



Waterbird communities and wetland dynamics in the Mexican Highlands, 1951–2006

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Abstract Many North American migratory waterbird species rely on wintering and stopover sites in the Northern Highlands of Mexico, several of which have experienced habitat loss or degradation over the last century. Despite this, the long-term patterns of waterbird abundance and the state of the wetlands themselves had not been analyzed. Changes in abundance and distribution of 3.4 million birds belonging to 19 waterbird taxa that winter in the Mexican Highlands were assessed using data from the United States Fish and Wildlife (USFWS) aerial surveys carried out between 1951 and 2006. Additionally, water occurrence at 29 wetlands used by these birds

was inferred from satellite imagery corresponding to the bird count dates by calculating water surface area using Google Earth Engine. Bird abundance between 1975 and 2006 and environmental variables were modelled using Generalized Linear Mixed Models to identify determinants of wetland use by these groups of wintering waterbirds. Total sampled abundance in the Highlands was between 125,000 and 500,000 individuals of the different species of waterbird per year, and their abundance was highly variable between sites and years. The sites with the highest average abundance were Laguna de Babícora and the wetland complexes from Laguna Bustillos to Laguna de los Mexicanos in the northwestern section of the Highlands, as well as the wetlands in the sierra of the state of Durango, to the south-southeast of the former. Water permanence was different between the six subregions into which the wetlands were grouped, despite waterbody size not being significantly different between them. Overall, waterbirds were more abundant in semi-permanent sites, and abundance was explained best by water surface area plus total precipitation of the previous 12 months. Geese in the area exhibited site fidelity and this reflected in site-specific variables included in the best model. Abundance of diving ducks was explained best by water surface area, while that of dabbling ducks was so by water permanence plus water surface area. Our work supports that most birds preferred reliable, natural wetlands over human-modified ones even if the latter

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were larger, and this has clear implications for habitat management in this semiarid region.

Keywords Historic changes · Wetlands · Semiarid and arid lands

Introduction

Many migratory waterbirds in North America rely on stopover sites during their yearly migrations, and some of these sites are critical for their survival (Myers 1983). Besides providing a place to rest, these sites must provide enough food for birds to replenish body resources so that they are able to continue their southward or northward journeys. Hence, disturbance or loss of such habitat patches can result in a suboptimal nutrition or a change in migrating route (Weber et al. 1999). As a result, many continental population sizes of migrating waterbirds are determined not by the conditions of the best sites along the route, but often by the worst (Myers 1983; Newton 2008). The dependence of migrating birds on the quality of the sites is especially acute in species that migrate through arid regions where water bodies are less abundant, and birds must fly over large areas of inhospitable terrain between them (Kirby et al. 2008). This is further complicated by the fact that in arid and semiarid regions, like those found in the Mexican Altiplano, there can be high year-to-year variation in wetland conditions. Reflecting such dynamics, for example, during drought events the Mexican Duck (*Anas platyrhynchos diazi*), concentrate in a few large and permanent waterbodies where they reach 10 times their usual abundance (Pérez Arteaga et al. 2002).

Waterbird dependence on wetlands is a matter of conservation concern as up to 57% of wetlands in the world have been lost or transformed since the beginning of the 18th Century (Davidson 2014). In Mexico, 62% of all wetlands known in historic times have been lost, and most of this loss has occurred in two major regions: the arid and semiarid regions of the highlands and the tropical southeast (Landgrave and Moreno-Casasola 2012). Such wetland loss has been caused mainly by water-extraction for agricultural and urban uses (Leopold 1959; Moreno-Casasola 2008). In contrast to the loss of natural wetlands, and often causing it, many artificial wetlands have been created for agricultural purposes and, although such wetlands

are used by waterbirds, they could be imperfect substitutes for unmodified sites (Kingsford et al. 2004).

Waterbird dynamics have long been studied in the United States and Canada, driven by the high levels of sport hunting and derived benefits. In contrast, published information on the same species during the non-breeding season in Mexico is scant, and restricted basically to the accounts of Leopold (1959) and Saunders and Saunders (1981), in addition to small-scale studies. The inland region whose waterbirds seem to have been better studied is El Llano in the states of Aguascalientes and Jalisco, where the main focus has been the Mexican duck (*Anas platyrhynchos diazi*) (Pérez-Arteaga et al. 2002a, b; Pérez-Arteaga and Gaston 2004; Medina-Torres et al. 2007), and for which recently 50 years of waterbird abundance were analyzed (Mellink et al. 2018). Other recent studies were carried out in Laguna Santiaguillo, Durango (Chacón de la Cruz et al. 2017), Laguna Bustillos, Chihuahua, (Mireles and Mellink 2017), the San Pedro river (Ramírez-Marfil 2016); sandhill cranes (*Antigone canadensis*) in Laguna Babícora (Drewien et al. 1996; Arizmendi and Márquez 2000) and in Zacatecas (Clemente-Sánchez et al. 2014); waterbird habitat and plovers nesting in San Luis Potosí's western arid section (Mellink and Valenzuela, 1991; Luévano et al. 2010, respectively); and genetics and habitat preference of the Mexican Duck in the state of Zacatecas (Mercado-Reyes 2012). Thus, the few studies carried out on waterbirds of the Mexican Altiplano have addressed single or few sites, been focused on a single species, or been of short duration. They have mostly involved species tallying, without analyzing mid- or long-term fluctuations and, or wide geographic scopes.

One consequence of the paucity of information and analysis of waterbird populations in Mexico has been that management has relied more on appreciation than on solid knowledge. Hence, the management strategies for waterbirds by successive Mexican administrations have changed through time, although more recent efforts to integrate a national strategy have been made (SEMARNAT 2008). Without solid knowledge, management decisions will continue to rely on appreciations and gut feelings and would, thus, have a high risk of not being adequate to best manage waterbird populations.

One source of information on the waterbirds of northern Mexico, which has not been extensively

tapped into, is the long-time mid-winter monitoring program carried out by the United States Fish and Wildlife Service (USFWS). Surveys under this program were initiated in 1948 and continued until 2006. Until 1982 they were performed yearly, and afterwards they were carried out every 3 years. These surveys were not always consistent in flight path, sampling scheme and several sites being visited only a few times (Eggeman and Johnson 1989; Otto and Frechtel 2001; Atkinson et al. 2006), but nevertheless they are still the main general source of waterbird abundance information in Mexico, and the only information that exists for many areas (Carrera-Gonzales and De la Fuente-De León, 2003). The USFWS surveys led to the first overview of the waterfowl areas in the country (Leopold 1959; Saunders and Saunders 1981) and formed the basis for proposals of protected sites (Pérez-Arteaga et al. 2002a, b). They have also provided information for local and regional analysis (v.gr. Mellink et al. 2009, 2018; Mireles and Mellink 2017). However, much of the information obtained during these surveys in Mexico, has not been interpreted.

We focused on the arid-semiarid northern half of the Mexican Altiplano that runs from north of the Trans-Mexican Volcanic Belt to Mexico's border with the United States. The objectives of our study were to analyze changes in abundance and distribution of waterbirds in a subset of comparable sites in this region that were surveyed aerially by the USFWS between 1951 and 2006 as well as analyze the relationship of waterbird numbers with inter-survey variation in the attributes of the sites, incorporating remote sensed data.

Methods

Study region and sites

The Mexican Altiplano is a large plateau in northern Mexico between the Sierra Madre Oriental and the Sierra Madre Occidental to the east and west respectively, north of the Mexican Transvolcanic belt. It has an average elevation of between 1000 and 2000 m above sea level and has predominantly arid and semi-arid climate which produces xeric shrublands for the most part. It is part of the central North American flyway of migratory waterbirds. In this region, dozens of

waterbodies that were known to harbor large amounts of waterbirds were selected to be inventoried at the onset of the USFWS' mid-winter monitoring program, in the 1940s (Saunders and Saunders 1981). These included natural wetlands such as marshes and bolson lakes to manmade reservoirs to support agriculture. From within this pool, we focused on 29 sites that were more uniformly surveyed since 1975 until 2006, ranging from the northern edges of the state of Jalisco in central Mexico to the border with the United States, grouped into 6 sub-regions (Fig. 1, Supplementary data). We classified waterbodies by quartiles as small (0–5.6 km²), medium (5.7–13.5), large (13.6–63.2), and very large (> 63.2). Winter permanence of each site was determined using the coefficient of variation (C.V.) of its size throughout the surveys. Categories were: permanent (< 0.6 C.V.), semi-permanent (0.6–1), temporary (1.5–1), ephemeral (> 1.5). Our sites occurred through 8 hydrological regions: Cuencas Cerradas del Norte, Sonora Sur, Bravo-Conchos, Mapimí, Nazas Aguanaval, Presidio San Pedro, El Salado and Lerma-Santiago (Comisión Nacional del Agua, 2018).

Waterbird abundance

Data on waterbirds abundance at each of the selected site or cluster of sites were gleaned from the USFWS mid-Winter inventories databases. Many surveys had changes in flight paths, sampling intensity and flight methods (Eggeman and Johnson 1989), adding to variation intrinsic to specific date (abundance could have been affected by recent disturbance at any site, for example). Thus, to minimize variation and create a subset of comparable data, we selected 19 bird taxa according to their total abundance (> 5000 total birds counted), as well as their conservation category according to the Mexican species-at-risk list (SEMARNAT 2010). Bird data was analyzed in four separate groups: geese, dabbling ducks, diving ducks and other, and were grouped by region.

Wetland dynamics

We derived information about water surface area from satellite images of each study site. For this purpose, we created site polygons using original site descriptions (Saunders and Saunders 1981) and flight data. Landsat 1–5 satellite imagery from between 1975 and

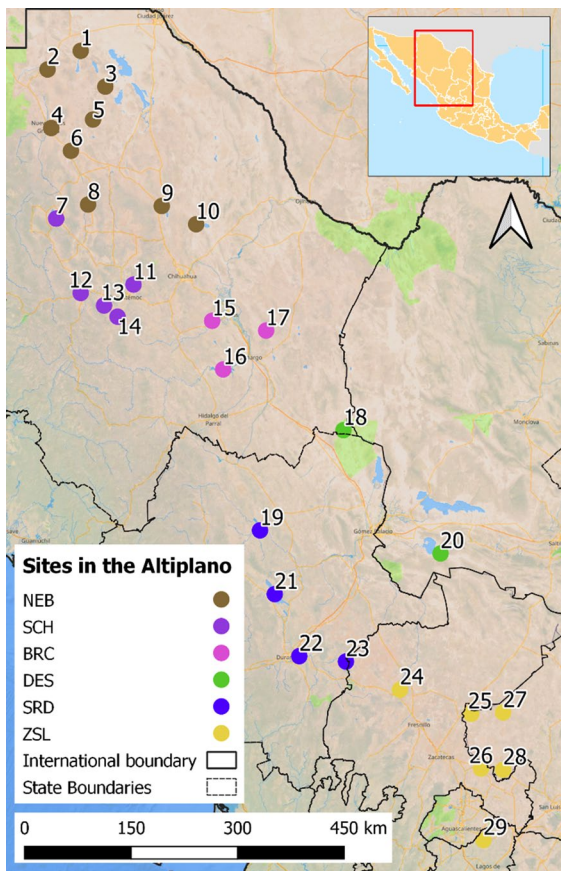


Fig. 1 Sites and subregions in the Mexican Altiplano. *Northern basins* (NEB, brown): 1 - Laguna de Guzmán, 2 - Ascensión, 3 - Laguna de Santa María, 4 - Casas Grandes, 5 - Rio de Santa María, 6 - Galeana, 8 - Presa el Tintero, 9 - Laguna de Encinillas and 10 - Laguna de Cuervo. *Sierra of Chihuahua* (SCH, purple): 7 - Laguna de Babícora, 11 - Laguna Bustillos, 12 - Presa Abraham Gonzales, 13 - Laguna San Rafael and 14 - Laguna de los Mexicanos. *Bravo - Conchos* (BRC, pink): 15 - Delicias, 16 - Presa la Boquilla and 17 - East la Cruz. *Deserts* (DES, green): 18 - Laguna de Palomas, 20 - Laguna de Viesca. *Sierra of Durango* (SRD, blue): 19 - Rio de Oro, 21 - Laguna de Santiaguillo, 22 - Durango and 23 - Presa Francisco Villa. *Zacatecas - San Luis Potosí* (ZSL, yellow): 24 - Presa El Cazadero, 25 - Villa de Cos, 26 - Saladillo, 27 - Lago de Perdido, 28 - Salinas and 29 - El Llano

2006 was obtained near each survey date. In addition to technological changes bearing on resolution, starting from a 60 m resolution on the Multi-spectral Scanner (MSS) on Landsat 1, the coverage of available images was not uniform, mainly due to policy changes in successive US government administrations (Wulder et al. 2012). A total of 266 surveys, out of the 464 that were carried out during the timespan studied,

had matching satellite images of sufficient quality for analysis, and were thus selected for analysis.

Normalized Difference Water Index (NDWI; Gao, 1996) was used to detect surface water area, and different thresholds were used depending on environmental factors such as turbidity and substrate. Preliminary tests had many false positives in hilly areas since shaded vegetation in canyons can be mistaken for water. Several methods have been proposed to fix this, including using digital elevation models or automating water detection models (Shahtahmassebi et al. 2013; Jiang et al. 2014). We used a modified version of the NDWI, applying a scaling factor to the green band, which was able to reduce >95% of false positives:

$$\frac{((\text{green} * \text{factor}) - \text{nir})}{((\text{green} * \text{factor}) + \text{nir})}$$

Water pixels were classified and water area was calculated. Sites were classified into quartiles by maximum winter size and winter water persistence using their coefficient of variation. Compound images were created using a color gradient to indicate water persistence. We performed all image processing using Google Earth Engine for image processing (Gorelick et al. 2017), a remote sensing analysis, cloud-based platform that is open for everyone.

Data analysis

We analyzed the relationships between bird abundance and water surface at each site, as described above, and climatic explanatory variables, through Generalized Linear Mixed Models (GLMMs). Historic climate data was obtained from the National Weather System of Mexico (Sistema Meteorológico Nacional 2019), including monthly maximum and minimum temperature, evaporation, precipitation, and El Niño-Southern Oscillation (ENSO) index values. An information theory approach (Burnham and Anderson 2002) was used where models were not randomly generated, but several plausible combinations of 11 fixed effects were tested, namely January precipitation, previous 6-month precipitation, previous year precipitation, November to January ENSO values before survey, previous year ENSO average, water surface area, sub-region, winter water permanence category, size category, and year. Since individual site characteristics were

expected to influence yearly winter abundance, site was used as a random effect.

Akaike Information Criterion (AIC) values were used to infer the best model and a parsimony criterion was used in cases where two or more models had similar values. Count data was transformed into its natural logarithm to ensure model assumption were met, and residuals were checked. The best/most parsimonious models were validated with unused original data. All analysis were carried out in R (R Core Team 2019), mostly with the *lme4* (Bates et al. 2015) and *pgirmess* (Giraudoux 2018) packages.

Results

Winter water levels

Of all sites, 14 were permanent while 5 each were ephemeral, temporary, or semipermanent. The sites in the Northern Basins were of all sizes and permanence. All 3 in Bravo-Conchos were semipermanent or permanent. Desert sites were ephemeral and medium-sized on average. Those in the sierras of Durango and Chihuahua were either semi-permanent or permanent. The Zacatecas - San Luis Potosi plains had sites of all sizes and permanence type. No clear link was found between size and permanence. Study-wise averages classified 8 sites as small, 7 as medium-sized, 6 as large and 8 as very large (Supplementary file).

Waterbirds, study-wide and per region

Birds of 19 species or species-groups counted at the selected sites from 1975 to 2006 summed nearly 3.4 million individuals. Laguna de Babicora, in Chihuahua, had the highest total abundance, with over 800,000 individuals. Two sites in the state of Durango followed: the wetland complex around the city of Durango and Laguna de Santiaguillo, each with nearly 700,000 birds. The complex around ciudad Cuauhtémoc, Chihuahua, had over 500,000 birds counted over this period.

Region-wide totals of between 125,000 and 500,000 individuals were recorded in each of the winter surveys, with data exhibiting high inter-year variation and no clear general trend (Fig. 2). Two bird species/species groups accounted for 50% of the total abundance in our dataset: Snow and Ross's Goose (31.8%) and Northern Pintail (18.3%). Five other species, accounted for an additional 40.8%: Green-Winged Teal (11.7%), American Coot (7.7), Sandhill Crane (7.5), Northern Shovelers (7.0), and Greater White-fronted Geese (6.8). The remaining 12 species/species groups accounted for less than 10%; and diving ducks were, overall, a minor component of the waterbird population in our study sites (Table 1).

There was regional segregation in some species: Snow and Ross's Geese reached the southern edge of the state of Durango and were sometimes recorded to the southeast of it, in the states of Zacatecas and San Luis. Gadwalls, Northern Pintails, and Green-winged Teals were distributed evenly except on the Zacatecas—San Luis Potosi plains, where their numbers were lower. Northern Shovelers were spread out evenly throughout the study region. American Coots were notably

Fig. 2 Total waterbird abundance at 29 survey sites in the Mexican Altiplano surveyed by the USFWS between 1975 and 2016. Solid lines indicate consecutive years

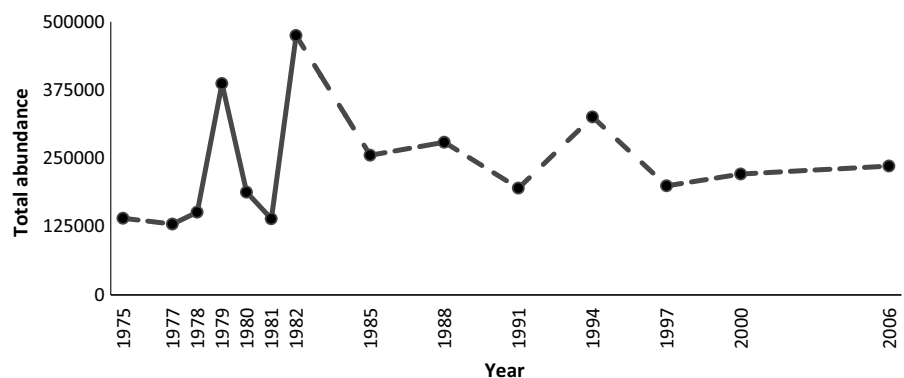


Table 1 Waterbird species studied on the Mexican Altiplano, according to their abundance recorded during USFW mid-winter aerial waterbird surveys. Within group, species are arranged from more to less abundant

Name	Abundance	%
<i>Geese</i>		
Snow/Ross's Goose (<i>Anser caerulescens/A. rossii</i>)	1,072,045	31.8
Greater White-fronted Goose (<i>Anser albifrons</i>)	228,068	6.8
<i>Dabbling ducks</i>		
Northern Pintail (<i>Anas acuta</i>)	617,647	18.3
American Green-Winged Teal (<i>Anas crecca</i>)	393,569	11.7
Northern Shoveler (<i>Spatula clypeata</i>)	235,109	7.0
Gadwall (<i>Mareca strepera</i>)	79,311	2.3
American Wigeon (<i>Mareca americana</i>)	76,469	2.3
Mexican Duck (<i>A. platyrhynchos diazi</i>)	69,608	2.1
Mallard (<i>A. platyrhynchos</i> , other subspecies)	41,276	1.2
Blue-winged/Cinnamon Teal (<i>Spatula discors/S. cyanoptera</i>)	17,358	0.5
<i>Diving ducks</i>		
Redhead (<i>Aythya americana</i>)	11,374	<0.5
Generic Scaup (<i>Aythya</i> sp.)	5,417	<0.5
Canvasback (<i>Aythya valisineria</i>)	3,674	<0.5
Ruddy Duck (<i>Oxyura jamaicensis</i>)	3,539	<0.5
Ring-necked Duck (<i>Aythya collaris</i>)	2,933	<0.5
Generic Merganser (<i>Mergus</i> sp.)	1,577	<0.5
<i>Other waterbirds</i>		
American Coot (<i>Fulica americana</i>)	259,133	7.7
Sandhill Crane (<i>Antigone canadensis</i>)	251,734	7.5
Generic small shorebird	5,143	<0.5
Total	3,374,984	

absent from northern Chihuahua and the Sierras de Chihuahua at the northern edge of the Altiplano. Greater White-fronted Geese were absent from the northern end of the study range and disappeared from the Zacatecas—San Luis Potosí plains, where they had wintered in the 1980 and 1990 s; mostly retracting to the wetlands of Durango and to Laguna de Babícora in Chihuahua. Mallards were identified only in Chihuahua, at the northernmost edges of the Altiplano; to the south they are substituted by the Mexican Duck.

Of the 28 models tested, total abundance was explained best by winter size of waterbody, along with wetland year-to-year permanence, and precipitation during the previous 12 months (Fig. 3). There was a positive correlation between waterbird abundance and the size of the water and precipitation. Bird abundance was slightly higher in semi-permanent sites than permanent ones, with temporary sites being lower and ephemeral sites, the lowest.

Waterbirds per species or species group

At species level, there were meaningful trends in geese populations between 1975 and 2006 (Fig. 4). Snow and Ross's Geese numbers either remained steady or increased in all sub-regions, while average Greater White-fronted Goose abundance dropped by more than 80% at the southern edge of the Altiplano. Mexican Duck numbers did not exhibit any trend but varied greatly each winter. Part of this fluctuation might have been caused by their pre-1982 lumping with mallards, which winter in northern Durango and Chihuahua, after which they began to be counted separately whenever this was possible. Sandhill cranes were concentrated in Laguna Babícora and Laguna de los Mexicanos; each of them had a higher average abundance than all other 27 sites combined. Laguna Babícora by itself holds almost 70% of all sandhill cranes tallied in Mexico, even more in certain years (Fig. 5); their total population seems to have had a

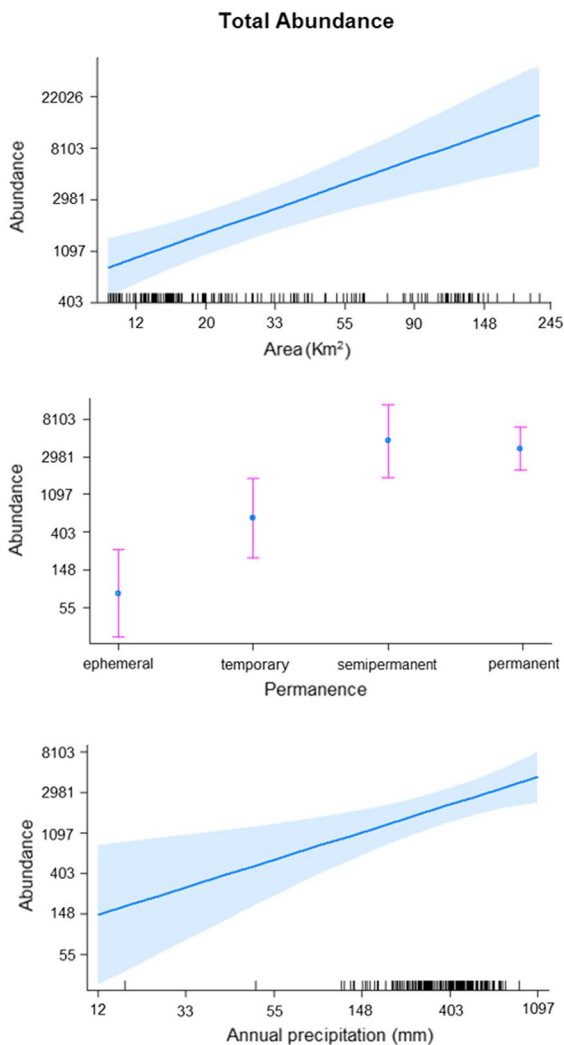


Fig. 3 Relationship between total waterbird abundance and permanence, water body, and the precipitation of the previous 12 months. The vertical lines on the horizontal axis indicate where data is located. Data is logarithmic

modest increase. Goose abundance was explained by maximum size of waterbody, wetland permanence, and sub-region (Fig. 6). Desert sites had the lowest average number of goose counts, but there was very high inter-year variation. Abundance of dabbling ducks was positively dependent on wetland size, and these were more abundant in semi-permanent sites and less abundant in ephemeral ones (Fig. 7) Average correlation between rainfall of the past 12 months and wetland size was 0.55. Abundance of each permanence category was modeled for dabbling ducks

(See supplementary file for site data) Abundance of diving ducks was explained only by surface area and numbers were small.

Discussion

Waterbird abundance

The role of changing environmental conditions and human water use in wetland dynamics and waterbird presence in northern Mexico has remained largely unexplored. Nevertheless, some data point at major changes during the last few centuries. Overall, the northern Altiplano and adjacent regions seem to have seen a slight increase in precipitation between 1970 and 2000, but also some of the increases in temperature in the country (Cuervo-Robayo et al. 2020). Other factors also come into play. Laguna de Viesca and neighboring Laguna Mayran were part of a wetland complex of hundreds of square kilometers as recently as the 19th and early 20th Centuries (Saunders and Saunders 1981) but have dried up because of the damming of the rivers that fed them (Descroix 2004), and Laguna de Viesca totaled only 770 birds in one count during the 20 years of USFWS data we explored.

Changes in the abundance of some species' numbers were driven by changes at much larger scales, as well as local factors. So, white goose (Snow and Ross's geese combined) went from an average of 50,000 birds in the late 1970 to around 100,000 in the 2000s in northern Mexico, coinciding with a tripling of their continental population over the same period (Bechet et al. 2004, Gauthier et al. 2005). Nevertheless, the abundance of this group of geese in northern Mexico varied between winters, increasing with time overall, indicating that, in addition to the continental population change, local conditions played a role. Availability of goose food in the bolson lakes of Chihuahua increased because of a 50% increase in grain production between 1980 and 2006 (SIAP, 2019), and this could have led to positive feedback loops as geese that use these sites are largely philopatric (Ely et al. 2013).

In contrast, Greater White-fronted Goose numbers decreased in the area from 30,000 individuals to fewer than 10,000, especially in the arid lands of Zacatecas and San Luis Potosi, in the southernmost edge of the

Fig. 4 Abundance of Snow Goose/Ross's Goose (*Anser caerulescens/A. rossii*) and Greater White-fronted Goose (*Anser albifrons*) on the Mexican Altiplano from 1975 to 2006, as recorded on USFWS mid-winter aerial surveys

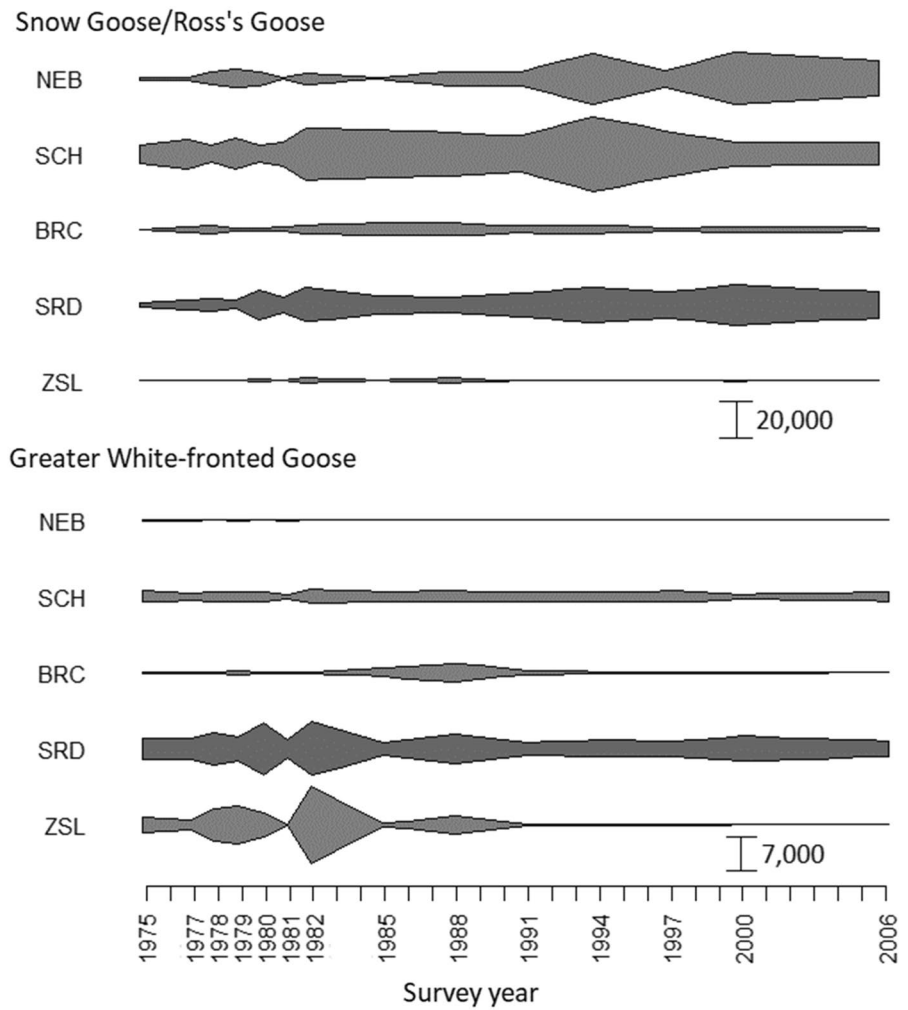
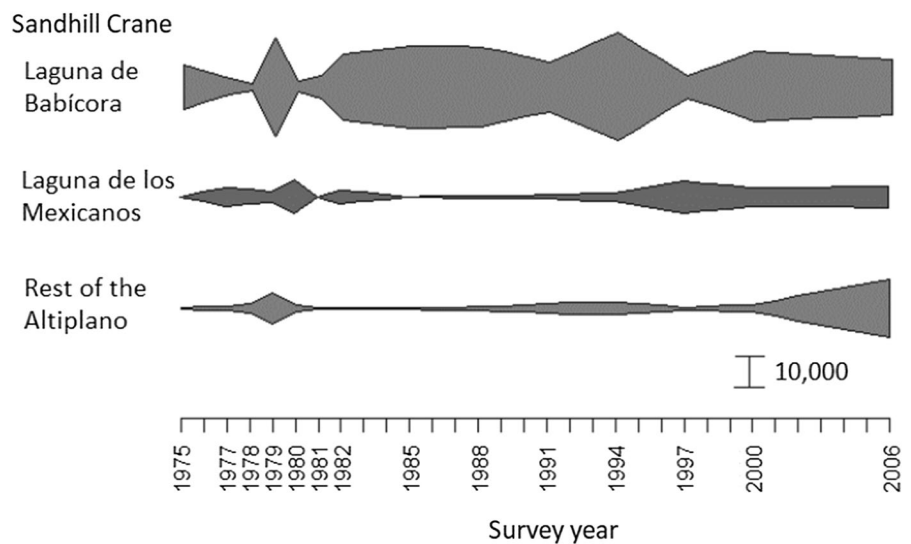


Fig. 5 Abundance of Sandhill Crane (*Antigone canadensis*) on the Mexican Altiplano from 1975 to 2006, as recorded on USFWS mid-winter aerial surveys



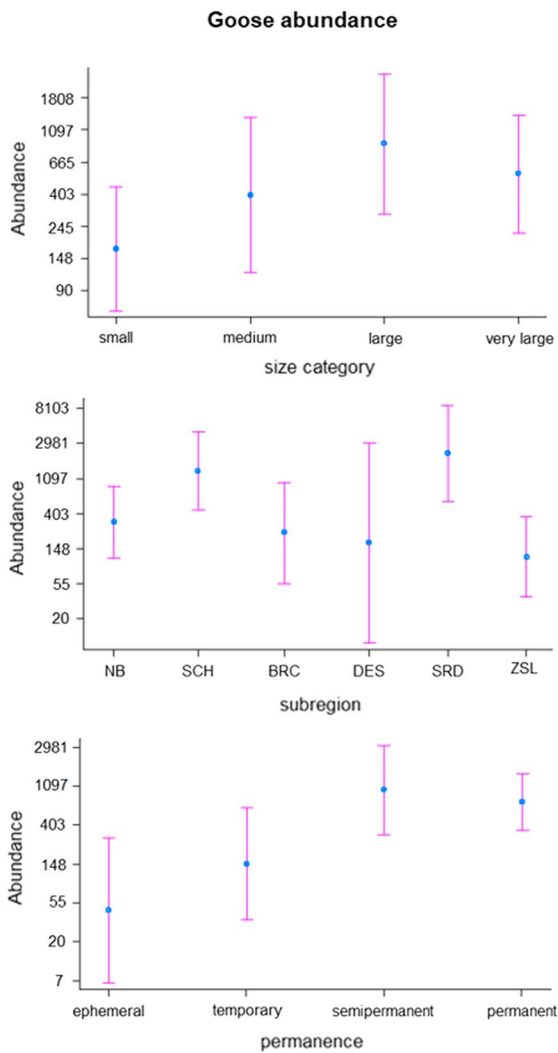


Fig. 6 Relationship between goose abundance and maximum size, water permanence and subregion of the Northern Highlands. Data scale is logarithmic

Northern Highlands. Here abundance dropped from 10,000 Greater White-fronted Geese in 1982 to less than 500 from 1988 onwards. This decrease coincides with a large decrease in available water surface as revealed by our satellite imagery analysis.

Yearly numbers of both dabbling and diving ducks varied greatly, likely resulting from a combination of factors as we discuss in the following sections, but few species exhibited relevant patterns or trends. Northern Pintails, Green-winged Teals and Gadwalls were mostly evenly distributed throughout the highlands in all years except in the Zacatecas—San Luis

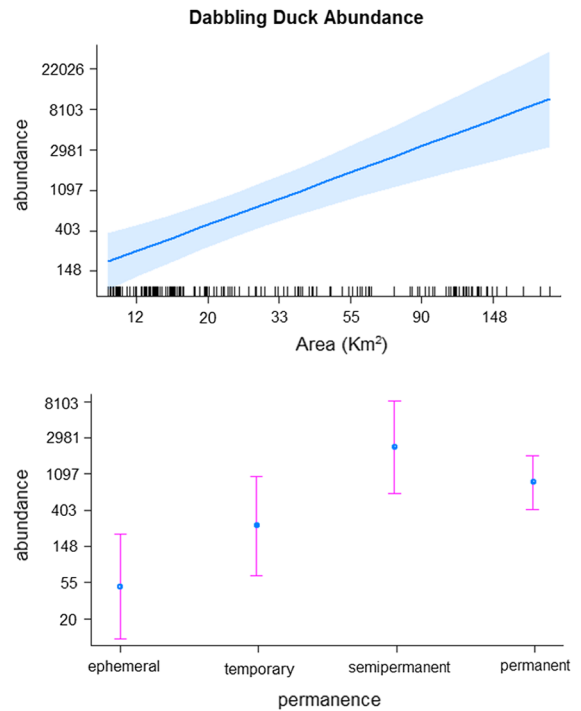


Fig. 7 Relationship between dabbling duck abundance and water surface area and permanence. Data scale is logarithmic

Potosí plains. The abundance of Northern Shovelers was strongly correlated with that of Pintails, although on the Zacatecas—San Luis Potosí plains they were present in higher numbers. Although American Coots are present throughout Mexico, they were mostly absent from northern Chihuahua and the western Sierras de Chihuahua. This is likely because nearly 90% of coots migrate either along the Pacific Coast or the Gulf of Mexico, with fewer migrating along the mountainous and arid areas north of Chihuahua. Mallards were recorded only in northern Chihuahua although they might have been confounded with the Mexican Duck at times further south.

Winter water change

Our use of satellite imagery to determine waterbird habitat presented several challenges. Chief among them were the varying characteristics of water bodies in Northern Highlands, such as size, depth, soil type and suspended solids that affected light reflectance. Topography and vegetation had to be dealt with to prevent overestimation of waterbody size. This was

particularly important at sites with dams, since they are usually surrounded by hilly terrain and our first attempts to determine their size produced many false positives (i.e., classifying areas in the shade as water). Water reflectance in the region is highly variable due to soil color, turbidity, sensor characteristics and other variables, so several thresholds were used manually for NDWI values, especially in older Landsat images, from -0.05 to 0.2 units. This method yields more precise results than automated analysis; its drawback being that it is more labor-intensive (Feyisa et al. 2014). Nevertheless, finding an appropriate threshold plainly justified the additional time and effort. The use of satellite images from only December–January, when waterbirds were monitored, provided adequate habitat information. In the 1970 and 1980s many sites were not satellite-imaged, or the images were of very low quality, cloudy, but later remote sensing programs produce more accurate information about wetland conditions.

Predictably, most permanent sites were in the more mountainous areas of the states of Durango and Chihuahua, which have lower temperatures and higher precipitation than the more arid parts of the plains. So, sites like Laguna de Babícora and Santiaguillo hosted much higher waterbird abundances by always being available.

Higher bird abundances coincided with waterbodies with irregular edges. Sites with irregular shapes or consisting of a series of smaller wetlands, such as Laguna Babícora and Laguna de los Mexicanos, had higher abundance than sites that were just as large or larger but had simpler shapes. This reflects the fact that more irregular perimeters lead to larger shallow areas, which are preferred by many species over the deeper water, and natural waterbodies generally have more space available for grazing by waterbirds (Colwell and Taft 2000; Froneman et al. 2001). Man-made waterbodies in the Altiplano, especially the larger ones, tend to have edges with much steeper slopes which, along with their simpler peripheries, led to lower use by shallow-water feeders.

Our data suggest a loss of water surface, especially in more arid sites like those of the desert and the Zacatecas—San Luis Potosí plains, paired with a corresponding drop in some bird populations, although further research would be needed to confirm this as a long-term trend. Oceanographic events such as El Niño and La Niña can cause periodic reductions in

precipitation in the region, but our data was inadequate to analyze this.

Different climate change scenarios for this region all predict an increase in temperature and evapotranspiration, a reduction in precipitation and more frequent extreme weather events (Comisión Nacional del Agua 2018, Rodríguez-González et al. 2018). Each of these would have negative effects on smaller wetlands that are already dry in many winters, and whose water is extracted for human use. Although some waterbird species might easily move to “wetter” sites in dry years and come back in wetter ones, philopatric species might effectively abandon these sites even if conditions improve at later years. The remote sensing information that is nowadays widely available would allow for the monitoring of wetland dynamics, but it is imperative to continue monitoring bird populations periodically, especially in the more arid and vulnerable sites.

Factors of winter wetland use by waterbirds in the Northern Highlands

In the four selected abundance models, total bird abundance was modelled best as a combination of precipitation in the previous 12 months, winter water surface area and site permanence type. Peaks in region-wide abundance, such as that of January 1982, coincided with an increase in water surface area for the whole region.

The fact that average waterbird abundance was higher in semi-permanent sites than permanent ones reflect that, while the previous are natural wetlands, the latter are generally manmade reservoirs, which have much less surface of shallow water that many migratory waterbirds prefer. Since data for the three variables that our analysis showed to be drivers of waterbird abundance in the region are available from years where no surveys took place, these can be used to give rough estimates of how many birds were present, although more data and calibration would be necessary to improve accuracy.

Goose numbers were explained best by subregion, maximum surface area in winter, and site permanence. Since all these variables are categorial, we inferred that geese preferred specific sites in the Altiplano, specifically those in the sierras. Drewien and others (2003) estimated that in 1998 and 1999, the whole altiplano region hosted 40–70% of the around

300,000 White Geese wintering in Mexico. High site fidelity has been reported for Lesser Snow and Ross's Geese, with yearly return rates of up to 97% (Williams et al. 2008). Under this scenario, conservation efforts should be directed at a few specific sites used by geese year after year. However, the abundance of geese before the 1980s at the southern edge of the Altiplano makes it unclear if the Sierra locations have always been the best sites for geese or if they are simply the most reliable wetlands remaining in the area.

Of the variables we examined, diving duck abundance was determined only by winter water surface area. Since these ducks have the capacity to feed in deeper water, they may use the wetlands in this region relatively indiscriminately or vary such use as a function of unexplored variables. Diving duck numbers were generally much lower than those of other waterbird types, and the data does not exhibit large concentrations of any species during any survey year. When performing validation test, these low numbers meant that even this "best" explanatory variable had very high margins of error and low predictive power.

On the other hand, dabbling duck abundance was explained best by a combination of water surface area and permanence type. Their higher abundance in semipermanent sites over permanent ones points at the importance of shallow water. In model validation more than 95% of count data not used in the model generation fell within one standard deviation of the mean values. While it is difficult to establish clear trends with the data at hand, a reduction in winter water size of the wetlands in the region due to a reduction in rainfall or due to human activities would clearly impact many of these species negatively. Conservation strategies for these birds might include modification of permanent manmade sites to provide shallower, more suitable areas for feeding.

Water depth was not studied but our data indicate that it plays a large role in selection of wintering sites for many species. Years with low precipitation and scarce available habitat may push many birds to gather in suboptimal sites that are more consistently available, such as dams. Several sites hosted large numbers of certain species, such as sandhill cranes and White Geese in the Sierra of Chihuahua locations and they should be the focus of conservation efforts in the region, especially during prolonged droughts. On the other hand, there are several sites in the more arid parts of the altiplano (eastern Zacatecas, Northwest

San Luis Potosi, and Coahuila states) that hosted considerable numbers of waterbirds in the past but seem to do so no longer.

The Mexican Altiplano has large changes in habitat availability and waterbird abundance throughout the last 70 years. Large-scale bird counts have been useful in identifying trends in migratory bird populations and coupled with new remote sensing tools for habitat monitoring, aid conservation and management initiatives. In the Northern Highlands of Mexico, where budgetary and safety concerns must be considered when visiting many wintering sites, satellite imagery can be an important complement to traditional waterbird surveys.

Conclusions

Our work allows us to conclude that waterbird abundance in the northern Altiplano was greatly variable between 1975 and 2006 between sites and years, with a few sites concentrating a large proportion of the bird abundance of the region. Few species displayed clear trends over time; rather, abundance, especially of dabbling ducks, was mainly a result of available habitat and conditions. Furthermore, sites in the more arid parts of the altiplano (eastern Zacatecas, Northwest San Luis Potosí and Coahuila) seem to be undergoing a degradation of wetland conditions, leading to habitat loss. Given that the scenarios for climate change predict an increase in surface temperature and the frequency of extreme weather events in the region, and that water consumption by humans in the area is increasing, this region will continue to provide appropriate conditions for migratory wintering birds only if active environmental management is done for that purpose.

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Data availability The datasets, maps and code generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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