC2 ( $\beta_{PC1:PC2} = 0.32$ , 95% CI = 0.12, 0.52; Fig. 8; Table 4), suggesting that predation rates were higher in areas with taller, more woody vegetation. Three models had a strong influence of year, such that 2018 had fewer bites per grid than 2017 ( $\beta_{year} = -0.67$ , 95%CI=-0.99, -0.35). One model also suggested that phantom and real ocean sites had higher rates of predation than control sites (ref. control  $\beta_{phantom} = 0.40$ , 95%CI= 0.05, 0.74;  $\beta_{real\ ocean} = 0.46$ , 85%CI=0.06, 0.85) and that shifted sites had lower rates of predation than phantom sites (ref. phantom,  $\beta_{shifted} = -0.28$ , 85% CI=-0.52, -0.04).

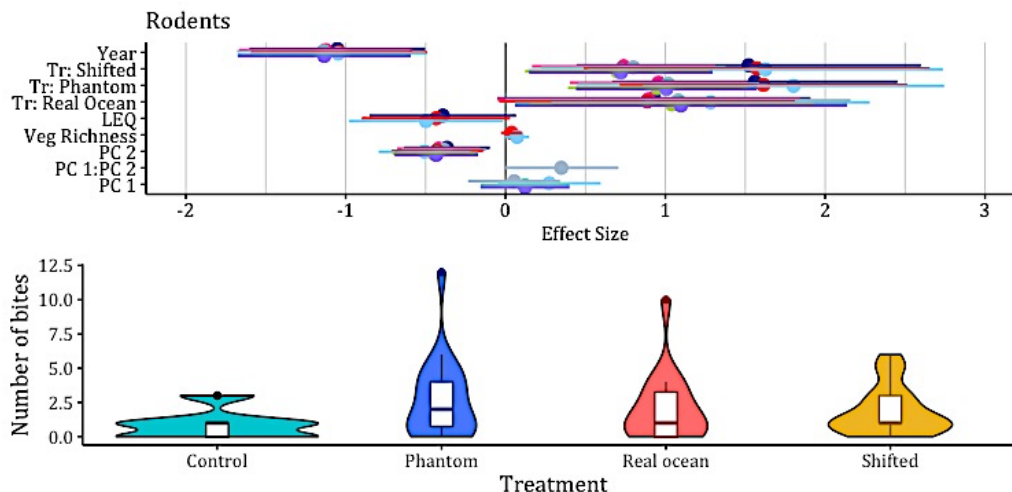


**Figure 8 | Top** | The influence of fixed effects on number of bites per grid by all taxa. Effects of all top models (Table 4) are plotted with model indicated by color. Dots represent the mean and horizontal bars represent 95% confidence intervals (95%CI). Those variables with 95%CI's that do not overlap zero indicate a strong effect. The strength of influence for each variable can be determined from the direction and magnitude from zero. See Table 2 for definition of model terms. Effects estimates are standardized by rescaling estimates by dividing each by two standard deviations.  
**Bottom** | Number of bites by all taxa for each acoustic treatment. Width shows data distribution.

**Table 4 |** Model selection table for bites of combined taxa on artificial caterpillars. Models are ranked using Akaike information criteria corrected for small sample sizes ( $AIC_c$ ). Bold indicates 95% confidence intervals that do not overlap zero and italic indicates 85% confidence intervals that don't overlap zero. See Table 2 for full variable definitions. Color indicates model in Fig. 8.

Combined Taxa Models	K	LogLik	$AIC_c$	$\Delta AIC_c$	$w_i$	Color
PC1 + PC2 + <b>PC1:PC2</b> + <b>Yr</b>	8	-173.49	365.16	0.00	0.43	Blue
PC1 + PC2 + <b>PC1:PC2</b>	7	-175.33	366.3	1.17	0.24	Teal
PC1 + PC2 + <b>PC1:PC2</b> + <b>Yr</b> + scale(LEQ)	9	-173.09	366.9	1.78	0.17	Green
PC1 + PC2 + <b>PC1:PC2</b> + <b>Yr</b> + Tr[P,S,O]	11	-170.45	367.1	1.93	0.16	Purple
Null – random effects only	4	-180.94	370.4	5.28	0.00	

All top models for predation by rodents revealed higher caterpillar predation rates on phantom and shifted treatments relative to controls ( $\beta_{\text{Phantom}} = 1.56$ , 95%CI=0.67, 2.45;  $\beta_{\text{Shifted}} = 1.52$ , 95%CI=0.44, 2.60; Fig. 9; Table 5).



**Figure 9 | Top |** The influence of fixed effects on number of bites per grid by rodents. Effects of all top models (Table 5) are plotted with model indicated by color. Dots represent the mean and horizontal bars represent 95% confidence intervals (95%CI). Those variables with 95%CI's that do not overlap zero indicate a strong effect. The strength of influence for each variable can be determined from the direction and magnitude from zero. See Table 2 for definition of model terms. Effects estimates are standardized by rescaling estimates by dividing each by two standard deviations.

**Bottom |** Number of bites by rodents for each acoustic treatment. Width shows data distribution.

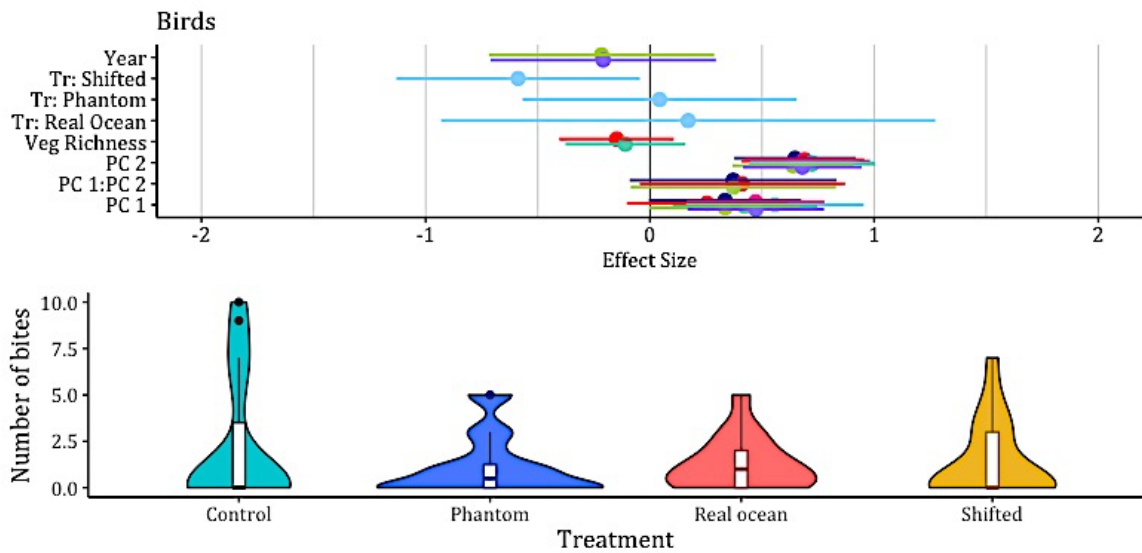


Predation by rodents did not differ among phantom, shifted, and real ocean sites in all well supported models.

PC2 had a strong negative effect on the number of caterpillars bit by rodents ( $\beta_{PC2} = -0.37$ , 95%CI=-0.63, -0.10) with less bites on sites with taller, woodier shrubs. Predation by rodents was lower in 2018 than 2017 ( $\beta_{Year} = -1.05$ , 95%CI=-1.60, -0.50). A subset of well-supported models also revealed a decrease in predation by rodents with sound level ( $\beta_{Leq} = -0.50$ , 95%CI=-0.98, -0.01) and a positive effect of PC1 and vegetation species richness ( $\beta_{PC1} = 0.27$ , 85%CI = 0.04, 0.51;  $\beta_{VegRich} = 0.07$ , 85%CI = 0.02, 0.13).

**Table 5 |** Model selection table for bites of rodents on artificial caterpillars. Models are ranked using Akaike information criteria corrected for small sample sizes ( $AIC_c$ ). Bold indicates 95% confidence intervals that do not overlap zero and italic indicates 85% confidence intervals that don't overlap zero. See Table 2 for full variable definitions. Color indicates model in figure 9.

Rodent Models	K	LogLik	$AIC_c$	$\Delta AIC_c$	$W_i$	Color
Tr[P,S,O] + <b>PC2</b> + Yr + <i>scale(LEQ)</i>	10	-113.47	250.38	0.00	0.22	<b>Violet</b>
Tr[P,S,O] + <b>PC2</b> + Yr	9	-114.84	250.44	0.06	0.21	<b>Pink</b>
Tr[P,S,O] + <b>PC2</b> + Yr + PC1 + <i>PC1:PC2</i>	11	-112.69	251.57	1.18	0.12	<b>Grey</b>
Tr[P,S,O] + <b>PC2</b> + Yr + <i>scale(LEQ)</i> + Vg	11	-112.88	251.96	1.57	0.10	<b>Red</b>
Tr[P,S,O] + <b>PC2</b> + Yr + <b>scale(LEQ)</b> + PC1 + Vg	12	-111.47	251.98	1.60	0.10	<b>Blue</b>
Tr[P,S,O] + <b>PC2</b> + Yr + PC1	11	-113.07	252.34	1.95	0.10	<b>Teal</b>
Tr[P,S,O] + <b>PC2</b>	8	-117.09	252.36	1.98	0.08	<b>Green</b>
Tr[P,S,O] + <b>PC2</b> + Yr + PC1	10	-114.47	252.38	1.99	0.08	<b>Purple</b>
Null – random effects only	4	-132.2	273.03	22.65	0.00	



**Figure 10 | Top |** The influence of fixed effects on number of bites per grid by birds. Effects of all top models (Table 6) are plotted with model indicated by color. Dots represent the mean and horizontal bars represent 95% confidence intervals (95%CI). Those variables with 95%CI's that do not overlap zero indicate a strong effect. The strength of influence for each variable can be determined from the direction and magnitude from zero. See Table 2 for definition of model terms. Effects estimates are standardized by rescaling estimates by dividing each by two standard deviations. **Bottom |** Number of bites by birds for each acoustic treatment. Width shows data distribution.

All top models for avian predation included a strong, positive effect of PC2 with more bites on taller, woodier grids ( $\beta_{PC2} = 0.65$ , 95%CI=0.38, 0.92; Fig. 10; Table 6). Also included in all top models was a positive strong effect of PC1 with more bites on taller, grassier grids ( $\beta_{PC1}=0.47$ , 95%CI = 0.16, 0.78). Several models included a positive effect of the interaction of PC1 and PC2 ( $\beta_{PC1:PC2} = 0.37$ , 85%CI = 0.03, 0.71) indicating more bites in grids with complex vegetation structure resulting from both taller woody shrubs and more grass coverage.

**Table 6** | Model selection table for bites of birds on artificial caterpillars. Models are ranked using Akaike information criteria corrected for small sample sizes ( $AIC_c$ ). Bold indicates 95% confidence intervals that do not overlap zero and italic indicates 85% confidence intervals that don't overlap zero. See Table 2 for full variable definitions. Color indicates model in Fig. 10.

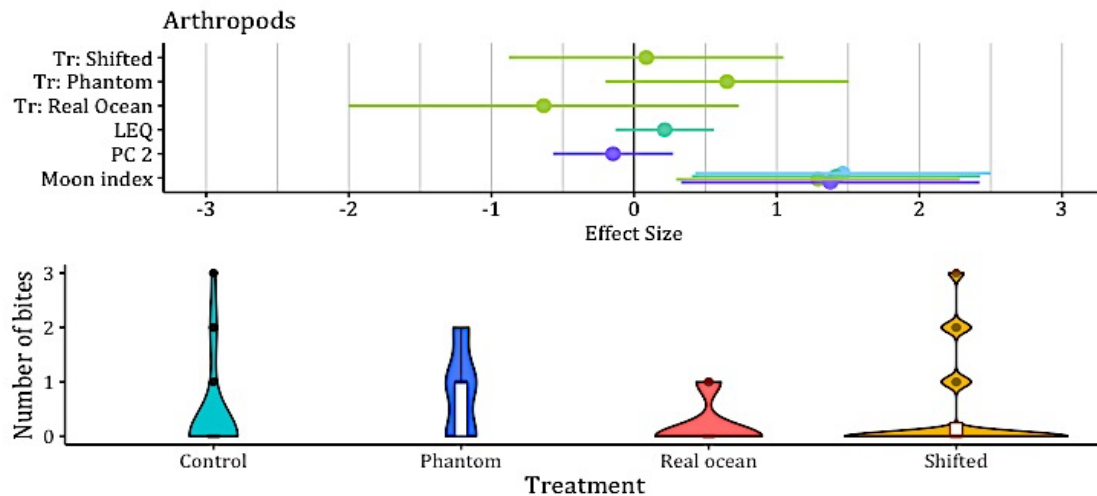
Bird Models	K	LogLik	$AIC_c$	$\Delta AIC_c$	$W_i$	Color
<i>PC1</i> + <b>PC2</b> + <i>PC1:PC2</i>	7	-125.08	265.84	0.00	0.24	Grey
<b>PC1</b> + <b>PC2</b>	6	-126.33	265.89	0.06	0.23	Pink
<i>PC1</i> + <b>PC2</b> + <i>PC1:PC2</i> + scale(Vg)	8	-124.44	267.06	1.22	0.13	Red
<b>PC1</b> + <b>PC2</b> + Tr(P,S,O)	9	-123.26	267.28	1.44	0.12	Blue
<b>PC1</b> + <b>PC2</b> + scale(Vg)	7	-125.98	267.62	1.79	0.10	Teal
<i>PC1</i> + <b>PC2</b> + <i>PC1:PC2</i> + Yr	8	-124.73	267.65	1.81	0.10	Green
<b>PC1</b> + <b>PC2</b> + Yr	7	-126.00	267.67	1.84	0.09	Purple
Null – random effects only	4	-149.40	307.36	41.52	0.00	

Caterpillar predation by birds was lower on shifted sites compared to control sites (ref. control,  $\beta_{\text{Shifted}} = -0.59$ , 95%CI = -1.13, -0.04) and phantom sites (ref. phantom,  $\beta_{\text{Shifted}} = -0.63$ , 85%CI = -1.11, -0.15). None of the models containing average sound level were well supported.

All well-supported models for arthropods included a strong positive effect of moon index, with more bites on nights with more moonlight ( $\beta_{\text{Moon}} = 1.46$ , 95%CI = 0.43, 2.50; Fig. 11, Table 7). There was also some support for arthropods biting more caterpillars on phantom sites relative to both control sites (ref. control,  $\beta_{\text{Phantom}} = 0.65$ , 85%CI = 0.03, 1.28) and real ocean sites (ref. real ocean,  $\beta_{\text{Phantom}} = 1.29$ , 95%CI = 0.01, 2.56).

**Table 7 |** Model selection table for bites of arthropods on artificial caterpillars. Models are ranked using Akaike information criteria corrected for small sample sizes ( $AIC_c$ ). Bold indicates 95% confidence intervals that do not overlap zero and italic indicates 85% confidence intervals that don't overlap zero. See Table 2 for full variable definitions. Color indicates model in Fig. 11.

Arthropod Models	K	LogLik	$AIC_c$	$\Delta AIC_c$	$W_i$	Color
<b>Moon</b>	5	-67.22	145.31	0.00	0.36	Blue
<b>Moon + scale(LEQ)</b>	6	-66.52	146.25	0.96	0.22	Teal
<b>Moon + Tr[P,S,O]</b>	8	-64.47	147.13	1.82	0.14	Green
<b>Moon + PC2</b>	6	-66.98	147.19	1.89	0.14	Purple
Null – random effects only	4	-71.08	150.74	5.43	0.00	



**Figure 11 | Top |** The influence of fixed effects on number of bites per grid by arthropods. Effects of all top models (Table 7) are plotted with model indicated by color. Dots represent the mean and horizontal bars represent 95% confidence intervals (95%CI). Those variables with 95%CI's that do not overlap zero indicate a strong effect. The strength of influence for each variables can be determined from the direction and magnitude from zero. See Table 2 for definition of model terms. Effects estimates are standardized by rescaling estimates by diving each by two standard deviations.

**Bottom |** Number of bites by arthropods for each acoustic treatment. Width shows data distribution.

## 5. DISCUSSION

Our experiment revealed that natural sounds alter foraging activity across multiple diverse taxa, and is the first study to our knowledge to do so. We observed more predation attempts on artificial caterpillars from all taxa combined under introduced phantom ocean conditions and ambient real ocean conditions, as well as fewer predation attempts under introduced high frequency shifted conditions compared to phantom. This combined analysis however masks the opposite and strong, taxon-specific responses among birds and rodents, suggesting that not all organisms share a common response to a background sound stimulus. Predatory foraging activity by birds declined under the introduced, high-frequency shifted conditions compared to ambient controls, while predatory foraging activity by rodents increased under both introduced phantom and shifted treatments, and real ocean conditions compared to controls. It may be that how a taxon's foraging activity is affected by natural sounds is a result of each one's different hearing sensitivity (Dooling, 2002; Dice & Barto, 1952; Heffner & Heffner, 1985; Masterton & Heffner, 1980), and ecological context including factors like trophic level and interspecific interactions (discussed below).

That rodents had increased foraging activity under both introduced phantom and shifted conditions and real ocean conditions relative to ambient controls was surprising, and thus we reject our hypothesis that foraging activity would decrease in natural sounds. With further consideration their increased activity appears likely to be a multi-trophic response with rodents perceiving a lower risk of being depredated

themselves by larger predators. In partial support of our predictions, we found that caterpillar predation by birds was lower on the introduced high-frequency shifted sites relative to all other site types, but not altered on the introduced phantom sites or ambient real ocean sites relative to controls. This decline in foraging is likely the result of increased visual vigilance being required, reducing time spent foraging time and decreasing perceived habitat value. Finally, the weaker evidence that predation by arthropods was higher on introduced phantom sites compared to ambient control and real ocean sites is partially consistent with our prediction of no effect of the soundscape. Potential mechanisms explaining these taxon-specific patterns include two non-mutually exclusive responses: differences in (i) foraging behavior (*i.e.*, functional response) or (ii) abundance (*i.e.*, numerical response). Although we are unable to confirm the active mechanism given our study design, support for both possibilities are discussed in more detail below.

### **Effects on Rodents**

We reject our hypothesis that rodents' foraging activity would decline in natural sounds, as their foraging activity actually increased under both introduced phantom and shifted stimuli, and real ocean conditions compared to controls. This was surprising not only because the response was the opposite of our prediction, but also that there was no difference in the strength of the response between the introduced phantom and shifted treatments. One possible explanation for these results is that while each

treatment impacts rodent's hearing ability differently, they are all recognized as an indirect cue of lower predation risk. Woodrats (*Neotoma floridana*), have a peak sensitivity for hearing at 8kHz (Heffner & Heffner, 1985) and deer mice, (*Peromyscus maniculatus*) have a peak sensitivity between 5-16 kHz (Dice & Barto, 1952). This means that much of the low-frequency energy of the introduced phantom treatment was below their peak hearing range and some of the lower frequencies may have been poorly audible. In contrast, the shifted treatment's higher frequencies strongly overlapped with rodent's peak hearing range, which is why we predicted a stronger response. So an alternative explanation to make sense of the increased foraging activity may be that it is via an indirect effect of the treatments mediated by a decline in the mesopredators that commonly prey on small rodents. Although we have no direct evidence of mesopredators' responses to our sound treatments, mesopredators common to our sites have high hearing sensitivities within the range of our playbacks: owls, (Strigiformes), at 2-3 kHz (Dooling, 2002), red fox (*Vulpes vulpes*), at 4 kHz (Malkemper *et al.*, 2015), Raccoon (*Procyon lotor*), at 1kHz (Wollack, 1965), domestic dog (*Canis lupus familiaris*; closest relative to coyote [*Canis latrans*], for which hearing sensitivity was available), at 8 kHz (Heffner, 1983) and Domestic cat (*Felis catus*; closest relative to bobcat [*Lynx rufous*], for which hearing sensitivity was available), at 8 kHz (Neff & Hind, 1955). Hearing sensitivities among predators of rodents are likely reflected by this general range (~1-8 kHz). Many predators target rodents using acoustic cues for prey detection (reviewed in Barber *et al.*, 2010) and interference from the soundscape is known to result in declines in prey detection and hunting success (Mason *et al.*, 2016;

Senzaki *et al.*, 2016). Lower prey capture success could lead to predators avoiding louder areas, which could then have direct effects on rodent populations and/or decrease rodents' perceived predation risk, changing their behavior. Both mechanisms could then lead to the increase in overall foraging activity by rodents.

Although there is evidence of increased vigilance among rodents in response to both anthropogenic and natural sounds (Shannon *et al.*, 2014; Le *et al.*, 2019), these studies involved larger, diurnal, semi-fossorial species of ground squirrels that forage in open habitats and have much lower frequency hearing than mice (Heffner *et al.*, 1994). Given the differences in both hearing ability and natural histories between ground-squirrels and mice, the observed response to elevated sound levels in ground squirrels is not likely to be generalizable to mice and rats. Research on the foraging-vigilance tradeoff among rodents has consistently demonstrated that individuals favor foraging in the areas where perceived predation risk is lowest (Brown, 1988). Vegetation structure, known to influence perceived predation risk (Johnson & De León, 2015), was influential in our system, with greater caterpillar predation by rodents in taller, grassier grids. However moonlight, which can influence perceived predation risk (Johnson & De León, 2015; Orrock *et al.*, 2004), had no effect. It is possible that the soundscape is another indirect cue rodents use to assess predation risk, and may be highly relevant given that we observed a strong effect of soundscape, but not moonlight. The potential importance of sound in rodents' perception of risk is evidenced by the fact that *Peromyscus* mice seem to be aware of how loud their own activity is and use quieter pathway substrates to reduce the likelihood of creating adventitious sounds that could



be heard by predators (Barnum *et al.*, 1992; Roche *et al.*, 1999). Parallel research provides ample evidence that predators use these prey-generated sounds when hunting (Goerlitz & Siemers, 2007; Knudsen & Konishi, 1979; Rice, 1982), thus rodents may recognize the lower signal-to-noise ratio of their own activity in louder conditions and in turn perceive a less risky environment. Whether rodents take advantage of the “acoustic cover” provided by loud background sounds while foraging is an intriguing prospect warranting further attention.

We also saw greater foraging activity on caterpillars by rodents on ambient real ocean sites relative to ambient control sites even though their sound levels were not meaningfully different at the time of the experiment. Although latent environmental variables could explain this difference, it is also possible that higher caterpillar predation by rodents on ocean sites could reflect a persistent response to higher sound levels that dominated these sites earlier in the season when swells were larger (Fig. S1). Also unclear is why caterpillar predation by rodents decreases with increasing sound level considering the strong increase in predation on treatment sites that had higher mean sound levels. It is possible that increased sound levels at amplitudes near the mean of our treatment sites serve as a predator shield, yet as has been discussed for avian reproductive success (Kleist *et al.* 2018), exposure to the highest sound levels still has direct negative effects on animal physiology like elevated stress hormones or lower body condition, and so these loudest areas are still avoided.

There are few studies to our knowledge on the direct effect of the soundscape on rodent physiology or populations. One study reported that stress hormones increase

in voles in response to wind farm noise (Łopucki *et al.*, 2018), but the investigators did not quantify the acoustic environment so it is impossible to conclude that noise and not another unmeasured variable was responsible for the physiological change. Another study showed increased foraging activity of *Peromyscus* mice in areas exposed to energy-sector noise (Francis *et al.*, 2012) consistent with our findings, however, their methods also precluded the researchers' ability to determine whether the change to foraging activity was due to changes in population density or alterations to individual behavior. Distinguishing between individual and population-level responses remains an important gap in our understanding of not only small mammal responses to noise, but those of most taxa.

### **Effects on Birds**

Partially consistent with our predictions, predation attempts by birds decreased under introduced, high frequency shifted conditions. However, this effect was not seen in the introduced phantom conditions, or ambient real ocean conditions, inconsistent with our predictions. Birds' responses to the frequency of background sounds are associated with the frequency of the birds' vocalizations and hearing sensitivities, both of which are related to body-size (Francis, *et al.*, 2011; Gleich *et al.*, 2005). It has been demonstrated that larger birds with lower frequency vocalizations are more adversely impacted by low-frequency anthropogenic sound than are smaller birds with higher-frequency vocalizations, since the lower frequency vocalizations experience greater

potential for acoustic masking given their spectral overlap with low-frequency anthropogenic sound (Francis *et al.*, 2011). Since the majority of gleaning, insectivorous birds in our system are smaller-bodied, their higher-frequency vocalizations and hearing range likely overlapped more with the shifted treatment, causing greater interference with communication and acoustic surveillance than the phantom treatment did. The observation that the phantom treatment did not differ in effect from control suggests that low frequency sound did not impact insectivorous birds in our system. Another possibility for the difference in caterpillar predation on shifted and phantom sites could be that mean sound levels were higher on shifted sites than phantom sites. This seems unlikely, however, because sound level did not occur in competitive models for avian predation of caterpillars, and, although shifted sites were louder, phantom sites' sound levels were elevated well above the level known to cause biological effects (Shannon *et al.*, 2016).

We also saw no difference in caterpillar predation by birds between control sites and real ocean sites, which may reflect the lack of differences in sound levels between these site types in late summer, when ocean swell is mild and creates substantially less acoustic energy than other times of the year (unpublished data). Whether patterns would change if we completed our experiment during the beginning of the avian breeding season (February-March) when ocean sites were louder is unknown (Fig. S1). The fact that foraging activity did not differ on introduced phantom sites from ambient controls is surprising given the abundance of evidence that similar frequency anthropogenic noise alters both bird behaviors and distributions (Patricelli & Blickley,

2006; Ortega, 2012; Francis *et al.*, 2009). It may be that the insectivorous birds in our system respond differently than other functional groups of birds or that surf sounds represent a less deleterious stimulus than traffic or infrastructure noise. Further research into different functional groups and sound stimuli will provide greater resolution to these questions.

As discussed for rodents, one way bird foraging activity could have been altered in shifted treatments is through a change in behavior due to heightened perceived predation risk (Brown, 1988). Passive acoustic surveillance is important because foraging posture often reduces visual vigilance (Krause & Godin, 1996), leaving individuals more vulnerable to attack from predators, especially in noise (Simpson *et al.*, 2016). When passive surveillance through audition is disrupted by noise, birds spend more time using visual surveillance at the expense of foraging (Evans *et al.*, 2018; Quinn *et al.*, 2006; Ware *et al.*, 2015), which could explain the patterns observed on the shifted treatment sites. Petrelli *et al.*, (2017) found that different foraging guilds of birds respond differently to perceived predation risk in noise, as a function of their foraging modality. Low-scrub insectivorous gleaners had decreased perception of predators and heightened predation risk in noise, so it is possible that the increase in visual vigilance in this group is not enough to offset the impairment of surveillance through loss of hearing.

Visual vigilance not only occupies time that could be spent foraging, but it is also cognitively demanding and energetically costly for birds. The outcome is that foraging patches that require increased attention are less valuable (Blumstein, 2003). As a result,

birds may relocate to more energetically profitable locations. Reduced foraging activity by birds in shifted sites could thus reflect reduced density of avian insectivores, consistent with declines observed in avian abundance due to anthropogenic noise (Francis *et al.* 2009, McClure *et al.* 2013; Proppe *et al.* 2013; Bayne *et al.* 2008). It is therefore likely a combination of lowered foraging activity and altered distributions that led to the observed decline on high-frequency shifted sites.

### **Effects on Arthropods**

Arthropods appeared largely unaffected by the acoustic treatments, with only one model indicating increased foraging activity in the introduced phantom treatment relative to ambient control and real ocean sites. Based off field observations the most likely taxon responsible for arthropod bites were ants (Formicidae) which can communicate acoustically using a behavior called stridulation, but only over very short distances (<100mm) and are deaf to far field sounds (Hickling & Brown, 2000). It is therefore unlikely our acoustic treatments would affect them. To our knowledge the only studies on ants and sound are related to their ability to perceive it with conflicting evidence on if vibrations are sensed through the substrate (Fielde & Parker, 1904; Hickling & Brown, 2000), but no studies focus on any behavioral or physiological effects of sound. Thus, we have limited insights on interpreting whether the increase in activity on introduced phantom sites is a direct effect of low frequency sound transmitted through the substrate, or an indirect effect such as lessened activity from predators or

competitors. Interestingly, moonlight had a strong positive effect on caterpillar predation activity by arthropods, potentially due to the prevalence of nocturnal ant species or behaviors triggered by ambient light levels (Klotz & Reid, 1993; Narendra *et al.*, 2010) though this response remains uncertain.

### **Indirect Community Effects**

It is important to consider that these taxa do not exist in a vacuum but as part of the same ecological community, and as such changes to one taxon may cause knock-on changes to others. When viewed in this light our results could reflect outcomes from competition between rodents and birds that share a foraging guild (Root, 1967). The competitive balance changes with environmental variation (Brown & Heske, 1990; Kotler *et al.*, 1993) and it may be that the soundscape is another environmental axis that shapes competition. The decline in bird foraging activity in louder areas may have resulted in competitive release for rodents, or alternatively, rodents' increased foraging activity in natural sounds may have outcompeted birds. However, competition between rodents and birds may be weak given the diverse diets of coastal scrub rodents (Meserve, 1976). Rodents' foraging activity increased in all other treatments relative to control while birds only declined in the introduced high frequency shifted conditions so this alternative hypothesis has weaker support from our results. Changes to bird and rodent foraging activity in anthropogenic sound have been shown to lead to changes in vegetation community processes like seedling recruitment (Francis *et al.*, 2012),

demonstrating that understanding community interactions in response to natural sounds will be of important future consideration.

## **Conclusions**

Our study demonstrates that natural sounds can lead to taxon-specific shifts in foraging activity. Because the effects of natural sounds remain largely unknown, several non-mutually exclusive mechanisms could explain our results. The increase in rodent foraging activity in introduced phantom surf, higher frequency shifted surf, and ambient real ocean conditions could be due to an indirect effect of decreased perceived predation risk. Decreased foraging activity among birds in the introduced higher-frequency shifted conditions is likely caused by both increased vigilance behavior and avoidance of loud areas. Arthropods' increased foraging activity on introduced phantom sites is poorly understood with no clear explanation at this time. Competition between rodents and birds could also have played a role, such that changes in foraging activity of one taxon in response to natural sounds resulted in changes to the other, though this seems less likely in our system. Although the precise mechanisms responsible must be sorted out with future research, our results provide a clear indication that natural sounds influence foraging activity, and it's likely that they also influence other ecological processes in ways waiting to be discovered.

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## CHAPTER 2

# NATURAL SOUNDS ALTER DETECTION AND OCCUPANCY PROBABILITIES ACROSS FUNCTIONAL GROUPS

## 6. ABSTRACT

Research into the effects of the soundscape continues to reveal ways in which animals are affected by the acoustic environment, and recently interest in the effects of natural sounds has been growing. A variety of behavioral and distributional changes have been observed in response to anthropogenic noise and it is likely that natural sounds can cause similar effects, although whether and how animals respond is largely unknown. We studied how natural sounds influenced animal detection ( $p$ ) and occupancy ( $\Psi$ ) probabilities using occupancy modeling and camera-traps set within four different acoustic environments: experimentally-introduced natural surf playbacks (phantom ocean) and higher-frequency playbacks (shifted ocean), ambient conditions found on sites inland where surf was not audible (control), and ambient conditions found on sites situated along the coastline where actual crashing waves were audible (real ocean). Detected animals were sorted into five “functional groups” based on their taxonomy, trophic level, or foraging modality: mesocarnivores, Cricetid rodents, kangaroo rats, ground foraging birds, and insectivorous birds. We found that with increasing sound levels, mesocarnivore detection probabilities declined, but occupancy probabilities increased. Cricetid rodent detection probabilities increased with increasing sound levels, and on all treatment types (phantom, shifted, and real ocean) relative to control, but their occupancy probabilities were unchanged. Kangaroo rats and ground foraging birds both had unchanged detection and occupancy probabilities. Insectivorous birds had decreased detection probabilities with increased sound levels. These patterns

likely reflect differences in risk-reward perception based on each group's hearing sensitivity and trophic position. Our results show that variation in natural sounds result in functional group-specific changes in detection and occupancy probabilities, and suggest that natural sounds are an important factor influencing animal behavior and distributions. Additionally our results reveal that the soundscape can influence both detection and occupancy estimates and should be incorporated into future sampling protocols, both for studies explicitly focused on acoustic questions and non-acoustic studies where background sound is a relevant nuisance variable.

## 7. INTRODUCTION

Research on acoustic environments continues to increase and a growing body of literature demonstrates that background sounds influence animals' behavior, distribution, and physiology (Barber et al., 2010; Kight & Swaddle, 2011; Shannon et al., 2016). Most of this research has focused on anthropogenic noise because it has been identified as a global conservation concern (Dominoni et al., 2020; Francis & Barber, 2013; Ortega, 2012; Swaddle et al., 2015), but far less attention has been given to understanding the effects of natural sounds for which research has mainly documented how natural sounds alter behavior (Davidson et al., 2017; Le et al., 2019). Natural sounds are a common element of the soundscape (Pijanowski et al., 2011) and include sounds generated by moving water in rivers and along coastlines, by vegetation rustling in the wind, or by chorusing animals. Natural sounds also have a massive spatial extent. For example, there are over 1.6 million kilometers of coastline worldwide (Pruett & Cimino, 2000) and sounds of moving water can dominate exposed coastline soundscapes. Because natural sound sources are so ubiquitous in nature, it is probable that animals cope or otherwise respond to the difficult acoustic conditions presented by natural sounds in similar ways to those that have been documented in response to anthropogenic noise.

Evolutionary adaptations for dealing with background sound do exist, such as signaling mechanisms that avoid background noise or hearing thresholds that exclude uninformative acoustic stimuli (Brumm & Slabbekoorn, 2005; Römer & Holderied, 2020;

Swaddle et al., 2015). Notwithstanding adaptations to difficult listening and signaling environments, elevated background sounds often select for plastic responses such as *i*) altering behavior; *ii*) altering distributions; or *iii*) altering both. Behavioral changes (*e.g.*, altered signaling (Patricelli & Blickley, 2006), altered foraging (Evans et al., 2018; Quinn et al., 2006; Shannon et al., 2014; Ware et al., 2015)), and altered distributions (Bayne et al., 2008; McClure et al., 2013; Shannon et al., 2016), are well documented in response to anthropogenic sound, and a small number of studies have even documented similar effects in response to the background sounds of surf and river noise (Davidson et al., 2017; Le et al., 2019). However, if animals' behavioral responses to natural sound stimuli are widespread, to date what form those responses take remains largely unknown.

Whether and how natural sounds alter animal behaviors and distributions is likely the result of not only the amplitude and spectral properties of the sound source but also its interaction with the animal's ecology. How different animal taxa respond to a stimulus depends on each one's trophic level, hearing sensitivity, and or foraging modality. For instance, moonlight can increase perceived predation risk by small rodents (Fanson, 2010; Johnson & De León, 2015) likely due to improved hunting success by predators (Clarke, 1983; Penteriani et al., 2013). Just as moonlight can influence behavior relevant to predator-prey interactions through relative changes in visibility, variation in natural sounds that can influence an animal's abilities to detect threats or find prey through audition is also highly relevant to animal behavior and distributions (Mason et al., 2016; Römer & Holderied, 2020; Siemers & Schaub, 2011).

There is growing evidence that animals alter their movement and foraging activities in response to background sound (Barnum et al., 1992; Le et al., 2019; McClure et al., 2013; Roche et al., 1999; Shannon et al., 2014) and that the soundscape can influence distributions and habitat use as well (Francis et al., 2011; Kleist et al., 2017; McClure et al., 2013). However, studying these effects can be challenging because it is not always clear if relationships between background sounds and positive detections (*i.e.*, observing the target animal) are the result of behavioral changes that influence detectability (*i.e.*, altered movement and foraging activity), or population dynamics like immigration or emigration (*i.e.*, changes in distribution), or shifts in home range use that numerically increase or decrease local abundance. For example, Shannon *et al.* (2014), found that when exposed to experimental road noise, prairie dogs (*Cynomys ludovicianus*) had less above ground activity. So a lower count of individuals above ground could mistakenly be attributed to a lower population size, when in fact the population size was unchanged but the detectability of each individual was reduced. One potentially fruitful approach to address this dilemma is through occupancy modeling (MacKenzie et al., 2002). These models use observation records from repeated surveys of a location to estimate occupancy ( $\Psi$ ), the probability that the target species is present at the location, and detection ( $p$ ), the probability of observing the target species when it is known to be present at that location. One of the key assumptions of this method is that if a species is positively detected on one visit, it must have been present for all visits, but may have gone unobserved on some. This creates a detection-error function, which can then be used to estimate the probability that an

individual was in fact present at sites where it was not actually observed. Using these models enables studying how environmental covariates affect occupancy ( $\Psi$ ) and detection ( $p$ ) probabilities (MacKenzie et al., 2002). This, therefore, allows us to study whether changes in observations of a species in natural sound are the result of altered patch use and distributions (i.e., a change in presence or absence represented by occupancy,  $\Psi$ ) or altered behavior that influences detectability (represented by detection,  $p$ ).

Occupancy models use observational histories as a single response variable, but incorporate two sets of related predictor variables integrated simultaneously: one set each for covariates affecting detection ( $p$ ) and occupancy ( $\Psi$ ) probabilities. The occupancy covariates are those factors believed to influence an animal's use of that habitat patch and therefore are related to its distributions; *i.e.*, the vegetation community, elevation, distance to urban areas, *etc.* Detection covariates are those elements believed to influence the likelihood of detecting an animal when it is present and therefore can plausibly relate to behavior, along with effects of the observer (*i.e.* sampling effort, visibility, weather, *etc.*) Background sounds are an important covariate affecting both detection and occupancy probabilities, but are especially relevant for detection probabilities as a human observer's ability to accurately detect animals is decreased in the presence of elevated background sound levels due to the soundscape's interference with the observer's hearing (Francis et al., 2017; Ortega & Francis, 2012). Background sounds are also known to alter animal behaviors in ways that can make them less detectable (Le et al., 2019; Shannon, et al., 2014). This makes background

sound an especially difficult variable to interpret as it is challenging to parse out whether the altered detections are due to a change in the study animals' behaviors, or merely the observer's limited hearing. It is plausible that this problem can be avoided if a study uses camera traps to make detections, because infrared-triggered cameras do not respond to acoustic stimuli. We therefore contend that when observed using camera-traps, changes to detection probabilities ( $p$ ) resulting from natural sounds can plausibly be interpreted as the result of changes to the animals' activity that makes them more or less detectable. This is because the device would have a constant probability of detection which would not be impacted by sound. This then allows for determining if natural sounds are altering foraging and movement behavior, and or patch occupancy, without the confounding effects of altered human observations.

To study how natural sounds influence animal behavior and distributions, we used a camera-trap array set within a "phantom ocean"- a landscape-level, acoustic manipulation of experimentally broadcasted crashing surf sounds. The phantom ocean allows us to separate the effects of surf sound from other confounding environmental covariates at the coastline (*e.g.* salt spray, sandy soil, increased fog). Additionally, because species' hearing and vocalization frequencies vary, different background sound frequencies can elicit unique responses among species (Francis *et al.*, 2011) so we therefore introduced a higher-frequency "shifted ocean" stimulus to examine whether responses change with variation in the frequency of the background sound. We compared both of these introduced acoustic treatments to ambient, endemic conditions



found on sites inland where crashing surf was not audible (control) and on sites along the coast where real, breaking waves were audible (real ocean).

Based on existing evidence and our *a priori* reasoning, we hypothesized that natural surf sounds would alter animal behavior and distributions, but all species would not share a common response to our surf sounds playbacks and that species may have distinct responses based on their taxonomy, foraging modality, and/ or trophic positions. While species-specific responses to natural sounds are probable, we as yet do not know if and how broad taxonomic groups, or community members with different ecological roles would respond. It is likely that broader patterns of response exist among similar species that are not based solely on taxonomy, trophic level, or foraging modality but a combination of these characteristics. Understanding these broader patterns will likely better inform future thinking and study design than individual species responses. Thus, we chose to analyze responses by grouping our detected species based on their shared attributes into “functional groups” that we believed would better explain the presumptive responses. We considered taxonomic relation, foraging modality, predatory status, trophic position, and hearing ability to sort species into groups for which members were more similar within than among groups. The five groups we defined were mesocarnivores, Cricetid rodents, kangaroo rats, ground foraging birds, and insectivorous birds. Because there is evidence of decreased hunting success for predators in noise (Mason et al., 2016; Senzaki et al., 2016; Siemers & Schaub, 2011; Tuttle et al., 1982) we expected that impaired hunting success would cause mesocarnivores to avoid natural sound treated areas. Thus, we predicted that both

detection ( $p$ ) and occupancy ( $\Psi$ ) probabilities of mesocarnivores would be lower in phantom, shifted, and real ocean conditions relative to control, with the lowest probabilities in shifted conditions due to the shifted treatment's higher frequency overlapping more strongly with mesocarnivores' hearing range and the rustling sounds these predators use to locate prey (Goerlitz & Siemers, 2007; Goerlitz et al., 2008; Heffner, 1983; Heffner & Heffner, 1985; Neff & Hind, 1955). Cricetid rodents, including two of the three genera considered here, have been observed at higher activity levels (whether it was increased per-capita foraging behavior, or increased population size is unknown) in areas with elevated sound levels (Francis et al., 2012; Wardle, 2020, chp. 1) and as such we predicted Cricetid rodents would increase in detection ( $p$ ) and or occupancy ( $\Psi$ ) probability. We did not make a prediction on how treatments would compare to each other or to control as driving mechanisms remain unclear. Because kangaroo rats have such sensitive hearing and rely so heavily on it for predator avoidance (Masterton & Heffner, 1980; Webster & Webster, 1971) we believed that kangaroo rats would be more cautious and remain in cover when exposed to elevated background sound levels. As such we predicted a decline in occupancy ( $\Psi$ ) and detection ( $p$ ) probabilities on all treatment sites relative to control, with the strongest decline on phantom sites due to kangaroo rats' unusually low frequency hearing sensitivity (Masterton & Heffner, 1980) and their use of low frequency foot drumming for intra-specific communication (Randall & Stevens, 1987). In louder areas with elevated background sound levels, birds have demonstrated more vigilance and less foraging activity (Evans et al., 2018; Quinn et al., 2006; Ware et al., 2015), thus we anticipated

**Table 1** | Summary of predictions and rationale for detection ( $p$ ) and occupancy ( $\Psi$ ) probabilities for each functional group. Strongest predicted treatment is listed relative to control: phantom (**P**), shifted (**S**), and Real ocean (**O**).

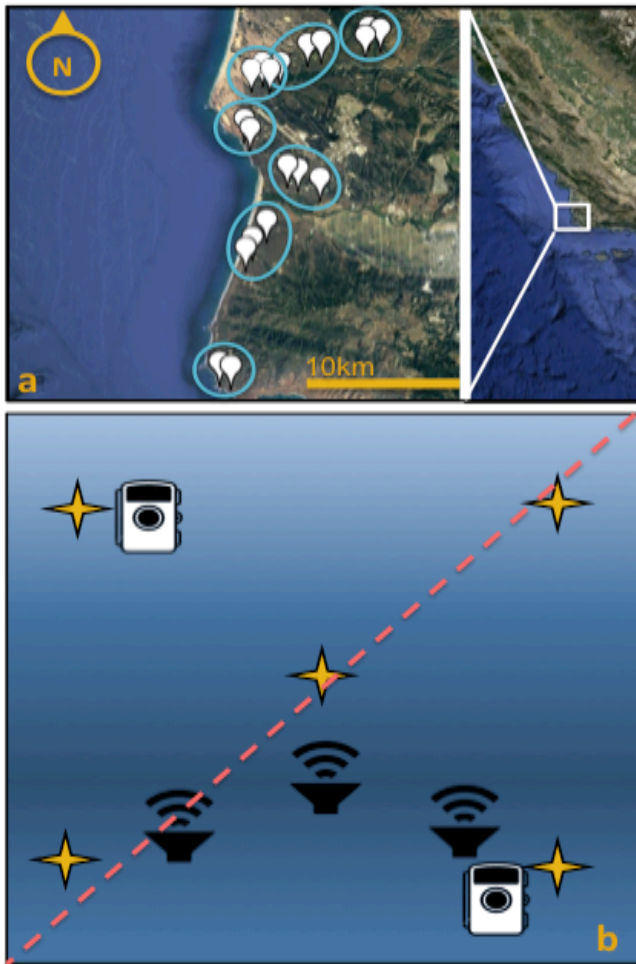
Functional Group	Det ( $p$ )	Occ ( $\Psi$ )	Rationale	References
Mesocarnivores	- <b>S</b>	- <b>S</b>	Impaired hunting ability, likely would seek quieter patches. Shifted treatment overlaps greater with peak hearing.	Mason et al., (2016); Senzaki et al., (2016); Siemers & Schaub, (2011); Tuttle et al., (1982)
Cricetid rodents	+	+	Increased activity documented in elevated background sounds	Francis et al., (2012); Wardle, Chp1 (2020)
Kangaroo rats	- <b>P</b>	- <b>P</b>	Rely heavily on hearing for predator avoidance, and intra-specific communication. Sensitive low frequency hearing likely overlapping more with phantom.	Masterton & Heffner, (1980); Webster & Webster, (1971); Randall & Stevens, (1987)
Ground-foraging birds	-	-	Decreased foraging and increased vigilance in noise; distributions and abundances decline in noise.	Evans et al., (2018); Quinn et al., (2006); Ware et al., (2015); Francis et al., (2009); McClure et al., (2013); Proppe et al., (2013)
Insectivorous birds	- <b>S</b>	- <b>S</b>	Same as for ground foraging birds, but stronger decline as insectivores appear more sensitive to noise. Likely higher frequency hearing overlapping more with shifted.	Canaday & Rivadeneyra, (2001); Karp & Guevara, (2011)

birds would perceive elevated predation risk in louder areas and would spend less time openly foraging. We therefore predicted a decrease in detection probability ( $p$ ) for both avian groups in all treatments reflecting these lower activity patterns. Also, elevated sound levels from anthropogenic sources has been shown to decrease bird abundance and alter distributions (Francis et al., 2009; McClure et al., 2013; Proppe et al., 2013), so we believed that birds would avoid settling in louder areas and thus predicted decreased occupancy probabilities ( $\Psi$ ) for both ground foraging and insectivorous birds, but likely with a stronger decline for insectivorous birds due to their apparent heightened sensitivity to sound (Canaday & Rivadeneyra, 2001; Karp & Guevara, 2011). Also the insectivorous birds in our system are mostly smaller bodied, and as such are likely more sensitive to higher frequencies, so we predicted the strongest declines for this group in the shifted treatments (Gleich et al., 2005; Wardle chp1, 2020). See Table 1 for a summary of predictions.

## 8. METHODS

### Treatments

We conducted our camera-trapping experiment during the spring (May 4th-June 29th) of 2018 across Vandenberg Air Force Base, Santa Barbara County, CA on sites representing four different acoustic environments: phantom, shifted, real ocean, and control (Fig. 1a).



**Fig. 1 | a.** Study area location on the California coast. Blue circles indicate locations of **clusters**. Each cluster includes a phantom treatment, shifted treatment and control site. Real ocean sounds sites are in two clusters of two. **Sites** are represented by white points. **b. Site Layout.** A simplified representation of each site. Each site was 250m x 250m in area. Speakers represent location of treatment speakers or sham control speakers. On control and real ocean sounds sites all three speakers were sham controls. On phantom sites the left and right location were treatment speakers, with a sham in the middle spot. On shifted sites all three locations were treatment speakers. Sites were divided in half diagonally (dashed line) and cameras were positioned with one in the lower left region and one in the upper right.

See Chapter 1 methods for full description of treatments, playback details, site layout and other environmental variables.

### Camera Deployment

We deployed two camera traps per site for a total of 38 cameras for five weeks each from May 4th- June 29th, 2018. We used Bushnell Trophy Cam HD Aggressors

(Bushnell, USA) with passive Infra-red (PIR) motion sensor and “no glow” black LED night-vision flash, powered by AA batteries. Sites were divided in half diagonally into lower-right and upper-left with one camera on each side (Fig. 1b). Given mesocarnivores have the largest relative territory size, they were expected to be the most elusive taxa in our system (relative to songbirds and rodents). Therefore, we determined the camera location on each side by walking from the geometric center of each triangular division, spiraling outward until we found a biologically relevant sign that indicated patch use by mesocarnivores. Typical signs included scat, carcass remains, or tracks. However, none were present within a 20 meter buffer, we selected the area with the best likelihood of capturing images, such as a game trail or open patch (Colyn et al., 2018).



**Fig. 2 |** Camera deployment. Cameras were positioned at 25cm high, at the end of a 2x2m area cleared of grass. Patches were not baited for three weeks if then baited for two.

However, none were present within a 20 meter buffer, we selected the area with the best likelihood of capturing images, such as a game trail or open patch (Colyn et al., 2018). This was done to standardize our ability to photograph animals. We positioned each camera 25cm above the ground on rebar (Hernández-Sánchez et al., 2017, Fig. 2). To

reduce the number of false triggers from moving vegetation and to aid in standardizing detections among cameras, we cleared a two by two meter patch, with the camera positioned at one edge of the clearing aimed along the game trail or towards the biologically relevant sign that identified the patch. Additionally, we modified the detection area of each PIR sensor to be constrained to the two by two meter area to further reduce false detections by placing opaque tape around the outer edges of the sensor. When triggered, cameras took three-photo bursts with a ten second interval between triggers. Cameras were left in clearings for several weeks prior to the start of the experiment to allow animals to acclimate to their presence. We passively surveyed for three weeks with no bait, then for two weeks baited with raw chicken pieces and juices, replenished weekly to potentially improve detections of any mesocarnivores that had not yet been detected (Buyaskas, 2020). No other bait was utilized at camera stations.

### **Environmental Variables**

We measured the sound level at the start of each week of camera trapping for a total of five measurements each using MicW i436 microphones (BSWA Technology, China) and the smartphone application SPLnFFT (ver. 6.9). The application and microphone combination was calibrated using a standardized playback and Larson Davis 831 sound pressure meter. We used the mean value from these measurements for subsequent analyses.

Because nocturnal mammal activity can be influenced by moonlight (Johnson & De León, 2015; Mukherjee et al., 2009; Orrock et al., 2004; Penteriani et al., 2013) we also obtained moon position and phase using the R package lunar (Lazaridis, 2014).

## **Image Analysis**

In order to process the myriad images collected, we developed a custom Python program using the Open CV package (Bradski, 2000) to screen for false positives, in which the camera was triggered by moving vegetation or litter, which was approximately 95% of the total images. To train the program-assisted approach, subsets of images were analyzed in parallel by an unassisted observer, compared to an observer aided by the program. The program-assisted observer found more events, especially during certain conditions such as when an animal took up only a small portion of the frame or the image had high contrast. After the data were filtered to only images containing animals, each detection was identified to the most specific taxonomic level possible. A detection was defined as the time that an individual of a given species occupied an unbroken sequence of images (*i.e.*, the animal never left the field of view between photos). Even if the same species was detected after a break in the image sequence it was considered a new detection. Multiple detections could be ongoing in the same frame, but there were never more than two species in the same image. The number of detections for each species can be found in Table 2.



## Functional Groups

We separated detected species into five “functional groups” for which we expected responses to natural sound conditions to be the most similar based on each species’ taxonomy, trophic level, foraging modality, and hearing ability. The five groups we defined were mesocarnivores, Cricetid rodents, kangaroo rats, ground foraging birds, and insectivorous birds (Table 2). The mesocarnivore group was comprised of bobcats, (*Lynx rufus*), coyotes, (*Canis latrans*), striped skunks, (*Mephitis mephitis*), spotted skunks, (*Spilogale gracilis*), American badgers, (*Taxidea taxus*), gray foxes, (*Urocyon cinereoargenteus*), and long-tailed weasels, (*Mustela frenata*). The Cricetid rodents were deer mice, (*Peromyscus spp.*), woodrats, (*Neotoma spp.*), and California voles, (*Microtus californicus*). Kangaroo rats were members of the genus *Dipodomys*. Ground foraging birds were spotted towhees, (*Pipilo maculatus*), California towhees, (*Melospiza crissalis*), white-crown sparrows, (*Zonotrichia leucophrys*), house finches, (*Haemorhous mexicanus*), and other unidentifiable new-world sparrows (Passerellidae). Lastly, the insectivorous bird group was made up of wrentits, (*Chamaea fasciata*), Bewick’s wrens, (*Thryomanes bewickii*), and California thrashers, (*Toxostoma redivivum*). Other species were detected but not included in analyses because their taxonomy, foraging, and trophic position differed enough to be excluded from any of these groups, and were detected too infrequently, or they failed to meet occupancy model assumptions.

**Table 2** | Species detections separated by functional group.

Common Name	Species/ Family	Dets.
<b>Mesocarnivores</b>		
Coyote	<i>Canis latrans</i>	6
Gray fox	<i>Urocyon cinereoargenteus</i>	9
Bobcat	<i>Lynx rufus</i>	21
Striped skunk	<i>Mephitis mephitis</i>	187
Spotted skunk	<i>Spilogale gracilis</i>	2
Long-tailed weasel	<i>Mustela frenata</i>	10
American badger	<i>Taxidea taxus</i>	24
<b>Cricetid rodents</b>		
Un-identifiable deer mouse	<i>Peromyscus</i> spp.	914
Un-identifiable woodrat	<i>Neotoma</i> spp.	192
California vole	<i>Microtus californicus</i>	60
<b>Kangaroo rats</b>		
Un-identifiable kangaroo rat	<i>Dipodomys</i> sp.	597
<b>Ground foraging birds</b>		
Un-identifiable sparrow	Passerellidae	6
Spotted towhee	<i>Pipilo maculatus</i>	18
California towhee	<i>Melospiza crissalis</i>	41
House finch	<i>Haemorhous mexicanus</i>	1
White-crowned sparrow	<i>Zonotrichia leucophrys</i>	58
<b>Insectivorous birds</b>		
Wrentit	<i>Chamaea fasciata</i>	3
California thrasher	<i>Toxostoma redivivum</i>	86
Bewick's wren	<i>Troglodytes aedon</i>	6

### Occupancy Modeling

For each functional group we performed single season occupancy modeling in RStudio (ver. 1.0.153) using the *unmarked* package (Fiske & Chandler, 2011). Estimating occupancy and detection probabilities requires repeated sampling occasions of a given area (MacKenzie et al., 2006). In our study “occasions” were defined as five continuous one-week sampling blocks at each camera with a functional group being considered

detected if any member of the functional group was positively identified during that week's sampling period. This record of whether or not a member of the functional group was observed during each week is the dependent variable in occupancy modeling. We used single-season occupancy models which assume that the population is closed (MacKenzie et al., 2006), and given the season (May-June) and duration (five weeks) of our experiment we feel this assumption is likely met. It is also assumed that each camera is independent (MacKenzie et al., 2002), with cameras being spaced far enough apart so that detecting the same individual at multiple cameras does not bias occupancy or detection probabilities. The average distance between cameras on each site was 150-200m, with sites being at least 750m to several kilometers apart, far enough to assume independence in Cricetid rodents, kangaroo rats, ground-foraging birds, and insectivorous birds, because typical home range size of small animals such as these are usually smaller than these distances and unlikely to overlap with multiple cameras (Mikesic & Drickamer, 1992; Sung & Handford, 2020). Mesocarnivores, however, may travel with varying spatial extent up to several kilometers (Riley et al., 2003). Given the relatively small area we sampled though, occupancy ( $\Psi$ ) can also be interpreted as the probability of the camera being located within the home range of at least one individual for the target group and an indication that the habitat patch is being utilized (Efford & Dawson, 2012; MacKenzie et al., 2002; Neilson et al., 2018). As a result of these relaxed model assumptions our inferences do not apply to changes in home range size or population estimates for any species detected, but simply apply to the dynamics related to patch use. Understanding how animals' patch use changes with acoustic covariates

will be informative for understanding how natural sounds influence habitat usage in heterogeneous acoustic conditions.

Included in occupancy modeling are site-specific covariates that differ between camera locations but are stable over time, and observational level covariates that are specific to each sampling period but change over time. Our site-specific covariates were vegetation richness, PC1 (negative values correlate with percentage forb cover, positive values correlate with mean height), PC2 (negative values correlate with percentage grass cover, positive values correlate with percentage woody shrub cover), mean sound level and acoustic treatment. Our observational level covariates were date, moon phase (first night of the week block), and whether the camera trap was baited or not. We generated global models for each functional group based on *a priori* reasoning of important covariates (Table 3).

**Table 3 |** Global occupancy models for functional groups. **Bt** = bait status, **Dt** = first Julian date of each week, **L<sub>eq</sub>** = mean sound level at camera, two-minute A weighted *L<sub>eq</sub>*, **Trt** = acoustic treatment: **P** = phantom, **S** = shifted, **O** = real ocean, **Mn1** = ordinal moon phase, **Mn2** = second order polynomial moon phase, **PC1** = vegetation component 1, **PC2** = vegetation component 2, **VR** = vegetation richness, **scl()** = scaled continuous variables.

Functional Group	Detection ( $p$ )	Occupancy ( $\Psi$ )
Mesocarnivores	$\sim Bt + Mn1 + Dt + L_{eq} + Trt + L_{eq}:Trt + L_{eq}:Mn1 + Trt:Mn1$	$\sim PC1 + PC2 + VR + L_{eq} + Trt + PC1:PC2 + PC2:VR + L_{eq}:Trt$
Cricetid rodents	$\sim Bt + Mn2 + Dt + L_{eq} + Trt + L_{eq}:Trt + L_{eq}:Mn2 + Trt:Mn2$	$\sim PC1 + PC2 + scl(VR) + L_{eq} + Trt + PC1:PC2 + PC1:scl(VR) + PC2:scl(VR) + L_{eq}:Trt$
Kangaroo rats	$\sim Bt + Mn1 + Dt + scl(L_{eq}) + Trt + L_{eq}:Trt + L_{eq}:Mn1 + Trt:Mn1$	$\sim PC1 + PC2 + scl(VR) + scl(L_{eq}) + Trt + PC1:PC2 + PC1:scl(VR) + PC2:scl(VR) + scl(L_{eq}):Trt$
Ground foraging birds	$\sim Bt + Dt + L_{eq} + Trt + L_{eq}:Trt$	$\sim PC1 + PC2 + scl(VR) + L_{eq} + PC1:PC2 + PC1:scl(VR) + PC2:scl(VR) + L_{eq}$
Insectivorous birds	$\sim Bt + Dt + L_{eq} + Trt + L_{eq}:Trt$	$\sim PC1 + PC2 + scl(VR) + L_{eq} + Trt + PC1:PC2 + PC1:scl(VR) + PC2:scl(VR) + L_{eq}:Trt$

Moon phase was included for mesocarnivores, Cricetid rodents and kangaroo rats, as these groups are known to change activity with moonlight (Mukherjee et al., 2009; Penteriani et al., 2013; Orrock et al., 2004; Lockard & Owings, 1974), but was not included for either diurnal avian group. Moon phase was divided into eight phases each representing one lunar stages beginning with new moon and ending with waning crescent. For each functional group with moon phase included, we tested for linear and non-linear responses to the lunar cycle using a linear effect of moon phase plus second and third order polynomials. Each potential response variant was fitted into a simplified occupancy model with constant occupancy ( $\Psi$ ), and detection ( $p$ ) only varying with moon phase. These simple models were then ranked using Akaike information criterion corrected for small sample size ( $AIC_c$ ). The top ranked moon phase variable for each functional group was included in the global model, unless the top ranked model was the null, in which case the next ranked model within  $\Delta 2AIC_c$  was used because we believed moon phase would be an important covariate for explaining detection probability ( $p$ ).

We also used a generalized linear mixed effects model to compare the mean sound level across treatments, accounting for geographic clustering as a random effect (Fig. 3). We analyzed acoustic treatment and mean sound level for multicollinearity in a single-season occupancy model with mean sound level and treatment as covariates in both detection ( $p$ ) and occupancy ( $\Psi$ ), which we determined to be independent for all groups ( $VIF < 10$ ; Dormann et al., 2007). Acoustic treatment and sound level were included for both occupancy ( $\Psi$ ) and detection ( $p$ ) because of the aforementioned evidence that background sound can alter animal activity patterns and foraging

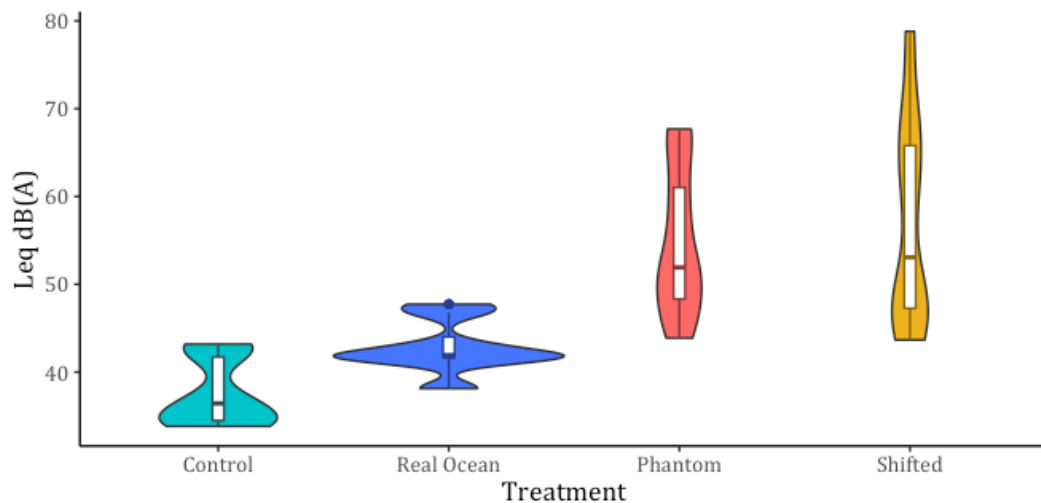
behavior (Evans et al., 2018; Francis et al., 2012; Le et al., 2019; Petrelli et al., 2017; Quinn et al., 2006; Shannon et al., 2014; Ware et al., 2015), which could lead to altered detection probabilities, and affect patch use (Barber et al., 2010; Francis et al., 2009; Ware et al., 2015) and hence lead to altered occupancy probabilities. Vegetation richness, PC1, PC2, and the interaction of PC1 and PC2 were used to model occupancy since vegetation community and structure play important roles in animal habitat usage (Meserve, 1976; Robinson & Holmes, 1982). Bait status and moon phase were used to model detection as they are known to influence risk assessment and behavior (Buyaskas et al., 2020; Johnson & De León, 2015; Orrock et al., 2004; Penteriani et al., 2013), which could alter detection probabilities as well. Date was also used to model detection to account for any seasonal change in detection probabilities. Vegetation species richness was scaled in all models except mesocarnivores and sound level was scaled in kangaroo rat models to aid in model convergence. We used a MacKenzie and Bailey goodness-of-fit on global models (MacKenzie & Bailey, 2004) using the AICcmodavg package (Mazerolle, 2019) to determine model fit and ensure model assumptions were met.

Subsets of each global model were performed, with occupancy ( $\Psi$ ) and detection ( $p$ ) being estimated for each (see Fiske & Chandler, 2011, for details). We then performed model selection based off  $AIC_c$  for each functional group using the MuMIn package (Bartoń, 2019) and considered models within  $\Delta 2AIC_c$  of the top-ranked model as well supported. We interpreted covariates to have effects and strong effects when the 85% and 95% confidence intervals (CI's) did not overlap zero, respectively (Arnold 2010). This approach narrows our conclusions to those models with improved fit, and

those variables for which we have high confidence in the response by excluding the interpretation of uninformative parameters, but still allows for a more nuanced consideration of all parameters with apparent effects. Model weights were calculated from the well-supported model sets. Detection ( $p$ ) and occupancy ( $\Psi$ ) probabilities were predicted for all variables with an effect or strong effect based off the top-ranked model in which they occurred.

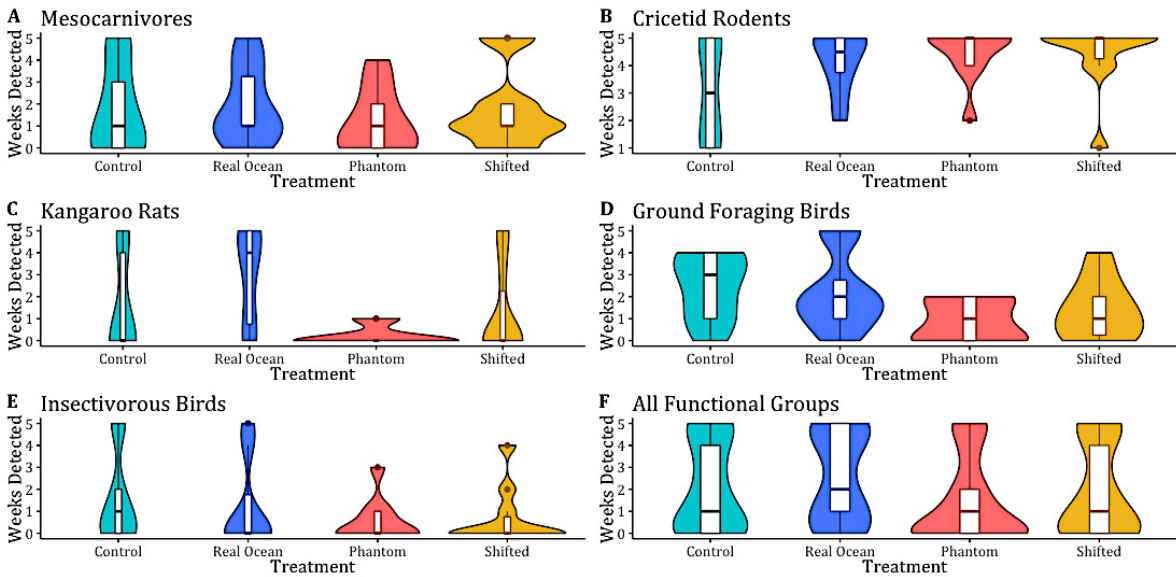
## 9. RESULTS

We deployed 38 cameras for five weeks each for a total of 190 camera-weeks, of which eight camera-weeks had to be removed due to technical issues for a total of 182 camera-weeks. Over the course of the experiment we had 5,103 detections of 34 species, 19 of which were selected for analyses (Table 2). There were 259 detections of



**Figure 3** | Mean sound level at each camera by treatment in dB(A). Sound levels are the average of five two-minute A-weighted  $L_{eq}$ 's taken at the start of each week period.

mesocarnivores, 1,166 of Cricetid rodents, 597 of kangaroo rats, 124 of ground foraging birds, and 95 of insectivorous birds. The quietest sound level recorded was 28.9 dB on a control site and the loudest was 82.7 dB on a shifted treatment site. The mean sound level was  $37.6 \pm 0.56$  dB on control sites,  $42.8 \pm 0.46$  dB on real ocean sites,  $54.8 \pm 1.18$  dB on phantom sites and  $56.9 \pm 1.63$  dB on shifted sites.



**Figure 4 |** The number of weeks each functional group had one (or more) detection(s) at each camera by treatment. All functional groups is the sum of the detections of each of the five analyzed functional groups.

The mean sound levels at each camera on real ocean, phantom, and shifted sites were louder than control sites (ref. control,  $\beta_{\text{ocean}}=5.06$ , 95%CI= 0.46, 9.67;  $\beta_{\text{phantom}}=17.10$ , 95%CI= 13.32, 20.87;  $\beta_{\text{shifted}}= 19.15$ , 95%CI= 15.41, 22.88; Fig. 3), and additionally phantom and shifted sites were louder than real ocean (ref. real ocean,  $\beta_{\text{phantom}}= 12.03$ , 95%CI= 7.46, 16.61;  $\beta_{\text{shifted}}= 14.08$ , 95%CI= 9.54, 18.62) but did not differ from each other (ref. phantom,  $\beta_{\text{shifted}}= 2.05$ , 95%CI= -1.65, 5.75). The mean number of weeks ( $\pm$  SE) mesocarnivores were detected was  $1.78 \pm 0.70$  on control sites,  $2.00 \pm 0.63$

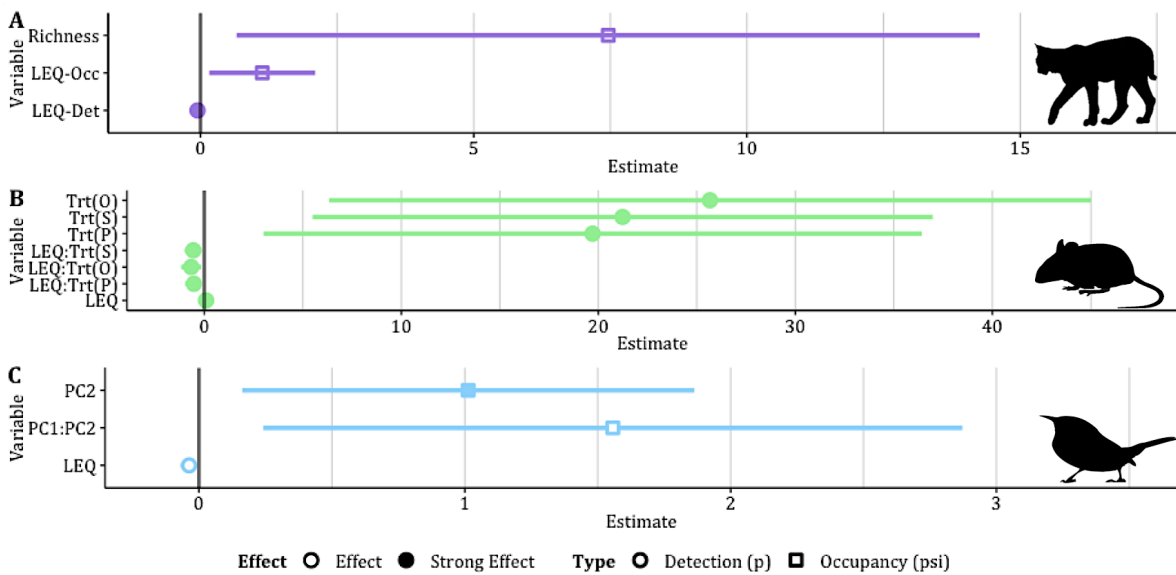


on real ocean sites,  $1.22 \pm 0.49$  on phantom sites, and  $1.80 \pm 0.57$  on shifted sites (Fig. 4A).

**Table 4 |** Well supported mesocarnivore models ranked based on  $AIC_c$ . Variables affecting detection ( $p$ ) are in the left column and those affecting occupancy ( $\Psi$ ) are in the right column. Bold and italics indicates a strong effect (95%CIs that do not overlap zero) and effect (85%CIs that do not overlap zero) respectively. A “1” indicates a constant state. The null model (constant detection and occupancy) is included for reference. Model weights are calculated from the well-supported model set. Variable definitions can be found in Table 3.

Mesocarnivore models		$k$	LogLik	$AIC_c$	$\Delta AIC_c$	$w_i$
<b><i>L<sub>eq</sub></i></b>	PC2 + VR + PC2:VR + Trt	9	-90.71	206.34	0.00	0.38
<b><i>L<sub>eq</sub></i></b>	<i>L<sub>eq</sub></i> + PC1 + PC2 + VR + PC1:PC2	8	-93.06	207.45	1.12	0.21
<b><i>L<sub>eq</sub></i></b>	PC1 + PC2 + VR + Trt + PC1:PC2	10	-89.38	207.55	1.21	0.21
1	1	2	-107.78	219.92	13.58	0.00

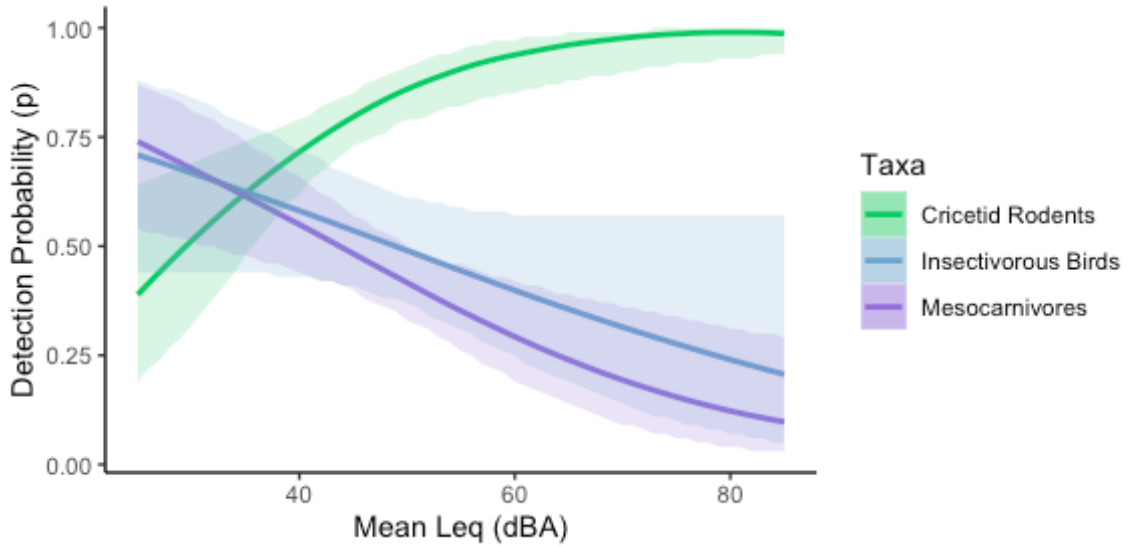
The mean number of weeks Cricetid rodents were detected was  $3.11 \pm 0.63$  on control sites,  $4.12 \pm 0.40$  on real ocean sites,  $4.44 \pm 0.34$  on phantom sites, and  $4.40 \pm 0.40$  on shifted sites (Fig. 4B). Kangaroo rats had  $1.56 \pm 0.78$  mean weeks detected on control sites,  $3.00 \pm 0.80$  weeks detected on real ocean sites,  $0.22 \pm 0.15$  weeks detected on phantom sites, and  $1.30 \pm 0.68$  weeks detected on shifted sites (Fig. 4C). Ground foraging birds’ mean weeks detected were  $2.44 \pm 0.50$  on control sites,  $2.25 \pm 0.65$  on real ocean sites,  $0.89 \pm 0.31$  on phantom sites, and  $1.40 \pm 0.43$  on shifted sites (Fig. 4D). Insectivorous birds’ mean weeks detected were  $1.56 \pm 0.69$  on control sites,  $1.25 \pm 0.73$  on real ocean sites,  $0.56 \pm 0.34$  on phantom sites, and  $0.70 \pm 0.42$  on shifted sites (Fig. 4E).



**Figure 5 |** Effects estimates for **A)** Mesocarnivores, **B)** Cricetid rodents, **C)** Insectivorous birds. Variables with effects (85% CI does not overlap zero, open shape) and strong effects (95% CI does not overlap zero, filled shape) are shown from the top ranked model in which they have the strongest effect. Squares represent occupancy ( $\Psi$ ) and circles represent detection ( $p$ ). Estimates are on the logit scale. Axes scales are different for each functional group. Kangaroo rat and ground foraging bird models had no effects and so are not visualized.

The top models for mesocarnivores all included the strong negative effect of sound level on detection probability ( $p$ ,  $\beta_{LEq} = -0.054$ , 95%CI= -0.09, -0.02; Fig.5A; Table 4), which led to a decline in predicted detection probability from  $0.74 \pm 0.09SE$  at 25 dB to  $0.10 \pm 0.06 SE$  at 85dB (Fig. 6). There was also a positive effect on occupancy by vegetation richness ( $\beta_{VegRich} = 7.46$ , 85%CI= 0.66, 14.26; Fig. 5A; Table 4) with a sharp increase from a predicted occupancy probability of  $0 \pm 0SE$  at patches with 15 species and below, to a probability of  $1 \pm 0.06SE$  at patches with 17 species and above. Sound level also had a positive effect on occupancy ( $\beta_{LEq} = 1.13$ , 85%CI= 0.16, 2.10; Fig. 5A; Table 4); however, the predicted increase in probability was dependent on vegetation richness with sites that had greater than three and less than thirteen species being affected by sound level. The same change to probability was generated from lower sound levels at higher richness and higher sound levels at lower richness (Fig. 7). The null model

assuming constant detection probability and occupancy rates received little support with a  $\Delta AIC_c = 13.58$ .



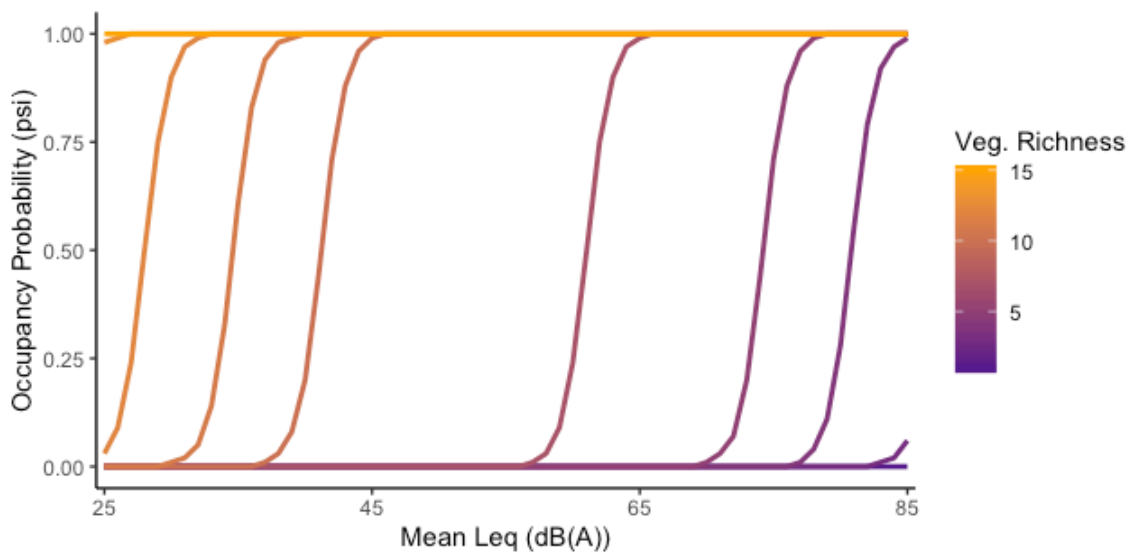
**Figure 6 |** Effects of mean sound level (2-minute A-weighted  $L_{eq}$ 's) on predicted detection probability ( $p$ ) for Cricetid rodents, insectivorous birds and mesocarnivores.

No variable had an effect on occupancy rates ( $\Psi$ ) for Cricetid rodents, but competitive models suggested that sound level had a strong positive effect on detection probabilities ( $p$ ,  $\beta_{Leq} = 0.09$ , 95% CI = -4.87, -0.41; Fig. 5B; Table 5) with a predicted increase from  $0.40 \pm 0.12$  SE at 25 dB to  $0.99 \pm 0.01$  SE at 85 dB (Fig. 6).

**Table 5 |** Well supported Cricetid rodent models ranked based on AICc. Variables affecting detection ( $p$ ) are in the left column and those affecting occupancy ( $\Psi$ ) are in the right column. Bold and italics indicates a strong effect (95% CIs that do not overlap zero) and effect (85% CIs that do not overlap zero) respectively. A "1" indicates a constant state. The null model (constant detection and occupancy) is included for reference at the bottom. Model weights are calculated from the well-supported model set. Variable definitions can be found in Table 3.

Cricetid rodent models	$k$	LogLik	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$	
$L_{eq}$	1	3	-80.42	167.6	0.00	0.55
<b><math>L_{eq} + Trt(P,S,O) + L_{eq}:Trt</math></b>	1	9	-72.17	169.3	1.67	0.24
<b><math>L_{eq} + bt</math></b>	1	4	-80.09	169.5	1.89	0.21
1	1	2	-88.67	181.70	14.1	0.00

Higher detection probabilities were also positively and strongly associated with all treatments relative to control ( $p$ , ref. control,  $\beta_{\text{real ocean}} = 25.67$ , 95%CI= 6.34, 44.99;  $\beta_{\text{phantom}} = 19.71$ , 95%CI= 3.01, 36.40;  $\beta_{\text{shifted}} = 21.23$ , 95%CI= 5.50, 36.97; Fig. 5B; Table 5). Predicted detection probability was  $<0.001$  on control sites,  $0.25 \pm 0.69$  SE on shifted sites,  $0.61 \pm 0.55$  SE on real ocean sites and  $0.99 \pm 0.05$  SE on phantom sites. These models also suggested a strong negative effect of the interaction between sound level and all treatments on detection probability ( $p$ , ref. control,  $\beta_{\text{Leq:real ocean}} = -0.66$ , 95%CI= -1.17, -0.15;  $\beta_{\text{Leq:phantom}} = -0.53$ , 95%CI= -0.97, -0.08;  $\beta_{\text{Leq:shifted}} = -0.56$ , 95%CI= -0.99, -0.12; Fig. 5B; Table 5). The null model was uncompetitive ( $\Delta\text{AIC}_c = 14.10$ ).



**Figure 7** | Effects of mean sound level ( $L_{eqA}$ ), and vegetation species richness on mesocarnivore occupancy probabilities. Species richness greater than 15 had no additional effect and was not plotted to increase contrast.

For kangaroo rats, although the null model was uncompetitive ( $\Delta\text{AIC}_c = 19.29$ ) and supported models included sound level, treatment, the interaction of sound level

and treatment and vegetation richness, no variables had any apparent effects on detection probability ( $p$ ) or occupancy ( $\Psi$ , Table 6).

**Table 6 |** Well supported kangaroo rat models ranked based on AICc. Variables affecting detection ( $p$ ) are in the left column and those affecting occupancy ( $\Psi$ ) are in the right column. Bold and italics indicates a strong effect (95%CIs that do not overlap zero) and effect (85%CIs that do not overlap zero) respectively. A “1” indicates a constant state. The null model (constant detection and occupancy) is included for reference at the bottom. Model weights are calculated from the well-supported model set. Variable definitions can be found in Table 3.

Kangaroo rat models		$k$	LogLik	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$
scl( <i>L<sub>eq</sub></i> ) + Trt(P,S,O) + scl( <i>L<sub>eq</sub></i> ):Trt	scl(VR)	10	-38.41	105.6	0.00	0.59
scl( <i>L<sub>eq</sub></i> ) + Trt(P,S,O) + scl( <i>L<sub>eq</sub></i> ):Trt	1	9	-40.58	106.1	0.46	0.41
1	1	2	-62.85	130.06	19.29	0.00

Supported occupancy models for ground foraging birds included PC1, PC2, vegetation richness, the interaction of PC2 and richness, and treatment, but none of these had an effect on occupancy ( $\Psi$ ), and detection probability was constant ( $p$ , Table 7). The null model had a  $\Delta$ AIC<sub>c</sub> = 5.21.

**Table 7 |** Well supported ground foraging bird models ranked based on AICc. Variables affecting detection ( $p$ ) are in the left column and those affecting occupancy ( $\Psi$ ) are in the right column. Bold and italics indicates a strong effect (95%CIs that do not overlap zero) and effect (85%CIs that do not overlap zero) respectively. A “1” indicates a constant state. The null model (constant detection and occupancy) is included for reference at the bottom. Model weights are calculated from the well-supported model set. Variable definitions can be found in Table 3.

Ground foraging bird models		$k$	LogLik	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$
1	PC1 + PC2 + scale(VR) + Trt(P,S,O) + PC2:scale(VR)	9	-99.04	223.01	0.00	1.00
1	1	2	-111.93	228.22	5.21	0.00

Lastly, sound level had a negative effect on insectivorous bird detection probability ( $p$ ,  $\beta_{L_{eq}} = -0.04$ , 85%CI= -0.07, -0.01; Fig. 5C; Table 8) with a predicted decline from  $0.71 \pm 0.12$  SE at 25 dB to  $0.21 \pm 0.14$  SE at 85 dB (Fig. 6). PC2 and the interaction between PC1 and PC2 had a strong positive effect on occupancy ( $\Psi$ ) with taller, shrubbier patches with greater grass coverage and more densely structured habitat having increased occupancy ( $\beta_{PC2} = 1.01$ , 95% CI = 0.16, 1.86;  $\beta_{PC1:PC2} = 1.56$ , 95% CI = 0.24, 2.87; Fig. 5C; Table 8). At low values (PC2 = -2) PC2 had a predicted occupancy probability of  $0.07 \pm 0.07$  SE, increasing to  $0.82 \pm 0.13$  SE at high values (PC2 = 2). The null model had a  $\Delta AIC_c = 5.93$ .

**Table 8** | Well supported insectivorous bird models ranked based on AICc. Variables affecting detection ( $p$ ) are in the left column and those affecting occupancy ( $\Psi$ ) are in the right column. Bold and italics indicates a strong effect (95%CIs that do not overlap zero) and effect (85%CIs that do not overlap zero) respectively. A “1” indicates a constant state. The null model (constant detection and occupancy) is included for reference at the bottom. Model weights are calculated from the well-supported model set. Variable definitions can be found in Table 3.

Insectivorous bird models		$k$	LogLik	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$
<i>L<sub>eq</sub></i>	<i>PC1 + PC2 + PC1:PC2</i>	6	-63.90	142.70	0.00	0.23
1	<i>PC1 + PC2 + PC1:PC2</i>	5	-65.40	142.80	0.10	0.22
<i>L<sub>eq</sub></i>	<b>PC2</b>	4	-67.21	143.71	1.01	0.14
<i>L<sub>eq</sub></i>	<b>PC1 + PC2</b>	5	-66.04	144.08	1.38	0.12
1	<b>PC2</b>	3	-68.75	144.25	1.55	0.11
1	<b>PC1 + PC2</b>	4	-67.56	144.41	1.71	0.10
<i>L<sub>eq</sub></i>	<i>L<sub>eq</sub> + PC1 + PC2 + PC1:PC2</i>	7	-63.35	144.70	2.00	0.09
1	1	2	-72.13	148.63	5.93	0.00

## 10. DISCUSSION

Our experiment demonstrated that natural sounds are capable of altering both detection ( $p$ ) and occupancy ( $\Psi$ ) probabilities for a variety of taxa, and that responses differ across groups defined by taxonomic and ecological characteristics. Furthermore, our methodology provides potential insights into how natural sounds influence habitat utilization by different functional groups and how animal behaviors and interactions are likely shaped by acoustic conditions. We accepted our hypothesis given that both detection ( $p$ ) and occupancy ( $\Psi$ ) probabilities were altered by natural surf sounds, and functional groups had different responses. However, we had mixed support for our group specific predictions. Consistent with our predictions, mesocarnivores were less likely to be detected with increasing sound levels. However, unexpectedly, they were more likely to occupy patches with elevated sound levels. Also supporting our predictions, Cricetid rodents were more likely to be detected with increasing sound levels, and in all treatments relative to controls, but they deviated from our predictions with a paradoxical decline in detection probabilities in treatment conditions at higher sound levels. Our detection prediction for insectivorous birds was also well supported, as insectivorous birds were less likely to be detected with increasing sound levels as well, but our occupancy predictions were not supported, as the birds did not appear to change in occupancy. Surprisingly, and in contrast to our predictions, effects from any environmental conditions on Kangaroo rats' and ground foraging birds' responses were both not supported. Below, we discuss how responses of each functional group could be

related to their ecology and how their ecology interfaces with their perceptions of risk versus reward under varying natural sound conditions.

### **Mesocarnivores**

Our predictions were partially supported for mesocarnivores in that they had decreased detection probability with increasing sound levels. Sampling methods using human observers, such as point counts, are subject to the strong influence of sound on detectability (Ortega & Francis, 2012), but because camera traps do not rely on sound for detections, changes to detection must be the result of altered animal behavior, suggesting mesocarnivores behaved in ways that made them less detectable in elevated background sound areas. That detection probabilities for mesocarnivores decreased with sound level suggests that these predators may have spent more time in cover and moving shorter distances in areas with higher sound levels, thus reducing their likelihood of detection by our cameras. Although the effects of acoustics on vigilance have not been observed for mesocarnivores, there is evidence that in response to elevated background sounds birds spend less time foraging and more time vigilant (Evans et al., 2018; Quinn et al., 2006; Ware et al., 2015), and ground squirrels move less and forage over smaller areas (Le et al., 2019; Shannon et al., 2014), so these more cautious behaviors may be true for mesocarnivores as well. Additionally, volant, nocturnal, acoustic predators' hunting success declines in noise (Mason et al., 2016; Senzaki et al., 2016; Siemers & Schaub, 2011), so mesocarnivores may be experiencing



similar impairments and choosing to forage more intensively in quieter habitat patches. Mesocarnivores are not avoiding these habitats however, and in fact are more likely to be utilizing them as evidenced by the increase in occupancy with sound level, rejecting our prediction of lowered patch use. Given the decreased detection probabilities and suspected hunting impairment, that occupancy actually increases suggests an alternative use of these habitat patches besides active foraging. Mesocarnivores may utilize elevated background sound levels themselves as a “predator shield” (Shannon *et al.*, 2014) for behaviors such as resting or hiding because mesocarnivores can be depredated by intra-guild species or by top-apex predators. Therefore, they have to balance their own potential of being depredated against the necessity of capturing prey in different conditions (Penteriani *et al.*, 2013).

Occupancy was also positively affected by vegetation species richness, with higher probability of occupancy on sites with higher richness. Interestingly though, lower levels of richness could also have increased occupancy probabilities when sound levels were elevated, and the lower the richness the higher the sound levels were required to be to increase occupancy (Fig. 10). This suggests some sort of trade off in habitat quality between vegetation species richness and background sound levels. Given the prevalence of aromatic secondary defense compounds found in Mediterranean climate plants (Regnault-Roger *et al.*, 2004) and that plant species richness can affect odor complexity (Randlkofer *et al.*, 2010) it may be that sites with high plant diversity mask mesocarnivore odors. It is possible that a multi-modal detection trade-off occurs, such that declining scent masking in lower vegetation richness patches is exchanged

with increased acoustic masking, leading to similar levels of detectability in both patches. This auditory-olfactory interaction has been documented in a mammalian mesocarnivore, the dwarf mongoose (*Helogale parvula*). Specifically, when exposed to traffic noise, mongooses took longer to detect predator odors and exhibited weaker responses to them (Morris-Drake *et al.*, 2016). It may be that auditory and olfactory interactions are more common among mammalian predators than previously thought.

### **Cricetid rodents**

Detection probabilities of Cricetid rodents increased in response to elevated sound levels and treatment level effects, in support of our predictions. This increase in detectability likely reflects a change towards more time spent engaged in active behaviors, like foraging, compared to more passive behaviors like hiding in a burrow, as cameras were only triggered when Cricetid rodents moved out from cover. Mice and rats are known to respond strongly to indirect cues of predation risk such as moonlight, vegetation cover, and weather (Fanson, 2010; Johnson & De León, 2015; Orrock *et al.*, 2004), and our results suggest that background sound levels are another habitat characteristic rodents are assessing to determine risk. This is supported by some evidence that rodents are aware of their own sound level transmission, choosing to move across quieter substrates (Fitzgerald & Wolff, 1988; Roche *et al.*, 1999). Minimizing the signal-to-noise ratio of their activity is important for Cricetid rodents because predators utilize rustling sounds to locate prey (Goerlitz & Siemers, 2007;

Goerlitz *et al.*, 2008), especially one of their most common predator groups, owls (Mason *et al.*, 2016; Senzaki *et al.*, 2016; Siemers & Schaub, 2011).

That Cricetid rodents were more detectable and likely more active with increasing sound levels and mesocarnivores' occupancy also increased with sound level outwardly appears at odds through the lens of predation risk. However, as discussed above, we suspect that lower detection rates of mesocarnivores with sound level reflects less activity, such as foraging. Additionally, conventional thought suggest that it would be unlikely that Cricetid rodents would be aware of variation in mesocarnivore foraging activity because they respond to the indirect environmental cues not direct predator cues for assessing predation risk (Orrock *et al.*, 2004). Nevertheless, the increase in Cricetid rodent detectability, likely a proxy for overall activity, is consistent with previous observations of greater foraging activity by *Peromyscus* mice in response to anthropogenic sound (Francis *et al.*, 2012). Precisely what causes increases in detectability and or activity with noise in this group warrants further investigation. One possible explanation of the increased detectability may involve hearing abilities. While there is evidence for altered movement and activity patterns in rodents in response to both anthropogenic and natural sounds, these responses were observed in ground squirrels (Le *et al.*, 2019; Shannon *et al.*, 2014). These larger, diurnal, semi-fossorial species have lower frequency hearing (Heffner *et al.*, 1994) and different ecological roles than do Cricetid rodents, so how movement and foraging of mice and rats change in the presence of natural sounds should be studied separately as well. Cricetid rodents were also the only functional group to have increased detections in response to all

treatments (phantom, shifted, real ocean) relative to control. This is interesting because much of the energy from the phantom and real ocean stimuli were below Cricetid rodents' peak hearing sensitivity of around 5-16kHz (Heffner & Heffner, 1985; Heffner *et al.*, 2001), yet all three stimuli (phantom, shifted, and real ocean) had similar increases in detection. Frequency differences of the background sound were therefore uninformative in explaining detectability, and hence activity, of this functional group.

Finally, and unexpectedly, the interaction between mean sound level and treatment led to a decline in Cricetid rodent detection probability for all treatment stimuli, such that on treatment sites with higher sound levels, detection probability declined. There are no simple explanations for this pattern, but it, along with the consistent response to all treatments, may highlight a problem in studying acoustic ecology using categorical treatments that vary in both sound level and frequency. A more appropriate methodology for future studies may be to measure sound level (dB) and frequency (Hz) as separate continuous variables because the properties of sound are dynamic as they propagate across the landscape and may not be well represented as a categorical level. That Cricetid rodent occupancy probabilities remained unchanged across sound level and treatments suggests that this group's distributions or presence in a patch may not be shaped by natural sounds. However, we did not estimate populations, thus, the possibility remains that natural sounds do not alter the probability of at least one individual being present at a site, but they do alter population structure or dynamics.

## **Kangaroo rats**

There were no variables with any apparent effect on kangaroo rats, with no changes to occupancy or detection probability. This contradicts our predicted decrease in both detection and occupancy with increases in natural sound. Kangaroo rats are known to have exceptional hearing (Masterton & Heffner, 1980) and to rely heavily on audition for predator detection (Webster & Webster, 1971) and intra-specific foot-drumming signals (Randall & Stevens, 1987; Ward & Randall, 1987). It may be that given their wide range of peak hearing sensitivity from 0.125kHz to 16kHz (Masterton & Heffner, 1980), no single treatment stimulus interfered with their ability to discriminate cues, or that they are not integrating background sounds when assessing predation risk. It is also surprising that factors known to alter behaviors and distributions, such as moonlight (Kaufman & Kaufman, 1982) or vegetation structure (Waser & Ayers, 2003) did not have any effect either. The lack of evidence for a response from this functional group to natural sounds seems anomalous and will require future study.

## **Ground foraging birds**

Our predictions for ground foraging birds were not supported, because no variables had an apparent effect on this functional group. The lack of response is surprising, considering that numerous studies have reported decreased foraging activity and increased vigilance of ground foraging birds in noise (Evans *et al.*, 2018; Quinn *et al.*,

2006; Ware *et al.*, 2015) and the decline in avian abundance in anthropogenic noise (Bayne *et al.*, 2008). It could be that the ground foraging birds in our study did not change their overall activity levels, but just partitioned it differently between foraging and vigilance such that detection probabilities were unaffected even though behavior may have been. Herbivorous, ground foraging bird species have also been shown to be less impacted by anthropogenic sound than omnivorous and insectivorous species (Francis, 2015) and so our natural sounds stimuli may not have been influential on our ground foraging birds' behavior or patch use. It is also possible that bird species within the ground foraging functional group have unique but opposing species-specific responses to natural sound. Avian responses to anthropogenic sound vary with vocal frequency and body-size (Francis *et al.*, 2011) so the variation in vocal frequency among species in this group may explain the lack of a consistent response. Ground foraging birds have also been shown to flush from an approaching predator later (*i.e.*, when a predator is closer) with increasing sound levels (Petrelli *et al.*, 2017), so it might be that increased visual vigilance still does not make up for the decline in passive acoustic surveillance. The lack of any vegetation effects on occupancy is somewhat surprising, although this too could be the result of species-specific habitat preferences cancelling one another out. An alternative explanation for these patterns is that camera traps are less commonly used to study avian occupancy than other survey methods, and as such may provide a plausible explanation for the lack of influential variables in our study.

## **Insectivorous birds**

Finally, our predictions for insectivorous birds were partially supported, because insectivorous birds did have lower detection probabilities with increasing sound levels; however, there was no support for our prediction that occupancy would decline with sound level. Insectivorous birds are known to be more sensitive to background sound than other functional groups (Francis, 2015), possibly because of their dependence on multi-modal foraging and passive acoustic surveillance while searching for prey. A low-scrub, gleaner, insectivore, the Pacific wren (*Troglodytes pacificus*), was demonstrated to flush from an approaching predator at closer distances with increasing sound levels (Petrelli *et al.*, 2017), suggesting that even if a bird increases visual vigilance it does not make up for the loss of passive acoustic surveillance. As a result, insectivorous birds may be spending more time in cover or engaging in other behaviors to reduce the probability of detection by a predator when living in louder conditions.

Insectivorous birds' occupancy probabilities increased with PC2 and the interaction between PC1 and PC2, indicating that sites with more taller, woody shrubs and greater structural complexity were more likely to be occupied, consistent with known habitat preferences for insectivorous gleaners (Robinson & Holmes, 1982). We did not observe a change in occupancy related to our natural sounds stimuli, suggesting that although insectivorous birds may have altered their behavior to avoid detection, they were not occupying louder patches less than quieter ones. This could be because the behavioral response represented by altered detections is enough to mitigate the

effects of natural sound. Alternatively, occupancy is not altered and insectivorous birds continue to live in louder patches, and rather than distributions being altered, birds incur physiological or reproductive costs, such as stress hormone dysregulation or lower reproductive success (Kleist *et al.*, 2018; Mulholland *et al.*, 2018).

Occupancy probabilities were not altered by natural sounds for either avian functional group, even though bird settlement has been shown to be strongly influenced by anthropogenic noise (Francis *et al.*, 2011; Kleist *et al.*, 2017). Anthropogenic noise and natural surf sound sources are similar in many ways but do vary in aspects like timing and periodicity. It could be that the natural rhythms of crashing surf provide quieter lulls in which listening and signaling are easier relative to acoustic conditions created by anthropogenic sources (Vélez & Bee, 2011; Versace *et al.*, 2008). Our results for both avian groups show that differences in response to anthropogenic and natural sound sources may exist, although how and why remain unclear.

## **Conclusions**

Background sound represents a particularly troublesome variable to incorporate into occupancy modeling not only because it can affect the detection and occupancy probabilities of the animals being observed, as our results suggest, but because it can also alter the ability of a human observer to detect said animals (Ortega & Francis, 2012). An occupancy modeling study design using a human observer making detections by ear adds a greater layer of ambiguity as altered detection probabilities can not be



determined to be the result of the observer's altered hearing or the focal species' altered behavior. For this reason, camera traps paired with sound level measurements should be considered alongside traditional survey techniques whenever possible in the study of soundscapes, because altered detections due to sound must be the result of a change to the animal, not the observer. It would also be of great benefit to the application of occupancy modeling to make certain that variance is being accurately partitioned between detection and occupancy when models are fit with a shared variable. This could be achieved by modeling the effects of background sound on occupancy ( $\Psi$ ) and detection ( $p$ ) probabilities from known or simulated data sets to explore how readily available occupancy model applications divide variance between occupancy and detection probabilities when fit with a shared variable. Additionally, considering our results show that background sound levels can influence both detection and occupancy probabilities, we suggest incorporating sound level measurements into most future camera-trapping and human observer occupancy study designs. Even if it is only included as a nuisance variable, explaining the variation in sound level could help reveal patterns of interest in future occupancy modeling applications.

Our results show that like anthropogenic noise, natural sounds have the ability to alter animal behavior and distributions, although the response is dependent on various ecological and taxonomic characteristics. It is clear that natural sounds play an important role in shaping ecological community interactions, and our findings that show altered detection and occupancy in response to natural sounds are likely to be expanded upon. Future research into the mechanisms by which natural sounds interact

with functional groups, trophic levels, hearing abilities, and other sensory modalities to alter behavior and distribution will be paramount in advancing our understanding of the role of natural sounds in shaping ecological communities.

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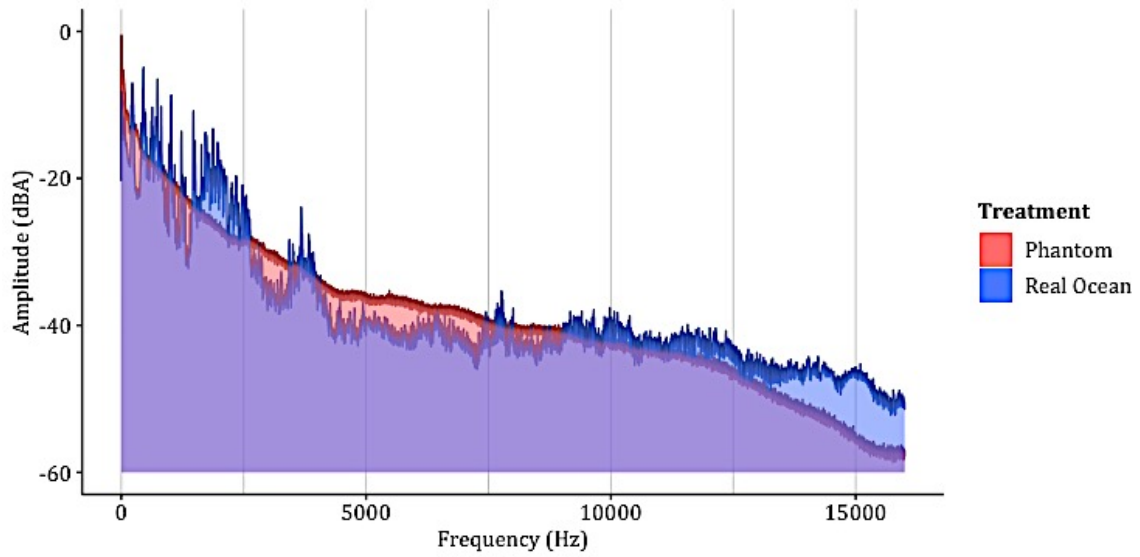
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## APPENDICES



**Figure S1** | Frequency of phantom treatment and recording taken at our real ocean sounds sites in early March 2017. Automated recording units had a cut of at 16 kHz.