Mechanisms underlying increased nest predation in natural gas fields: a test of the mesopredator release hypothesis

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Abstract. Anthropogenic activities are changing landscapes and the context in which predator–prey dynamics evolved, thereby altering key ecological processes and community structure. Yet, the specific mechanisms underlying such changes are rarely understood. We tested whether a mesopredator release explained increased rodent density and concomitant predation of songbird nests near natural gas development. From 2015 to 2016, we surveyed apex predators (coyotes, badgers, raptors, and corvids) and measured apparent survival and perceived predation risk of deer mice (Peromyscus maniculatus; a primary nest predator), at 12 plots spanning a gradient of surface disturbance caused by energy development in Wyoming, USA. Additionally, we measured densities of three nest predators: deer mice, least chipmunks (Tamias minimus), and thirteen-lined ground squirrels (Ictidomys tridecemlineatus). Contrary to the mesopredator release hypothesis, counts of apex predators and perceived predation risk of deer mice increased with surface disturbance from energy development, whereas apparent survival of mice decreased. Densities of mice and ground squirrels, however, increased with surface disturbance, despite increased predation pressure. We therefore rejected the mesopredator release hypothesis as a potential mechanism underlying altered trophic dynamics near energy development. Our results suggest that apex predator control measures would not benefit declining songbirds on natural gas fields. Rather, apex predator abundance may be regulated from the bottom-up by rodents in this system. Our results corroborate a pattern showing weakened effects of mesopredator release in habitats modified by humans. Understanding how predator–prey dynamics may be altered in novel environments requires an understanding of how predators and prey alike respond to habitat change under different contexts.

Key words: anthropogenic disturbance; apex predators; deer mouse; energy development; human-induced rapid environmental change; predator–prey; rodent; sagebrush; songbird; surface disturbance.

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INTRODUCTION

The rapid pace at which contemporary habitat change is occurring impedes the ability of many wildlife species to adapt or acclimate (Sih et al. 2011). The effects of human-induced rapid environmental change (HIREC; Sih et al. 2011) have been far-reaching, resulting in population declines, reduced fitness, and extinction of species across many taxa (Tilman et al. 1994). Patterns of population decline and negative fitness outcomes caused by HIREC are regularly documented, yet the specific mechanisms underlying these patterns are rarely understood (Mitchell et al. 2013). Without such understanding, the development of management actions to
successfully ameliorate the negative effects of habitat change on focal species is hampered.

Understanding processes with important fitness outcomes, such as predation, is particularly critical in the face of HIREC (Dorrestein et al. 2015). Predation can be a strong regulatory force for populations and therefore community structure and function (Young et al. 2015). Changes in apex predator abundance can lead to trophic cascades that drive population cycles, limit growth of prey populations, and alter vegetation communities (Berger et al. 2001). Reductions in the abundance of apex predators, for example, can alleviate consumptive and non-consumptive pressures on populations of medium-sized predators, with negative effects on underlying prey communities—a phenomenon known as a mesopredator release (Soule et al. 1988). A clearer understanding of how processes such as the mesopredator release may be elicited by HIREC, and the contexts under which a mesopredator release is most likely to manifest, however, are still lacking (Ryall and Fahrig 2006).

Habitat loss and fragmentation do not manifest in the same manner across all systems, so understanding how different forms of habitat alteration affect species interactions is critical for effective management. Energy development is one rapidly growing form of habitat disturbance, with energy production projected to expand up to 30% in the next decade (IEA 2015). In North America, species reliant on sagebrush habitats for key stages of their life history are particularly vulnerable to habitat changes caused by energy development (Knick and Rotenberry 2002), as energy development has high spatial overlap with the sagebrush steppe (Knick et al. 2003). In particular, populations of sagebrush-obligate songbirds (Brewer’s sparrow, Spizella breweri, sagebrush sparrow, Artemisiospiza nevadensis, and sage thrasher, Oreoscoptes montanus) are declining in many parts of their range (Sauer et al. 2017) and have exhibited decreased occupancy (Mutter et al. 2015), density (Gilbert and Chalfoun 2011), and nest survival (Hethcoat and Chalfoun 2015a) with energy development.

Decreases in nest survival of sagebrush songbirds in Wyoming were associated with surrounding surface disturbance caused by natural gas development (Hethcoat and Chalfoun 2015a). Nest predation was the primary cause of nest failure, and over 75% of nest depredations were attributed to rodents (mice, chipmunks, and ground squirrels), with other predator taxa (i.e., American badger, Taxidea taxus, common raccoon, Procyon lotor, loggerhead shrike, Lanius ludovicianus, black-billed magpie, Pica hudsonia, and raptors) displaying only intermittent depredations (Hethcoat and Chalfoun 2015b). Captures of rodents increased with increasing surface disturbance from energy development, and songbird nest survival decreased with concomitant increases in rodent captures (Hethcoat and Chalfoun 2015b). The mechanism underlying the increased rodent abundance near energy development, however, was unknown.

Here, we had a unique opportunity to test whether habitat changes associated with energy development may alter interactions between predators and prey, and investigate the implications of an altered predation regime on community structure. Although in most contexts the mesopredator release has referred to a release of medium-sized mammals from predation pressure (Crooks and Soule 1999), in our system the medium-sized mammals (coyote, Canis latrans, and badger) are actually at the apex of a trophic interaction and their prey (rodents) represent the mesopredator. Responses of medium-sized mammals to habitat alteration caused by humans can vary by species and disturbance type. In some contexts, predators such as corvids and coyotes can be drawn to the food and nesting resources associated with human disturbance (Ordenana et al. 2010, Coates et al. 2014). In other contexts, however, coyotes, badgers, and raptors shift their distributions and behaviors away from disturbed areas, presumably to minimize contact with humans (Gehrt et al. 2009, Garvin et al. 2011, Brodie et al. 2015, Hipólito et al. 2016). If apex predators present on natural gas fields, including coyotes, badgers, raptors, and corvids, are less prevalent near energy development, reduced risk of predation may facilitate increased mesopredator (i.e., rodent) densities.

We tested whether a mesopredator release may explain patterns of rodent abundance and thus songbird nest survival near natural gas development. We specifically predicted the following patterns across a gradient of surface disturbance from energy development: (1) decreased counts of apex predators, (2) increased apparent rodent
survival, (3) increased rodent densities, and (4) decreased perceived predation risk for rodents.

**METHODS**

**Study area**

We conducted our research within the Jonah-Pinedale Development Area in Sublette County, Wyoming, USA (42°38' N, 109°45' W; Appendix S1: Fig. S1). The area was dominated by sagebrush habitat (*Artemisia* spp.; Lyon and Anderson 2003) and contained two of the most concentrated and productive natural gas fields in the country (U.S. EIA 2015): the Pinedale Anticline Project Area (hereafter Pinedale Anticline) and the Jonah Field. We established six 25-ha study plots within each natural gas field, separated by 2–6 km (Appendix S1: Fig. S2). Plots were spread across a gradient, ranging from 0 to 38 ha of surrounding surface disturbance from energy development within 1 km² of study plot centers (Hethcoat and Chalfoun 2015a). We defined surface disturbance as any area that had been converted from sagebrush habitat as a result of development activities, including roads, pipelines, well pads, and reclaimed areas (in which mature sagebrush habitat had been removed during well, road, or pipeline construction and re-seeded). Whereas areas where habitat has been disturbed by energy development activities may represent habitat loss for sagebrush-obligate songbirds (which breed and forage exclusively in the shrub layer), these areas represent altered, but still useable habitat for rodents (Sanders and Chalfoun 2018).

Using ArcGIS 10.0 (ESRI 2011), we calculated the amount of surface disturbance within a 1-km² area centered over each study plot. We hand-digitized surface disturbance using National Agricultural Imagery Program files (USDA Geospatial Data Gateway 2017) and calculated total surface disturbance per area (ha/km²) surrounding each plot. Additional details on how we calculated this metric can be found in Hethcoat and Chalfoun (2015a).

We also established two plots located 3 km and two plots located 5 km from the nearest energy development infrastructure, which we used exclusively for conducting apex predator surveys. Apex predators (coyotes, badgers, raptors, and corvids) present at these four plots likely did not encounter energy development activities anywhere within their home range (Windberg and Knowlton 1988, Goodrich and Buskirk 1998, Boarman and Heinrich 1999, Preston and Beane 2009), allowing us to assess apex predator activity in areas devoid of nearby energy development.

**Apex predator surveys**

We conducted counts of the four most common taxa of apex predators in our system: coyotes, badgers, raptors, and corvids. Other predators (such as foxes, bobcats, and snakes) were either not present at our sites or were not present in large enough numbers to be detected during surveys. To quantify the relative abundance of the primary terrestrial predators of rodents present in our study area (coyotes and badgers), we used scent stations with camera traps. We placed two scent stations concurrently on opposite sides of a study plot, 250 m outside plot edges (1.0–1.3 km apart; Appendix S1: Fig S2). We deployed scent stations for seven consecutive days per month from May to August in 2015 and 2016, and moved locations of scent stations 45° around each plot each month to more accurately represent relative abundance of apex predators surrounding the entire plot. Scent stations consisted of a motion-activated trail camera (Browning, Morgan, Utah, USA; Bushnell Outdoor Products, Overland Park, Missouri, USA) mounted on a post ~30 cm above the ground. We placed a scent lure consisting of one Predator Survey Disk scented with fatty acid (USDA APHIS, Pocatello, Idaho, USA) and 1/16 ounce of Caven’s gusto (Minnesota Trapline Products, Pennock, Minnesota, USA) in front of each camera unit under a rock or cow pie to minimize weathering. Cameras took 3–4 consecutive photographs every time the motion sensor was triggered.

We conducted aerial predator surveys (point counts) at the center of all study plots from May–August 2015 and 2016 to assess counts of the primary avian predators of rodents in our study area (raptors and corvids). Each plot was visited every 3–14 d throughout the season, with variation in total number of visits (6–18 per year) between plots. Surveys did not occur during inclement weather (i.e., rain, high winds; Ralph et al. 1995). Observers recorded the location,
behavior, and number of individuals of all species that could potentially depredate rodents, including raptors, ravens, and magpies (Appendix S2: Table S1), taking care not to double-count individuals. Surveys lasted 10 min and were completed between 09:00 and 14:00 hours, when many raptors are most active (Fuller and Mosher 1987). We recorded horizontal distance from the observer to the initial location of detection using laser range finders (Ralph et al. 1995).

Rodent survival and density

We trapped both nocturnal and diurnal rodents to obtain density and survival estimates for three important nest predators of sagebrush-obligate songbirds (Hethcoat and Chalfoun 2015b): deer mice (Peromyscus maniculatus), least chipmunks (Tamias minimus), and thirteen-lined ground squirrels (Ictidomys tridecemlineatus). We trapped separate 150×150-m trapping grids at each plot in each year. We placed rodent trapping grids adjacent to study plots in similar habitat during 2015, and inside study plots in 2016 to facilitate a concurrent study (Appendix S1: Fig S2). We trapped three grids spanning our development gradient simultaneously to control for potential weather effects. Each nocturnal trapping grid contained 49 Sherman traps (LFA Folding Trap; H.B. Sherman Traps, Tallahassee, Florida, USA; 7×7 trap array) with 25-m spacing between traps. Diurnal trapping grids contained 28 Tomahawk traps (Model 102; Tomahawk Live Trap, Hazelhurst, Wisconsin, USA; 7×4 trap array) with alternating 25- and 50-m spacing between traps (Appendix S1: Fig S3). Nocturnal and diurnal trapping grids occupied the same spatial footprint each year, but efforts did not overlap temporally.

We used a robust trapping design (Williams et al. 2002), with two nocturnal sampling periods per year (summer 2015 and 2016) separated by approximately six weeks, each consisting of three trap nights. Both nocturnal (deer mice) and diurnal rodents (chipmunks and ground squirrels) were captured during nocturnal trapping efforts, as nocturnal traps were open for daylight hours in the mornings and/or evenings. To more specifically target diurnal rodents, we also trapped one diurnal period per year, which consisted of four trap days. This resulted in two primary trapping periods for nocturnal rodents and three primary periods for diurnal rodents (Appendix S2: Fig S1). We opened nocturnal traps in the late afternoon and checked for captures the following morning. We opened diurnal traps within one hour of sunrise and checked for captures 6–8 h later. We baited all traps with a rolled oats and peanut butter mixture. Nocturnal traps also contained polyester batting as bedding material, and diurnal traps contained an apple slice to provide hydration. Each trap was covered with a small plywood board or tarp to minimize direct sun exposure. We identified all captured animals to species, marked individuals with a 9-mm PIT tag (passive integrated transponder; Biomark, Boise, Idaho, USA) and released animals at their location of capture. All animal handling was conducted with the approval of the Wyoming Game and Fish Department (permit #1015) and the Institutional Animal Care and Use Committee (permit #20140602AC00107-03).

The perceived risk of a site and thus its suitability for rodents can be affected by many factors, including vegetative cover, nighttime brightness, and weather conditions (Orrock and Danielson 2004, Doherty et al. 2015). To account for habitat covariates that could influence rodent density and survival, we estimated percent sagebrush (Artemisia tridentata) and tumbleweed (dead Russian thistle, Kali tragus) cover at each trapping grid using line-intercept surveys (Etchberger and Krausman 1997) along 20-m transects centered in the four quadrants of each grid. We measured the maximum height of the nearest sagebrush shrub every 2 m along each transect to determine average shrub height. We obtained estimates of moon illumination from the U.S. Naval Observatory (2014). Daily temperature and precipitation measurements were obtained from the weather station at the Pinedale Ralph Wentz Field Airport (9–60 km from study plots; NOAA 2016).

We calculated total surface disturbance within a 100-, 250-, and 564-m buffer around each trapping grid using the methods described under study area above for use as predictors. Because trapping grids moved locations between years, we calculated surface disturbance metrics for 2015 and 2016 separately. The three buffer distances around trapping grids were used to assess the most relevant spatial scale of surface disturbance for our three rodent taxa, which have
varying home range sizes and foraging strategies (Harris and Leitner 2004, Wood et al. 2010, Locker et al. 2016). The 564-m buffer is the scale at which sagebrush songbirds were previously affected by surface disturbance from energy development (Hethcoat and Chalfoun 2015a).

**Perceived predation risk experiment**

We conducted a giving-up density (GUD; Brown 1988) experiment during summer 2015 to determine whether perceived predation risk of nocturnal rodents varied across our development gradient. The giving-up density is the food density at which an animal stops foraging in a food patch, that is, the point at which the potential costs of foraging (predation) outweigh the benefits (continued food harvest). Using a paired design, we compared the GUD at a food patch in a safe microhabitat (a food tray located under a shrub) with a nearby food patch in a risky microhabitat (a food tray located in the open; Brown 1988). If more food was consumed at the safe patch than at the risky patch (i.e., rodents minimized time spent in risky foraging activity), we concluded that rodents experienced an increase in their perceived risk of predation. We were thus primarily interested in the foraging effort at safe foraging trays relative to their paired risky trays.

We implemented the GUD experiment within trapping grids at 11 study plots for three consecutive nights at each grid during the upper and lower quarter of moon illumination, to account for variation in perceived predation risk with moon phase (Orrock and Danielson 2004). Giving-up density experiments did not overlap temporally with nocturnal trapping efforts. At five plots, we conducted the experiment for only two nights during the moon’s upper quarter due to poor weather conditions. Each plot contained 6–7 pairs of foraging trays (stations) per night. All stations within a plot were separated by 50–75 m to reduce the likelihood that an individual rodent would visit multiple stations in the same night, based on average home range size for deer mice (Wood et al. 2010). Deer mice represented ~90% of nocturnal rodents at our sites (L.E. Sanders and A.D. Chalfoun unpublished data), and thus, the GUD experiment primarily tested perceived risk for deer mice. Trays were placed in pairs, with one tray placed fully under a shrub (safe tray) and the second placed in the open (risky tray; Appendix S2: Fig S2; Orrock and Danielson 2004). We placed risky trays ~1 m away from paired safe trays with as little vegetation in the surrounding 1 m radius as possible, ensuring that a rodent approaching a station was likely to encounter both trays.

Trays were filled with a homogenized mixture containing one liter of play sand (Pavestone, Tyron, Georgia, USA) and 5.00 g of sterilized sunflower seed in the husk (Jacob and Brown 2000). For tray construction details, see Appendix S2: Fig S2. We opened trays after sunset and closed trays the following morning before sunrise to ensure that only nocturnal rodents accessed stations. We recorded any signs of visitation at foraging trays (see Ceradini and Chalfoun 2017) and observed no sign of animals other than rodents foraging in trays. We sifted sand from visited trays to collect remaining seeds and dried all seed in an oven for 24 h at 60°C before weighing. We defined a giving-up density as the amount of seed remaining in the tray after one night of foraging by nocturnal rodents, that is, the food density at which rodents gave up their foraging efforts.

We recorded vegetation metrics at each station for use as covariates in analyses to ensure that observed differences in seed consumption were not a product of variation in microhabitat. At each station, we measured shrub height (for the shrub covering the safe tray), shrub volume, and minimum space between the top of the safe tray and the closest vegetation.

**Statistical analyses**

**Apex predator surveys.**—All analyses were conducted in Program R (R Core Team 2017) version 3.3.3. We calculated an index of abundance for mammalian apex predators by summing the number of times coyotes and badgers were detected during each survey event (n = 166 surveys), and for avian predators by summing the number of times raptors and corvids were observed within 1 km of the sampling point during each survey (n = 210 surveys). We considered counts of coyotes and badgers independent if they were separated by ≥1 h. Although we could not identify individual coyotes and badgers in photographs, our count metric was
intended to index relative coyote and badger activity in the vicinity of study plots. We determined that counts were similar between camera models \((n = 2)\) for coyotes and badgers using Kruskal-Wallis tests for non-parametric data (Appendix S2: Table S2). Counts of raptors and corvids were similar between observers \((n = 6)\), wind levels \((n = 7)\), Beaufort wind scale \(0–6, WMO 1970\), cloud cover \((n = 4; 0–25\%, 25–50\%, 50–75\%, 75–100\% \text{ cloud cover})\), time of day (range: \(09:00–14:00\) hours), and Julian date (range: April 30–August 13; Appendix S2: Table S2). We thus created an index of abundance for coyotes, badgers, raptors, and corvids separately by summing counts from all surveys at each plot in each year \((n = 32 \text{ plot-year combinations})\). This approach of summarizing the data before analysis more clearly exposes the underlying constraints of the data than a mixed-effects approach and allowed us to conduct analyses at the plot scale where we intended to make inference (Murtaugh 2007). We tested for an effect of surface disturbance (measured within \(1 \text{ km}^2\) of study plot centers) on counts of coyotes, badgers, and raptors separately using generalized linear regressions (Poisson) with a log-link function (lme4 package; Bates et al. 2015). We chose to run fixed effects models (rather than mixed-effects models with study plot as a random effect) given only two estimates per plot, which is not a sufficient number of replicates for a random effect (Zuur et al. 2009). To account for over-dispersion of the data, we modeled counts of corvids using a negative binomial distribution (Zuur et al. 2009) with a log-link function (MASS package; Venables and Ripley 2002). Coyote and badger models were offset by the number of days cameras were active at each plot in each year (log-transformed), while raptor and corvid models were offset by the number of surveys conducted at each plot in each year (log-transformed; Zuur et al. 2009). We created separate model suites for all four apex predator taxa. Model suites contained six models, including univariate predictors of year, gas field, and surface disturbance, two additive models (surface disturbance + year, surface disturbance + gas field), and an intercept-only model. Models contained two or fewer predictors to reduce the potential of overfitting (Burnham and Anderson 2002). We used Akaike's information criterion corrected for small sample size \((\text{AIC}_c)\) for model selection (AICmodavg package; Mazerolle 2019), model probabilities \((w_i)\), and evidence ratios \((E_r)\) to assess model support for each group of apex predators (Burnham and Anderson 2002). We determined goodness of fit by visually inspecting residuals versus fitted values and quantile-quantile plots for our top model (Zuur and Ieno 2016), which we used to make inference about the effect of predictor variables on apex predator counts.

**Rodent survival and density.**—To quantify how surface disturbance from energy development influenced the density of rodents, we used mark-recapture models (Program MARK, White and Burnham 1999; RMark package, Laake 2013) with Huggins robust design (Williams et al. 2002) and a logit link function to estimate capture \((p)\) and recapture \((c)\) probability, survival \((\Phi)\), and abundance \((N)\) for three common nest predators in our study area: deer mice (effective \(n = 1272\)), least chipmunks (effective \(n = 307\)), and thirteen-lined ground squirrels (effective \(n = 110\)). Deer mice were caught exclusively during nocturnal trapping, and therefore, only two primary periods were used for estimating model parameters, necessitating that temporary emigration parameters \((\gamma'\text{ and } \gamma'')\) be fixed to zero. Temporary emigration parameters for chipmunks and ground squirrels were also fixed to zero due to model convergence issues. We thus estimated apparent survival, since emigration and death are confounded when temporary emigration parameters are inestimable (Williams et al. 2002). We calculated within-season apparent survival, that is, apparent survival between primary trapping sessions in the same season (6-week period for deer mice). We used a two-stage modeling approach to model detection and apparent survival of deer mice (Doherty et al. 2012). Our first stage followed the methodologies of Sanders and Chalfoun (2018) to model detection probabilities (see Appendix S2: Methods for details; Appendix S3: Table S1 for predictor variables). We moved the final capture/recapture probability model forward into apparent survival analyses. To model apparent survival, we used \(\text{AIC}_c\) model selection to compare univariate and bivariate (additive) models containing all combinations of predictor variables \((n = 56 \text{ models})\), see Appendix S3:
Table S1 for covariate descriptions). We measured surface disturbance for apparent survival models at a 564-m scale, which has previously been informative for songbird nest survival in this system (Hethcoat and Chalfoun 2015a). We model-averaged predicted abundance for deer mice based on the final model set, and estimated predicted abundance for each plot-year combination. We repeated these steps separately for chipmunks and ground squirrels, though we skipped model selection and set apparent survival for both species to the intercept-only model due to issues with parameter estimation.

We analyzed the natural logarithm of rodent densities using linear models, and ensured residuals fit the Gaussian distribution from visual observation of quantile-quantile and residual plots (Zuur and Ieno 2016). We calculated effective trapping area for each species by adding the mean maximum distance traveled across individuals to total grid size, and divided abundance by effective trapping area to determine rodent densities. Because our response variable was an estimate, we weighted all models by the inverse of the standard error. We only captured thirteen-lined ground squirrels at the Jonah Field, so did not include trapping grids from the Pinedale Anticline in ground squirrel analyses. For grids at the Jonah Field where no ground squirrels were captured, we estimated standard error as the minimum standard error observed at other trapping grids (0.31).

We used a two-staged approach to model rodent density, which allowed us to test how rodent densities (n = 24 estimates for deer mice and chipmunks, n = 12 estimates for ground squirrels) varied across many covariates (Burnham and Anderson 2002). To determine the spatial scale at which deer mice responded to development, we first compared surface disturbance as a predictor of density at three different scales (a buffer from the edge of the trapping grid measuring 100, 250, and 564 m) using AICc model selection. Second, we modeled deer mouse density as a function of the top-performing surface disturbance metric from stage 1 and additional predictors including year, gas field, and habitat covariates (Appendix S3: Table S1).

We compared the relative performance of all univariate models (n = 8), along with bivariate models containing surface disturbance and each additional predictor variable in additive (n = 7) and interactive combinations (n = 7) and an intercept-only model (n = 1). We used AICc model selection, model probabilities (wi), and evidence ratios (Ei) to compare competing models. We repeated both modeling stages for chipmunks and ground squirrels separately, excluding bivariate models for ground squirrels in stage 2.

Perceived predation risk experiment.—We calculated perceived predation risk for nocturnal rodents based on giving-up densities at paired foraging trays (stations). We excluded from analyses all station-nights where neither foraging tray was visited by a rodent (n = 17 out of 391 station-nights; Mattos and Orrock 2010) and where seed weights were unreliable (n = 11 station-nights). We averaged the amount of seed eaten at each tray across the 2–3 nights surveyed during each moon phase, resulting in 142 foraging station-moon phase combinations. To take advantage of our paired study design, we calculated the change in the odds that a safe tray had a lower giving-up density than its paired risky tray (see Appendix S2: Methods for details on this calculation). We log-transformed this value to account for non-normality in the residuals. Thus, we calculated the log change in the odds of a safe tray having a lower giving-up density than its paired risky tray at any given station (hereafter perceived predation risk). If nocturnal rodents had a lower giving-up density at the safe tray than the paired risky tray, perceived predation risk would be higher.

We used Kruskal-Wallis tests to determine that perceived predation risk did not vary at individual foraging stations with moon phase (df = 1, χ² = 1.23, P = 0.27) or minimum temperature (df = 3, χ² = 4.31, P = 0.23). As such, we averaged perceived predation risk ratios across all stations and moon phases within each study plot to generate one metric of perceived predation risk per plot (n = 11 plots). We averaged vegetation metrics for all stations at each plot to produce one measure per plot for use as predictor variables. We developed linear models using a Gaussian distribution to test for a relationship between perceived predation risk and surrounding surface disturbance (within a 564-m buffer around trapping grids, based on results from
deer mouse density analyses), gas field, all vegetation metrics, and deer mouse density (to test for any density dependent effects, as calculated under Rodent survival and density above). We used AICc model selection, model probabilities ($w_i$), and evidence ratios ($E_i$) to compare competing models. Based on our relatively small sample size ($n = 11$ plots) and our inability to confirm that data conformed to parametric normality assumptions, we determined whether perceived predation risk varied by our top predictors with bootstrapped 95% confidence intervals (CIs; 1000 resampling events; Zuur et al. 2009). We back-transformed estimates and confidence intervals from the log-scale for interpretation as odds ratios, and report the change in the odds across our entire gradient of surface disturbance (0–38 ha/km$^2$).

**RESULTS**

**Apex predator counts**

Coyote counts increased 80% across our gradient of surrounding surface disturbance ($\beta = 0.02$ for every ha/km$^2$ of surface disturbance, 95% CI = 0.003–0.04, $z = 2.21$; Fig. 1a), based on results from our top-performing model ($w_i = 0.43$; Table 1), which contained a univariate effect of surface disturbance. The top three models in this suite all contained surface disturbance as a predictor and together held 78% of model weights, indicating support for the effect of surface disturbance on coyote counts.

Badger counts also tended to increase with surface disturbance ($\beta = 0.03$ for every ha/km$^2$ of surface disturbance, 95% CI = −0.001–0.06, $z = 1.88$; Fig. 1b) according to the top-ranked
model in this suite ($w_i = 0.46$; Table 1) which contained an additive effect of surface disturbance and gas field. We counted 2.7 times more badgers at the Jonah Field than the Pinedale Anticline ($b = 0.99$, 95% CI = 0.17–1.82, $z = 2.37$).

Our top two models both contained an effect of gas field and together contained 72% of model weights, with a relatively low evidence ratio for the third-ranked model ($E_i = 4.18$), indicating strong support for the effect of gas field on observed badger counts, and some support for the effect of surface disturbance.

Raptor counts increased 1.2 times across our gradient of surrounding surface disturbance ($\beta = 0.03$ for every ha/km$^2$ of surface disturbance, 95% CI = 0.01–0.06, $z = 3.12$; Fig. 1c), based on results from the top-performing model ($w_i = 0.42$; Table 1), which contained an additive effect of surface disturbance and gas field. Raptor counts tended to be higher at the Pinedale Anticline than the Jonah Field ($b = 0.58$, 95% CI = −0.04–1.20, $z = −1.84$). The top three models in this suite all contained surface disturbance as a predictor, contained 97% of combined model weights, and outperformed the null model, with a very low evidence ratio for the fourth-ranked model ($E_i = 42.00$), indicating strong support for an effect of surface disturbance on raptor counts.

Counts of corvids increased 80% across our gradient of surrounding surface disturbance ($\beta = 0.02$ for every ha/km$^2$ of surface disturbance, 95% CI = 0.002–0.05, $z = 2.17$; Fig. 1d),

| Competing model                     | log(L) | $k$ | $\Delta$AIC$_c$ | $w_i$ | $E_i$ |
|-------------------------------------|--------|-----|-----------------|-------|-------|
| Coyote                              |        |     |                 |       |       |
| Surface disturbance                 | −49.35 | 2   | 0.00            | 0.43  | N/A   |
| Surface disturbance + gas field     | −48.78 | 3   | 1.30            | 0.22  | 1.95  |
| Surface disturbance + year          | −49.33 | 3   | 2.41            | 0.13  | 3.31  |
| Null                               | −51.76 | 1   | 2.55            | 0.12  | 3.58  |
| Gas field                           | −51.23 | 2   | 3.77            | 0.06  | 7.17  |
| Year                               | −51.76 | 2   | 4.82            | 0.04  | 10.75 |
| Badger                             |        |     |                 |       |       |
| Surface disturbance + gas field     | −37.16 | 3   | 0.00            | 0.46  | N/A   |
| Gas field                           | −38.96 | 2   | 1.16            | 0.26  | 1.77  |
| Surface disturbance + year          | −38.57 | 3   | 2.81            | 0.11  | 4.18  |
| Surface disturbance                 | −40.28 | 2   | 3.79            | 0.07  | 6.57  |
| Year                               | −40.38 | 2   | 3.99            | 0.06  | 7.67  |
| Null                               | −41.96 | 1   | 4.87            | 0.04  | 11.50 |
| Raptor                             |        |     |                 |       |       |
| Surface disturbance + gas field     | −44.65 | 3   | 0.00            | 0.42  | N/A   |
| Surface disturbance + year          | −44.95 | 3   | 0.60            | 0.31  | 1.35  |
| Surface disturbance                 | −46.43 | 2   | 1.11            | 0.24  | 1.75  |
| Gas field                           | −49.54 | 2   | 7.34            | 0.01  | 42.00 |
| Year                               | −50.07 | 2   | 8.41            | 0.01  | 42.00 |
| Null                               | −51.65 | 1   | 9.29            | 0.00  | Undefined |
| Corvid                             |        |     |                 |       |       |
| Surface disturbance + gas field     | −71.55 | 4   | 0.00            | 0.93  | N/A   |
| Year                               | −73.66 | 3   | 2.21            | 0.07  | 13.29 |
| Surface disturbance                 | −79.54 | 3   | 13.98           | 0.00  | Undefined |
| Null                               | −80.96 | 2   | 14.82           | 0.00  | Undefined |
| Surface disturbance + year          | −79.30 | 4   | 15.50           | 0.00  | Undefined |
| Gas field                           | −80.65 | 3   | 16.20           | 0.00  | Undefined |

Notes: Surface disturbance was measured as total habitat altered by energy development activities within a 1 km$^2$ of study plot centers. We report log-likelihood values log(L), number of parameters $k$, the difference in Akaike’s information criterion corrected for small sample size (AIC$_c$) values between the top model and model $i$ (AIC$_c$), the AIC$_c$ weight indicating relative support for the model $w_i$, and the weight of evidence for each model compared with the top model ($E_i = w_{top}/w_i$). Data were collected at 16 study plots within two natural gas fields in western Wyoming, USA, 2015–2016.
based on the top-performing model ($w_i = 0.93$; Table 1), which contained an additive effect of surface disturbance and gas field. Corvid counts were 4.3 times higher at the Jonah Field than the Pinedale Anticline ($\beta = 1.46$, 95% CI = 0.87–2.05, $z = 4.86$). Our top model had 13.29 times the evidence of the second-ranked model, indicating strong support for an effect of surface disturbance and gas field on corvid counts.

**Rodent apparent survival**

Within-season apparent survival for deer mice decreased 60% across our gradient of surface disturbance ($\beta = -0.02$ for every ha/km² of surface disturbance, 95% CI = -0.04 to -0.01, $z = 2.68$; Fig. 2), according to the top-performing model ($w_i = 0.55$; Table 2, full model set in Appendix S3: Table S2, detection probabilities in Appendix S3: Table S3). Apparent survival also varied by year ($\beta = -1.03$, 95% CI = -1.42 to -0.63, $z = 5.11$), with lower apparent survival in 2016 than 2015. Our second-ranked model had a relatively low evidence ratio ($E_i = 5.00$), indicating support for the effect of surface disturbance and year on apparent survival of deer mice.

**Rodent density**

Surface disturbance at a 564-m scale was the best energy development metric for predicting deer mouse density ($w_i = 0.46$; Appendix S3: Table S4). Deer mouse densities doubled across our gradient of surface disturbance in 2016, but not 2015 ($\beta = 0.03$ for every ha/km² of surface disturbance, 95% CI = 0.01–0.04, $t = 2.55$, adj-$R^2 = 0.27$; Fig. 3a, detection probabilities in Appendix S3: Table S3), according to our top-ranked model ($w_i = 0.27$; Table 3, full model set in Appendix S3: Table S5). Our top model outperformed the second-ranked model (univariate year-effect) by $\Delta AIC_c = 3.00$, and only these two models outperformed the null, indicating support for the effect of surface disturbance and year on deer mouse densities.

Surface disturbance at a 250-m scale was the best energy development metric for predicting least chipmunk density ($w_i = 0.39$; Appendix S3: Table S4). Chipmunk densities were 1.6 times

Table 2. Subset of deer mouse (Peromyscus maniculatus) apparent survival ($\Phi$) models from stage two Huggins robust design analysis (90% confidence set).

| Competing model | $k$ | $\Delta AIC_c$ | $w_i$ | Deviance | $E_i$ |
|-----------------|-----|----------------|-------|----------|------|
| $\Phi$ (surface disturbance + year) | 12  | 0.00           | 0.55  | 6263.01  | N/A  |
| $\Phi$ (year + AT cover [SD]) | 12  | 3.25           | 0.11  | 6266.26  | 5.00 |
| $\Phi$ (surface disturbance + AT cover [SD]) | 12  | 3.79           | 0.08  | 6266.80  | 6.88 |
| $\Phi$ (year) | 11  | 5.33           | 0.04  | 6270.36  | 13.75|
| $\Phi$ (year + AT height [avg]) | 12  | 6.06           | 0.03  | 6269.07  | 18.33|
| $\Phi$ (year + gas field) | 12  | 6.09           | 0.03  | 6269.10  | 18.33|
| $\Phi$ (year + AT cover [avg]) | 12  | 6.28           | 0.02  | 6269.29  | 27.50|
| $\Phi$ (year + age) | 12  | 6.79           | 0.02  | 6269.80  | 27.50|
| $\Phi$ (gas field + AT cover [sd]) | 12  | 7.17           | 0.02  | 6270.18  | 27.50|

Notes: Covariates include average sagebrush (Artemisia tridentata) cover (AT cover [avg]), standard deviation of sagebrush cover (AT cover [SD]), average sagebrush height (AT height [avg]), gas field, year, deer mouse age, and surface disturbance. Surface disturbance was measured as total habitat altered by energy development activities within a 564-m buffer around trapping grids. We report number of parameters $k$, the difference in Akaike’s information criterion corrected for small sample size ($AIC_c$) values between the top model and model $+ \Delta AIC_c$, the $AIC_c$ weight indicating relative support for the model $w_i$, model deviance, and the weight of evidence for each model compared with the top model ($E_i = \frac{w_{top}/w_i}{\Sigma w_j}$). Data were collected at 12 study plots within two natural gas fields in western Wyoming, USA, 2015–2016.

Fig. 2. Predicted apparent survival for deer mice (Peromyscus maniculatus) in relation to surrounding surface disturbance (ha/km²) caused by natural gas development (measured within a 564-m buffer around trapping grids). Apparent survival estimates from 2015 are in gray and 2016 are in black. Dotted lines indicate 95% confidence intervals. Data were collected at 12 study plots within two natural gas fields in western Wyoming, USA, 2015–2016.
higher at the Jonah Field than the Pinedale Anticline ($b = 0.45$, 95% CI = 0.26–0.66, $z = 4.12$, adj-$R^2 = 0.41$; detection probabilities in Appendix S3: Table S3), according to our top-supported model ($w_i = 0.61$; Table 3, full model set in Appendix S3: Table S5). Our top-supported model including surface disturbance ranked second ($w_i = 0.31$) and contained additive effects of gas field and surface disturbance, indicating a non-significant decrease in chipmunk density with increasing surface disturbance ($b = −0.01$ for every ha/km$^2$ of surface disturbance, 95% CI = −0.02−0.01, $z = −1.66$, adj-$R^2 = 0.45$; Fig. 3b, Table 3). The top two models together contained over 90% of model weights, indicating strong support for the effect of gas field on chipmunk densities.

Table 3. Top generalized linear regression models for deer mouse (*Peromyscus maniculatus*), least chipmunk (*Tamias minimus*), and thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*) densities.

| Competing model | log(L) | $k$ | ΔAICc | $w_i$ | $E_i$ |
|-----------------|--------|-----|--------|------|------|
| Deer mouse      |        |     |        |      |      |
| Surface disturbance × year | −0.33 | 5   | 0.00   | 0.27 | N/A  |
| Year            | −4.47  | 3   | 2.15   | 0.09 | 3.00 |
| Null            | −5.81  | 2   | 2.19   | 0.09 | 3.00 |
| Chipmunk        |        |     |        |      |      |
| Gas field       | −2.02  | 3   | 0.00   | 0.61 | N/A  |
| Surface disturbance + gas field | −1.25 | 4   | 1.37   | 0.31 | 1.96 |
| Surface disturbance × gas field | −1.13 | 5   | 4.36   | 0.07 | 8.71 |
| Null            | −8.88  | 2   | 11.10  | 0.00 | Undefined |
| Ground Squirrel |        |     |        |      |      |
| Surface disturbance | −23.71 | 3   | 0.00  | 0.68 | N/A  |
| AT height [SD]  | −25.33 | 3   | 3.23   | 0.13 | 5.23 |
| AT cover [SD]   | −26.24 | 3   | 5.05   | 0.05 | 13.60 |
| Null            | −28.19 | 2   | 5.28   | 0.05 | 13.60 |

Notes: All models outperforming and including the null model are shown. Covariates include standard deviation of sagebrush (*Artemisia tridentata*) cover (AT cover [SD]), standard deviation of sagebrush height (AT height [SD]), gas field, year, and surface disturbance. Surface disturbance was measured as the total habitat altered by energy development activities within a 250-m buffer of trapping grids for chipmunks and within a 564-m buffer for deer mice and ground squirrels. We report log-likelihood values log(L), number of parameters $k$, the difference in Akaike’s information criterion corrected for small sample size (AICc) values between the top model and model $i$ $Δ$AICc, the AICc weight indicating relative support for the model $w_i$, and the weight of evidence for each model compared with the top model ($E_i = w_{top}/w_i$). Data were collected at 12 study plots within two natural gas fields in western Wyoming, USA, 2015–2016.
Surface disturbance at a 564-m scale was the best energy development metric for predicting thirteen-lined ground squirrel density \( (w_i = 0.80; \text{Appendix S3: Table S4}) \). Ground squirrel densities increased 4.5 times across our gradient of surface disturbance \( (\beta = 0.12 \text{ for every ha/km}^2 \text{ of surface disturbance, 95% CI } 0.01–0.20, z = 3.33, \text{adj-R}^2 = 0.48; \text{Fig. 3c, detection probabilities in Appendix S3: Table S3}) \) according to our top-supported model \( (w_i = 0.68; \text{Table 3, full model set in Appendix S3: Table S5}) \). Our second-ranked models had a relatively low evidence ratio \( (E_i = 5.23) \), indicating support for the effect of surface disturbance on ground squirrel densities.

**Perceived predation risk**

Perceived predation risk of nocturnal rodents increased with surface disturbance \( (\beta = 0.02 \text{ for every ha/km}^2 \text{ of surface disturbance, 95% CI } 0.001–0.03, t = 2.08; \text{Fig. 4}) \), according to our top-ranked model \( (w_i = 0.33; \text{Table 4}) \). Across our gradient of surface disturbance \( (0–38 \text{ ha/km}^2) \), the odds that perceived predation risk would be lower at a safe tray than its paired risky tray increased by 142% \( (95\% \text{ CI } 8–282\%) \). We had considerable uncertainty in our model suite, however, with the top-ranked model having only 1.22 times the evidence of the intercept-only model, indicating a lack of strong support for the effect of surface disturbance on perceived predation risk.

**DISCUSSION**

Habitat change and fragmentation have affected nearly every environment worldwide and can alter historic species interactions, including predation regimes (Tylianakis et al. 2008, Dorresteijn et al. 2015). A mesopredator release is one potential phenomenon responsible for altered community structure near human disturbance (Crooks and Soulé 1999), though results of tests have been mixed (Cove et al. 2012, Wang et al. 2015). Relatively few studies, moreover, have explicitly investigated the mesopredator release hypothesis in altered landscapes (Crooks and Soulé 1999, Wang et al. 2015, Krofel et al. 2017), such as those resulting from energy development. We investigated whether a mesopredator release was responsible for shifts in prey communities near energy development by testing whether trends in rodent density and concomitant songbird nest survival (Hethcoat and Chalfoun 2015a) were related to a decrease in

![Fig. 4. Perceived predation risk for nocturnal rodents in relation to surrounding surface disturbance (ha/km²) caused by natural gas development. Perceived predation risk was measured as the log change in the odds of a safe foraging tray having a lower giving-up density than its paired risky tray. Surface disturbance was measured as total habitat altered by energy development activities within a 564-m buffer around trapping grids. Dotted lines indicate 95% confidence intervals. Data were collected at 11 study plots within two natural gas fields in western Wyoming, USA, 2015.](image)

### Table 4. Linear regression model suite for perceived predation risk of nocturnal rodents.

| Competing model | \( \log(L) \) | \( k \) | \( \Delta \text{AIC}_c \) | \( w_i \) | \( E_i \) |
|-----------------|--------------|------|-----------------|------|---------|
| Surface disturbance | -1.56 | 3 | 0.00 | 0.33 | N/A |
| Null | -3.72 | 2 | 0.39 | 0.27 | 1.22 |
| Deer mouse density | -2.34 | 3 | 1.57 | 0.15 | 2.20 |
| Gas field | -2.69 | 3 | 2.27 | 0.11 | 3.00 |
| Distance to shrub above tray | -3.25 | 3 | 3.38 | 0.06 | 5.50 |
| Shrub volume | -3.64 | 3 | 4.16 | 0.04 | 8.25 |
| Shrub height | -3.72 | 3 | 4.32 | 0.04 | 8.25 |

**Notes:** Covariates include gas field, surface disturbance, deer mouse (Peromyscus maniculatus) density, and vegetation metrics. Surface disturbance was measured as total habitat altered by energy development activities within a 564-m buffer around trapping grids. We report log-likelihood values \( \log(L) \), number of parameters \( k \), the difference in Akaike’s information criterion corrected for small sample size \( (\text{AIC}_c) \) values between the top model and model \( i \) \( \Delta \text{AIC}_c \), the AIC\(_c\) weight indicating relative support for the model \( w_i \) and the weight of evidence for each model compared with the top model \( E_i = w_{\text{top}}/w_i \). Data were collected at 11 study plots within two natural gas fields in western Wyoming, USA, 2015.
mammalian and/or avian apex predators. As surrounding surface disturbance from natural gas development increased, plots generally had higher counts of apex predators, higher perceived predation risk for rodents, lower apparent survival of rodents, and higher rodent densities. Combined, our four lines of evidence suggest rejection of the mesopredator release hypothesis.

Contrary to our predictions, coyotes, badgers, raptors, and corvids were generally detected more often in areas with more surface disturbance caused by energy development. Rodents provide important food resources for many apex predators (Brillhart and Kaufman 1995, Laudet and Selva 2005, Sidorovich et al. 2011), particularly in arid environments where other food resources may be scarce. Because badgers and coyotes avoid some types of human activity (Crooks 2002, Gehrt and Clark 2003, Hipólito et al. 2016), their presence near energy development suggests that anthropogenic disturbance can modify behaviors in surprising ways—potentially via increased availability of desirable prey (live rodents and roadkill). Our results corroborate other work, moreover, suggesting that common raven densities increase in the sagebrush steppe near human disturbance, with ravens accounting for nearly half of predatory birds in some areas (Coates et al. 2014). As raven populations continue to increase, corvids may become even more important predators for small mammals (Laudet and Selva 2005). Some apex predators also depredate sagebrush songbird nests in this system (e.g., American badger, Short-eared Owl, Asio flammeus, Northern harrier, Circus hudsonius, American kestrel, Falco sparverius, Common raven, Corvus corax, and Black-billed magpie; Hethcoat and Chalfoun 2015b, A. D. Chalfoun unpublished data). The combined effects of apex predators on songbird nest survival, however, appear to be negligible compared to rodents.

Concomitant with the apex predator results, apparent survival of deer mice decreased and perceived predation risk increased with surface disturbance from energy development. Mice therefore appeared to recognize that areas with more surface disturbance represented increased predation risk (Lima and Dill 1990). Nonetheless, we found higher rodent densities in more dangerous habitats. Rodents may be receiving some benefit (e.g., higher quality food resources) when living near energy development, leading to increased reproductive output and/or increased immigration into areas with high levels of habitat change, thereby counter-balancing the effect that decreased survival would have on local densities (Fraser and Huntingford 1986). Indeed, habitat modifications that lead to increased edge habitat and food resources, such as urbanization, agriculture, and energy development, tend to have the most positive effects on synanthropic species, such as deer mice and ground squirrels (Eagan et al. 2011). See Sanders and Chalfoun (2018) for further investigation into this potential mechanism. Because we could not estimate emigration and immigration rates for deer mice, our estimates of apparent survival could be confounded (Williams et al. 2002). Daily movements within trapping grids, though, did not vary across our development gradient (Appendix S2: Fig S3), and the congruence between our apparent survival and perceived predation risk results suggests that our apparent survival estimates were legitimate.

Mesopredator response to habitat alteration varied by species in our system: Two out of three rodent taxa (deer mice and ground squirrels) were more abundant in areas with more surface disturbance caused by energy development, whereas chipmunks trended in the opposite direction, though not significantly. Competitive pressures among taxa may explain the varying responses across mesopredators in our study (Heske et al. 1994), as chipmunks are a medium-sized rodent whose resource requirements likely overlap both deer mice and ground squirrels. Mesopredators in our system may therefore have somewhat complementary local distributions (Sozio and Mortelliti 2016), with deer mice and ground squirrels displacing chipmunks in more fragmented areas. Generalist species such as deer mice tend to thrive near human disturbance, often at the expense of more sensitive or specialist species which are unable to adapt as quickly to novel environments (Crooks 2002, Ceradini and Chalfoun 2017).

Patterns of mesopredator abundance near energy development varied across spatial scales, with deer mice and ground squirrels responding most strongly at the largest scale (564 m). The 250-m spatial scale was most important for
chipmunks, though their abundance was not significantly related to the surface disturbance gradient. Notably, none of the mesopredators showed a strong response to the development gradient at the smallest spatial scale (100 m), although our model suites did contain considerable uncertainty. Preferences for local microhabitat characteristics such as food resources or cover can lead to increased abundance and fitness at scales much larger than individual resource use, especially in fragmented systems (Fauteux et al. 2012). Rodents responded to surface disturbance at fairly large spatial scales, implying that species with relatively small home ranges (i.e., deer mice; Wood et al. 2010) can respond to habitat alteration at a scale up to ten times larger than their home range size. Rodents in disturbed systems may therefore need to be managed at much larger spatial scales than the resources to which they are attracted.

The mesopredator release phenomenon may be mediated by ecosystem productivity, where apex predators have fewer controls on community structure in areas with limited or patchy food resources, such as the xeric landscape of the sagebrush steppe (Elmhagen and Rushton 2007, Letnic and Dworjanyn 2011). Apex predators may actually move into developed areas while searching for food resources, drawn by the large numbers of rodent prey. Rodents may therefore be helping to regulate apex predator abundance from the bottom-up in this system, rather than the opposite (Holbrook et al. 2016). The extent to which top-down and bottom-up forces affect local trophic dynamics remains a seminal question in ecology (Elmhagen and Rushton 2007), particularly within the context of habitat alteration.

Our research contributes to understanding of how predator-prey interactions and resulting trophic dynamics can change as human disturbance alters the context in which species evolved. The mesopredator release phenomenon may not manifest in many fragmented landscapes where apex predators and mesopredators alike may be drawn to human activities (Krofel et al. 2017), as was the case in this study. Indeed, our research corroborates an emerging pattern of the mesopredator release being dampened or non-existent near human disturbance (Cove et al. 2012, Krofel et al. 2017). Given our results, apex predators living near energy development do not need to be controlled to protect declining songbird populations (sensu Dinkins et al. 2016)—rather, apex predators may actually be helping to regulate rodents on natural gas fields. Moreover, our elimination of the mesopredator release hypothesis is important for strong inference and clears a path for the assessment of alternate explanations for observed patterns in mesopredator density and altered species interactions with energy extraction (Sanders and Chalfoun 2018). Effective strategies for the mitigation of negative effects of human-induced habitat change on species of concern rely on such mechanistic understanding.

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LITERATURE CITED

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson. 2001. A mammalian predator-prey imbalance: Grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications 11:947–960.

Boarman, W. I., and B. Heinrich. 1999. Common raven (Corvus corax). In A. Poole and F. Gill, editors. The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

Brillhart, D. E., and D. W. Kaufman. 1995. Spatial and seasonal variation in prey use by coyotes in north-central Kansas. Southwestern Naturalist 40:160–166.

Brodie, J. F., A. J. Giordano, and L. Ambu. 2015. Differential responses of large mammals to logging and edge effects. Mammalian Biology 80:7–13.
Hipólito, D., M. Santos-Reis, and L. M. Rosalino. 2016. Effects of agro-forestry activities, cattle-raising practices and food-related factors in badger sett location and use in Portugal. Mammalian Biology 81:194–200.

Holbrook, J. D., R. S. Arkle, J. L. Rachlow, K. T. Vierling, D. S. Pilliod, and M. M. Wiest. 2016. Occupancy and abundance of predator and prey: implications of the fire-creatgrass cycle in sagebrush ecosystems. Ecography 7:e01307.

IEA (International Energy Agency). 2015. Energy and climate change. World Energy Outlook Special Report, Paris, France.

Jacob, J., and J. S. Brown. 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. Oikos 91:131–138.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. I. Riper. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611–634.

Knick, S. T., and J. T. Rotenberry. 2002. Effects of habitat fragmentation on passerine birds breeding in Intermountain shrubsteppe. Studies in Avian Biology 25:130–140.

Krofel, M., G. Giannatos, D. Cirovic, S. Stoyanov, and T. M. Newsome. 2017. Golden jackal expansion in Europe: A case of mesopredator release triggered by continent-wide wolf persecution? Hystrix, the Italian Journal of Mammalogy 28:9–15.

Laake, J. L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle, Washington, USA.

Laudet, F., and N. Selva. 2005. Ravens as small mammal bone accumulators: First taphonomic study on mammal remains in raven pellets. Palaeoecography, Palaeoclimatology, Palaeoecology 226:272–286.

Letnic, M., and S. A. Dworjanyn. 2011. Does a top predator reduce the predatory impact of an invasive mesopredator on an endangered rodent? Ecography 34:827–835.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Locker, S. M., G. Smith, and M. Ben-David. 2016. Space use and home-range overlap of least chipmunks in the Laramie Range. Final report: Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.

Mattos, K. J., and J. L. Orrock. 2010. Behavioral consequences of plant invasion: an invasive plant alters rodent antipredator behavior. Behavioral Ecology 21:556–561.

Mazerolle, M. J. 2019. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.2-1. https://cran.r-project.org/package=AICcmodavg

Mitchell, M. G. E., E. M. Bennett, and A. Gonzalez. 2013. Linking landscape connectivity and ecosystem service provision: current knowledge and research gaps. Ecosystems 16:894–908.

Murtaugh, P. A. 2007. Simplicity and complexity in ecological data analysis. Ecology 88:56–62.

Mutter, M., D. C. Pavlacky, N. J. Van Lanen, and R. Grenyer. 2015. Evaluating the impact of gas extraction infrastructure on the occupancy of sagebrush-obligate songbirds. Ecological Applications 25:1175–1186.

NOAA (National Oceanic and Atmospheric Administration). 2016. National Climatic Data Center. https://www.ncdc.noaa.gov/cdo-web/

Ordeñana, M. A., et al. 2010. Effects of urbanization on carnivore species distribution and richness. Journal of Mammalogy 91:1322–1331.

Orrock, J. L., and B. J. Danielson. 2004. Rodents balancing a variety of risks: invasive fire ants and indirect and direct indicators of predation risk. Oecologia 140:662–667.

Preston, C. R., and R. D. Beane. 2009. Red-tailed hawk (Buteo jamaicensis). In A. Poole and F. Gill, editors. The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ralph, C. J., S. Droege, and J. R. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications. Gen. Tech. Rep. PSW-GTR-149. USDA Forest Service, Albany, California, USA.

Ryall, K. L., and L. Fahrig. 2006. Response of predators to loss and fragmentation of prey habitat: a review of theory. Ecology 87:1086–1093.

Sanders, L. E., and A. D. Chalfoun. 2018. Novel landscape elements within natural gas fields increase densities but not fitness of an important songbird nest predator. Biological Conservation 228:132–141.

Sauer, J. R., D. K. Niven, J. E. Hines, K. L. Pardieck, J. E. Fallon, W. A. Link, and D. J. J. Ziolkowski. 2017. The North American breeding bird survey: results and analysis 1966–2015. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.
Sidorovich, V. E., I. I. Rotenko, and D. A. Krasko. 2011. Badger Meles meles spatial structure and diet in an area of low earthworm biomass and high predation risk. Annales Zoologici Fennici 48:1–16.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications 4:367–387.

Soulé, M., D. Bolger, A. Alberts, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2:75–92.

Sozio, G., and A. Mortelliti. 2016. Empirical evaluation of the strength of interspecific competition in shaping small mammal communities in fragmented landscapes. Landscape Ecology 31:775–789.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65–66.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

U.S. EIA (U.S. Energy Information Administration). 2015. Top 100 U.S. Oil and Gas Fields. Washington, D.C., USA.

U.S. Naval Observatory. 2014. Naval Oceanography Portal. www.usno.navy.mil

USDA Geospatial Data Gateway (U.S. Department of Agriculture). 2017 National Agricultural Imagery Program Mosaic. https://gdg.sc.egov.usda.gov/

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth Edition. Springer, New York, New York, USA.

Wang, Y., M. L. Allen, and C. C. Wilmers. 2015. Meso-predator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biological Conservation 190:23–33.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, California, USA.

Windberg, L. A., and F. F. Knowlton. 1988. Management implication of coyote spacing patterns in southern Texas. Journal of Wildlife Management 52:632–640.

WMO (World Meteorological Organization). 1970. The beaufort scale of wind force (technical and operational aspects). Reports on marine science affairs (MSA)- No. 03. Geneva, Switzerland.

Wood, B. A., L. Cao, and M. D. Dearing. 2010. Deer mouse (Peromyscus maniculatus) home-range size and fidelity in sage-steppe habitat. Western North American Naturalist 70:345–354.

Young, H. S., et al. 2015. Context-dependent effects of large-wildlife declines on small-mammal communities in central Kenya. Ecological Applications 25:348–360.

Zuur, A. F., and E. N. Ieno. 2016. A protocol for conducting and presenting results of regression-type analyses. Methods in Ecology and Evolution 7:636–645.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2738/full