



Duck Use of Saline Wetlands Created by Irrigation in a Semiarid Landscape

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Abstract

Throughout semiarid western North America, flood irrigation and associated small reservoirs have created or augmented many wetlands that otherwise would not exist or persist through summer. Diversion of mountain snowmelt from rivers has thereby created widely scattered hotspots of biodiversity. Increased urban water demands, higher profits from sprinkler irrigation, and climate-driven declines in mountain snowpack threaten these wetlands. Knowledge of unique functions of different wetland types and their spatial interactions would aid conservation of wetland complexes. We characterized use by ducks of wetlands with varying salinities, vegetation, nearby land use, and spatial relations in the Laramie Basin, Wyoming, USA. All duck species and social groups had higher densities in smaller wetlands. Pairs and broods of diving ducks and some dabbling ducks had highest densities in oligosaline wetlands (0.5–5 ‰ salinity) which have emergent plants for nesting cover. However, these ducks were commonly observed in mesosaline wetlands (5–18 ‰) which lack emergent cover but have higher availability of near-surface foods, suggesting differential use of wetland types for nesting and feeding. Accordingly, densities of some dabbling and diving ducks were higher when mesosaline wetlands were within 1 km. Hayfields or livestock grazing nearby seldom affected duck densities in wetlands, suggesting that with sparse upland cover in shortgrass steppe, many upland nesters sought cover in dry portions of the emergent fringe. For ducks in such intermountain basins, mesosaline wetlands with less stable water levels but high prey availability should be maintained in complexes near oligosaline wetlands with variably flooded emergent cover.

Keywords Flood irrigation · Nesting cover · Hayfields · Salinity · Saline wetlands · Waterfowl · Wetland complexes

Introduction

Across semiarid western North America, flood irrigation and associated small reservoirs have created many wetlands that did not exist previously, and have made many temporarily or seasonally flooded wetlands more permanently flooded (cf. Cowardin et al. 1979). In intermountain basins with limited direct precipitation, water from mountain snowmelt has been diverted from rivers and distributed over broad areas by irrigation systems (Lovvorn and Hart 2004; Kendy 2006; Downard and Endter-Wada 2013). In the common case of flood irrigation for hay production, many wetlands

are maintained by direct input from ditches, or by groundwater recharged from irrigated fields or unlined ditches (Peck and Lovvorn 2001; Sueltenfuss et al. 2013). These wetlands function as hotspots of biodiversity scattered across broad areas of otherwise dry and wind-scoured shortgrass steppe. Although many of these intermountain wetlands were mostly seasonally flooded or did not exist before Euro-American settlement in the late 1800s, today they provide summer-long refugia for taxa diminished by loss of scarce natural wetlands, and in some cases allow persistence of threatened species that now depend on these novel habitats (Parker and Anderson 2003). Indeed, although wetlands may comprise only 1% of land area in the American West, at least half of the region's endangered species depend on them (Kendy 2006). In dryland regions worldwide, diverting water from rivers often adversely affects naturally occurring wetlands (Williams 1999). However, in watersheds driven by mountain snowmelt (Qin et al. 2020), traditional flood irrigation and associated small reservoirs can afford important wetland

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functions and conservation benefits (Kendy 2006; Sueltenfuss et al. 2013).

Rapid expansion of urban areas and water demands, conversion from flood to sprinkler-irrigated crops, and severe ongoing and projected declines in mountain snowpack threaten these valuable wetlands (Baker et al. 2014; Fyfe et al. 2017; Kendy et al. 2018; Mote et al. 2018). Sprinkler irrigation uses less water for the same crop yield (higher “irrigation efficiency”); however, this practice decreases local groundwater recharge and return flows that maintain adjacent wetlands (Grafton et al. 2018). Mandates to achieve higher instream flows in spring to benefit protected species far downstream can demand reduced water diversions in the upper watershed (Aiken 1999), thereby decreasing water to support a range of more common species through the summer. Conserving a complement of wetland breeding habitats throughout semiarid intermountain basins requires understanding the unique functions of various wetland types and their spatial interactions, to guide planning of wetland complexes and projection of the amount and timing of water they require (Fairbairn and Dinsmore 2001; Fortuna et al. 2006; Kendy et al. 2018).

The Laramie Basin, Wyoming, USA is a high intermountain basin dominated by flood irrigation which supports an array of wetlands scattered across the landscape (Peck and Lovvorn 2001; Lovvorn and Hart 2004). As part of a suite of studies of these wetlands (Lovvorn and Hart 2004 and references therein), this paper characterizes effects of wetland type, adjacent land use, and spatial relations on wetland use by dabbling ducks (Anatini) and diving ducks (Aythini and Oxyurini) during the breeding season. Other research has used satellite remote sensing of surface water to document availability and use of flood-irrigated areas by ducks during migration at a scale encompassing portions of several states (Donnelly et al. 2019). However, after spring-flooded hayfields are drained for harvest in early to midsummer, it is often the small reservoirs associated with irrigation that provide wetland habitat through the breeding season (Peck and Lovvorn 2001, Lovvorn and Hart 2004). On-the-ground acquisition and management of water at a local scale to sustain wetlands suitable for a range of species during the breeding season requires information on use of different wetland types by different species and social groups.

Our observations over three decades have indicated that, with episodic droughts and variable water levels among subsequent years, vegetation and invertebrate prey communities in these wetlands are often in varying stages of recovery after major perturbations. Resulting transient states and heterogeneity may weaken associations between duck use and specific habitat features. Nevertheless, our analysis revealed insights for the design and conservation of wetland complexes important to strategic actions to offset ongoing and anticipated system-wide losses.

Methods

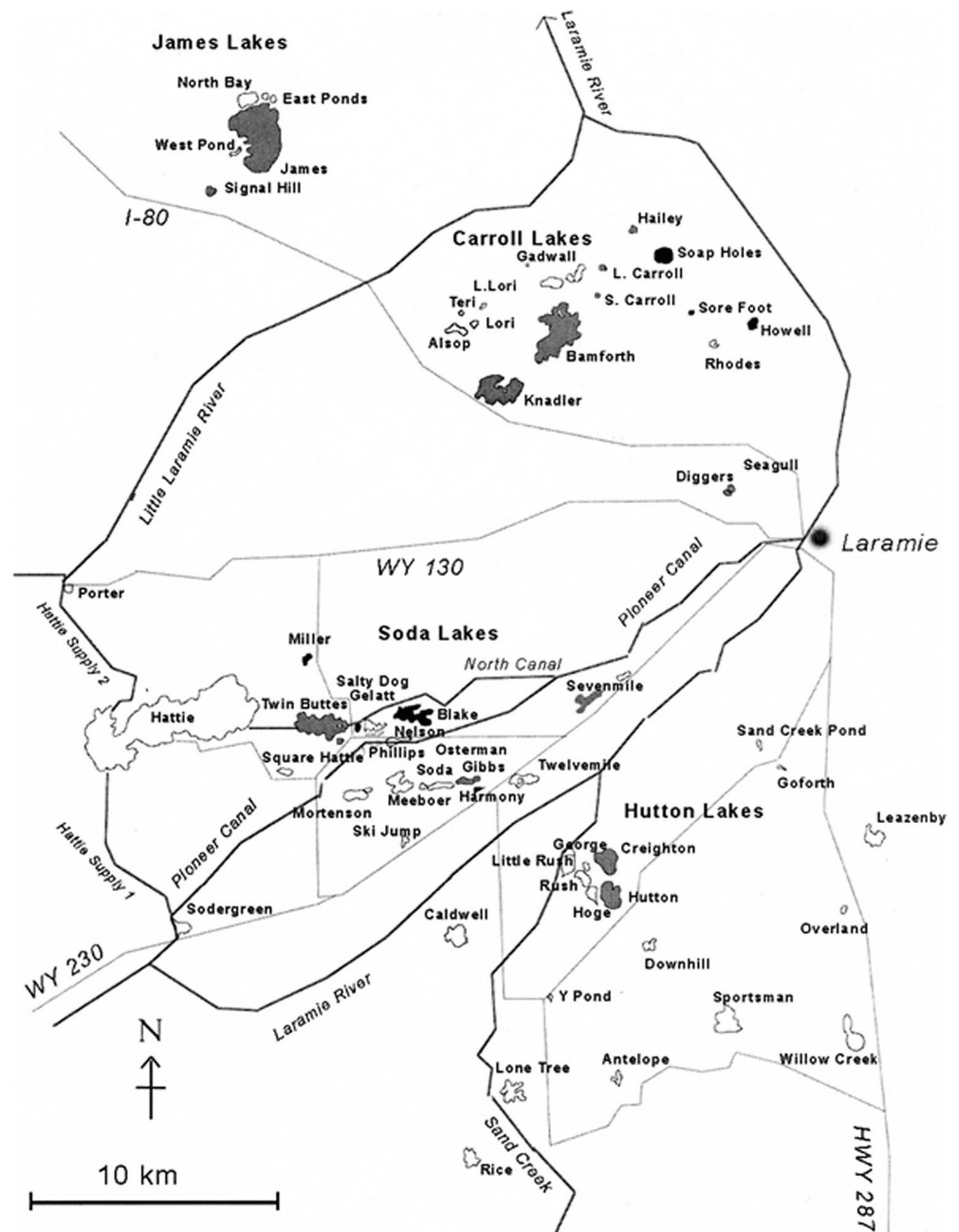
Study Area and Expected Habitat Effects

The Laramie Basin (Fig. 1) is in southeast Wyoming at an elevation of 2000–2400 m between the Laramie Range to the east and the Medicine Bow Range to the west (Lovvorn and Hart 2004). Crop production is restricted by the short, cool growing season (mean 81 days, mean temperature May–September of 14.6 °C), so the main land uses are cattle grazing and hay production through flood irrigation. Snowmelt runoff (and thus water for flood irrigation) rises rapidly to a peak in May and June, and declines quickly thereafter (Kuhn et al. 1983). Because irrigation demand peaks in July and remains high through September, a number of small reservoirs have been built to hold water through the summer and extend the irrigation season (States West Water Resources Corporation 1991).

Wind-eroded depressions that are normally dry or flooded briefly in the spring are distributed throughout the Laramie Basin. However, these deflation hollows have often been modified by ditches, dikes, and water-control structures to become flooded in most years when they receive irrigation flows directly from ditches, or via seepage from unlined ditches or groundwater recharged by flood irrigation (Peck and Lovvorn 2001; Fernald et al. 2010). Unlike some other areas in the intermountain region (e.g. the San Luis Valley in Colorado), very little water for irrigation is pumped from groundwater in the Laramie Basin. Both natural riparian flooding and flood irrigation (mostly in current or former floodplains) can distribute water over large areas starting in May; however, natural floodwaters subside in June and flood-irrigated hayfields are typically drained and harvested in July. The spring-flooded areas support many migrating waterbirds (cf. Donnelly et al. 2019), but in the Laramie Basin it is typically the small reservoirs associated with irrigation that maintain water through the summer to support breeding birds. These small reservoirs depend on direct input of surface water from ditches, and on shallow groundwater fed by seepage from ditches and flooded fields. About 61% of palustrine and lacustrine wetlands (excluding seasonal riparian wetlands) are on private land and the rest are on state or federal property (Peck and Lovvorn 2001).

Plant and invertebrate communities in Laramie Basin wetlands are determined largely by variations in freshwater inflow, which governs salinity and the frequency of drying events. Mean evaporation from mostly lacustrine wetlands (130 cm y^{-1}) is almost five times total precipitation (27 cm y^{-1}) (Wyoming Climate Atlas 2004), so almost all wetlands are saline ($>0.8 \text{ mS cm}^{-1}$ or $>0.5 \text{ ‰}$ total dissolved solids, TDS). Hypersaline ($>40 \text{ ‰}$) wetlands

Fig. 1 Map of wetland study sites within the Laramie Basin, Wyoming. For each wetland, clear indicates oligosaline (0.5–5 ‰, 0.8–8 mS cm⁻¹), gray indicates mesosaline (5–18 ‰, 8–30 mS cm⁻¹), and black indicates higher salinity sites (>18 ‰ or 30 mS cm⁻¹). Roads and major waterways are included. Elevation is highest in the southwest, and waterways flow to the northeast



in the area are often temporarily flooded, and have little vegetation, simple invertebrate communities (e.g. anostracan fairy shrimp), and low use by waterfowl. Eusaline (30 to 40 ‰) and polysaline (18 to 30 ‰) wetlands are rare in the Laramie Basin. Oligosaline wetlands (0.5 to 5 ‰) receive direct surface inflows from irrigation almost every year. Mesosaline wetlands (5 to 18 ‰) receive inflows directly from ditches only in intermittent years, or only as groundwater or interflow seeping from ditches, irrigated fields, or other wetlands. (Salinity classifications are from Cowardin et al. 1979.) Owing to inconsistent inflow, water levels are much more variable in mesosaline wetlands, which occasionally experience severe drawdowns. Ducks

use mainly oligosaline and mesosaline wetlands, which are by far the dominant types in the Laramie Basin (Fig. 1; Peck and Lovvorn 2001).

Oligosaline and mesosaline wetlands differ substantially in vegetation and invertebrate community structure (Wollheim and Lovvorn 1995; Hart and Lovvorn 2000). Oligosaline wetlands generally have a fringe of emergent hardstem bulrush (*Scirpus acutus*), and are dominated by a near-bottom canopy of the submersed macroalgae *Chara* spp. Mesosaline wetlands typically lack an emergent fringe, being surrounded by unvegetated mudflat often with a crust of salt. Rather than low-growing *Chara*, the submersed vegetation in mesosaline wetlands is mainly the erect vascular

plant *Potamogeton pectinatus*, which often forms a dense canopy near the water surface. Along with differences in canopy structure and production by planktonic, epiphytic, and benthic algae (Wollheim and Lovvorn 1996; Hart and Lovvorn 2000), oligosaline and mesosaline wetlands have different invertebrate communities. Oligosaline wetlands are dominated by amphipods, have abundant snails, and have much lower biomass of chironomid larvae, zooplankton, and predatory insects. In mesosaline wetlands amphipods and snails are uncommon, chironomid larvae dominate total biomass, and both zooplankton and predatory insects are much more abundant (Wollheim and Lovvorn 1995).

Although large areas in the Rocky Mountain region contain little or no waterfowl habitat, intermountain basins with flood irrigation can host high densities of breeding ducks (Gilbert et al. 1996). In an aerial survey in 1994 that preceded this study in 1998–1999, the Laramie Basin supported a breeding duck population of about 52,000 (Prenzlowl 1994); breeding duck densities here are among the highest in the state (Copeland et al. 2010). Except for lesser scaup (*Aythya affinis*), diving ducks build floating nests over water within bulrush stands. For upland nesters (scaup and all dabbling ducks), the moist, saline soils in low-lying uplands surrounding wetlands are often dominated by short stands of halophytic saltwort (*Salicornia rubra*) and saltgrass (*Distichlis stricta*), with higher elevations vegetated mostly by short grasses and sometimes scattered greasewood (*Sarcobatus vermiculatus*); neither of these habitats generally provide good nesting cover (Gilbert et al. 1996). Alternative cover for upland nesters includes peripheral stands of hardstem bulrush whose outer edges are partially dewatered in most years (cf. Arnold et al. 1993), or nearby hayfields (Duebbert and Lokemoen 1976). Cattle are grazed in shortgrass vegetation and in harvested hayfields adjacent to some wetlands.

Several duck species have been reported to move their broods overland among wetlands, thereby taking advantage of high food densities in wetlands other than those used for nesting (Duncan 1987; Rotella and Ratti 1992; Leonard et al. 1996). In Manitoba, female redheads (*Aythya americana*) nesting in small semi-permanent wetlands with wide bands of emergent cover were more successful in brood-rearing if they moved their young to larger semipermanent wetlands (Yerkes 2000). Perhaps as a result, the size and proximity of wetlands have been shown to be important to their use by ducks and other waterbirds, and to survival of mobile duckling broods (Rotella and Ratti 1992; Fairbairn and Dinmore 2001).

Bird Observations

In a 200-km² area of the Laramie Basin (Fig. 1), we counted ducks in most wetlands identified on a USGS hydrologic map (1:100,000). Some wetlands on private land could not

be accessed. The 64 wetlands ranged from 2125 to 2400 m in elevation, from 0.1 to 4 km² in surface area (see Peck and Lovvorn 2001), and from 0.1 to 5 km away from other wetlands. We conducted a pilot survey in summer 1998; however, because sampling in summer 1999 was much more comprehensive and standardized, most analyses in this paper were restricted to data from 1999. Sample sizes for waterbirds other than ducks were more limited, so in this paper we report data only for ducks. Ducks were surveyed at each wetland once per week, alternating between morning and afternoon visits.

Each adult duck was observed through a 15–60× spotting scope for about 10 s to determine its species, gender, and social group. Social groups recorded were male-female pairs, broods, and “unassociated adults” (all-male or mixed-gender groups in which no pairs were apparent). The latter category included single males which were spaced apart from other unassociated adults during the observation period, but for which no associated female was seen. Thus, unassociated adults might have included some paired males that were waiting for their mates to return during incubation breaks. Females of teal species were typically accompanied by either a mate or unassociated adults that included males, allowing species identification. Broods attended by canvasback (*Aythya valisineria*) hens were considered canvasback broods, even if some of the ducklings were redheads owing to nest parasitism. We analyzed numbers of broods (whose habitat use was determined by the attending hen) and not numbers of ducklings. For each duck species, we determined the first and last dates when Class I broods (Southwick 1953) were first observed, and the date with the highest number of ducklings counted. As the latter analyses did not depend on standardized sampling of all wetlands, we supplemented data from 1999 with data from the pilot study in 1998. Dates of hay harvest were determined by our observations and by interviews with landowners. As wetlands varied greatly in size, we standardized duck counts per unit area of wetland to evaluate effects of wetland type.

Habitat Measurements

Our analyses included 23 habitat variables (Table 1). We determined the area and perimeter of wetlands with the ESRI ArcView Geographic Information System using a hydrographic coverage of the Laramie Basin based on a U.S. Geological Survey topographic map. Also, aerial photographs were taken of each wetland with a handheld camera on 8 August 1999. Polygons in the coverage were revised according to these photographs if there were appreciable changes in size or shape of surface water during the current year, and small temporary ponds were added if they were not shown on the original topographic map. Wetland area and perimeter were log-transformed to correct heterogeneous

Table 1 Attributes of wetlands that were analyzed for their influence on wetland use by ducks in the Laramie Basin, Wyoming, summer 1999

Variable	Min	Max	Mean	SD	Description
Shape, hydrology, salinity					
LnAREA	0.01	8.86	0.4	1.19	ln (surface area), (km ²)
LnPERI	0.34	22.14	2.26	3.11	ln (perimeter), (km)
SINUOUS	2.5	65	18.4	12.5	Perimeter ÷ area
DEPTH	0	2			Temporary, <2 m, or > 2 m
INFLOWpa	0	1			Presence or absence of surface inflow
SALCLASS	1	3			Oligosaline, mesosaline, or higher salinity
Wetland Vegetation					
EMERGpa	0	1			Presence or absence of emergent vegetation
EMERGcov	0	7			Areal cover of emergent vegetation (%)
EMERGshor	0	100	23.5	31.2	Shoreline covered by emergent veg (%)
SAVpa	0	1			Presence (>25%) or absence (<25%) of SAV ^a
SAVcov	0	7			Areal cover of SAV (%)
CHARA	0	1			Dominance by <i>Chara</i> spp.
POTAMO	0	1			Dominance by <i>Potamogeton pectinatus</i>
MUDFLATpa	0	1			Presence or absence of mudflat
Upland cover					
HAYFIELDpa	0	1			Presence or absence of hayfields
LGRAZEpa	0	1			Presence or absence of infrequent grazing
HGRAZEpa	0	1			Presence/absence of heavy, weekly grazing
Wetland complex					
NEAREST	0.05	4.1	0.73	0.97	Distance to nearest wetland (km)
WIN1	0	7	2.39	2.16	Number of wetlands within 1 km
OLIWIN1	0	5	1.62	1.76	Number of oligosaline wetlands within 1 km
OLIAREA	0	8.86	0.4	1.29	Area of oligosaline wetlands within 1 km
MESWIN1	0	3	0.51	0.7	Number of mesosaline wetlands within 1 km
MESAREA	0	4.27	0.49	1.08	Area of mesosaline wetlands within 1 km

^aSubmersed aquatic vegetation

variances. Sinuosity (SINUOUS) was the ratio of perimeter to surface area. DEPTH was classified as temporary if the wetland dried up during part of the summer, shallow if it was <2 m deep, and deep if it was >2 m deep at any point (based on field sampling). Presence or absence of surface inflows from streams or ditches were determined from site visits and aerial photographs (Peck and Lovvorn 2001).

Biweekly at each site in summer 1999, we used a handheld meter to record the conductivity of surface water. Wetlands were then classified (SALCLASS) as oligosaline (0.8–8 mS cm⁻¹), mesosaline (8–30 mS cm⁻¹), or high-salinity (>30 mS cm⁻¹). In terms of total dissolved solids, these conductivity classes correspond approximately to 0.5–5 ‰, 5–18 ‰, and > 18 ‰ (Cowardin et al. 1979).

From field observations, areal coverage of emergent vegetation (hardstem bulrush) was scored at 10% intervals from 0 (none) to 7 (≥70%). From aerial photographs, we measured the percentage of each wetland's perimeter occupied by bulrush. Areal cover of submersed aquatic vegetation (SAV) was also rated subjectively from 0 to 7 (≥70%). Submersed vegetation was evaluated for dominance by *Chara* spp. or by

P. pectinatus (0 = not dominant, 1 = dominant). Presence or absence of mudflats was recorded.

From aerial photographs and ground truthing, we determined presence or absence of hayfields (mainly grass with little alfalfa) in adjacent uplands. Cattle grazing occurred in both shortgrass vegetation and in hayfields after harvest. Grazing intensity was scored by presence or absence of light grazing (LGRAZEpa) or heavy grazing (HGRAZEpa). LGRAZEpa applied to sites where cattle were observed for less than a month of the study period, and to sites where cattle were near but did not have direct access to the wetland. HGRAZEpa applied to sites where cattle grazed each week of the study period and had direct access to the wetland. Our assessments of grazing intensity were not intended as a metric of vegetation cover, as grazing occurred both in recently hayed fields as well as in native (but impacted by grazing) shortgrass prairie. We considered grazing mainly in terms of disturbance to ducks nesting in cover near the periphery of wetlands. Cattle tend to congregate near water, and they trample bulrush and other cover and disturb ducks which nest mostly in that

peripheral vegetation. We measured distance to nearest wetland, and numbers and total area of wetlands within 1 km, both for all wetland types and for oligosaline and mesosaline wetlands separately (Table 1).

Statistical Analyses

We used stepwise regression (with bidirectional addition or removal of variables) to relate the mean density (mean number of individuals per km² of wetland per observation visit) of the different social groups of each duck species to different wetland characteristics. The α value for inclusion or exclusion from the models was 0.15. Only sites where a particular species or social group occurred were included in regression analyses. Thus, these analyses evaluated factors affecting the relative attractiveness of sites that were generally suitable for a species or social group.

For model selection, many authors have argued the relative merits of comparing a collection of multiparameter models by information-theoretic approaches (specifically Akaike's Information Criterion or AIC) vs. iterative assessment of the amount of variance explained independently by individual variables as in stepwise regression. Although advocacy among methods is often polarized, a collection of reviews has concluded that the appropriate method depends on goals of the analysis (Stephens et al. 2005; Shmueli 2010; Murtaugh 2009, 2014). For analyses in this paper, we were not interested in the *relative* predictive value of a series of multiparameter models, of which the "best" model selected by AIC may in fact be a poor model in terms of the *absolute* amount of variance explained (Stephens et al. 2005, Mundry 2011, Symonds and Moussalli 2011). Rather, our intent was to identify individual variables that accounted for appreciable absolute fractions of variation in duck use of different wetland types.

Explanatory power and predictive accuracy are different properties (Shmueli 2010). AIC may be better for model selection if the goal is to evaluate the *relative* predictive success of specified combinations of variables that have been identified a priori as important. [However, see Murtaugh (2009) and Raffalovich et al. (2008) for studies in which AIC yielded the same or less accurate predictive capability.] In contrast, our goal was to conduct exploratory analyses to identify variables important to explaining use of different wetland types by different duck species and social groups (cf. Eberhardt 2003, Stephens et al. 2005). We did not intend our regressions to be used for quantitative prediction, but rather to indicate variables that were consistently important in absolute terms during our study. Inference from AIC vs. stepwise regression is often quite similar (Murtaugh 2009, Richards et al. 2011); however, the methods differ in intent.

Results

Relative Numbers and Chronology of Ducks

Diving ducks represented 40% of adult dabbling and diving ducks observed during the survey period, and 35% of juveniles (Fig. 2). Throughout the summer, scattered observations were made of other duck species including ring-necked ducks (*Aythya collaris*) and various sea ducks (Mergini); however, their numbers were low and are not reported here. Gadwalls (*Mareca strepera*) were by far the most common species. Adult canvasbacks, redheads, and lesser scaup were more numerous than all dabbling duck species except gadwalls. Gadwalls and canvasbacks had larger relative proportions of offspring than adults, whereas redheads and lesser scaup produced relatively few young compared with adult numbers (Fig. 2). Almost all newly hatched dabbling ducks and scaup, which generally nest in uplands, appeared on wetlands late during the hay harvest from early July to early August (Fig. 3).

To analyze effects of habitat attributes on duck use of wetlands, we wished to focus on summer residents that bred locally, excluding use patterns that might exist only during molt, staging, or migration including non-residents. Based on chronology of numbers, most spring migrants of dabbling and diving ducks had passed through by 15 May, so we began habitat analyses on that date. In August, dabbling

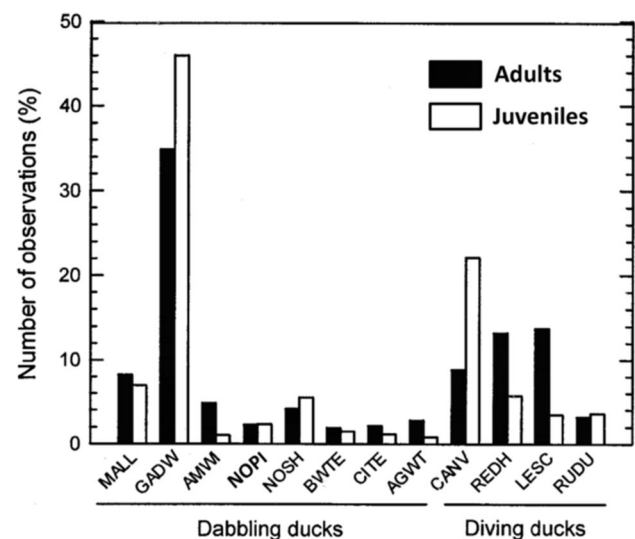


Fig. 2 Percentages of adult ($n=21,096$) and juvenile ($n=1789$) dabbling and diving ducks observed in the Laramie Basin, Wyoming, 15 May–24 August 1999. Species codes are MALL mallard, GADW gadwall, AMWI (American wigeon), NOPI (northern pintail), NOSH (northern shoveler), BWTE (blue-winged teal), CITE (cinamon teal), AGWT (American green-winged teal), CANV (canvasback), REDH (redhead), LESC (lesser scaup), and RUDU (ruddy duck)

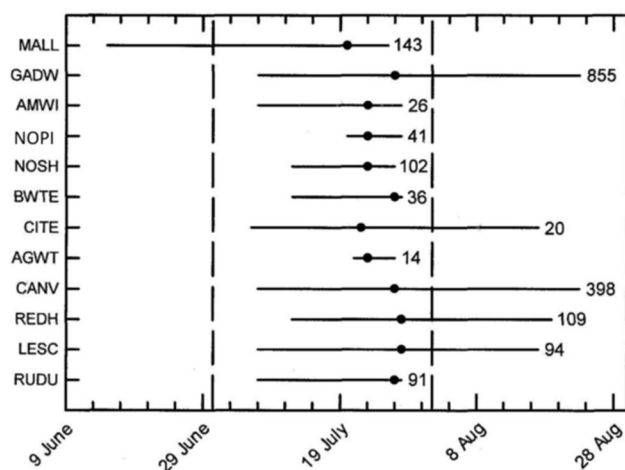


Fig. 3 Range of hatching dates (first observations of Class I broods) of ducks in the Laramie Basin, Wyoming with respect to the haying period for 1998 and 1999 combined. Numbers of Class I juveniles are annotated, as well as the date the largest number of Class I juveniles was observed for each species (solid circles). The range of hatching dates is enclosed by the horizontal dotted lines. Species codes are in Fig. 2

ducks tended to shift from smaller to larger lakes. These concentrations may have included local individuals that were molting or preparing to migrate, and possibly non-residents that were molting or staging in the area. At the same time, we were still seeing new broods of diving ducks appear. Consequently, in contrast to Fig. 2 which includes counts from 15 May to 24 August for all species, multiple regressions reported below are based on data from 15 May to 15 July for dabbling ducks, and from 15 May to 24 August for diving ducks.

Wetland Use by Dabbling Ducks

For densities (number per wetland area) of all species and social groups of dabbling ducks, the most consistent factors in almost all regression models were positive associations with sinuosity or negative associations with wetland area or perimeter (Table 2). Sinuosity (perimeter ÷ area) increases with declining wetland area, so these correlations collectively suggest that all species and social groups of dabbling ducks preferred smaller wetlands, especially if shorelines were irregular. Other habitat factors were more variable among species and social groups – note that sample sizes for dabbling broods were inadequate except for mallards (*Anas platyrhynchos*), gadwalls, and northern shovelers (*Spatula clypeata*). For all dabbling species except mallards and shovelers, pairs showed positive correlations with higher salinity class, while unassociated adults of gadwall, American wigeon (*Mareca americana*), northern pintail (*Anas acuta*),

and American green-winged teal (*Anas carolinensis*) were negatively affected by the presence of surface inflow. As there were very few wetlands with salinities higher than mesosaline (>18 ‰ or 30 mS cm⁻¹, Fig. 1), these correlations indicate a general preference for mesosaline wetlands with no freshwater inflow during the year of the survey.

Pair densities of wigeon, cinnamon teal (*Anas cyanoptera*), and green-winged teal were positively correlated with presence or areal cover of emergent vegetation, but pairs of the other species were not. When presence or areal cover of submersed aquatic vegetation (SAV) were influential, correlations with duck density were mostly negative. However, there were concurrent positive correlations with dominance by *P. pectinatus* for pairs of gadwalls and ruddy ducks (*Oxyura jamaicensis*) (Table 3), and negative correlations with dominance by *Chara* in discriminant functions for presence-absence of canvasback broods and unassociated adult scaup (not shown). These patterns suggest that the negative association with SAV coverage reflected negative influence of the areal extent of *Chara*. Presence or absence of nearby hayfields had no effects on densities of any species or social group of dabblers. Heavy grazing around wetlands positively affected pair densities of pintails, whereas light grazing negatively affected brood densities of shovelers; however, grazing had no apparent effects on other species or social groups.

Pairs and broods of gadwalls, the most common species, were positively related to higher numbers or area of mesosaline (but not oligosaline) wetlands within 1 km. However, densities of shoveler pairs were lower on wetlands with higher area of mesosaline wetlands within 1 km. No other species or social groups of dabblers were affected by the proximity of other wetlands.

Wetland Use by Diving Ducks

For densities of diving ducks, negative correlations with wetland area and positive correlations with sinuosity (perimeter ÷ area) again indicated overall greater use of smaller wetlands by all species and social groups. Pairs and broods of all species (except broods of scaup) were positively associated with the percentage of shoreline with emergent vegetation, or the mere presence of emergent vegetation (canvasback pairs). This pattern is consistent with overwater nesting by canvasbacks, redheads, and ruddy ducks, or nesting in dry portions of the emergent fringe by lesser scaup. Among divers, canvasbacks were unique in that both pairs and broods were also associated with higher salinities. Densities of redhead and scaup pairs, and of unassociated adult canvasbacks, were higher on wetlands with mudflats; mudflats are more common in mesosaline wetlands which lack an emergent fringe, suggesting feeding by these species in mesosaline wetlands. Scaup pairs were

Table 2 Stepwise multiple regressions of counts of dabbling ducks (Anatini) per km² on attributes (Table 1) of each wetland, for counts averaged over 8 weekly visits from 15 May to 15 July 1999, analyzed for different social groups at each site where they were present (n = number of sites). Data for broods are not reported if number of

sites was too low for analyses (2 to 4 sites). Variable codes are in Table 1. Social groups were paired males and females, broods, and unassociated (not accompanied by a mate) adults. For all regressions, $P < 0.01$

Species, social group	Model equation	adj r^2	n
Mallard			
Pairs	$-1.16 - 3.17 \text{ LnAREA}$	0.43	49
Broods	$-1.93 + 1.30 \text{ SINUOUS} - 6.01 \text{ DEPTH}$	0.89	12
Unassociated adults	$-0.870 + 1.19 \text{ SINUOUS} - 6.09 \text{ MESAREA} - 1.71 \text{ SAVcov}$	0.72	42
Gadwall			
Pairs	$-21.8 - 7.86 \text{ LnAREA} + 10.1 \text{ POTAMO} + 2.27 \text{ MESWIN1} + 6.99 \text{ SALCLASS}$	0.62	52
Broods	$20.8 + 0.391 \text{ SINUOUS} - 19.6 \text{ SAVpa} + 4.7 \text{ MESAREA}$	0.47	30
Unassociated adults	$7.7 - 14.7 \text{ LnAREA} - 21.5 \text{ INFLOWpa} + 14.2 \text{ MUDFLATpa}$	0.32	44
Northern shoveler			
Pairs	$0.029 + 0.298 \text{ SINUOUS} - 0.822 \text{ MESAREA} - 0.307 \text{ SAVcov}$	0.86	36
Broods	$1.08 + 0.498 \text{ SINUOUS} - 5.27 \text{ LGRAZEpa}$	0.81	8
Unassociated adults	$8.03 - 2.86 \text{ LnPERI} - 3.09 \text{ SAVpa} + 0.956 \text{ MUDFLATpa}$	0.78	22
American wigeon			
Pairs	$-12.4 + 0.491 \text{ SINUOUS} + 5.86 \text{ SALCLASS} + 0.0566 \text{ EMERGshor}$	0.62	31
Unassociated adults	$35.8 - 11.5 \text{ DEPTH} - 12.2 \text{ INFLOWpa} - 0.974 \text{ SAVcov}$	0.62	24
Northern pintail			
Pairs	$-8.00 - 2.48 \text{ LnAREA} + 4.82 \text{ SALCLASS} + 2.74 \text{ HGRAZEpa}$	0.74	25
Unassociated adults	$-5.77 - 1.91 \text{ LnAREA} + 3.85 \text{ SALCLASS} - 4.55 \text{ INFLOWpa} + 5.55 \text{ SAVpa}$	0.90	12
Blue-winged teal			
Pairs	$-2.39 + 0.240 \text{ SINUOUS} + 1.98 \text{ SALCLASS} - 1.10 \text{ DEPTH}$	0.91	22
Unassociated adults	$2.68 - 1.46 \text{ LnPERI} + 0.00868 \text{ EMERGshor}$	0.71	19
Cinnamon teal			
Pairs	$-5.02 - 1.78 \text{ LnAREA} + 2.91 \text{ SALCLASS} + 1.24 \text{ EMERGpa}$	0.59	26
Unassociated adults	$-2.20 + 0.308 \text{ SINUOUS} + 2.29 \text{ MUDFLATpa}$	0.96	16
American green-winged teal			
Pairs	$-5.23 + 0.156 \text{ SINUOUS} + 3.22 \text{ EMERGpa} + 2.44 \text{ SALCLASS}$	0.81	23
Unassociated adults	$2.77 + 0.214 \text{ SINUOUS} - 2.27 \text{ INFLOW}$	0.65	16

uniquely associated with the presence of nearby hayfields, but scaup broods were less common when there were adjacent hayfields. No effects of hayfields on other species, or of cattle grazing on any diver species, were detected. Although these results suggest that canvasbacks commonly moved with their broods to mesosaline wetlands after nesting and also fed there as pairs, there was no correlation for any diver species with the number or area of mesosaline wetlands within 1 km. Among divers, only broods and unassociated adults of ruddy ducks were affected by nearby wetlands, and the correlations were with oligosaline and not mesosaline wetlands.

Discussion

Effects of Nesting Cover, Hayfields, and Grazing

Beyond wetland area, salinity class and associated presence or extent of emergent vegetation were the most influential habitat variables for most species. Diving ducks nest overwater in bulrush, and lesser scaup probably nest on the ground in dry portions of the bulrush fringe. Moreover, dabbling ducks and scaup were probably limited by the

Table 3 Stepwise multiple regressions of counts of diving ducks (Aythya) per km² on attributes (Table 1) of each wetland, for counts averaged over 14 weekly visits from 15 May to 24 August 1999, analyzed for different social groups at each site where they were present

(n =number of sites). Variable codes are in Table 1. Social groups analyzed were paired males and females, broods, and unassociated (not accompanied by a mate) adults. For all regressions, $P < 0.01$

Species, social group	Model equation	adj r^2	n
Canvasback			
Pairs	$-10.5 - 2.03 \text{ LnAREA} + 2.18 \text{ EMERGpa} + 3.42 \text{ SAVpa} + 4.03 \text{ SALCLASS}$	0.65	38
Broods	$-29.4 - 8.51 \text{ LnAREA} + 15.5 \text{ SALCLASS} + 0.130 \text{ EMERGshor}$	0.58	26
Unassociated adults	$-14.0 - 11.9 \text{ LnAREA} + 32.1 \text{ MUDFLATpa} + 0.252 \text{ EMERGshor} - 8.64 \text{ SALCLASS}$	0.64	34
Redhead			
Pairs	$-10.1 - 3.29 \text{ LnAREA} + 0.0778 \text{ EMERGshor} + 4.22 \text{ MUDFLATpa} + 3.10 \text{ DEPTH}$	0.73	38
Broods	$1.80 + 0.302 \text{ SINUOUS} + 0.0267 \text{ EMERGshor} - 4.26 \text{ SAVpa}$	0.84	10
Unassociated adults	$-6.63 - 7.71 \text{ LnAREA} + 17.6 \text{ MUDFLATpa}$	0.29	41
Lesser scaup			
Pairs	$-22.5 - 15.1 \text{ LnAREA} + 0.404 \text{ EMERGshor} + 21.7 \text{ MUDFLATpa} + 11.8 \text{ HAYpa}$	0.57	37
Broods	$-3.52 + 0.664 \text{ SINUOUS} - 20.6 \text{ HAYpa}$	0.83	8
Unassociated adults	$-6.05 + 1.19 \text{ SINUOUS} + 0.200 \text{ EMERGshor}$	0.38	39
Ruddy duck			
Pairs	$-4.73 + 0.425 \text{ SINUOUS} + 0.0519 \text{ EMERGshor} + 2.27 \text{ POTAMO}$	0.75	20
Broods	$-0.156 + 0.399 \text{ EMERGcov} + 0.341 \text{ WIN1}$	0.88	8
Unassociated adults	$-3.33 - 3.10 \text{ LnAREA} + 1.65 \text{ OLIWIN1} + 0.587 \text{ NEAREST}$	0.43	22

sparse upland cover in shortgrass steppe. Use of shortgrass habitat by upland-nesting ducks is rarely documented, although nest success in taller mixed-grass prairie can be high (Ball et al. 1995). In the San Luis Valley of Colorado, rushes and sedges were more available than in the Laramie Basin and supported most nests of dabbling ducks, while upland habitats of saltgrass and greasewood were little used (Gilbert et al. 1996; Setash et al. 2020). In the Laramie Basin, it is likely that dabbling ducks often nest in landward portions of the bulrush fringe that are not flooded in drier years, and mallards may nest over water in flooded bulrush (Arnold et al. 1993).

Studies elsewhere have shown that hayfields can provide valuable upland nesting cover (Duebbert and Lokemoen 1976). As a result, cattle grazing that degrades hayfield cover (except perhaps for pintails, Table 2) has been reported to reduce numbers of pairs and broods on intermountain and mixed-grass prairie wetlands (Gjersing 1975; Harrison et al. 2017), and to decrease nest densities and nest survival in the eastern prairies (Kruse and Bowen 1996; Bloom et al. 2013). However, in the Laramie Basin, presence of hayfields or grazing cattle had little or no influence on duck use of adjacent wetlands except by scaup pairs. For upland-nesting dabbling ducks and lesser scaup, most hatching occurred during haying operations, and peak of hatching was late in the harvest period (Fig. 3). Thus, if hens tried to nest in hayfields, their nests might have been destroyed or abandoned during harvest. Dugger et al. (2016) reported that nests of mallards in the Columbia Basin of Washington state were not successful because of haying. Broods were not

associated with hayfields in our analyses; however, if ducks nest in hayfields but lose their nests, this behavior would not be apparent from numbers of juveniles observed. For example, nearby hayfields had positive effects on scaup pairs but negative effects on scaup broods (Table 3), and production of scaup juveniles was low relative to adult numbers (Fig. 2). Thus, scaup may have been attracted to nest in hayfields, but did not nest successfully. Lack of hayfield effects suggests that dabbling ducks were not using hayfields disproportionately as nest sites. Research is needed to determine the fraction of different species that attempt to nest in hayfields in shortgrass steppe environments, and the fraction of nests destroyed or abandoned during hay harvest.

Differences in Prey Availability

In oligosaline wetlands of the Laramie Basin, biomass of invertebrate prey (g C m^{-2}) is dominated by amphipods (mainly *Hyalella azteca*), with abundant snails and far lower biomass of chironomid larvae. In mesosaline wetlands, snails are essentially absent, amphipods are much less abundant, and chironomid larvae are the dominant taxon. *H. azteca*, which can tolerate higher salinities but lacks a dispersal stage, appears to have difficulty recolonizing mesosaline wetlands after their more frequent drawdowns; thus, instability of water levels may be more important than salinity per se in regulating abundance of some taxa (Hart and Lovvorn 2005). Snails also lack a dispersal stage, but may also be excluded by higher salinities.

Diets of ducks in the Laramie Basin have not been studied, so the significance of loss of snails and replacement of amphipods by chironomid larvae as the dominant potential prey is unclear. During the breeding season ducks tend to feed opportunistically and have quite varied diets (review in Wollheim and Lovvorn 1995). Much of the invertebrate biomass in Laramie Basin wetlands is in the foliage of submersed vegetation (Wollheim and Lovvorn 1995). The total invertebrate biomass in *P. pectinatus* stands in mesosaline wetlands is over twice as high as in *Chara* stands in oligosaline wetlands (Wollheim and Lovvorn 1996). Moreover, the foliage, seed heads, and invertebrates in the near-surface canopy of *P. pectinatus* are often more accessible to surface-feeding adults and broods than in the low canopy of *Chara*. Although costs of osmoregulation at higher salinities can have important negative effects on duckling growth (Swanson et al. 1984; Mitcham and Wobeser 1988; Moorman et al. 1991), these costs might be offset by higher food availability for surface-feeders in mesosaline lakes. Note that in the nonbreeding period when invertebrates are less important than in the diet of nesting hens and broods, and in shallower waters where *Chara* is accessible, *Chara* foliage and oogonia can be a predominant food for herbivorous adults of both dabbling and diving ducks (Bailey and Titman 1984; Noordhuis et al. 2002).

As we have found in the Laramie Basin, total abundance or biomass of invertebrates were higher in mesosaline than in oligosaline wetlands of the Canadian prairies and North Dakota (Hammer et al. 1990; Mushet et al. 2015). Further studies are needed to confirm that food availability and duck responses to salinity-related habitat types that we observed apply consistently to other areas of the intermountain region.

Proximity of Oligosaline Vs. Mesosaline Wetlands

For dabbling ducks, we often saw pairs and unassociated adults on mesosaline wetlands that lacked an emergent fringe (Table 2). Moreover, densities of pairs and broods of gadwalls, by far the most common duck species, increased with higher numbers or area of mesosaline (but not oligosaline) wetlands within 1 km. Pairs and broods of canvasbacks, the next most abundant species, were positively related to higher salinities. These observations suggest that (1) some dabbling ducks often nested around mesosaline wetlands in the sparse cover provided by shortgrass steppe, or (2) some dabbling ducks and canvasbacks that nested in emergent stands around oligosaline wetlands often fed in mesosaline wetlands, and often moved their broods to mesosaline wetlands despite scant cover for overland travel (Duncan 1987; Rotella and Ratti 1992; Leonard et al. 1996). As noted above, available evidence suggests that hayfields or shortgrass upland cover in this area support few successful nests. In the wet year of this study (1999), only 16% of our

study wetlands were mesosaline while 73% were fresh or oligosaline (Fig. 1; Peck and Lovvorn 2001). Thus, for some dabbling ducks and canvasbacks, in particular, mesosaline wetlands appear to provide exceptional resources in wetland complexes, despite their lack of emergent cover for nesting or brood-rearing.

The Future of Flood-Irrigated Wetlands

Throughout the western United States, mountain snowpack declined by 10–20% from the 1980s to 2000s, and further loss of up to 60% is projected within the next 30 years (Fyfe et al. 2017; Mote et al. 2018). In addition to reduced total runoff, the timing of runoff is increasingly occurring over a shortened period earlier in the spring, so that both the amount and duration of water availability is declining in high intermountain basins worldwide (Qin et al. 2020; Muselman et al. 2021). Higher temperatures will also increase evapotranspiration from irrigated crops (Elliott et al. 2014), and increase conveyance losses via evaporation from transport canals (Moghazi & Ismail 1997). These trends will greatly intensify competition for water between irrigated agriculture, rapidly growing urban areas, and efforts to sustain networks of wetland biodiversity and federally protected species (Aiken 1999; Parker and Anderson 2003; Matchett and Fleskes 2017).

Ironically, attempts to reduce water demands of irrigation by installing sprinklers and lining ditches generally do not decrease water consumption. Such improvements more often result in planting of more valuable crops with higher water demands, or expansion of irrigated area (Grafton et al. 2018). Moreover, although forgoing flood irrigation can increase instream flows during the spring peak of snowmelt, the lack of groundwater recharge by percolation of water distributed over large areas reduces return flows to ditches later in the season (Fernald et al. 2010; Gordon et al. 2020). Thus, elimination of flood irrigation also eliminates a transient storage and release function previously supported by more gradual over-summer melting of mountain snowpack. Loss of flood irrigation not only deprives fishes of higher instream flows later in summer when temperatures are warmer, but also eliminates important wetland habitat for birds and amphibians important to recreation and conservation interests (Kendy et al. 2018). Because a substantial fraction of water used to flood-irrigate fields eventually flows back into ditches and canals (Kendy 2006; Fernald et al. 2010; Gordon et al. 2020), lining ditches and eliminating flood irrigation by installing sprinklers are not a general solution to water shortages (Kendy 2006). Nevertheless, declining mountain snowpack and increased evaporation with higher temperatures will severely reduce availability of water for all uses, so that reductions in flood irrigation and associated filling of small reservoirs appear inevitable.

To counter such losses by strategically creating or conserving key wetland complexes, our study in the Laramie Basin indicates the importance of including both oligosaline and mesosaline wetlands separated by only hundreds of meters. Part of the overall approach may be to identify important complexes that now exist, and to implement long-term efforts to acquire consistent water supplies. Most nature preserves and refuges in this region have very junior water rights, as they were created long after most water was appropriated during Euro-American settlement; thus, direct flows to conservation areas currently have low priority if overall water supplies are scarce. To protect direct surface flows locally, landowners may in some cases be compensated for profits lost in retiring land from irrigation (Peck et al. 2005). Incentive payments to holders of both junior and senior water rights might also be used to perpetuate flood irrigation that keeps local reservoirs filled through the summer, sustains return flows, and elevates water tables that provide seepage to nearby wetlands (King et al. 2021). Nevertheless, declines in mountain snowpack may eventually leave holders of junior rights with no water to maintain flood irrigation or to transfer to wetland conservation. Thus, despite legal, political, and economic impediments, acquiring more reliable senior water rights may be critical to maintaining adequate water availability for wetlands (Downard and Endter-Wada 2013; Kendy et al. 2018; Richter et al. 2020).

Planning and implementing such efforts will require forecasts of climate trends, models of local hydrology and water-rights priorities, knowledge of conditions needed to support different biotic communities, and close cooperation with local water users (Downard and Endter-Wada 2013; Kendy et al. 2018). In urbanizing locales where the public desires access to ecologically diverse nature preserves and visible wildlife, wetland complexes might be developed or enhanced where pre-existing hydrology and soils are amenable (Johnson et al. 2013). Some insights exist into wetland management in this region where biotic communities are structured by the timing of episodic drawdowns and resulting salinities (Kadlec and Smith 1989; Lovvorn and Hart 2004). However, much work is needed to identify factors that mediate the dormancy, dispersal, and community interactions of fauna in these variable environments (Hart and Lovvorn 2005; Chase 2007; Strachan et al. 2015). In all these endeavors, maintaining diverse wetland bird populations may be the most visible indicator of success in preserving overall biodiversity and meeting societal demands in this semiarid region.

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MLC: Methodology, Investigation, Writing – original draft, Visualization. Both authors read and approved the final manuscript.

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