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Learning Differences between Feral Pigeons and Zenaida Doves: The Role of Neophobia and Human Proximity

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Abstract

Learning differences predicted from ecological variables can be confounded with differences in wariness of novel stimuli (neophobia). Previous work on feral pigeons (*Columba livia*), as well as on group-feeding and territorial zenaida doves (Zenaida aurita), reported individual and social learning differences predicted from social foraging mode. In the present study, we show that speed of learning a foraging task covaries with neophobia and latency to feed from a familiar dish in the three types of columbids. Pigeons were much faster than either territorial or groupfeeding zenaida doves on all tests conducted in captivity, but showed unexpectedly strong neophobia in some urban flocks during field tests. Human proximity strongly affected performance in group-feeding doves both in the field and in captivity. They were slightly faster at learning than their territorial conspecifics in cage tests. In multiple regressions, species identity, but not social foraging mode, significantly predicted individual variation in learning, as did individual variation in neophobia. Wariness of novel stimuli and species differences associated with artificial selection appear to be more important than foraging mode and wariness of humans in accounting for learning differences between these columbids.

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Introduction

Some animals feed less willingly than others in unfamiliar situations. This wariness of novel stimuli (neophobia) can have important consequences for ecological plasticity. Neophobic animals may encounter and use a narrower range of food types than neophilic ones, and learn less rapidly about cues and rewards

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associated with novel situations they face in the field and in the laboratory (Greenberg & Mettke-Hoffmann 2000). As a consequence, learning differences predicted from differences in diet breadth (Rozin & Schull 1988) can be confounded by differences in willingness to eat new foods (Daly et al. 1982).

Inter- and intraspecific comparisons on wild-caught pigeons (Columba livia) and zenaida doves (Zenaida aurita) suggest that differences in social foraging can also predict differences in learning, but the confounding effect of neophobia on these trends has not been examined. Gregarious feral pigeons (Lefebvre et al. 1996) and group-feeding populations of zenaida doves (Carlier & Lefebvre 1996) learn faster by themselves than do territorial zenaida doves. They also learn socially from different tutor species. Group-feeding doves and pigeons learn well from conspecifics, while territorial doves learn best from the birds they most often feed with in mixed-species assemblages, Carib grackles (Quiscalus lugubris; Dolman et al. 1996; Lefebvre et al. 1996; Carlier & Lefebvre 1997). Pigeons feed more willingly from a simple open dish than do territorial doves (Lefebvre et al. 1996), suggesting that simple motivation to feed in captivity could underlie the apparent species learning differences. These differences could in turn be caused by differences in artificial selection. Feral pigeons and Barbados zenaida doves show a striking similarity in urbanisation, opportunism and reliance on food provided by humans in city streets (Pinchon 1963; Evans 1990), parks and harbour storage areas (Murton et al. 1972; Lévesque & McNeil 1985; Dolman et al. 1996). The species do, however, have very different histories of selection: all pigeons in the New World descend from captive individuals presumably bred in part for tolerance of human proximity (Johnston & Janiga 1995). In contrast, zenaida doves come from wild populations, one of which is clearly considered to be a pest at our harbour study site in Barbados where it roosts, breeds and feeds in flocks. A further problem is that social foraging has been inferred as the common variable behind the fast, conspecific-oriented learning of feral pigeons and group-feeding zenaida doves, but this inference is based on studies using different methodologies.

In the present study, we addressed all of these problems by assessing neophobia in captivity and in the field in territorial and group-feeding zenaida doves in Barbados and gregarious feral pigeons in Canada. We also assessed individual learning speed in the three columbids with the same apparatus used in the neophobia trials. We investigated whether group- and individual-level differences in learning speed could be predicted from differences in neophobia, and whether species identity or social foraging mode best account for learning differences between the three columbids.

Methods

Experiments in Captivity

Subjects

Twenty-two adult feral pigeons were obtained from a commercial dealer (S. Wright, Richmond Hill, Ontario). All birds were wild-trapped on farms in the

vicinity of Richmond Hill and are from the same origin as those used in previous work (Lefebvre et al. 1996). Thirty-nine adult zenaida doves were caught in Barbados in baited walk-in traps between Apr. and June 1997; all birds were removed from the traps within 10 s of capture. Nineteen doves were caught at the Barbados Mills compound, Deep Water Harbour (DWH), in the parish of St-Michael; the remaining 20 doves were caught 9 km away in coastal St-James (StJ). The DWH birds feed at a landfilled site that consists of docking, grain loading, milling and storage facilities; there is little natural vegetation at this site, but as a result of transport and storage operations at the Barbados Mills plant, doves routinely feed in homospecific flocks (mean size 60; Dolman et al. 1996) on large, temporally unpredictable patches of spilled grain (maize, rice and wheat), legumes and commercial meal. A majority of DWH doves roost overnight on building ledges at the harbour. Nesting pairs are also frequently seen, suggesting that the DWH population is not a simple temporary feeding aggregation of nonbreeding floaters (Goldberg 1998).

The doves captured at StJ inhabit an area that includes a public park, hotel and church grounds, as well as the Bellairs Research Institute of McGill University. Vegetation in this area is coastal woodland, dominated by manchineel, mahogany, casuarina and coconut trees. The area provides roosting, nesting and feeding resources that allow year-round territoriality: mated pairs of zenaida doves aggressively defend their territory against conspecifics (Goldberg 1998), showing very high rates of intraspecific aggression.

Experimental procedure

Following capture (for doves) or transport (for pigeons), each bird was banded, weighed, housed in an individual cage and allowed to feed and drink ad libitum for 6 days. Mean weights of the two zenaida dove samples did not differ, suggesting that social foraging mode is not confounded with differences in age class or resource-holding potential. On day 7, food was withheld for 24 h and all birds were progressively brought down to 90% of their maximum weight; this level was maintained throughout the experimental period through adjustments in the individual's daily ration. The testing period began when birds had reached their target deprivation weight. On each testing day, birds were transferred from the housing to the experimental room and individually given a 10-min habituation period before that day's session commenced. Birds were returned to the housing room after each test session and fed the appropriate quantity of commercial mixed seed.

Each subject experienced three tests in the same order: feeding latency, neophobia and learning. The feeding latency test was designed to measure willingness to eat in captivity, with and without the experimenter being visible. Food (20 g of mixed seed) was presented to the birds in their usual feeding dish for a series of 2-min trials, with a maximum of eight trials per day over four consecutive days. The food dish was removed for a 30-s interval after each trial. On the first and third day of the test, the experimenter was visible, standing 2 m

from the bird's cage. On days 2 and 4, the experimenter was hidden behind a door and could observe the birds only through a small aperture. The number of trials required before the bird fed was recorded in each daily session.

The second test, neophobia, was conducted over five consecutive days, with a maximum of eight 2-min trials per day. The experimenter was hidden behind a door during all trials. On each trial, food (2 g of mixed seed) was presented in an apparatus the birds had never seen. The apparatus was a black, opaque Plexiglas box measuring $5.5 \times 5.5 \times 5$ cm (see Carlier & Lefebvre 1996 and Hatch & Lefebvre 1997 for a more complete description). This is the apparatus that birds would later be exposed to again in the learning test. Since our goal was to assess neophobia in the same conditions the birds would encounter during learning, this was the only novel object in our neophobia test, contrary to the procedure devised by Greenberg (1983). Food was available in the apparatus in a small circular depression (1 cm deep and 1.5 cm diameter) on the upper surface; it was easily visible and accessible and the animal therefore simply needed to approach the novel stimulus. Like the feeding latency test, the number of 2-min trials required by the bird before it fed from the new apparatus was recorded; a 30-s interval separated the trials during a given day.

The final test used a second feeder hidden in the side of the black Plexiglas box; the animal was required to learn a new response, ring or drawer pulling, to open this feeder (Carlier & Lefebvre 1996; Hatch & Lefebvre 1997). In this test, food was enclosed in a $5.5 \times 5.5 \times 1.5$ cm drawer fitted with a metal ring; when pulled, the ring gave access to a depression (1 cm deep and 1.5 cm diameter) in the drawer which contained 2 g of mixed seed. Because the food was hidden and ringpulling is an extremely low probability behaviour for columbids, each bird was run through a series of four successive steps in the task (modified from the nine steps used by Carlier & Lefebvre 1996; steps 1, 4, 6 and 8 in Carlier & Lefebvre's Table 1, respectively, represent steps 1, 2, 3 and 4 in the present study). Each step differed in the position of the drawer, the ease of access to the seed and the behaviour needed to acquire the seed. Each bird was first started at level 1 and graduated to the next level of difficulty if it consumed seed in two trials; the lowest possible number of trials needed to reach level 4 was thus 8. The maximum number of trials given was 40, at a rate of 8 trials per day over five consecutive days; the highest possible latency was 41 trials at level 1 (i.e. the 40 trials + 1, to distinguish a bird that failed from a bird that succeeded on its very last trial). When a bird graduated to an upper level but failed to eat on its first two trials there, it was brought back down to the previous level of difficulty (Carlier & Lefebvre 1996). In this test, the dependent variable was the trial at which each bird reached each of the four levels of the learning task.

Two types of analyses were conducted: first, the three types of columbids were compared with a multivariate analysis of variance (MANOVA, Wilkinson 1992) on latency to feed in the familiar dish (experimenter hidden), latency to feed upon first presentation of the box (neophobia) and latency to open the drawer. If group-feeding favours learning, we predict a significant effect of columbid type on the univariate F for trials on learning; in the comparisons between means, both

pigeons and DWH doves should learn faster than should StJ doves. If instead species identity is the major source of variance, then pigeons should learn faster than both types of doves. If learning is confounded with neophobia and latency to feed in captivity, then trends in the three tests should covary in the MANOVA; the multivariate F in the MANOVA should be significant, indicating common variance in the three dependent variables.

Similar predictions can be made for the second type of analysis, multiple regression. This analysis ascertains the extent to which individual differences in learning (the dependent variable in the regression) can be predicted from four independent variables: neophobia (latency to feed in the novel apparatus), latency to feed in captivity (experimenter hidden, as in the learning and neophobia tests), species identity (pigeon vs. zenaida dove) and social foraging mode (group-feeding vs. territorial). Neophobia and latency to feed in captivity should be significant predictors in the multiple regression if they are confounds of learning. The relative roles of species identity and social foraging mode can be assessed by their significance levels in the regression.

Experiments in the Field

The goal of these experiments was to validate the tests used in captivity by assessing feeding latencies of the three columbids in the field. In captivity, birds may be forced to respond to a test situation they would normally avoid in the wild. Birds that feed in groups in the wild are also placed in an abnormal situation when they are housed and tested alone in a cage.

Sites

For zenaida doves, field experiments were conducted on the island of Barbados during the month of May and June 1999 (late dry season), in the same two areas as described above (StJ and DWH). For pigeons, the experiments were conducted at 10 sites in Montréal, Québec, from July to Sept. 1999; previous work in our lab shows very similar performance in pigeons caught in Montréal and the Richmond Hill area, where subjects for the experiments in captivity originated. At StJ, experiments were run on haphazardly selected dove territories situated on the grounds of the Bellairs Research Institute and four adjacent areas, Folkstone Park, St-James Church, the Coral Reef Club and the Colony Club. The approximate boundaries of the territories and the identity of most resident doves were known from an earlier study on banded individuals (Goldberg 1998). A maximum of two trials was conducted on each territory to prevent habituation. For the DWH population, experiments were run on five hapazardly selected sites situated on the grounds of the Barbados Mills compound. In Montréal, pigeons were given a maximum of five trials at each of 10 sites throughout the city: Square Bethune, Square Dorchester, Square St-Louis, Square Phillips, Parc Ahuntsic, Parc Lafontaine, Parc Claude-Jutra, Réservoir MacTavish, Métro Place-des-Arts and Métro Peel.

Experimental procedure

We used a procedure similar to the one described by Greenberg (1989). The three columbids were compared on their latency to feed from a patch containing only seed and one where seed was available only in the Plexiglas box used in the laboratory experiments (described above). Because pilot work suggested that DWH doves were more familiar with maize and soybean (both frequent spillage at DWH), we used either a mix of these two foods or the commercial seed mix employed in the laboratory experiments on successive days at each site for each of the three columbids. On each test day, birds were first attracted with a 20-g patch of either soybean and maize or mixed commercial seed, presented on a green leaf background to facilitate both seed detection by the birds and seed removal by the experimenter. When birds started feeding (usually a single dove at StJ and groups of birds at DWH and Montréal), the experimenter, standing 15 m from the patch, randomly (by coin flipping) decided whether a food-only trial or a box trial would follow. The experimenter then slowly approached the patch at a constant pace, placing a marker at the spot where he was when the last bird at the patch stopped feeding and either walked or flew away; he then either simply replenished the patch to 20 g (if the trial was food only) or removed all seed and replaced it with the Plexiglas box, filled with 2 g of the same food type in the recessed hole on the upper surface (see neophobia trials described above). The experimenter then moved back to his initial position, 15 m from the patch and measured the time it took for at least one pigeon or dove to return and feed. The trial was ended after 20 min if no bird came back and assigned the ceiling latency of 1201 s. Distance (in m) between the feeding interruption marker and the patch was measured at the end of each trial. A second trial was then conducted on each test day, repeating the same procedures as above, including the random determination of food only or box presentations. A total of 41 tests (each with attraction + two randomly determined trials with either food only or box) were conducted at StJ, 32 at DWH and 40 in Montréal; an average of 3 d separated tests conducted at the same site.

Time to return and feed (latency) was normalized using log₁₀ transformations prior to analysis. The results were analysed as a food (mixed seed or maize/ soybean) by patch type (food only or box) by columbid type (pigeon, DWH dove or StJ dove) factorial ANOVA on log feeding latency. We assumed that the data were independent cases, since it is impossible to assure repeated presence of the same individuals in field trials on pigeons and DWH doves.

Results

Experiments in Captivity

Pigeons showed the fastest mean performance on the three tests (Fig. 1). Group-feeding doves performed slightly faster than did territorial doves and, as predicted, differences between the three columbids were in the same direction on the three tests. Due to lack of variance in at least one group for learning criteria 3

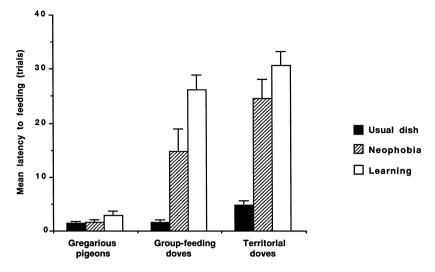


Fig. 1: Mean (+ SE) latency to feeding in the three tests conducted in captivity for the three columbids

and 4, as well as the second measure of feeding latency with the experimenter absent (day 4), we used mean trials on criteria 1 and 2 as our measure of learning and latency to feed on the first trial with experimenter absent (day 2) as our measure of response to captivity. The MANOVA yielded significant effects for both the multivariate ($F_{6,112} = 16.72$, p < 0.01) and the univariate effects of the three tests (feeding latency: $F_{2,58} = 11.40$, p < 0.001; neophobia: $F_{2,58} = 14.97$, p < 0.001; learning: $F_{2,58} = 52.77$, p < 0.001). Comparisons between means (Tukey tests, all at p = 0.01) on the univariate tests showed that pigeons were significantly faster than both territorial (StJ) and group-feeding (DWH) doves in the neophobia and learning tests, whereas the territorial StJ doves were significantly slower than both pigeons and group-feeding DWH doves in the feeding latency test.

Zenaida doves from both populations showed very poor performance on criteria 3 and 4 of the learning task, yielding means very close to the 40-trial ceiling (Fig. 2). In contrast, all pigeons reached criterion 1 extremely rapidly. In the feeding latency test (Fig. 3), territorial doves from StJ showed the slowest overall performance. All pigeons ate on the very first presentation of food on day 4 (experimenter hidden), precluding the use of these data in an ANOVA for lack of variance; intergroup differences in the visibility of the experimenter are thus statistically examined on days 1–3 only. A factorial analysis of variance (3 columbid types by 3 repeated days) revealed significant main effects of columbid type ($F_{2,58} = 11.16$, p < 0.001). The only significant comparison between means (Tukey test p < 0.05) shows a lower overall latency in pigeons than in territorial StJ doves. The significant effects of trials ($F_{2,116} = 16.47$, p < 0.001), as well as the groups-by-trials interaction ($F_{4,116} = 5.45$, p < 0.001) suggest that presence or

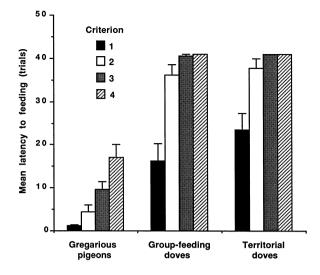


Fig. 2: Mean (+ SE) trials-to-criterion for the three types of columbids on the four criteria of the learning task

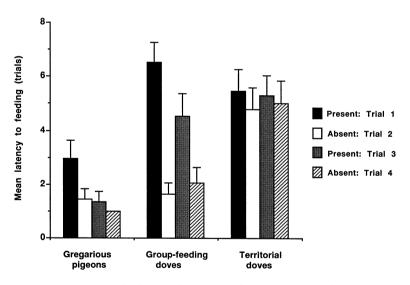


Fig. 3: Mean (+ SE) latency to feeding in a familiar dish for the three types of columbids in both the presence and absence of the experimenter over the course of four consecutive feeding trials

absence of the experimenter had a strong effect on group-feeding doves, but practically no effect on either territorial doves or pigeons. There were no significant differences between trial means for either pigeons or territorial doves; group-feeding doves took longer to feed on their first trial with the experimenter present than when she was hidden (Tukey test, p < 0.01), then increased their latency when the experimenter was again visible on trial 3 (Tukey test, p < 0.05).

The multiple regression confirms the trends revealed by the MANOVA. Neophobia covaries with learning (overall $F_{4,56} = 52.68$, p < 0.001, $R^2 = 0.775$). Pigeons differ from the two types of zenaida doves to a much greater extent than the two types of group-feeding columbids differ from the territorial one. Only species (p < 0.001) and neophobia (p < 0.001) were significant predictors of learning performance; feeding latency and social organization were not (p = 0.624 and 0.859, respectively). Feeding latency was correlated with neophobia (r = 0.555, $F_{1,59} = 26.33$, p < 0.001), which is why it dropped out of the final regression model.

Experiments in the Field

Group-feeding doves from DWH fled sooner than the other two columbids (Fig. 4a) and returned later when the patches contained only food (Fig. 4b). The ANOVA conducted on interruption distance revealed a highly significant effect of columbid type ($F_{2,214} = 178.83$, p < 0.001), with significant differences between all three group means (Tukey test, p < 0.01). There was also a weak effect of food type ($F_{1,214} = 4.30$, p = 0.039), with birds fleeing sooner from the approaching human if the patch contained mixed seed instead of maize and soybean.

The ANOVA conducted on latency to return showed significant main effects of all variables, as well a significant patch by columbid type interaction ($F_{2,214} = 8.55$, p < 0.001). None of the other interaction effects were significant. Overall, birds were slower to return when the patch featured the unfamiliar box than when it contained only food ($F_{1,214} = 187.350$, p < 0.001). Birds again showed a preference for maize and soybean over mixed seed ($F_{1,214} = 8.66$,

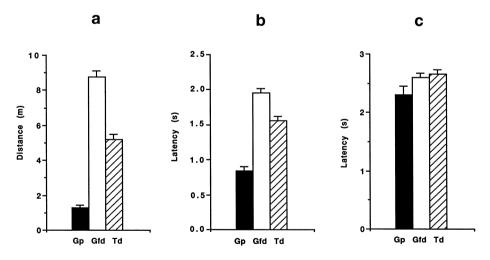


Fig. 4: Mean (+ SE) interruption distance (a) and mean latency to feed in the absence (b) or presence (c) of the novel box for the three columbids. Latency is expressed as log₁₀ time (seconds). Gp: Gregarious pigeons; Gfd: Group-feeding doves; Td: Territorial doves

p = 0.004). The three columbids differed significantly from each other in foodonly trials (Tukey test, p < 0.05). In trials with the box, pigeons ate faster on average, followed by group-feeding doves and territorial doves; only the pigeonterritorial dove difference was significant, however (Tukey test, p < 0.05). Although these average trends are ordered in the same way as they were in the experiments in captivity, this should not obscure the fact that, on several field trials, pigeon flocks failed to feed at the box within the 20-min limit of the test, a behaviour that was never seen in individually caged pigeons.

Discussion

Our results show that species identity is a much stronger predictor of observed differences in learning between pigeons and zenaida doves than is social foraging mode. Group-feeding doves from DWH were slightly faster learners than were territorial doves from StJ, but pigeons were much faster than either type of dove. Learning covaried with neophobia and latency to feed. Tests in captivity and in the field yielded broadly comparable results. Pigeons fed rapidly in cages, whether the experimenter was visible or not and whether food was presented in a familiar dish or a new apparatus. In the field, pigeons were the fastest to respond in food-only trials and tolerated a much closer approach by the experimenter. Territorial (StJ) doves consistently ranked last in all the cage tests, as well as in the novel apparatus test in the field. Group-feeding (DWH) doves also showed consistent responses to human proximity both in the field and captivity. They were the first to flee from an approaching human in the field and showed clear effects of experimenter presence in cage tests. This wariness of humans is likely due to the pest status of zenaida doves at the harbour, where they constantly have to avoid vehicles and personnel (Carlier & Lefebvre 1997).

Overall, our results confirm the differences between DWH and StJ doves reported previously (Carlier & Lefebvre 1996; Dolman et al. 1996). The learning difference clearly covaries with wariness of the new apparatus, but not with tolerance of humans, DWH doves ranking behind StJ doves when the experimenter is more salient than the apparatus (Fig. 4a and trial 1 in Fig. 3). Sparrows, Melospiza melodia and M. georgiana (Greenberg 1989) and sunfish, Lepomis gibbosus (Coleman & Wilson 1998) also differ in their response to novel objects and predation threat, suggesting that the link between neophobia and wariness of predators (including human experimenters) is more variable than the one between neophobia and learning. Only future work on marked individuals in the field can determine if factors other than social foraging mode affect the learning difference between the two types of zenaida doves. For the moment, resource distribution seems to be a key variable. DWH doves normally feed unaggressively at the large, unpredictable patches available at the harbour. However, nest sites situated on ledges only a few meters above these food spillage areas are strongly defended. Furthermore, if small patches of spatially and temporally predictable seed are offered at the harbour, DWH doves can be experimentally induced to fight off conspecifics as aggressively as StJ doves do

(Goldberg 1998). In the long run, changes in neophobia and learning should logically follow these resource-driven changes in foraging mode.

The difference between DWH and StJ doves may be robust, but it is modest compared to the overall interspecific difference between feral pigeons and zenaida doves. Artificial selection is probably an important factor here; selection for reduced neophobia has been shown in other domesticated birds, such as quails, Coturnix coturnix (Marples & Brakefield 1995), mallards, Anas platyrhynchos (Desforges & Wood-Gush 1975) and chickens, Gallus gallus (Murphy 1977). A complicating factor, however, is the unexpectedly strong effect of the novel apparatus on urban flocks of pigeon (Fig. 4c). At some of our sites (and at all sites in a pilot study conducted before this one, E. Marzinotto, unpubl. data), pigeons never came to feed within the 20-min limit of a novel object trial, despite fast responses in the food-only condition (Fig. 4b) and close tolerance of the approaching human (Fig. 4a). In the field, neophobia thus appears to be socially facilitated by a flocking effect that causes pigeons to all stay perched at the place where they fled after experimenter approach. Overall, however, this effect is sufficiently compensated for by the opposite tendency to all flock down on other trials for pigeons to maintain their mean position as the fastest of the three columbids. Despite the similarity in ordinal trends in Fig. 1 and Fig. 4c, pigeons probably achieve their relatively faster response to novel feeding situations through separate mechanisms in field flocks and in individual cages. Only future studies can tease apart the mix of individual and social factors that affect response to novelty in a gregarious bird like the pigeon.

The most important finding of our study is the positive relationship between neophobia and learning, confirmed both by the MANOVA and the multiple regression. All other things being equal, a bird that is slow to feed from a novel apparatus the first time it sees it will also be slower at learning to open it; latency to feed from the unfamiliar apparatus is in turn correlated with latency to feed from a familiar dish. Other variables not measured in this study (e.g. vigilance, attention, exploration, opportunism) could also have important effects. For example, the Lesser-Antillean bullfinch (*Loxigilla noctis*), a dietary generalist, feeds more rapidly near novel objects in the field than does the bananaquit (*Coereba flaveola*), a more specialised nectar-feeder; the bullfinch also arrives first on most field tests, however, suggesting that it is not only less neophobic, but also faster at detecting and responding to feeding opportunities (Webster & Lefebvre 2000).

The results of our multiple regression analysis are similar to those of a comparative study on finch species that differ in their use of aggression while feeding: cutthroat finches (*Amadina fasciata*) are much more aggressive than are zebra finches (*Taeniopygia guttata*), but do not show the predicted interspecific differences in either neophobia, individual learning or social learning (Whittle 1996). At the individual level, however, a re-analysis of Whittle's data shows that social learning latency can be predicted by individual learning latency, which can be predicted in turn by neophobia (both effects p = 0.03 in multiple regressions, n = 40; Whittle, Redman & Lefebvre, unpubl. data).

Several studies point to the key intervening role of neophobia in learning. The precise nature of the relationship between these two phenomena remains unknown: do they covary because initial response to novel food-related stimuli determines future performance differences in learning tasks, or because animals that learn frequently and rapidly are reinforced for initial approach to novel objects (thus showing learned neophilia, Greenberg 1992), or because neophobia and individual learning are both part of a broad set of traits that also includes social learning and innovativeness (Lefebvre 2000; Reader & Laland 1999)? Experimental manipulation of food predictability in space and time (e.g. Gray 1981; Goldberg 1998) could answer some of these questions, by testing for correlated changes in an array of traits that allow animals rapidly to track changes in resource distribution.

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