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Research

Plausible causes of seed preferences and diet composition in seed-eating passerines

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We evaluated whether seed mass, handling time, handling efficiency and profitability account for (a) preferences in controlled experiments and (b) field-diet composition of four bird species of the Monte desert, Argentina. The question of whether birds maximise their energy intake rates while feeding on seeds is assessed. We used feeding experiments with six native seed species of 0.07–0.75 mg (i.e. the seed-size range consumed in nature), which account for 0.59–0.84 of the field diet of the four birds. We measured seed-handling times and used published information on bird preferences and diets, and on seed chemistry, for further calculations. Bird preferences were always positively related to seed mass and also to seed profitability in the two intermediate-sized birds. Diet composition correlated positively with seed mass and negatively with seed profitability in three species, but some birds also showed a flexible behaviour eating the most attractive seeds according to their availability. This behaviour is not genuinely opportunistic because it only focuses on a restricted fraction of the total seed species present in the field. Contrary to expectations of species coexistence due to resource partitioning, small and large birds showed similar feeding efficiencies when eating the smaller and the larger seeds. The positive association between seed mass and profitability in several studies suggests that most birds can maximise their energy reward, on average and in the long-term, by preferring the larger seeds. A combination of potential feeding optimisation with certain flexibility in the field may characterise the feeding ecology of desert seed-eating birds.

Keywords: feeding experiments, handling time, seed availability, seed mass, seed profitability

Introduction

Knowledge about why seed-eating animals prefer and consume seeds from certain plants and avoid others is crucial to predict top-down and bottom-up consequences



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of the process of granivory. However, understanding of the mechanisms of seed preferences and consumption in the field in birds, along with the establishment of their degree of generality, remains fragmentary and poorly integrated (Marone et al. 2000, Eraud et al. 2015, Young and Schlesinger 2018).

Optimal foraging theory perhaps offers the more general, simple framework to account for animal seed choices (Radtke 2011). It assumes that consumers maximise their energy intake per unit foraging time (Díaz 1996), and one way that birds can maximise energy intake is by selecting the seeds they process the fastest. Through morphological co-adaptations of seeds and bills, birds with smaller bills could process small seeds faster than larger-billed birds because of their greater dexterity in positioning small seeds in their bills for dehusking or cracking (Díaz 1990), and birds with larger bills could handle larger seeds faster than small-billed species because they are able to apply greater pressure on the seeds (Grant 1986, van der Meij and Bout 2004). Thus, some bill sizes and morphologies can optimise the processing speed of some seeds (Ziswiler 1965, Grant 1986, Díaz 1990, 1996), and birds might prefer seeds that require less handling time (Willson and Harneson 1973, Keating et al. 1992, De Nagy Koves Hrabar and Perrin 2002, Carrillo et al. 2007, Titulaer et al. 2018a).

Another way birds can maximise the energy intake rate is by choosing seeds with a higher energy reward (Glück 1985, Díaz 1996): if the availability of seed species is equal, seed choice would be positively related to seed profitability. Some evidence agrees with this prediction (Glück 1985, Shuman et al. 1990, Young and Schlesinger 2018), although several authors suggest that the energy content might be less important than the morphological traits of seeds and birds in determining seed preferences (Díaz 1996, De Nagy Koves Hrabar and Perrin 2002, Soobramoney and Perrin 2007, Titulaer et al. 2018b). Certainly, birds could maximise their energy intake rate by optimising several possible combinations of handling time and energy reward, but the influence of each tactic remains little known because most studies address them one by one instead of trying to weigh their relative importance (Díaz 1996). Moreover, energy reward has sometimes been inferred indirectly by using the seed mass (Wang and Chen 2009, Titulaer et al. 2018a, b) or the mass intake per unit of time (Schluter 1982, Pulliam 1985) as indicators of profitability. Although such assumptions are plausible, the hypothesis that birds maximise energy intake rate by choosing the seeds with a higher energy reward deserves direct testing.

Grant et al. (1976) discuss two possible relationships between seed mass, body (and bill) size and feeding efficiency. In their model 1, small birds are more efficient than large ones with small seeds and large birds are more efficient than small ones with large seeds (Schluter 1982, Díaz 1990, Soobramoney and Perrin 2007), but in model 2, large birds are more efficient with larger seeds, but both large and small birds are equally efficient with smaller seeds (Pulliam 1985). Every model suggests different degrees of diet overlap between

bird species in the field, with likely implications on species competition and coexistence (Schluter 1982, Pulliam 1985).

The most abundant seed-eating bird species inhabiting the central Monte desert, Argentina, that mainly search for the seeds from the ground (Lopez de Casenave et al. 2008, Milesi et al. 2008) are *Zonotrichia capensis* (Emberizidae), *Poospiza ornata*, *Saltatricula multicolor* and *Diuca diuca* (Thraupidae). They all prefer grass seeds (Cueto et al. 2006, Camín et al. 2015), although *P. ornata* (25%), *Z. capensis* (45%) and *D. diuca* (22%) incorporate a fraction of forb seeds in their diet (Marone et al. 2008). Bird–seed preferences seem to be positively associated with the size of grass seeds in some species (Cueto et al. 2006, Camín et al. 2015), and independent of the composition of seed patches, which suggests that birds have the potential to behave as rational feeders (Marone et al. 2015). Grass-seed specialists prefer starch-rich seeds, and they avoid the phenolic compounds and alkaloids typical of forb seeds (Ríos et al. 2012). Although these results help unveil some causes of seed preferences and consumption in the field, a more comprehensive and systemic approach (i.e. one that tests several plausible causes at the same time) should be used to assess patterns and causes thoroughly.

Here we evaluate the effect of several mechanisms that can affect bird–seed preferences and the composition of the granivorous fraction of their diets simultaneously. The influence of four ‘explanatory variables’ (i.e. seed mass, seed handling time, seed handling efficiency and seed profitability) on seed preferences and diet is weighed to test the hypothesis that seed-eating birds maximise energy intake rates while feeding. We also evaluate whether small and large birds feed more efficiently on seeds of different sizes, and we assess the ecological consequences of the foraging decisions of these organisms.

Methods

Seed species

Birds and seeds tested came from the Ñacuñán Biosphere Reserve (34°03’S, 67°54’W), Mendoza province, Argentina, which is in the central Monte desert and has been effectively excluded from domestic grazing since 1972. The climate is dry and temperate, with hot summers and cold winters. On average, >75% of the annual rainfall occurs during the growing season (October–March; 273 ± 95 (SE) mm, $n = 47$ years). The main habitat type in the reserve is open woodland with dispersed *Prosopis flexuosa* and *Geoffroea decorticans* trees. The shrub stratum is dominated by *Larrea divaricata*, and the herbaceous stratum is mainly composed of perennial grasses and annual forbs (Supporting information).

Seeds offered in the laboratory trials came from six herbaceous plant species that are common in the soil seed bank of the reserve (Pol et al. 2014). Four of them are from perennial C_4 native grasses (*Sporobolus cryptandrus*, *Pappophorum* spp., *Digitaria californica* and *Setaria leucopila*) and the other two are from annual native forbs (*Chenopodium papulosum* and *Parthenium hysterophorus*) (Table 1). The seed-size range

Table 1. Properties of the seeds used in the experiments. Data about seed mass, length and width were taken from Cueto et al. (2006), whereas energy content of seeds was obtained from Ríos et al. (2012). Standard deviations of morphological measurements did not surpass 10% of mean values in any case.

	Mass (mg)	Length (mm)	Width (mm)	Energy (kJ g ⁻¹)
<i>Sporobolus cryptandrus</i>	0.07	0.68	0.40	14.90
<i>Chenopodium papulosum</i>	0.25	0.94	0.82	12.34
<i>Digitaria californica</i>	0.40	1.67	0.98	18.28
<i>Parthenium hysterophorus</i>	0.42	2.45	1.18	23.22
<i>Pappophorum</i> spp. ^a	0.70	1.32	0.47	24.07
<i>Setaria leucopila</i>	0.75	1.18	1.04	7.41

^aA propagule of *Pappophorum* spp. may have 1–4 cariopses of variable mass (0.20 to >1 mg). We report average dimensions and the modal mass of all cariopses in a propagule.

(0.07–0.75 mg) offered was identical to the natural range of herbaceous seeds consumed by the birds in the reserve (Marone et al. 2008). The seeds used account for a high percentage of the granivorous fraction of the bird diets: 84% (*P. ornata*), 68–77% (*Z. capensis*), 59–69% (*S. multicolor*) and 76–79% (*D. diuca*) (Marone et al. 2008, 2017). The grass seeds are protected by glumes and glumellas that surround the round (*S. leucopila*), oval (*S. cryptandrus*) or elongated (*Pappophorum* spp., *D. californica*) cariopses. The kernel of *P. hysterophorus* is surrounded by an achene or cypsela with two membranous glumellas, whereas the kernel of *C. papulosum* is suborbicular and covered by a thin, fragile membranous pericarp. Although the birds used in our trials always dehusk the seeds when feeding, eating the whole grain, most seeds of *S. cryptandrus* and *C. papulosum* lose their seed coats during primary dispersal, arriving at the soil dehusked (L. Marone, pers. obs.), and so, we offered dehusked seeds of *S. cryptandrus* and *C. papulosum* in our experiments. References to large and small seeds in the text correspond to seeds with high and low mass, respectively (Table 1) (Supporting information).

Seed-handling time experiments

We carried out handling-time experiments on *P. ornata*, *Z. capensis*, *S. multicolor* and *D. diuca*, which differ in several body-size measurements (Table 2). Thirty-five individuals (8–10 for each species) were mist-netted in the Ñacuñán Reserve and kept in individual cages (30 × 20 × 20 cm) with a natural photoperiod for one week before the trials were carried out. At the lab, we provided all birds with

commercial seeds (*Setaria italica* or *Phalaris canariensis*) and vitamin-enriched water ad libitum. The experiments for all the combinations of bird per seed species were made during the following 3–4 weeks to prevent captive individuals from becoming used to the laboratory diet (Cueto et al. 2001). After the experiments, we released all the birds in the same area where we caught them.

Before each experiment, each bird was maintained without food for 2–5 h. At the beginning of every trial, we moved one individual to an observational acrylic cage (40 × 40 × 40 cm) in darkness and, after 1 min, the observer turned the light on and left the bird to feed for 10 min. In every trial, there were 50 seeds of one plant species on the ground of the cage. We assigned the order in which seed species were offered randomly, and we did not test the same individual with other seed species during the following 24 h. Bird feeding activity was filmed using a video camera with a chronometer (± 0.1 s), at a velocity of 30 photograms per second. Images were digitalised and assessed using a photogram-by-photogram inspection. Handling time for seeds that disperse with husks was the interval from when the bird picked it up from the ground with its bill until it was peeled and swallowed (Benkman and Pulliam 1988). For seeds that disperse without any structures attached, handling time was the interval from when the seed was picked up until the bird started the head movement to search for another seed. Data were not collected when seeds were not eaten (Benkman and Pulliam 1988). Given that several seeds were usually eaten by the same individual during a trial, handling times were averaged for every individual and seed species. We used these averages to calculate bird species-specific mean handling time ($n =$ number of individuals of a given bird species assessed).

The calculation of seed handling time by the four seed-eating birds allowed us to estimate (a) seed handling efficiency (mg s⁻¹), which is the amount of mass of each seed species incorporated by a given bird species per unit of time and (b) seed profitability (kJ s⁻¹), which is the energy that a bird species gains per unit of time when eating a certain food item. To estimate the profitability values, we used the calculations of the energy per unit of mass (kJ g⁻¹) provided by seeds of every plant species, reported in Ríos et al. (2012). Seed masses used for these estimations were measured on dehusked seeds (Table 1).

Bird–seed preferences and diet

Information on preferences for the six-seed species by the four-bird species comes from the published levels of seed

Table 2. Averages (\pm SE) of three bill dimensions and body mass of four seed-eating bird species of the Monte desert, Argentina. Data from Lopez de Casenave (2001).

	Bill length (mm)	Bill with (mm)	Bill height (mm)	Body mass (g)
<i>Poospiza ornata</i>	9.31 \pm 0.11	5.20 \pm 0.07	5.38 \pm 0.07	12.68 \pm 0.21
<i>Zonotrichia capensis</i>	9.62 \pm 0.04	5.53 \pm 0.02	5.76 \pm 0.03	19.23 \pm 0.13
<i>Saltatricula multicolor</i>	11.21 \pm 0.09	6.79 \pm 0.07	7.26 \pm 0.05	22.41 \pm 0.20
<i>Diuca diuca</i>	11.40 \pm 0.10	7.28 \pm 0.08	7.86 \pm 0.07	25.02 \pm 0.17

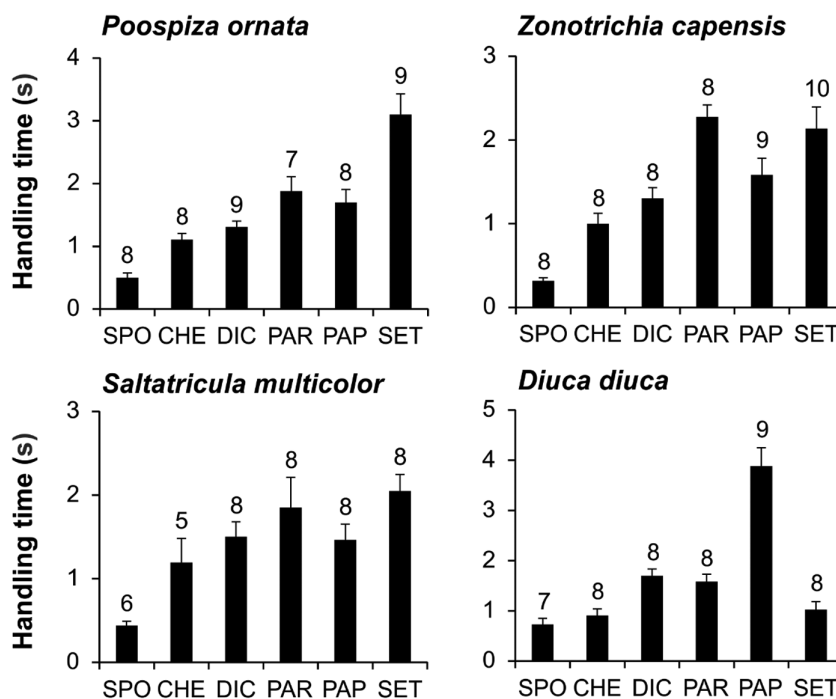


Figure 1. Handling times of four seed-eating bird species of the Monte desert, Argentina, consuming seeds from six different herbaceous species. Values shown are mean + SE. Seeds are ranked in order of increasing mass. Plant-species acronyms: SPO, *Sporobolus cryptandrus*; CHE, *Chenopodium papulosum*; DIC, *Digitaria californica*; PAR, *Parthenium hysterophorus*; PAP, *Pappophorum* spp.; SET, *Setaria leucopila*. The number of birds tested with the seeds of each plant species is shown on the bars. *S. cryptandrus* and *C. papulosum* seeds lose their seed coats during primary dispersal and were offered dehusked in our experiments.

consumption in a choice experiment (Fig. 1 in Cueto et al. 2006). In those experiments, we offered an equal number of seeds (20) of every plant species simultaneously, which were dispersed homogeneously on the experimental arena, avoiding the biases of uncontrolled studies (Díaz 1990, Cueto et al. 2001). Seed preferences were established according to the mean proportion of seeds of each species consumed by each bird species. Field-bird diets in the Ñacuñán Reserve have been already published (Table 2 in Marone et al. 2008) and are expressed as the proportion of the total seed mass eaten by each bird species that corresponds to each of the six plant species evaluated.

Data analysis

Plausible causes of bird–seed preferences and of the granivorous composition of the bird diets were explored by evaluating their relationship with four independent or ‘explanatory’ variables (i.e. seed mass, seed-handling time, seed-handling efficiency, seed profitability) by using generalized linear models (GLMs) with binomial distribution due to preferences and diets expressed as proportions (Crawley 2013). Each bird species was modelled in a separate GLM. Independent variables were standardised to make the estimates of the regression coefficients comparable, directly weighing the effect of each variable on the response. Variable selection was carried out by stepwise regression. The values of some of the independent variables were correlated according to the Spearman ordinal

test: seed mass with seed-handling time in *P. ornata* ($r=0.94$, $p < 0.05$) and seed mass with seed-handling efficiency in *S. multicolor* ($r=0.89$, $p < 0.05$), so we only retained one of the variables in the final models of both preference and diet to avoid problems with multicollinearity. In such cases, the variable with the highest standardised regression coefficient was retained (Montgomery et al. 2021). All statistical calculations were conducted in R with the ‘glm’ function – ‘stats’ base package, and ‘stepAIC’ function – ‘MASS’ package (Venables and Ripley 2002).

Different indicators of feeding efficiency may be used to assess whether birds fit model 1 or 2 for seed consumption: the time taken to deal with a food item (Grant et al. 1976), the number of seeds consumed per unit of time (Grant 1986) or the mass of seeds consumed per unit of time (Schluter 1982, Pulliam 1985). We assessed the way feeding efficiency of different-sized birds varies with small and large seeds using three indicators: handling time, handling efficiency and seed profitability, which made it possible to test the robustness of different indicators when the four bird species ate the smaller (*S. cryptandrus*, *C. papulosum*) or the larger seeds (*Pappophorum* spp., *S. leucopila*). As we were interested in contrasting feeding efficiency with the largest and smallest seeds, the two intermediate-sized seeds (*D. californica*, *P. hysterophorus*) were discarded for this analysis. The averages of each indicator for different bird species were compared with one-way ANOVA. Raw data were log-transformed on some occasions to accomplish ANOVA assumptions. Simple linear

Table 3. Results of generalised linear models with a binomial distribution: multiple regression coefficients and p-values, estimated parameters, standard errors (SE), z-values and p-values for seed preferences of four seed-eating bird species of the Monte desert, Argentina. Values are shown only for variables which were retained in the final models.

	Estimate	SE	z-value	p-value
<i>Poospiza ornata</i> R=0.99; p=0.003				
Intercept	0.13	0.13	0.95	0.340
Seed mass	12.19	1.44	8.47	0.000
Seed profitability	-2.88	0.50	-5.70	0.000
Seed-handling efficiency	-2.36	0.73	-3.25	0.001
<i>Zonotrichia capensis</i> R=0.99; p=0.003				
Intercept	2.16	0.23	9.42	0.000
Seed mass	4.08	1.83	2.23	0.026
Seed profitability	1.31	0.45	2.90	0.004
<i>Saltatricula multicolor</i> R=0.94; p=0.017				
Intercept	-0.12	-0.13	-0.95	0.340
Seed mass	4.39	1.03	4.27	0.000
Seed-handling time	-0.91	0.46	-1.98	0.048
Seed profitability	0.86	0.35	2.44	0.015
<i>Diuca diuca</i> R=0.94; p=0.017				
Intercept	-0.10	0.11	-0.95	0.343
Seed mass	3.66	1.44	2.55	0.011

correlations reported in the text are always Spearman ordinal correlations.

Results

Seed preferences were significantly and positively related to seed mass in all bird species, and this simple relationship showed the highest standardised coefficients in all four models (Table 3; Supporting information). Preferences also associated positively with seed profitability in *Z. capensis* and *S. multicolor* but were negatively correlated with profitability

(and with seed handling efficiency) in *P. ornata* and with seed-handling time in *S. multicolor* (Table 3; Supporting information).

The models with the field-seed diets retained more independent variables than those with preferences in *Z. capensis* and *D. diuca* (Table 4; Supporting information). However, seed mass was related positively (also with the highest standardised coefficients) with bird diets in *P. ornata*, *S. multicolor* and *D. diuca*. Although the multiple regression coefficient of the *Z. capensis* model was the lowest in our analyses, the model retained several independent variables. Remarkably, and opposite to seed preference results, the diet of *Z. capensis*

Table 4. Results of generalised linear models with a binomial distribution: multiple regression coefficients and p-values, estimated parameters, standard errors (SE), z-values and p-values for seed diets of four seed-eating bird species of the Monte desert, Argentina. Values are shown only for variables which were retained in the final models.

	Estimate	SE	z-value	p-value
<i>Poospiza ornata</i> , R=0.94; p=0.017				
Intercept	-2.79	0.17	-16.14	0.000
Seed mass	8.58	1.70	5.05	0.000
Seed profitability	-5.64	0.97	-5.79	0.000
<i>Zonotrichia capensis</i> , R=0.71; p=0.136				
Intercept	-2.91	0.17	-17.49	0.000
Seed-handling efficiency	6.19	1.05	5.90	0.000
Seed mass	-4.60	0.93	-4.96	0.000
Seed profitability	-2.84	0.32	-8.78	0.000
Seed-handling time	1.07	0.42	2.54	0.011
<i>Saltatricula multicolor</i> , R=0.94; p=0.017				
Intercept	-2.99	0.09	-34.10	0.000
Seed mass	5.38	0.69	7.75	0.000
Seed-handling time	-3.96	0.25	-15.74	0.000
Seed profitability	0.96	0.30	3.21	0.001
<i>Diuca diuca</i> , R=0.99; p < 0.001				
Intercept	-3.40	0.24	-14.17	0.000
Seed mass	15.73	2.81	5.61	0.000
Seed-handling efficiency	-10.88	2.06	-5.28	0.000
Seed-handling time	-9.68	1.92	-5.04	0.000
Seed profitability	-1.05	0.22	-4.77	0.000

was negatively related to both seed mass (the strongest relationship) and profitability. Diet and seed profitability were also negatively related in *P. ornata* and *D. diuca*. Only *S. multicolor* retained the positive relationship in its diet with profitability observed with seed preferences. In the field, *S. multicolor* and *D. diuca* consumed more of the seeds with less handling times and *D. diuca* also consumed the seeds that provide more mass per unit of time (Table 4; Supporting information).

Seed mass tended to be positively correlated with handling time in *P. ornata* ($r=0.94$, $p=0.005$, $n=6$), *Z. capensis* ($r=0.81$, $p=0.05$), *S. multicolor* ($r=0.83$, $p=0.04$) and *D. diuca* ($r=0.60$, $p=0.21$). Seed-handling time for the same seed species usually changed moderately between the bird species, with some notable exceptions (these comparisons were not assessed statistically to avoid making multiple inferences; see below) (Fig. 1). For example, the smallest bird (*P. ornata*) was not the fastest with the smallest seed (*S. cryptandrus*), but it was the slowest with the largest seed (*S. leucopila*), whereas the largest bird (*D. diuca*) was the slowest not only with the tiny *S. cryptandrus* seeds but also with one of the larger seeds (*Pappophorum* spp.) (Fig. 1).

There was evidence neither of small birds handling the smaller seeds significantly more efficiently (seed-handling time $F_{3,57}=0.490$, $p=0.69$; handling efficiency $F_{3,57}=0.978$, $p=0.41$; profitability $F_{3,57}=1.398$, $p=0.25$) nor of the large birds handling the larger seeds more efficiently (seed-handling time $F_{3,68}=2.244$, $p=0.09$; handling efficiency

$F_{3,68}=1.088$, $p=0.36$; profitability $F_{3,68}=0.730$, $p=0.54$) (Fig. 2). Birds with small and large bills fed on seeds in each group with similar efficiency measured by any of the indicators and, therefore, they did not fit the models 1 or 2 of Grant et al. (1976).

Discussion

The empirical variance in our data was usually greater than that predicted by the binomial models (i.e. results often exhibited over dispersion). However, and despite the low number of seed species tested, over dispersion was especially restrictive in only one case (*Zonotrichia capensis* diet). Other analytical challenges of GLMs like multicollinearity or the correct assignment of relative weights to the estimates of each independent variable included in the models could be solved, but over dispersion remained and quasi-binomial distributions produced some unsatisfactory results. Therefore, we opted for robustness as a criterion for maintaining the current analyses and outputs (Marone et al. 2019). The main results of the GLMs with binomial distribution were consistent with those of simple correlation analyses (Supporting information) as well as multiple regression analyses. Furthermore, and probably most important, some of the strongest relationships reported here had been previously found using independent data sets, like the positive association of seed mass with seed preferences (Camín et al. 2015) and seed diet

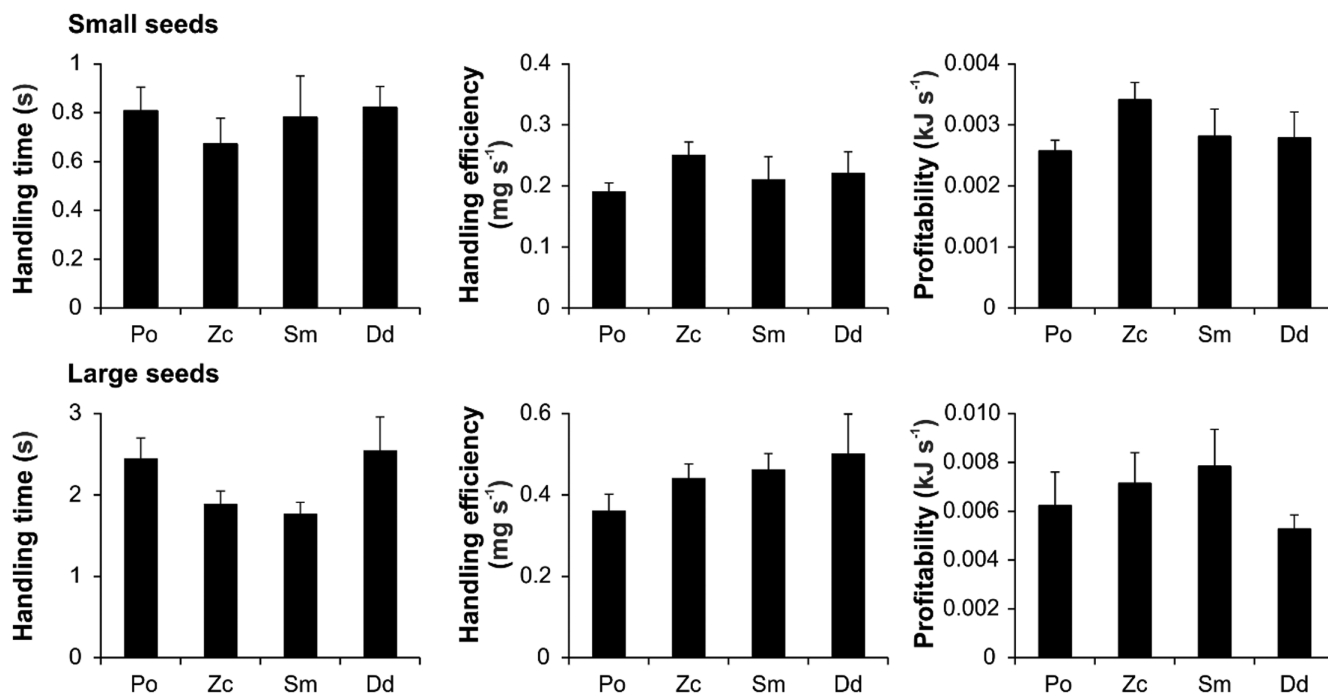


Figure 2. Feeding efficiency (measured as handling time, handling efficiency and profitability) of four seed-eating bird species of the Monte desert, Argentina, consuming the smallest seeds (*Sporobolus cryptandrus* and *Chenopodium papulosum*; above), and the largest seeds (*Pappophorum* spp. and *Setaria leucopila*; below). Values shown are mean + SE. Bird species are ranked in order of increasing mass. Bird-species acronyms: Po (*Poospiza ornata*), Zc (*Zonotrichia capensis*), Sm (*Saltatricula multicolor*), Dd (*Diuca diuca*). Comparisons of small-seed consumption were based on $n=58$, and of large-seed consumption on $n=69$; see Results).

(Marone et al. 2017) for the larger birds. Despite some degree of over dispersion, the main results of the binomial models proved highly robust within our research programme.

Four bird species belonging to two different families, with different body masses (12.7–25.0 g), preferred the largest seeds within the natural seed-size range. The two intermediate-sized birds (*Z. capensis*, *S. multicolor*) also preferred the seeds with more energy reward per unit of time. Preferences, on the contrary, were only occasionally associated with seed-handling time or efficiency. In previous experiments with eight native grass seeds, preferences were also positively and significantly related to seed mass in *S. multicolor* ($r=0.97$, $p < 0.001$) and *D. diuca* ($r=0.92$, $p=0.001$), and they showed a positive although non-significant relationship in *Z. capensis* ($r=0.35$, $p=0.40$) (Camín et al. 2015). Mammals, birds and some ants that consume seeds from plants of the herbaceous stratum often prefer the larger seeds (Wang and Chen 2009, Pirk and Lopez de Casenave 2010, Radtke 2011).

Bird species prefer the largest seeds despite it taking more time to handle them: they did not optimise their energy intake by selecting the seeds that they can process faster. The selection of seeds that are difficult to handle is not rare in nature (Pulliam 1985, Soobramoney and Perrin 2007) since complex propagules requiring longer handling times for dehusking are typical of some normally preferred large seeds (Benkman and Pulliam 1988, Radtke 2011). For example, *D. diuca* delays more than any other species in handling the tiny *S. cryptandrus* seeds, whereas it handles one of the larger seeds (*S. leucopila*) the fastest, as was expected according to the hypothesis that birds with large bills will manage the small seeds inefficiently and the large ones efficiently. Unexpectedly, however, *D. diuca* uses twice the time employed by any other species to handle the other preferred large seed (*Pappophorum* spp.). This was because *D. diuca* only makes $9.6 (\pm 2.4, \text{SE})$ mandibulations per second, half the number made by the other large bird (*S. multicolor*; 18.8 ± 3.6) when handling *Pappophorum* spp. seeds. The average number of mandibulations needed to dehusk a kernel (van

der Meij and Bout 2004) or the maximum number a bird can make per unit of time determines the handling time of seeds with intricate propagules for organisms that dehusk the seeds before eating them. This behaviour can affect handling times independently of dehusked seed mass, blurring otherwise linear relationships between these variables (Pulliam 1985, Carrillo et al. 2007, Soobramoney and Perrin 2007).

Our results suggest that only two bird species (*Z. capensis*, *S. multicolor*) maximise energy intake rates in the lab, but this result requires a broader assessment. Apart from certain contingencies in most local studies, such as the existence of some preferred large seeds of low energy content, e.g. *Dicantelium angustifolium* (DiMiceli et al. 2007), *Echinochloa frumentacea* (Soobramoney and Perrin 2007) or *S. leucopila* (in this study), the birds that prefer the larger seeds could, on average, be eating the most profitable seeds: seed mass may often be an empirical indicator or proxy of energy content (Pulliam 1985). This could explain why the large seed of *S. leucopila* is preferred (Cueto et al. 2006) and is selected in the field (Marone et al. 2008) by the four-bird species examined here, even though it has the lowest energy content (7.41 kJ g^{-1} against a mean of 18.56 kJ g^{-1} of the other five seeds; Table 1). If this atypical seed (in terms of its mass–energy relationship) had not been included in our analyses, the seed mass and energy content of the remaining seeds would have correlated positively and significantly ($r=0.99$, $p < 0.001$, $n=5$). Among all the most common Monte grasses, including *S. leucopila*, the seed mass and energy content also correlated significantly ($r=0.83$, $p=0.01$, $n=8$; Ríos et al. 2012). This does not mean that in our experiments all bird species preferred the most profitable seeds: model outputs do not support that hypothesis in two cases. We suggest notwithstanding that the preference of seeds according to their size within the natural seed-size range may be an evolutionary strategy that, on average, may render a long-term positive outcome in terms of profitability because few plant species will have large seeds of low profitability (Pulliam 1985). In our study, for example, when the four-bird species eat the

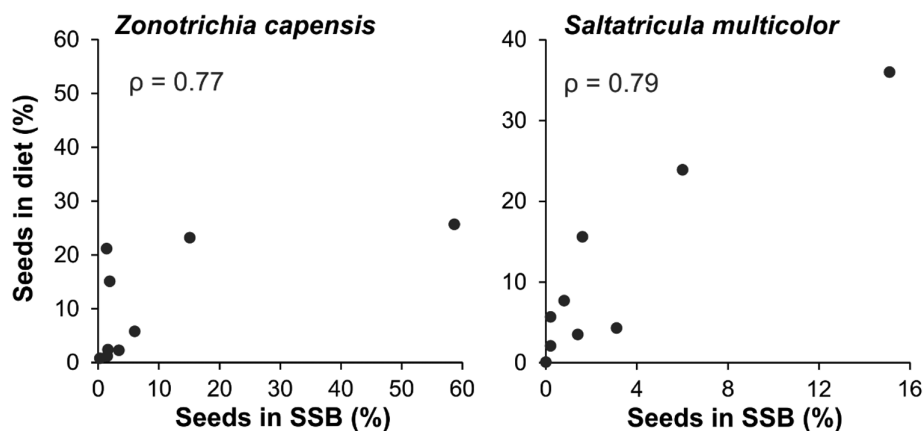


Figure 3. Relationship between seed availability in the soil seed bank (SSB) and in the field diet of *Zonotrichia capensis* and *Saltatricula multicolor*, seed-eating bird species of the Monte desert, Argentina. Percentages in the soil and in the diet come from Marone et al. (2008, Table 2, 3).

largest seeds, they obtain more than twice as much energy per unit of time, on average, than when they eat the smallest seeds (Fig. 2).

The field-diet composition of each bird species does not associate with a unique joint variable, although three out of the four species consume the seeds according to their mass (positively) and profitability (negatively). Both the preferences and diets of *P. ornata* and *S. multicolor* are related to the main 'explanatory' variables in a similar way, which was expected since, for example, *S. multicolor* is a stereotyped seedeater (Camín et al. 2015, Marone et al. 2017). By contrast, *Z. capensis* prefers seeds according to their mass and energy reward but consumes them in the field in an opposite way, which was also expected because *Z. capensis* has the most flexible feeding behaviour of the seed-eating birds of the central Monte desert (Cueto et al. 2013, Marone et al. 2017).

Even though some general patterns exist on the effect of seed mass on seed diet, the more complex feeding behaviour of birds in realistic situations was expected because other factors intervene in the field. For example, predation pressure on adult birds might shape flexible feeding decisions like gathering most of the suitable seeds that the bird encounters rather than being highly selective (Willson and Harmeson 1973). In such cases, differences in relative seed availability may shape the diet of a flexible consumer, keeping it away from its preferences (Desmond et al. 2008, Eraud et al. 2015) and eventually promoting negative relations of seed diet with profitability like those observed here.

When the relative abundance of all grass and forb seeds in the Monte soil seed bank is considered, bird species do not consume them accordingly (Fig. 1 in Marone et al. 2008). The presence of several abundant seed species in the soil that the birds avoid, prefer less or barely eat deters any correlations (Pulliam 1985). However, if only the nine most consumed seed species are included in the analyses, then diet composition follows seed availability or the abundance of seeds that could be eaten effectively (Cueto et al. 2013) in two species: *Z. capensis* ($r=0.77$, $p=0.015$) and *S. multicolor* ($r=0.79$, $p=0.010$) (those seeds account for 98% of *Z. capensis* diet, and 91% of *S. multicolor* diet; Marone et al. 2008) (Fig. 3). *Zonotrichia capensis* is an expansive feeding specialist, i.e. a species that feeds on preferred seeds until they fall below some threshold value when the bird begins to include less preferred or alternative food types (Heller 1980, Camín et al. 2015), that consumes both grass and forb seeds in the field (Marone et al. 2017), and *S. multicolor* is a grass-seed specialist (Marone et al. 2017) that consumes the preferred grass seeds according to field availability. Although feeding flexibility (i.e. a context-dependent behaviour sensu Marone et al. 2015) appeared to be 'opportunism', it occurred within a restricted range of attractive seeds and therefore it should not be considered as genuine opportunism.

The birds do not fit any of the models of feeding efficiency of Grant et al. (1976) when confronted with natural seeds. The four-bird species show similar handling time, handling

efficiency and profitability with the smaller and larger seeds, separately. The pattern seems to be reliable since the three indicators of feeding efficiency behaved robustly in all the comparisons. The feeding choice of large bird species like *D. diuca*, that consume a high proportion of large seeds in the field compared to small birds (Marone et al. 2008), should not then be ascribed to a higher feeding efficiency of the larger birds when eating the larger seeds but to other causes (Ríos et al. 2012). For example, as noted above, the strong bill of *D. diuca* could be especially suitable and inadequate, respectively, when dealing with the larger and smaller seeds. The shared preferences of all bird species for the larger seeds, as well as the similar feeding efficiency that large and small birds show for seeds of the same size group, constitute unfavourable evidence for resource partitioning as a mechanism of species coexistence in the seed-eating birds of the central Monte desert (Pulliam 1985).

There was a general attraction of birds for the larger natural seeds in the lab and in the field, which suggests that some morphological seed traits are important in determining seed choices (Díaz 1990, 1996). The partially flexible foraging behaviour of some bird species results in them also consuming seeds according to availability in nature, although within a restricted group of attractive seeds. Bird foraging behaviour could eventually have top-down community effects by changing the relative proportion of seed species in the soil seed bank, especially in disturbed habitats or during lean periods (Marone et al. 2008). Birds' preferences for the larger natural seeds, which are frequently profitable seeds, may be common in floristic communities around the world, suggesting that animals with those preferences are, on average and through the evolutionary time, maximising their energy reward. At the same time, such preferences can explain the pervasive bottom-up effect provoked by the reduction of large seeds under continuous cattle grazing on both the behaviour (i.e. diet switching; Marone et al. 2017) and the abundance of seed-eating birds in the central Monte desert (Zarco et al. 2019, Sagario et al. 2020).

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Author contributions

Luis Marone: Conceptualization (lead). **Victor Cueto:** Conceptualization (equal). **Javier Lopez de Casenave:** Conceptualization (equal). **Agustín Zarco:** Conceptualization (supporting). **Sergio Camín:** Conceptualization (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.0k6djhb1n>> (Marone et al. 2021).

Supporting information

Any supporting information associated with this article is available from the online version.

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