

# Exploring food preferences and the limits of feeding flexibility of seed-eating desert birds

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**Abstract.** Habitat degradation caused by cattle grazing may be a serious threat for seed-eating birds because the availability of beneficial seeds usually diminishes in grazed areas. Ecologically plastic species might, however, circumvent food deprivation via changes in foraging behaviour. We studied the limits of feeding flexibility and factors affecting seed preferences in *Zonotrichia capensis*, *Diuca diuca*, and *Saltatricula multicolor*. We experimentally assessed preferences for seeds of eight grass and eight forb species by using a protocol that combines choice and non-choice trials, and employed a different batch of experiments to evaluate some plausible causes of different feeding flexibility. On average, birds consumed 45–140% more grass than forb seeds, confirming previous results. *Z. capensis* preferred several grass and forb seeds, and showed maximum feeding flexibility. *S. multicolor* and, to a lesser extent, *D. diuca*, were grass specialists that preferred large and medium-sized grass seeds. The size of forb seeds did not affect preferences. Coat thickness of grass seeds did not seriously reduce consumption levels. Birds showed low ability to feed on resources characteristic of degraded environments (i.e. annual grass seeds). Species-specific differences in behavioural flexibility could be used to predict dietary and numerical responses of seed-eating birds to habitat degradation.

**Additional keywords:** Argentina, choice and non-choice trials, forb seeds, grass seeds, habitat degradation, seed size.

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## Introduction

Human-induced rapid environmental change (Sih *et al.* 2011) such as climate change, species invasions, pollution and habitat degradation, has notable effects on the abundance and distribution of plant and animal species (Clavel *et al.* 2011). A key issue for conservation and management is to understand why some species are doing so badly while others are doing so well in coping with habitat change. In some cases, the answer is behaviour (Sih 2013): plastic organisms can respond effectively to habitat degradation via changes in their patterns of resource use (e.g. foraging behaviour and diet). Understanding the limits of an organism's flexibility and the mechanisms affecting their resource preferences are important goals for basic and applied ecology (Charmantier *et al.* 2008).

Grazing by domestic animals is the most globally widespread land use and a major driver of global vegetation change (Díaz *et al.* 2007). In the central Monte desert of Argentina, livestock consumes a high proportion of herbaceous biomass, reducing the cover and seed bank size of numerous herbaceous plants

(Pol *et al.* 2014). In a 3-year study at two localities in the central Monte desert, Pol *et al.* (2014) reported average reductions of 63–83% (grass seeds) and 25–100% (forb seeds) in the seed bank. Most seed species reduced by grazing are the same as those that prevail in the diet of seed-eating birds (Marone *et al.* 2008), which suggests that cattle grazing could lead to declines in bird populations if the bird species are not sufficiently flexible to cope with resource changes in these degraded environments.

Previous studies on the winter diet of granivorous bird species in undisturbed habitats of the Biosphere Reserve of Ñacuñán, central Monte desert, suggest that birds can be placed along a continuum, from grass seed specialists to generalists. The Many-coloured Chaco-Finch (*Saltatricula multicolor*) has a granivorous diet composed of 100% grass seeds, whereas Common Diuca-Finch (*Diuca diuca*) (78%) and Rufous-collared Sparrow (*Zonotrichia capensis*) (55%) have more mixed granivorous diets composed of both grass and forb seeds (Marone *et al.* 1998, 2008). In experiments in which eight seed species were offered (four grasses and four forbs), all birds showed preferences for some

grass seeds such as those in the genera *Setaria* or *Pappophorum*, though *D. diuca* and *Z. capensis* were also able to consume many forb seeds such as *Chenopodium* and *Parthenium* (Cueto *et al.* 2006).

Although these patterns are consistent with bird species showing different degrees of specialisation in foraging behaviour, the limits of their feeding flexibility are still mostly unknown. On the one hand, realised field diet is usually a poor estimator of the potential diet breadth of a species, particularly when it comes from undisturbed habitats (Díaz 1994). In these environments, birds are not usually subjected to food deprivation (Lopez de Casenave 2001), and may be mostly consuming the abundant, most beneficial seeds (Marone *et al.* 2008). On the other hand, the determination of preference or avoidance of any particular food type depends critically upon the array of types included in the experiment (Johnson 1980). We previously assessed seed preferences with only eight seed species (Cueto *et al.* 2006), whereas birds can consume up to 24 seed species in certain locations of the central Monte (Marone *et al.* 2008; Sánchez and Blendinger 2014).

We assessed bird preferences for seeds of eight grass species and eight forb species offered in separate experiments that combine choice and non-choice trials (Cueto *et al.* 2001). Our main aim was to confirm previous inferences on bird seed preferences, and determine the limits of feeding flexibility of three common (Marone 1992) granivorous bird species. Our hypothesis was that all bird species prefer grass seeds over forb seeds of similar sizes, but that bird species also show important differences in feeding flexibility. After testing this idea, we used previous information (Cueto *et al.* 2006; Marone *et al.* 2008; this study) and a different batch of choice experiments to evaluate some plausible causes of seed preferences and differences in feeding flexibility. One experiment was designed to test a prediction based on optimal foraging theory relating seed and bill properties: namely that smaller seed-eating birds should specialise on smaller seeds whereas larger seed-eaters should have a broader range of seed-size use (i.e. should use both small and large seeds), being more flexible than smaller seed-eaters (Grant *et al.* 1976; Pulliam 1985; Díaz 1994). A second experiment evaluates Pulliam's (1980) prediction that the presence of seed-covering structures (e.g. seed-coat thickness) will discourage seed consumption, owing to an increase of food handling time. Finally, we assessed preference levels of seeds from an annual versus several perennial grasses, to determine whether seed resources that usually increase in abundance in degraded environments (i.e. seeds from annual grasses) could be an alternative food for birds, increasing bird resilience to the changes that occur in such environments.

## Materials and methods

### *Bird species and environment*

The three bird species used in feeding experiments were *Z. capensis* (bodyweight 18 g), *S. multicolor* (22 g), and *D. diuca* (25 g). All three species were formerly in the family Emberizidae, but *S. multicolor* and *D. diuca* are now placed in Thraupidae (Burns *et al.* 2014). All are members of a ground-foraging guild that mainly search for and obtain seeds from the soil (Lopez de Casenave *et al.* 2008). We caught individuals

with mist nets and cage traps during winter months in the open *Prosopis flexuosa* woodland of the Biosphere Reserve of Ñacuñán (34°03'S, 67°54'W). The open woodland is composed of scattered *P. flexuosa* and *Geoffroea decorticans* trees within a shrub matrix mainly of *Larrea divaricata* (Marone 1991). The herbaceous stratum is dominated by perennial grasses (genera *Setaria*, *Trichloris*, *Pappophorum*, *Digitaria*, *Sporobolus*, *Jarava*, *Aristida*, *Eragrostis*), and secondarily by annual or biennial forbs (genera *Chenopodium*, *Parthenium*, *Sphaeralcea*, *Lappula*, *Glandularia*, *Descurainia*, *Phacelia*, *Plantago*). Ñacuñán has a dry temperate climate, with cold winters and hot summers. On average, >75% of the annual rainfall (263 mm,  $n=31$  years) occurs in spring and summer (October–March) (Lopez de Casenave 2001).

### *Preferences among grass species and among forb species*

We used an experimental design that combined both choice and non-choice feeding trials to detect seed preferences of the three sparrow species (Cueto *et al.* 2001). This combined design can overcome the limitations and biases of using only one of the experimental approaches, which is crucial when the species under study has partial or conditional preferences (e.g. when the use of an item depends on the availability of others). Birds were kept in individual cages (45 × 30 × 30 cm) for no more than 30 days in an indoor room with artificial photoperiod (12 h L:12 h D), fed with commercial seeds (*Setaria italica* or *Panicum milliaceum*) and vitamin-enriched water *ad libitum*. After the trials, we released all birds in the same area where they were caught. Seeds tested (8 species in every trial) were collected in the same area where we had captured the birds. In one experiment, we offered only grass seeds of *Setaria leucopila* (0.75 mg), *Pappophorum* spp. (0.35 mg), *Trichloris crinita* (0.23 mg), *Digitaria californica* (0.40 mg), *Aristida mendocina* (0.46 mg), *Sporobolus cryptandrus* (0.07 mg), *Jarava ichu* (0.12 mg), and *Eragrostis* sp. (0.07 mg). In another experiment, we tested seeds of annual or biennial forbs of *Chenopodium papulosum* (0.25 mg), *Parthenium hysterophorus* (0.42 mg), *Lappula redowskii* (0.40 mg), *Sphaeralcea miniata* (0.20 mg), *Glandularia mendocina* (0.40 mg), *Descurainia* sp. (0.07 mg), *Phacelia artemisioides* (0.50 mg) and *Plantago mendocina* (0.65 mg). Hereafter, the generic name will be used to identify the species employed.

In every experiment we placed each individual in an observational cage made of see-through acrylic (40 × 40 × 40 cm), with acrylic floor and a single perch. Prior to the trial, all birds were subjected to a food-deprivation period of 2–5 h, depending on body mass and general behaviour (e.g. the reluctance to feed under experimental conditions) of the species and organisms tested. In choice trials, we simultaneously presented 50 seeds of the eight food options (a total of 400 seeds) scattered randomly on the cage floor, and an individual bird was placed in the cage in darkness. After 1 min, a hidden observer turned on the light, and the bird was allowed to feed for 10 min. At the end of the trial, we removed all remaining seeds and recorded the number of seeds of each species consumed. Offering seeds on the cage floor allows comparing seed consumption rates among the three bird species since all of them are capable of detecting and consuming seeds placed on the soil surface, but *S. multicolor*

and *D. diuca* do not detect or are unable to extract buried seeds (Cueto *et al.* 2013). In non-choice trials, we used the same procedure but offered 50 seeds of a single plant species to a bird for 5 min, testing the seeds of the eight plant species separately. We randomised the order in which each seed species was assayed. In choice trials, we presented more seeds per unit time than in non-choice ones (40 versus 10 seeds per minute) to prevent a significant decrease in abundance of the most-preferred species, which could force birds to consume other species at higher rates than expected because there was nothing else to eat.

Following the recommendations of Roa (1992) and Lockwood (1998), we analysed data of choice trials with a Friedman's test (Zar 1996), given that the treatments (i.e. the different food options) were not independent (Roa 1992). We used the same statistical test for analyses of non-choice data, because we tested each food item with the same individual bird, thereby using a repeated-measure (Zar 1996). Given that the detailed results of *a posteriori* multiple-comparison tests are difficult to summarise and interpret when several (8) options are compared, we applied a graphical approach that combined both kinds of trials to distinguish among preferred, less-preferred and avoided seed species (Cueto *et al.* 2001). The average percentage of seeds consumed by each granivorous bird species was represented on the *x* (non-choice) and *y* (choice) axes of a 2D scatterplot. The combined graph gives a more informed picture of species-specific seed preferences since non-choice trials usually overestimate the consumption of some food items that may not be strictly preferred (Roa 1992), whereas choice experiments may underestimate the use of some items whose consumption depends on the presence or absence of preferred food in the foraging microhabitat (Cueto *et al.* 2001). In the graph space we classified seed species as preferred (i.e. those consumed more than 50% in non-choice as well as choice trials), less preferred (i.e. seeds consumed more than 50% in non-choice trials, and between 25 and 50% in choice trials), and not preferred or avoided (i.e. seeds consumed less than 50% in non-choice trials, and between 0 and 25% in choice trials).

#### The effect of seed size on seed preferences

First, we determined correlations between the level of consumption in choice trials (see above) and seed masses, separately for grass and forb seeds, to test the prediction that the range of seed-size use differs in smaller and larger bird species. In a second step, we employed a new set of choice trials in which 50 seeds of three types were offered simultaneously to individuals of the three bird species: *S. cryptandrus* seeds (0.07 mg), *Sporobolus phleoides* seeds (0.21 mg), and two *S. cryptandrus* seeds, along with a paste of flour and water (0.15 mg). We used morphologically identical grass seeds of different sizes from the same genus (*Sporobolus*) under the assumption that related phylogeny implies similar chemical composition. We analysed the results with Friedman's test, and a multiple-comparison *a posteriori* analysis of ranked data (Zar 1996). We tested the assumption that the paste does not discourage seed consumption by simultaneously offering 20 *Pappophorum* seeds smeared with paste and 20 without paste to *Z. capensis* ( $n=9$ ) and *S. multicolor* ( $n=5$ ) individuals.

Comparison between control and treatment for each bird species was carried out with a Mann–Whitney test.

#### The effect of seed-coat thickness on seed preferences

We tested the effect of coat thickness on seed consumption rates by using a choice trial with three options: whole *Digitaria* seeds, husked *Digitaria* seeds (only the cariopses, without any glumes), and partially husked seeds (without external glumes and papus but with internal green glumes). We analysed results with a Friedman's test, and a multiple-comparison *a posteriori* analysis of ranked data (Zar 1996).

#### Preferences for seeds from annual grasses

In some locations of the Monte desert, some annual grass species such as *Bouteloua aristidoides* are abundant in the soil seed bank (Pol *et al.* 2014; Sánchez and Blendinger 2014). It is an annual caespitose grass species widely distributed in arid South and North America, which usually grows in degraded (e.g. grazed) environments (Herrera-Arrieta *et al.* 2004). It has elongated cariopses placed in propagules with conspicuous awns. Seed mass and general appearance are like those of the preferred *Trichloris* seed. We tested preferences for two bird species using a choice trial where *Bouteloua* was offered together with three other grass seed species whose preference level is known (Cueto *et al.* 2006; this study): *Setaria*, *Trichloris* and *Sporobolus cryptandrus* (*Z. capensis*); and *Setaria*, *Trichloris* and *Pappophorum* (*S. multicolor*). We analysed results with a Friedman's test, and a multiple-comparison *a posteriori* analysis of ranked data (Zar 1996).

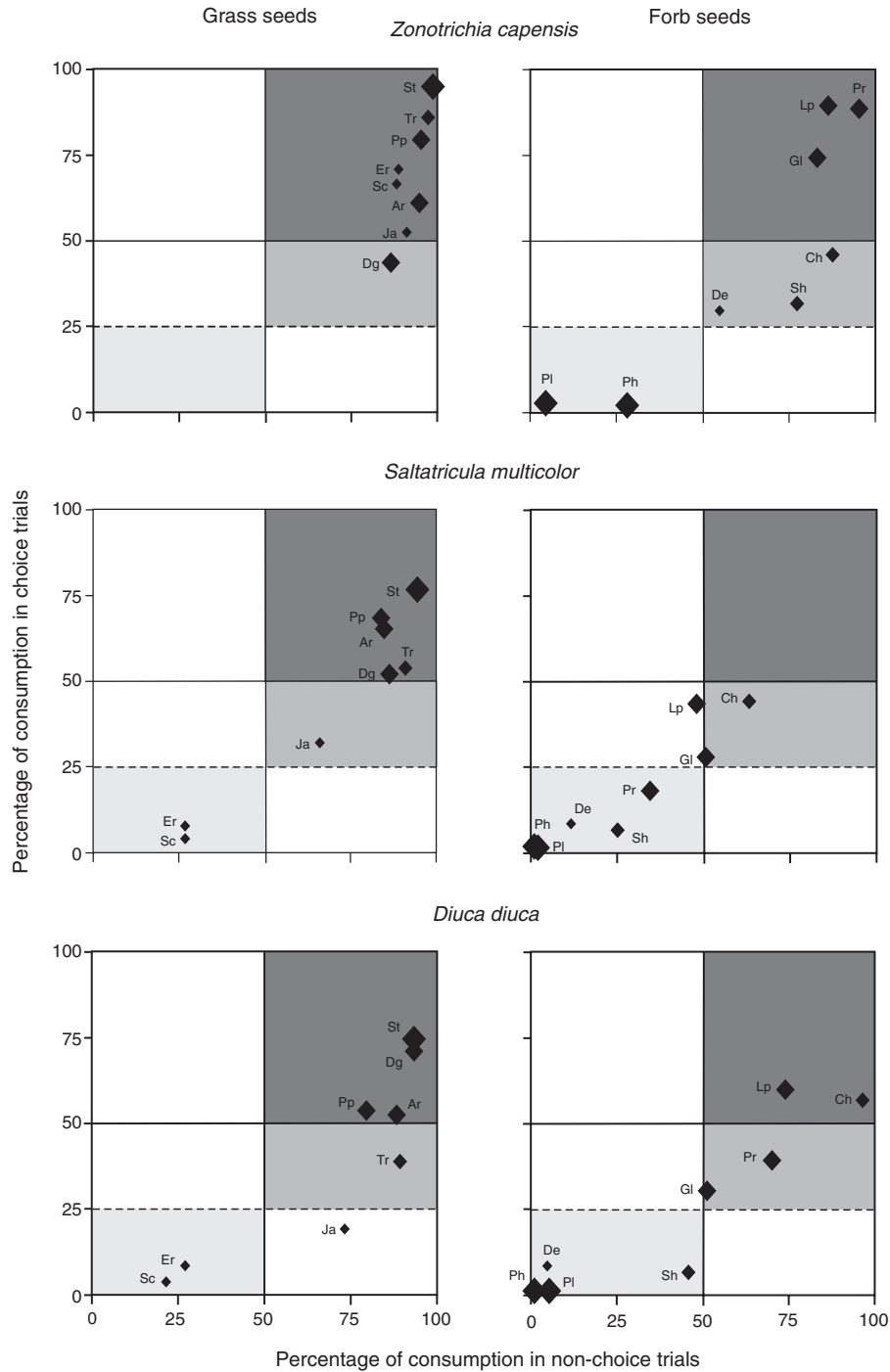
## Results

#### Preferences of grass versus forb seeds

In non-choice trials, *Z. capensis* consumed, on average, 92% of the offered grass seeds but only 65% of the forb seeds, whereas in choice trials, it ate 70% of the grass seeds and 46% of the forb seeds (this species consumed 45–50% more grass seeds than forb seeds in both trials). Figures for *S. multicolor* were 70% and 29% in non-choice, and 45% and 19% in choice tests (135–140% more grass seeds). *D. diuca* ate 71% of grass seeds but only 43% of forb seeds in non-choice trials, and 40% of grass seeds but only 24% of forb seeds in choice trials (65–70% more grass seeds).

#### Preferences among grass seed species

Choice and non-choice trials showed that the three bird species have clear preferences when searching for seeds. *Z. capensis* (choice Friedman test  $\chi^2=41.01$ ,  $P<0.001$ ,  $n=12$  individuals employed; non-choice Friedman test  $\chi^2=20.25$ ,  $P=0.005$ ,  $n=12$ ), *S. multicolor* (choice  $\chi^2=54.94$ ,  $P<0.001$ ,  $n=13$ ; non-choice  $\chi^2=41.75$ ,  $P<0.001$ ,  $n=13$ ), *D. diuca* (choice  $\chi^2=45.43$ ,  $P<0.001$ ,  $n=10$ ; non-choice  $\chi^2=46.03$ ,  $P<0.001$ ,  $n=10$ ) (Fig. 1). *Z. capensis* preferred *Setaria*, *Trichloris*, *Pappophorum*, *Eragrostis*, *Sporobolus*, *Aristida* and *Jarava*, whereas it preferred *Digitaria* less (i.e. 8 species with some level of preference). *S. multicolor* preferred *Setaria*, *Pappophorum*, *Aristida*, *Trichloris* and *Digitaria*, and preferred *Jarava* less (i.e. 6 species), while it showed negative preference for *Eragrostis* and *Sporobolus*. *D. diuca* preferred *Setaria*, *Digitaria*, *Pappophorum* and *Aristida*, and preferred *Trichloris* less (5 species),



**Fig. 1.** Scatter plots combining the average percentage of seeds consumed in choice and non-choice trials by three seed-eating bird species inhabiting the central Monte desert, Argentina. Grass seed species (left graphs) are *Setaria leucopila* (St), *Pappophorum* spp. (Pp), *Trichloris crinita* (Tr), *Aristida* spp. (Ar), *Digitaria californica* (Dg), *Jarava ichu* (Ja), *Sporobolus cryptandrus* (Sp), *Eragrostis* sp. (Er). Forb seed species (right graphs) are *Parthenium hysterophorus* (Pr), *Chenopodium papulosum* (Ch), *Lappula redowskii* (Lp), *Glandularia mendocina* (Gl), *Sphaeralcea miniata* (Sh), *Descurainia* sp. (De), *Plantago patagonica* (Pl), and *Phacelia artemisioides* (Ph). Sizes of symbols are directly proportional to seed weights (see the text for species-specific seed weights). Preferred seeds are consumed more than 50% in non-choice as well as choice trials, less preferred seeds are consumed more than 50% in non-choice trials, and between 25 and 50% in choice trials, and not preferred or avoided seeds are consumed less than 50% in non-choice trials, and between 0 and 25% in choice trials (indicated with different grey tones).

whereas it avoided *Jarava*, *Eragrostis* and *Sporobolus*. All bird species showed some degree of preference for medium- and large-sized seeds (*Setaria*, *Pappophorum*, *Aristida*, *Trichloris*, *Digitaria*) (Fig. 1).

#### Preferences among forb seed species

Choice and non-choice tests showed that the three bird species also have preferences among forb seeds. *Z. capensis* (choice Friedman test  $\chi^2 = 51.32$ ,  $P < 0.001$ ,  $n = 11$ ; non-choice Friedman test  $\chi^2 = 40.0$ ,  $P < 0.001$ ,  $n = 11$ ), *S. multicolor* (choice  $\chi^2 = 18.74$ ,  $P = 0.009$ ,  $n = 9$ ; non-choice  $\chi^2 = 33.28$ ,  $P < 0.001$ ,  $n = 9$ ), *D. diuca* (choice  $\chi^2 = 27.42$ ,  $P < 0.001$ ,  $n = 9$ ; non-choice  $\chi^2 = 40.66$ ,  $P < 0.001$ ,  $n = 9$ ) (Fig. 1). *Z. capensis* preferred *Parthenium*, *Lappula* and *Glandularia*, and preferred *Chenopodium*, *Sphaeralcea* and *Descurainia* less, while it showed negative preferences for *Plantago* and *Phacelia*. *S. multicolor* did not prefer any of the forb seed species, and preferred only *Chenopodium* and *Glandularia* less. *D. diuca* showed an intermediate behaviour regarding forb seed consumption. It preferred (*Chenopodium*, *Lappula*) or preferred less (*Parthenium*, *Glandularia*) four (50%) of the species offered, and avoided another four (*Sphaeralcea*, *Descurainia*, *Plantago*, *Phacelia*). *Chenopodium* and *Glandularia* were the only genera with some degree of preference by all bird species (Fig. 1).

#### The effect of seed size on seed preferences

Preferences of *Z. capensis* (i.e. the level of seed consumption in choice experiments) did not correlate with seed mass of grasses (Pearson Correlation Coefficient  $r = 0.316$ ,  $n = 8$ ,  $P = 0.450$ ). By contrast, seed mass correlated positively with grass seed preferences in *S. multicolor* ( $r = 0.877$ ,  $n = 8$ ,  $P = 0.004$ ) and *D. diuca* ( $r = 0.923$ ,  $n = 8$ ,  $P = 0.001$ ). Seed mass of forbs did not correlate with preferences of *Z. capensis* ( $r = -0.224$ ,  $n = 8$ ,  $P = 0.594$ ), *S. multicolor* ( $r = -0.219$ ,  $n = 8$ ,  $P = 0.273$ ) nor *D. diuca* ( $r = -0.394$ ,  $n = 8$ ,  $P = 0.334$ ) (Fig. 1).

Every bird species consumed different amounts of the three food options tested: *Z. capensis* (choice Friedman test  $\chi^2 = 12.64$ ,  $P = 0.002$ ,  $n = 9$ ), *S. multicolor* ( $\chi^2 = 7.142$ ,  $P = 0.02$ ,  $n = 7$ ), and *D. diuca* ( $\chi^2 = 11.56$ ,  $P = 0.003$ ,  $n = 6$ ) (Fig. 2, left). The larger *S. phleoides* seeds were always more consumed than the tiny *S. cryptandrus* seeds, and there was a tendency to consume more *S. cryptandrus* seeds when together than when separate (Fig. 2, left). Independent trials showed that the presence of paste did not increase seed consumption. *Z. capensis* ate  $79 \pm 10\%$  (mean s.d.) of the seeds without paste and  $55 \pm 14\%$  with paste (Mann–Whitney test  $Z = 0.97$ ,  $P = 0.33$ ,  $n = 9$ ), whereas *S. multicolor* consumed  $86 \pm 43\%$  of the seeds without paste and  $47 \pm 26\%$  with paste ( $Z = 0.10$ ,  $P = 0.92$ ,  $n = 5$ ). Therefore, the tendency of *S. multicolor* and *D. diuca* to eat more seeds when together than separate (see Fig. 2, left) is unlikely to constitute a methodological artefact.

#### The effect of seed-coat thickness on seed preferences

Seed consumption by *Z. capensis* of the three food options assayed differed statistically (choice Friedman test  $\chi^2 = 6.81$ ,  $P = 0.03$ ,  $n = 9$ ), although multiple-comparison ranked tests did not discriminate among the items. By contrast, seed consumption did not differ for *S. multicolor* ( $\chi^2 = 2.60$ ,  $P = 0.272$ ,  $n = 8$ ) or

*D. diuca* ( $\chi^2 = 4.66$ ,  $P = 0.09$ ,  $n = 7$ ) (Fig. 2, right). Although birds showed a slight tendency to eat more husked seeds, the effect of seed-coat thickness could be not significant biologically, since all types of seeds (including entire seeds) were highly consumed (usually >70%) by the three bird species.

#### Preferences of seeds from annual grasses

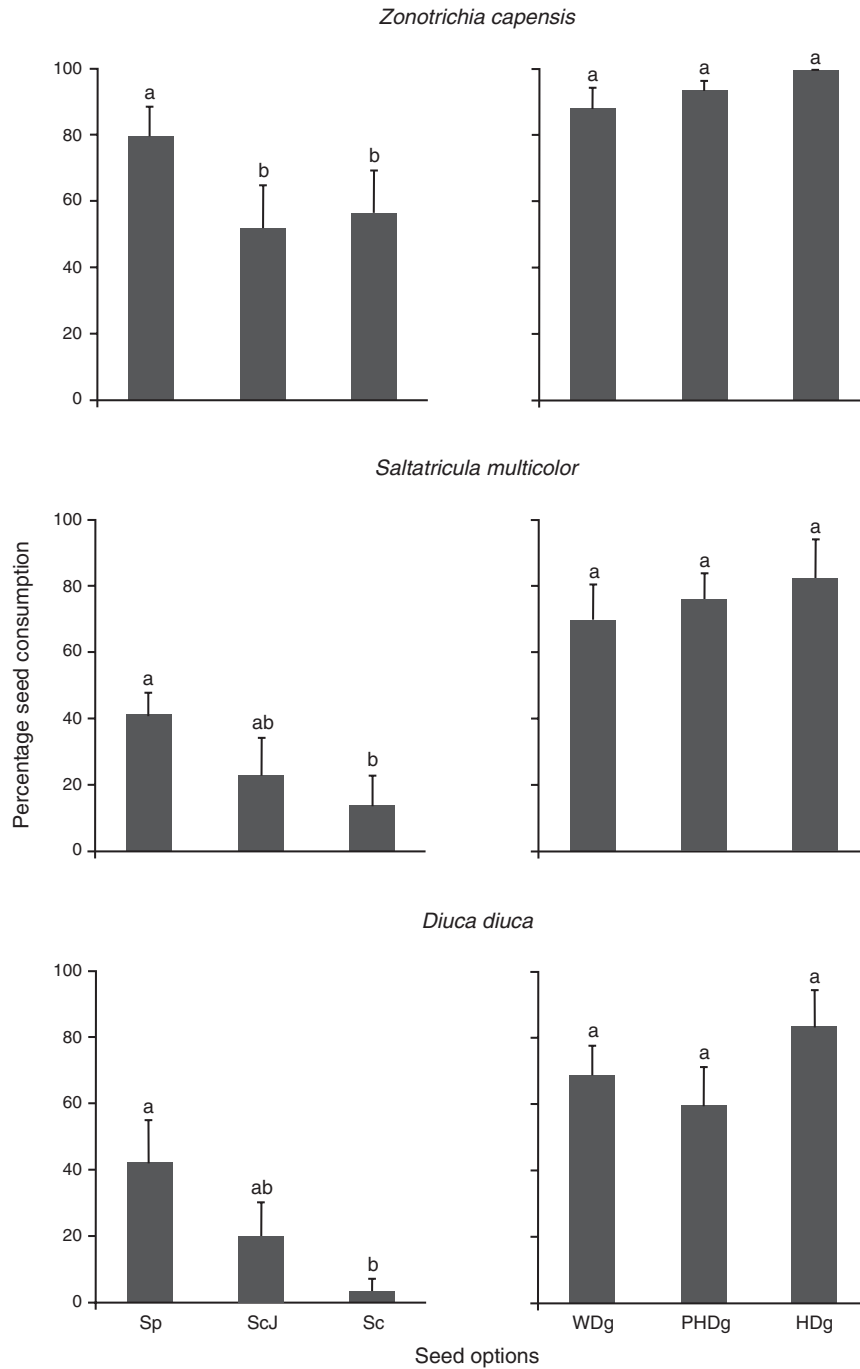
The offered seeds were differentially consumed by *Z. capensis* (choice Friedman test  $\chi^2 = 25.62$ ,  $P < 0.001$ ,  $n = 9$ ) and *S. multicolor* ( $\chi^2 = 13.39$ ,  $P = 0.003$ ,  $n = 6$ ) (Fig. 3). The former species was able to eat 42%, whereas the latter consumed only 7% of the tested *Bouteloua* seeds. According to *a posteriori* ranked tests, *Z. capensis* ate significantly less *Bouteloua* than *Setaria* and *Trichloris*, whereas *S. multicolor* consumed more *Setaria* than *Bouteloua*.

#### Discussion

Although all three bird species often preferred grass over forb seeds, they also differed in feeding flexibility. The most stereotyped forager (*S. multicolor*) strongly preferred medium-sized and large grass seeds, the same seeds that suffer the highest reductions in the soil bank of grazed habitats of the Monte desert (Pol *et al.* 2014). The feeding behaviour of *S. multicolor* might not be sufficiently flexible to cope with resource depletion in those degraded environments.

Bird species consumed 45–140% more grass seeds than forb seeds in our trials, and all three birds preferred five grass seed species to a certain degree. Among forbs, only *Chenopodium* and *Glandularia* were consistently preferred or preferred less by the three species, whereas the seeds of *Phacelia*, *Plantago*, *Descurainia* and *Sphaeralcea* (which constitute <2% of the granivorous field diet of Monte's birds: Marone *et al.* 2008) were avoided by at least two of the three species. Grass seeds were preferred according to their size by the larger bird species (*S. multicolor* and *D. diuca*), while the smaller *Z. capensis* highly consumed grass seeds in all sizes. Finally, the level of preference of forb seeds was independent of seed size for all birds. Within some chemically homogeneous groups of seeds (e.g. grasses: Díaz 1996; Ríos *et al.* 2012a), seed size could positively define preference levels by the larger bird species, plausibly because birds can optimise energy intake rate per unit time by eating the larger seeds. By contrast, when chemically heterogeneous seeds were considered (e.g. forbs), seed size alone seemed insufficient to account for preferences. Multiple causal mechanisms affect seed preferences, the feeding flexibility of seed-eating birds and the realised field diet (Dimiceli *et al.* 2007; Runia *et al.* 2007; Ríos *et al.* 2012a).

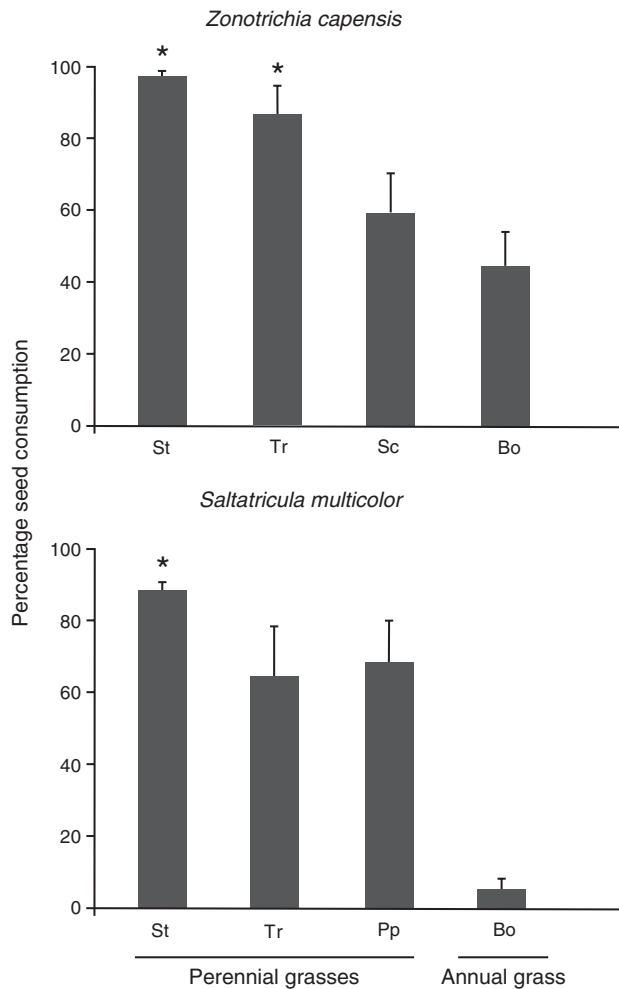
Despite the plausible interaction of causal factors, ecologists have long searched for simple and intuitive rules for seed preferences. For example, the prediction of a direct correlation between seed size preferences and bird body mass or bill size inspired several interesting studies (e.g. Díaz 1990), although the evidence to support it remains ambiguous (Lopez de Casenave 2001). The related prediction that smaller seed-eaters should specialise on smaller seeds whereas larger ones should increase the range of seed sizes preferred was supported in an experimental study with a group of European passerines belonging to three families (Díaz 1994). By contrast, we experimentally showed



**Fig. 2.** Percentage consumption of seeds differing in individual mass (left graphs) and coat thickness (right graphs) by three seed-eating bird species. Seed consumption was measured in choice trials. Vertical lines indicate standard errors. Food items for assessing the effect of seed size on consumption level are *Sporobolus phleoides* (Sp), two *Sporobolus cryptandrus* joined by paste (ScJ), and *Sporobolus cryptandrus* (Sc). Food items for evaluating the effect of coat thickness are Whole *Digitaria* (WDg), Partially Husked *Digitaria* (PHDg), and Husked *Digitaria* (HDg). Bars sharing the same letter are not significantly different (multiple-comparison analyses of ranked data,  $P < 0.05$ ).

that the smaller *Z. capensis* preferred grass seeds in a wide range of sizes, and that the larger birds (*S. multicolor*, *D. diuca*) avoided the smallest grass seeds. Moreover, Lopez de Casenave (2001) had failed to find any relationship between bill features

of these birds and the size of seeds consumed, both at the individual and species level. He suggested that Monte's birds are opportunistic feeders exploiting abundant resources, a situation that could have prevented a tight coupling between



**Fig. 3.** Percentage consumption of seeds from annual and perennial grass species by two seed-eating bird species. Seed consumption was measured in choice trials. Seed species offered were *Setaria leucopila* (St), *Trichloris crinita* (Tr), *Sporobolus cryptandrus* (Sc), *Pappophorum* spp. (Pp) (perennial grasses), and *Bouteloua aristidoides* (Bo) (annual grass). Vertical lines indicate standard errors. Bars with an asterisk indicate that the number of seeds consumed was significantly higher than the number of *B. aristidoides* seeds eaten (multiple-comparison analyses of ranked data,  $P < 0.05$ ).

morphology and diet in this group. Díaz (1994) experimented mostly with fringillids, which have a very different seed-handling behaviour compared with emberizids and thraupids due to beak structure (see a review in Lopez de Casenave 2001). Differences in feeding preferences between European and South American birds could then be due to birds in distinct families having a different scaling of seed-handling ability with seed size (Díaz 1990), as was also shown by Benkman and Pulliam (1988) for North American cardueline finches versus emberizine sparrows. Notwithstanding, in a survey of seed consumption by several New World sparrows (emberizids) of New Mexico, Desmond *et al.* (2008) also claimed that small-bodied sparrows specialised on small seeds, larger-bodied sparrows exhibited preferences for seeds representing a great diversity of sizes, and most birds preferred the tiny seeds of *Sporobolus cryptandrus*. At first glance, these results seem to imply that rules of preference are

very limited in scope and contingent to location and bird species considered. This conclusion, however, deserves deeper assessment because some methodological decisions of the researchers might be affecting the inferences.

The assessment of bird diet (i.e. the proportion of various food types in stomachs) is not enough to make conclusions about food preferences because birds may be feeding opportunistically (Johnson 1980; Díaz 1990). The comparison of the proportion of every seed species in the field and in bird diets to determine whether birds are feeding opportunistically or are being selective (e.g. Desmond *et al.* 2008) is certainly a more reliable way to approach bird preferences. Notwithstanding, the most appropriate method for analysing food preferences is feeding experiments in which food types are presented under controlled conditions and equally available (Díaz 1990; Cueto *et al.* 2001; Soobramoney and Perrin 2007). Thus, the consumer can express foraging choices, permitting a distinction among preferred, less preferred and avoided food items (Cueto *et al.* 2001). As Desmond *et al.* (2008) reported for the Chihuahuan desert, we also found that birds select *S. cryptandrus* seeds in the Monte desert (Marone *et al.* 2008; Fig. 1) but, under controlled conditions, we were able to determine that these seeds were less preferred (Cueto *et al.* 2006) or preferred (this study) only by *Z. capensis*, while they were avoided by *S. multicolor* and *D. diuca* (Cueto *et al.* 2006; this study). When Desmond *et al.* (2008) assert that small as well as large-bodied sparrows in New Mexico preferred the tiny *Sporobolus* seeds, they are actually stressing that the sparrows ‘selected’ the seeds (i.e. consumed them disproportionately according to availability). The high proportion of *Sporobolus* seeds in the stomachs of several bird species in the Monte desert (Marone *et al.* 1998, 2008; Sánchez and Blendinger 2014) as well as in the Chihuahuan desert (Niemela 2002; Desmond *et al.* 2008) might be a consequence of the opportunistic consumption (from the soil bank or directly from the panicles: Lopez de Casenave *et al.* 2008; Milesi *et al.* 2008) of an abundant seed item that is, however, a suboptimal or less preferred and not a highly preferred seed for those bird species.

Birds showed clear species-specific differences in behavioural flexibility. *Z. capensis* was the most flexible forager. It preferred most grass seeds but also preferred, or preferred to a lesser degree, six forbs, and had no limitations in eating the smallest seeds. By contrast, *S. multicolor* was a grass-seed specialist that showed minimum feeding flexibility (i.e. it preferred five grass seeds but none of the forb seeds). *D. diuca* was a graminivorous bird also (i.e. it preferred, or preferred to a lesser degree, all medium-sized or large grass species) but also preferred two forb seeds. The feeding flexibility of the three bird species clearly corresponded with the incidence of forb seeds in their field diet and with the breadth of their dietary niche (Marone *et al.* 2008), suggesting that the extrapolation of experimental results to field conditions is largely reliable.

Some physiological and behavioural mechanisms can enhance or restrict ecological flexibility. Grass-seed specialists usually prefer high-starch diets (Brzek *et al.* 2010), and their seed intake is reduced by the presence of some secondary chemical compounds. Among Monte’s birds, the generalist *Z. capensis* is able to eat seeds regardless of starch content, has higher tolerance to several secondary compounds (Rios *et al.*

2012a) and higher detoxification capability than *S. multicolor* and *D. diuca* (Ríos *et al.* 2012b). The last two species, however, preferred diets with high starch content, possibly because they entailed two advantages: obtaining easily digestible energy with low cost of absorption, and a relative gain in terms of thermogenesis during the cold season (Ríos *et al.* 2012a). Physiological flexibility of *Z. capensis* certainly enhances its ecological flexibility.

Regarding behaviour, Cueto *et al.* (2013) verified that *Z. capensis* is the only species capable of recovering buried seeds, and is more efficient in recovering seeds mixed with litter, owing to its capability of 'double scratching' (i.e. quickly moving both legs at the same time, backwards and forwards). The higher physiological and behavioural plasticity of *Z. capensis* may then account for several of its flexible ecological characteristics: it behaves as an opportunistic feeder (Cueto *et al.* 2006), uses the full range of available foraging microsites (Milesi *et al.* 2008), has the greatest diet breadth in the field (Marone *et al.* 2008) and a higher winter abundance (Marone 1992) in the Monte desert, and it adapts successfully to new habitats created by human activities such as agriculture and ranching (Bellocq *et al.* 2011). Following the same line of thinking, niche theory predicts that, under severe grazing conditions, the less flexible and specialised *S. multicolor* would not respond through changes in behaviour (i.e. it should maintain its foraging tactics and realised diet mostly unchanged), and consequently would suffer numerical declines (Clavel *et al.* 2011).

Additional experiments allow us to deepen the investigation on plausible causes of seed preferences that contribute to shaping the species-specific limits of feeding flexibility. Although the three bird species preferred the larger *S. phleoides* seeds over the tiny *S. cryptandrus* seeds, *Z. capensis* was able to consume almost 60% of the smaller seeds, but *S. multicolor* (15%) and *D. diuca* (5%) barely consumed the smaller seeds (Fig. 2, left side). The great ability of *Z. capensis* to consume tiny seeds, despite its significant preference for the largest seeds, shows its higher foraging flexibility, and not surprisingly the field diet of *Z. capensis* has abundant *S. cryptandrus* seeds (23.2%) whereas that of *D. diuca* has none (Marone *et al.* 2008). Surprisingly, the stomach contents of *S. multicolor* can have a high proportion (36%) of *S. cryptandrus* seeds. The explanation, however, is that *S. multicolor* usually eats numerous seeds in a single bout directly from the panicles and not from the soil (Lopez de Casenave *et al.* 2008; Milesi *et al.* 2008), which is how seeds were offered in our experiments. The ability to consume an important proportion of seeds from the panicles is a flexible component of the otherwise stereotyped foraging behaviour of *S. multicolor*.

Seed handling of coated seeds might also account for differences in preferences. Under risky field conditions (e.g. in the presence of competitors or predators), birds that eat husked seeds or seeds with propagules that are easy to manipulate could have an advantage, since they can consume the seeds faster, optimising energy intake rate per unit time (Díaz 1996; Carrillo *et al.* 2007). Our results show a slight tendency for all bird species to consume more husked *Digitaria* seeds than other options, although it was only significant for *Z. capensis*. The most important conclusion, however, is that all bird species were able to consume at least 70% of the entire seeds offered, suggesting that coat thickness of grasses is not an obstacle to eating the seeds and that behavioural

tools of all these birds are flexible enough to allow the efficient handling of both entire and husked propagules. Comparative studies of seed handling capability of these birds are needed to strengthen this conclusion.

Finally, our results showed clearly that *Bouteloua* seeds were consumed less than most other seeds of perennial grasses offered in the experiments. *Bouteloua* may be a less preferred (*Z. capensis*) or even avoided (*S. multicolor*) seed for the two species assayed. If bird species had showed clear preferences for the seeds of the opportunistic *Bouteloua* grass, the impact of habitat degradation might be moderated, but this did not occur. The modest presence of *Bouteloua* in the field diet of some Monte desert birds (Sánchez and Blendinger 2014) could again be the consequence of birds feeding on a suboptimal and only occasionally abundant resource (Pol *et al.* 2014). Whether diet choices based on suboptimal items have negative consequences on the physical condition of seed-eating birds, and could provoke population declines like those reported in temperate farmlands (Julliard *et al.* 2004), is a question that certainly deserves scrutiny.

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