Do neophobia and dietary wariness explain ecological flexibility? An analysis with two seed-eating birds of contrasting habits

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The neophobia threshold hypothesis (NTH) suggests that the acquisition and maintenance of a high behavioral and ecological flexibility in the evolutionary and adaptive history of a species is the consequence of lower levels of neophobia towards new micro-habitats and of dietary wariness of novel foods. To test this idea we assessed the degree of neophobia and dietary wariness in two seed-eating bird species with contrasting degrees of ecological flexibility that inhabit the central Monte desert (Argentina): a grass-seed specialist, the many-colored chaco-finch, and a generalist feeder, the rufous-collared sparrow. We expected that both species would exhibit neophobia and wariness when faced with new foraging opportunities but that the rufous-collared sparrow would be less neophobic and less wary than the specialized many-colored chaco-finch. Experimental indicators of neophobia and dietary wariness included willingness to eat near novel objects and willingness to eat novel seeds, respectively. Both species showed similar levels of reluctance to novelty, although the sparrow could be slightly more reluctant than the finch. Contrary to our predictions, the sparrow was neither less hesitant nor faster or greedier than the finch. This experimental evidence does not support a negative relationship between neophobia/wariness and ecological flexibility in these two seed-eating birds and it coincides with the growing evidence that challenges the NTH. Some of our results provide support for the dangerous niche hypothesis, especially as the rufous-collared sparrow, that feeds on more diverse and potentially dangerous food, showed higher levels of neophobia in some cases. Although the idea of neophobia and wariness being plausible causes of ecological specialization sounds attractive, the current situation calls for further research so that the causes of ecological flexibility in granivorous birds can be better understood.

Behavioral flexibility, which includes the ability of organisms to use new resources such as microhabitat or food (e.g. made available through human induced environmental change), has drawn the attention of ornithologists who have reported differences in this attribute within and among bird species (Terraube and Arroyo 2011, Viol et al. 2012). Birds with more flexible foraging behavior normally have broader niches and are more resilient to habitat change than birds with stereotyped behavior (Mayr 1974, Sol and Lefebvre 2000, Sol et al. 2002, Greenberg 2003). So, the study of the mechanisms that foster foraging flexibility may help to understand the ecological responses of organisms to environmental change (Charmantier et al. 2008).

Two aspects of foraging flexibility are the ability to adopt new foods (i.e. consumer innovation; Sol et al. 2011) and to feed near unfamiliar stimuli (Webster and Lefebvre 2001). Animals can be attracted (neophilic), deterred (neophobic), or indifferent to unfamiliar stimuli (Echeverría and Vassallo 2008). Neophilia is the spontaneous attraction of an animal to a food item, object, or place because it is novel. Neophobia, on the contrary, is the aversion that an animal displays towards approaching a food item, object, or place simply because it is novel (Greenberg 2003). Neophilia and neophobia are not necessarily the ends of a single behavioral continuum (Russell 1973, Greenberg and Mettke-Hofmann 2001, Greenberg 2003) but could be different animal responses to novelty caused by independent motivations (Griffin and Guez 2014).

When faced with a novel foraging place, birds normally exhibit neophobia and the adoption of the new place would imply overcoming neophobia. When faced with a novel food, in turn, birds show a transient aversion to approaching it (i.e. food neophobia), and a normally longer lasting reluctance to consume the novel food (i.e. dietary conservatism) even once food neophobia has waned. The overall period of food neophobia plus dietary conservatism is dietary wariness, so that the entire process of novel food acceptance implies overcoming dietary wariness (McMahon et al. 2014).

High levels of neophobia and dietary wariness might promote low foraging flexibility. Greenberg (1983) encapsulated

this idea in the neophobia threshold hypothesis (NTH), which proposes that the degree of aversion to novelty plays a key role in the probability that a new foraging opportunity will be explored and incorporated into the niche of a bird. More specialized birds will remain so because of high levels of neophobia and wariness. On the contrary, low levels of neophobia and wariness should be the hallmark trait of generalists. The prediction that species with less neophobia are more flexible than related neophobic ones has been confirmed in several tests. For example, the specialized insectivore *Setophaga pensylvanica* showed a higher degree of neophobia than its generalist congener *S. castanea* (Greenberg 1983, 1984), the specialized granivore *Melospiza georgiana* was more neophobic than the generalist *M. melodia* (Greenberg 1989, 1990a), and the specialized nectarivore *Coereba flaveola* exhibited more neophobia than the generalist *Loxigilla noctis* (Webster and Lefebvre 2000).

Cases exist, however, where generalized foragers showed high levels of neophobia: house sparrow *Passer domesticus* (Rana 1989, Echeverría et al. 2006), raven *Corvus corax* (Heinrich 1988), shiny cowbird *Molothrus bonariensis* (Echeverría et al. 2006), generalist species in the genera *Melospiza* (Greenberg 1992) and *Anas* (Greenberg 2003) and blackbirds (Icterids: Mettke-Hofmann et al. 2013). These patterns have been explained by the dangerous niche hypothesis (DNH: Barnett 1958). It predicts that species living in dangerous habitats or feeding on potentially dangerous food (e.g. toxic) will show high levels of neophobia that protects an individual from the unknown potential danger of new things (Greenberg 2003). Generalist species, for example those living in close proximity to humans, are exposed to a variety of unfamiliar situations and are therefore more likely to encounter dangerous situations. As a consequence, generalists may be more neophobic than specialists (Greenberg 2003). The DNH framework proposes that mechanisms other than neophobia (e.g. innate templates, neophilia, digestive constraints) might control ecological flexibility.

Two conspicuous birds of the central Monte desert (Argentina), the rufous-collared sparrow *Zonotrichia capensis* (body weight: 18 g) and the many-colored chaco-finch *Saltatricula multicolor* (body weight: 22 g) appear to be reliable experimental models for testing the neophobia threshold hypothesis (Greenberg 1983, 2003, Sol et al. 2011). Both species were formerly placed in the family Emberizidae but *S. multicolor* has now been moved to Thraupidae (Burns et al. 2014). Although the two species are sympatric in the central Monte desert and feed on seed to a great extent, they differ in several behavioral and ecologica characteristics (Table 1). Given that the rufous-collared sparrow has a broad diet and generalized foraging behavior and habitat use, we wanted to find out whether it is less neophobic and less wary than the many-colored chaco-finch as proposed by the NTH.

Under the hypothesis that both species are neophobic and wary, but that the specialized many-colored chaco-finch would be so to a greater extent than the rufous-collared sparrow, we performed tests in captivity to estimate the willingness to eat usual seeds close to a novel object (i.e. neophobia test) and the willingness to eat novel seeds (i.e. dietary wariness test). We predicted that: 1) both bird species will take more time to touch usual seeds when there were novel objects nearby, and to eat novel seeds in the experimental arena, 2) the rufous-collared sparrow will be faster than the many-colored chaco-finch to touch usual seeds with novel objects nearby, 3) the rufous-collared sparrow will be faster than the many-colored chaco-finch to eat novel seeds, and 4) both bird species will eat a smaller mass of novel seeds than usual seeds but the rufous-collared sparrow will eat a larger mass of novel seeds than the many-colored chaco-finch.

Methods

Capture and maintenance of birds

In the winters of 2010, 2011, 2012 and 2013 we caught 34 mature birds (18 rufous-collared sparrows, of a resident subspecies: *Z. c. hypoleuca* and 16 many-colored chaco-finches) using mist nets in the open *Prosopis flexuosa* woodland, at the Biosphere Reserve of Ñacuñán (34°03′S, 67°54.5′W). Birds were then placed in individual cages ($50 \times 40 \times 40$ cm), each of which was equipped with a perch, a feeding dish ($5 \times 4 \times 3$ cm) and a water bowl in an inner room under an artificial winter photoperiod (10L:14D). Birds were kept visually isolated from one another using black plastic sheets throughout the experimental period of < 30 d, which included a habituation phase of 5–10 d. We provided birds with water enriched with vitamins and commercial seeds of foxtail millet *Setaria italica* (weight $= 2.40$ mg) or european millet *Panicum milliaceum* (weight $= 4.52$ mg) ad libitum during the entire experimental period. After completion of the experiments, we released all birds in the same area where we had caught them in compliance with the permit issued by the Direction of Renewable Natural Resources of the Government of Mendoza, Argentina (research permits numbers 956-10 and numbers 486-11). Captures and experiments comply with the current guidelines for the use of wild birds in research (Fair et al. 2010).

We deprived the birds of food during the night before running each test for a minimum fasting time of 14 h (i.e. winter darkness period). In order to account for the differences in specific metabolic rate, the fasting time was increased for the species with a larger body mass (i.e. with lower metabolic rate) as they would have a higher capability to resist starving periods (Webster and Lefebvre 2001). The rufous-collared sparrow and many-colored chaco-finch were subjected to fasting for 14 and 16 h respectively.

Object neophobia test

In order to estimate neophobia for novel objects for each bird species and then compare it between species, in the winter of 2010 we conducted a trial based on Greenberg (1983, 1990a) and Webster and Lefebvre (2001) in which we used 18 individuals (8 many-colored chaco-finches and 10 rufous-collared sparrows). We measured latencies to touch seeds supplied in a feeding dish without (i.e. control) or with (i.e. treatment) of a novel object. So, on the morning (8:00 am) following the fasting period (Greenberg and Mettke-Hofmann 2001) we offered the usual feeding dish to each bird in its cage with ≈ 20 g of foxtail millet seeds. The experimenter was located 2 m away, hidden behind a screen, to be able to observe without being seen. If the bird ate within the first 20 min, the maximum time limit

Table 1. Ecological characteristics of rufous-collared sparrow and many-colored chaco-finch, the two experimental models used in this study to test the general hypothesis that the acquisition of different levels of ecological flexibility over the evolutionary and adaptive history of a species is the result of different levels of neophobia and/or dietary wariness towards novel foraging microsites or foods.

Ecological characteristics	Rufous-collared sparrow	Many-colored chaco-finch	Reference
Granivorous field diet			
Trophic Niche	Generalized	Specialized	Marone et al. 2008
Percentage of grass/forbs seeds	50%, 50%	100%, 0%	Marone et al. 2008
Preferences	Grasses + forbs	Only grasses	Cueto et al. 2006, Camín et al. 2015a
Digestive physiology			
Preference for seeds rich in starch	No	Yes	Ríos et al. 2012a
Ability to detoxify plant secondary compounds	Yes	No	Ríos et al. 2012b
Foraging behavior			
Capability of double scratching	Yes	No	Cueto et al. 2013
Context dependence foraging	Low	Nil	Marone et al. 2015
Social behavior			
Breeding season	Territorial	Territorial	Sagario and Cueto 2014
No-breeding season	Mainly in flocks	Mainly alone	Sagario and Cueto 2014
Geographical distribution			
Latitude	Wide (10°N to 55°S)	Narrow (20°S to 32°S)	Cracraft 1985, Lougheed et al. 2013
Migratory strategy			
Migratory	No (one subspecies); Yes (two subspecies)	No	Sagario et al. 2014
Response to human activities			
Negative	Low	High	Milesi et al. 2002, Bellocq et al. 2011

established for the first stage, we allowed it to eat for 5 s, after which the experimenter approached the cage at a slow and steady pace, and randomly offered either a control test (consisting of simply moving the feeder 2 cm) or a treatment test (consisting of moving the feeder 2 cm and placing one of three novel objects at 2 cm from it).

The objects were 1) three 10 cm long springs vertically placed next to each other, 2) three 10 cm long sticks of different colors embedded at their base in a small ball of expanded polystyrene, and 3) a handful of curly white paper, all mounted on cardboard bases of 8 × 8 cm (Webster and Lefebvre 2001). We chose different types of objects to maximize the reaction to novelty rather than to a single object (Martin and Fitzgerald 2005, Mettke-Hofmann et al. 2013). We carried out one experiment per day with each individual, accumulating a total of six days of trials with the same individual (three controls and three treatments).

For controls and treatments, we recorded latency to touch the seeds (1st peck), within a maximum time of 20 min- second stage. If after 20 min the birds had not touched the seeds, we assigned them a latency of 1201 s. The birds were fed normally after the experiments until a new food deprivation period started in the evening. The following day another control or treatment experiment was conducted.

Dietary wariness and consumption tests

In order to estimate dietary wariness in each bird species and compare it between species, we ran a second trial in the winters of 2012 and 2013, with a similar protocol to the first one, but based on Martin and Fitzgerald (2005) and Marples et al. (2007). In this trial we used 16 birds (8 many-colored chaco-finches and 8 rufous-collared sparrows) to record latency to eat usual seeds and novel seeds. The morning following the fasting period, we provided each subject with 20 g of usual (i.e. control, european millet) or novel (i.e. treatment) seeds in cardboard feeders (already present during

the habituation phase) designed ad-hoc (40 × 5 × 2 cm) to be accessed from the cage floor. Seeds could be seen by the bird from any position. During the deprivation period the feeders remained covered with cardboard that was removed a few minutes before starting the experiments. The novel seeds, absent from the birds' natural diet (Marone et al. 2008), were: 1) oats *Avena sativa* (weight = 24.84 mg ± 1.18), 2) flax *Linum usitatissimum* (weight = 6.96 mg ± 0.12), 3) quinoa *Chenopodium quinoa* (weight = 3.72 mg ± 0.29) and 4) chia *Salvia hispanica* (weight = 1.36 mg ± 0.06). This selection of seed allowed us to maximize diversity in sizes, shapes, textures, colors and flavors (Martin and Fitzgerald 2005) in relation to usual seeds (Greenberg and Mettke-Hofmann 2001). We performed one experiment per day with every individual, accumulating a total of eight days of trials with the same individual (four controls and four treatments).

We controlled and video-recorded the bird's behavior from behind a perforated screen. For each bird we recorded latency to touch (i.e. for novel seeds: the end of food neophobia, 1st peck) and latency to eat (i.e. for novel seeds: the end of dietary wariness, active pecking, ≥ 5 pecks in a row) usual seeds and novel seeds. In addition, we calculated the dietary conservatism for each bird by subtracting the time to touch novel seeds from the time to eat novel seeds. If after 2 h birds had not consumed the seeds, we assigned them a maximum score of 7201 s. After the 2 h had passed, we removed the seeds from the cages and estimated the mass consumed by difference, with a 0.01 g precision. The birds were fed again on usual seeds for the rest of the day until the start of a new deprivation period. We repeated the trial the following day, but with a different kind of seed.

Design and statistical analyses

To estimate object neophobia, dietary wariness and consumption levels for each bird species, we removed any

possible effects of individual variation by using each individual as its own control. We considered that the different types of objects or seeds employed were different instances of the same treatment type so that a single average for control as well as treatment was calculated for every individual. We considered a species to be neophobic and dietary wary when, under treatment conditions, its latencies and consumption were significantly higher and lower, respectively, than in the control. To compare latencies or consumption levels between control and treatment conditions we used t-test for paired samples.

To compare neophobia, wariness and consumption levels between bird species we first subtracted the control latency (i.e. without objects) or consumption level (i.e. of usual seeds) from the treatment latency (i.e. with novel objects) or consumption level (i.e. of novel seeds) for each bird tested. We considered a bird as more neophobic or more wary when the latency was significantly higher and consumption level lower than its counterpart. We compared latency and consumption differences between species and types of objects or seeds with two-factor ANOVA (n = number of birds tested).

To compare the duration of food neophobia with dietary conservatism in each bird species we used t-test for paired samples.

We determined whether raw data met the assumptions of parametric statistics using one-sample Kolmogorov–Smirnov and Levene tests. Log-transformed data of latency (neophobia as well as dietary wariness) and of seed consumption met normality and homocedasticity. Statistical tests were two-tailed, and the alpha level to determine significance was 0.05. We performed all tests with Statistica (ver. 5.0, 1998). Data are reported as averages $\pm$ SE.

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.v48m0 > (Camín et al. 2015b).

Results

Object neophobia test

All individuals fed in the first stage of the experiments. In the second stage, all the many-colored chaco-finches touched the food within the first 20 min in both control and treatment trials. All rufous-collared sparrows touched the food within the period in control trials, but one of them did not touch the food in a treatment trial.

Latency to touch was greater in the presence of novel objects than in their absence in rufous-collared sparrow ($t_9 = -10.61$, p < 0.001; Fig. 1a), as well as in many-colored chaco-finch ($t_7 = -4.30$, p < 0.001; Fig. 1b).

Latency to touch did not differ between bird species ($F_{1,16} = 0.19$, p = 0.66; Fig. 1c) and was affected by object type ($F_{2,16} = 6.94$, p = 0.003). The interaction between object type and bird species was nearly significant ($F_{2,32} = 3.17$, p = 0.055), which suggest that an increase in the sample size could show that rufous-collared sparrow had a more aversive reaction to some treatments than many-colored chaco-finch.

Dietary wariness and consumption tests

The rufous-collared sparrow and many-colored chaco-finch exhibited dietary wariness (i.e. food neophobia plus dietary conservatism) before eating novel seeds. The average duration of food neophobia (527.6 ± 266.1 s) and dietary conservatism (868.0 ± 385.7 s) were similar in the rufous-collared sparrows ($t_7 = -0.18$, p = 0.85). The figures for the many-colored chaco-finches (306.1 ± 263.6 s and 497.2 ± 430.6 s, respectively) were also statistically indistinguishable ($t_7 = 0.22$, p = 0.82).

Latency to eat was significantly larger for novel than for usual seeds in rufous-collared sparrow ($t_7 = -5.25$, p = 0.001; Fig. 1d) but not in many-colored chaco-finch ($t_7 = -1.34$, p = 0.22; Fig. 1e).

Latency to eat was not affected by species ($F_{1,14} = 2.17$, p = 0.16; Fig. 1f), nor by the type of food ($F_{3,14} = 0.41$, p = 0.74). We detected no significant interaction between food type and bird species ($F_{3,42} = 1.94$, p = 0.13).

Both bird species ate detectable quantities of novel seeds, but consumed significantly more usual than novel seeds: rufous-collared sparrow ($t_7 = 9.94$, p < 0.001; Fig. 1g), and many-colored chaco-finch ($t_7 = 10.17$, p < 0.001; Fig. 1h). The consumption of novel seeds was not affected by the type of seed ($F_{3,14} = 1.83$, p = 0.15) nor by the species ($F_{1,14} = 0.12$, p = 0.72; Fig. 1i). We detected no significant interaction between seed type and bird species ($F_{3,42} = 1.43$, p = 0.24).

Discussion

We provide information about the foraging behavior of the rufous-collared sparrow and many-colored chaco-finch, little known thus far, when they faced new foraging opportunities. When birds faced unknown objects, both species exhibited neophobia to forage nearby, but rufous-collared sparrow could have been more reluctant to start eating in some treatments. When birds were given novel seeds the rufous-collared sparrow took more time to start eating them, although dietary wariness did not differ between species, and both species consumed low and similar amounts of novel seeds. To sum up, the rufous-collared sparrow and many-colored chaco-finch showed similar levels of reluctance to novelty, although the sparrow could be slightly more reluctant than the finch.

These results did not support the NTH, that the higher ecological flexibility of the rufous-collared sparrow is an evolutionary and adaptive consequence of being less neophobic and less wary than the many-colored chaco-finch. The idea that neophobia and dietary wariness cause and/or maintain ecological flexibility in the rufous-collared sparrow does not fit, specifically, with three kinds of evidence: on average 1) the rufous-collared sparrow did not react to novel foraging microsites with less neophobia (Fig. 1c), 2) nor was it less wary when faced with novel seeds (Fig. 1f), 3) nor was it greedier when consuming novel seeds than the many-colored chaco-finch (Fig. 1i). These patterns recorded at the population level were confirmed when the foraging strategies of consumer individuals were taken into account (Lee et al. 2010). Considering that foragers may exhibit two stable foraging strategies, adventurous consumers that rapidly accept novel food or conservative consumers with prolonged or even boundless dietary conservatism (McMahon et al. 2014), the percentage of individuals with dietary conservatism was 37% in rufous-collared sparrow and 12% in many-colored
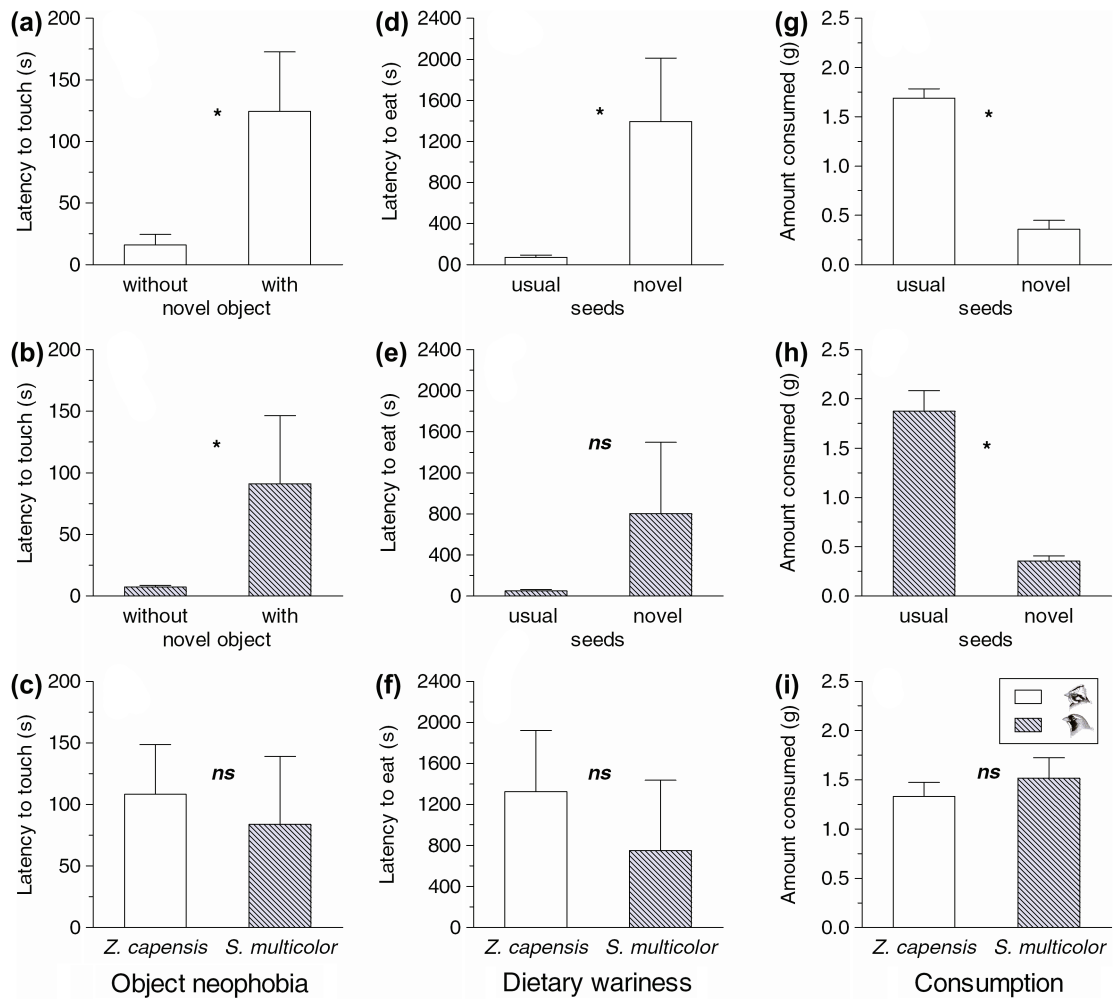
Figure 1. Latencies (average + SE) and consumption (average + SE) in (a–c) object neophobia tests and (d–i) dietary wariness and consumption tests by rufous collared-sparrow (white bars) and many-colored chaco-finch (dashed bars). Latency to touch food without (i.e. control) or with (i.e. treatment) a novel object for (a) rufous-collared sparrow, (b) many-colored chaco-finch, and (c) rufous-collared sparrow and many-colored chaco-finch in treatment tests. Latency to eat usual (i.e. control) and novel (i.e. treatment) seeds for (d) rufous-collared sparrow, (e) many-colored chaco-finch, and (f) rufous-collared sparrow and many-colored chaco-finch in treatment tests. Amount consumed of usual (control) and novel (treatment) seeds for (g) rufous-collared sparrow, (h) many-colored chaco-finch and (i) rufous-collared sparrow and many-colored chaco-finch in treatment tests. The direct comparison between species is based on the difference in latency with/without novel object and the difference in latency to consume familiar/novel food and the difference in consumption of familiar/novel food. Significant and non-significant differences, detected by t-test or ANOVA, are indicated by '*' or 'ns' respectively. See methods for a detailed description.

chaco-finch, whereas the percentage of adventurous consumers was twice the number in many-colored chaco-finch (75%) than in rufous-collared sparrow (37%). The overall results reject a causal link between low neophobia or wariness and high ecological flexibility.

Echeverría et al. (2006), Sol et al. (2011), and Mettke-Hofmann et al. (2013) showed results that also contradict NTH. Echeverría et al. (2006) studied the responses to novelty in a bird assemblage inhabiting a suburban marsh. They tested the NTH by presenting food in the presence of novel objects with the prediction that the more specialized species will show a greater aversion to feeding near novel objects than generalist species (Greenberg 1983, 1984). Contrary to expectations, Echeverría et al. (2006) found higher levels of neophobia in highly generalist, urbanized species, such as the house sparrow and shiny cowbird. Mettke-Hofmann et al. (2013) noted that such evidence

may be explained by the DNH, a hypothesis that has received support in several studies. For example, Sol et al. (2011) worked under the umbrella of the 'two factor model' of Greenberg and Mettke-Hofmann (2001), and contrasted common mynas *Acridotheres tristis* from a risky habitat with others from a safe area. Mynas from safe environments were less fearful of predators and solved technical tasks faster, a result consistent with the idea that birds from risky environments are more neophobic. Recently, Mettke-Hofmann et al. (2013) studied neophobic reactions to experimentally-induced changes in the natural environment of six closely-related blackbird species, including two species represented by two distinct populations. For the analyses, the neophobic reactions (measured as the difference in the number of birds feeding and the time spent feeding with and without novel objects) were related to several measures of ecological flexibility and migratory strategy. The degree of neophobia was

higher in migrant mynas than in the resident mynas and in diet generalist mynas than in specialist mynas, supporting the DNH.

Although our experiments highlight similar responses to novelty by both the species tested, some results would support the DNH, in particular the idea that organisms feeding on potentially dangerous food will show high levels of neophobia. The species that showed longer latencies, the rufous-collared sparrow, is a diet generalist that can consume both grass and forb seeds in the Monte desert (Marone et al. 2008, Camín et al. 2015a), whereas the many-colored chaco-finch is a grass-seed specialist that would rarely face dangerous food in the field since, on average, grass seeds have less toxic secondary compounds than forb seeds (Díaz 1996, Ríos et al. 2012a). The tendency of the rufous-collared sparrow to develop higher neophobia or wariness (Fig. 1), together with its great tolerance to secondary compounds and its detoxification capacity (Ríos et al. 2012a, b), are properties that could have evolved under a potentially 'dangerous niche' condition (Mettke-Hofmann et al. 2013). However, the robustness of this tendency should be confirmed by several kinds of independent studies. For example, if hesitation to start feeding was increased under experimental conditions (e.g. birds tested feeding alone as in our trials) in organisms like the rufous-collared sparrow which feed in flocks in the field in some seasons (Sagario and Cueto 2014), the behavior of rufous-collared sparrow and many-colored chaco finch in the field would be even more similar than our results showed. The social environment may facilitate the approach to novel foods or objects because the presence of group members enables them to learn about the palatability of novel items socially (Stöwe et al. 2006, Voelkl et al. 2006), reducing the stress of individual birds while feeding (Greenberg 1990a, b, Cadieu et al. 1995).

Our study was restricted to a single comparison between two species differing in general behavior, and it was intended to explain the plausible relationships between wary reactions and foraging flexibility (Greenberg 1983, 1984, 1989, Webster and Lefebvre 2000). A single comparison between two species is, however, insufficient to make broad inferences about these relationships. Notwithstanding, our experimental model is fertile because one of the species compared is clearly a generalist, whereas the other is a highly specialized consumer, as well as a habitat dweller (Table 1). This clear contrast would help the incorporation of our study into a meta-analysis intended to elucidate the evolutionary relationship between the inability to adopt new foraging opportunities by birds and their ecological specialization (Rezende and Garland 2003).

Knowledge of the causes of foraging flexibility is an important issue for basic and applied ecology (Charmantier et al. 2008), since the establishment of the limits of behavioral flexibility would allow predictions to be made about population responses to global change (Camín et al. 2015a). The idea of neophobia and wariness as plausible causes of ecological specialization sounds attractive because of its simplicity and explanatory power. However, our study does not support it, coinciding with the growing evidence that challenges the NTH. The current situation calls for further research in order to understand better the causes of ecological flexibility in granivorous birds.

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