



Novel landscape elements within natural gas fields increase densities but not fitness of an important songbird nest predator

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ABSTRACT

Identifying the elements within human-altered landscapes most associated with population and community changes is critical for conservation and management of sensitive species. We investigated which features of habitat change from natural gas development best explained the density of deer mice (*Peromyscus maniculatus*), an important nest predator of declining sagebrush-obligate songbirds. During 2014–2016, we quantified the spatial extent of habitat change (well pads, roads, and reclaimed areas [i.e., reseeded soils]) surrounding 12 sites spanning two natural gas fields in Wyoming, USA. We further tested whether the altered plant communities within reclaimed areas provided benefits to deer mice, by assessing multiple fitness indices. Deer mouse density increased with surrounding reclaimed area. Powder tracking and dietary analyses confirmed that mice moved through and consumed plant species found exclusively within reclaimed areas. Concomitant fitness metrics of mice, however, were neutrally or negatively related to the amount of surrounding reclaimed area. Mice therefore did not derive any apparent fitness benefits associated with living near reclaimed areas, despite the presence of novel food resources, indicating that increased abundance may be a product of mice dispersing toward reseeded soils. Our study contributes mechanistic insights into the complexities of how human-induced changes to landscapes can influence community dynamics. Minimizing total habitat disturbed during construction, expediting reclamation practices, and using only native and regionally-local seed mixes would likely help minimize increases in synanthropic rodent predators within energy fields. More efficient restoration of disturbed habitat, moreover, may help ameliorate altered predator-prey relationships that affect the success of sensitive species.

1. Introduction

Landscape composition can affect species distributions (Mortelliti and Boitani, 2008), inter-specific interactions (Baggio et al., 2011), and trophic dynamics (Liao et al., 2017). Understanding such relationships has become particularly urgent, given the rapid pace and large scale at which humans are altering habitat structure and availability (Sih, 2013). Habitat loss, fragmentation, and degradation can affect co-occurring organisms via changes in resource availability (Anteau et al., 2011), barriers to movement (McGregor et al., 2003), and altered predation risk (Baggio et al., 2011). Identifying the particular elements within human-altered landscapes most associated with shifts in resource availability and species interactions, particularly those affecting vulnerable species, is critical for a mechanistic understanding of wildlife responses to human disturbance and effective mitigation (Lindenmayer and Fischer, 2007).

One way in which habitat change can affect community composition and dynamics is by altering the availability, quality, and distribution of food resources. Food can limit the population growth and distribution of consumers (Richardson, 1991). Augmented food resources can increase the suitability of habitat, especially for dietary generalists within fragmented systems (Mortelliti and Boitani, 2008). Increased heterogeneity of food resources within human-altered landscapes may benefit synanthropic species by introducing new resources and changing existing resource distribution. Human-associated food subsidies are provided by, among other sources, agricultural fields (Anteau et al., 2011), garbage (Kirby et al., 2016), and reclamation activities (Monroe and Ritchison, 2005). When a high-quality food supply becomes readily available in a relatively nutrient-poor system, populations that exploit those resources can increase dramatically via immigration and/or higher individual fitness and reproductive capacity (Marcello et al., 2008). Common ravens (*Corvus corax*) receiving food

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subsidies near human development (e.g., from landfills), for example, can increase in territory occupancy and density, with negative implications for sensitive prey species (such as the Greater sage-grouse, *Centrocercus urophasianus*; Bui et al., 2010). Generalist omnivores, such as rodents, are often the first species to take advantage of human-provided food resources (Shaner and Macko, 2011), and local abundances can subsequently increase rapidly given their short generation times (Pearson and Fletcher, 2008). Such effects may subsequently influence other trophic levels (Spiller et al., 2010).

Oil and natural gas extraction is one form of human land use that can lead to extensive habitat alteration. Natural gas is a large and still growing form of energy production worldwide, making understanding of its ecological effects critical. Over 5.2 million ha of federal lands in the U.S. alone produced natural gas in 2015 (Humphries, 2016), with production projected to continue expanding (International Energy Agency, 2015). Habitat loss, fragmentation and degradation within natural gas fields result from land conversion to well pads, roads, and reclaimed areas (reseeded soils around well pads, roadsides, and pipelines), leading to fragments of intact habitat contained within a matrix of development (Bender et al., 1998; Liao et al., 2017). Very little is known, however, about how energy fields influence food resources, population densities, and concomitant species interactions.

Oil and natural gas development in western North America has altered large swaths of habitat where the sagebrush steppe and natural resource reserves overlap (Braun et al., 2002). Sagebrush-obligate songbirds, including the Brewer's sparrow (*Spizella breweri*), sagebrush sparrow (*Artemisiospiza nevadensis*), and sage thrasher (*Oreoscoptes montanus*), rely on sagebrush (*Artemisia* spp.) and associated shrubs for nesting, and have experienced population declines across their range (Sauer et al., 2017). Landscape changes from natural gas development in Wyoming, USA, can result in decreased densities and increased nest predation of sagebrush songbirds (Ingelfinger and Anderson, 2004; Gilbert and Chalfoun, 2011; Hethcoat and Chalfoun, 2015a). Rodents were responsible for over three quarters of nest depredations in one study (Hethcoat and Chalfoun, 2015b). Deer mice (*Peromyscus maniculatus*), the smallest predator (15–25 g) and a dietary generalist, accounted for over 40% of observed nest losses (Hethcoat and Chalfoun, 2015b; A.D. Chalfoun, unpublished data), even killing older nestlings of the largest songbird (sage thrasher). In the same study, nest survival of all three sagebrush songbirds decreased with rodent density (Hethcoat and Chalfoun, 2015b). Deer mouse densities also increased with sagebrush habitat loss caused by natural gas development (Sanders and Chalfoun, in review). A critical next step is to identify the specific component(s) of landscape change within natural gas fields associated with increased nest predator abundance and subsequent decreases in songbird nest survival, and the possible mechanisms.

We first assessed which component of landscape alteration within natural gas fields (reclaimed areas, well pads, roads, or open areas) was most associated with higher deer mouse densities. Each landscape component represented one plausible hypothesis to explain deer mouse abundance. Re-seeded (i.e., reclaimed) areas, for example, may provide food subsidies for mice. Small structures on well pads could provide covered refuges from predators and the elements. Mice may avoid crossing roads due to traffic and noise, leading to increased local abundance associated with barriers to dispersal (Ascensão et al., 2017). Lastly, the open areas on roads and well pads could elevate actual and/or perceived predation risk due to insufficient cover (Hinkelman et al., 2012), leading to increased mouse densities in remaining habitat patches. We predicted that the amount of surrounding reclaimed area would best explain observed variation in mouse density. Reclaimed areas often contain different plant species and higher herbaceous cover (which could be consumed by generalist predators) than adjacent native habitat (Parmenter and MacMahon, 1983) and could be augmenting rodent diets.

We further tested three critical assumptions of our food augmentation hypothesis (that reclaimed areas may be providing food subsidies

for deer mice). We examined whether (1) reclaimed areas contained higher cover of grasses and forbs than adjacent sagebrush understoreys, (2) deer mice entered and used habitat within reclaimed areas, and (3) deer mice consumed the plants within reclaimed areas. We reasoned that mice likely would not be attracted to reclaimed areas for increased refugia from predators, as reclaimed areas typically are largely devoid of a shrub layer and are therefore more open than adjacent sagebrush patches (Minnick and Alward, 2015). Nonetheless, we compared shrub and bare ground cover between reclaimed and sagebrush areas. Finally, we investigated whether deer mice living near reclaimed areas received any fitness benefits that could explain density patterns. Life history theory suggests, however, that many components of fitness can tradeoff with one another. For example, proximate allocation of food resources to mating and reproduction can result in decreased individual body condition (Tatar and Promislow, 1997) or survival (Roff, 1992) as increased reproductive output can mean fewer resources are available to sustain the adult individual. As such, we expected to see a relationship between amount of surrounding reclaimed area and some, but potentially not all relevant fitness outcomes. As the amount of surrounding reclaimed area increased, we specifically predicted:

1. Higher apparent survival of mice;
2. Mice in better body condition;
3. More reproductive adult mice; and/or
4. More immature mice per female (i.e., higher reproductive output).

2. Materials and methods

2.1. Study area

We conducted our research within the Jonah-Pinedale Development Area in Sublette County, Wyoming, USA (42°38'N, 109°45'W), an area which contained two of the most productive natural gas fields in the country (U.S. Energy Information Administration, 2015). The Pinedale Anticline Project Area (hereafter Pinedale Anticline) covered 252 km² of surface area with an average density of 13.4 wells/km² in 2016, while the Jonah Field covered 140 km² and averaged 17.2 wells/km² (Wyoming Oil and Gas Conservation Commission, 2016). The landscape was dominated by big sagebrush (*Artemisia tridentata*) habitat with an understorey of grasses and forbs (see Lyon and Anderson, 2003).

2.2. Trapping efforts

2.2.1. Small mammal trapping grids

We conducted our primary trapping efforts at six study plots per natural gas field (n = 12 plots), separated by 2–6 km. Study plots were originally established in 2008 and 2011 as part of a long-term study (Hethcoat and Chalfoun, 2015a). Study plots were randomly placed across four development strata within each gas field (see Hethcoat and Chalfoun, 2015a for details), to provide a gradient of habitat change from development across plots. Sagebrush cover and height showed no systematic variation across study plots (Hethcoat and Chalfoun, 2015a).

During 2014–2016 we established small mammal trapping grids (hereafter primary trapping grids) associated with each study plot to determine density and fitness estimates for the most important nest predator of sagebrush-obligate songbirds at our sites—deer mice (Hethcoat and Chalfoun, 2015b; Sanders and Chalfoun, in review). Primary trapping grids measured 60 × 60 m in 2014 (0.36 ha), and 150 × 150 m in 2015 and 2016 (2.25 ha). We increased grid size after 2014 to increase capture numbers. Each primary trapping grid contained 49 Sherman traps (LFA Folding Trap, H.B. Sherman Traps Inc., Tallahassee, FL, USA; 7 × 7 array) with 10-m spacing between traps in 2014, and 25-m spacing in 2015–2016. We moved primary trapping grids within each study plot 75–650 m between years to facilitate a concurrent study, and trapped one grid per plot each year. We trapped three grids spanning our development gradient simultaneously to

control for potential weather effects.

We used a robust trapping design (Williams et al., 2002), with two sampling periods per plot each year (May 22–June 25 and July 7–Aug 6) consisting of three trap nights and separated by approximately six weeks. We set traps after 1530 and checked for captures before 1030 the following morning. We baited all traps with a rolled oats and peanut butter mixture, with polyester batting as bedding material. Traps were covered with a plywood board to minimize direct sun exposure. All animal handling was approved by the Institutional Animal Care and Use Committee (permits #20140602 AC00107–03 and #20170517LS0071–01). We identified all captured animals to species, marked individuals with a 9-mm PIT tag (passive integrated transponder; Biomark Inc., Boise, ID, USA), collected demographic (age, gender, reproductive status) and morphometric measurements (mass, body length), and released animals at their capture location.

2.2.2. Diet sampling plots

We conducted additional trapping efforts at six separate study plots per gas field ($n = 12$; see Fig. A.1) during 2017 to assess the diets and movement patterns of mice with access to both sagebrush understory and reclaimed areas (hereafter diet sampling plots; used to assess critical assumptions 1–3 of the food augmentation hypothesis). Diet sampling plots consisted of a 25×190 -m grid (0.48 ha) in sagebrush habitat with the long side bordering an adjacent reclaimed area. We placed plots adjacent to reclaimed areas varying in their vegetative composition and age since initial reclamation (1–8 years). Specifically, at each natural gas field we placed 1–3 diet sampling plots (depending on availability) adjacent to reclaimed areas from each of three vegetative cover classes: tumbleweed dominant (i.e., > 10% ground cover of dead *Kali tragus*), sparse grass cover (< 50% ground cover) and heavy grass cover (> 50% ground cover; see Fig. A.2 for photos of reclaimed area vegetation). Cover class was determined during initial site visits. Plot edges were located at least 100 m away from any other reclamation activity, to reduce the likelihood that captured mice had access to multiple reclaimed areas. Diet sampling plots contained one line of 18 Sherman traps with 10-m spacing between traps and 5-m spacing from the edge of the adjacent reclaimed area. Traps were placed 5 m from habitat edges to ensure reclaimed areas fell within the potential home-range of all captured mice (home range radius = 11–43 m; Wood et al., 2010). Reclaimed area edges were identified by a distinct change in the vegetation community (primarily the lack of mature sagebrush shrubs) and available GIS layers (Pinedale Anticline Project Office, 2017; USGS, 2015). Trapping efforts at diet sampling plots lasted for 1–4 consecutive nights in June 2017, and trapping ceased at each plot once we had captured 5–10 unique individuals. We used the same trapping protocols as described in Section 2.2.1.

2.3. Habitat covariates

2.3.1. Landscape-scale habitat change

We quantified the total area around primary trapping grids consisting of novel infrastructure or habitat. We calculated separately the area within 564 m of each primary trapping grid that consisted of reclaimed areas, well pads, roads (excluding 2-tracks), and open area (disturbed soil on roads and well pads) using National Agricultural Imagery Program files (USDA Geospatial Data Gateway, 2015) in ArcGIS 10.0 (ESRI, 2011). A 564-m buffer was the most relevant scale of habitat loss for sagebrush songbirds (Hethcoat and Chalfoun, 2015a) and deer mice (Sanders and Chalfoun, in review) in concurrent studies, and represented a measure of development in the surrounding landscape at a scale much larger than a single animal's home range (Wood et al., 2010). Because primary trapping grids moved locations between years, we re-calculated landscape composition (amount of reclaimed area, well pad, road, and open area) surrounding each primary trapping grid each year. Grids spanned a gradient of surrounding habitat change

caused by all infrastructure metrics: reclaimed areas (0–27 ha/km²), well pads (0–0.4 ha/km²), roads (0.1–0.5 ha/km²), and open area (0.1–0.8 ha/km²). For reference, 27 ha/km² is equivalent to conversion of 27% of the habitat surrounding a primary trapping grid to reclaimed area.

2.3.2. Local shrub cover

We quantified shrub cover at all primary trapping grids, because shrub cover can influence deer mouse capture rates, survival, and fitness via changes to perceived predation risk (Orrock et al., 2004; Ceradini and Chalfoun, 2017). Big sagebrush was the primary vegetation cover growing within our study area, thus we estimated percent sagebrush cover at each primary trapping grid using line-intercept surveys along 20-m transects centered in the four quadrants of each grid (Etchberger and Krausman, 1997).

2.4. Reclaimed v. sagebrush understory vegetation composition

We quantified differences in vegetation composition between the sagebrush understory and adjacent reclaimed areas (to assess the 1st critical assumption of the food augmentation hypothesis). We measured percent cover of plant functional groups that deer mice could consume (grasses and forbs; Kelrick et al., 1986) or that could influence predation risk (shrub cover and bare ground; Orrock et al., 2004) in the sagebrush understory and in adjacent reclaimed areas at diet sampling plots on the Pinedale Anticline ($n = 10$; 6 original diet sampling plots plus 4 additional plots selected using criteria described in Section 2.2.2 above) in July 2016. Within each diet sampling plot and a 50-m buffer inside the adjacent reclaimed area, we took photos of a 1×1 -m quadrat on the ground at 30 random points using a digital camera (Sony Corporation of America, New York, USA). We quantified vegetation cover in each photo using SamplePoint software (Booth et al., 2006; Pilliod and Arkle, 2013), which randomly placed 30 points in each photo for observers to manually classify to cover type (grass, forb, shrub, or bare ground).

2.5. Deer mouse tracking

We assessed deer mouse habitat use (2nd critical assumption of food hypothesis) by powder tracking mice, following Stapp (1997). Powder tracking efforts occurred at the original 12 diet sampling plots in 2017 ($n = 6$ each at the Pinedale Anticline and Jonah Field, Fig. A.1). Rather than releasing all mice after capture, a subset (excluding lactating females) were removed from the plot and placed in a quiet, shaded location with food, water, and bedding for the remainder of the day. At 1–2 h before sunset, we coated mice with a fluorescent powder (Radiant Color Inc., Richmond, CA) using paintbrushes and released individuals at the trap location where they were originally captured. To ensure that we tracked exclusively nighttime movements, we marked the last known daytime location of individuals at sunset. Beginning 2–4 h after sunset, we tracked mice from their last known daytime location using an ultraviolet LED flashlight (<https://ledwholesalers.com>) and placed pin flags at one meter intervals along each track for 130 m or until tracks were no longer visible. We measured distance (in meters) to the nearest reclaimed area along each track.

2.6. Deer mouse diet

To determine plant matter consumed by deer mice (3rd critical assumption of food hypothesis), we collected fecal samples from inside the traps of 50 deer mice captured during deer mouse tracking at diet sampling plots. Fecal samples were transported on ice and frozen within 6 h of collection. Although deer mice are dietary generalists, plant material generally comprises 40–80% of diets during the summer (Hingten and Clark, 1984), making assessment of plant foods very relevant to understanding the dietary inputs of mice. We sent fecal

samples to Jonah Ventures, LLC (Boulder, CO) for analyses of plant chloroplast DNA (*trnL* approach). For additional details on this process, see Craine et al. (2016). The analyses generated DNA sequences, which were clustered into operational taxonomic units (OTUs) at the $\geq 97\%$ similarity level. We used the National Center for Biotechnology Information's Standard Nucleotide BLAST database to assign OTUs to their corresponding genera. We removed all OTUs with unclassified taxonomy and OTUs belonging to species that did not occur within our study sites (e.g., pollen from nearby forested habitats). We also removed all OTUs associated with *Artemisia* spp. due to possible contamination during sample collection. Food trial studies, moreover, have found *Artemisia* to be an undesirable food resource for deer mice (Kelrick et al., 1986).

All OTUs were reported with an abundance of DNA reads, and we summarized all data using the abundance of reads for each OTU relative to the total number of reads in the sample (hereafter relative read abundance). After filtering, samples had an average of 9,933 reads per sample (104–24,003 reads). Read abundance corresponds to the amount of protein from a diet item, rather than biomass, and thus we were unable to infer the prevalence of genera in mouse diets. Instead, we considered a food items' presence in diet samples to indicate its potential as a food source for deer mice. Some OTUs contained multiple species found at our study sites, and are presented as 'complexes.' In reality these complexes represent some, though likely not all of the genera listed within.

We measured vegetation at 11 diet sampling plots (5 at the Pinedale Anticline and 6 at the Jonah Field) to compare the availability of plant foods between reclaimed areas and the sagebrush understory. We were specifically interested in determining the availability of plant genera identified during dietary analyses. We selected 10 random points in the sagebrush understory and 10 in the adjacent reclaimed area at each plot. We placed a 50 × 50-cm quadrat at each point and conducted a point-line intercept survey at 36 equally spaced marks within the quadrat (Damgaard, 2014), identifying all grasses, forbs and shrubs to genus or species.

2.7. Deer mouse fitness

We assessed one grid-level metric of fitness (survival; 2014–2016) and three capture-level metrics of fitness (body condition, reproductive status of adults, and number of immature individuals per female, hereafter age; 2015–2016) at primary trapping grids to assess our suite of fitness-metric predictions. We calculated body condition for all captures (excluding pregnant females) as the residuals from a regression of mass against body length (Schulte-Hostedde et al., 2005). When multiple body length and mass measurements were available, we averaged across the primary period. We identified all individuals in each primary period as reproductive (females: pregnant, lactating, vagina perforated; males: scrotal) or non-reproductive, and as an adult or immature. Deer mice in the sagebrush primarily disperse as adults (Waltee et al., 2009), so sub-adults present at a site likely represented recent reproductive output. Sub-adults and juveniles were therefore grouped together as immatures for this analysis. We excluded individuals assigned multiple reproductive states or ages in the same primary period to minimize human error. We randomly chose one primary period to include in capture-level fitness analyses per individual to avoid pseudoreplication.

2.8. Statistical analyses

2.8.1. Deer mouse density and survival

All analyses were conducted in Program R (R Core Team, 2017) version 3.3.3. To quantify the importance of individual components of habitat change within natural gas fields, we used mark-recapture models (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 (Φ), and abundance (\hat{N}) of deer mice (effective $n = 1488$). Temporary emigration parameters (γ' and γ'') were inestimable given only two primary periods, and were fixed to zero. We thus estimated apparent within-season survival between primary periods each year (six-week survival), which may be an underestimate of true survival, because emigration and death were confounded (Williams et al., 2002).

We used a two-stage approach to model capture/recapture probability and survival of deer mice. We used backward stepwise selection to model capture (p) and recapture (c) probability (Hocking, 1976), beginning with global models for p and c containing variables that could potentially influence capture probability: year, gas field, % moon illumination, minimum temperature, precipitation, trapping effort, seasonality (primary period), trap night (secondary period), and capture age, gender, and reproductive status. We removed the least predictive variables in succession, using AIC_c model selection (AICcmodavg package; Mazerolle, 2017) to compare the previous model (i) to the current model (i-1) after each removal, until model i outperformed model i-1. We moved the final capture-recapture model into our survival analysis. To model survival, we developed one model containing additive effects of reclaimed area (within 564 m of primary trapping grids), year, gas field, average sagebrush cover, and individual age, gender, and reproductive status. We chose predictor variables based on their likely relevance to small mammal predation risk, capture probability, and survival in our system (Hethcoat and Chalfoun, 2015b; Ceradini and Chalfoun, 2017; Sanders and Chalfoun, in review). We inspected model output and 95% confidence intervals to determine the importance of reclaimed area on deer mouse survival.

We calculated effective trapping area by adding the mean maximum distance moved to total grid size each year, and divided abundance at each grid by the effective trapping area to calculate deer mouse density. We predicted density using a linear model (Gaussian distribution). Because our response variable was an estimate, we weighted all models by the inverse standard error of abundance to account for potential bias. We log-transformed density estimates to account for non-normality in the residuals, and back-transformed for beta interpretation. We used AIC_c model selection (Mazerolle, 2017) to determine which of four a priori development metrics best explained patterns in deer mouse density across our development gradient. As such, we only included one development metric in each model of our model suite. We compared four univariate measures of habitat change surrounding primary trapping grids: area (ha/km²) consisting of reclaimed areas, well pads, roads, and open area. We used model probabilities (w_i), and evidence ratios ($E_i = w_{top}/w_i$) to assess model support (Burnham and Anderson, 2002).

2.8.2. Reclaimed v. sagebrush vegetation composition

To assess the first critical assumption of the food augmentation hypothesis, we compared the difference in mean cover of grasses, forbs, shrubs, and bare ground between the reclaimed area and sagebrush understory at diet sampling plots, and bootstrapped 95% confidence intervals (*boot* package; Canty and Ripley, 2017). Confidence intervals that fell above zero indicated significantly higher plant cover in reclaimed areas than sagebrush understories.

2.8.3. Deer mouse tracking

We ran a generalized linear regression (logistic; logit link) to assess whether vegetative cover class within a reclaimed area (tumbleweed dominant, high grass cover, or sparse grass cover) affected the likelihood that a deer mouse entered a reclaimed area. The model included vegetative cover class and initial distance from reclaimed area edge (meters; measured from last known daytime location) as fixed effects. We verified model assumptions by visually inspecting residuals versus fitted values and quantile-quantile plots (Zuur and Ieno, 2016). We assessed model output and 95% confidence intervals for predictor significance.

2.8.4. Deer mouse diet

We summarized relative DNA read abundance from all diet samples to identify plant genera in deer mouse diets. We removed samples with fewer than 300 reads from analysis, as the likelihood of a false positive with these data was high. We present plant genera that represent $\geq 0.1\%$ of all mouse diets sampled. All genera were classified as native or non-native to the sagebrush steppe (Dorn, 2001; Skinner, 2010). We focused on quantifying differences in % cover of plants known to be in deer mouse diets (i.e., plant genera identified in diet analyses) between reclaimed areas and sagebrush understory. We bootstrapped 95% confidence intervals for plant cover in both reclaimed areas and sagebrush understory for each plant genera identified in mouse diets, based on vegetation surveys from 11 diet sampling plots.

2.8.5. Deer mouse fitness

We assessed four fitness metrics for deer mice at primary trapping grids: survival (see Section 2.8.1), body condition, reproductive status of adults, and number of immature individuals per female. We ran generalized linear regressions for body condition ($n = 1053$; gamma distribution), adult reproductive status ($n = 725$; logistic with logit link), and age ($n = 875$; binomial with complimentary log-log link) metrics with trapping grid/year combination ($n = 24$) as a random effect using the *lme4* package (Bates et al., 2015). We used a complimentary log-log link for our age model to account for the asymmetrical distribution of adult and juvenile mice in our dataset. We developed one model for each fitness metric of interest. Our body condition model contained additive fixed effects of: amount of surrounding reclaimed area, mouse gender, Julian date, year, surrounding deer mouse density and surrounding sagebrush % cover. Our reproductive status model and age model contained these same six covariates, and also included body condition as a fixed effect. We offset age models by number of adult females at each primary trapping grid to determine the number of immature individuals per female. We rescaled reclaimed area, Julian date, mouse density, and sagebrush cover between 0 and 1 for all analyses to aid in model convergence, and back-transformed for beta interpretation. We verified model assumptions by visually inspecting residuals versus fitted values and quantile-quantile plots (Zuur and Ieno, 2016). We inspected model outputs and 95% confidence intervals to determine the importance of reclaimed area to each fitness metric separately, and converted pertinent parameter estimates to odds ratios for interpretation. We generated sensitivity and specificity values for logistic and binomial regression models, and assessed area under the receiver operating characteristic curve (hereafter AUC) to determine model performance.

3. Results

3.1. Deer mouse density

Reclaimed area was the top performing development metric in predicting deer mouse densities ($w_i = 0.85$, $E_{i+1} = 9.44$; Table 1). Deer mouse density increased with surrounding reclaimed area ($\beta = 0.03$ for each ha/km^2 of reclaimed area, 95% CI: 0.01–0.04, range = 6–46 mice/ha; Fig. 1, detection results in Table A.1).

3.2. Critical assumptions of the food augmentation hypothesis

3.2.1. Reclaimed v sagebrush vegetation composition

Reclaimed areas had higher percent cover of grasses (95% CI: 0.05–0.14; Fig. 2a) and forbs (95% CI: 0.03–0.1; Fig. 2b) than adjacent sagebrush understories. Additionally, reclaimed areas contained substantially lower percent cover of live sagebrush (95% CI: -11.99–7.79; Fig. 2c) and higher cover of bare ground (95% CI: 0.11–0.19; Fig. 2d) than the sagebrush understory.

Table 1

Ranking and relative support for linear models explaining variation in deer mouse density (*Peromyscus maniculatus*; Huggins robust design, $n = 36$) using metrics of landscape change. Competing metrics include total area (ha/km^2) covered by reclaimed areas, well pads, roads, and open area within 564 m of primary trapping grids. All models were weighted by the inverse standard error of abundance. We report log-likelihood values $\log(L)$, number of parameters k , the difference in AIC_c values between the top model and model i ΔAIC_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 from 12 sites within the Pinedale Anticline and Jonah natural gas fields in western Wyoming, USA, 2014–2016.

Competing model	$\log(L)$	k	ΔAIC_c	w_i	E_i
Reclaimed area	-22.28	3	0.00	0.85	n/a
Well pads	-24.48	3	4.40	0.09	9.44
Open area	-25.28	3	5.99	0.04	21.25
Roads	-26.81	3	9.05	0.01	85.00

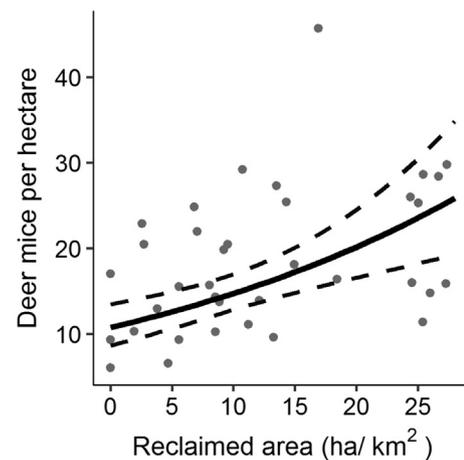


Fig. 1. Density estimates for deer mice (*Peromyscus maniculatus*; Huggins robust design). Reclaimed area was measured within 564 m of primary trapping grids. Dotted lines indicate 95% confidence intervals. Data were collected from 12 sites within the Pinedale Anticline and Jonah natural gas fields in western Wyoming, USA, 2014–2016 ($n = 36$ grids). Grids covered 0.36 ha in 2014, and 2.25 ha in 2015–2016.

3.2.2. Deer mouse habitat use

We powder tracked 42 deer mice in 2017 for an average 76.1 ± 4.7 m (range 25–136 m). We tracked 26% of mice into a reclaimed area (up to 40 m into reclaimed area interiors), and 62% of all individuals traveled within 5 m of a reclaimed area edge (average distance to reclaimed area across all tracks = 16 m). We did not identify any differences in likelihood of mice entering a reclaimed area between plots dominated by Russian thistle ($\beta = -0.85$, 95% CI: -2.24–0.54; see Fig. A.2 for distinction between cover types), plots with high grass cover ($\beta = -1.25$, 95% CI: -2.66–0.17), sparse grass cover ($\beta = -1.21$, 95% CI: -2.85–0.43 \pm 0.95), or by initial distance to habitat edge ($\beta = -0.01$, 95% CI: -0.09–0.08; range 1–60 m).

3.2.3. Deer mouse diet

Mouse diet samples ($n = 48$) contained DNA from 27 plant genera and complexes (Table A.2), seven of which were non-native to the sagebrush steppe: *Phleum*, *Leymus*, *Kali*, *Descurania*, *Chenopodium*, *Lappula*, and *Bromus*. Non-native genera were found exclusively within reclaimed areas during vegetation surveys, whereas nearly all native genera, with the exception of *Pseudoroegneria* grasses, were present either equally between habitat types, or were more common in the sagebrush understory (Fig. 3, Table A.2).

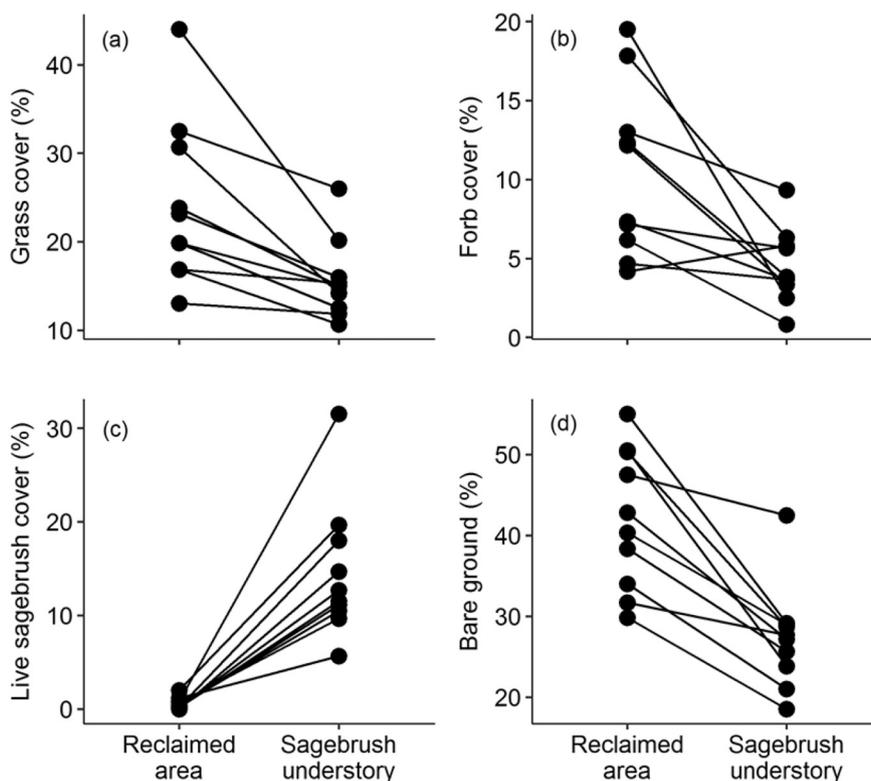


Fig. 2. Percent cover of (a) grasses, (b) forbs, (c) live sagebrush (*Artemisia tridentata*), and (d) bare ground at paired sites within reclaimed areas and sagebrush understories. Data were collected from 10 diet sampling plots within the Pinedale Anticline in western Wyoming, USA, 2016.

3.3. Deer mouse fitness

Within-season apparent survival of deer mice decreased as surrounding reclaimed area increased ($\beta = -0.04$ for each ha/km² of reclaimed area, 95% CI: -0.06 to -0.01 ; Fig. 4a). Deer mouse survival did not vary with year ($\beta = 0.39$, 95% CI: -0.23 – 1.01), gas field ($\beta = 0.11$, 95% CI: -0.35 – 0.57), surrounding sagebrush cover ($\beta = -0.06$, 95% CI: -0.24 – 0.13), reproductive status ($\beta = -0.09$, 95% CI: -0.21 – 0.03), age ($\beta = 0.02$, 95% CI: -0.23 – 0.27), or gender

($\beta = -0.02$, 95% CI: -0.12 – 0.07).

Reclaimed area was not an important predictor of body condition ($\beta = -0.001$ for each ha/km² of reclaimed area, 95% CI: -0.005 – 0.002 ; Fig. 4b). Body condition was not density dependent ($\beta = -0.0005$, 95% CI: -0.002 – 0.001) and did not vary with gender ($\beta = -0.01$, 95% CI: -0.03 – 0.02), year ($\beta = -0.05$, 95% CI: -0.10 – 0.01), Julian date ($\beta = -0.0002$, 95% CI: -0.0008 – 0.0003), or surrounding sagebrush cover ($\beta = 0.02$, 95% CI: -0.06 – 0.02).

Reclaimed area was an important predictor of reproductive status,

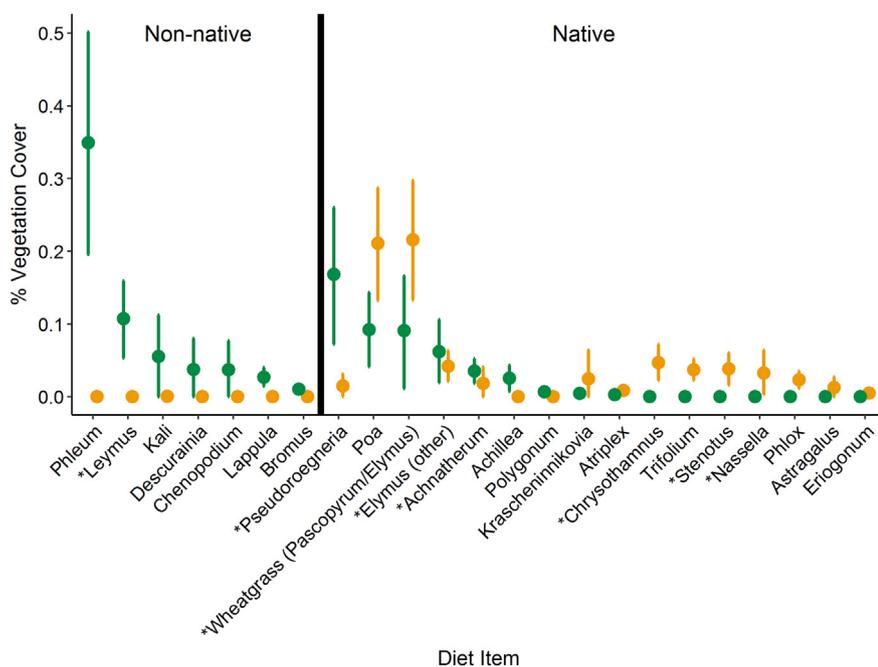


Fig. 3. Bootstrapped 95% confidence intervals for percent vegetative cover of deer mouse (*Peromyscus maniculatus*) plant foods within reclaimed areas (green) and sagebrush understories (yellow). Plant foods shown here were determined from deer mouse fecal samples (n = 48). An asterisk (*) indicates a genera contained within a complex. Each complex contains multiple genera which could not be differentiated in dietary analyses. We report % vegetation cover (as measured during vegetation surveys) for all plant foods identified in deer mouse diets. Plant genera are grouped by native status. Both fecal sample collection and vegetation surveys were conducted at 11 diet sampling plots within the Pinedale Anticline and Jonah natural gas fields in Wyoming, USA, 2017. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

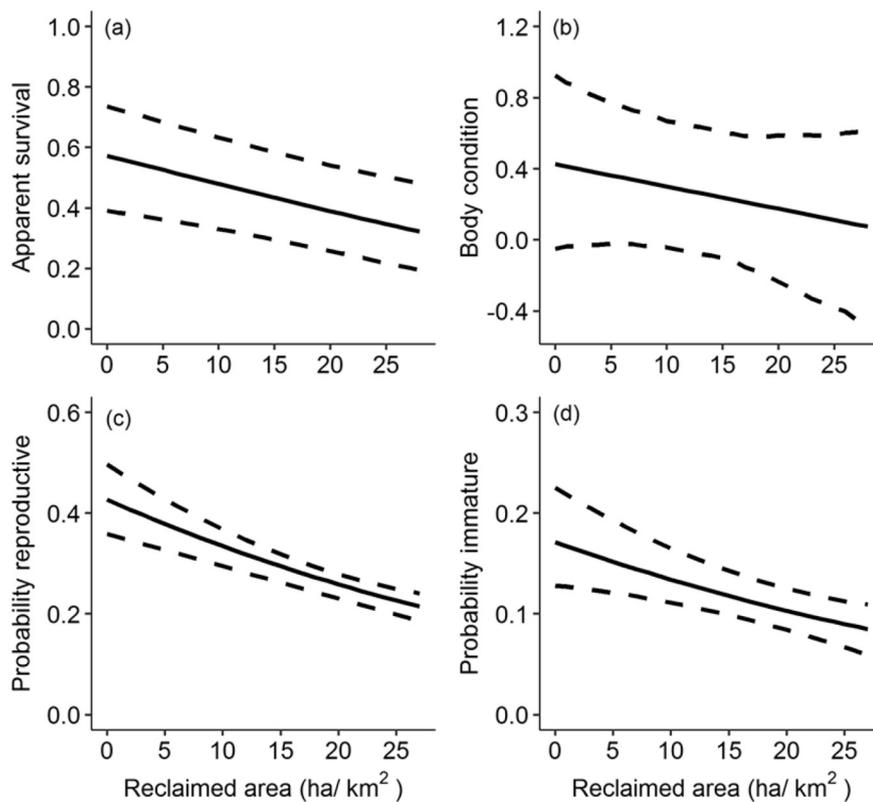


Fig. 4. Deer mouse (*Peromyscus maniculatus*) fitness metrics measured across a gradient of surrounding reclaimed area. Fitness metrics include a) predicted apparent survival (within-season, Huggins robust design), b) body condition, c) number of reproductively active adults, and d) number of immature individuals per female (hereafter age). Apparent survival data were collected during 2014–2016 ($n = 36$ grids), whereas body condition, reproductive status, and age data were collected during 2015–2016 ($n = 24$ grids). Reclaimed area was measured within 564 m of primary trapping grids. Body condition was calculated as the residuals from a regression of body mass by body length. Results for each fitness metric are presented with all additional variables held at their means. Dotted lines indicate 95% confidence intervals. Data were collected from 12 sites within the Pinedale Anticline and Jonah natural gas fields in western Wyoming, USA.

with the odds that an adult was reproductively active decreasing 55% across our gradient of surrounding reclaimed area ($\beta = -0.03$ for each ha/km^2 of reclaimed area, 95% CI: -0.06 to -0.005 , AUC = 0.8; Fig. 4c). Reproductive adults were more likely to be males ($\beta = -1.35$, 95% CI: -1.80 to -0.90), trapped earlier in the summer ($\beta = -0.03$, 95% CI: -0.04 to -0.02), trapped in 2015 ($\beta = -1.04$, 95% CI: -1.47 to -0.60), and in better body condition ($\beta = 0.26$, 95% CI: 0.17 – 0.34). Reproductive status was not density dependent ($\beta = -0.003$, 95% CI: -0.01 – 0.01), and did not vary with surrounding sagebrush cover ($\beta = 0.14$, 95% CI: -0.42 – 0.15).

Reclaimed area was not an important predictor of the number of immature individuals captured per female ($\beta = -0.03$ for each ha/km^2 of reclaimed area, 95% CI: -0.06 – 0.01 , AUC = 0.7; Fig. 4d). Immature individuals were more likely to be females ($\beta = 0.76$, 95% CI: 0.38 – 1.14), trapped earlier in the summer ($\beta = -0.02$, 95% CI: -0.02 to -0.01), and in better body condition ($\beta = 0.09$, 95% CI: 0.02 – 0.15). The number of immature individuals captured per female was not density dependent ($\beta = 0.001$, 95% CI: -0.01 – 0.02) and did not vary with year ($\beta = -0.20$, 95% CI: -0.77 – 0.36) or surrounding sagebrush cover ($\beta = -0.09$, 95% CI: -0.48 – 0.31).

4. Discussion

Identifying the specific elements of human-induced habitat changes that affect species' distributions and success is important for effective management (Baggio et al., 2011). We investigated the components of landscape change within natural gas fields that contributed to increased nest predation of sagebrush-obligate songbirds by a primary nest predator (Hethcoat and Chalfoun, 2015b). Rodents, particularly deer mice, were the most common nest predator in our study system, and rodent densities have been linked to reduced songbird nest success (Hethcoat and Chalfoun, 2015b). Deer mouse densities, moreover, tended to increase with surface disturbance caused by energy development (Sanders and Chalfoun, in review). We aimed to clarify the mechanism underlying the increase in deer mouse densities within natural gas

fields. Deer mice were more positively associated with reclaimed areas than any other aspect of habitat conversion assessed. Reclaimed areas contained more herbaceous food resources than adjacent sagebrush understories, and we documented mice using, and foraging within, reseeded habitat. Deer mice, however, experienced lower apparent survival and productivity when surrounded by more reclaimed area, possibly due to a decrease in available refugia from predators. Reclaimed areas were therefore the most relevant component of landscape change for an important nest predator within natural gas fields, but no benefits of utilizing reclaimed areas were realized by deer mice via increased fitness within the timeframe evaluated. Our findings demonstrate the complex and somewhat counter-intuitive trophic dynamics that can occur with, and may be exacerbated by, human-induced, rapid environmental change (Tylianakis et al., 2008).

The increased deer mouse densities that we documented near reclaimed areas may have been related to habitat structure and/or augmented food availability (Doherty et al., 2015; Monroe and Ritchison, 2005). Plant community composition and diversity can change dramatically following reclamation, as observed in this study. The lack of shrub cover and large amount of bare ground that we documented in reclaimed areas suggests that rodents likely did not use reclaimed areas as refuges from predators, as perceived risk typically increases under such conditions (Orrock et al., 2004; Ceradini and Chalfoun, 2017). Some large bunch grasses (such as timothy-grass, *Phleum pretense* and basin wildrye, *Leymus cinereus*) could provide protection from predators in place of shrubs, given their tall stalks and wide bunch diameter (Bush, 2009; Ogle et al., 2012). The perceived predation risk of rodents in reseeded areas would likely still have been higher than the adjacent shrubland patches, however, given the virtual absence of shrubs and amount of bare ground (Conner et al., 2011). Moreover, concomitant surveys of predators of rodents (raptors, corvids, canids and badgers) and a giving-up density experiment at the same sites documented higher actual and perceived predation risk for rodents with increased surrounding habitat loss from energy development (Sanders and Chalfoun, in review).

The cover of plants (forbs and grasses) that can serve as food resources for rodents (Hingtgen and Clark, 1984) was higher in reclaimed areas than native sagebrush patches, which supports the food augmentation hypothesis. Although we did not assess food resources via actual plant biomass (Turchin and Batzli, 2001), higher cover of plant foods in reclaimed areas indicates the potential for increased food availability for mice (Antunes et al., 2016). We identified seven genera of non-native plants, found exclusively within the reclaimed portions of our study landscape during vegetation surveys, in mouse diets—confirming that deer mice were indeed foraging within reclaimed areas. Many non-native grasses and forbs provide exceptional forage for livestock and wild ungulates, and also may render reclaimed areas more desirable for small mammals. Non-native bunchgrasses such as timothy-grass and basin wildrye, for example, are highly nutritious and intentionally planted during reclamation efforts (Bush, 2009; Ogle et al., 2012; P. Guernsey, pers. comm.). Non-native forbs such as Russian thistle (*Kali tragus*) and herb sophia (*Descurainia sophia*), grow on their own in recently disturbed soils and are also highly nutritious (Howard, 1992; Invasive Species Compendium, 2015). Many native species, found in both reclaimed areas and the sagebrush understory, were also represented in deer mouse diets, including native bunch grasses (*Pseudoroegneria* spp, *Poa* spp, *Elymus elymoides*, *Achnatherum hymenoides*), clover (*Trifolium* spp) and yarrow (*Achillia* spp). The inclusion of very palatable forb species, especially those that are relatively rare within undisturbed portions of the landscape, in seed mixes may serve as a strong attractant for opportunistic, generalist species such as deer mice.

If reclaimed areas were providing food subsidies for deer mice on natural gas fields, we expected that mice would experience increased survival, body condition and/or reproductive output compared to undisturbed areas (Arcese and Smith, 1988). We found no evidence, however, that the amount of surrounding reclaimed area provided fitness benefits to individual mice. To the contrary, we documented lower mouse survival and numbers of reproductively active individuals associated with more reclaimed area in the vicinity. Increased predation pressure (Sanders and Chalfoun, in review) may therefore be modulating the individual benefits mice experience while living near energy development (Elmhagen and Rushton, 2007). Regardless, given the higher mouse densities near reclaimed areas, the aggregate population growth (which is a product of the number of individuals and their fitness; Levin and Ellner, 2008) may be comparable or become higher than in areas without extensive habitat alteration. Moreover, we only measured fitness metrics during the summer months. Reclaimed areas could increase deer mouse survival or body condition during other seasons, which could carry-over and influence demography during the breeding season (Johnsen et al., 2017).

Steady dispersal into habitat near reclaimed soils may at least partly explain the deer mouse density patterns we observed during our study. Local populations are determined by survival, reproductive output, and/or rates of immigration and emigration (Levin and Ellner, 2008). We observed decreased survival and reproductive output of deer mice associated with reclaimed areas, leaving dispersal as the most plausible explanation for increased local abundance. We were unfortunately unable to directly measure dispersal, however, given only two primary periods of trapping in our study design (Williams et al., 2002). Given the patterns documented herein, however, we suspect that mice may be dispersing toward reclaimed areas, possibly via attraction to desirable herbaceous food resources (Taitt, 1981). As such, reclaimed areas may represent severe or equal-preference ecological traps for deer mice (Robertson et al., 2013), if individuals are preferentially dispersing into natural gas fields despite the decreased resulting fitness outcomes. Cumulatively, our results suggest an interplay between top-down and bottom-up forces within natural gas fields (Zhang and Richardson, 2011), whereby apex predators may be preventing mice from taking full advantage of available food resources. Regardless, mice still maintained high enough population densities to negatively affect the productivity

of sagebrush songbirds near energy development (Hethcoat and Chalfoun, 2015a).

Successful habitat restoration is a difficult task, and practitioners require better tools to aid in, and monitor, the reclamation of lands disturbed by energy extraction (Curran et al., 2013). Our findings accentuate the importance of minimizing the amount of land that is initially disturbed during development (Bender et al., 1998), especially because twenty or more years are regularly needed for reclaimed sites to begin resembling native habitat within arid systems (Arkle et al., 2014). We suggest that seed mixes contain only species native to the region and habitat type being re-seeded, and that efforts are made to prevent the establishment of non-native species in the seed bank. Such practices would likely minimize the attraction of synanthropic rodents to reclaimed areas near energy development, and could alleviate increased nest predation pressure experienced by nesting birds.

Our research contributes to a broader understanding of how species interactions and communities can change within human-altered landscapes, especially when novel resources become available. We identified increases in the abundance of a generalist species associated with reseeded areas within natural gas fields, which helps clarify the mechanisms responsible for a previously-documented altered predator-prey relationship (Hethcoat and Chalfoun, 2015b). Reclaimed areas appear to be an important component of habitat change within energy fields that can significantly influence wildlife populations. Simultaneous studies of predators, prey, and vegetation communities can yield key insights into species interactions and resulting community composition in altered landscapes (Zhang and Richardson, 2011). Targeted land management strategies based on an understanding of which components of habitat change most affect the abundance and fitness of species of concern will be imperative for successful mitigation.

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Conflicts of interest

The authors have no conflicts of interest to report.

Role of funding sources

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.10.020>.

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