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Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados

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Previous research suggests a link between innovation rate, neophobia and behavioural flexibility in the field and in captivity. In this paper we examine three correlates of flexibility in five opportunistic avian species that feed together in Barbados: three Passeriformes (the Carib grackle, *Quiscalus lugubris*, the Lesser Antillean bullfinch, *Loxigilla noctis*, and the shiny cowbird, *Molothrus bonariensis*) and two Columbiformes (the zenaida dove, *Zenaida aurita* and the common ground dove, *Columbina passerina*). The flexibility measures are habituation to a new food patch, willingness to feed near a novel object (neophobia) and ability to obtain food from a new apparatus (problem solving). Passeriformes (in particular grackles and bullfinches), as predicted from their high innovation rate in anecdotal data, outperformed Columbiformes on all three measures. The three tests yielded similar results in the field and in captivity. Grackles, which are members of the most innovative passeriform genus in North America after *Corvus*, were by far the most successful species on the problem solving test. Individual variation in attempts to obtain food from the new apparatus was predicted by latency to approach it, which was in turn predicted by latency to feed near novel objects. This study provides experimental evidence, both in the field and in captivity, for the taxonomic differences in innovative flexibility seen in anecdotal data and suggests that neophobia is an important intervening variable in response to new feeding problems.

Animals vary in the flexibility of their foraging behaviour. Some species will, much more rapidly than others, feed near unfamiliar stimuli, opportunistically adopt new foods or foraging techniques, and modify their behaviour as a result of environmental cues and rewards. In birds, different comparative programmes have been conducted on each of these aspects of flexibility. For example, Greenberg (1983, 1984, 1990a) has shown that generalist species of warblers (e.g. chestnut-sided warbler, Dendroica pensylvanica) and sparrows (e.g. song sparrow, Melospiza melodia) will approach a food patch placed near a novel object more quickly than will congeneric specialists (respectively, bay-breasted warbler, D. castanea and swamp sparrow, *M. georgiana*). Lefebvre et al. (1997, 1998) report that new food items and unusual foraging techniques are more often observed in avian taxa with larger forebrains. Sasvari (1985a, b) has shown that urbanized species of passerines learn faster in captivity than less urbanized ones.

These comparative programmes are based on very different methodologies. Work on neophobia uses naturalistic experiments conducted in the field and in captivity,

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work on feeding innovations relies on field anecdotes collected from ornithological journals, while learning experiments routinely present captive animals with arbitrary tasks in laboratory settings. Anecdotes can be problematical because they carry a risk of overinterpretation and are subject to biases coming both from the scientist and the animal (reviewed in Mitchell et al. 1997 and the open peer commentary following Whiten & Byrne 1988). Comparative experiments on captive animals are more controlled, but can have low ecological relevance (Shettleworth & Krebs 1986). These comparative experiments also can be biased by differences in motivation and response to testing procedures that could lead to type I or type II error (summarized by MacPhail 1982; Kamil 1988). It is thus difficult to know whether comparative trends in neophobia, innovation and learning depend on the particular methods by which each flexibility measure is studied.

In this paper, we minimize these problems by combining positive features of the anecdotal and experimental approaches. To ensure ecological relevance we base our predictions on comparative trends in innovation anecdotes and develop an experimental task that mimics innovative foraging in the field. Contrary to the anecdotal method, however, we conduct systematic experiments on wild-caught birds in controlled conditions. Following Greenberg (1983, 1984, 1990a), we measure readiness to feed near novel stimuli and ask whether differences in neophobia are associated with differences in innovative problem solving. Finally, we validate the results of the cage experiments by replicating them in the field. We focus on five avian species that feed together in developed areas of Barbados (Dolman et al. 1996): three Passeriformes (the Carib grackle, Quiscalus lugubris; the Lesser Antillean bullfinch, Loxigilla noctis; the shiny cowbird, Molothrus bonariensis; taxonomy according to Sibley & Monroe 1990) and two Columbiformes (the zenaida dove, Zenaida aurita; the common ground dove, Columbina passerina). The species differ in two traits that are thought to affect behavioural flexibility, diet breadth and innovation rate, but are relatively similar for two other traits, tameness and opportunism. In Barbados, the five species readily feed close to humans and rapidly cue in on food made available in parks, restaurants and housing areas (ffrench 1991; Lefebvre 1996). In terms of diet, however, the two Columbiformes are primarily seed and legume eaters, whereas the three Passeriformes also feed on invertebrates, Q. lugubris adding vertebrate predation to its repertoire (ffrench 1991; personal observation) and L. noctis adding nectar feeding (Webster & Lefebvre 2000). More importantly, Columbiformes and Passeriformes show large differences in innovation frequency in the field, learning abilities in captivity and relative size of neural structures involved in learning and cognition. Passeriformes show a much higher innovation rate than Columbiformes (Lefebvre et al. 1997, 1998). Within Passeriformes, the genus Quiscalus is particularly innovative, yielding the second highest number of anecdotal reports (14) in North America after the genus Corvus (19). Passeriformes also have a larger forebrain than Columbiformes (Portmann 1947), as well as a larger hyperstriatum ventrale-neostriatum complex (Boire 1989; Rehkämper et al. 1991; Timmermans et al. 2000), the structure thought to be equivalent to the mammalian neocortex in birds (Rehkämper & Zilles 1991). In captive experiments on various forms of learning and cognition, Gossette (1968, 1969); Powell (1974); Wilson & Boakes (1985); Wilson et al. (1985) and Plowright et al. (1998) all report a faster and less error-prone performance in Passeriformes compared with Columbiformes.

In this study, we present birds, both in the field and in captivity, with an apparatus containing visible food that can be obtained by manipulating several lids and drawers. We assess innovative problem solving in two ways: success or failure at reaching the food and flexibility in opening attempts, measured by the number of lids, drawers and other sections of the apparatus contacted by the bird. If our task is a valid experimental analogue of innovative foraging in the field, then passeriform species (especially the Carib grackle, a member of the highly innovative genus Quiscalus) should outperform columbiforms. To ensure ecological relevance of the experiments, we present the same feeding problem to wild-caught, caged individuals and to free-moving birds in the field. Individual caging, with visual isolation from others, ensures that all subjects perform on their own, without social information or competition. Field testing allows us to see whether differences measured in captivity can be reproduced in a more natural setting; a conservative species, for example, has the option of avoiding our apparatus in the field, while its only alternative to temporary hunger in captivity is to interact with it. Finally, if neophobia is a key intervening variable in novel feeding situations (reviewed in Greenberg & Mettke-Hofmann, in press), interspecific and individual differences in innovative problem solving should be associated with differences in latency to feed near unfamiliar stimuli. Several authors have suggested that opportunistic generalism, innovation rate, learning, neural substrate size and neophobia are all correlated components of ecological flexibility. Species with larger neural structures should innovate and learn more readily (Wyles et al. 1983; Wilson 1985; Fitzpatrick 1988; Reader & Laland 1999), approaching new stimuli more quickly to incorporate more food types in their diet opportunistically (Greenberg 1990b) and colonize new habitats (Sol & Lefebvre 2000).

EXPERIMENTS IN CAPTIVITY

Methods

Subjects

We captured 15 individuals from each of the five species in baited, walk-in traps on the grounds of the Bellairs Research Institute, St James, Barbados, between May and July 1999. All individuals were adults. For four of the five species, we tested the first 15 adults caught in our traps, without attempting to equalize sex ratios. For the only species where we had a priori reasons to expect sex differences in at least one form of learning, the shiny cowbird, the sample included equivalent numbers of males (N=7) and females (N=8). Reboreda et al. (1996) have shown that female shiny cowbirds have a larger hippocampus than males; only females search for heterospecific nests in this brood-parasitic species, potentially requiring more spatial memory than the male.

Experimental procedures

Birds were removed from the traps immediately after capture, weighed, identified with individually coloured leg bands and housed in individual cages $(2.25 \times 2.15 \times 0.76 \text{ m})$ in an outdoor aviary at Bellairs. The cages were visually isolated from one another by black plastic sheets and each contained a branch perch and a shelf $(0.25 \times 0.83 \times 0.76 \text{ m})$ where food and water dishes could be placed. The birds were first given a period of habituation to captivity, in which they fed and drank ad libitum for a minimum of 24 h or until sufficiently comfortable to feed from the dish shortly after presentation (maximum: 8 days). Subjects were fed a speciesspecific diet; bullfinches were given a commercial seed mix for finches, the two columbid species were fed a seed mix for doves, and the grackles and cowbirds were fed a combination of seed, bread, cooked rice and pieces of chicken. After the habituation phase, the birds were food deprived (late afternoon to the next morning) before each

testing day. To equalize the effects of hunger on the five species, we based deprivation times on body size and presence (Columbiformes) or absence (Passeriformes) of a seed-storing crop. A larger species with a seed-storing crop can endure a longer period of time without food than a smaller species with no crop storing. Bullfinches had the smallest body weight (mean=19.8 g) and, therefore, the shortest deprivation time (mean=14.5 h). Zenaida doves had the longest deprivation time (23.9 h), since their body weight is the highest among the five species (mean=158.0 g) and they can store seed in their crop. The other three species were given deprivation times between the two extremes (grackles: mean deprivation=16.6 h, mean weight=51.8 g; cowbirds: 17.3 h, 41.0 g; ground doves (seed-storing crop): 19.7 h, 43.6 g).

Testing began the morning following food deprivation and started every day with the bullfinches, followed by the grackles, cowbirds, ground doves and zenaida doves in that order. Two tasks were given to each subject, neophobia and problem solving. The neophobia tests involved three novel objects, whose order of presentation was randomly determined. The problem solving task was given to each bird between the second and third neophobia trial. This allowed us to test for order effects in the task sequence by comparing neophobia results before and after the problem solving task.

Neophobia test

The neophobia tests followed procedures developed by Greenberg (1984) and compared the latency to feed in trials randomly featuring either a novel object or no novel object placed next to a dish of food. Each trial began with the presentation of the subject's usual feeding dish, containing approximately 50 g of the food mix used for each species. Latency to approach this dish was recorded for each subject, with the experimenter standing 2 m away, hidden behind a screen pierced with a small hole allowing observation. If the subject fed within the 20-min limit of the trial, we allowed it to eat for 5 s. If the bird did not feed, we allowed it up to two more 20-min trials that day, separated by approximately 1.5 h. If the subject still failed to feed, we allowed it up to three 20-min trials per day on successive days, after the usual overnight food deprivation. We recorded the number of days required before each bird fed as its habituation time to this task.

Once the birds had fed for 5 s, each neophobia trial then involved the experimenter approaching the cage at a constant, slow pace and randomly (by a coin toss) presenting either a control trial (which simply involved rotating the food dish) or a novel object trial (which involved rotating the dish and placing one of three objects 2 cm from the dish). The following trial would then involve the opposite condition of the one that had been randomly determined in the preceding trial. On novel object trials, we tossed the coin again to determine which of three novel objects would be used. The objects (based on Greenberg 1990a) were three straws of different colours sticking vertically out of a ball of paper, three springs approximately 2.5 cm in diameter and 10 cm tall, and a handful of curly white paper; the objects were



Figure 1. Schematic view of the clear Plexiglas box that was used for the problem solving test in captivity and in the field. Black dots represent handles that could be used to pull open the drawer or lid and to push or pull open the middle compartment. Numbers 1–13 and letters A–G, respectively, indicate the parts of the box used for the two definitions of attempts to problem solve.

mounted on pieces of cardboard that measured 8×8 cm. We recorded latency to feed from the dish (in seconds, this and all other latencies log transformed for normalization) for all trials. Birds were again given a maximum of 20 min to return to the dish in either type of trial; a failure to return was scored as a latency of 1201 s. We conducted one trial per day for each bird, for a total of six testing days (three controls and three novel objects).

Problem solving test

The second task tested each bird's problem solving performance by presenting it with a clear, $18 \times 6.5 \times$ 4.5 cm Plexiglas box (Fig. 1) filled with visible food, identical to the species-specific mix used in the neophobia task. The box could be opened and the food reached by lifting or pushing one of two lids each fitted with a metal ring (tops of the two end sections) and by pulling or pushing drawers also fitted with a metal ring (sides of the middle section and extremes of the end sections; see Fig. 1). Pushing, pulling and lifting are probably not novel motor acts for the five species, but the application of the techniques to metal rings and clear Plexiglas is likely to be unfamiliar to the birds. We first presented the box to the birds with all lids and drawers open (and the food thus accessible) after completion of the second neophobia test. If a subject did not eat from the box in the 5–6 h that followed this first presentation, we presented the open apparatus again on successive days (maximum: 3 days), after the usual overnight food deprivation. Once each subject had fed once from the open box, it was food deprived overnight and given the closed box on the following day for a maximum of 15 min. We recorded latency to first contact the box in this session, as well as two operational measures of innovative problem solving: success or failure at reaching the food and flexibility in attempts to open, assessed by counting the number of sections of the box contacted. To increase the robustness of the analyses, we used two different definitions of a section, one that split the box into 13 possible areas (numbered 1–13 in Fig. 1), the other that lumped the 13 areas into seven larger units (labelled A-G in Fig. 1). Only the pecks following the initial exploratory peck were recorded as attempts to problem solve. The maximum number of attempts for the two conditions was thus 12 and 6, respectively. Repeated pecks at a single area were counted only once. For example, a bird that pecked 25 times at one of the Plexiglas areas would be given a score of zero, since the only area contacted is the one counted for the initial exploratory peck. In contrast, a bird that pecked once at each of the 13 areas would be given the maximum flexibility score of 12. Subjects were given a single 15-min session with the box if they contacted it at least once, whether or not this led to successful feeding. Subjects that did not touch the box within the 15-min limit were given a maximum of two more 15-min sessions that day. If they still failed to contact the box, they were presented again with the open box until they fed. This was followed by the usual overnight food deprivation and testing the next day. All subjects eventually contacted the apparatus at least once. During all sessions, the experimenter was hidden behind the same screen used in the neophobia trials and recorded all dependent variables manually. To ensure observer reliability, we recorded the trials on a Panasonic PV-A208-K Camcorder and checked the manual data after the experiments. We released all birds at their site of capture at the end of the experiments; total captivity time varied between 7 and 20 days.

We conducted two types of analysis, one focusing on between-species differences in neophobia and problem solving, the other on predictors of individual differences. In the first approach we used analyses of variance (ANOVAs) and tested for interspecific differences in the two tasks and in habituation to captivity. We conducted one-way ANOVAs on (1) number of days it took birds to first feed after capture, (2) latency to initial feeding (before experimenter interruption) in the neophobia task, (3) latency to first contact of the closed Plexiglas box in the problem solving task, (4) problem solving attempts (12-area and 6-area criteria), and (5) success or failure at reaching the food. We assessed neophobia by a patch type (food only or novel object) by species factorial ANOVA on latency to feed after experimenter interruption.

For the second type of analysis, we used multiple regressions. We used individual differences in problem solving success and number of attempts successively as dependent variables. We used a logistic regression for problem solving success, because this variable was all or none, whereas we used a linear regression for number of areas contacted, which was normally distributed. We used taxonomic group of the individual (entered as a dichotomous nominal variable, Passeriformes or Columbiformes), latency to approach the box, latency to return to the novel objects, latency to first feed in the neophobia test and latency to habituate to captivity as independent variables. If neophobia and taxonomy are major determinants of problem solving, then individual variation in success and attempts to open the Plexiglas box should, in a multiple regression, be predicted by these variables.

Results

All 75 birds eventually completed the experiments. Consistent interspecific differences were found in all dependent variables (Fig. 2), with bullfinches and grackles generally scoring better than zenaida doves and ground doves, and cowbirds occupying an intermediate position. This trend was apparent in the very first measure taken after capture, the latency to eat in the ad libitum feeding phase of familiarization to captivity (ANOVA: $F_{4,70}$ =11.64, P<0.001). In Tukey tests for differences between means, grackles, bullfinches and cowbirds fed significantly sooner after capture than did zenaida doves, while grackles and bullfinches fed significantly sooner than did ground doves (P<0.05).

The first component of the neophobia task, latency to initial feeding (before experimenter interruption), revealed a significant species main effect (ANOVA: $F_{4,70}$ =12.85, P<0.001; Fig. 2a); in this case, the only significant difference between species means (Tukey test: P < 0.05) showed that grackles fed significantly faster than the other four species. For the latency to return after experimenter interruption, the factorial ANOVA revealed significant main effects for patch type (subjects slower in the presence of novel objects: $F_{1,70}$ =16.275, P<0.001) and species (F_{4,70}=13.527, P<0.001; Fig. 2b), but no significant interaction between these variables ($F_{4,70}=0.124$, P=0.304). There was no significant difference (ANOVA: $F_{1,70}=0.582$, P=0.448) in latency to feed in the neophobia tests (two and three) conducted before and after the problem solving task, which suggests that order effects between the tests were negligible. There were also no significant differences in response to the three objects used in these tests (ANOVA: $F_{2,22}$ =0.052, P=0.950).

Eight subjects solved the closed box task, six grackles, one cowbird and one zenaida dove. Grackles and bullfinches were significantly faster at approaching the box than either ground doves or zenaida doves, while grackles were significantly faster than cowbirds (Tukey test: P<0.05; species main effect, ANOVA: $F_{4,70}$ =8.94, P<0.001; Fig. 2c). The interspecific differences in number of attempts to open (ANOVA: 12 pecks: $F_{4,70}$ =5.51, P=0.001; 6 pecks: $F_{4,70}$ =5.224, P<0.001; Fig. 2d) diverged slightly from previous patterns: bullfinches made significantly more attempts than zenaida doves or cowbirds (for 12 and 6 pecks) and ground doves made significantly more attempts than cowbirds (for 12 pecks; Tukey test: all P<0.05).

None of the independent variables included in the logistic regression significantly predicted failure or success to open the box, probably because of the small number of subjects that succeeded. In contrast, individual differences in number of attempts to open the box, measured by the 12-area criterion, were significantly predicted by latency to approach the box (P=0.037). Taxonomic group differences, as well as other latency measures in the experiments, were nonsignificant in this analysis (total R^2 of the regression=0.177, $F_{5,69}$ =2.977, P=0.017). The significant predictors of latency to approach the box were latency to return to the novel object (P<0.001) and latency to feed before interruption in the neophobia trials (P=0.008; total R^2 of the regression=0.720, F_{4.70}=44.965, P<0.001). Latency to feed before interruption (P<0.001) and taxonomic group (P=0.013) were the only significant predictors of



Figure 2. Mean±SE performance in the different phases of the captive test in bullfinches (BF), grackles (GR), cowbirds (CB), ground doves (GD) and zenaida doves (ZD). (a) Latency (s) to arrive and feed before interruption; (b) latency (s) to return to food after interruption; (c) latency (s) to approach the Plexiglas box; (d) number of attempts made to open the Plexiglas box (12-area criterion).

latency to return to the novel object (total R^2 of the regression=0.552, $F_{3,71}$ =29.161, P<0.001). All multiple regressions conducted with the 6-area criterion were nonsignificant.

EXPERIMENTS IN THE FIELD

Methods

Sites

We conducted experiments in July and August 1999 in areas adjacent to the ones used for capture in the preceding section. We chose 15 sites in three neighbouring areas of St James: Folkestone Park, St James Church and a part of the Bellairs Research Institute. Distance between sites was at least 20 m, the mean diameter of ground areas defended by zenaida doves at Bellairs (Goldberg 1998), to decrease the probability of repeated sampling of territorial birds.

Experimental procedures

The experiments followed a similar format to those conducted in captivity. They began with a habituation phase in which each site was baited with 40 g of grain, finch food, bread and rice. The food (hereafter referred to as mixed food, suitable for all five species) was presented on a large green leaf to facilitate detection by the birds and removal by the experimenter. Sites were checked after 24 h to determine whether all food had been consumed. This was the case at 14 of the 15 sites, which, we consequently retained for the rest of the study.

Neophobia test

We conducted three matched pairs of neophobia trials on different days at each of the sites. We presented a 40-g patch (10 cm in diameter) of mixed food at a site and recorded the feeding latency of the first bird to arrive. If no bird fed within 20 min, we terminated the trial and repeated it the next day. Once a bird started to feed, the experimenter waited for approximately 10 s to determine whether any other birds in the vicinity (either perching in trees or on the ground nearby) were likely to approach the site. If other birds were in the vicinity, the experimenter waited until the birds arrived at the patch. If not, or when the arriving birds had started to feed, the experimenter then approached the feeding station at a constant slow pace and randomly (by coin tossing) presented either a control trial (which involved touching the food) or a novel object trial (which involved touching the food and placing one of three novel objects 2 cm from it). The following trial would then involve the opposite condition of the one that had been randomly determined in the preceding trial. On the novel object trials, we tossed the coin again to determine which of the three novel objects would be used. The novel objects were the same as those used in the experiments conducted in captivity. Birds were given a maximum of 20 min to return to the food. We recorded latency to feed from the dish (in seconds, log transformed for normalization) for all trials, as well as the species identity of all birds. Failure to return after interruption was scored as a latency of 1201 s. Field conditions allowed an additional dependent variable to be recorded, the distance at which the birds interrupted their initial feeding when the experimenter walked towards the patch; as the experimenter approached, she dropped a marker at the spot where she was when the last bird of each species stopped feeding and moved away, either on foot (typical of Columbiformes) or in flight (typical of Passeriformes). Distance between the marker and the dish was measured with a tape at the end of each trial. One trial was conducted per day at each of the 14 sites, for a total of six testing days per site (three controls, three novel objects). Except for the approach phase, the experimenter was located 15 m away from the patch during all trials.

Problem solving test

The second experiment tested problem solving performance in the field with the same Plexiglas box used in captivity. As in the tests conducted in captivity, this task was presented between the second and third neophobia trial. Each trial again began with the presentation of the box with all drawers open and lids removed, allowing the birds to reach the 85 g of mixed food placed inside. Once at least one bird pecked at the box, the experimenter waited for approximately 10 s to determine whether any other birds in the vicinity were likely to approach. The experimenter then approached the box at a constant slow pace and closed all of the drawers and lids. The latency and species identity of the birds returning to the box was then recorded, along with the number of attempts (12and 6-area criteria, as in captivity) made by the bird to reach the food. The birds were given 10 min to solve the problem. If a bird was successful it was allowed to feed for 30 s, after which the box was removed and 20 g of food was left at the site. If a bird attempted to open the box but was unsuccessful within the 10-min limit, the box was removed and 20 g of food was left at the site. If a bird made no attempt to contact the box in 10 min, the apparatus was removed and presented again at the site 2 h later, for a maximum of three trials per day on successive days.

All five species were present at all 14 sites. However, successful completion of all tests by all species occurred at only four of the sites; at the remaining 10 sites, anywhere between two and four of the species were present on any given trial, leading to unequal sample sizes for the species. For a given species at a given site, we kept only those cases where the entire sequence of habituation,

neophobia and problem solving tests were completed. This yielded a sample size of 10 complete cases for bullfinches, 8 for grackles, 6 for cowbirds, 10 for ground doves and 12 for zenaida doves. Only one complete test sequence per species was run at each site. Because the field experiments were conducted after the tests conducted in captivity, a total of 15 banded individuals per species could possibly visit the test sites. The identity of these individuals was noted if they came to the patches. Banded individuals were seen on 15% of the tests. When a banded bird was noted at one site, it had a 75% probability of being present only at that site, which suggests strong site fidelity; this probability increased to 84% in the territorial zenaida doves, 80% in ground doves and to 100% in bullfinches. Because of these high probabilities, we used in our ANOVAs a repeated measures assumption for the sequence of tests conducted at a particular site. This assumption is statistically more conservative than that of independent cases and reduces our chance of finding a significant result. Contrary to our experiments in captivity, however, no multiple regressions were conducted on these repeated measures. This is because we cannot be as certain in the field as we can in captivity that a score for the different variables recorded at one site is yielded by exactly the same individual.

Results

Bullfinches were the first species to arrive at the patches on 76% of the trials they attended (Fig. 3); grackles arrived first on 39% of trials. The probability of later arrival by these two species declined linearly, while the order of arrival for the other three species peaked at intermediate ranks (Fig. 3): cowbirds were most likely to arrive third (43%), while ground doves and zenaida doves were most commonly the second species to arrive (45 and 49%, respectively).

As in the experiments in captivity, consistent interspecific differences were seen in all phases of the field tests. Again, grackles and bullfinches generally scored higher on most tests, ground doves and zenaida doves lowest, and cowbirds occupied an intermediate position (Fig. 4). The ANOVA on latency to initial feeding at the patches revealed a significant difference between species ($F_{4,44}$ =9.20, P<0.001; Fig. 4a). A Tukey test on differences between means showed that bullfinches fed significantly faster than the other species (P<0.001). The ANOVA on interruption distance again revealed a highly significant effect of species ($F_{4,44}$ =13.45, P<0.001); zenaida doves and cowbirds fled sooner than grackles and bullfinches, and ground doves fled sooner than bullfinches (Tukey test: P<0.05).

The neophobia test revealed a significant interspecific difference in latency to return and to feed after the interruption (ANOVA: $F_{4,44}$ =12.510, P<0.001; Fig. 4b), as well as a significant effect of presence versus absence of the novel object (birds were slower to return and feed in the presence of the novel object: $F_{1,44}$ =13.124, P=0.001); the interaction between these two variables was nonsignificant ($F_{4,44}$ =1.352, P=0.266). Grackles were significantly faster at returning to the patch than cowbirds,



Figure 3. Percentage of trials in which each species arrived at a feeding site as a function of other species present.

ground doves and zenaida doves, whereas bullfinches were significantly faster than either of the doves (Tukey test: *P*<0.05). An ANOVA on the performance of tagged versus untagged birds indicated that previous experiences in captivity had no effect on performance in the field (latency to arrive: $F_{1,35}$ =2.511, *P*=0.122, latency to return: $F_{1,35}$ =0.093, *P*=0.762).

In the box task, five individuals, two grackles and three bullfinches, successfully opened and reached the food. None of these birds had been part of the tests that were conducted in captivity. Of the 13 birds that opened the box in the tests conducted in the field and in captivity, 12 were Passeriformes and only one a Columbiforme; this frequency difference was significant at the 0.05 level (Yates corrected: χ_1^2 =5.88). The ANOVAs conducted on latency to contact the box and on number of areas contacted on the box (12- and 6-area criteria) revealed no significant differences between species (12 pecks: $F_{4,41}$ =2.317, P=0.073; 6 pecks: $F_{4,41}$ =1.950, P=0.120; latency to approach: $F_{4,41}$ =1.746, P=0.158), but trends were in the same direction as they were in captivity for all species except ground doves (Fig. 4c, d).

DISCUSSION

Three conclusions can be drawn from the results of the field and cage experiments: (1) innovative problem solving ability varies with taxonomic group in the direction predicted by our hypothesis; (2) interspecific and individual differences in problem solving are in the same direction as are differences in neophobia and

habituation; and (3) results from the field and from captivity were very similar. Table 1 summarizes these findings in a simplified format, ranking the five species on their relative performance on each dependent variable; reducing interspecific differences to the ordinal level removes some of the detail of the interval level analyses, but it also allows patterns to emerge more easily.

Table 1 shows that, over all tests, performance of the three Passeriformes outranked that of the two Columbiformes. Either grackles or bullfinches ranked first on almost all tests, while zenaida doves or ground doves ranked last. The only major outlier in this pattern was the contrasting success rate of bullfinches on the Plexiglas box in captivity and in the field. The overall trends parallel the differences between Passeriformes and Columbiformes in innovation rate, size of the forebrain (Lefebvre et al. 1997, 1998) and hyperstriatum ventraleneostriatum complex (Boire 1989; Timmermans et al. 2000), as well as learning and cognition (Gossette 1968, 1969; Powell 1974; Wilson & Boakes 1985; Wilson et al. 1985; Plowright et al. 1998). The results suggest that problem solving performance may be a good experimental estimate of innovation, which is by definition rare and impossible to elicit at will in controlled conditions. The fact that grackles were more successful than any other species on the box opening test further supports this idea. Innovation data are not available for the West Indies, but in the closest area, North America, the genus Quiscalus has the highest innovation frequency (14) in the parvorder Passerida, coming second only to the genus Corvus (19 innovations) when all Passeriformes are included (L.



Figure 4. Mean±SE performance in the different phases of the field test in bullfinches (BF), grackles (GR), cowbirds (CB), ground doves (GD) and zenaida doves (ZD). (a) Latency (s) to arrive and feed before interruption; (b) latency (s) to return to food after interruption; (c) latency (s) to approach the Plexiglas box; (d) number of attempts made to open the Plexiglas box (12-area criterion).

Table 1. Ranking of bullfinches (BF), grackles (GR), cowbirds (CB), ground doves (GD) and zenaida doves (ZD) on their relative performance on dependent variables tested in the field and in captivity

| | Tests in captivity | | | | | Tests in the field | | | | |
|-----------------------------|--------------------|----|-----|-----|-----|--------------------|----|----|----|----|
| | BF | GR | СВ | GD | ZD | BF | GR | СВ | GD | ZD |
| Habituation | 2 | 1 | 3 | 4 | 5 | _ | _ | _ | _ | _ |
| Interruption distance | _ | | _ | _ | _ | 1 | 2 | 5 | 4 | 3 |
| Latency to arrive | 2 | 1 | 3 | 5 | 4 | 1 | 2 | 4 | 5 | 3 |
| Latency to return | 2 | 1 | 3 | 5 | 4 | 2 | 1 | 3 | 5 | 4 |
| Latency to approach | 2 | 1 | 3 | 5 | 4 | 1 | 2 | 3 | 5 | 4 |
| Attempts to open (12 areas) | 1 | 3 | 4 | 2 | 5 | 1 | 2 | 3 | 4 | 5 |
| Success at opening box | 4.5 | 1 | 2.5 | 4.5 | 2.5 | 1 | 2 | 4 | 4 | 4 |

Lefebvre, unpublished data). In contrast, *Zenaida* and *Columbina* show no innovations, *Molothrus* shows only one, the genus *Loxigilla* being absent from North America.

Despite this overall similarity between success rate in our task and innovation rate in the field, some of our results need to be clarified. For example, the fact that only one of our five species, the grackle, showed a high success rate in the problem solving task suggests that the task may have been too difficult for the four other species. Future studies using multiple tasks with greater variation in the level of difficulty than that used in the present study may reveal that species predicted to be less innovative than other species will show reasonable levels of success on at least one task. Secondly, our assumption that flexibility in attempts to open the box is a valid operational measure of innovation is supported by the results of the linear regression conducted on captive birds, but not by those of the logistic regression. As predicted, flexibility in attempts (number of different areas contacted) is associated both with neophobia and taxonomic group, but its relationship with opening success in the logistic regression failed to reach significance. This result may be an artefact of low variance in opening success, but it may also mean that success does not depend on the variability of the means used to solve the problem. Other predictors of success need to be considered (looking, for example, at the motor acts that immediately precede successful opening), and the best ones retained for future studies.

Overall, the differences between Passeriformes and Columbiformes in our tests cannot be attributed to motivation or features of the captive testing situation. First, field tests yield very similar results to cage tests, with the exception of box opening success in bullfinches. Potentially confounding variables in the captive testing situation, such as the stress of captivity, the close proximity of a human experimenter, the controlled food deprivation schedule, the absence of feeding alternatives outside the test, and the social isolation of single cages, were all eliminated in the field, yet the results from the field and the captive testing situations showed very similar interspecific differences. Body weight differences within taxa are also large, potentially causing differences in motivational effects despite our efforts to adjust deprivation time. Grackles weigh on average three times as much as bullfinches, and zenaida doves have triple the body weight of ground doves, yet the two Passeriformes and the two Columbiformes show very similar performances. Our experiments also include three novel objects in the neophobia test and three ways of reaching the food in the problem solving test. Varying experimental conditions is one of the controls suggested by Kamil (1988) against confounds caused by features of the testing situation. Our use of a box that allowed pulling, pushing or lifting was a further guard against favouring particular species, a frequent problem in comparative tests. If ring pulling had been the only option, Quiscalus and Molothrus may have been favoured because of the strength and/or greater manipulative ability of their beaks, but pushing the drawer or pecking off the lightweight lid was simultaneously available to the smaller Loxigilla and the less manipulative beaks of Columbiformes. The fact that three individuals from the smallest species, the bullfinch, successfully opened the box is additional evidence that all birds could technically solve the task and that failure to do so reflects problem solving performance rather than physical limitations.

An important issue in comparative research (Shettleworth 1998) is the extent to which different aspects of learning and cognition are correlated. Like Greenberg (1990a) and Daly et al. (1982), we found that flexibility was correlated with neophobia. As seen in Table 1, the five species showed similar ranks on all tests presented. Multiple regressions also showed similar trends at the individual level. Contrary to the most stringent criterion for neophobia, however, there was no significant interaction between species and presence or absence of a novel object. Differences were also seen in the food-only controls, in flight distance and latency to arrive. Similar trends were found in a recent study

comparing bullfinches and bananaquits, *Coereba flaveola*, at artificial nectar sources (Webster & Lefebvre 2000). These trends suggest that neophobia may sometimes be confounded with small differences in tameness and latency to detect new feeding opportunities, despite the broad interspecific similarities in opportunism and anthropophilia that we assumed at the start of this study. Such confounds are not present in all cases. In columbids (*C. livia* and *Z. aurita*; Seferta et al., in press), sparrows (*M. melodia* and *M. georgiana*; Greenberg 1989), and sunfish (*Lepomis gibbosus*; Coleman & Wilson 1998), neophobia and response to possible predators do not show correlated trends.

Multiple regressions further revealed that individual variance in problem solving attempts could be predicted from latency to approach the box, which could in turn be predicted by latency to feed near novel objects. The lack of significant differences between the neophobia trial conducted before the box test and the one conducted after suggests that the result of the regression does not simply reflect task order. The results confirm Greenberg's (1983, 1984) suggestion that neophobia is a key intervening variable in flexible responses to new feeding situations. Whether an animal has to approach unfamiliar stimuli while foraging (neophobia), try a new food type or foraging technique (innovations), or modify its behaviour as a result on positive or negative consequences (learning), similar or correlated processes may be occurring. Support for this view is provided by a recent study showing that innovation rate, social learning, tool use and neocortex size are all correlated across primate species (Reader & Laland 1999).

Comparative data on feeding innovations in the field can be criticized for their anecdotal and uncontrolled nature. Conversely, learning tests on captive species often have low ecological validity. Our study combines field and cage tests on multiple species from two widely divergent taxa that feed together in the wild. Through its methodology and choice of species, the study bridges the gap between anecdotal field data and learning tests in captivity. Several complementary lines of evidence in birds and primates (Reader & Laland 1999) now suggest consistent taxonomic differences in behavioural flexibility that could be associated with information processing capacity and opportunism.

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