ARTICLE

Context-dependent foraging by seed-eating birds does not necessarily mean low ecological predictability

L. Marone, S.R. Camín, and V.R. Cueto

Abstract: Flexibility of foraging behaviour affects our capacity to predict ecological outputs such as population responses to habitat change. Some birds forage following rules of absolute value of the food item (i.e., absolute valuation). Their realized diet is strongly correlated with the profitability of the food item and it is predictable. Consumers, however, do not always follow absolute rules. Opportunistic foragers adjust food consumption based on the availability of the food item. Their diet is still predictable but more elusive. Relativistic or context-dependent foragers change the ranks of food preferences depending on the presence of alternative food options in the choice set. Predicting their contingent diet is particularly difficult. We tested if the context of seed availability affects foraging decisions of three seed-eating bird species (the Rufous-collared Sparrow (*Zonotrichia capensis* (Statius Muller, 1776)), the Many-colored Chaco Finch (*Saltatricula multicolor* (Burmeister, 1860)), and the Common Diuca Finch (*Diuca diuca* (Molina, 1782))) using choice experiments aimed at detecting if seed preferences for two types of target seeds changed according to context. Birds showed very similar rankings of preferences for target seeds; however, preferences for attractive food items were not fixed but often increased in less valuable contexts. Although results imply some degree of context-dependent behaviour, predictability of bird diet was preserved because the ranking of preferences remained mostly unchanged between contexts (and among bird species), and the higher consumption of target grass seeds in a less attractive context was widely expected from the intrinsic properties of the seeds.

Key words: context dependence, ecological predictability, environmental change, feeding experiments, rational food choice.

Résumé : La souplesse du comportement d'approvisionnement a une incidence sur la capacité de prédire des conséquences écologiques telles que les réactions d'une population aux modifications de l'habitat. Certains oiseaux s'approvisionnent en suivant des règles basées sur la valeur absolue de l'aliment. Leur alimentation réelle est fortement corrélée à la profitabilité de l'aliment et est prévisible. Toutefois, les consommateurs n'observent pas toujours des règles absolues. Les animaux opportunistes ajustent leur consommation de nourriture en fonction de la disponibilité de l'aliment. Leur régime alimentaire demeure prévisible, mais plus difficile à définir. Les animaux relativistes ou dépendants du contexte changent le classement des aliments qu'ils préfèrent selon la présence d'autres options d'aliments parmi les choix possibles. Il est particulièrement difficile de prédire leur régime alimentaire. Nous avons vérifié si le contexte de disponibilité de graines avait une incidence sur les décisions d'approvisionnement de trois espèces d'oiseaux granivores (le bruant chingolo (*Zonotrichia capensis* (Statius Muller, 1776)), le saltatricule du chaco (*Saltatricula multicolor* (Burmeister, 1860)) et le diuca gris (*Diuca diuca* (Molina, 1782))) avec des expériences de sélection ayant pour but de déterminer si les préférences pour deux types de graines cibles changeaient selon le contexte. Les oiseaux présentaient des classements de préférence des graines cibles très semblables. Cependant, la préférence d'aliments très attrayants n'était pas fixée, augmentant souvent dans des contextes de moins grande valeur. Si les résultats indiquent un certain degré de dépendance du comportement sur le contexte, la prévisibilité du régime alimentaire des oiseaux était conservée parce que le classement des préférences demeurait principalement inchangé d'un contexte à l'autre (et d'une espèce d'oiseau à l'autre), et qu'une consommation plus élevée de graines cibles dans un contexte moins attrayant était largement prévisible à la lumière des propriétés intrinsèques des graines. [Traduit par la Rédaction]

Mots-clés : dépendance du contexte, prévisibilité écologique, modification du milieu, expériences d'alimentation, sélection rationnelle d'aliments.

Introduction

Classical models of animal foraging assume that consumers are economically rational because they make choices based on the absolute values of foods (i.e., absolute valuation), independent of the type and number of other food alternatives available (Stephens and Krebs 1986). An ecological corollary of absolute valuation is that preferences are consistent across different environmental con- texts, a concept encapsulated in two major principles (Latty and Beekman 2011): transitivity and independence of irrelevant alternatives (IIA). Transitivity is the idea that animal preferences show a consistent, internally coherent ranking order, often associated with the intrinsic profitability of the food option (Shafir 1994). IIA is the principle by which the preference for a target option should not be increased when the consumer faces other options of "lesser

Table 1. Main characteristics of rational, opportunistic, and relativistic food-choice behaviours.

Choice type	Description	Selection key	Selection type	Type of effect
Rational	Organisms assign absolute utilities to food options	Profitability	Absolute	Direct. Option profitability on food choice
Opportunistic	Organisms adjust food choice according to local availability of food options	Target food abundance	Target-dependent	Direct. Target food abundance on food choice
Relativistic	Organisms consume a target food or its competitor according to the presence of a third food option (decoy)	Presence and absence of decoy food options	Context-dependent	Indirect. Context characteristics on food choice

value" in the choice set (Luce 1959; Bateson et al. 2003). Absolute valuation and context independence are violated to some degree by at least two types of organisms: (1) opportunistic or target-dependent foragers that do not employ absolute valuation but adjust the consumption of different target food options based on their availability in the field and (2) relativistic or context-dependent foragers that change the rank of preference between food options (and, incidentally, their diet) depending on the presence of alternative food options in the choice set (Table 1).

In a broad sense, changing environments are the contexts to which organisms often respond through behaviour (Gordon 2011). A species of bird forages on grass seeds in an arid scrubland when some areas begin to be exploited by cattle, which result in a decrease in availability of grass seeds. As a result, the bird changes its behaviour in response to the new condition, i.e., it changes its diet by incorporating forb seeds. The response would be opportunistic (Table 1) if the bird chooses forb seeds according to their "new" (from the cognitive perspective of the consumer) abundances, but it would be context-dependent (Table 1) if the bird changes its previous preferences for seed options A and B because of the appearance of a new seed species (C) as a consequence of intense grazing.

While both rational and irrational consumers may evolutionarily maximize expected gains (Waksberg et al. 2009), their behavioural differences have particular ecological consequences. Rational choosers usually have specialized diets, feeding primarily on a few preferred food resources, are more efficient when foraging on their preferred foods (Terraube and Arroyo 2011), and suffer more from habitat disturbance than species capable of consuming a wider range of food resources (Ondine et al. 2009). By contrast, opportunistic consumers have more generalized diets because they eat less-preferred food items when preferred ones become scarcer or spacer (Levey et al. 1984; Cueto et al. 2006), have access to a wider and more abundant resource base, and are capable of facing variable (Egan and Funk 2006) or disturbed environments (Sol et al. 2012). This black-or-white scheme is, however, an oversimplification. In practice there is a continuum from specialists to generalists within and between species (Egan and Funk 2006).

The ecological consequences of context dependence are more elusive. Context dependence hinders the development of general ecological theory because under such circumstances hard-won insights about natural history may become radically local or contingent (Werner and Peacor 2003; Noda 2004; Heithaus et al. 2009; Gordon 2011). A plausible approach to study the potential diet of a context-dependent organism is to abstract the whole consumer–resource system into component parts, to develop an understanding of the interactions between them (e.g., assessing changes in food preferences across contexts), and then reassemble the system. Conceivably, however, the number of pairwise interactions to be considered when exploring the potential diet of an organism could be so high as to make the approach unmanageable (Werner and Peacor 2003).

Notwithstanding the logical virtues of these abstract arguments on the implications of context-dependent behaviour on ecological

predictability, the extent to which the former inhibits predictive capability is a matter of empirical research. Let us suppose that we are facing the question "how will animal diet change as food items are added or deleted from a precise environmental context"? When animals assign absolute utilities to food options, we could expect maximum ecological predictability based on well-founded hypotheses regarding animal food preferences and general qualitative knowledge of available resources. When animal choice is opportunistic, we can also expect reasonable predictability based on seed preferences (and the limits of foraging flexibility) of the consumer and a more detailed knowledge of the quantitative composition and dynamics of the resource base. Finally, when animals are radically context-dependent, diet predictability might certainly decline (Gordon 2011). Nevertheless, the effect of changes in the context of food availability on animal behaviour should be carefully established through experimentation before drawing conclusions regarding the contingency of ecological outputs.

Granivorous bird species inhabiting the central Monte Desert of Argentina consume high proportions of grass seeds: 100%, 78%, and 55% of the seeds eaten by Many-colored Chaco Finches (*Saltatricula multicolor* (Burmeister, 1860)), Common Diuca Finches (*Diuca diuca* (Molina, 1782)), and Rufous-collared Sparrows (*Zonotrichia capensis* (Statius Muller, 1776)), respectively (Marone et al. 1998, 2008). These birds also prefer grass seeds, although *Z. capensis* shows a wider range of preferences that includes several forb seeds (Cueto et al. 2006) and the proportion of seed species in its diet correlates positively with the proportion of seed species available in the soil seed bank (Cueto et al. 2001). The evidence suggests that *S. multicolor* is a grass specialist and *Z. capensis* is an opportunistic consumer, whereas *D. diuca* is somewhere in between. This natural-history knowledge may substantiate useful predictions about the response of bird populations to disturbances, like grazing, that reduces the density of grass plants and the availability of grass seeds in the Monte desert (Pol et al. 2014). To date, however, we do not know to what extent foraging choices of those bird species are context-dependent. Consequently, predictions remain uncertain.

Here we assess the hypothesis that *S. multicolor*, *D. diuca*, and *Z. capensis* do not develop meaningful context-dependent food choices. That is, the context of seed availability in the microhabitat where they forage does not affect their seed preferences. Specifically, we tested two predictions of the hypothesis: (1) bird preferences for different target seed species show a consistent and internally coherent ranking order across two contrasting, experimentally manipulated, choice sets (an expectation akin to transitivity), and (2) preferences for target seeds do not change when new options of "lesser value" are added to the choice set (a prediction akin to the IIA principle).

Materials and methods

Bird species and environment

The three bird species used in feeding experiments were *Z. capensis* (body mass 18 g), *S. multicolor* (body mass 22 g), and

Table 2. Composition of target seeds and context seeds in homogeneous and mixed seed trials.

Type of experiment	Target seed	Context seed decoy
Homogeneous grasses	Streambed bristlegrass, *Setaria leucopila* (0.75) Pappusgrass, *Pappophorum* spp. (0.35) Arizona cottontop, *Digitaria californica* (0.40) Sand dropseed, *Sporobolus cryptandrus* (0.07)	*Aristida mendocina* Phil. (0.46) *Trichloris crinita* (Lag.) Parodi (0.23) Peruvian feather grass, *Stipa ichu* (Ruiz & Pav.) Kunth (0.12) Lehmann's lovegrass, *Eragrostis lehmanniana* Nees (0.07)
Mixed grasses (to be compared with homogeneous grasses)	*Setaria leucopila* *Pappophorum* spp. *Digitaria californica* *Sporobolus cryptandrus*	*Parthenium hysterophorus* *Chenopodium papulosum* *Phacelia artemisioides* *Plantago patagonica*
Homogeneous forbs	Santa Maria feverfew, *Parthenium hysterophorus* (0.42) *Chenopodium papulosum* (0.25) *Phacelia artemisioides* (0.50) Woolly Indianwheat, *Plantago patagonica* (0.65)	*Sphaeralcea miniata* (Cav.) Spach (0.20) Stickseed, *Lappula redowskii* (Hornem.) Greene (0.40) *Glandularia mendocina* (Phil.) Covas & Schnack (0.40) Species of *Descurainia* Webb & Berthel. (0.07)
Mixed forbs (to be compared with homogeneous forbs)	*Parthenium hysterophorus* *Chenopodium papulosum* *Phacelia artemisioides* *Plantago patagonica*	*Setaria leucopila* *Pappophorum* spp. *Digitaria californica* *Sporobolus cryptandrus*

Note: We made pairwise comparisons of consumption of target seeds between homogeneous and mixed seed experiments to assess if seed preferences change when the context of seed availability was experimentally manipulated. Species-specific seed masses (mg) are indicated in parentheses. Mixed seed experiments were initially reported by Cueto et al. (2006).

D. diuca (body mass 25 g). All three species were formerly classified in the family Emberizidae, but *S. multicolor* and *D. diuca* are now placed in the family Thraupidae (Burns et al. 2014). All of them 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 in the Biosphere Reserve of Ñacuñán, central Monte Desert, Argentina (34°03′S, 67°54′W). The general habitat in the reserve consists of scattered algarrobo dulce (*Prosopis flexuosa* DC.) and chañar (*Geoffroea decorticans* (Gillies ex Hook. & Arn) Burkart.) trees within a scrub matrix of jarilla (*Larrea divaricata* Cav.). The herbaceous stratum is dominated by perennial grasses (genera *Setaria* P. Beauv. (bristle-grass), *Trichloris* E. Fourn. Ex Benth., *Pappophorum* Schreb. (pappus-grass), *Digitaria* Haller (crabgrass), *Aristida* L. (threeawn), *Sporobolus* R. Br. (dropseed)) and, secondarily, annual or biennial forbs (genera *Chenopodium* L. (goosefoot), *Sphaeralcea* A. St.-Hil. (globemallow), *Glandularia* J.F. Gmel. (mock vervain), *Parthenium* L. (feverfew), *Phacelia* Juss. (scorpion-weed)) (Marone 1991). 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).

Experimental design

We used multiple-choice feeding experiments to detect the level of seed consumption by the three bird species (Cueto et al. 2001). In every trial, birds faced simultaneously eight seed species, four "target" seeds and four "context" seeds (Table 2). To test the prediction that bird preferences for target seeds were consistent across contexts, we compared the ranking order of consumption of the four target seeds (grasses or forbs) in two sets of contrasting experiments: homogeneous grasses versus mixed seeds and homogeneous forbs versus mixed seeds (Table 2). The consumption of grass and forb seeds in the mixed experiments was the same as originally reported by Cueto et al. (2006). In the homogeneous trials, we assessed percent seed consumption of target seeds by every bird species when they were mixed with other seeds of the same functional group (i.e., all grasses or all forbs). In the mixed trials, percent seed consumption of target seeds of one functional group (e.g., grasses) was assessed when mixed with seeds of the other functional group (i.e., forbs) (Table 2).

Experiments followed the protocol of choice trials described by Cueto et al. (2001, 2006). Birds tested were kept in individual cages (45 cm × 30 cm × 30 cm) for no more than 30 days in an indoor room with an artificial photoperiod (12 h light : 12 h dark). We provided all birds with commercial seeds (Italian bristlegrass,

Setaria italica (L.) P. Beauv.) and vitamin-enriched water ad libitum. After the trials, we released all birds in the same area where they were caught. Seeds employed are frequent in the soil seed bank of Ñacuñán (Marone and Horno 1997) and were collected in the same area where we had caught the birds. In every experiment, we placed an individual bird in an observational cage made of transparent acrylic (40 cm × 40 cm × 40 cm), with an acrylic floor and a single perch. Previous to the trial, all birds were food-deprived for a period of 2–5 h. The heaviest species (*D. diuca*) and the tame, more reluctant to feed species (*S. multicolor*) were food-deprived for a longer period.

In the homogeneous trials, we scattered randomly 50 seeds of each plant species (Table 2) on the 0.16 m² cage floor (400 seeds in total, which is a similar seed density to that found in the soil seed bank of Ñacuñán; see Marone et al. 2008, Pol et al. 2014). Birds were placed in the cage in darkness and, 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 consumed by each species (consumed seeds = initial seeds − remaining seeds). We randomized the order in which each experiment was carried out. In the mixed trials, Cueto et al. (2006) had offered 20 seeds of every plant species (Table 2; 160 seeds in total) and the birds were allowed to feed for 5 min. Although the birds faced 400 seeds in the homogeneous trials compared with only 120 seeds in the mixed trails (Cueto et al. 2006), a similar number of offered seeds per unit of time was maintained (i.e., 40 seeds/min in the homogeneous trials and 32 seeds/min in the mixed trials). All other experimental decisions were identical in both sets of trials.
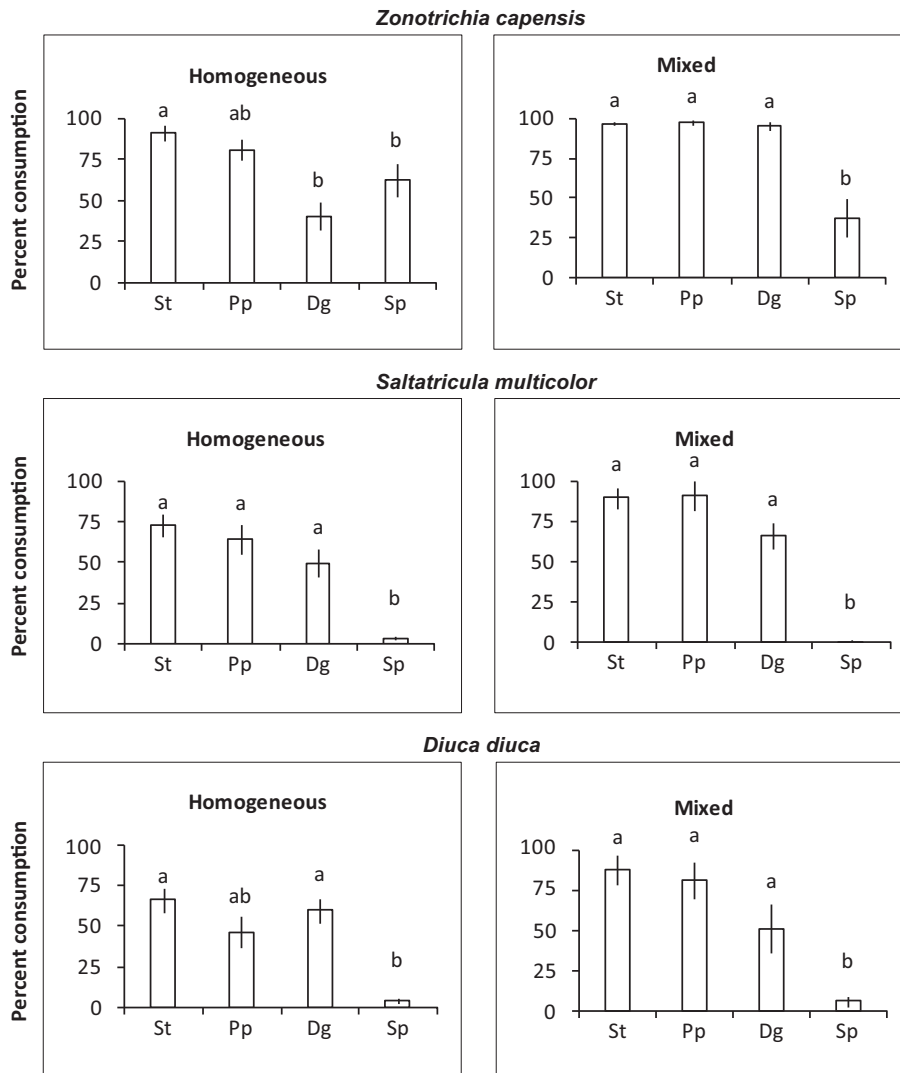
Fieldwork and laboratory work complied with the requirements of the "Guidelines to the use of wild birds in research" (Fair et al. 2010) and was carried out with permission of the Dirección de Recursos Naturales del Gobierno de la Provincia de Mendoza (resolutions 956/10, 486/11, and 654/13).

Data analysis

Consistency of ranking order of preferences (transitivity)

Pairwise comparison of the proportion of target seeds consumed in the homogeneous and mixed trials would provide evidence of context-dependent foraging if (*i*) species A is more consumed than species B in one trial, but species B is more consumed than species A in the other trial (strong context-dependent effect), and (*ii*) species A is more consumed than species B in one trial, but consumption of species A and species B does not differ in

Fig. 1. Percent consumption of target grass seeds in homogeneous and mixed experiments by three sparrow species (Rufous-collared Sparrow, *Zonotrichia capensis*; Many-colored Chaco Finch, *Saltatricula multicolor*; Common Diuca Finch, *Diuca diuca*) of the central Monte Desert, Argentina. Error bars indicate ±1 SE. Species of target seeds are the streambed bristlegrass (*Setaria leucopila*) (St), species of pappusgrass (genus *Pappophorum*) (Pp), Arizona cottontop (*Digitaria californica*) (Dg), and sand dropseed (*Sporobolus cryptandrus*) (Sp). Bars sharing the same letter are not significantly different (multiple-comparison analysis of ranked data, *P* < 0.05). The consumption of grass seeds in mixed experiments was originally reported by Cueto et al. (2006).

the other trial (weak context-dependent effect). Higher consumption of species A than species B, or equal consumption of both species in both trials are evidence of context independence, which suggests that birds have absolute or stereotyped foraging behaviour. Following Roa (1992) and Lockwood (1998), we analyzed data from the multiple-choice experiments with Friedman's test (Zar 1996), because treatments (i.e., different food options being offered simultaneously) were not independent (Roa 1992). A multiple-comparison analysis of ranked data (Zar 1996) was used to ascertain differences in the consumption of target seeds separately in the homogeneous and mixed trials to compare the ranking of preferences. When paired preferences for two seed species remained the same in the homogeneous and mixed trials, we considered transitivity to be mostly preserved for that contrast. Differences were statistically significant when *P* < 0.05.

Effect of a lesser value option on the consumption of target seeds (IIA)

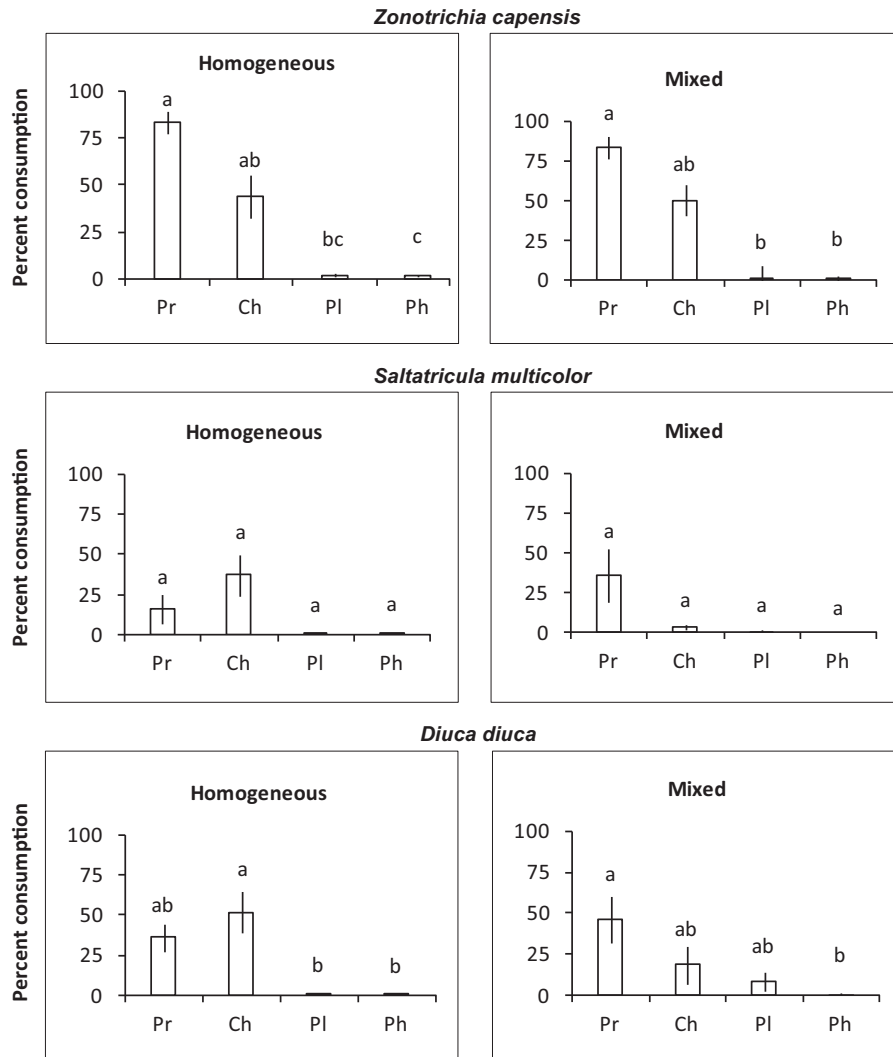We compared the mean percent consumption of the attractive target grass seeds in the homogeneous and mixed trials to deter-mine whether the IIA was violated (i.e., whether the consumption of target seeds was higher in the mixed trial, where target seeds were offered within an unfavourable context). We did not use statistical hypotheses testing to avoid "simultaneous inferences" because the same raw data were used to test for transitivity (Rice 1989).

Results

Consistency of ranking order of preferences (transitivity)

Consumption of seed species by *Z. capensis* differed in the homogeneous trials (grasses: Friedman test, $\chi^2 = 45.89$, $P < 0.001$, $n = 13$ individuals tested; forbs: $\chi^2 = 57.21$, $P < 0.001$, $n = 13$) and the mixed trials ($\chi^2 = 70.0$, $P < 0.001$, $n = 14$). Consumption of seed species by *D. diuca* also differed in the homogeneous trials (grasses: $\chi^2 = 46.05$, $P < 0.001$, $n = 13$; forbs: $\chi^2 = 26.2$, $P < 0.001$, $n = 10$) and the mixed trials ($\chi^2 = 39.2$, $P < 0.001$, $n = 7$). Consumption of seed species by *S. multicolor* also differed in the homogeneous trials (grasses: $\chi^2 = 64.61$, $P < 0.001$, $n = 15$; forbs: $\chi^2 = 20.22$, $P < 0.01$, $n = 11$) and the mixed trials ($\chi^2 = 39.7$, $P < 0.001$, $n = 7$). Regarding a

Fig. 2. Percent consumption of target forb seeds in homogeneous and mixed experiments by three sparrow species (Rufous-collared Sparrow, *Zonotrichia capensis*; Many-colored Chaco Finch, *Saltatricula multicolor*; Common Diuca Finch, *Diuca diuca*) of the central Monte Desert, Argentina. Error bars indicate ±1 SE. Species of target seeds are the Santa Maria feverfew (*Parthenium hysterophorus* L.) (Pr), *Chenopodium papulosum* Moq. (Ch), woolly Indianwheat (*Plantago patagonica* Jacq.) (Pl), and *Phacelia artemisioides* Griseb. (Ph). Bars sharing the same letter are not significantly different (multiple-comparison analysis of ranked data, *P* < 0.05). The consumption of forb seeds in mixed experiments was originally reported by Cueto et al. (2006).

posteriori multiple-comparison tests, all 12 pairwise contrasts of target seed species remained without changes in both kinds of trials in *S. multicolor* (Figs. 1, 2), whereas *D. diuca* (four changes) and *Z. capensis* (four changes) showed only changes that involved weak context-dependent behaviour. In other words, preferences were not reversed in any case, but consumption trends for *Z. capensis* were not totally preserved in the contrasts of *Setaria–Digitaria*, *Pappophorum–Sporobolus*, *Digitaria–Sporobolus* (Fig. 1), and *Chenopodium–Phacelia* (Fig. 2), and consumption trends for *D. diuca* were not totally preserved in the contrasts of *Pappophorum–Sporobolus* (Fig. 1), *Parthenium–Phacelia*, *Chenopodium–Plantago*, and *Chenopodium–Phacelia* (Fig. 2). In summary, there was no evidence of strong context dependence as a result of violation of the transitivity hypothesis and 78% of contrasts were clearly transitive or context independent.

Seed choices were not only generally consistent between contexts for individual bird species, but also remain similar among bird species in every experiment. For example, the three birds usually ate >50% of *Setaria*, *Pappophorum*, and *Digitaria* seeds in the two contexts, *S. multicolor* and *D. diuca* ate <10% of *Sporobolus* seeds,

and the three bird species always consumed <10% of *Phacelia* and *Plantago* seeds (Figs. 1, 2).

Effect of a lesser value option on the consumption of target seeds (IIA)

Sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray) seeds were not systematically consumed by *S. multicolor* and *D. diuca* (i.e., they ate about 5% of the offered seeds) and, therefore, we did not make inferences with *Sporobolus cryptandrus* as a target seed (Table 3). According to the consumption of the three target seed species, birds moderately violate the IIA principle. In other words, mean seed consumption was higher in the mixed trials in 8 out of 9 comparisons (Table 3): *Z. capensis* (36%), *S. multicolor* (32%), and *D. diuca* (28%) consumed more grass seeds in the mixed trials, while the mean consumption of streambed bristlegrass (*Setaria leucopila* (Scribn. & Merr.) K. Schum.) (21%), *Pappophorum* spp. (46%), and Arizona cottontop (*Digitaria californica* (Benth.) Henrard) (52%) increased when offered in mixed trials with less attractive seeds.

Table 3. Mean (±SE) percent consumption of three species of target grass seeds in homogeneous and mixed seed experiments by three bird species (Rufous-collared Sparrow, *Zonotrichia capensis*; Many-colored Chaco Finch, *Saltatricula multicolor*; Common Diuca Finch, *Diuca diuca*).

	Zonotrichia capensis		*Saltatricula multicolor*		*Diuca diuca*	
	Homogeneous	Mixed	Homogeneous	Mixed	Homogeneous	Mixed
Streambed bristlegrass, *Setaria leucopila*	90.8±4.9	96.8±1.1	72.5±6.9	89.3±3.3	66.3±7.5	87.9±9.0
Pappusgrass, *Pappophorum* spp.	80.9±6.2	97.5±1.4	64.1±9.3	90.7±9.3	46.5±9.3	81.4±11.2
Arizona cottontop, *Digitaria californica*	40.6±8.6	95.4±2.4	49.7±8.2	66.4±11.9	59.7±7.2	51.4±15.5
Total consumption (mean ± SE)	70.8±8.9	96.6±0.4	62.1±3.8	82.1±4.5	57.5±3.4	73.6±6.5

Note: In the mixed seed experiments, target grass seeds were mixed with a less attractive decoy (species of forb seeds), whereas in the homogeneous seed experiments, target grass seeds were scattered among other grass seeds with similar attractiveness (see Table 2).

Discussion

The test of transitivity showed that preferences remained unchanged in 28 out of 36 contrasts and suffered only weak modifications in the other 8 contrasts. *Saltatricula multicolor* was the most stereotyped seed chooser (i.e., preferences remained the same in 12 out of 12 contrasts). Furthermore, all bird species had similar patterns of consumption of target seed species in the two contexts (i.e., they usually preferred or avoided the same seeds). Birds therefore showed a mostly consistent, internally coherent ranking order of preferences, which suggests that some intrinsic characteristics of the seeds guided such preferences (Cueto et al. 2006; Ríos et al. 2012).

The level of consumption of attractive focal food options, by contrast, often increased when seeds were offered within a context of inferior quality. This particular result is consistent with the idea that birds can use relativistic choice mechanisms in which options are not assigned fixed or absolute values, a context-dependent process that implies a refutation of the IIA hypotheses (Shafir 1994; Bateson et al. 2003; Latty and Beekman 2011). Our work assessed the prevalence of absolute or comparative valuation rules in nature and contributed to the increasing conviction that both human and animal decisionmakers can sometimes deviate from absolute selective behaviour (i.e., they do not assign fixed utilities to food options) by making context-dependent choices (Latty and Beekman 2011; Freidin and Kacelnik 2011; Kluen and Brommer 2013).

However, our work also showed that one of the mechanisms of context-dependent foraging (i.e., IIA) does not lead to unpredictability in realistic field situations (e.g., situations in which we are interested in determining how behaviour changes across different environmental contexts). Although violation of the IIA principle supported context dependence (Latty and Beekman 2011), such violation did not hinder but reinforced our capacity to predict bird diet. In other words, an increased consumption of grass seeds in a less attractive seed context was clearly expected from previous knowledge of seed selection and preferences of birds. Birds select most grass seeds under field conditions (Marone et al. 1998, 2008) and also prefer them over forb seeds in the laboratory (Cueto et al. 2006). Although ecological predictability would decline when transitivity does not fit, it would be mostly preserved (or even reinforced) when the IIA principle is violated.

Birds foraging in a nonattractive food context may increase consumption rates of optimal items if they are present as focal food. As implied previously, this type of context dependence could hardly be considered an irrational behaviour. For example and similar to other seed-eating birds (Brzek et al. 2010), *S. multicolor* and *D. diuca* prefer seeds with high starch content, a decision that allow these two bird species to obtain easily digestible energy with low cost of absorption (Ríos et al. 2012). In this study, the grass seeds, whose consumption rates increased in the less attractive context, usually have high starch content (Ríos et al. 2012), and their augmented consumption may be considered simultaneously a context-dependent and a rational decision (i.e., their consumption was guided by the intrinsic nutritional properties of the seeds).

The fusion of ecology and behaviour (Gordon 2011) is undoubtedly welcomed, because it advances joint ecological descriptive studies with theoretical and experimental works on the behavioural causes of ecological patterns (Werner 1998). Although these patterns may be sometimes elusive or contingent because of context-dependent behaviour (Gordon 2011), the radical localness of natural history should be empirically evaluated before establishing it as an ecological axiom. The kind of context dependence that is associated with violation of the IIA principle may be ubiquitous among biological decisionmakers (Latty and Beekman 2011), but the foraging behaviour of seed-eating birds of the Monte desert offers an example of comfortable coexistence of this type of context-dependent behaviour and ecological predictability. The prediction that grass seed specialists like *S. multicolor* will suffer population declines in areas where reserves of grass seeds are reduced, while more generalist birds like *Z. capensis* and *D. diuca* would be less affected, was reinforced by the low incidence of the transitivity component of context dependence and violation of the IIA component, which paradoxically implies a context-dependent effect.

Acknowledgements

References

Bateson, M., Healy, S.D., and Hurly, T.A. 2003. Context-dependent foraging decisions in rufous hummingbirds. Proc. R. Soc. B Biol. Sci. **270**(1521): 1271–1276. doi:10.1098/rspb.2003.2365.

Brzek, P., Lessner, K.N., Caviedes-Vidal, E., and Karasov, W.K. 2010. Low plasticity in digestive physiology constrains feeding ecology in diet specialist, zebra finch (*Taeniopygia guttata*). J. Exp. Biol. **213**(5): 798–807. doi:10.1242/jeb.037259.

Burns, K.J., Shultz, A.J., Title, P.O., Mason, N.A., Barker, F.K., Klicka, J., Lanyon, S.M., and Lovette, I.J. 2014. Phylogenetics and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds. Mol. Phylogenet. Evol. **75**(1): 41–77. doi:10.1016/j.ympev.2014.02.006.

Cueto, V.R., Marone, L., and Lopez de Casenave, J. 2001. Seed preferences by birds: effects of the design of feeding-preference experiments. J. Avian Biol. **32**(3): 275–278. doi:10.1111/j.0908-8857.2001.320311.x.

Cueto, V.R., Marone, L., and Lopez de Casenave, J. 2006. Seed preferences in sparrow species of the Monte Desert, Argentina: implications for seed–granivore interactions. Auk, **123**(2): 358–367. doi:10.1642/0004-8038(2006)123[358:SPISSO]2.0.CO;2.

Egan, S.P., and Funk, D.J. 2006. Individual advantages to ecological specialization: insights on cognitive constraints from three conspecific taxa. Proc. R. Soc. B Biol. Sci. **273**(1588): 843–848. doi:10.1098/rspb.2005.3382.

Fair, J.M., Paul, E., and Jones, J. (*Editors*). 2010. Guidelines to the use of wild birds in research. The Ornithological Council, Washington, D.C. Available from http://www.nmnh.si.edu/BIRDNET/guide/ [accessed 16 April 2015].

Freidin, E., and Kacelnik, A. 2011. Rational choice, context dependence, and the value of information in European starlings (*Sturnus vulgaris*). Science, **334**(6058): 1000–1002. doi:10.1126/science.1209626. PMID:22096203.

Gordon, D. 2011. The fusion of behavioral ecology and ecology. Behav. Ecol. **22**(2): 225–230. doi:10.1093/beheco/arq172.

Heithaus, M.R., Wirsing, A.J., Burkholder, D., Thomson, J., and Dill, L.M. 2009. Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. J. Anim. Ecol. **78**(3): 556–562. doi:10.1111/j.1365-2656.2008.01512.x. PMID:19076259.

Kluen, E., and Brommer, J.E. 2013. Context-specific repeatability of personality traits in a wild bird: a reaction-norm perspective. Behav. Ecol. **24**(3): 650–658. doi:10.1093/beheco/ars221.

Latty, T., and Beekman, M. 2011. Irrational decision-making in an amoeboid organism: transitivity and context-dependent preferences. Proc. R. Soc. B Biol. Sci. **278**(1703): 307–312. doi:10.1098/rspb.2010.1045.

Levey, D.J., Moermond, T.C., and Denslow, J.S. 1984. Fruit choice in Neotropical birds: the effect of distance between fruits on preference patterns. Ecology, **65**(3): 844–850. doi:10.2307/1938058.

Lockwood, J.R. 1998. On the statistical analysis of multiple-choice feeding preference experiments. Oecologia, **116**(4): 475–481. doi:10.1007/s004420050612.

Lopez de Casenave, J. 2001. Estructura gremial y organización de un ensamble de aves del desierto del Monte. Ph.D. thesis, Universidad de Buenos Aires, Buenos Aires, Argentina.

Lopez de Casenave, J., Cueto, V.R., and Marone, L. 2008. Seasonal dynamics of guild structure in a bird assemblage of the central Monte desert. Basic Appl. Ecol. **9**(1): 78–90. doi:10.1016/j.baae.2006.08.006.

Luce, R.D. 1959. Individual choice behavior: a theoretical analysis. Wiley, New York.

Marone, L. 1991. Habitat features affecting bird species distributions in the Monte desert, Argentina. Ecol. Austral, **1**(2): 77–86.

Marone, L., and Horno, M.E. 1997. Seed reserves in the central Monte Desert, Argentina: implications for granivory. J. Arid Environ. **36**(4): 661–670. doi:10.1006/jare.1996.0187.

Marone, L., Rossi, B.E., and Lopez de Casenave, J. 1998. Granivore impact on soil-seed reserves in the central Monte desert, Argentina. Funct. Ecol. **12**(4): 640–645. doi:10.1046/j.1365-2435.1998.00226.x.

Marone, L., Lopez de Casenave, J., Milesi, F.A., and Cueto, V.R. 2008. Can seed-eating birds exert top-down effects on grasses of the Monte desert? Oikos, **117**(4): 611–619. doi:10.1111/j.0030-1299.2008.16506.x.

Noda, T. 2004. Spatial hierarchical approach in community ecology: a way beyond high context-dependency and low predictability in local phenomena. Popul. Ecol. **46**(2): 105–117. doi:10.1007/s10144-004-0184-x.

Ondine, F.-C., Jean, C., and Romain, J. 2009. Effects of organic and soil conservation management on specialist bird species. Agric. Ecosyst. Environ. **129**(1–3): 140–143. doi:10.1016/j.agee.2008.08.004.

Pol, R.G., Sagario, M.C., and Marone, L. 2014. Grazing impact on desert plants and soil seed banks: implications for seed-eating animals. Acta Oecol. **55**(1): 58–65. doi:10.1016/j.actao.2013.11.009.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, **43**(1): 223–225. doi:10.2307/2409177.

Ríos, J.M., Mangione, A.M., and Marone, L. 2012. Effects of nutritional and anti-nutritional properties of seeds on the feeding ecology of seed-eating birds of the Monte desert, Argentina. Condor, **114**(1): 44–55. doi:10.1525/cond.2012.110043.

Roa, R. 1992. Design and analysis of multiple-choice feeding-preference experiments. Oecologia, **89**(4): 509–515. doi:10.1007/BF00317157.

Shafir, S. 1994. Intransitivity of preferences in honey bees: support for "comparative" evaluation of foraging options. Anim. Behav. **48**(1): 55–67. doi:10.1006/anbe.1994.1211.

Sol, D., Bartomeus, I., and Griffin, A.S. 2012. The paradox of invasion in birds: competitive superiority or ecological opportunism? Oecologia, **169**(2): 553–564. doi:10.1007/s00442-011-2203-x. PMID:22139450.

Stephens, D.W., and Krebs, J.R. 1986. Foraging theory. Princeton University Press, Princeton, N.J.

Terraube, J., and Arroyo, B. 2011. Factors influencing diet variation in a generalist predator across its range distribution. Biodivers. Conserv. **20**(10): 2111–2131. doi:10.1007/s10531-011-0077-1.

Waksberg, A., Smith, A., and Burd, M. 2009. Can irrational behaviour maximise fitness? Behav. Ecol. Sociobiol. **63**(3): 461–471. doi:10.1007/s00265-008-0681-6.

Werner, E.E. 1998. Ecological experiments and a research program in community ecology. *In* Experimental ecology: issues and perspectives. *Edited by* W.J. Resetarits and J. Bernardo. Oxford University Press, Oxford, UK. pp. 3–26.

Werner, E.E., and Peacor, S.D. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology, **84**(5): 1083–1100. doi:10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2.

Zar, Z.H. 1996. Biostatistical analysis. 3rd ed. Prentice-Hall, Inc., Upper Saddle River, N.J.