

Livestock grazing in intermountain depressional wetlands: effects on breeding waterfowl

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Abstract Livestock grazing is a prevalent land use in western North American intermountain wetlands, and physical and biotic changes related to grazing-related disturbance can potentially limit wetland habitat value for waterfowl. We evaluated breeding waterfowl use in 34 wetlands in relation to water retention, amount of wetlands on the landscape, and livestock grazing intensity. The study was conducted over 2 years in the southern intermountain region of British Columbia, Canada. For a subset of 17 wetlands, we measured aquatic invertebrate abundance over 1 year. Waterfowl breeding pairs and broods were classified into three functional groups: dabbling ducks, and two types of diving ducks, overwater and cavity nesters. We evaluated candidate models with variables considered singly and in combination using the Akaike Information Criterion. When selected, bare ground (an indicator of grazing

intensity) and wetland density were negatively associated with breeding use while wetland fullness and invertebrate density were positively associated. Each factor was a significant predictor in at least one of the models, but unexpectedly, grazing intensity was the most consistent predictor of waterfowl wetland use (e.g., it was present in more ‘best models’ than wetland fullness). Grazing was associated with declines in the number of waterfowl pairs and broods, likely mediated through effects on wetland vegetation and aquatic macroinvertebrates. Models with site- and landscape-scale variables generally performed better than simpler models. Waterfowl breeding use of wetlands can be improved by reduced livestock grazing intensity adjacent to wetlands and by grazing later in the season. Wetland water retention is also an important constraint on waterfowl use of wetlands and may become more limiting with a shifting climate.

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Introduction

In the past three decades there have been notable declines among some migratory waterfowl species nesting in Alaska and the Canadian prairie and parklands (US Fish and Wildlife Service 2015). The extent to which cattle grazing in these regions might

be responsible is unclear. Considering that livestock grazing is one of the most widespread land uses in Western North America (Fleischner 1994), and that wetlands are an important water source for cattle, as well as essential habitat for migratory waterfowl, a better understanding of how grazing affects wetlands and waterfowl is necessary for managing its potential ecologic costs.

Intermountain depressional wetlands in western North America are primarily managed for livestock production and are commonly used by the ranching industry for cattle watering and forage. Grazing by livestock can alter wetland productivity and diversity by removing or trampling vegetation, compacting soil, increasing erosion, and adding nutrients and sediments, all of which can negatively affect waterfowl breeding success (Kantrud 1986; Nader et al. 1998; Steinman et al. 2003; Marty 2005; Morris and Reich 2013). For example, as grazing intensity at these wetlands increases, vegetation structure changes and biomass declines (Jones et al. 2011), which potentially affects their habitat quality.

We have limited knowledge of cattle grazing effects on intermountain wetland ecosystems in general, and breeding waterfowl in particular. Research results on grazing effects on waterfowl have been inconsistent. Grazing in North Dakota and Colorado was detrimental to dabbler nest densities and success (Kirsch 1969; Gilbert et al. 1996), but duck production in the aspen parkland of Canada was maximized in idled or lightly grazed pastures (Warren et al. 2008). In wetlands, grazing has been negatively associated with the presence of waterfowl pairs (Kirsch 1969; Munding 1976) and broods (Gjersing 1975; Munding 1976), and Ryan et al. (2002) categorized many dabbler species as relatively grazing intolerant in the American Midwest. However, Duebber et al. (1986) found that light to moderate levels of grazing (<3 animal unit months (AUM)/ha) were compatible with nesting dabblers in North Dakota, and it's possible that grazing may be used to maintain open water in areas where shallow wetlands would otherwise be filled in with emergent vegetation (Murkin et al. 1997; Morris and Reich 2013). There is some consensus that grazing at higher levels is detrimental to waterfowl, but it is unclear whether the impact of grazing on waterfowl increases linearly.

The objective of this research was to explore the linkages between waterfowl breeding use of wetlands

and cattle grazing intensity. We conceived that grazing effects would be expressed as a disturbance to the biotic community which supports waterfowl (emergent vegetation, aquatic invertebrates), and to underlying abiotic elements of the environment (e.g., water-borne nutrients, wetland hydrology) which play a strong role in determining wetland communities (Mitsch and Gosselink 2000). We evaluated variables that are potentially useful as indicators for waterfowl use of interior wetlands and that are measurable with reasonable effort in the field. Specifically, we hypothesized that (1) livestock grazing diminishes waterfowl breeding pair use of wetlands, primarily through reducing wetland vegetation biomass that provides waterfowl habitat cover and decreasing the abundance of aquatic invertebrates, (2) wetland water levels is more important than livestock grazing in determining waterfowl brood use of wetlands due to the importance of water availability and its importance to waterfowl resource availability in a landscape which typically becomes dryer as broods come of age, and (3) wetlands with high density of surrounding wetlands is positively associated with waterfowl breeding use through the provision of additional pair-formation, foraging, nesting and rearing sites.

Methods

Study area

The study area was located near the city of Kamloops in the southern interior of British Columbia, Canada. Mean summer temperatures range from 21 to 28 degrees celcius and mean annual precipitation is 280 mm. Livestock grazing is ubiquitous at low to moderate elevations (350–1000 m a.s.l.). The study was conducted in 2007 and 2008, during a period of several years in which the study area experienced relative drought conditions: precipitation levels during the sampling period were below the 1971–2000 average in both 2007 (75%) and 2008 (52%), as well as in the preceding year 2006 (70%).

We examined 34 depressional wetlands, all of which were somewhat to moderately alkaline (mean pH: 7.7–10.6; mean specific conductance: 0.9–11.8 mS/cm), and either semi-permanent or permanent (Stewart and Kantrud 1971) except for two seasonally-flooded sites. Tall emergent vegetation was

dominated by hard-stemmed and seacoast bulrush (*Schoenoplectus acutus* and *Bolboschoenus maritimus*). Adjacent uplands were primarily bunch-grass-dominated grasslands (*Festuca scabrella*, *Pseudoroegneria spicata*, *Achnatherum richardsonii*). Annual cropping is rare in the study area.

Sampling design

There was no experimental manipulation of grazing intensity or season, but wetlands were selected based on general grazing intensity: ‘lightly grazed’ and ‘heavily grazed’. Pasture stocking densities ranged from 0 to 2.9 cattle/ha. Lightly grazed pastures were typically publicly owned, large in size (up to 1200 hectares) and averaged less than 0.5 AUM/ha, with most grazing in fall. Heavily grazed pastures were typically privately owned, less than 100 hectares in size and averaged over 7 AUM/ha, with grazing in spring and summer.

Sample collection

Waterfowl breeding pairs and broods were counted between April 26 and June 3 and between June 2 and August 16, respectively. Each wetland was surveyed at approximately equal intervals six times for pairs and five times for broods by a single observer. All 34 wetlands were counted before the next round of surveying began. All waterfowl were identified to species, sex, social status, and plumage class (Gollop and Marshall 1954; Smith 1995). Detection probabilities were not formally estimated but we believe they were high due to the large number of visits in each season and excellent observation conditions at all wetlands, which were small to moderate in size and offered good vantage points due to the rolling topography of the area. We expected that any detection bias would lead to fewer detections at lightly grazed (more vegetated) wetlands; hence, our inferences may be conservative. For each species on a given wetland, the overall pair or brood count was the maximum number observed on any single visit.

We classified breeding waterfowl into three functional groups. Dabbling ducks were compared to overwater and cavity nesters (both diving ducks) because we believed that cattle grazing might affect these groups differently based on their nesting, foraging and escape behaviour. We contrasted overwater and cavity nesters because we thought the former would be

much more susceptible to grazing disturbance. Consistent with standard procedures for waterfowl breeding ground surveys (e.g., Canadian Wildlife Service and U.S. Fish and Wildlife Service 1987), breeding pairs were calculated as the sum of observed pairs + lone males + groups of two males \times 2 + groups of three males \times 3 + groups of four males \times 4. The small groups of flocked males are post-breeders seen after incubation begins, and each individual indicates a breeding pair. For species with skewed sex ratios, namely redhead (*Aythya americana*), ring-necked duck (*Aythya collaris*), ruddy duck (*Oxyura jamaicensis*), and lesser scaup (*Aythya affinis*), we used a slightly modified formula: observed pairs + lone males/2 + groups of two males \times 2/2 + groups of three males \times 3/2 + groups of four males \times 4/2.

We sampled aboveground vegetation biomass in 2007 at 12 locations around each of the 34 ponds, 6 within the marsh zone and 6 within the wet meadow zone, using species-hydrology associations summarized in Kantrud et al. (1989). The 6 locations within each zone were selected randomly, and at each location we clipped aboveground biomass to a height of 1 cm from a 0.25 m² quadrat. Biomass samples were oven-dried at 65 °C for at least 72 h to a constant dry mass.

Although we had information on pasture stocking rates, we observed that this metric was not always a reliable indicator of grazing pressure on a given wetland. Cattle use of wetlands within pastures of similar stocking rate could vary significantly due to wetland density, water chemistry and topographic considerations; therefore, we sought a more wetland-specific indicator. The amount of bare ground and soil bulk density have both been found to be good indicators of grazing intensity (Tate et al. 2004; Manier and Hobbs 2007; Jones et al. 2011; Skaer et al. 2013). For example, Jones et al. (2011) demonstrated predictable plant functional group response (an increase in shorter-lived and smaller plants) to an increase in bare ground as a surrogate of grazing intensity. Bare ground was measured at 60 0.5 m² randomly located quadrats placed within the wetland zone of each pond and was calculated as the mean number of quadrat corners that intersected bare ground. To improve the interpretability of this measure, it was rescaled so that it ranged from 0 to 100. Soil bulk density collected in 2007 was measured at three random locations within the wet meadow zone of each of the 34 wetlands.

Aquatic invertebrates were sampled in 2008 over 2-week periods in early and mid-summer to correspond with waterfowl nesting and brood rearing periods. A total of 17 wetlands, encompassing a range of grazing intensities, were sampled in May to June. Three sweep and three core samples were collected from each wetland during each session. Sweep net samples of the nektonic community were collected 2 m from the wetted edge of the wetland using a sweep net placed just above the substrate surface and rapidly pulled vertically to the water surface (Rader 2001; Merritt et al. 2008; Silver and Vamosi 2012). Water depth was measured at sweep sites to determine organisms/m³. Core samples (5.1 cm diameter × 10.2 cm deep) were collected 2 m from the wetland edge using a benthic hand corer.

Wetland water level was measured via ocular estimate in spring and summer as the percent fullness of a wetland to the nearest decile, and in 2008 was also combined with field groundwater measurements. Water level meters, constructed of 3 cm diameter perforated PVC pipes, were installed within a meter of the water's edge to an average depth of 160 cm. Water levels were collected every 2 weeks from mid-June to late-August. Wetland fullness was initially measured on a 10-point scale, but because waterfowl use was zero at low water levels we therefore binned this variable into two categories, drying or full.

Using ortho-corrected aerial photography, we measured wetland density and percent wetland cover on all 34 wetlands in 500, 1000, and 2000 m buffers using ArcGIS 9.3 software (ESRI, Redlands, California). Study ponds were excluded from these measurements within their own buffers. Buffer sizes were selected to bracket a conservative estimate (300 ha) for the home range of a mallard in the Canadian Prairie Parkland region (*Anas platyrhynchos*; Mack and Clark 2006); data were lacking for other species and more proximal locations, and mallards were considered inclusive of most duck species due to their large body size. We also measured length of roads (50 and 100 m buffers), percent deciduous and/or coniferous tree cover (50, 100, and 250 m buffers). Landscape metrics were ground-truthed for accuracy in the field.

Statistical analyses and modeling

For our full data set of 34 wetlands sampled in both 2007 and 2008, we used generalized linear mixed

models to evaluate waterfowl breeding use (glmer function in the lme4 package; Bates et al. 2011). We modeled the number of dabbler, overwater nester, and cavity nester breeding pairs and broods in relation to three explanatory variables: wetland fullness (Krapu et al. 2000), bare ground (Lapointe et al. 2000; West and Messmer 2006), and the amount of wetlands on the landscape (Naugle et al. 2000), as measured by either the percentage of wetland cover within a 500 m buffer of each wetland (for broods) or the density of wetlands within a 2000 m buffer (for breeding pairs). Other potential landscape predictors such as road density and tree cover were only weakly correlated with waterfowl breeding use. Wetland zone was included as a grouping factor. It was necessary to control for wetland size in some fashion, but given our limited number of samples, we chose to include wetland size in all models as an offset term (a continuous covariate with a known slope, added to the equations to convert breeding rates to counts) rather than as an independent variable (Kneib et al. 2011). To account for correlation between the number of breeding pairs and the number of broods, we included the number of pairs as an offset term in brood models. For cavity nesters, we also considered percent tree cover in the surrounding landscape at 50, 100, and 250 m buffer widths. We found no meaningful correlation between cavity nester abundance and tree cover and so did not include this variable in the models.

For a subset of 17 wetlands, sampled in 2008, for which we had aquatic invertebrate data, we evaluated the number of breeding pairs using generalized linear models. We considered the same predictors as for the full data set but added total invertebrate density (sweep and core samples separately and combined). To confirm that this subset was representative of the full dataset sampled in both years, we also analyzed the subset with the same candidate models used for the full set. The best models were almost identical, with the exception of dabbler pairs, but model performance was relatively weak for this functional group regardless of wetland set. Due to the high degree of correlation between bare ground and invertebrate abundance ($R = -0.59$), we expected the variances of the coefficients to be inflated, and we therefore calculated variance inflation factors for the most heavily parameterized models for each waterfowl group. Before models were evaluated, maximum likelihood estimates of unconditional Box–Cox

transformations to multinormality were calculated for all covariates. Based on this, values for all numeric variables were centered and log transformed. We used a Poisson error structure with the most heavily parameterized models and tested for overdispersion. We used likelihood ratio χ^2 tests to determine whether we needed to model extra-Poisson variation using either an additional observation-level grouping factor for mixed models or a negative binomial parameterization for generalized linear models. We found that the Poisson parameterization was sufficient in all cases.

The Akaike Information Criterion (AIC) was used to select the best candidate model(s). We followed the recommendation by Arnold (2009) to use 85% Confidence Intervals when reporting model parameter estimates. Candidate models for the full data set included all possible combinations of variables. For overwater nester breeding pairs, candidate models did not include wetland fullness, as this group was observed only at full wetlands. For the subset of wetlands with invertebrate data, we limited each model to three predictors and did not include the global model. Candidate models within six AIC units of the lowest ranked model were considered; more complex models were only retained if they had a lower AIC value than all simpler models nested within them (Richards 2008). There is considerable uncertainty estimating the appropriate degrees of freedom for random effects. Given the population-level (vs. group-level) focus of this study, we assigned one degree of freedom to the wetland site random effect (Spiegelhalter et al. 2002). All modeling was done in the R statistical environment (version 2.13.0; R Development Core Team 2011).

Results

We surveyed fifteen species of breeding waterfowl in our study wetlands in 2008 and 2009 (Table 1). Wetlands ranged in size from 0.4 ha to 12.7 ha ($\bar{x} = 2.4$, $SD = 2.4$). In spring, the number of full wetlands was consistent between 2007 (79%) and 2008 (82%), but summer fullness was higher in 2007 (66%) than in 2008 (41%). In terms of landscape composition, wetlands/ha (within 2000 m) ranged from 0.01 to 0.04, ($\bar{x} = 0.02$, $SD = 0.01$), whereas wetland percent cover (within 500 m) ranged from 1.0 to 10.0 ($\bar{x} = 4.2$,

$SD = 2.4$). Total mean aquatic invertebrate density ranged from 4.5 to 29.1 organisms/m³ ($\bar{x} = 12.5$, $SD = 6.9$).

Bare ground ($\bar{x} = 21.04$, $SD = 17.91$) ranged from 0 to 66.25 and was strongly negatively associated with vegetation biomass ($F_{1,32} = 53.33$, $R^2 = 0.61$, $P < 0.001$) and was strongly positively associated with soil bulk density ($F_{1,32} = 68.39$, $R^2 = 0.68$, $P < 0.001$). It appears to be a good indicator of grazing intensity (consistent with Manier and Hobbs 2007, and discussed in greater depth in Jones et al. 2011). Mean aboveground vegetation biomass (± 1 SD) ranged from 36 ± 26 to 537 ± 192 g/m². The contrast between heavily grazed wetlands (mean vegetation biomass = 36 ± 26 g/m²) and lightly grazed wetlands (mean vegetation biomass = 442 ± 232 g/m²) was marked.

Waterfowl models—all wetlands

Candidate models with bare ground were selected for five out of the six waterfowl response variables analyzed, those with wetland abundance were selected in four out of six cases, and those with wetland fullness were selected in three out of five cases (models for overwater nester pairs did not include wetland fullness; Tables 2 and 3). Model weights for the best approximating models were generally strong (>50%), except for dabbler pairs (25%) and cavity nester broods (19%). Generally, the models explained more than a third of the total variation in the data. There was little model uncertainty, with the notable exception of dabbler pairs, where the null model (pairs were approximated by a constant due to lack of statistical dependence on any of the explanatory variables) was almost the best model (although no model performed well for this functional group).

The effect of bare ground was strongly negative for all functional groups except cavity nester broods: an increase of 2 SD in bare ground decreased the response variables between 38 and 87%. The effect was most pronounced for overwater nester broods, where the number of broods associated with the 25th quantile of bare ground (the lightest 25% of grazing intensity) was 0.30 versus 0.06 for the 75th quantile.

An increase in wetland % cover or density at the landscape level had a negative effect on most groups. An increase of 2 SD in landscape wetland cover decreased brood numbers between 51 and 77%,

Table 1 Mean number of breeding pairs and broods (± 1 SD) by species and functional group per wetland surveyed in British Columbia in 2007 and 2008

Functional group/species	Pairs		Broods	
	2007	2008	2007	2008
<i>Dabblers</i>				
American wigeon (<i>Anas americana</i>)	0.26 \pm 0.45	0.29 \pm 0.46	0.06 \pm 0.35	0.06 \pm 0.25
Blue-winged teal (<i>Anas discors</i>)	0.29 \pm 0.52	0.47 \pm 0.71	0.13 \pm 0.34	0.00 \pm 0.00
Cinnamon teal (<i>Anas cyanoptera</i>)	0.29 \pm 0.52	0.38 \pm 0.74	0.09 \pm 0.39	0.00 \pm 0.00
Gadwall (<i>Anas strepera</i>)	0.35 \pm 0.49	0.38 \pm 0.49	0.06 \pm 0.25	0.09 \pm 0.39
Green-winged teal (<i>Anas crecca</i>)	0.35 \pm 0.64	0.24 \pm 0.43	0.19 \pm 0.47	0.03 \pm 0.18
Mallard (<i>Anas platyrhynchos</i>)	0.76 \pm 0.78	0.74 \pm 0.57	0.41 \pm 0.71	0.19 \pm 0.47
Northern pintail (<i>Anas acuta</i>)	0.06 \pm 0.24	0.03 \pm 0.17	0.00 \pm 0.00	0.00 \pm 0.00
Northern shoveler (<i>Anas clypeata</i>)	0.06 \pm 0.24	0.18 \pm 0.39	0.03 \pm 0.18	0.03 \pm 0.18
<i>Overwater nesters</i>				
Canvasback (<i>Aythya valisineria</i>)	0.00 \pm 0.00	0.00 \pm 0.00	0.03 \pm 0.18	0.00 \pm 0.00
Redhead (<i>Aythya americana</i>)	0.21 \pm 0.54	0.27 \pm 0.51	0.19 \pm 0.54	0.25 \pm 0.57
Ring-necked duck (<i>Aythya collaris</i>)	0.12 \pm 0.33	0.06 \pm 0.24	0.00 \pm 0.00	0.00 \pm 0.00
Ruddy duck (<i>Oxyura jamaicensis</i>)	0.71 \pm 1.12	0.50 \pm 0.86	0.72 \pm 1.14	0.53 \pm 0.88
Lesser scaup (<i>Aythya affinis</i>)	0.12 \pm 0.41	0.32 \pm 0.59	0.09 \pm 0.39	0.09 \pm 0.30
<i>Cavity nesters</i>				
Barrow's goldeneye (<i>Bucephala islandica</i>)	0.71 \pm 0.84	0.77 \pm 0.56	0.28 \pm 0.77	0.34 \pm 0.65
Bufflehead (<i>Bucephala albeola</i>)	0.26 \pm 0.57	0.30 \pm 0.55	0.09 \pm 0.30	0.19 \pm 0.47

whereas an increase of 2 SD in landscape wetland density decreased breeding pair numbers by 45 and 47%. The effect was most pronounced for overwater nester broods, where the number of broods associated with the 25th quantile of landscape wetland cover was 0.21 versus 0.07 for the 75th quantile.

Conversely, an increase in wetland fullness had a strong positive effect on all functional groups where it appeared in the best models: as wetlands changed from drying to full, the response variables (pairs or broods) increased between 109 and 211% when other covariates were held at their mean values. The effect was most pronounced for cavity nester pairs, where the number of pairs associated with drying wetlands was 0.14 compared to 0.44 pairs for full wetlands. For overwater nester pairs, we couldn't evaluate the importance of fullness numerically because all non-zero observations were associated with full wetlands. However, the fact that overwater nester pairs only occurred when wetlands were full affirms the importance of fullness for this functional group.

Standardizing the parameter estimates (Gelman 2008) enables comparisons of the relative importance

of predictors within functional groups. For dabbler broods, for example, bare ground (-1.36) was roughly equivalent to buffer wetland density (-1.35) and about 1.5 times as important as wetland fullness (0.87). For waterfowl breeding pairs in general, bare ground was a strong predictor and the most consistently selected. For waterfowl broods, bare ground and wetland cover were the most consistently included and strongest predictors.

Waterfowl models—vertebrate subset

For dabbler and overwater nester pairs, invertebrate abundance was a strong predictor and models with this variable explained a large amount of model deviance (Tables 4, 5). Results were similar whether we used sweep and core densities separately or combined, and therefore we used an aggregate, averaged predictor to simplify the models. Bare ground, the most consistently selected predictor variable for the full set of wetlands, was mostly not included in the best models. For dabbling pairs, it was included in models within $\Delta AIC < 6$ of the best approximating model; however,

Table 2 Best models (non-nested models within 6 Akaike Information Criterion (AIC) units of the top ranked model) from a set of candidate models evaluating the number ofwaterfowl pairs and broods surveyed in British Columbia in 2007 and 2008 ($n = 34$ wetlands/year for breeding pairs and 32 wetlands/year for broods)

Waterfowl functional group	Δ AIC	Model terms ^a	Parameters ^b	Model weight	Deviance explained
Breeding pairs					
Dabblers	0.0	bare	3	0.25	0.03
	0.8	null	2	0.17	
Overwater nesters	0.0	bare	3	0.68	0.09
Cavity nesters	0.0	full + bare + buffdens	5	0.63	0.27
	3.5	full + bare	4	0.11	0.18
	3.5	full + buffdens	4	0.11	0.18
	3.8	full	3	0.09	0.14
	5.4	bare + buffdens	4	0.04	0.15
Broods					
Dabblers	0.0	full + bare + buff%	5	0.69	0.22
	2.6	bare + buff%	4	0.18	0.16
	5.9	full + bare	4	0.04	0.12
Overwater nesters	0.0	bare + buff%	4	0.69	0.32
Cavity nesters	0.0	full + buff%	4	0.19	0.09
	0.5	full	3	0.15	0.05
	0.6	bare + buff%	4	0.14	0.08
	1.2	null	2	0.10	

Nested models within 6 AIC units are not shown

^a *full* wetland fullness level, *bare* bare ground, *buffdens* density of wetlands within a 2000 m buffer, *buff%* percentage of wetland cover within a 500 m buffer; all models, including the null, contained wetland size as an offset term

^b All models included an intercept and a random effect for site

these models were excluded because the best model (with only invertebrate abundance) was a simpler nested model. For cavity nesters, models with bare ground and fullness were less supported than the null model. Variance inflation factors for the most heavily parameterized models were less than 1.9 for all functional groups.

The effect of invertebrate density was strongly positive for dabblers and overwater nesters. The effect was most pronounced for overwater nester pairs, where the number of pairs associated with the 25th quantile of invertebrate density was 0.04 versus 0.27 for the 75th quantile.

The effect of bare ground was negative for overwater nesters, where an increase of 2 SD in bare ground decreased the response variables by 99%. The number of pairs associated with the 25th quantile of bare ground was 0.36 versus 0.02 for the 75th quantile.

The effect of wetland density was negative for cavity nesters, where an increase of 2 SD in wetland density decreased the response variables by 84%. The

number of pairs associated with the 25th quantile of wetland density was 0.46 versus 0.11 for the 75th quantile.

Discussion

The most important factors correlated with breeding waterfowl use of wetlands were grazing intensity, as represented by bare ground, and the abundance of aquatic invertebrates followed by wetland water levels and wetland density. For the full data set, bare ground was more consistently represented among the best models and tended to be the strongest predictor for functional groups where it appeared in the best model.

Does livestock grazing diminish waterfowl breeding pair use of wetlands?

Results were consistent with our first hypothesis, that increased grazing would diminish breeding use of

Table 3 Parameter estimates, standard errors, and 85% confidence intervals for the best approximating model evaluating the number of waterfowl breeding pairs and broods surveyed in British Columbia in 2007 and 2008 in terms of wetlandfullness, bare ground, and density/percent of buffer wetlands ($n = 34$ wetlands/year for breeding pairs and 32 wetlands/year for broods over 2 years)

Waterfowl functional group/parameter ^a	Breeding pairs				Broods			
	Estimate ^b	SE	85% CI		Estimate	SE	85% CI	
			Lower	Upper			Lower	Upper
Dabblers								
Intercept	0.02	0.15	-0.19	0.24	-3.15	0.38	-3.70	-2.61
Full					0.87	0.43	0.25	1.49
Bare	-0.48	0.27	-0.88	-0.09	-1.36	0.39	-1.91	-0.80
Buff%					-1.35	0.36	-1.87	-0.83
Overwater nesters								
Intercept	-1.35	0.27	-1.74	-0.97	-2.02	0.18	-2.29	-1.75
Bare	-1.64	0.42	-2.25	-1.03	-2.02	0.38	-2.56	-1.47
Buff%					-1.47	0.32	-1.93	-1.00
Cavity nesters								
Intercept	-1.38	0.22	-1.70	-1.06	-2.97	0.38	-3.52	-2.42
Full	1.13	0.44	0.50	1.77	0.74	0.43	0.11	1.36
Bare	-0.68	0.44	-1.10	-0.26				
Buffdens	-0.63	0.28	-1.03	-0.23				
Buff%					-0.71	0.43	-1.32	-0.10

^a *intercept* estimated number of pairs/broods when included predictors are at their mean values, *full* wetland fullness level, *bare* bare ground, *buffden* density of wetlands within a 2000 m buffer, *buff%* percentage of wetland cover within a 500 m buffer; all models, including the null, contained wetland size as an offset term

^b All estimates are on the scale of the linear predictor and have been standardized to be roughly comparable to one another; estimates represent changes to the response associated with a change of 2 SD of selected covariates and/or a change from drying to full for wetland full when selected

Table 4 Best models (non-nested models within 6 small-sample corrected Akaike Information Criterion (AIC_c) units of the top ranked model) from a set of candidate modelsevaluating the number of waterfowl breeding pairs surveyed in British Columbia in 2008 ($n = 17$ wetlands)

Waterfowl functional group	ΔAIC_c	Model terms ^a	Parameters	Model weight	Deviance explained
Dabblers	0.0	Invert	2	0.38	0.45
Overwater nesters	0.0	Bare + invert	3	0.74	0.81
	4.7	Invert	2	0.07	0.58
Cavity nesters	0.0	Buffdens	2	0.36	0.31
	1.8	Null	1	0.15	

Nested models within 6 AIC units are not shown

^a *bare* bare ground, *buffdens* density of wetlands within a 2000 m buffer, *invert* total invertebrate density; all models, including the null, contained wetland size as an offset term

wetlands. Although we measured bare ground as our index of livestock disturbance, we think cattle grazing effects on waterfowl were expressed primarily via their influence on wetland vegetation, which had

significant (and generally negative) effects on critical waterfowl cover and foraging needs. Wetland use by grazers increases turbidity/siltation and decreases aquatic vegetation complexity (Declerck et al. 2006;

Table 5 Parameter estimates, standard errors, and 85% confidence intervals for the best approximating model evaluating the number of waterfowl breeding pairs surveyed in BritishColumbia in 2008 in terms of wetland fullness, bare ground, density of buffer wetlands, and invertebrate density ($n = 17$ wetlands)

Waterfowl functional group/ Parameter ^a	Estimate ^b	SE	85% CI	
			Lower	Upper
Dabblers				
Intercept	0.35	0.21	0.05	0.64
Invert	1.15	0.37	0.61	1.69
Overwater nesters				
Intercept	-2.33	1.33	-4.24	-0.41
Bare	-4.25	2.23	-7.46	-1.03
Invert	3.20	1.39	1.20	5.20
Cavity nesters				
Intercept	-1.40	0.56	-2.20	-0.59
Buffdens	-1.85	0.98	-3.26	-0.44

^a *intercept* estimated number of pairs when included predictors are at their mean values, *bare* bare ground, *buffden* density of wetlands within a 2000 m buffer, *invert* total invertebrate density; all models, including the null, contained wetland size as an offset term

^b All estimates are on the scale of the linear predictor and have been standardized to be roughly comparable to one another; estimates represent changes to the response associated with a change of 2 SD of selected covariates

Bouahim et al. 2010), thereby reducing the availability of food (e.g., macroinvertebrates, seeds) and nesting and escape cover for waterfowl (Ryan et al. 2006). At this study location, Clark (2015) demonstrated that the loss of emergent vegetation decreased total abundance, biomass, richness and diversity of aquatic macroinvertebrates in the wetlands.

Direct effects via nest trampling or waterfowl avoidance of cattle are rare (see Bleho et al. 2014). Although periodic disturbance through grazing can have positive effects on nutrient cycling and forage production (Hillhouse et al. 2010), we found a very strong negative association between bare ground and aboveground vegetation biomass. Vegetation structure and functional composition was also strongly related to bare ground, with frequency of both rhizomatous and tall species, which comprise most of the dominant emergent vegetation, decreasing with increased bare ground (Jones et al. 2011).

Most waterfowl groups showed a strong negative association with bare ground. For pairs, grazing-associated reductions in wetland vegetative cover presumably limited the number of potential nest sites, or led to decreased success of initiated nests (Gilbert et al. 1996; Warren et al. 2008). In adjacent grasslands, simulated grazing (clipping) significantly decreased visual obscurity, especially for taller vegetation

(Carlyle et al. 2010). The effect of bare ground was stronger for overwater nesters than for dabbler pairs and cavity nesters. Since overwater nesters rarely nest in upland habitats, this may reflect differential grazing effects between uplands and wetlands. Grazing presumably has no direct effect on cavity nesters.

Except for cavity nesters, brood responses to grazing were even stronger than those for pairs, with the effect most pronounced for overwater nesters. Wetland vegetation abundance has been positively associated with waterfowl brood survival (Hudson 1983) as well as mallard brood density (Lillie 2004) and survival (Simpson et al. 2007). Grazing-related reductions in brood use were likely caused by changes to wetland vegetation that diminished plant and invertebrate food sources for young ducklings (Murkin and Ross 2000). Among dabbler broods in particular, the response may also have involved reductions in the escape cover offered by emergent vegetation (Murkin and Caldwell 2000; Simpson et al. 2007); divers tend to move to open water as an escape technique (Murkin and Caldwell 2000).

Aquatic macroinvertebrate abundance strongly influenced waterfowl pair use of wetlands. When added to the set of variables considered for 17 wetlands in 2008, this metric was the most important predictor and improved model performance in terms

of the amount of variation explained for all functional groups except cavity nesters. The effect was strongest for overwater nester pairs, which was expected given the reliance of most diving species on invertebrate food sources (Krapu and Reinecke 1992), although their use by dabbling species is also well documented (Murkin and Batt 1987; Krapu and Reinecke 1992; Lillie 2004). In our study, macroinvertebrate taxa were dominated by insects (dipterans and odonates) and crustaceans (ostracods) which have been shown as major waterfowl protein sources during the breeding period (Krapu and Reinecke 1992; Batzer and Wisinger 1996). We also found large biomass contributions from gastropods, which are important to laying hens as sources of protein and calcium for egg production (Swanson et al. 1985; Murkin and Batt 1987; Krapu and Reinecke 1992).

There have been relatively few direct wetland examinations of grazing effects on invertebrates, but some studies have shown that increased grazing intensity lowers aquatic invertebrate abundance, diversity and richness (Andresen et al. 1990; Ausden et al. 2005; Foote and Hornung 2005; Morrison and Bohlen 2010) and a related study confirmed these effects at our location (Clark 2015). Grazing alters the structure of wetland vegetation, which is used as a growth substrate for invertebrate communities (Murkin and Ross 2000; Foote and Hornung 2005), and can increase wetland nutrient levels, which in turn can change macrophyte and algal communities that are used by aquatic invertebrates as habitat (Steinman et al. 2003). Other studies have found that grazing only changed the community structure (but not overall abundance) of benthic invertebrates within streams in native grasslands (Scrimgeour and Kendall 2003), or have associated grazing with increased species richness (Marty 2005; Davis and Bidwell 2008). One study found no discernable effect of grazing on crustacean species assemblages (Bagella et al. 2010).

Are wetland water levels more important than livestock grazing in determining waterfowl brood use of wetlands?

As wetlands lost water and began to dry, their capacity to support pairs and broods dropped dramatically. Waterfowl appeared to recognize and respond to drying wetlands by moving elsewhere. Fullness was strongly positively associated with the number of

breeding pairs and broods for cavity nesters, as well as the number of dabbling broods. Our second hypothesis, that water levels would be more important than grazing in determining waterfowl brood use, was partially validated, and although we were not able to explicitly evaluate the effects of wetland water level for overwater nester pairs, we expect it to be important, given their association with deeper wetlands. The importance of wetland fullness to mallard broods was expected: Dzus and Clark (1998) documented an increase in mallard brood mortality as wetland abundance declined over the summer, and Sayler and Willms (1997) found higher mallard duckling survival when high water levels increased access to flooded emergent vegetation.

Wetland permanence played a factor in waterfowl brood occurrence between years. In our study, semipermanent wetlands were drying by summer in 2008 (vs. 2007 when only half were drying), and overall brood numbers declined for dabblers (33–22) and overwater nesters (33–28) over this period. In the Canadian Prairie-Parklands, Raven et al. (2007) found that mallard broods selected deeper, more permanent wetlands. Similarly, permanent and full wetlands in our study accounted for >75% of broods in both years.

Are wetlands with high density of surrounding wetlands positively associated with waterfowl breeding use?

Landscape wetland abundance appeared in the best model for four of six functional groups, but the direction of influence was counter to our third hypothesis. It was more important for broods, where it was negatively associated with all functional groups. Considering that wetland abundance has been demonstrated as a positive predictor of waterfowl abundance (Naugle et al. 2000), brood use (Mulhern et al. 1985) and/or brood survival (Dzus and Clark 1998; Krapu et al. 2000), these results were unexpected, but not unique (Mack and Clark 2006; Bartzen 2008), and may have resulted from a tendency to “spread out” among available wetlands, reducing overall brood density. Alternatively, predators may have concentrated their efforts on wetland-dense areas, but this is a complex issue and we have little knowledge of local predator numbers and nest/brood predation rates. In addition, spatial scale is an important factor in our analysis.

Models that included variables measured at the site and landscape scale generally performed better than simpler models that included only site-level variables. Similar patterns have been observed in the aspen parklands of Canada (Howerter et al. 2008) and in North Dakota (Stephens et al. 2005). Conversely, Koper and Schmiegelow (2006) found that duck nest success in the mixed grass Canadian prairie depended more on local habitat variables. Regional context may ultimately determine the relative strength and nature of the roles played by site and landscape factors (Wiens et al. 1987); environmental conditions in the study area may impose conditions that dictate that multi-scale associations assume greater importance for waterfowl there.

We considered that the spatial proximity of similar grazing intensity wetlands near each other (in discrete ‘low intensity’ and ‘high intensity’ zones) could lead to a lack of independence among sampling locations, and potentially introduce findings which are more a result of correlations with confounding variables such as soil productivity. This sampling design was unavoidable due to local patterns of land ownership/use, and we are confident that all sites were relatively similar in terms of environmental attributes (e.g., soil productivity, latitude, elevation) that may have predisposed sites to grazing impacts or waterfowl presence in the absence of grazing.

Management implications

Grazing intensity was the most consistent predictor of breeding waterfowl use in this study. Although aquatic macroinvertebrate abundance was a more important predictor when added for a subset of wetlands, this factor was shown by Clark (2015) to be strongly driven by grazing intensity/bare ground. As grazing intensity increased, we observed a continuous reduction in the value of a wetland for waterfowl, and even a moderate amount of grazing appeared to decrease waterfowl pair and brood use noticeably, reinforcing the conservation value of managing cattle ingress.

To improve waterfowl use of wetlands, we recommend reducing grazing pressure in wetlands and using off-site watering to provide appropriate controls over cattle distribution, residual vegetative cover and wetland nutrient inputs. A reduction in grazing pressure can be achieved via a number of techniques,

including riparian exclusion fencing and seasonal restrictions. We recommend that grazing should be limited in spring, when it most destabilizes riparian slopes due to higher moisture content (Marlow et al. 1987). Other grazing systems such as rest rotation grazing (Vallentine 2001) can improve streambank stability and instream vegetation (Scrimgeour and Kendall 2003), but the evidence for waterfowl benefits is mixed. Positive responses in relation to grazing pressure have been observed for waterfowl nest success (Lapointe et al. 2000), pairs (Mundinger 1976) and broods (Gjersing 1975; Mundinger 1976) due to increases in residual vegetation. However, a review by Williams et al. (1999) found no studies where rotational grazing systems had significant positive effects on waterfowl productivity.

Translating recommendations for light/moderate grazing intensity into guidelines for cattle stocking rates is a difficult exercise, and is probably region-specific. We found that cattle use of wetlands also depended on local topography and wetland chemistry (B. Harrison, personal observation), and therefore the stocking rates we observed might not apply in areas with dissimilar environments. Furthermore, although our correlational data are excellent for detecting trends, controlled manipulative studies are needed to address specific stocking rate recommendations.

Where included in models, wetland fullness was an important limitation on waterfowl use of wetlands. This highlights the necessity of ensuring adequate wetland water levels in drought-prone areas, whether via reducing extractions for agricultural irrigation or watering, or via the provision of water to supplement natural sources. Periodic drying in semi-arid environments is necessary for wetland productivity and function (van der Valk 2005), but where the drying cycle has been accelerated by large scale water extraction and climate change, intervention may be necessary.

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