Impact of cattle grazing on the occupancy of a cryptic, threatened rail

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Abstract. Impacts of livestock grazing in arid and semiarid environments are often concentrated in and around wetlands where animals congregate for water, cooler temperatures, and green forage. We assessed the impacts of winter–spring (November–May) cattle grazing on marsh vegetation cover and occupancy of a highly secretive marsh bird that relies on dense vegetation cover, the California Black Rail (*Laterallus jamaicensis coturniculus*), in the northern Sierra Nevada foothills of California, USA. Using detection–nondetection data collected during repeated call playback surveys at grazed vs. ungrazed marshes and a "random changes in occupancy" parameterization of a multi-season occupancy model, we examined relationships between occupancy and habitat covariates, while accounting for imperfect detection. Marsh vegetation cover was significantly lower at grazed marshes than at ungrazed marshes during the grazing season in 2007 but not in 2008. Winter–spring grazing had little effect on Black Rail occupancy at irrigated marshes. However, at nonirrigated marshes fed by natural springs and streams, grazed sites had lower occupancy than ungrazed sites. Black Rail occupancy was positively associated with marsh area, irrigation as a water source, and summer vegetation cover, and negatively associated with marsh isolation. Residual dry matter (RDM), a commonly used metric of grazing intensity, was significantly associated with summer marsh vegetation cover at grazed sites but not spring cover. Direct monitoring of marsh vegetation cover, particularly at natural spring- or stream-fed marshes, is recommended to prevent negative impacts to rails from overgrazing.

Key words: Black Rail; detection probability; Laterallus jamaicensis coturniculus; *livestock grazing; marsh vegetation cover; multi-season occupancy models; random changes in occupancy; residual dry matter.*

INTRODUCTION

The impact of livestock grazing on wildlife is an issue of concern for both ecologists and natural resource managers. Cattle can act as vectors for diseases and parasites, degrade important wildlife habitats such as riparian forests, and contribute to the decline of native plant species through overgrazing (Fleischner 1994, Saab et al. 1995, Carrier and Czech 1996, Ohmart 1996). However, cattle grazing can also be used as a management tool to remove senescent vegetation, maintain native plant and aquatic diversity (Marty 2005), and improve water quality (Jackson et al. 2006). In arid environments, the impacts of grazing are often concentrated in wetlands and riparian areas where cattle congregate for water, cooler temperatures, and green forage (Kauffman and Krueger 1984, Belsky et al. 1999). In wetlands, cattle grazing results in reduced herbaceous vegetation height, cover, and biomass (Chabreck 1968,

Reimold et al. 1975, Hoffman and Stanley 1978), reduced residual litter (Gjersing 1975, Reimold et al. 1975, Mundinger 1976), reduced woody cover (Taylor 1986), increased productivity and N uptake (Schultz et al. 1994, Jackson et al. 2006), and increased or decreased plant species richness (Bakker and Ruyter 1981, Andresen et al. 1990, Marty 2005, Jackson and Allen-Diaz 2006). The impacts of grazing on wetlands are of particular concern because these ecosystems have experienced substantial historical declines in extent (Lemly et al. 2000), and they provide critical habitat for wildlife, including migratory birds and other wetland-dependent species (Mitsch and Gosselink 2000).

Grazing in wetlands is generally expected to negatively impact birds by reducing vegetation, which provides cover and nesting sites, although direct trampling of birds or nests and secondary changes to invertebrate communities may also be important (Weller 1996). However, previous studies found contrasting impacts on birds due to differences among species in their habitat requirements related to vegetation structure, and due to variation in the intensity, timing, and duration of grazing. Birds that require herbaceous vegetation or dense litter for nesting or foraging (e.g., dabbling ducks, bitterns, and rails) tend to decrease in abundance with increased grazing intensity, while species that prefer

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more open habitats (e.g., shorebirds) tend to increase in abundance (Kirsch 1969, Whyte and Cain 1979, Colwell and Dodd 1995, Belanger and Picard 1999, Warren et al. 2008). Light to moderate grazing in the emergent zone can improve waterfowl productivity in wetlands with dense, overgrown vegetation stands by increasing the interspersion of cover and open water for nesting and brooding (Kantrud 1986, Payne 1992, Schultz et al. 1994). The timing and duration of grazing are important determinants of impacts to waterbirds; rest-rotation grazing can result in higher waterfowl productivity than continuous (year-round) grazing (Gjersing 1975, Mundinger 1976, Lapointe et al. 2000, Carroll et al. 2007), but Ignatiuk and Duncan (2001) found no difference in productivity between these regimes. Heavy late-summer or fall grazing negatively impacts early-nesting duck species that rely on residual vegetation for nesting (Gjersing 1975, Mundinger 1976), while winter–spring grazing negatively impacts early- but not late-nesting duck species (West and Messmer 2006). While the effects of grazing on waterfowl have been fairly well studied, much less is known about grazing impacts on nongame waterbirds, particularly secretive species like rails.

We assessed the impacts of winter–spring grazing on a recently discovered resident metapopulation of California Black Rails (*Laterallus jamaicensis coturniculus*; hereafter "Black Rail") inhabiting a network of freshwater palustrine emergent persistent wetlands (Cowardin et al. 1979; hereafter "marshes") in the northern Sierra Nevada foothills of California (Richmond et al. 2008, Girard et al. 2010, Risk et al. 2011). This state-threatened and highly secretive subspecies (CDFG 2008) nests on the ground and depends on very dense emergent vegetation in permanent shallow marsh zones for cover (Eddleman et al. 1994, Flores and Eddleman 1995). Grazing has been identified as a threat to Black Rails because of their dependence on dense cover and their preference for the shallowest margins of marshes that are the most accessible to cattle (Eddleman et al. 1988). Furthermore, winter-spring grazing is expected to be especially detrimental because it occurs immediately prior to and during the Black Rail breeding season, which extends from approximately March–July. The primary aims of the study were to: (1) assess the relative intensity of winter-spring grazing; (2) evaluate the effects of grazing on marsh vegetation cover over the growing season; and (3) evaluate the effects of grazing on monthly Black Rail occupancy. We assessed grazing intensity by measuring upland residual plant biomass in annual grasslands adjacent to wetland sites and predicted that biomass would be lower at grazed marshes vs. ungrazed marshes. We predicted that marsh vegetation cover at grazed sites would be lower during the grazing season (November–May) and higher during the non-grazing season (June–October) as vegetation regrowth occurred. At grazed marshes, Black Rail occupancy should track changes in marsh vegetation cover during

the year if rails respond quickly to changes in vegetation structure, or remain lower throughout the year than at ungrazed marshes if rails do not respond rapidly to changes in cover. Overall, we predicted that ungrazed marshes would have greater marsh vegetation cover than grazed marshes and higher Black Rail occupancy.

METHODS

Study area

We surveyed 34 marshes in 2007 and 2008 in Nevada and Yuba counties in the Sierra foothills, California (for a detailed description of the study area see Richmond et al. 2008, 2010a). The region's mediterranean climate is characterized by hot, dry summers and cool, wet winters with an average annual precipitation of 76 cm that mostly falls between October and March (Lewis et al. 2000). Of the 34 marshes, 18 marshes received water primarily from irrigation inputs, while 16 marshes received water primarily from natural springs or streams. The marshes were small (1.08 ± 0.24 ha, mean ± SE; range 0.088–6.26 ha) and were surrounded by a variety of land cover types (oak woodland, annual grassland, riparian forest, agricultural, and residential). Most marshes (23) were located at Spenceville Wildlife Area (SWA), managed by the California Department of Fish and Game, while six marshes were located on a private ranch and five marshes were located at the Sierra Foothill Research and Extension Center (SFREC), managed by the University of California.

Estimating the effect of grazing on Black Rail habitat structure

We compared two grazing regimes: ungrazed (14 marshes; 10 irrigated marshes and 4 nonirrigated marshes) and winter–spring grazed (20 marshes; 8 irrigated marshes and 12 nonirrigated marshes). Ungrazed marshes had been fenced between 1998 and 2005 to exclude cattle. Grazed marshes had historically similar winter–spring grazing histories and were grazed from November to May in 2007 and 2008. Based on information provided by land managers, target stocking rates in grazed pastures ranged from 1.2 to 2.2 animal unit months (AUM)/ha. Target stocking rates give a general indication of grazing intensity at the pasture level, but may not necessarily relate to grazing impacts at specific locations within a pasture due to spatial heterogeneity in utilization (Barnes et al. 2008).

To estimate marsh-specific levels of grazing intensity, we measured residual dry matter (RDM) in annual grasslands adjacent to 27 marshes in October 2008. RDM is the amount of dead plant biomass left on the land surface at the end of a growing season, and it represents the total forage production from the previous growing season minus plant biomass removed by grazers. It is also a commonly used metric for assessing grazing intensity on rangelands in California (Bartolome et al. 2002), and therefore might be a useful tool for setting optimal grazing levels. To measure RDM, we

clipped dead plant material (excluding tree leaves and twigs) at five 30 × 30 cm plots randomly placed within a buffer of 50 m in the upland zone surrounding each marsh. At ungrazed marshes, RDM plots were located in upland areas within 50 m of the marsh edge where grazing was excluded. We dried all samples at 65°C for 48 hours, weighed each sample immediately after removal from the oven, and averaged the five sample masses from each site to obtain an average RDM value, expressed in units of pounds per acre. From previous studies in this region of California, RDM values between 0 and 600 pounds/acre (673 kg/ha) indicate heavy grazing, 600–800 pounds/acre (673–897 kg/ha) indicate moderate grazing, 800–1200 pounds/acre (897–1345 kg/ha) indicate light grazing, and >1200 pounds/acre (1345 kg/ha) indicate ungrazed conditions (Allen-Diaz et al. 2004).

To assess the effect of grazing on marsh vegetation, we sampled vegetation cover at 19 marshes monthly from April to July in 2007 and at 27 marshes in March and August of 2008. At each marsh, a zig-zag transect was walked and, at 10-m intervals, we recorded the presence or absence of vegetation touching a vertically held 1.2-m pole in three height strata: (1) 0–50; (2) 50–100; and (3) >100 cm. The first transect segment was walked from the marsh edge toward the marsh center in the direction of the initial bearing plus 45°. When the marsh boundary was reached, the surveyor rotated 225° and walked the second segment in a straight line until again reaching the marsh boundary, rotating 225° and walking the third segment, repeating this procedure until the entire marsh was covered. Vegetation cover was calculated by averaging the proportion of height strata where vegetation had touched the pole across all points at each marsh.

Black Rail occupancy surveys

To estimate Black Rail occupancy, we conducted call playback surveys, which are a standard method for monitoring trends in populations of secretive marsh birds (Gibbs and Melvin 1997, Lor and Malecki 2002, Conway and Gibbs 2005). In 2007, playback surveys were conducted twice monthly at 20 marshes from April to August and at least once monthly at 14 marshes in June and July, for a total of 239 visits. In 2008, playback surveys were conducted twice monthly at 27 marshes from February to October, excluding September, and at least once monthly from June to August at seven marshes, for a total of 416 visits. Visits within a month were separated by 1–3 days. Playback surveys were conducted from 30 min before until 210 min after sunrise and from 180 min before until 30 min after sunset. During playback surveys, locally recorded Black Rail vocalizations were broadcast at stations spaced 50 m apart within each marsh. If we did not detect a Black Rail at the first station, we walked 50 m farther into suitable habitat and repeated the playback sequence. Occupancy surveys ended at a marsh either when we

detected one or more rails, or when we had surveyed the entire marsh. A detailed description of the call playback protocol is available in Richmond et al. (2008). For each marsh, we also recorded whether it received irrigation water as the primary water source and calculated marsh area and isolation. Isolation was calculated as the log geometric mean distance to the nearest three marshes in the mapped network of over 200 marshes (Richmond et al. 2008) that were occupied in 2007 or 2008. Marsh perimeters had previously been mapped using a backpack Trimble GPS unit (Sunnyvale, California, USA) capable of determining three-dimensional positions with 0.5-m accuracy (Richmond et al. 2008, 2010b). Non-rail habitat, including zones of open water and areas with non-hydrophytic vegetation, were excluded from marsh area calculations.

Analyzing the effect of grazing on habitat structure

We used a t test to determine if mean RDM differed significantly between grazed and ungrazed sites, after determining that our data met the assumptions required for parametric tests by examining Q-Q plots and the variance across grazing regime groups. We examined the association between marsh vegetation cover, measured in March and August of 2008, and RDM, measured in October 2008, using Pearson's correlation coefficient. To analyze the effects of grazing regime on marsh vegetation cover across months, we performed repeated-measures ANOVAs for 2007 and 2008. Statistical analyses were performed in Program R version 2.10.1 (R Development Core Team 2008) and Systat 12 (Systat Software 2004).

Analyzing the effect of grazing on Black Rail occupancy

We modeled Black Rail occupancy (ψ_t) using the "random changes in occupancy" multi-season model parameterization developed by MacKenzie et al. (2006) and fit the models in Program Presence, version 4.1 (Hines 2006). The random changes in occupancy parameterization is considered an implicit dynamics model because colonization and extinction dynamics are not explicitly modeled; it is essentially equivalent to fitting a series of single-season occupancy models. While changes in marsh occupancy in our study system probably depend on occupancy in the previous time step, suggesting that a Markov model would be superior, we were unable to fit models with explicit occupancy dynamics because they were overparameterized given the data and resulted in inestimable parameters. The random changes in occupancy parameterization has fewer parameters than the multi-season occupancy model parameterization with explicit dynamics. This facilitates model fitting when occupancy data are available but consist of few colonization or extinction events, which described our data set. For a more detailed description of this model parameterization, see Appendix A.

Like other multi-season occupancy models, the random changes in occupancy parameterization allows
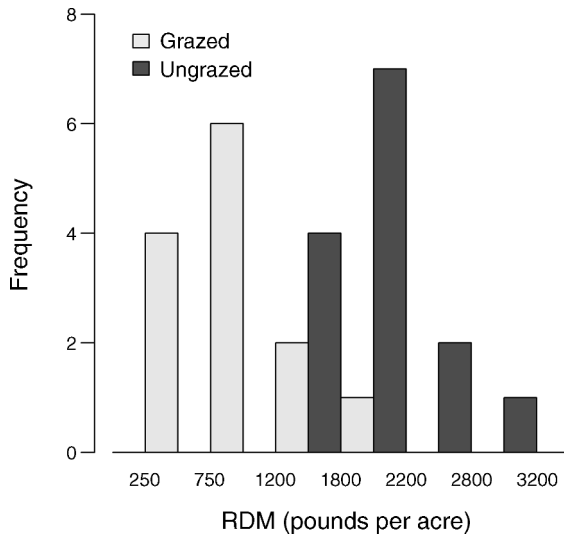
FIG. 1. Histograms of residual dry matter (RDM) measured adjacent to ungrazed ($N = 14$) and winter–spring grazed ($N = 13$) marshes in 2008 in the northern Sierra Nevada foothills, California, USA. One pound per acre = 1.12 kg/ha.

for changes in occupancy among seasons (sampling periods), but sites are assumed to be closed to changes in occupancy within seasons. This is a reasonable assumption in our study because repeated visits conducted during each season (month) were separated by only 1–3 days. We first evaluated the effects of day of year (1 January equals day 1), year, and month on detection probability (p) with a set of eight models. Year was strongly supported as a covariate for detection (cumulative AIC_c weight of 0.99), while day of year and month received less support as detection covariates (Appendix B).

Using the best detection model, with year as a covariate for detection, we then fit a set of 21 candidate models to test the effects of grazing regime, month, and year on occupancy (ψ_t). From previous studies in this system, we knew that Black Rail occupancy was strongly positively associated with area and irrigation water as a primary source, and was negatively associated with isolation (Richmond et al. 2010*a*, *b*), a measure of spatial covariation typically used in metapopulation models (Hanski 1999, Risk et al. 2011). Thus, we accounted for these important covariates by including them in all models in the set. We predicted that marsh vegetation cover at marshes fed primarily by irrigation water would be more resilient to grazing than at nonirrigated marshes due to higher water availability during the summer growing season, so we tested a grazing × irrigation interaction. We predicted that larger marshes might maintain more residual cover in the presence of grazing than smaller marshes, so we also tested a grazing × area interaction. Competing models were ranked using Akaike's Information Criterion (Burnham and Anderson 2002) corrected for small sample size (AIC_c) using the

number of sites surveyed (34 sites) as a conservative estimate of sample size. The relative importance of each model parameter was determined by summing the Akaike weights for each model that contained the parameter of interest (Burnham and Anderson 2002). To compare effect sizes of parameters, parameter estimates were averaged across the top four models using AIC_c weights, and model-averaged unconditional standard errors were obtained using Eq. 4.3 in Burnham and Anderson (2002:159). Finally, predicted values for Black Rail occupancy were averaged over the top four models in the candidate set, which had a cumulative Akaike weight of 0.96, using AIC_c weights (Burnham and Anderson 2002). In a post hoc analysis, we fit a set of four candidate models using the random changes in occupancy parameterization to examine the effect of spring vs. summer marsh vegetation cover on Black Rail occupancy as a test of the general hypothesis that Black Rails are associated with dense vegetative cover. For this model set, we included area, isolation, and irrigation as covariates for occupancy, and year as a covariate for detection in all models. Competing models were ranked using AIC_c and the top model was used to obtain estimates of occupancy as a function of marsh vegetation cover. Our two-step approach to model selection (fitting detection models first and then occupancy models) allowed us to simplify the structure of nuisance (detection) parameters when examining the comparisons of greatest biological interest. Unless otherwise specified, means are presented ±SE.

RESULTS

Effect of grazing on habitat structure

RDM measured in annual grasslands adjacent to marshes was significantly greater at ungrazed than at grazed sites ($t = 8.25$, $P < 0.001$; Fig. 1). Six marshes were characterized as heavily grazed (RDM <600 pounds/acre [673 kg/ha]), two marshes were moderately grazed (RDM 600–800 pounds/acre [673–897 kg/ha]), two marshes were lightly grazed (RDM 800–1200 pounds/acre [897–1345 kg/ha]), and 17 marshes had RDM values consistent with ungrazed pastures (RDM >1200 pounds/acre [1345 kg/ha]). RDM was not significantly correlated with marsh vegetation cover in March at ungrazed ($r = -0.02$, $P = 0.96$) or grazed sites ($r = 0.28$, $P = 0.36$). In contrast, RDM was significantly positively correlated with August marsh vegetation cover at grazed ($r = 0.61$, $P = 0.026$) but not at ungrazed marshes ($r = -0.41$, $P = 0.15$).

Grazed marshes had less marsh vegetation cover than ungrazed marshes in 2007 but not in 2008 (Fig. 2). Marsh vegetation cover differed significantly by grazing regime (repeated-measures ANOVA, $F_{1,19} = 8.14$, $P = 0.011$) and by month ($F_{3,19} = 12.51$, $P < 0.001$) in 2007. There was also a significant grazing regime × month interaction ($F_{3,19} = 8.26$, $P = 0.001$); ungrazed marshes maintained high marsh vegetation cover, while grazed marshes started with lower marsh vegetation cover than
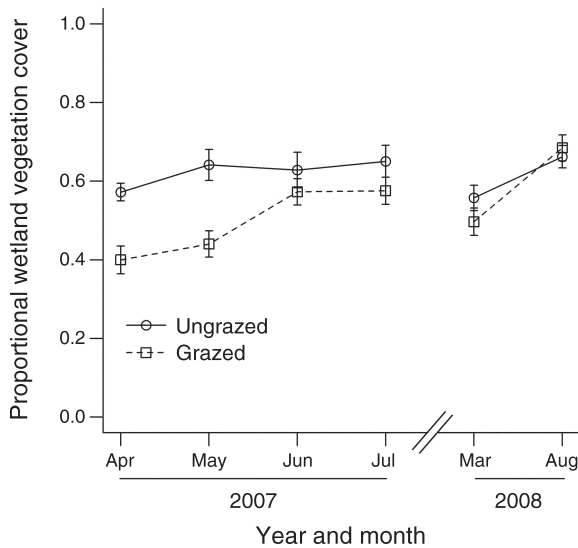
FIG. 2. Marsh vegetation cover at ungrazed ($N = 7$ and $N = 14$) and winter–spring grazed ($N = 12$ and $N = 13$) marshes in 2007 and 2008, respectively, in the northern Sierra Nevada foothills, California, USA. Error bars represent ±SE.

ungrazed marshes in April and May, but by June and July the vegetation at grazed marshes recovered almost to the level of the ungrazed sites (Fig. 2). In 2008, marsh vegetation cover did not differ significantly by grazing regime (repeated-measures ANOVA, $F_{2,31} = 0.63$, $P = 0.54$), did differ significantly by time ($F_{2,31} = 29.40$, $P < 0.001$), and did not show a significant grazing regime × month interaction ($F_{2,31} = 2.18$, $P = 0.13$). In 2008, marsh vegetation cover increased at both ungrazed and grazed marshes from March to August (Fig. 2).

When we examined the same data set taking water source into account (irrigated vs. nonirrigated), marsh vegetation cover again differed significantly by grazing regime (repeated-measures ANOVA, $F_{1,15} = 6.45$, $P = 0.023$) and by month ($F_{3,45} = 18.97$, $P < 0.001$), and there was a significant grazing regime × month interaction ($F_{3,45} = 7.22$, $P < 0.001$) but no significant effect of water source ($F_{1,15} = 0.15$, $P = 0.701$; Fig. 3). In 2008, marsh vegetation cover differed significantly by month ($F_{1,23} = 4.48$, $P < 0.001$), but there was no significant effect of grazing regime or water source.

Effect of grazing on Black Rail occupancy

Grazing regime was included in the top four models, with a cumulative Akaike weight of 0.97 (Table 1). There was strong support for models that included a grazing × irrigation interaction parameter (cumulative Akaike weight = 0.96), while models that included grazing regime but did not include this interaction received little support (cumulative Akaike weight = 0.01). Month received almost no support as a covariate for occupancy (cumulative AIC_c weight <0.01), while year received moderate support (cumulative AIC_c weight = 0.43), with slightly higher occupancy estimated

for 2008. Parameters with the largest effect sizes were marsh area (positive effect), the grazing × irrigation interaction (positive effect), grazing alone (negative effect), and isolation (negative effect; Table 2).

Black Rail occupancy at irrigated sites was positively impacted by winter–spring grazing, whereas occupancy at nonirrigated sites was negatively impacted by grazing. This result was consistent across the range of values for marsh area and isolation that were represented in our data set (Figs. 4 and 5, respectively). Consequently, sites that were both irrigated and grazed had the highest levels of occupancy, whereas sites that were not irrigated yet grazed had the lowest levels of occupancy (Figs. 4 and 5).

In a post hoc analysis of the effect of marsh vegetation cover on Black Rail occupancy, there was strong support for a model that included summer vegetation cover (Akaike weight = 0.71) as a covariate for occupancy and weaker support for a model including spring vegetation cover (Akaike weight = 0.29; Appendix C). Occupancy rose substantially at irrigated marshes with summer cover greater than ~60%, holding area and isolation constant at their medians, but summer cover had little effect on occupancy at nonirrigated sites (Fig. 6).

DISCUSSION

Effect of grazing on habitat structure

As expected, upland annual grasslands adjacent to marshes that were grazed had lower residual biomass than grasslands adjacent to ungrazed marshes (Fig. 1). This is consistent with previous studies that have documented reduced herbaceous biomass in the pres-
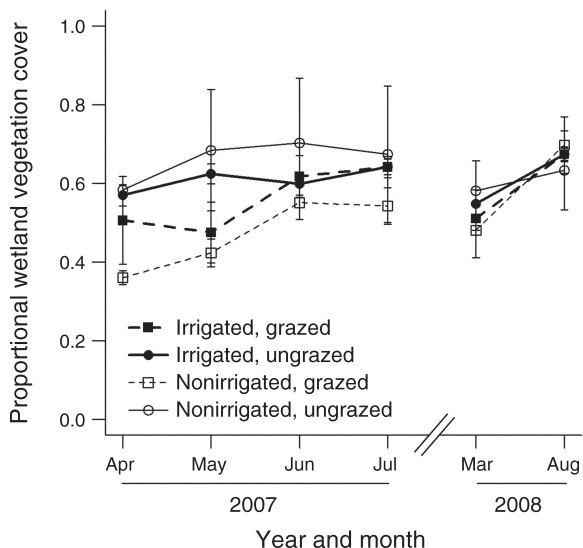

FIG. 3. Marsh vegetation cover at irrigated and winter–spring grazed ($N = 8$), irrigated and ungrazed ($N = 10$), nonirrigated and winter–spring grazed ($N = 12$), and nonirrigated and ungrazed ($N = 4$) marshes in 2007 and 2008 in the northern Sierra Nevada foothills, California. Error bars represent ±SE.

TABLE 1. Model selection results for 21 occupancy models fit to 2007–2008 California Black Rail (*Laterallus jamaicensis coturniculus*) detection data from 34 marshes in the Sierra Nevada foothills, California, USA.

Model	K	AIC_c	ΔAIC_c	w	Model likelihood
ψ(Area, Isol, Irr, Grz, Grz × Irr), p(Year)	8	345.01	0.00	0.48	1.00
ψ(Area, Isol, Irr, Grz, Grz × Irr, Year), p(Year)	9	345.58	0.57	0.36	0.75
ψ(Area, Isol, Irr, Grz, Grz × Irr, Grz × Area), p(Year)	9	348.70	3.69	0.08	0.16
ψ(Area, Isol, Irr, Grz, Grz × Irr, Grz × Area, Year), p(Year)	10	349.57	4.56	0.05	0.10
ψ(Area, Isol, Irr, Year), p(Year)	7	351.38	6.37	0.02	0.04
ψ(Area, Isol, Irr), p(Year)	6	352.02	7.01	0.01	0.03
ψ(Area, Isol, Irr, Grz, Year), p(Year)	8	354.83	9.82	0.00	0.01
ψ(Area, Isol, Irr, Grz), p(Year)	7	355.20	10.19	0.00	0.01
ψ(Area, Isol, Irr, Grz, Grz × Area, Year), p(Year)	9	358.55	13.54	0.00	0.00
ψ(Area, Isol, Irr, Grz, Grz × Area), p(Year)	8	358.65	13.64	0.00	0.00
ψ(Area, Isol, Irr, Grz, Grz × Irr, Month), p(Year)	15	372.28	27.27	0.00	0.00
ψ(Area, Isol, Irr, Month), p(Year)	13	373.35	28.34	0.00	0.00
ψ(Area, Isol, Irr, Month, Year), p(Year)	14	377.40	32.39	0.00	0.00
ψ(Area, Isol, Irr, Grz, Grz × Irr, Year, Month), p(Year)	16	378.07	33.06	0.00	0.00
ψ(Area, Isol, Irr, Grz, Month), p(Year)	14	379.26	34.25	0.00	0.00
ψ(Area, Isol, Irr, Grz, Grz × Irr, Grz × Area, Month), p(Year)	16	379.50	34.49	0.00	0.00
ψ(Area, Isol, Irr, Month, Year, Grz), p(Year)	15	383.96	38.95	0.00	0.00
ψ(Area, Isol, Irr, Grz, Grz × Area, Month), p(Year)	15	385.80	40.79	0.00	0.00
ψ(Area, Isol, Irr, Grz, Grz × Irr, Grz × Area, Year, Month), p(Year)	17	386.20	41.19	0.00	0.00
ψ(Area, Isol, Irr, Grz, Grz × Area, Year, Month), p(Year)	16	391.24	46.23	0.00	0.00
ψ(.), p(Year)	3	511.32	166.31	0.00	0.00

Notes: The model set compared the effects of winter–spring grazing (Grz), month, and year on Black Rail occupancy (ψ) using the random changes in occupancy multi-season parameterization. Two interactions, grazing regime × irrigation (Grz × Irr) and grazing regime × area (Grz × Area), were also tested. All models in the set included marsh area (Area), isolation (Isol), and irrigation (Irr) as covariates. ΔAIC_c is the difference in AIC_c relative to the best model, w is the Akaike weight that indicates the relative support for each model, and K is the number of parameters. Detection probability (p) was modeled as a function of year.

ence of grazing (Jones 2000). Differences in phenology complicated our efforts to examine correlations between upland and marsh vegetation. While we expected to find a correlation between upland grassland residual biomass (RDM; a cumulative measure of grazing intensity throughout one growing season) and marsh vegetation cover, instead we found that this relationship differed depending on when marsh cover was measured. We found no significant correlation between RDM and marsh vegetation cover in March (Fig. 2), but RDM was positively correlated with marsh vegetation cover in August at grazed sites (Fig. 3). Marshes measured for cover in March were subsequently grazed for two additional months (April and May), while marshes measured for cover in August had received their total

amount of livestock grazing for the year. It was, nevertheless, somewhat surprising that RDM was significantly associated with August marsh vegetation cover given the substantial amount of marsh vegetation regrowth that we observed by July in 2007 and by August in 2008 (Fig. 2).

From a management standpoint, it would be useful to know if RDM can be used to approximate grazing impacts on marsh vegetation cover because RDM guidelines are already used by managers to assess rangeland condition and ensure forage sustainability (Allen-Diaz and Jackson 2005). One previous study found that optimal levels of residual upland vegetation for maintaining riparian habitats varied with elevation and stream bank stability (e.g., Clary and Leininger

TABLE 2. Parameter estimates under the top four multi-season occupancy models in Table 1.

Parameter	Model 1† Estimate	SE	Model 2‡ Estimate	SE	Model 3§ Estimate	SE	Model 4¶ Estimate	SE	Model averaged Estimate	SE
Intercept	−1.36	0.82	−1.20	0.82	−1.34	0.82	−1.16	0.83	−1.29	0.79
Area	11.19	2.22	10.73	2.31	10.64	3.39	9.85	3.79	10.91	2.34
Isolation	−2.42	1.22	−2.44	1.21	−2.43	1.22	−2.46	1.21	−2.43	1.17
Grazing	−3.61	1.09	−3.51	1.11	−3.74	1.28	−3.68	1.29	−3.59	1.08
Irrigation	0.68	0.67	0.71	0.67	0.71	0.69	0.76	0.69	0.70	0.64
Grazing × Area					0.93	4.43	1.36	4.73	1.10	4.55
Grazing × Irr	4.06	1.18	3.97	1.19	4.11	1.23	4.04	1.24	4.03	1.14
Year			−0.74	0.41			−0.75	0.42	−0.74	0.41

Note: Model-averaged parameter estimates and standard errors were averaged over all four models using their AIC_c weights (Table 1).
† Model 1: ψ(Area, Isol, Irr, Grz, Grz × Irr), p(Year).
‡ Model 2: ψ(Area, Isol, Irr, Grz, Grz × Irr, Year), p(Year).
§ Model 3: ψ(Area, Isol, Irr, Grz, Grz × Irr, Grz × Area), p(Year).
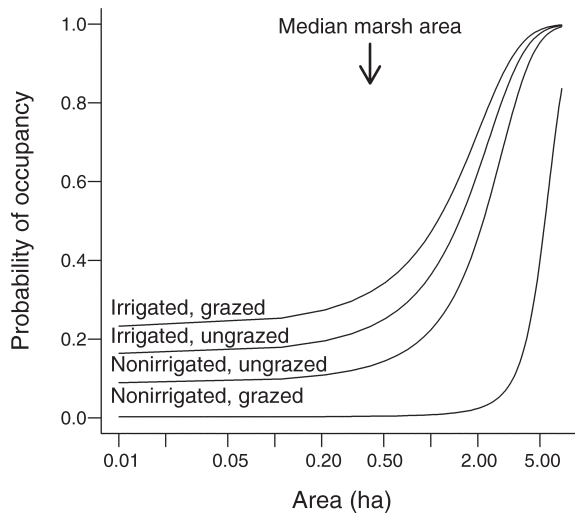¶ Model 4: ψ(Area, Isol, Irr, Grz, Grz × Irr, Grz × Area, Year), p(Year).

FIG. 4. The effect of area, irrigation, and grazing regime on model-averaged Black Rail (*Laterallus jamaicensis coturniculus*) occupancy (averaging over the top four models from Table 1) for ungrazed and winter–spring grazed marshes, holding marsh isolation constant at the median and averaging across years (2007 and 2008).

FIG. 6. The effect of summer marsh vegetation cover and irrigation on model-averaged Black Rail occupancy, holding area and isolation constant at the median and averaging across years.

2000). Our results indicate that RDM may be an indicator of summer marsh vegetation cover; however, spring cover was not associated with RDM and is likely to be more critical for breeding success for Black Rails and other ground-nesting birds (West and Messmer 2006). Consequently, we do not believe that measuring RDM is an adequate substitute for direct monitoring of marsh cover, particularly spring marsh cover.
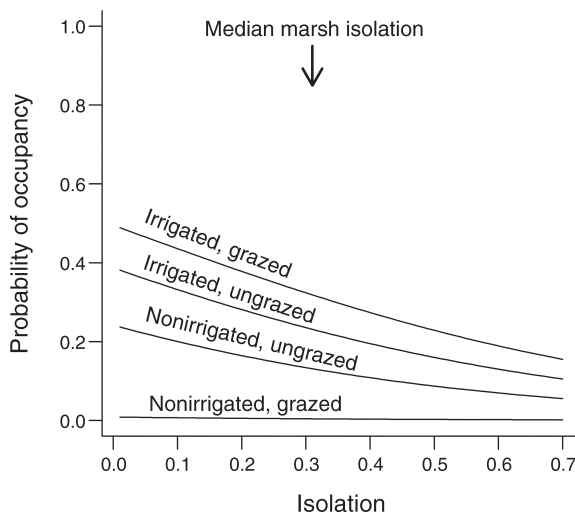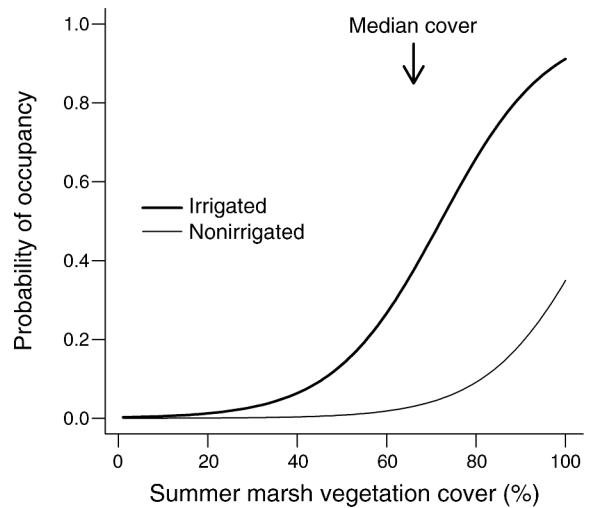

FIG. 5. The effect of isolation (log of geometric mean distance [originally measured in km] to the nearest three marshes that were occupied in 2007 or 2008), irrigation, and grazing regime on model-averaged Black Rail occupancy (averaging over the top four models from Table 1) for ungrazed and winter–spring grazed marshes, holding marsh area constant at the median and averaging across years (2007 and 2008).

While winter–spring grazing had a significant effect on marsh vegetation cover in 2007, it did not have a significant effect in 2008. In 2007, grazed marshes had lower marsh vegetation cover during and immediately following the winter–spring grazing season than ungrazed marshes, but then recovered after cattle were removed (Figs. 2 and 3). In 2008, the lack of a significant grazing effect on marsh vegetation may be due to the fact that spring marsh cover was measured only once and earlier (March) than in 2007 (April and May). We anecdotally observed that some grazed marshes in 2008 were not heavily used by cattle until April and May, after marsh cover had already been measured. Thus, the 2008 marsh vegetation data likely do not accurately reflect the full grazing impacts for that year.

Effect of grazing on Black Rail occupancy

The effect of grazing on Black Rail occupancy differed between irrigated and nonirrigated marshes (Figs. 4 and 5), which provokes at least two questions. First, why was Black Rail occupancy higher overall at irrigated vs. nonirrigated marshes? Second, why was winter–spring grazing more detrimental to Black Rail occupancy at nonirrigated vs. irrigated marshes? For the first question, it is reasonable to expect that marsh vegetation cover at irrigated sites would be enhanced by additional water supplied during the dry summer months, when temperatures are warmest and marsh plant growth rates in California are fastest (Goulden et al. 2007). From previous work, we knew that water inflows at nonirrigated marshes tend to decline during the summer as natural springs and seasonal creeks dry up (Richmond et al. 2010a). However, in both years marsh vegetation cover at nonirrigated, ungrazed marshes was comparable to cover at irrigated, ungrazed

marshes (Fig. 3), suggesting that observed differences in rail occupancy were not driven by differences in wetland vegetation cover alone. Further research is needed to investigate whether other variables, such as invertebrate density, may be partially responsible for the higher levels of Black Rail occupancy observed at irrigated marshes.

Winter–spring grazing was more detrimental to Black Rail occupancy at nonirrigated vs. irrigated marshes. Grazing may be expected to have a more detrimental effect on vegetation cover at sites lacking irrigation water inputs because plant regrowth should be slower with less water available. While grazing did appear to reduce marsh vegetation cover at nonirrigated sites to a greater degree than at irrigated sites in 2007 (Fig. 3), this difference was not significant. Furthermore, most of our nonirrigated marshes (12 out of 16) were grazed, so if the regrowth of marsh vegetation at these sites was inhibited following grazing due to a lack of water, then we should have been able to detect this effect. Further research is needed to elucidate precisely why nonirrigated marshes appear to be poorer habitat for Black Rails, and why grazing appears to be particularly detrimental at nonirrigated marshes. Interestingly, occupancy at grazed marshes did not vary by month (i.e., there was no increase in occupancy after cattle were removed), despite significant regrowth of marsh vegetation (Figs. 2 and 3), suggesting either that: (1) negative effects to the habitat persisted after the grazing period despite some vegetation regrowth, making them unsuitable for colonization; or (2) rails are unlikely to colonize marshes on the timescale examined in this study. Aside from winter–spring grazing, area, isolation, and irrigation had substantial effects on Black Rail occupancy in our study system (Figs. 4 and 5). Large (>0.5 ha), irrigated marshes that were close to neighboring occupied marshes had the highest probability of being occupied, thus marshes with these characteristics should be prioritized for conservation.

This analysis of Black Rail occupancy patterns could be advanced by examining rail demographic parameters and by covering a wider range of grazing intensities. We did not consider the influence of grazing on Black Rail abundance, density, or reproductive success. Changes in these variables may not necessarily be detected by examining changes in occupancy alone, especially over short timescales. Hart et al. (2002) found that even at very low stocking densities, livestock reduced breeding densities of adult Lapwings (*Vanellus vanellus*) and increased the risk of nest loss due to predation. However, measuring demographic parameters for secretive marsh birds is difficult and very costly, which resulted in our reliance on presence–absence data. We found a wide spectrum of grazing intensities in the study area, but only three marshes had RDM values in the nearby upland that were below the recommended minimum guidelines, 400–500 RDM, for annual grassland/hardwood range in California (Bartolome et al. 2002). Consequently, this study mainly assessed the effects of light to moderate, but not heavy, grazing pressure. The relatively rapid recovery of marsh vegetation cover in both years indicates that the vegetation in these freshwater marshes is fairly resilient to the light and moderate grazing pressures that we observed. However, the results that we report here may not hold under more intensive levels of livestock grazing.

Grazing is an important agent of disturbance in ecosystems, acting to create spatial heterogeneity in vegetation types, modulate successional processes, influence fire regimes, and control transitions of ecosystems between alternative states (Hobbs 1996). The question is not simply whether disturbance to marsh vegetation through grazing or other means is beneficial or detrimental to marsh birds, but rather what intensity, duration, and timing of disturbance minimizes impacts or maximizes benefits. For example, Conway et al. (2010) found that disturbance to marsh vegetation via fire increased numbers of Yuma Clapper Rails (*Rallus longirostris yumanensis*) and Virginia Rails (*Rallus limicola*) within the Lower Colorado River basin by setting back succession of emergent marshes, helping to mimic the natural disturbance regime. Further research is needed to examine the long-term effects that grazing may have on marsh succession and habitat quality. The light to moderate grazing levels that we examined in this study had no significant impacts on Black Rail occupancy at irrigated marshes but had negative impacts at nonirrigated marshes. We recommend that marsh vegetation cover in the northern Sierra foothills be monitored during the rail breeding season (March–July) so that stocking rates can be adjusted if marsh vegetation cover is reduced below 60%. Based on our findings, managers should aim to control grazing at natural spring- or stream-fed permanent marshes, perhaps using fencing and by providing alternate water sources for livestock, to minimize negative impacts to rails.

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Supplemental Material

Appendix A

Description of the "random changes in occupancy" multi-season occupancy model (*Ecological Archives* A022-087-A1).

Appendix B

Detection model set testing the effects of day of year, year, and month on detection probability of Black Rails from February to October, 2007–2008 (*Ecological Archives* A022-087-A2).

Appendix C

Occupancy model set testing the effects spring and summer marsh vegetation cover on occupancy of Black Rails from February to October, 2007–2008 (*Ecological Archives* A022-087-A3).