

Removal of cattle grazing correlates with increases in vegetation productivity and in abundance of imperiled breeding birds

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ABSTRACT

Livestock grazing is the most prevalent land use practice in the western United States and a widespread cause of degradation of riparian vegetation. Riparian areas provide high-quality habitat for many species of declining migratory breeding birds. We analyzed changes in vegetation and bird abundance at a wildlife refuge in southeastern Oregon over 24 years, following cessation of 120 years of livestock grazing. We quantified long-term changes in overall avian abundance and species richness and, specifically, in the abundances of 20 focal species. We then compared the local responses of the focal species to population-scale trends of the same species at three different large spatial scales. Overall avian abundance increased 23% during the 12 years after removal and remained consistent from then through year 24. Three times as many species colonized the survey sites as dropped out. Of the focal species, most riparian woodland-tree or shrub dependent, sagebrush obligate, and grassland or meadow taxa increased in abundance or remained stable locally. As these species were generally of conservation concern, the population increases contradicted regionally declining or stable trends. In contrast, most riparian woodland-cavity nester species decreased in abundance locally, reflecting disruption of aspen stand dynamics by decades of grazing. Avian nest parasites and competitors of native species declined in abundance locally, matching regional trends. Restoring riparian ecosystems by removing livestock appeared to be beneficial to the conservation of many of these declining populations of migratory birds.

1. Introduction

Livestock grazing is the most widespread land use practice in the arid western conterminous United States, and it has had a profound influence on native ecosystems (Fleischner, 1994; Saab et al., 1995). Unmanaged grazing can affect landscapes through loss of native plant and animal species, erosion of soil, reduction of water infiltration, and degradation of native plant and wildlife habitat (Belsky and Blumenthal, 1997; Yong-Zhong et al., 2005). Long-term grazing can alter the structure of grasses and shrubs, but these effects can have both positive and negative consequences for sagebrush and grassland communities (Davies et al., 2018). Grazing also can disrupt ecological succession by transforming a landscape into vegetation communities with a prolonged early seral stage (Fleischner, 1994; Belsky and Blumenthal, 1997). Furthermore, grazing has been linked to the invasion of non-native plant and animal species (Hobbs, 2001). Thus, habitat degradation from unmanaged grazing is one of the primary threats to biological diversity in the western United States (Fleischner, 1994).

The ecological impacts of grazing increase especially in riparian

ecosystems (Hansen et al., 2019), which are among the most biologically rich habitats in arid lands (Fleischner, 1994). In the United States, livestock were introduced into these ecosystems between one and two centuries ago (Belsky et al., 1999). Since then, grazed streams and riparian zones have been extensively affected by loss of streamside vegetation and streambed and channel alteration (Armour et al., 1994; Wyman et al., 2006). These disturbances reduce the amount and connectivity of habitat for riparian plants and animals, leading to the local decline or extirpation of many native species (Armour et al., 1994; Belsky et al., 1999). Riparian areas evolved with a low level of grazing by native herbivores, but high levels of grazing can be detrimental to these ecosystems (Swanson et al., 2015). The cumulative effects of livestock grazing have caused some to propose that it is the most prevalent source of habitat degradation in riparian areas in the western United States (Belsky et al., 1999). Because few riparian communities have been unaffected by grazing, opportunities to quantify the impacts of grazing on these ecosystems are rare.

Populations of many migrant bird species are declining across North America (Sauer et al., 2013, 2017). Although evidence of bird declines

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is well documented, the functional causes of these declines are not well understood. The most prevalent hypotheses to explain declines in migratory birds are habitat alteration or loss, and related demographic processes, on (i) breeding grounds (Vander Haegen, 2007); (ii) wintering grounds (Dybala et al., 2015); and (iii) during migration (Hutto, 2000). Some riparian areas are reported to have the highest densities of breeding birds in North America, and conservation of these bird species relies on protection of their riparian habitats (Saab et al., 1995). Livestock grazing affects riparian vegetation, which, in turn, limits bird abundance and productivity (Saab et al., 1995; Dobkin et al., 1998; Tewksbury et al., 2002; Krueper et al., 2003; Earnst et al., 2012; Hansen et al., 2019), and therefore limits the capacity of riparian ecosystems to support birds.

We tested the hypothesis that passive habitat restoration (i.e., the cessation of anthropogenic activities causing degradation [Kauffman et al., 1997]) on breeding grounds would be correlated with increasing local trends of migratory bird species that occupy riparian areas in western North America. To do this, we evaluated a 24-year dataset on bird populations at a wildlife refuge located in the Great Basin ecoregion of the western United States and that has undergone dramatic long-term habitat change. Grazing by cattle (*Bos taurus*), sheep (*Ovis aries*), and native herbivores occurred at the 1100 km² Hart Mountain National Antelope Refuge (HMNAR; Fig. 1) in southeastern Oregon, USA, during much of the 20th century (Supplementary Information Historical Grazing). Cattle were removed from HMNAR in 1990 after approximately 120 years of grazing. A long-term study began in 1991, and continued for 24 years, to investigate the consequences of cattle removal on the riparian areas of HMNAR and on avian abundance (Dobkin et al., 1998; Earnst et al., 2012). Although a few studies have measured recovery of plant communities post-grazing and within small-scale enclosure plots (e.g., Dobkin et al., 1998), we are not aware of any studies that have tracked indicators of riparian recovery at such large spatial scales and over multiple decades. In testing our hypothesis, our objectives were to (i) quantify the long-term changes in overall avian abundance, species richness, and the abundance of 20 key avian species (i.e., “focal species”) after removal of cattle grazing and to ascribe a functional mechanism for those changes; and (ii) compare the local trends of the focal species to population-scale trends of the same species at three different large spatial scales, each of which encompassed HMNAR.

2. Methods

2.1. Study area and design

HMNAR is located in the Great Basin ecoregion in southeastern Oregon, USA (Fig. 1). Details of the study area have been described elsewhere (Earnst et al., 2012). Generally, HMNAR consists of high-desert sagebrush (*Artemisia* spp.) shrub-steppe systems (dominated by low sagebrush [*A. arbuscula*] and big sagebrush [*A. tridentata*]) with riparian aspen (*Populus tremuloides*) and willow (*Salix* spp.) woodlands and snow-pocket aspen stands.

Riparian plots were established within HMNAR in 1991 (Dobkin and Rich, 1998) and 2000 (Earnst et al., 2012) to sample the study area. Plots were 150 × 100 m and were placed in six land cover types that represented the range of riparian vegetation present at HMNAR (described as riparian aspen, willow, meadow, shrub, deciduous, and snowpocket aspen in Earnst et al., 2005). The center line of each plot ran near (within approximately 15 m) and parallel to a stream for 150 m. Birds were monitored on these plots during three phases: 1–3 years after cattle removal (1991–1993; hereafter, phase 1), 10–12 years after cattle removal (2000–2002; hereafter, phase 2), and 22–24 years after cattle removal (2012–2014; hereafter, phase 3). During phase 1, 47 plots (“original plots”) were surveyed, and during phases 2 and 3, the original plots plus an additional 59 plots (“new plots”) were surveyed. Elevation of the plots ranged from 1520 m to 2231 m.

2.2. Avian surveys

The bird community at HMNAR was surveyed with modified fixed-width transect surveys (this was a common sampling approach when this study was designed in 1991). Observers walked slowly along the center line (transect) of each plot for 25 min and recorded the number of aurally or visually detected individuals of each bird species within 50 m of the transect (Dobkin and Rich, 1998; Earnst et al., 2012). In phase 1, each of the 47 plots was surveyed six times, twice in each of three survey rounds, during each of the three years (seven plots were only surveyed five times in 1993 and one plot was not surveyed in 1991 or 1992). In phases 2 and 3, because additional plots were added, the 106 plots were surveyed three times during each of the three years of the phases (58 plots were not surveyed in 2000, five plots were only surveyed two times in 2001, and one plot was not surveyed in 2014). Thus, the number of times a plot was visited varied by phase, but total survey effort did not substantially differ among the three phases (similar to the survey design of Hansen et al., 2019). Surveys were conducted from May to July each year (breeding season), as weather conditions allowed (Ralph et al., 1995).

For each plot, we estimated bird abundance, bird species richness, and bird species diversity. To capture broad-scale variation across phases, we estimated bird abundance as the mean number of individuals of all species detected per visit during each phase, bird species richness as the number of positively-identified species detected per phase, and bird species diversity per phase with Simpson's index of diversity (Simpson, 1949; Krebs, 2014). For both species richness and diversity, we did not include in our calculations those species detected at only one plot and during only one phase (Krebs, 2014).

We also calculated the percentage of plots surveyed in a given phase in which each species was detected. Changes in species composition can reflect environmental change, so we summarized species turnover in terms of species that colonized the study site and those that dropped out over the duration of the study. We defined species that colonized as those that occurred at either (i) 0 plots in phase 1 and > 1 original plot in phase 3 or (ii) 0 plots in phases 1 and 2 and > 1 plot (original or new) in phase 3. We defined species that dropped out as those that occurred at > 1 plot in phase 1 and 0 plots in phase 3.

We additionally estimated bird abundances of 20 focal species separately (see Table 1 for list of species; number of species was chosen a priori). We chose focal species that occupied a variety of habitat types representing the range of possible responses to cattle grazing and subsequent removal and that were well-represented in our dataset. We defined abundance as the maximum number of individuals of a species detected during a visit to a plot within each phase (count-based abundance). We used maximum abundance because, when considering individual species, it is a more sensitive index of abundance than mean abundance, and it has been shown to produce better-fitting models (Toms et al., 2006). We placed each of these 20 species into one of the following functional groups (GBBO, 2010): (i) riparian woodland-tree or shrub dependent; (ii) riparian woodland-cavity nester; (iii) grassland or meadow; (iv) sagebrush obligate; and (v) avian nest parasite or native species competitor.

2.3. Vegetation data

We used the Normalized Difference Vegetation Index (NDVI) to measure changes in vegetation productivity during the three phases of our study. NDVI is calculated from surface reflectance data in visible and near-infrared bands that are acquired by sensors on satellites, such as Landsat (Robinson et al., 2017). It has been used as a proxy for a wide range of vegetation characteristics related to productivity, including canopy greenness and gross primary productivity (St-Louis et al., 2009, 2014). Avian populations also are known to respond to changes in vegetation as measured by NDVI. For example, NDVI accounted for > 80% of the variability in bird species richness in a semi-

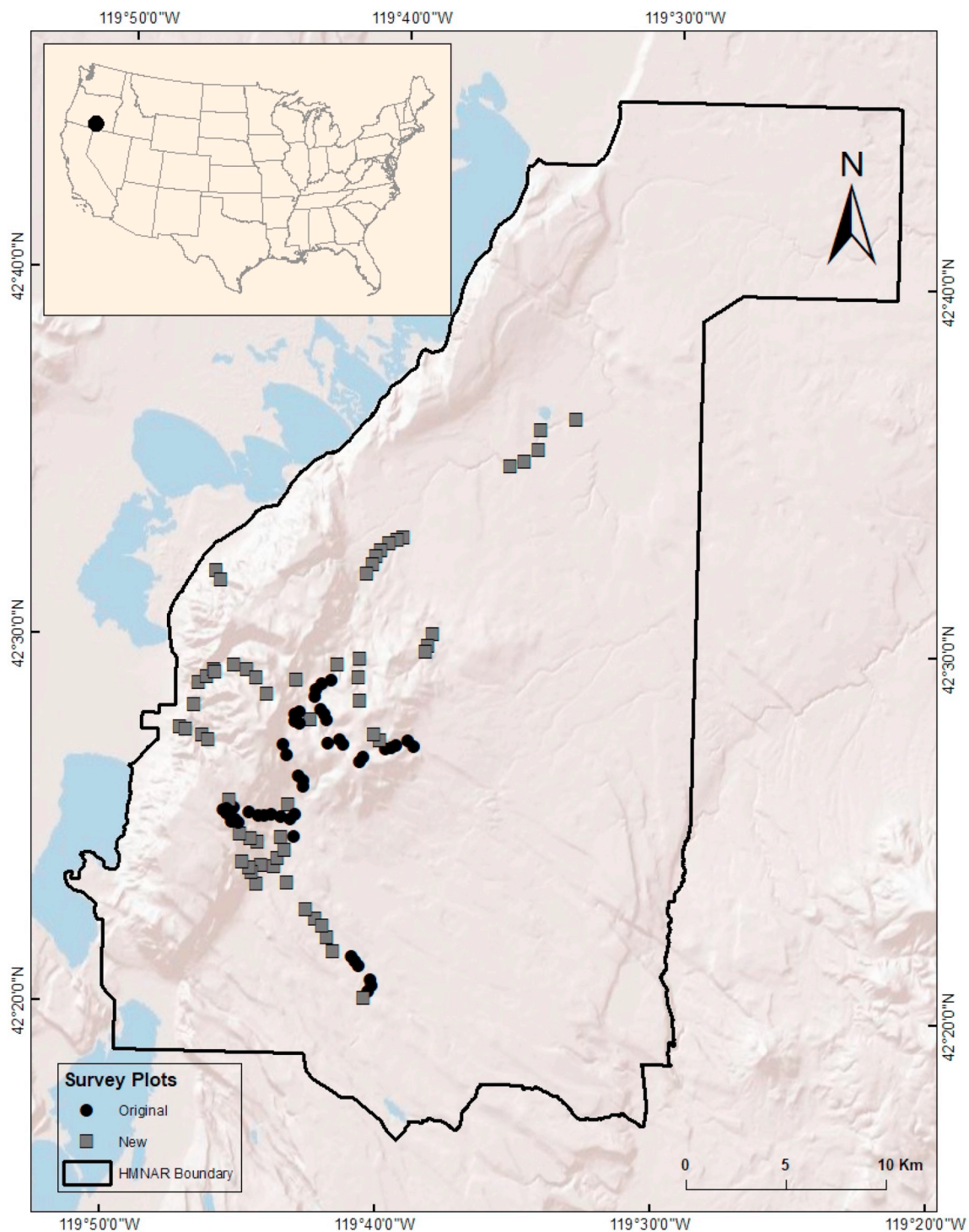


Fig. 1. Locations of the 106 survey plots (47 original, 59 new) at which bird surveys were conducted in Hart Mountain National Antelope Refuge (HMNAR), 1991–2014. Inset map shows the location of HMNAR (represented by black circle) in southeastern Oregon, USA.

arid landscape (St-Louis et al., 2009). NDVI has also been used to identify changes in community-scale cover of photosynthetic vegetation after changes in livestock grazing practices (Bradley and O'Sullivan, 2011).

We obtained NDVI data from the Landsat NDVI web application (<https://ndvi.ntsg.umn.edu/>), which produces, for each 30-m pixel on the landscape, 16-day composites of all available Landsat surface reflectance images (Robinson et al., 2017). If no images are available in the 16-day period, or all images in the period are covered by clouds or shadows, then the web application calculates the median NDVI of

available images over the same 16-day period from a user-specified number of previous years (the web application refers to this as a “climatology”). NDVI values are adjusted to account for radiometric differences across Landsat sensors (Robinson et al., 2017).

We downloaded NDVI data for each plot for each of the nine years of our study for three specific days of each year (days 145, 161, and 177), representing the end of May to the beginning of July. We chose this period because we expected vegetation (especially trees) then to be at maximum green-up. We chose a climatology of two years, and we also selected that the data be smoothed to account for atmospheric

Table 1

Local abundance response, regional population trends, and conservation concern score for 20 focal bird species within five functional groups during three phases of study after cattle removal at Hart Mountain National Antelope Refuge, 1991–2014.

Increase ^a				Decrease ^a			BBS trend ^b				Concern score ^c	
Functional group and common name		Early	Late	Steady	Early	Late	Steady	No change ^a	Oregon	Great Basin		Western BBS
Riparian Woodland-Tree or Shrub Dependent												
American robin	<i>Turdus migratorius</i>						X		Declining	Stable	Declining	5
Dusky flycatcher	<i>Empidonax oberholseri</i>		X						Stable	Declining	Stable	11
Green-tailed towhee ^d	<i>Pipilo chlorurus</i>		X						Declining	Declining	Stable	11
MacGillivray's warbler	<i>Geothlypis tolmiei</i>			X					Declining	Stable	Declining	12
Orange-crowned warbler	<i>Oreothlypis celata</i>		X						Declining	Deficient	Declining	9
Spotted towhee	<i>Pipilo maculatus</i>	X							Declining	Increasing	Stable	8
Warbling vireo	<i>Vireo gilvus</i>		X						Stable	Increasing	Increasing	9
Western wood-pewee	<i>Contopus sordidulus</i>							X	Declining	Increasing	Declining	11
Yellow warbler	<i>Setophaga petechia</i>			X					Declining	Stable	Declining	8
Riparian Woodland-Cavity Nester												
Mountain bluebird	<i>Sialia currucoides</i>					X			Stable	Increasing	Stable	12
Northern flicker	<i>Colaptes auratus</i>				X				Declining	Stable	Declining	9
Sapsuckers ^e	<i>Sphyrapicus</i> spp.				X				Deficient	Deficient	inc./stable	9, 11
Swallows ^f	<i>Tachycineta</i> spp.							X	Declining	Stable	Declining	10, 9
Grassland or Meadow												
Savannah sparrow	<i>Passerculus sandwichensis</i>		X						Declining	Declining	Declining	8
Vesper sparrow	<i>Poocetes gramineus</i>							X	Declining	Declining	Declining	11
Western meadowlark	<i>Sturnella neglecta</i>				X				Declining	Declining	Declining	10
Sagebrush Obligate												
Brewer's sparrow	<i>Spizella breweri</i>		X						Declining	Stable	Stable	11
Sage thrasher	<i>Oreoscoptes montanus</i>							X	Declining	Declining	Declining	11
Avian Nest Parasite or Native Species Competitor												
Brown-headed cowbird	<i>Molothrus ater</i>						X		Declining	Declining	Declining	7
European starling	<i>Sturnus vulgaris</i>				X				Declining	Declining	Declining	NA

^a Early increase or decrease indicates the most change between phases 1 and 2, late increase or decrease indicates the most change between phases 1 or 2 and 3, steady increase or decrease indicates a consistent change throughout all phases, and no change indicates no significant change throughout all phases.

^b BBS trend is the North American Breeding Bird Survey trend for populations of each species in Oregon, Great Basin, and Western BBS regions for 1966–2015. 'Deficient' indicates that insufficient BBS data were available, so no trend is reported. For the Western BBS region, one sapsucker species was increasing ('inc.') and the other was stable (see footnote *e* for description of the two sapsucker species).

^c Conservation concern scores were obtained from the State of North America's Birds 2016. Higher scores indicate greater conservation concern. Invasive European starlings were not scored.

^d Green-tailed towhee uses montane shrub and riparian habitats with a diversity of shrub species (GBBO, 2010).

^e Sapsucker species were primarily red-naped sapsucker (*Sphyrapicus nuchalis*) and hybrids with red-breasted sapsucker (*S. ruber*), although some birds were not identified to species and pure red-breasted sapsuckers may also be present.

^f Swallow species include tree swallow (*Tachycineta bicolor*) and violet-green swallow (*T. thalassina*).

contamination or poor data quality (Robinson et al., 2017).

Each study plot contained between 17 and 26 Landsat pixels. To obtain one NDVI value per plot per phase, we averaged, for each pixel, the nine NDVI values (three days for each of three years within a phase). We then calculated, for each phase, the mean of the average values of all pixels within the plot.

2.4. Statistical analyses

We tested our research hypothesis with three sets of models fit using R (R Core Team, 2017). In the first model set, we tested whether bird indices changed over time. We fit three models, one with each of the three bird metrics (abundance, species richness, and species diversity) as the response variable and phase (1, 2 or 3) as the predictor variable. For the bird abundance model, we log-transformed the response variable to meet distributional assumptions of linear models and used a Gaussian distribution. For the species richness model, we used a Poisson distribution because the response variable was a count of bird species. We ran linear mixed-effects models using the 'lme4' package (Bates et al., 2015) for both the bird abundance and species richness data, with the individual plot as a random effect in each model to account for multiple observations within a plot. For the species diversity model, no transformation allowed us to meet distributional assumptions, so we ran a non-parametric Kruskal-Wallis test (R Core Team, 2017).

In the second model set, we tested whether the vegetation index changed over time. We again used the 'lme4' package (Bates et al., 2015) to run one model with mean NDVI as the response variable, phase as the predictor variable, and plot as a random effect. We log-transformed the response variable to meet distributional assumptions and specified a Gaussian distribution.

For the first and second model sets, we used multiple comparisons to test whether phase was associated with the response variables. For the bird abundance, species richness, and vegetation index models, we used the emmeans function in the 'emmeans' package (Lenth, 2017) to run all pairwise comparisons of the phase variable with a Tukey adjustment. For the species diversity model, if the Kruskal-Wallis test was significant ($P < 0.05$), we used the dunn.test function in the 'dunn.test' package (Dinno, 2017) to run all pairwise comparisons of the phase variable with a Bonferroni adjustment.

In the third model set, we tested whether abundance of each of the 20 focal bird species responded to elevation, time, and changes in vegetation (as represented by NDVI) over time ($n = 47$ plots in phase 1 and 106 plots in phases 2 and 3). We included elevation as a fixed effect because of its known associations with bird species distributions (Martin, 2001). We averaged the ground elevation for each pixel in a given plot from a 30-m resolution digital elevation model (USGS, 2015). For modeling purposes, we rescaled the NDVI and elevation values by subtracting the mean and dividing by two times the standard

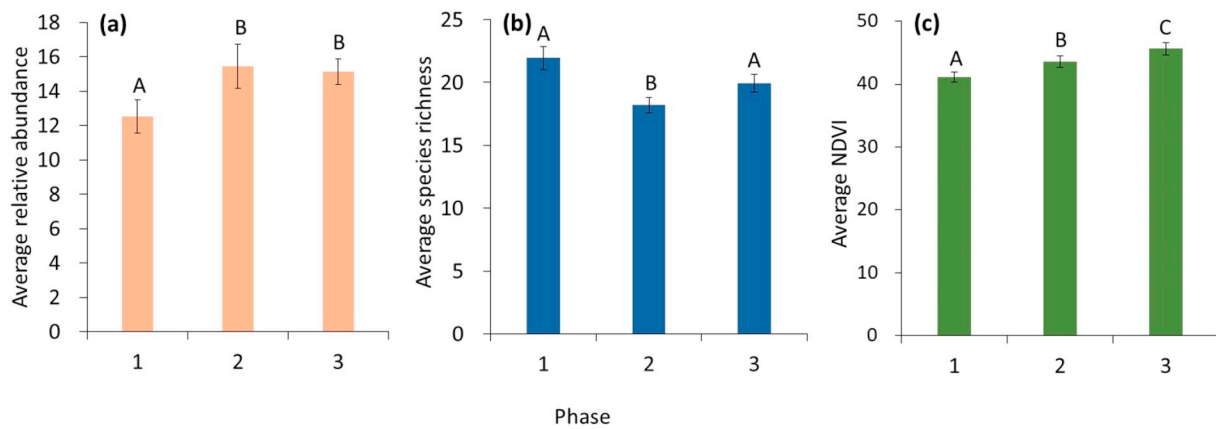


Fig. 2. Average (\pm SE) (a) relative abundance of birds detected per plot (all species combined), (b) species richness of birds per plot, and (c) Normalized Difference Vegetation Index (NDVI) per plot during three phases of study at Hart Mountain National Antelope Refuge, 1991–2014. Phase 1 occurred during 1991–1993, phase 2 occurred during 2000–2002, and phase 3 occurred during 2012–2014. Sample size in phase 1 was 47 plots in (a) and (b) and 106 plots in (c). Sample size in phases 2 and 3 was 106 plots. Within each panel, phases with different capital letters above bars are those that differ in statistical significance (see Supplementary Information Table S4).

deviation (Gelman, 2008).

We used a fixed-area survey method to generate our abundance index (Hutto, 2016). We assumed that all birds observed within a 50-m radius of either side of the transect in each plot had equal detectability (Norvell et al., 2003). The fixed-area survey is considered an effective way to control for potential distance-based detectability biases (Hutto, 2016, 2017).

Because the abundance data for each of the 20 focal species contained multiple zeroes (many plots had no detections of a species), we analyzed these data with zero-inflated models in the ‘glmmTMB’ package (Brooks et al., 2017). These models consist of two parts, a conditional model and a zero-inflation model. The conditional model is similar to a generalized linear mixed model (consisting of a response variable, one or more fixed effects, and one or more random effects). The zero-inflation model describes the probability of observing an extra zero. For each species, we ran 20 models with a combination of distributions (Supplementary Information Table S1) and zero-inflation parameters, including no zero-inflation (Supplementary Information Table S2). In each conditional model, we used the abundance of each species in a plot during each phase as the response variable, the rescaled NDVI nested within phase and the rescaled elevation as the fixed effect predictor variables, and plot as a random effect. We also tested for an effect of differing number of surveys between phases, but as this parameter did not improve model fit, we did not include the number of surveys in our final models (see Supplementary Information Model Selection for details). We nested NDVI within phase because of the positive association between these two variables (see Results; Schielzeth and Nakagawa, 2013).

For those models that converged, we then used Akaike's Information Criterion corrected for small sample size (AICc) to rank the models, and we based our inference on the best-performing model for each species (Burnham and Anderson, 2002; Anderson, 2008; Supplementary Information Model Selection, Table S3). We did not average among models because they specified different distributions. We categorized the response of each species as “early increase” or “early decrease” (a statistically significant change in the phase coefficients between phases 1 and 2 only), “late increase” or “late decrease” (significant change between phases 1 or 2 and 3 only), “steady increase” or “steady decrease” (consistent significant change throughout all phases), or “no change” (no significant change throughout all phases).

2.5. Population trends

We used North American Breeding Bird Survey (BBS) data to place

the responses of our focal species in the context of larger-scale population trends. The BBS is a joint effort between the U.S. Geological Survey and Environment Canada to monitor bird populations in the two countries. Long-term trends in avian populations are designated as declining, increasing, or stable based on analysis of survey data (Sauer et al., 2017). We obtained BBS trends for three regions, Oregon, Great Basin, and Western BBS, for 1966–2015 for each of the 20 focal species (Sauer et al., 2017). Oregon represents the “state-level” where wildlife conservation and management decisions are made but contains multiple vegetation types not present at HMNAR. The “Great Basin ecoregion-level” is representative of a smaller variety of land cover types and similar historical management practices as at HMNAR, but it includes a variety of vegetation types determined by differing elevations, precipitation, and phenologies. Finally, the Western BBS region represents a “semi-continent-level” that may influence smaller-scale habitat occupancy dynamics and trends in local abundance but, like Oregon, includes many vegetation types that were not sampled. For each species, we compared all three BBS trends to trends documented at HMNAR. We defined a “positive contradiction” as a population benefit at HMNAR compared to BBS (either an increasing or stable response at HMNAR when the BBS trend was declining, or an increasing response at HMNAR when the BBS trend was stable). We defined a “negative contradiction” as a population decline at HMNAR compared to BBS (either a decreasing or stable response at HMNAR when the BBS trend was increasing, or a decreasing response at HMNAR when the BBS trend was stable). A matching response was the same response at HMNAR as the BBS trend.

We obtained the conservation status of each species from the State of North America's Birds (NABCI, 2016). This report assigns a conservation concern score to each avian species. We evaluated the conservation concern status of each of the 20 focal species in the context of the change in abundance at HMNAR during the study and the BBS trend.

3. Results

Average bird abundance of all species increased between phases 1 and 2 ($P < 0.001$) and did not change between phases 2 and 3 (Fig. 2a; Supplementary Information Abundance and Species Richness by Phase, Table S4). Although the total number of bird species was higher in each phase than in the previous phase, species richness per plot decreased from phase 1 to phase 2 ($P = 0.007$) but increased from phase 2 to phase 3 ($P = 0.010$; Fig. 2b; Supplementary Information Abundance and Species Richness by Phase, Table S4). Species diversity did not

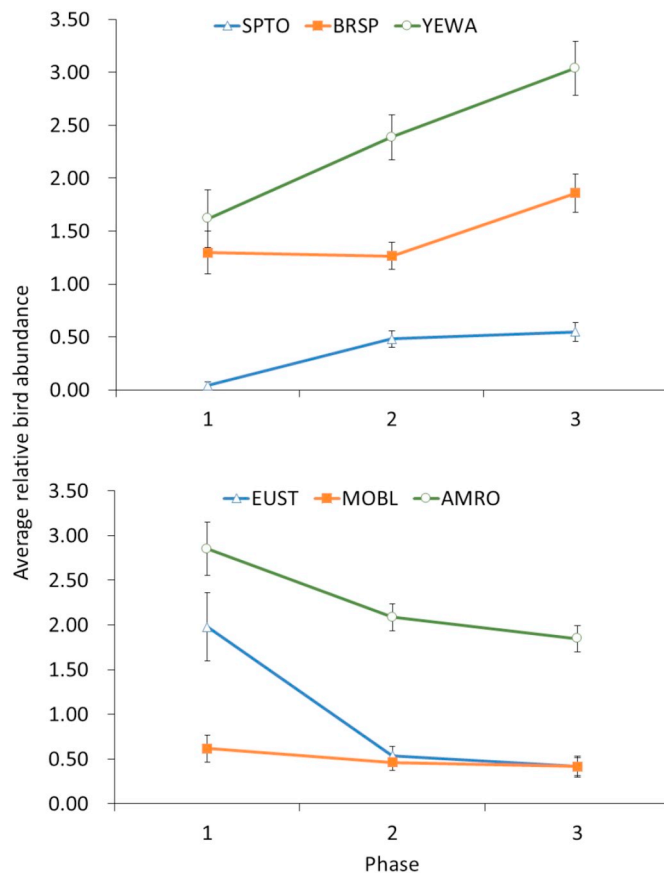


Fig. 3. Average (\pm SE) relative abundances of six bird species representing different types of responses during three phases of study after cattle removal at Hart Mountain National Antelope Refuge, 1991–2014. These represent: (a) early increase (spotted towhee [SPTO]; no other species showed this response), late increase (Brewer's sparrow [BRSP]; five other species responded similarly), and steady increase (yellow warbler [YEWA] and one other species) and (b) early decrease (European starling [EUST] and three other species), late decrease (mountain bluebird [MOBL] and no other species), and steady decrease (American robin [AMRO] and one other species). Phase 1 occurred during 1991–1993, phase 2 occurred during 2000–2002, and phase 3 occurred during 2012–2014. Sample size was 47 plots in phase 1 and 106 plots in both phases 2 and 3.

change among any of the three phases ($P = 0.482$; Supplementary Information Table S4). Over the course of the study, 12 species colonized study plots, but only four species dropped out (Supplementary Information Table S5). Average NDVI increased with time, indicating increases in vegetation productivity (phase 1 vs. phase 3: $P < 0.001$; Fig. 2c; Supplementary Information Fig. S1, Table S4).

Most riparian woodland-tree or shrub dependent focal avian species

increased in abundance after phase 1 (78%), and, of these, the majority increased late (Fig. 3a; Table 1; Supplementary Information Fig. S2; for specific species, see referenced figures). Most of these species also tended, within at least one phase, to be more abundant in areas with higher NDVI (Supplementary Information Table S6). Abundances of some species were correlated with elevation. However, we included elevation in our models to account for a potential source of variation in avian abundance, but we do not interpret its effect as it was not relevant to our focal research question.

The majority of riparian woodland-cavity nester focal species decreased in abundance after phase 1 (75%), usually decreasing early (Fig. 3b; Table 1; Supplementary Information Fig. S3). Abundances of most of these species were, within at least one phase, positively associated with NDVI (Supplementary Information Table S7). The abundances of grassland or meadow focal species varied following grazing removal, with one species showing a late increase, another showing an early decrease, and the third showing no change in abundance (Table 1; Supplementary Information Fig. S4). Abundances of most of these species were, within at least one phase, negatively associated with NDVI (Supplementary Information Table S8). One of the sagebrush obligate focal species showed a late increase in abundance following grazing removal and the other did not change (Fig. 3a; Table 1; Supplementary Information Fig. S5). Abundances of both of these species were, within at least one phase, negatively associated with NDVI (Supplementary Information Table S9). Both of the avian nest parasite or native species competitors decreased in abundance following removal of grazing, one early and one consistently throughout the study (Fig. 3b; Table 1; Supplementary Information Fig. S6). Abundances of both species were, within at least one phase, positively associated with NDVI (Supplementary Information Table S10).

Population trends at HMNAR were often opposite of declining large-scale trends. We observed positive contradiction of “state-level” population trends for 68% of focal species at HMNAR (i.e., trends at HMNAR were positive and opposite of trends from BBS data; Table 1; Supplementary Information Table S11). Five percent showed negative contradiction (HMNAR trends were negative and opposite of BBS trends), and one species had insufficient data to determine a BBS trend. Trends for the remaining five species matched those for BBS. We observed positive contradiction of “Great Basin ecoregion-level” population trends for 44% of focal species and negative contradiction for 22% (Table 1; Supplementary Information Table S11). Two species had insufficient data to determine a BBS trend. Finally, we observed positive contradiction of “western semi-continent-level” population trends for 60% of focal species and negative contradiction for 10% (Table 1; Supplementary Information Table S11).

We combined BBS trends across all spatial scales to represent the multiple spatial contexts relevant to evaluation of abundance changes at HMNAR within broader bird population dynamics. Of the 57 combined BBS trends (19 state-level, 18 ecoregion-level, and 20 semi-continent level), positive contradictions (58% of trends) were far more common than matching trends (30%) or negative contradictions (12%;

Table 2

Number of combined North American Breeding Bird Survey (BBS) trends at three spatial scales (Oregon, Great Basin, and Western BBS) and responses in abundances of 20 focal bird species during three phases of study after cattle removal at Hart Mountain National Antelope Refuge, 1991–2014. Light gray shaded cells indicate positive contradiction of trends, dark gray shaded cells indicate negative contradiction of trends, and cells with no fill (white) indicate matching response (no contradiction). Because trends are combined across spatial scales, each avian species is represented up to three times. In the Western BBS region, each of the two sapsucker species (see Table 1, footnote e for description of the two sapsucker species) had a different trend, one stable and one increasing. We assigned a stable trend (the more conservative of the two trends) to sapsuckers as a whole.

	Hart Mountain National Antelope Refuge		
BBS Combined	Decreasing	Stable	Increasing
Declining trend	13	10	14
Stable trend	5	1	9
Increasing trend	1	1	3

Table 2). The majority (58%) of positive contradictions were for riparian woodland-tree or shrub dependent species (Supplementary Information Table S12). The majority (71%) of negative contradictions were for riparian woodland-cavity nester species. All responses were positive for sagebrush obligate species, as were 67% of responses for grassland or meadow species. All responses for the avian nest parasite or native species competitors matched the BBS trends (declining; Supplementary Information Table S12).

Of the 14 focal species we studied that were of high or moderate conservation concern (conservation score > 8 [NABCI, 2016]), populations of six (43%) increased and four (28%) remained stable (Table 1). Of these species, 77% showed positive contradictions at the state level, 8% showed negative contradictions, and one species had insufficient data (Supplementary Information Table S11). Likewise, at the ecoregion level, 50% had positive contradictions, 25% had negative contradictions, and two species had insufficient data (Supplementary Information Table S11). Finally, at the semi-continent level, 64% showed positive contradictions and 14% showed negative contradictions (Supplementary Information Table S11).

4. Discussion

Our data suggest that removal of cattle was correlated with increases in vegetation productivity and in local abundances of many regionally declining avian species of conservation concern in the arid western United States. This is consistent with the hypothesis that these local trends were driven, at least in part, by restoring habitat on breeding grounds. Such patterns do not obviate the possibility that these declining bird populations are influenced by processes across the full annual cycle (both breeding and non-breeding seasons; Hostetler et al., 2015), but they provide a mechanism for how habitat alterations on breeding grounds might contribute to ongoing bird declines.

Although vegetation productivity, as measured by NDVI, recovered consistently across the three phases of the study (see Supplementary Information Alternative Explanations for Vegetation Change), we observed a broad range of temporal response patterns in the avian community. Overall avian abundance increased primarily between phases 1 and 2, indicating an immediate, relatively rapid positive response following the removal of cattle grazing. However, the three different responses of the focal bird species we observed – early, late, or steady – suggested differences in rates of change of key habitat elements. An increase in species richness per plot later in the study, and numbers of colonizing species that were 3 times higher than the numbers of species that dropped out, may have corresponded to increases in aspen tree diameter and the gradual development of habitat complexity over time (Tews et al., 2004). These patterns suggest that although responses of vegetation and some bird species can be rapid after removal of livestock grazing, ecosystem change can continue over many years in a long-term, dynamic process. Thus, some species at HMNAR may still be recovering > 24 years after cattle removal.

Riparian woodland-tree or shrub dependent species were most frequently affected positively after removal of cattle grazing, and the majority of these positive responses were delayed. The likely mechanism for the increase in abundance of these species was recovery of the riparian vegetation (i.e., tall, dense shrubs and trees; Supplementary Information Fig. S1) that these species rely upon for nesting and foraging (Martin and Possingham, 2005). Our work suggests that grazing may play at least a partial role in population-level declines observed at broader spatial scales of five species in this group – dusky flycatcher (*Empidonax oberholseri*), green-tailed towhee (*Pipilo chlorurus*), MacGillivray's warbler (*Geothlypis tolmiei*), orange-crowned warbler (*Oreothlypis celata*), and yellow warbler (*Setophaga petechia*; Table 1). In contrast, American robin (*Turdus migratorius*), the most abundant and broadly distributed thrush in North America (Vanderhoff et al., 2016), is the one species in this group that decreased in abundance. This response was not unexpected because robins are ubiquitous in pastures,

farmyards, and other agricultural landscapes and benefit from conversion of riparian forests to pastureland (Tewksbury et al., 2002).

The decline in cavity-nesting species may also reflect structural habitat change. Old aspen trees are susceptible to heart rot (*Phellinus tremulae*) infection, and primary cavity-nesting birds (northern flickers [*Colaptes auratus*] and red-naped sapsuckers [*Sphyrapicus nuchalis*]) are associated with rot-infected trees (Witt, 2010). Grazing appeared to cause a recruitment gap in riparian aspen stands at HMNAR. By phase 3 of our study, because of mortality of overstory trees, aspen stands were dominated by small- and medium-sized trees, resulting in only a few older individuals, and thus a near absence of heart rot (Beschta et al., 2014). Hence, the declines in primary cavity-nesting species likely reflect a deficit of suitable nest trees as a consequence of a disruption in aspen stand dynamics caused by a century of grazing (Dobkin et al., 1995). The current two-layered condition of aspen stands at HMNAR, with an upper layer of sparsely occurring mature trees and a dense understory of small trees, reflects recruitment of aspen since grazing removal (Beschta et al., 2014). However, these younger trees will need to mature over the next several years before they can provide suitable structural conditions for cavity-nesting species that prefer large-diameter trees (Earnst et al., 2012).

In addition to vegetation regrowth, decreases in both of the avian nest parasite or native species competitors after removal of cattle may have benefited other avian species by decreasing risk of nest failure. Brown-headed cowbirds (*Molothrus ater*) have a commensal feeding relationship with cattle and often abandon a site when cattle are removed (Goguen and Mathews, 2001). Furthermore, because cowbirds parasitize nests and reduce productivity of other bird species, declines in cowbirds may have thus contributed to increases in abundances of these species (Cox et al., 2012). European starlings (*Sturnus vulgaris*) rely upon short grasses to access their prey, and regional declines in starling abundance have been correlated with reductions in grazing pressure (Heldbjerg et al., 2016).

Finally, the sagebrush obligates and grassland or meadow species showed mixed responses after cattle removal. Although sagebrush cover declined in riparian areas (Earnst et al., 2012; Batchelor et al., 2015), removal of cattle likely allowed the recovery of adjacent sagebrush and meadow communities (Anderson and Holte, 1981). Recovery of depleted upland shrub-steppe landscapes can take a long time, a temporal lag that likely explains the lack of change or late increases in abundances of some of these species (i.e., vesper sparrow [*Pooecetes gramineus*; a grassland species] and Brewer's sparrow [*Spizella breweri*; a sagebrush species]).

The responses of avian species after regeneration of vegetation that followed grazing removal at HMNAR were consistent with findings in other studies. In New South Wales, Australia, avian species richness increased after restoration of vegetation by plantings of trees and shrubs (Ikin et al., 2019). Likewise, in Victoria, Australia, the opposite pattern was detected – woodland species decreased, and non-woodland species increased, in riparian zones where vegetation was denuded by heavy grazing (Hansen et al., 2019). Finally, in ranchlands near HMNAR, abundances of focal riparian bird species (including yellow warblers) declined since the 1990s, consistent with the state-level BBS trends (Ellis et al., 2019) and opposite of the trends we documented.

The changes in abundance that we observed over the study should be considered in the context of regional population dynamics. The majority of BBS trends were positively contradicted at HMNAR after removal of cattle. This pattern was particularly evident for those species of highest conservation concern and for riparian woodland-tree or shrub dependent species, sagebrush obligates, and grassland or meadow species. Such contradictions not only indicate potential causative agents for ongoing bird declines, but they also inform management options to restore avian populations. However, because each of the three regions we included in our comparison to HMNAR had different habitat types and climatic environments than did HMNAR, these regional trends may not be indicative of trends in riparian areas at each of these spatial scales.

5. Conclusions

Landscape-scale removal of livestock at HMNAR provided a rare opportunity to observe the potential effectiveness of passive restoration in riparian areas at a large spatial and temporal scale (Kauffman et al., 1997; Beschta et al., 2014; Batchelor et al., 2015). This work also illustrates the long temporal scales required to assess species responses to these types of habitat disturbances. In particular, the effects of cattle grazing endured for more than two decades after release from grazing pressure, and the abundance and occurrence of some species still appear to be in flux. On a global scale, riparian areas that have been damaged by livestock grazing and are in the process of recovery can be maintained by either continuing to exclude grazing or by implementing grazing systems that reduce impacts to riparian zones (George et al., 2011). Such maintained riparian areas may therefore function as refuges for avian populations that are otherwise declining across their range. Programs that further such protection can be an important strategy for conservation of imperiled migratory birds.

CRedit authorship contribution statement

Sharon A. Poessel: Methodology, Formal analysis, Data curation, Writing - original draft. **Joan C. Hagar:** Methodology, Supervision, Writing - review & editing. **Patricia K. Haggerty:** Data curation, Writing - review & editing. **Todd E. Katzner:** Methodology, Supervision, Writing - review & editing.

Declaration of competing interest

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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.2019.108378>.

References

- Anderson, D.R., 2008. *Model Based Inference in the Life Sciences: A Primer on Evidence*. Springer Science + Business Media LLC, New York, NY.
- Anderson, J.E., Holte, K.E., 1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangeland in southeastern Idaho. *J. Range Manag.* 34, 25–29.
- Armour, C.L., Duff, D.A., Elmore, W., 1994. The effects of livestock grazing on western riparian and stream ecosystem. *Fisheries* 19, 9–12.
- Batchelor, J.L., Ripple, W.J., Wilson, T.M., Painter, L.E., 2015. Restoration of riparian areas following the removal of cattle in the northwestern Great Basin. *Environ. Manag.* 55, 930–942.
- Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48.
- Belsky, A.J., Blumenthal, D.M., 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. *Conserv. Biol.* 11, 315–327.
- Belsky, A.J., Matzke, A., Uselman, S., 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. *J. Soil Water Conserv.* 54, 419–431.
- Beschta, R.L., Kauffman, J.B., Dobkin, D.S., Ellsworth, L.M., 2014. Long-term livestock grazing alters aspen age structure in the northwestern Great Basin. *For. Ecol. Manag.* 329, 30–36.
- Bradley, B.A., O'Sullivan, M.T., 2011. Assessing the short-term impacts of changing grazing regime at the landscape scale with remote sensing. *Int. J. Remote Sens.* 32, 5797–5813.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. Modeling zero-inflated count data with glmmTMB. *Ecol. Modelling*. BioRxiv. <https://doi.org/10.1101/132753>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, second ed. Springer, New York, NY.
- Cox, W.A., Thompson III, F.R., Root, B., Faaborg, J., 2012. Declining brown-headed cowbird (*Molothrus ater*) populations are associated with landscape-specific reductions in brood parasitism and increases in songbird productivity. *PLoS One* 7, e47591.
- Davies, K.W., Boyd, C.S., Bates, J.D., 2018. Eighty years of grazing by cattle modifies sagebrush and bunchgrass structure. *Rangeland Ecol. Manage.* 71, 275–280.
- Dinno, A., 2017. DunnTest: Dunn's test of multiple comparisons using rank sums (R package version 1.3.5). Available at: <https://cran.r-project.org/web/packages/dunnTest/index.html>.
- Dobkin, D.S., Rich, A.C., 1998. Comparison of line-transect, spot-map, and point-count surveys for birds in riparian habitats of the Great Basin. *J. Field Ornithol.* 69, 430–443.
- Dobkin, D.S., Rich, A.C., Pretare, J.A., Pyle, W.H., 1995. Nest-site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern Great Basin. *Condor* 97, 694–707.
- Dobkin, D.S., Rich, A.C., Pyle, W.H., 1998. Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the northwestern Great Basin. *Conserv. Biol.* 12, 209–221.
- Dybala, K.E., Truan, M.L., Engilis Jr., A., 2015. Summer vs. winter: examining the temporal distribution of avian biodiversity to inform conservation. *Condor* 117, 560–576.
- Earnst, S.L., Ballard, J.A., Dobkin, D.S., 2005. Riparian songbird abundance a decade after cattle removal on Hart Mountain and Sheldon National Wildlife Refuges. In: Ralph, C.J., Rich, T.D. (Eds.), *Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference*. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 550–558 Gen. Tech. Rep. PSW-GTR-191.
- Earnst, S.L., Dobkin, D.S., Ballard, J.A., 2012. Changes in avian and plant communities of aspen woodlands over 12 years after livestock removal in the northwestern Great Basin. *Conserv. Biol.* 26, 862–872.
- Ellis, M.S., Kennedy, P.L., Edge, W.D., Sanders, T.A., 2019. Twenty-year changes in riparian bird communities of east-central Oregon. *Wilson J. Ornithol.* 131, 43–61.
- Fleischner, T.L., 1994. Ecological costs of livestock grazing in western North America. *Conserv. Biol.* 8, 629–644.
- Gelman, A., 2008. Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* 27, 2865–2873.
- George, M.R., Jackson, R.D., Boyd, C.S., Tate, K.W., 2011. A scientific assessment of the effectiveness of riparian management practices. In: Briske, D.D. (Ed.), *Conservation Benefits of Rangeland Practices: Assessment, Recommendations, and Knowledge Gaps*. U.S. Department of Agriculture, Natural Resources Conservation Service. Allen Press Inc., Lawrence, KS, pp. 213–252.
- Goguen, C.B., Mathews, N.E., 2001. Brown-headed cowbird behavior and movements in relation to livestock grazing. *Ecol. Appl.* 11, 1533–1544.
- Great Basin Bird Observatory (GBBO), 2010. Nevada Comprehensive Bird Conservation Plan (Version 1.0). Great Basin Bird Observatory, Reno, NV Available at: <https://www.gbbo.org/bird-conservation-plan>, Accessed date: 20 April 2018.
- Hansen, B.D., Fraser, H.S., Jones, C.S., 2019. Livestock grazing effects on riparian bird breeding behaviour in agricultural landscapes. *Agric. Ecosyst. Environ.* 270–271, 93–102.
- Heldbjerg, H., Fox, A.D., Levin, G., Nyegaard, T., 2016. The decline of the Starling *Sturnus vulgaris* in Denmark is related to changes in grassland extent and intensity of cattle grazing. *Agric. Ecosyst. Environ.* 230, 24–31.
- Hobbs, R.J., 2001. Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. *Conserv. Biol.* 15, 1522–1528.
- Hostetler, J.A., Sillett, T.S., Marra, P.P., 2015. Full-annual-cycle population models for migratory birds. *Auk* 132, 433–449.
- Hutto, R.L., 2000. On the importance of en route periods to the conservation of migratory landbirds. *Stud. Avian Biol.* 20, 109–114.
- Hutto, R.L., 2016. Should scientists be required to use a model-based solution to adjust for possible distance-based detectability bias? *Ecol. Appl.* 26, 1287–1294.
- Hutto, R.L., 2017. Reply to Marques et al. (2017): how to best handle potential detectability bias. *Ecol. Appl.* 27, 1699–1702.
- Ikin, K., Barton, P.S., Blanchard, W., Crane, M., Stein, J., Lindenmayer, D.B., 2019. Avian functional responses to landscape recovery. *Proc. R. Soc. B* 286, 20190114.
- Kauffman, J.B., Beschta, R.L., Otting, N., Lytjen, D., 1997. An ecological perspective of riparian and stream restoration in the western United States. *Fisheries* 22, 12–24.
- Krebs, C.J., 2014. *Ecological Methodology*, third ed. (in prep). Available at: <https://www.zoology.ubc.ca/~krebs/books.html>, Accessed date: 22 November 2019.

- Krueper, D., Bart, J., Rich, T.D., 2003. Response of vegetation and breeding birds to the removal of cattle on the San Pedro River, Arizona (U.S.A.). *Conserv. Biol.* 17, 607–615.
- Lenth, R., 2017. emmeans: Estimated marginal means, aka least-squares means (R package version 1.0). <https://cran.r-project.org/web/packages/emmeans/index.html>.
- Martin, T.E., 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? *Ecology* 82, 175–188.
- Martin, T.G., Possingham, H.P., 2005. Predicting the impact of livestock grazing on birds using foraging height data. *J. Appl. Ecol.* 42, 400–408.
- North American Bird Conservation Initiative (NABCI), 2016. The state of North America's birds 2016. Available at: <http://www.stateofthebirds.org/2016>, Accessed date: 5 March 2018.
- Norvell, R.E., Howe, F.P., Parrish, J.R., 2003. A seven-year comparison of relative abundance and distance-sampling methods. *Auk* 120, 1013–1028.
- R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria Available at: <http://www.R-project.org>.
- Ralph, C.J., Droege, S., Sauer, J.R., 1995. Managing and monitoring birds using point counts: standards and applications. In: Ralph, C.J., Sauer, J.R., Droege, S. (Eds.), *Monitoring Bird Populations by Point Counts*. Gen. Tech. Rep. PSW-GTR-149. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 161–168.
- Robinson, N.P., Allred, B.W., Jones, M.O., Moreno, A., Kimball, J.S., Naugle, D.E., Erickson, T.A., Richardson, A.D., 2017. A dynamic Landsat derived Normalized Difference Vegetation Index (NDVI) product for the conterminous United States. *Remote Sens.* 9, 863.
- Saab, V.A., Bock, C.E., Rich, T.D., Dobkin, D.S., 1995. Livestock grazing effects in western North America. In: Martin, T.E., Finch, D.M. (Eds.), *Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues*. Oxford University Press, New York, NY, pp. 311–353.
- Sauer, J.R., Link, W.A., Fallon, J.E., Pardieck, K.L., Ziolkowski Jr., D.J., 2013. The North American Breeding Bird Survey 1966–2011: summary analysis and species accounts. *N. Am. Fauna* 79, 1–32.
- Sauer, J.R., Niven, D.K., Hines, J.E., Ziolkowski Jr., D.J., Pardieck, K.L., Fallon, J.E., Link, W.A., 2017. The North American Breeding Bird Survey, Results and Analysis 1966–2015 (Version 2.07.2017). U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD Available at: <https://www.pwrc.usgs.gov/bbs/index.cfm>, Accessed date: 3 May 2018.
- Schielzeth, H., Nakagawa, S., 2013. Nested by design: model fitting and interpretation in a mixed model era. *Methods Ecol. Evol.* 4, 14–24.
- Simpson, E.H., 1949. Measurement of diversity. *Nature* 163, 688.
- St-Louis, V., Pidgeon, A.M., Clayton, M.K., Locke, B.A., Bash, D., Radeloff, V.C., 2009. Satellite image texture and a vegetation index predict avian biodiversity in the Chihuahuan Desert of New Mexico. *Ecography* 32, 468–480.
- St-Louis, V., Pidgeon, A.M., Kuemmerle, T., Sonnenschein, R., Radeloff, V.C., Clayton, M.K., Locke, B.A., Bash, D., Hostert, P., 2014. Modelling avian biodiversity using raw, unclassified satellite imagery. *Philos. Trans. R. Soc. B* 369, 20130197.
- Swanson, S., Wyman, S., Evans, C., 2015. Practical grazing management to maintain or restore riparian functions and values on rangelands. *J. Range. Appl.* 2, 1–28.
- Tewksbury, J.J., Black, A.E., Nur, N., Saab, V.A., Logan, B.D., Dobkin, D.S., 2002. Effects of anthropogenic fragmentation and livestock grazing on western riparian bird communities. *Stud. Avian Biol.* 25, 158–202.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31, 79–92.
- Toms, J.D., Schmiegelow, F.K.A., Hannon, S.J., Villard, M.-A., 2006. Are point counts of boreal songbirds reliable proxies for more intensive abundance estimators? *Auk* 123, 438–454.
- U.S. Geological Survey (USGS), 2015. The National map, 3D elevation program. Available at: <http://nationalmap.gov/3dep.prodserv.html>, Accessed date: 11 January 2016.
- Vander Haegen, W.M., 2007. Fragmentation by agriculture influences reproductive success of birds in a shrubsteppe landscape. *Ecol. Appl.* 17, 934–947.
- Vanderhoff, N., Pyle, P., Patten, M.A., Sallabanks, R., James, F.C., 2016. American robin (*Turdus migratorius*) version 2.0. In: Rodewald, P.G. (Ed.), *The Birds of North America*. Cornell Lab of Ornithology, Ithaca, NY Available at <https://doi.org/10.2173/bna.462> (accessed 13 July 2018).
- Witt, C., 2010. Characteristics of aspen infected with heartrot: implications for cavity-nesting birds. *For. Ecol. Manag.* 260, 1010–1016.
- Wyman, S., Bailey, D.W., Borman, M., Cote, S., Eisner, J., Elmore, W., Leinard, B., Leonard, S., Reed, F., Swanson, S., Van Riper, L., Westfall, T., Wiley, R., Winward, A., 2006. Riparian area management: grazing management processes and strategies for riparian-wetland areas. Technical Reference 1737-20 Bureau of Land Management, Denver, CO.
- Yong-Zhong, S., Yu-Lin, L., Jian-Yuan, C., Wen-Zhi, Z., 2005. Influences of continuous grazing and livestock exclusion on soil properties in a degraded sandy grassland, Inner Mongolia, northern China. *Catena* 59, 267–278.