Towards a mechanistic understanding of human-induced rapid environmental change: a case study linking energy development, nest predation and predators

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Summary

1. Demographic consequences of human-induced rapid environmental change (HIREC) have been widely documented for many populations. The mechanisms underlying such patterns, however, are rarely investigated and yet are critical to understand for effective conservation and management.

2. We investigated the mechanisms underlying reduced avian nest survival with intensification of natural gas development, an increasing source of human-induced rapid environmental change globally. We tested the hypothesis that energy development increased the local activity of important nest predator species, thereby elevating nest predation rates. During 2011–2012, we surveyed predators and monitored 668 nests of Brewer's sparrows *Spizella breweri* (BRSP), sagebrush sparrows *Artemisiospiza nevadensis* (SASPs) and sage thrashers *Oreoscoptes montanus* (SATHs) breeding at twelve sites spanning a gradient of habitat loss from energy development in western Wyoming, USA.

3. Nine species, representing four mammalian and three avian families, were video-recorded depredating eggs and nestlings. Important nest predator species differed across songbird species, despite similar nesting habitats. Approximately 75% of depredation events were by rodents.

4. Consistent with our predictions, detections of most rodent nest predators increased with surrounding habitat loss due to natural gas development, which was associated with increased probability of nest predation for our three focal bird species.

5. An altered nest predator assemblage was therefore at least partly responsible for elevated avian nest predation risk in areas with more surrounding energy development.

6. *Synthesis and applications.* We demonstrate one mechanism, that is the local augmentation of predators, by which human-induced rapid environmental change can influence the demography of local populations. Given the accelerating trajectory of global energy demands, an important next step will be to understand why the activity and/or abundance of rodent predators increased with surrounding habitat loss from energy development activities.

Key-words: anthropogenic disturbance, birds, energy development, habitat loss, nest predation, predator–prey, sagebrush steppe, species interactions

Introduction

Addressing the impacts of habitat loss, fragmentation and alteration is a salient feature of conservation ecology, as human-induced modifications remain the greatest threat to global biodiversity (Tilman *et al*. 1994; Pimm & Raven 2000). While there has been significant progress in describing patterns of species' responses to human-induced rapid environmental change (HIREC; Sih, Ferrari & Harris 2011) over the last 30 years, few analyses

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explicitly test hypotheses regarding the mechanisms generating such patterns (Wu & Hobbs 2002; Lindenmayer & Fischer 2007; Tscharntke *et al.* 2012). Given the accelerating trajectory of land-use change forecasts (Sala *et al.* 2000; McLaughlin 2011), researchers will increasingly be tasked with evaluating the ways in which HIREC can impact species within a host of landscape contexts.

A growing source of HIREC globally is the result of energy extraction activities. World energy production has nearly doubled since 1980 and is forecast to increase an additional 40% in the next 20 years (Northrup & Wittemyer 2013; United States Energy Information Administration 2013). With the advancement of new energy technologies, a steady expansion of unconventional oil and gas (e.g. oil sands, tight gas, shale gas and coalbed methane) extraction has progressed throughout North America (Kerr 2010). As a consequence, a variety of habitats have been reduced and fragmented by the road networks, pipelines, drill pads, waste pits and other components associated with energy extraction. Unconventional oil and gas reserves exist, in largely unknown quantities, on every continent and are poised to become a major global energy sector (World Energy Council 2010). Thus, understanding how expanding energy activities can impact populations and systems will be a key challenge.

Broadly, the majority of research on energy impacts to wildlife has documented negative effects via direct habitat loss, fragmentation of remaining habitats, behavioural avoidance and aiding further disturbance via increased public access (reviewed in Northrup & Wittemyer 2013). The initial surge of research on the potential impacts of oil and gas development to wildlife was generally focused on game species (large mammals, ungulates and gamebirds) of western North America. Recently however, increased attention has been given to a growing list of non-game species (Northrup & Wittemyer 2013).

Since 2008, we have studied sagebrush-obligate songbirds breeding in energy field landscapes of western Wyoming, USA. In Wyoming, petroleum resources overlap approximately 70% of the state's sagebrush steppe habitat (Northrup & Wittemyer 2013). Moreover, oil and natural gas resources co-occur with approximately one-third of North America's sagebrush steppe (Northrup & Wittemyer 2013); a conservation concern given that more than half of the original range-wide extent of sagebrush steppe has already been converted to other land types with concomitant population declines (Knick *et al.* 2003). Our prior work in this system has documented declines in abundance for two breeding sagebrush-obligate songbirds, BRSP and SASPs *Artemisiospiza nevadensis*, with increased intensification of energy development (Gilbert & Chalfoun 2011). In addition, we identified reduced nest survival (i.e. nest predation) as a possible mechanism for observed declines in abundance of these species, as well as SATHs *Oreoscoptes montanus* (Hethcoat & Chalfoun 2015a).

Songbird eggs and nestlings are typically susceptible to a remarkable suite of potential nest predators (Ribic, Thompson & Piets 2012). Predation is the principal cause of passerine nest failure and is therefore a key factor for reproductive success and population viability (Ricklefs 1969; Martin 1995). Nest predation risk can be influenced by a variety of factors including nest site selection, the availability of suitable nest sites, the local predator assemblage and the availability of alternative prey for important predators. Thus, habitat change can influence nest predation risk via a number of non-mutually exclusive pathways. From a conservation and management perspective, understanding the mechanisms by which predation risk can be altered within the context of anthropogenic disturbance is essential for targeted mitigation because a species' ability to assess and respond to shifting fitness consequences may lag behind the rate of change occurring within a landscape (Schlaepfer, Runge & Sherman 2002).

In this study, we examined why nest predation increased with intensification of energy development. Specifically, we tested the hypothesis that energy extraction activities may elevate local nest predation risk by increasing the prevalence of at least some important nest predator species. We studied breeding songbirds and nest predators along a gradient of habitat loss associated with natural gas extraction. To demonstrate support for the predator activity hypothesis, three lines of evidence were required. First, we identified what species were important nest predators, a rare component of most nest survival studies (Ribic, Thompson & Piets 2012). Secondly, we tested the prediction that nest predator activity was higher in areas with greater amounts of surrounding habitat loss from energy development. Finally, we evaluated the assumption that increased predator activity resulted in decreased local nest survival rates.

Materials and methods

STUDY AREA

Our study took place within sagebrush (*Artemisia* spp.) habitats overlapping energy development activities in the Upper Green River basin of Sublette County, Wyoming, USA. The Jonah-Pinedale Anticline Development area consists of two large natural gas fields, the Pinedale Anticline Project Area (PAPA) and the Jonah Field (hereafter Jonah), which rank among the highest concentrated and most productive energy fields in the country (United States Energy Information Administration 2013). Our two study sites, PAPA and Jonah, each contained six 25-ha study plots separated by ≥2 km. Study plots spanned a gradient of surrounding habitat loss from energy activities. As part of a complementary study, we calculated habitat loss within a 1-km^2 area centred over each study plot using National Agriculture Imagery Program imagery files (Hethcoat & Chalfoun 2015a). To ensure the presence of nesting birds, study plots were required to meet the following habitat criteria: (i) minimum average shrub cover of approximately 20% and (ii) average shrub height of 35 cm or greater (Wiens, Rotenberry & Van Horne 1987; Chalfoun & Mar-

tin 2007). Study plots showed no systematic declines in either average shrub height ($\beta = -0.038 \pm 0.035$ SE, $P = 0.28$) or density of sagebrush shrubs ($\beta = -0.11 \pm 0.14$ SE, $P = 0.41$) with increased surrounding habitat loss. Plot level shrub cover showed a trivial decline with increased habitat loss ($\beta = -0.078 \pm 0.028$ SE, $P = 0.006$). The effect size translated to a difference in shrub cover of 2.8% between plots with the most and least surrounding habitat loss (Figs. S1 and S2, Supporting Information). We consider this to be a statistical effect of the large number of vegetation samples involved (nearly 600 points) and not of biological significance (Appendix S1).

NEST SEARCHING AND MONITORING

Nest searching efforts were focused on the three sagebrush-obligate songbird species; Brewer's sparrow (BRSP hereafter), sagebrush sparrow (SASP) and sage thrasher (SATH) during May–August, 2011 and 2012. Nests were located using behavioural observations of adults and systematic searches. We monitored active nests every 2–3 days until failure or success (Martin *et al.* 1997). Nest success was confirmed by the presence of fledglings, scolding adults carrying food or the sounds of begging calls from fledglings. A nest was considered successful if at least one nestling fledged.

PREDATOR IDENTIFICATION

We identified nest predators at a subset of nests using custom-built 24-h infrared video monitoring systems. Systems included an infrared (950 nanometres, and thus invisible to vertebrates) bullet camera for filming in darkness, a digital video recording (DVR) unit which transferred video images to an SD card and a battery supply in a weatherproof case. Cameras were set up shortly after the onset of incubation, and nests in earlier stages of development were prioritized when moving a camera after a predation event. Nest cameras were highly camouflaged, deployed in small numbers (1–2 cameras per study plot) and widely dispersed to minimize potential biases in nest survival (Richardson, Gardali & Jenkins 2009). We deployed nest cameras exclusively on BRSP and SATH nests, which represented opposite ends of the body size spectrum (approximately 11 and 40 g, respectively) for our focal species. We assumed that the main nest predators of the intermediate-sized SASP would overlap those of the BRSP and SATH. Separately for each species, we tested if camera presence influenced nest survival by comparing survival estimates for all nests with and without cameras.

PREDATOR ACTIVITY

We assessed nest predator activity at each study plot using techniques specific to predator taxa and their respective activity period. The following indices were generated based upon number of detections and therefore better represented relative activity rather than actual densities of predators across study plots. Moreover, because study plots showed no strong systematic declines in vegetation characteristics (shrub height, shrub density and shrub cover), we assumed no differences in the detection probability of potential predators among study plots (Appendix S1).

We used systematic searches (adapted from Rodewald, Kearns & Shustack 2011) to sample diurnally active small mammal nest predators (e.g. chipmunks and ground squirrels) at weekly intervals from May through July. An observer searched one-quarter of a study plot over a 30-min period, covering 1.5 km. Using a GPS with reference points as a guide, surveyors systematically traversed a plot quadrant, switching back at approximately 50-m intervals, while taking care to not double-count predators. Surveys were randomly assigned to a plot quadrant and time between 06.00 and 11.00 h. We grouped predators detected as chipmunks *Tamias minimus* or ground squirrels (*Ictidomys tridecemlineatus* and *Urocitellus armatus*).

We used scent stations with camera traps to assess the relative activity of diurnal and nocturnal mesocarnivores (e.g. *Canis latrans*, *Taxidea taxus* and *Vulpes vulpes*). Plots were sampled biweekly from May through July. Two camera trap units (Bushnell Trophy Cam®, Overland Park, KS, USA) were placed outside each study plot and run for a 72-h period during each sampling period. Stations were baited with a fatty-acid tablet from USDA Pocatello and a tongue depressor that had been soaked in cod-liver oil. Scent stations were located 250 m from the plot edge to minimize luring predators onto study plots and potentially biasing nest predation rates. The location of one camera unit was randomly selected, and the second camera unit was positioned outside the opposite edge of the plot (along a relative bearing of 180°). Scent stations on a plot were approximately 1 km apart (mean = 1132.4 m, $n = 104$ pairs) and were treated as independent sample units. Each species was recorded only once per 24-h period regardless of the number of photos, unless more than one individual was observed in the frame, to ensure we were not double-counting individuals. These data thus represented the relative activity of mesocarnivores around a study plot and were assumed to be representative of the plot itself, as their home ranges would easily overlap with the study plot.

In 2012, we added a series of streamlined trapping sessions to assess the relative activity of nocturnal small mammals (e.g. *Peromyscus maniculatus*) across our study sites after video recordings revealed mice depredating several nests in 2011. Live-trapping grids were randomly placed adjacent to study plots, at a distance of 50 m, so as not to hold nest predators overnight and potentially bias nest survival estimates. We assumed data from our randomly placed trapping grid were representative of the activity of nocturnal small mammals on adjacent study plots. Grids consisted of a 7×7 arrangement of Havahart® (model 1020, Lititz, PA, USA) traps ($n = 49$) with 10-m spacing. Traps were baited with peanut butter and rolled oats and contained polyester bedding material for thermoregulation. Traps were opened at dusk and checked for captures the following morning. During a trapping session, each grid was sampled for a single night. Three grids were trapped simultaneously, and all grids ($n = 12$) were randomly sampled within four nights to reduce temporal effects within a trapping session. Grids were sampled three times throughout the season, at approximately 6-week intervals (early-May, mid-June and late-July), to account for temporal fluctuations. Traps that were sprung but empty were recorded and counted as 0.5 trap nights to adjust for trapping effort (Beauvais & Buskirk 1999). We identified each capture to species and, after adjusting for trapping effort, calculated the number of individuals captured per 100 trap nights as our index of activity. We only considered mouse (*P. maniculatus* and *Reithrodontomys megalotis*) captures in our analyses (84.3% of captures) because nocturnal trapping sessions could not accurately assess the activity of diurnal small mammals (e.g. *I. tridecemlineatus* and *T. minimus*).

DATA ANALYSES

All analyses were done in Program R (R Core Team 2014), and all estimates of effect are means ± 1 SE. We tested for a relationship between predator activity and surrounding habitat loss, separately for each predator group (chipmunks, ground squirrels and mesocarnivores), using a generalized estimating equation (i.e. a marginal model with a Poisson distribution) with the geepack package (Højsgaard, Halekoh & Yan 2006). Study plot was used as a grouping variable to acknowledge potential correlations (auto-regressive) in predators detected on a study plot between survey events. Additional explanatory variables included site (PAPA vs. Jonah), year and possible interactions. In our analysis of nocturnal small mammals, we pooled captures per 100 trap nights for the two mouse species within a trapping session (early, mid and late season) to generate a single metric per trapping occasion of total mouse captures. Model structure was the same as other predator models noted above, except a Gaussian distribution was used. Wald chi-squared was used to determine the significance of predictors and model coefficients.

We used the logistic exposure model (Shaffer 2004) to estimate nest survival. The logistic exposure method utilizes a modified link function that is adjusted for the length of exposure for each nest. This method accounts for the potential bias of nests being found at varying stages of development by calculating survival as a daily rate. Separately for each species, we calculated a daily nest survival rate for each study plot in each year (Table S1). For ease of interpretation, in some cases we converted the daily nest survival rate to an overall nest survival percentage. Overall, nest survival was calculated by raising the daily rate to the exponent of the average nest cycle length. Nest cycle lengths were 23 (mean = 23·1, n = 346), 25 (mean = 24·9, n = 100) and 29 (mean = 28·6, n = 111) days for BRSPs, SASPs and SATH, respectively.

We tested the relationship between songbird nest survival and the activity of predators using a separate generalized estimating equation (i.e. a marginal model with a Gaussian distribution) for each songbird species utilizing the geepack package (Højsgaard, Halekoh & Yan 2006). First, we created annual indices of predator activity by dividing the total number of detections within a season by the number of surveys conducted for each group. Thus, each study plot in each year had a unique index of predator activity for each predator type. We then used the daily nest survival rate on a study plot in a given year as the response and our annual indices of predator activities as predictors (Table S2). Study plot was used as a grouping variable to acknowledge potential correlations in nest survival rates on a plot across years. We initially fit a global model with additive and interactive combinations of predators and then removed insignificant predictors in successive steps using the ANOVA command to settle on a final model (Zuur *et al.* 2009). Wald chi-squared was used to determine the significance of predictors and model coefficients.

Results

NEST SEARCHING AND MONITORING

We monitored 668 nests of our three focal species during 2011–2012. Thirty-seven nests (5·5%) were excluded from analyses due to failure from researcher activities (abandonment), insufficient information to determine fate or inviable eggs. In total, 361 BRSP, 121 SASP and 149 SATH nests were used in calculating nest survival estimates (Table S1).

PREDATOR IDENTIFICATION

We deployed video cameras at 144 nests during 2011–2012. We excluded 17 nests from survival analyses because of abandonment by adults or nest failure for reasons other than predation (e.g. eggs failed to hatch; n = 10 BRSP and 7 SATH). We identified nest predators from 31 predation events and confirmed nine species depredating eggs and nestlings (Table 1). Rodents were the majority of predators for both species, composing 89% of predation events at BRSP nests and 54% at SATH nests. Nests with and without camera units had similar rates of survival for BRSP (t = 1·67, d.f. = 1026, P = 0·10), while SATH nests with camera units were more likely to fledge (t = 3·48, d.f. = 2051, P = 0·001; Fig. 1).

PREDATOR ACTIVITY

We conducted 84 diurnal predator surveys in 2011 and 88 in 2012. Chipmunk detections decreased slightly with increased habitat loss within 1 km^2 (β = −0·0196 ± 0·013; Wald χ = 2·42, d.f. = 170, P = 0·12). On average, chipmunk detections halved across the gradient of habitat loss (Fig. 2a). Conversely, ground squirrel detections increased significantly with surrounding habitat loss (β = −0·024 ± 0·80; Wald χ = 9·40, d.f. = 169, P = 0·002). On average, ground squirrel detections more than doubled across the habitat loss gradient (Fig. 2b). The additive effect of site

Table 1. Species confirmed depredating Brewer's sparrow *Spizella breweri* (BRSP) and sage thrasher *Oreoscoptes montanus* (SATH) nests in natural gas field landscapes within Sublette County, Wyoming, USA, 2011–2012. The number of predation events documented for each predator species is represented by *n*. In total, 82 BRSP and 62 SATH nests were video-monitored

|	n	
Nest predator	BRSP	SATH
Deer mouse *Peromyscus maniculatus*	3	3
Unknown mouse – *P. maniculatus* or *Reithrodontomys megalotis*	1	1
Least chipmunk *Tamias minimus*	7	0
Thirteen-lined ground squirrel *Ictidomys tridecemlineatus*	1	1
Unknown sciurid – *T. minimus* or *I. tridecemlineatus*	2	2
Uinta ground squirrel *Urocitellus armatus*	2	0
Raccoon *Procyon lotor*	0	1
American badger *Taxidea taxus*	0	3
Loggerhead shrike *Lanius ludovicianus*	2	0
American kestrel *Falco sparverius*	0	1
Short-eared owl *Asio flammeus*	0	1
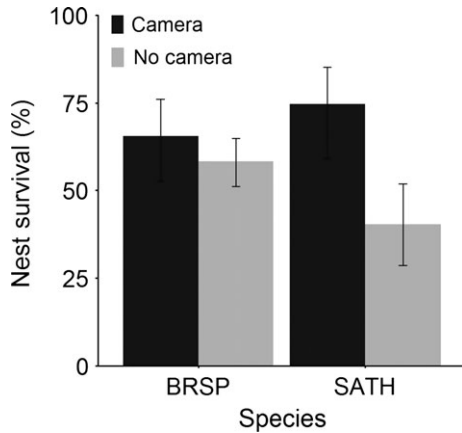
Fig. 1. Nest survival of Brewer's sparrow *Spizella breweri* (BRSP) and sage thrasher *Oreoscoptes montanus* (SATH) nests with (black bars) and without (grey bars) 24-h infrared video camera units at twelve study locations in 2011 and 2012 in western Wyoming, USA. Error bars represent 95% confidence intervals.
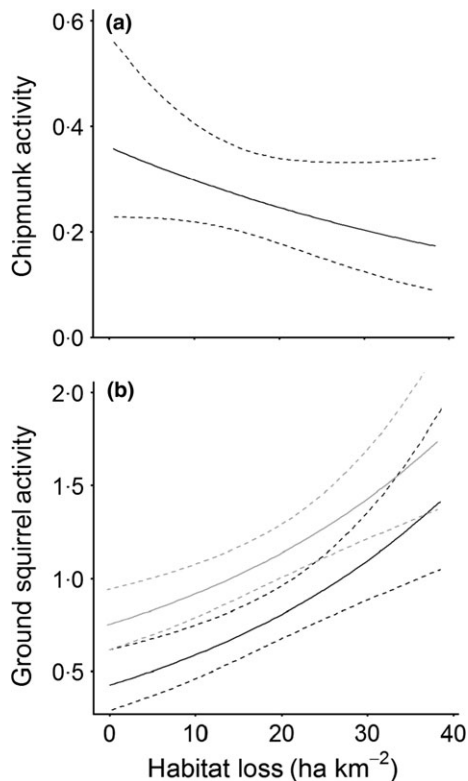
Fig. 2. Poisson regression modelling the effect of habitat loss on the activity (number of detections per survey) of (a) chipmunks *Tamias minimus* and (b) ground squirrels (*Urocitellus armatus* and *Ictidomys tridecemlineatus*) at twelve study locations in 2011 and 2012 in western Wyoming, USA. Ground squirrel estimates from the Pinedale Anticline Project Area (PAPA) are in grey and estimates from the Jonah Field (Jonah) are shown in black. Study plots spanned an existing gradient of habitat loss from energy extraction activities. Dashed lines represent 95% confidence intervals.

was also significant ($\beta = -1.144 \pm 0.26$; Wald $\chi = 18.66$, d.f. = 169, $P < 0.001$), with higher ground squirrel detections in PAPA.
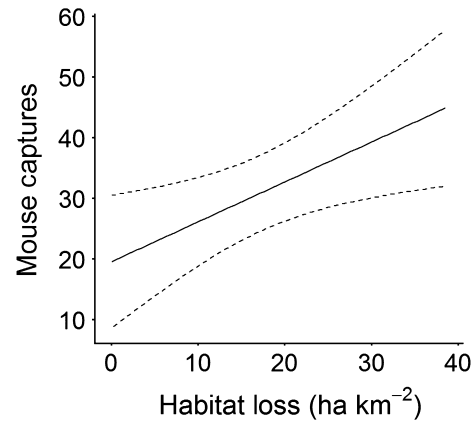
Fig. 3. Mouse (*Peromyscus maniculatus* and *Reithrodontomys megalotis*) captures per 100 trap nights from twelve study locations in 2012 in western Wyoming, USA. Study plots spanned an existing gradient of habitat loss from energy extraction activities. Dashed lines represent 95% confidence intervals.

We deployed 208 scent stations and recorded 36 visitations of mesocarnivores (*n* = 17 *C. latrans* and 19 *T. taxus*) during the 2 years. There was no relationship between mesocarnivore activity and surrounding habitat loss ($\beta = -0.0089 \pm 0.016$; Wald $\chi = 0.31$, d.f. = 206, $P = 0.58$).

Mouse captures increased with increased habitat loss within 1 km^2 ($\beta = 0.657 \pm 0.23$; Wald $\chi = 7.94$, d.f. = 34, $P = 0.005$). On average, mouse captures were twice as high in areas with the most surrounding habitat loss relative to areas with little habitat loss from energy activities (Fig. 3).

NEST SURVIVAL AND PREDATOR ACTIVITY

Daily nest survival for BRSP decreased with chipmunk activity ($\beta = -0.033 \pm 0.012$, Wald $\chi = 7.63$, d.f. = 22, $P = 0.006$). The probability of overall nest survival decreased 4.3% (95% CI = −6.8 to −1.9) with every 0.1 unit increase in the index of chipmunk activity (Fig. 4).

Daily nest survival for SASP decreased with ground squirrel activity ($\beta = -0.021 \pm 0.0062$, Wald $\chi = 11.2$, d.f. = 21, $P < 0.001$). The probability of overall nest survival decreased 2.2% (95% CI = −3.5 to −0.9) with every 0.1 unit increase in the index of ground squirrel activity (Fig. 4).

Daily nest survival for SATH decreased marginally with ground squirrel activity ($\beta = -0.0085 \pm 0.0047$, Wald $\chi = 3.33$, d.f. = 22, $P = 0.068$). The probability of overall nest survival decreased 1.3% (95% CI = −2.8 to 0.2) with every 0.1 unit increase in the index of ground squirrel activity (Fig. 4).

Discussion

Human alteration of habitats has the potential to influence important ecological processes, such as predator–prey relationships, and negatively affect fitness (Tylianakis
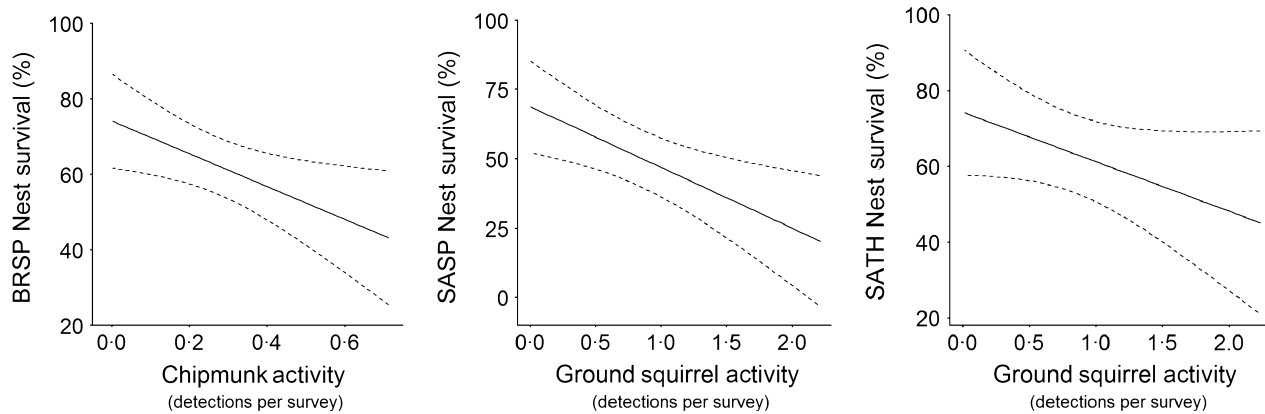
Fig. 4. Brewer's sparrow *Spizella breweri* (BRSP), sagebrush sparrow *Artemisiospiza nevadensis* (SASP) and sage thrasher *Oreoscoptes montanus* (SATH) nest survival in relation to predator activity at twelve study locations in 2011 and 2012 in western Wyoming, USA. Dashed lines represent 95% confidence intervals.

et al. 2008). Meanwhile, expanding unconventional energy infrastructure is expected to remain a major land-use driver in North America, with an estimated 200 000 km^2 of new land expected to be developed by 2035 (McDonald *et al.* 2009; Northrup & Wittemyer 2013). Understanding the mechanisms underlying concomitant effects on predator–prey dynamics involving sensitive species will therefore be critical for successful conservation efforts. We tested, and found support for, the hypothesis that increased predator activity was one mechanism underlying previously documented declines in sagebrush songbird nest survival (Hethcoat & Chalfoun 2015a), and therefore, possibly decreased songbird abundance (Gilbert & Chalfoun 2011). Rodents were the main predators captured on video depredating nests, and the activity of most rodent species increased with habitat loss caused by energy development. Higher nest predator activity was also inversely related to nest survival of our focal species (BRSP, SASP and SATH).

Determining the identity of important nest predators has been rare yet is critical for the development and testing of alternative hypotheses for nest predation patterns (Benson, Brown & Bednarz 2010; Ribic, Thompson & Piets 2012). A wide variety of species can depredate nests (Rodewald, Kearns & Shustack 2011; Ribic, Thompson & Piets 2012), and the identity of predators has historically often been assumed and/or based on the nature of nest remains, which can be inaccurate and misleading (Larivière 1999). One species that we did not observe depredating any nests, to our surprise, was the common raven *Corvus corax*. Ravens have been implicated (with video evidence) as an important predator on greater sage-grouse *Centrocercus urophasianus* nests within the same habitat type (Coates, Connelly & Delehanty 2008; Coates & Delehanty 2010). While ravens may account for some proportion of nest failures in our study system, we are confident that our lack of documented predations is an accurate reflection of the relative risk this species poses to the songbirds we studied. Approximately one-quarter of nests with a camera unit were depredated during our study. This number is within the range (approximately 20–50%) documented from other camera studies (Ribic, Thompson & Piets 2012). Video-monitored SATH nests were significantly more likely to successfully fledge. A number of other studies have found survival rates to be higher for nests with camera units (reviewed in Richardson, Gardali & Jenkins 2009). Thus, we cannot rule out the possibility that some facet of the predator community avoided cameras and biased our understanding of important predators for SATH.

Peromyscus mice, despite their small size, were one of the most important predators we captured on camera, even taking 5- to 6-day-old nestlings. The preceding decade has brought an increased understanding of the role rodents can play as nest predators, thanks in large part to the growing use and affordability of camera systems that document predation events (Ribic, Thompson & Piets 2012). As such, there is increasing recognition that *Peromyscus* mice can be important predators on passerine eggs and nestlings (Thompson, Dijak & Burhans 1999; Drever *et al.* 2000; Thompson & Burhans 2003, 2004; Cox, Thompson & Faaborg 2012). However, we also documented two occasions (one per focal species) where a mouse made repeated attacks on the adult defending nest contents. Neither incident recorded the mortality of the adult within the camera's field of view; however, both occasions clearly show a level of aggression not often ascribed to *Peromyscus* spp.

Rodent taxa did not respond uniformly to habitat loss from energy development activities. Chipmunk activity decreased with increased surrounding habitat loss, whereas both ground squirrel and mouse (in 2012) activity increased. Predator assemblages often show complex and species-specific responses to anthropogenic habitat alteration (Robinson *et al.* 1992; Andren 1994; Diffendorfer, Gaines & Holt 1995; Chalfoun, Thompson & Ratnaswamy 2002; Tewksbury *et al.* 2006). These findings highlight the potential risk in pooling predator species when seeking a mechanistic understanding of predation

patterns. Researchers frequently group species into predator guilds, such as mesopredators, raptors or rodents (e.g. Rodewald, Kearns & Shustack 2011; Cox, Thompson & Faaborg 2012). Such decisions are often driven by sample size and statistical power considerations. However, pooling species has the potential to mask meaningful variation, and our study suggests carefully considering how predator taxa are grouped for analyses. Cox, Thompson & Faaborg (2012), for example, pooled predations by *Peromyscus* and flying squirrels *Glaucomys volans* into a rodent group. The authors acknowledged that these species showed different responses to important predictors of nest survival and thus may have contributed to the unexpected patterns in nest survival they observed. An important caveat worth noting, however, is that our predator activity data are not distance based (i.e. adjusted for detection probability) and do not reflect true densities. Nevertheless, patterns reported here are preliminarily consistent with ongoing work in this study system wherein formal mark–recapture analyses are underway (Chalfoun, A.D., Johnson, T.N. & Sanders, L.E., unpublished data).

We found a correlation between the activity of nest predators and nest survival rates, though the importance of a particular predator and strength of effects were unique, for each of our focal species. For example, nest survival for BRSP was negatively associated with chipmunk activity, whereas nest survival for SASP and SATH was negatively associated with ground squirrel activity. These songbirds utilize many of the same habitat features, often have overlapping territories, and yet, nest survival responded uniquely to the activity of particular predators. These results suggest that disentangling the mechanisms for variation in nest survival both across landscapes and among species requires careful study of the interactions between specific prey species, their predators and important habitat attributes.

Since 2008, nest survival for BRSP has shown significant annual variation in response to habitat loss (Hethcoat & Chalfoun 2015a). Given our results here, which rodents accounted for 89% of predations and their activity affected survival, BRSP nest survival may be tied to annual variation in the abundance or activity of rodent nest predators. In contrast, nest survival for SATH was only marginally associated with predator activity. During 4 years of study, nest survival for SATH has shown the sharpest and most consistent declines with increased habitat loss from energy development (Hethcoat & Chalfoun 2015a). We therefore expected steep declines in nest survival with increased activity of predators. However, SATH nests were depredated by a broader suite of species (Table 1), which may have dampened relationships with individual predator species or groups. Additional factors beyond the activity of predators alone, such as microhabitat features at nest sites, may be also important for SATH nest survival.

The interactions between predators and prey are likely to continue to be altered with the expansion of human-modified landscapes. An important next step is to investigate why the activity and/or abundance of rodent species increased with surrounding habitat loss from energy extraction, so that management practices may be implemented that discourage the local accumulation of rodent nest predators. The mesopredator-release hypothesis (Crooks & Soulé 1999) suggests that the abundance or activity of species that are themselves predators on rodents (e.g. *C. latrans*, *T. taxus*, *V. vulpes* and/or raptors) may decrease across the same gradient of habitat loss from energy development. Our scent station data preliminarily suggest that mammalian mesocarnivore species were relatively rare within the study area. Alternatively, differences in rodent activity or abundance may be the result of the concentrating of individuals in remaining habitat patches and/or food subsidies from reclaimed areas.

Given the accelerating trajectory of global energy demands, understanding how processes with clear fitness consequences, such as predation, are altered by HIREC from energy development will be essential for ecologists tasked with conservation and management of co-occurring wildlife populations. Predation plays a pivotal role in community organization and maintenance, both as an important evolutionary force and as the driver of energy through food webs (Lindeman 1942; Hairston, Smith & Slobodkin 1960; Paine 1966; Sih *et al.* 1985; Fretwell 1987). Taken together, our results demonstrate the importance of simultaneous study of habitat change, predators and prey for understanding the mechanisms by which evolved predator–prey relationships can be affected by HIREC.

Acknowledgements

Data accessibility

Data available from the Dryad Digital Repository: doi:10.5061/dryad.97d13 (Hethcoat & Chalfoun 2015b).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Daily nest survival rates at each study plot in each year for each species.

Table S2. Annual indices of predator activity at each study plot.

Appendix S1. Methods associated with vegetation sampling at study plots and nest sites.