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RESEARCH ARTICLE

Diet switching of seed-eating birds wintering in grazed habitats of the central Monte Desert, Argentina

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ABSTRACT

Although bird population declines associated with land degradation are common, the initial response of organisms to rapid human-induced environmental change is usually behavioral. Reductions in seed availability due to cattle grazing may trigger diet switching in seed-eating birds, but empirical examples of such behavior are lacking. We asked whether cattle grazing changed the composition and reduced the size of seed reserves, and whether seed shortage caused diet shifts in 4 species of seed-eating birds wintering in the central Monte Desert, Argentina. We assessed the soil seed bank composition and the granivorous fraction of each species' diet. Digestive tract or crop contents were obtained by using the flushing method on individuals captured with mist nets, and seeds were sorted and assigned to 1 of 3 functional groups (small grass seeds, large and medium-sized grass seeds, or forb seeds). Cattle grazing reduced the abundance of the preferred large and medium-sized grass seeds by 60–90%. The grass-seed specialists Many-colored Chaco Finch (*Saltatricula multicolor*) and Ringed Warbling-Finch (*Microspingus torquatus*) did not change their diets in grazed areas, but the expanding specialists Common Diuca-Finch (*Diuca diuca*) and Rufous-collared Sparrow (*Zonotrichia capensis*) incorporated increased proportions of small grass seeds as well as forb seeds into their diets. These results were correctly predicted from species-specific differences in feeding flexibility previously established in cafeteria experiments. Based on species-specific diet composition, the energy reward of seeds by unit mass consumed decreased moderately (5–21%) in the grazed sites for *S. multicolor*, *M. torquatus*, and *D. diuca*. Starch content was similar between grazing conditions for all 3 birds. Although such deficits might be compensated for by a slight increase in absolute mass of seeds or alternative food items consumed in degraded lands, substantial reduction in the availability of grass seeds may reduce the capacity of degraded lands to support specialist granivorous birds.

Keywords: feeding flexibility, expanding specialists, seed shortage, seed preferences, grass seeds, forb seeds, energetics, land degradation

Modificación de la dieta invernal de las aves granívoras en hábitats sujetos a pastoreo de la porción central del Desierto del Monte, Argentina

RESUMEN

Aunque las reducciones poblacionales de aves asociadas a la degradación de la tierra son usuales, la respuesta inicial de los organismos al cambio ambiental antrópico es a menudo conductual. La disminución de semillas en ambientes pastoreados puede disparar cambios en la dieta de las aves granívoras, pero no hay datos que respalden esa expectativa. Evaluamos si el pastoreo cambia la composición y reduce la abundancia de las reservas de semillas, y si la escasez de semillas provoca cambios en la dieta invernal de cuatro especies de aves granívoras en la porción central del desierto del Monte, Argentina. Medimos el banco de semillas y establecimos la fracción granívora de la dieta (proporción de semillas de gramíneas pequeñas, gramíneas medianas y grandes y dicotiledóneas herbáceas) a través del lavado del tracto digestivo de aves cazadas con redes de niebla. El pastoreo redujo 60–90% la abundancia de las semillas preferidas (i.e. medianas y grandes de gramíneas). Las aves especialistas en esas semillas (*Saltatricula multicolor* y *Microspingus torquatus*) no modificaron su dieta en los sitios pastoreados, pero las especialistas expansivas (*Diuca diuca* y *Zonotrichia capensis*) sí incorporaron fracciones significativas de semillas no preferidas (e.g. pequeñas de gramíneas y de dicotiledóneas herbáceas). Estos resultados se preveían según las diferencias en flexibilidad alimentaria de las aves establecidas experimentalmente con anterioridad. Según la composición especie-específica de las dietas de *S. multicolor*, *M. torquatus* y *D. diuca* la recompensa energética por unidad de masa disminuye moderadamente (5–21%) en los ambientes pastoreados. El contenido de almidón por unidad de masa fue similar en ambas condiciones de pastoreo para las tres aves. Esos déficits podrían compensarse mediante un leve incremento de la masa total consumida tanto de semillas como de recursos alternativos pero, dada la notablemente menor disponibilidad de semillas preferidas de gramíneas en los ambientes degradados, el pastoreo podría reducir la capacidad de esos ambientes de mantener aves especialistas.

Palabras clave: flexibilidad alimentaria, especialistas expansivos, escasez de semillas, preferencia de semillas, semillas de gramíneas, semillas de dicotiledóneas herbáceas, energética, degradación de la tierra

INTRODUCTION

Despite the increasing importance of climate change, land degradation continues to be a major driver of biodiversity loss and the homogenization of bird communities (BirdLife International 2008, Lebbin et al. 2010, da Silva et al. 2015). Numerical declines of bird species associated with land degradation have been reported in arid and semiarid areas of different continents (Bock and Bock 1999, Gonnet 2001, Martin and Possingham 2005, Seymour and Dean 2010, Dvorak et al. 2012), but the initial response of organisms to rapid human-induced environmental change is usually behavioral: Changes in resource availability due to habitat disturbance often trigger modifications in the foraging behavior, movement, or habitat choice of animals (Tuomainen and Candolin 2011). The ability to behave appropriately under novel conditions is crucial for the success or failure of bird species in new habitats (Sih et al. 2011), where flexible or plastic organisms can respond more effectively to changes in resources than stereotyped ones.

Diet switching is an example of flexible behavior (Whelan et al. 2000) and a topic of interest for community ecology (Wiens 1989), predator–prey dynamics (Reif et al. 2004, Garrott et al. 2007), and competition theory (Schoener 1982, Wiens 1993, Dhondt 2012). Despite this, most studies on ecological guilds consider guild membership as a fixed attribute of a species (Lopez de Casenave et al. 2008), without examination of temporal (e.g., Farias and Jaksic 2007, Lopez de Casenave et al. 2008) or spatial diet switching (e.g., Monserrat et al. 2005 in birds, Abbas et al. 2011 in mammals, Delariva et al. 2007 in fishes). Moreover, empirical field studies of diet switching by birds living in disturbed habitats are rare, even though diet switching could be a key mechanism for avoiding population declines and local extinctions.

Seed-eating birds wintering in the central Monte Desert of Argentina offer an opportunity to assess feeding flexibility as a mechanism for enduring the effects of land degradation. The diet and seed selection behavior of several bird species is well known (Lopez de Casenave 2001, Marone et al. 2008, Sánchez and Blendinger 2014), and seed preferences—or the levels of consumption of different seed species when offered simultaneously and with equal availability—have been established using cafeteria experiments (Cueto et al. 2006, Camín et al. 2015). Further, the nutritional and antinutritional composition of seeds is known and allows us to understand some of the causes of seed selection and bird diet composition (Ríos et al. 2012). Most seed-eating birds consume, select, and prefer grass seeds, but some species are grass-seed specialists whereas others have broader diets. High trophic specialization on grass seeds can be, at least in part, a consequence of digestive adaptation to processing and taking advantage of a starch-rich diet (Brzęk et al. 2010). Broader diets, on the other hand, may occur when a forager selectively harvests its preferred food (e.g., grass seeds) when its abundance is high, but expands its diet to include less-preferred foods when the preferred food is depleted to a critical level (i.e. the 'expanding specialist' strategy; Heller 1980, Brown and Mitchell 1989). This occurs because it may no longer be beneficial for the forager to feed as a specialist below the diet expansion point determined by the abundance of the preferred food (Mitchell 1990, Molokwu et al. 2011). Among the Monte Desert's birds, the Many-colored Chaco Finch (*Saltatricula multicolor*) and Ringed Warbling-Finch (*Microspingus torquatus*) are large and medium-sized grass-seed specialists, while the Common Diuca-Finch (*Diuca diuca*) and Rufous-collared Sparrow (*Zonotrichia capensis*) are expanding specialists that prefer large and medium-sized grass seeds but also consume less-preferred seeds (e.g., tiny grass or forb seeds; Cueto et al. 2006, Camín et al. 2015).

Grazing by domestic animals is the main economic activity in the central Monte Desert. Grazing usually provokes inconsistent minor changes in the cover and structure of woody vegetation, and it reduces the abundance of several seed species in the soil bank, especially perennial grass seeds (Gonnet 2001, Pol et al. 2014, 2017). Given that cattle grazing could reduce the number of spikes of preferred grass seeds, we expected changes to occur in the feeding behavior of seed-eating birds in degraded lands. Specifically, we expected more diet switching by wintering bird species with flexible feeding behavior (*D. diuca* and *Z. capensis*) and less diet switching by more stereotyped, grass-seed specialists (*S. multicolor* and *M. torquatus*). Here, we tested these expectations using field data on seed reserves and bird diets. We then considered the energy reward and starch content available to birds in grazed and ungrazed habitats depending on whether or not the birds switched diets.

METHODS

We studied bird diets in the Biosphere Reserve of Ñacuñán, central Monte Desert, Argentina (34°03′S, 67°54′W), which has been without any domestic grazers for the last 40 yr, and on 2 cattle ranches subject to continuous grazing adjacent to the west and east sides of the reserve. The general habitat has a tree stratum made up of scattered individuals of *Prosopis flexuosa* and *Geoffroea decorticans* within a dense matrix of tall shrubs (>1 m; *Larrea divaricata*, *L. cuneifolia*, *Atamisquea emarginata*, *Condalia microphylla*, and *Atriplex lampa*) and low shrubs (<1 m; *Lycium* spp., *Verbena aspera*, and *Acantholippia seriphioides*). The most common Poaceae species are C4 perennial grasses: *Pappophorum* spp., *Trichloris crinita*, *Setaria leucopila*, *Digitaria californica*, *Sporobolus cryptandrus*, *Aristida mendocina*, *Diplachne dubia*, and *Neobouteloua lophostachya*. Most forbs are annual or biennial, including *Chenopodium papulosum*, *Phacelia artemisioides*, *Descurainia* spp., *Glandularia mendocina*, *Sphaeralcea miniata*, *Parthenium hysterophorus*, *Lappula redowskii*, *Heliotropium mendocinum*, and *Plantago patagonica* (Lopez de Casenave 2001). The climate is dry and temperate, with cold winters. Around 75% of the annual rainfall occurs in the warmer months of October to March, which coincides with the plant growing season. Average rainfall in the growing season is 266 mm ($n = 32$ yr). Most grass and forb seeds disperse and enter the soil in late summer and early autumn (Marone et al. 1998).

We studied the composition and size of the soil seed bank in grazed and ungrazed sites in October–November, 2010–2014. Each year, we collected 120 soil samples from both types of site; we randomly allocated sampling points for soil core samples according to the cover of the main microhabitats on the landscape: beneath the tree canopy (15% in both grazing conditions) and the tall shrub canopy (35% in both grazing conditions), under low shrubs (13% in both grazing conditions) and grasses (17% and 7% in ungrazed and grazed sites, respectively), and on bare soil (20% and 30% in ungrazed and grazed sites, respectively). We collected soil samples using a cylindrical sampler, 3.2 cm in diameter and 2.0 cm deep (80% of seeds are found in the upper 2 cm of soil). In the laboratory, soil samples were sifted through a 0.27-mm mesh sieve (the smallest seeds recorded from each microhabitat did not pass through the sieve), washed in the same sieve under water pressure, and air-dried. We searched for sound seeds under a stereoscopic microscope and identified these seeds to the species or genus level using a reference collection, following Marone and Horno (1997). Seeds were ascribed to 1 of 3 plant groups that corresponded to different degrees of seed selection and preferences of birds: small grass seeds (<0.15 mg), large and medium-sized grass seeds (0.15–0.75 mg), and forb seeds of different sizes (0.16–0.65 mg; Cueto et al. 2006, Marone et al. 2008, Camín et al. 2015). Results of this sampling have been partially published in Pol et al. (2014).

We assessed the granivorous fraction of the avian diet by counting seeds from the digestive tracts of individuals of 4 seed-eating wintering bird species captured with mist nets: *M. torquatus* (mean weight 10.5 g), *Z. capensis* (19.2 g), *S. multicolor* (22.4 g), and *D. diuca* (25.0 g; Lopez de Casenave 2001). Sampling was conducted in autumn and winter (May–August) in the grazed and ungrazed sites. Birds were caught within the reserve (ungrazed control sites) in 1993–1998 and 2014, and in the grazed locations (treatment sites) in 2011–2012 and 2014. In the reserve, we obtained 116 digestive tract or crop contents (DTC) from *Z. capensis* ($n = 78$ in 1993–1998, $n = 38$ in 2014), 30 DTC from *M. torquatus* ($n = 30$ in 1993–1998), 27 DTC from *S. multicolor* ($n = 20$ in 1993–1998, $n = 7$ in 2014), and 19 DTC from *D. diuca* ($n = 15$ in 1993–1998, $n = 4$ in 2014). In the grazed locations, we obtained 128 DTC from *Z. capensis* ($n = 48$ in 2011–2012, $n = 80$ in 2014), 54 DTC from *M. torquatus* ($n = 54$ in 2011–2012), 51 DTC from *D. diuca* ($n = 25$ in 2011–2012, $n = 26$ in 2014), and 19 DTC from *S. multicolor* ($n = 7$ in 2011–2012, $n = 12$ in 2014).

The contents of the digestive tract were obtained by using the flushing method (Moody 1970), a nondestructive technique that allows the effective collection of different food items (Zach and Falls 1976, Zann and Straw 1984, Rosenberg and Cooper 1990, Lopez de Casenave 2001), with low adverse effects on birds compared with other techniques such as the use of emetics (Moody 1970, Zach and Falls 1976, Zann and Straw 1984, Jenni et al. 1990, Rosenberg and Cooper 1990, Durães and Marini 2003). Fair et al. (2010), for instance, recommended emetics only when fecal analysis or flushing is either not practical or not advisable. We carefully flushed the digestive tract and evacuated it completely using warm water. A flexible plastic nasogastric tube (1.44 or 2.00 mm in diameter, depending on species) was inserted gently into the esophagus until the tip rested against the stomach. This process was facilitated by holding the bird's head and slightly stretching its neck. The bird was held with a receptacle under the cloaca and its body upward to facilitate flushing. After the tube was inserted, warm water was forced gradually into the digestive tract using a disposable plastic syringe until water started to flow from the cloaca. Pressure was then increased, forcing the water through the digestive tract and out of the cloaca, carrying the ingested material, which was collected into the receptacle. When this procedure failed we quickly extracted the tube, allowing the bird to regurgitate. Birds for which the flushing process was unsuccessful were released after 2 attempts, following a brief recovery period. A key to success for this technique is the careful use of plastic tubing to deliver the water (Gionfriddo et al. 1995, Fair et al. 2010). Our skill with the technique and our knowledge of the species studied were important to obtain a very low mortality rate: only 10 of 935 (~1%) birds sampled using flushing died during handling in the 1993–1998, 2011–2012, and 2014 sampling periods. When the flushing process failed, we collected the water and partial contents that were regurgitated by the bird. We also collected any fecal material produced while we were handling a bird, and incorporated it into the corresponding sample. Finally, we removed the entire digestive tract of the few individuals that died during the study. Therefore, although our primary technique was flushing, we attempted to obtain the maximum information from every individual by combining several procedures. We preserved all collected tract contents in alcohol. Seed items were taxonomically identified and sorted in the laboratory under a dissecting microscope. Since our goal was to depict the granivorous fraction of the diet, which constitutes the bulk of the diet of wintering birds (Lopez de Casenave 2001), the remains of arthropods and fleshy fruits were not considered in our analyses.

Every seed was classified into 1 of the following 3 categories: small grass seeds (*S. cryptandrus*, *N. lophostachya*, *Jarava ichu*, *Eragrostis pilosa*, and *Schismus barbatus*), large and medium-sized grass seeds (*Pappophorum* spp., *D. californica*, *A. mendocina*, *S. leucopila*, *T. crinita*, and *D. dubia*), and forb seeds (*C. papulosum*, *P. hysterophorus*, *G. mendocina*, *L. redowskii*, *S. miniata*, *P. artemisioides*, *H. mendocinum*, *Parietaria debilis,* and *Conyza* spp.). We considered the mass of seeds of every species in each DTC and expressed the contribution of seeds in each category to the diet of every individual as the percentage of seed mass (mg of seeds in each category divided by the total seed mass in that stomach times 100). We then obtained the contribution of each category to the diet of each bird species by averaging the individual values, as suggested by Rosenberg and Cooper (1990), excluding the samples that lacked quantifiable seed remains.

We employed published information on the energy reward (kJ mg^{-1}) and starch content (% of mass) of every seed species eaten by the 4 birds analyzed (Ríos et al. 2012) in the grazed and ungrazed areas in order to calculate the amount of energy and starch provided on average in each grazing condition. Given that the species-specific composition of the avian diet can vary between grazing conditions, and that the energy and starch content vary among seed species, the energy reward and starch content per unit mass consumed can vary for each bird species under different grazing conditions. We had data on the energy and starch content of 15 seed species (Ríos et al. 2012), but we lacked such data for another 3 seeds present in the birds' stomachs. For *N. lophostachya*, *D. dubia*, and *P. debilis*, we used the average energy and starch content provided for seeds belonging to the same functional group (i.e. small grass seeds, large and medium-sized grass seeds, and forb seeds, respectively). Given that *N. lophostachia*, *D. dubia*, and *P. debilis* combined represented, on average, <9% of the diets of *M. torquatus* and *D. diuca*, and ~22% of the diet of *S. multicolor* (Table 1), we assumed that the use of a coarse estimator of energy and starch content for these 3 seed species introduced only a minor bias into the total calculations for the 3 bird species. In contrast, *P. debilis* seeds alone averaged 18% and 46% of the total seed mass consumed by *Z. capensis* in ungrazed and grazed sites, respectively. For *Z. capensis*, the use of a coarse surrogate for this seed species might have produced more serious biases in the calculations. Thus, we did not estimate the energy reward and starch content of the mean diet of *Z. capensis*.

We used one-way ANOVAs to compare seed mass in the soil bank between the 2 grazing conditions, and one-way ANOVAs with a step-down sequential Bonferroni correction for each bird species (global alpha level = 0.05; Holm 1979, García 2004) to compare the mean percentage of seeds in every functional group in the diet under the 2 grazing conditions. We transformed raw data using square-root or log-10 when they did not meet the assumptions of normality and homoscedasticity.

RESULTS

The comparison of soil seed banks in the reserve and cattle ranches showed a clear pattern: The mass of large and medium-sized grass seeds was 60–90% higher in ungrazed areas in all 5 comparisons, showing a general, negative, and consistent effect of domestic grazers on the seeds that the birds most prefer (Figure 1). This consistent pattern for large and medium-sized grass seeds constitutes a robust and convincing tendency despite multiple comparisons. Although small grass seeds appeared to be more abundant in some years in the reserve, differences between grazing conditions were not significant (Figure 1). Forb seeds were negatively affected in the grazed area in 2 out of 5 years (Figure 1).

Grass seed species constituted most of the granivorous component of the diets of *S. multicolor* and *M. torquatus* (>95%) under both grazing conditions, and of *D. diuca* (>85%) in the reserve (Table 1). In the grazed areas, ~25% of the seeds consumed by *D. diuca* were of the dicot *C. papulosum*, but, even so, grass species predominated in its diet (>70%), with an increase in the proportion of small grass seed species (Table 1). The dicots *C. papulosum* and *P. debilis* prevailed in the diet of *Z. capensis* in the grazed areas (where they summed to ~67% of the diet) as well as in the ungrazed reserve (~52%; Table 1).

When assessing the consumption of seeds in the 3 functional groups, *S. multicolor* and *M. torquatus* con-

TABLE 1. Species-specific contribution (as percentage based on mg of seeds consumed) of different seed species to the granivorous fraction of the diet of 4 seed-eating birds in ungrazed and grazed *Prosopis* open woodlands of the central Monte Desert, Argentina.

	Saltatricula multicolor		*Microspingus torquatus*		*Diuca diuca*		*Zonotrichia capensis*	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Small grasses								
Jarava ichu		0.19		1.94		1.24	0.03	3.20
Eragrostis pilosa		0.14	1.67		0.73		2.34	
Sporobolus cryptandrus	26.73	9.26	52.59	35.95		4.54	12.07	9.59
Neobouteloua lophostachya	3.80	21.33		9.21		5.44	1.03	3.07
Schismus barbatus		0.12				3.92	0.47	1.07
Total	30.54	31.03	54.26	47.10	0.73	15.14	15.94	16.93
Large and medium-sized grasses								
Pappophorum spp.	22.81	8.18	24.87	4.92	36.14	18.47	7.01	2.84
Digitaria californica	0.30	1.27	4.40		11.59	1.64	1.23	0.32
Aristida spp.	19.29	23.20			10.04	20.81	2.01	1.14
Setaria leucopila	7.42	18.53	8.65	13.07	24.04	5.75	12.56	7.42
Trichloris crinita	10.34	1.44	3.11	22.99	1.82	2.31	2.65	1.78
Diplachne dubia	7.62	10.85	0.63	8.36	1.43	7.91	2.18	0.97
Chloris castilloniana								0.02
Total	67.78	63.46	41.66	49.34	85.06	56.89	27.64	14.48
Forbs								
Parthenium hysterophorus					7.15		1.61	
Plantago patagonica						0.29		0.20
Glandularia mendocina							2.52	0.20
Lappula redowskii					5.31		0.15	0.35
Sphaeralcea miniata		0.14			1.75		0.37	
Phacelia artemisioides								0.77
Chenopodium papulosum	1.49	1.07		3.56		24.64	33.37	20.93
Parietaria debilis	0.19	4.29				1.96	18.29	45.94
Conyza spp.			4.07					
Heliotropium mendocinum						1.08	0.12	0.19
Total	1.68	5.50	4.07	3.56	14.22	27.97	56.42	68.59
n	27	19	30	54	19	51	116	128

sumed similar proportions of every seed group under both grazing conditions (Figure 2). Both species always ate grass seeds almost exclusively (forbs represented <5% of their diets under both environmental conditions; Figure 2). In contrast, *D. diuca* and *Z. capensis* showed some degree of foraging flexibility under grazing conditions. *Zonotrichia capensis* ate a smaller amount of the preferred large and medium-sized grass seeds and more forb seeds in the grazed sites. *Diuca diuca* also significantly reduced its consumption of the preferred large and medium-sized grass seeds in grazed sites. In ungrazed vs. grazed areas, *D. diuca* and *Z. capensis* consumed 14% and 56% vs. 28% and 69% forb seeds, respectively (Figure 2).

With regard to the species-specific composition of the diet, the energy reward by unit mass of the mean diet of *S. multicolor*, *M. torquatus*, *and D. diuca* was 21%, 5%, and 19% higher in the reserve than in the grazed sites, respectively (Figure 3). Conversely, *S. multicolor* consumed 6% more starch in the reserve than in the grazed sites, *M. torquatus* ate similar proportions of starch under both grazing conditions, and *D. diuca* consumed 7% more starch in the grazed sites than in the reserve (Figure 3).

DISCUSSION

Although the reported effects of cattle grazing on the structure and composition of vegetation and the soil seed bank in deserts are not always consistent (Oesterheld and Semmartin 2011), some of these effects were strong and clear in Ñacuñán: The cover of perennial grasses fell by 50% and the number of spikes by 90% (Pol et al. 2014), and large and medium-sized grass seeds suffered a drastic and consistent cutback in the soil seed bank across the 5 yr of our study. This was the period during which all of the DTC were obtained in the grazed sites, but some DTC in the ungrazed site (i.e. the control diet in the reserve) were obtained in 1993–1998, and our experimental design could therefore be criticized because some of the control diets were collected during a time that did not match the period when the treatment diets were established. This criticism should, however, be put into a wider context. The mean mass of grass seeds in the winters of 2010–2014 (measured in the soil seed bank) was ∼590 mg m^{-2} in the reserve and ∼160 mg m^{-2} in the grazed areas (Figure 1), whereas in the winters of 1995 and 1996 the mean mass of grass seeds (measured on plant stalks) was ∼300 mg m^{-2} in the

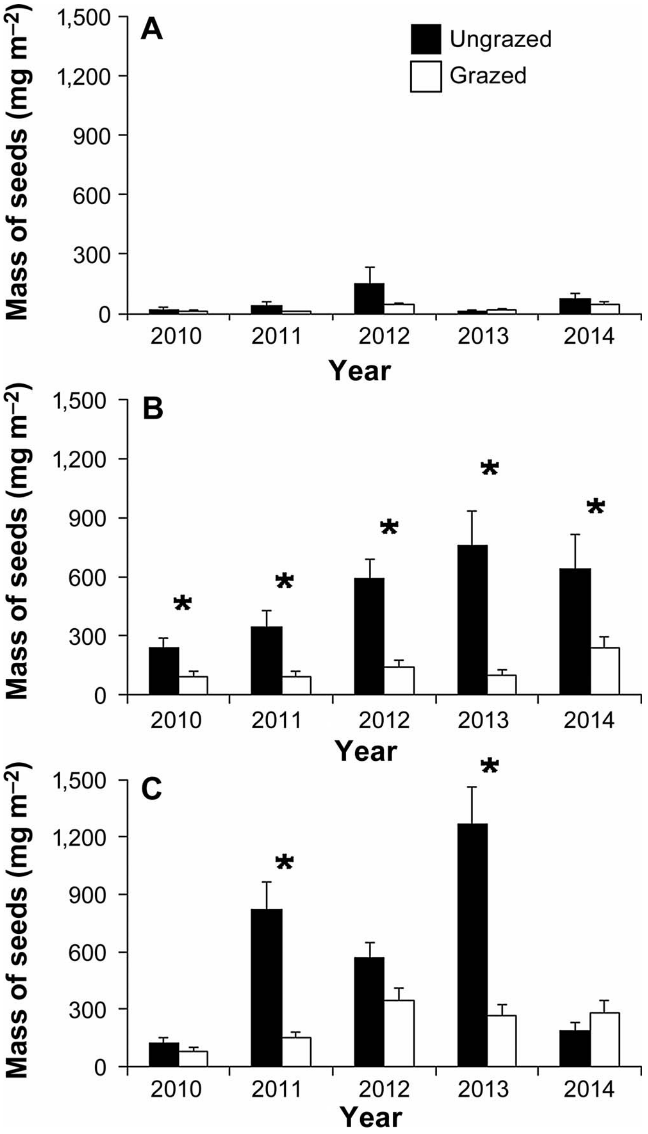

FIGURE 1. Soil seed bank size (mean + SE) measured as the mass of seeds in the 3 functional groups consumed by seed-eating birds (small grass seeds, large and medium-sized grass seeds, and forb seeds) in ungrazed (black bars) and grazed (white bars) *Prosopis* open woodlands of the central Monte Desert, Argentina. (**A**) Small grass seeds, (**B**) Large and medium-sized grass seeds, and (**C**) Forb seeds. Asterisks indicate a significant difference between grazing regimes (one-way ANOVA, $P < 0.05$).

reserve and ~70 mg m^{-2} in 2 grazed paddocks near the reserve (table 2 in Gonnet 2001). Both datasets come from the same area but from different decades, and they suggest that grass seed availability is ~4 times lower in the grazed areas than in the control sites. The estimations of seed mass were based on different techniques in 1995–1996 and 2010–2014, and therefore the comparison of absolute values is inappropriate (e.g., seed reserves measured in the soil seed bank are usually higher than on plant stalks). However, the comparison of the relative availability of grass seeds under both grazing conditions strongly suggests that DTC samples from the reserve were efficient controls for the entire study period.

As expected, *S. multicolor* and *M. torquatus* fed on grass seed species almost exclusively under both grazing conditions. At the species level, the consumption of some particular seeds could have differed between grazing conditions in spite of some seeds being equally attractive to the birds (Cueto et al. 2006, Camín et al. 2015). This was more likely due to patchy local spatial distributions of the seeds in the soil (Marone et al. 2004) rather than subtle context-dependent seed preferences by the birds (Marone et al. 2015). In contrast, the appearance of the dicot *C. papulosum* and of the small grasses (*S. cryptandrus*, *J. ichu*, *N. lophostachya*, and *S. barbatus*) in the stomachs of *D. diuca* in grazed areas seems to be a clear example of the diet switching that can happen with the depletion of preferred seeds, as *C. papulosum* is a less-preferred seed for *D. diuca* and small grass seeds are also not preferred (Cueto et al. 2006, Camín et al. 2015), and these seeds were rarely eaten in the reserve, or not at all, despite their high availability (Pol et al. 2014). Finally, the 2 species most frequently consumed by *Z. capensis* were dicots, *C. papulosum* and *P. debilis*. The former is a less-preferred seed for *Z. capensis* (Cueto et al. 2006, Camín et al. 2015) and, although we do not know the preference level of *P. debilis* in cafeteria experiments, forb seeds are rarely preferred seeds, even for *Z. capensis* (Cueto et al. 2006, Camín et al. 2015). Therefore, less-preferred seed species prevailed in the *Z. capensis* diet under both habitat conditions.

At the level of the functional groups, *S. multicolor* and *M. torquatus* maintained a high and similar consumption of grass seeds of all sizes and almost no consumption of forb seeds under both grazing conditions, which is in agreement with the results at the species-specific level. This might imply a rational or fixed feeding behavior because birds did not change their granivorous diets under habitat disturbance, which is not surprising since, for example, *S. multicolor* showed the most stereotyped feeding behavior in previous studies (Camín et al. 2015, Marone et al. 2015). However, when the radical reduction (~80%) of the preferred grass seeds in grazed sites is taken into account, the high consumption of preferred seeds in grazed areas by *S. multicolor* and *M. torquatus* may also be interpreted as resulting from context-dependent foraging behavior: Birds increased their search for and consumption of the preferred (target) seeds in a context (the grazed site) in which they faced a high proportion of options of lesser value (Marone et al. 2015). Whatever the behavior involved (stereotyped, context-dependent, or a combination of both), the numerical predictions for *S. multicolor* and *M. torquatus* in degraded areas are the same: both species

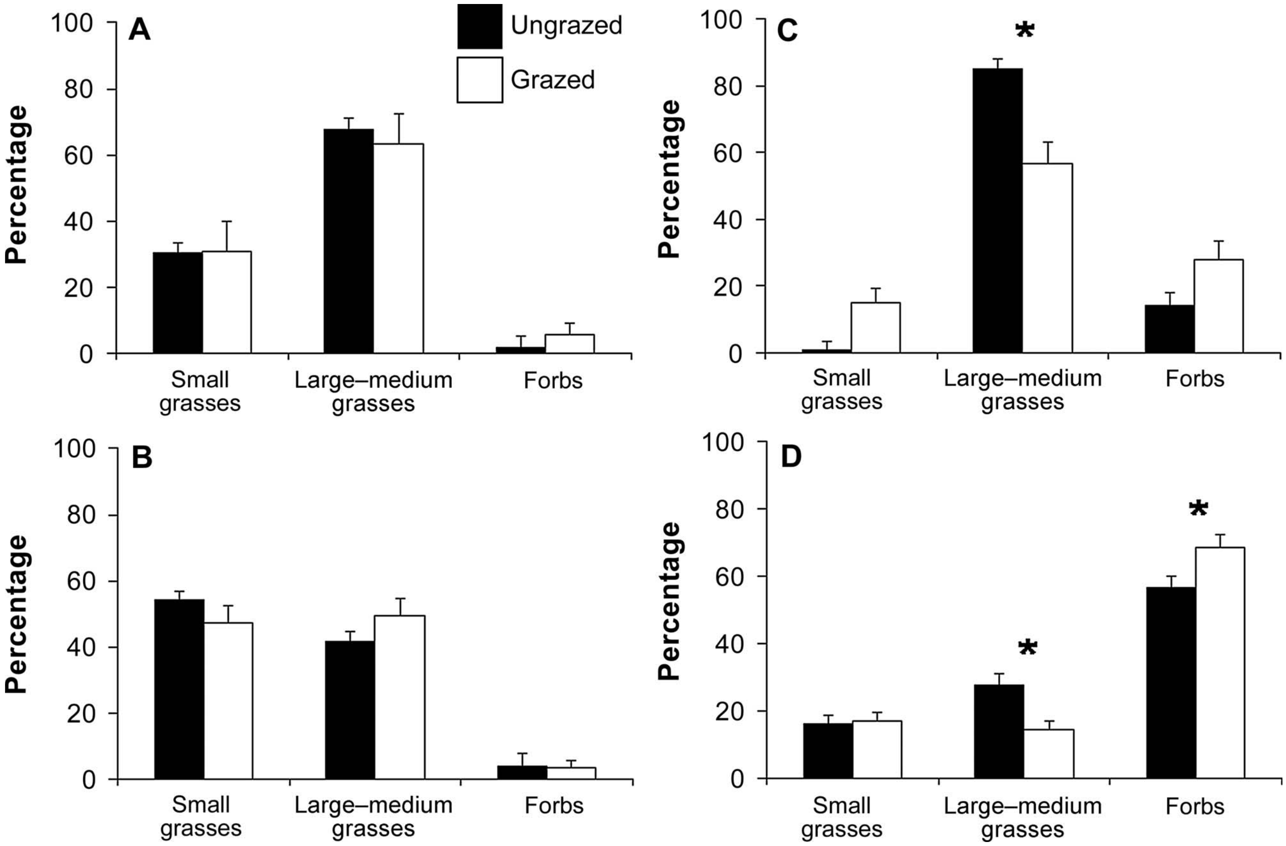

FIGURE 2. Percentage (mean + SE) of small grass seeds, large and medium-sized grass seeds, and forb seeds in the diets of 4 seed-eating bird species wintering in ungrazed (black bars) and grazed (white bars) *Prosopis* open woodlands of the central Monte Desert, Argentina: (**A**) *Saltatricula multicolor*, (**B**) *Microspingus torquatus*, (**C**) *Diuca diuca*, and (**D**) *Zonotrichia capensis*. Asterisks indicate a significant difference between grazing regimes (one-way ANOVAs with a step-down sequential Bonferroni correction for each bird species, global alpha level = 0.05; Holm 1979, García 2004).

should suffer numerical declines due to their high dependence on the grass seeds whose abundance diminishes under domestic grazing regimes.

In degraded habitat conditions, *D. diuca* and *Z. capensis* reduced their consumption of the preferred large and medium-sized grass seeds, and *Z. capensis* increased consumption of less-preferred or not preferred seeds. Despite the large reduction in the proportion of large and medium-sized grass seeds consumed by *D. diuca* in the grazed sites, the proportions of the other 2 functional seed groups consumed did not rise significantly in such sites. This pattern might have arisen from the reduced power of our statistical analysis, however, and *D. diuca* could be considered to be an expanding specialist: Facing a decline in the availability of its preferred seeds, *D. diuca* reduced consumption of these seeds and increased consumption of less-preferred seeds. Interestingly, a similar diet switch has been reported for a seed-eating ant of the Monte Desert. *Pogonomyrmex mendozanus* also behaved as an expanding specialist, consuming less-preferred seeds when the availability of preferred grasses declined due to heavy grazing (Pol et al. 2017).

Intriguingly, in the reserve, *Z. capensis* ate ~60% forb seeds (half of them the less-preferred *C. papulosum* seed), without expressing the preference for grass seeds that it clearly showed in laboratory trials (Cueto et al. 2006, Camín et al. 2015). Low consumption of preferred grass seeds, even when they were abundant in the reserve, might have been associated with maximum feeding and foraging flexibility of *Z. capensis*, or may have been due to competition from other seed-eating organisms in undisturbed habitats. Regarding foraging flexibility, *Z. capensis* is the only species included in this study capable of recovering buried seeds, which it accesses through double scratching (i.e. quickly and simultaneously moving both legs forwards and backwards; Whalen and Watts 2000, Cueto et al. 2013). Given that most seeds in Ñacuñán buried in the soil or trapped in the topsoil are forb seeds (Marone et al. 1998), double scratching might facilitate the expression of a wider and more generalized diet in *Z. capensis*, even in undisturbed environments. However,

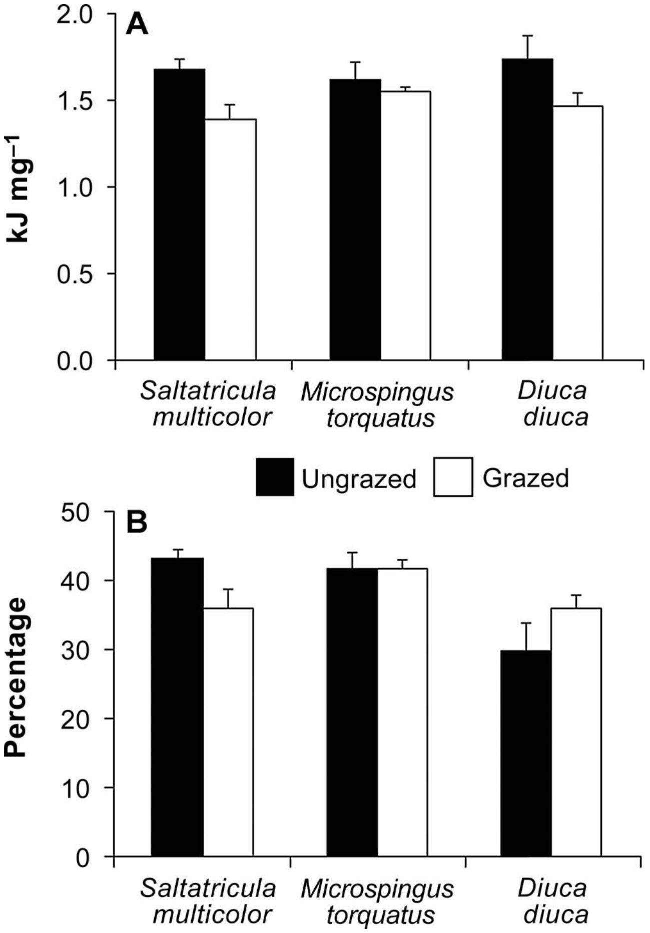

FIGURE 3. Average (+ SE) (**A**) energy reward measured as kJ mg^{-1}, and (**B**) starch content measured as percentage of seed mass in the diets of 3 seed-eating bird species wintering in ungrazed (black bars) and grazed (white bars) *Prosopis* open woodlands of the central Monte Desert, Argentina.

despite its relatively wide niche in the reserve, *Z. capensis* reached maximum feeding flexibility in the grazed sites, where it consumed a smaller amount of the preferred grass seeds and more forb seeds. Feeding flexibility was apparent in disturbed as well as undisturbed habitats, but the combination of results from cafeteria experiments (*Z. capensis* prefers grass seeds) and realized diets (the species shows high flexibility) suggests that *Z. capensis* is also an expanding specialist.

The low capacity of diet switching shown by *S. multicolor* and *M. torquatus* and the moderate but clear capacity of diet switching of *D. diuca* and *Z. capensis* were expected due to previous results from seed selection studies in the field (Marone et al. 2008) and seed preference trials under controlled laboratory conditions (Cueto et al. 2006, Camín et al. 2015). Quantification of species-specific diet switching by birds enables us to foresee which species will be more vulnerable to reduction of preferred resources under habitat degradation, an important issue for applied ornithology. It is worth noting that our predictions were developed using a mechanismic approach that needed laborious studies on the size of seed reserves under different grazing conditions, the energy reward and starch content of consumed seeds, and subtle differences in the feeding behavior of bird species. Mechanisms acted as causal links between niche properties and habitat alteration, offering a priori hypotheses on plausible responses of bird species (Martin and Possingham 2005, Marone et al. 2008, Pol et al. 2014). This allowed us to look for energetic and nutritional consequences of diet switching in degraded lands. The average diet of all birds in the grazed areas contributed a smaller proportion of energy per unit mass than the diet in the ungrazed area and, for 1 out of 3 bird species, a lower starch content. The reduction in energy reward in grazed areas was, however, low to moderate, and it could be compensated for by a minor increase in the absolute seed mass consumed, or by incorporating higher fractions of alternative food resources (e.g., arthropods). Strictly according to diet switching theory, the physical condition of individual birds might then be barely, or not at all, affected under grazing regimes. Nevertheless, the substantial reduction in the availability of grass seeds (60–90%) in degraded lands, together with the low to moderate capacity of diet switching by several seed-eating birds, may reduce the capacity of degraded habitats to support the most granivorous birds.

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