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ORIGINAL PAPER

Innovativeness and the effects of urbanization on risk-taking behaviors in wild Barbados birds

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Abstract The effects of urbanization on avian cognition remain poorly understood. Risk-taking behaviors like boldness, neophobia and flight distance are thought to affect opportunism and innovativeness, and should also vary with urbanization. Here, we investigate variation in risk-taking behaviors in the field in an avian assemblage of nine species that forage together in Barbados and for which innovation rate is known from previous work. We predicted that birds from highly urbanized areas would show more risk-taking behavior than conspecifics from less urbanized parts of the island and that the differences would be strongest in the most innovative of the species. Overall, we found that urban birds are bolder, less neophobic and have shorter flight distances than their less urbanized conspecifics. Additionally, we detected between-species differences in the effect of urbanization on flight distance, more innovative species showing *smaller* differences in flight distance between areas. Our results suggest that, within successful urban colonizers, species differences in innovativeness may affect the way species change their risk-taking behaviors in response to the urban environment.

Keywords Urbanization · Innovation · Neophobia · Flight initiation distance

Introduction

Urbanization and human-induced environmental changes in general have strong effects on biodiversity (Chace and Walsh 2006; McKinney 2002; Shochat et al. 2006; Sol et al. 2014). Although urbanization is known to cause important loss of species diversity (Shochat et al. 2010a, b), some species are able to thrive in urban ecosystems. Accumulation of evidence showing differences in behavior between organisms living in the cities and their rural conspecifics suggests that behavioral adjustments may explain the success of these species [see Sol et al. (2013) for a review]. Many of these behavioral changes imply adjustments of risk-taking behaviors, whereby urban populations tend to be less risk-averse than rural ones. For instance, urban Barbados bullfinches *Loxigilla barbadensis* are bolder than their rural counterparts (Audet et al. 2016), and the neophobia of a bird assemblage in the Pampas region in Argentina is higher in suburban compared to urban areas (Echeverría et al. 2006). Similarly, within species, flight distances from humans decrease in urban compared to rural areas (Møller 2008b; Samia et al. 2015a, b).

These behavioral traits are also expected to affect innovativeness and cognitive performance. The risk-reward continuum that shapes behavioral variation is thought to be associated with the speed-accuracy trade-off that partly explains inter-individual and inter-species differences in

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cognition (see Sih and del Giudice 2012). Urbanization may thus also alter an individual's cognition and innovativeness. Alternatively, innovativeness and cognitive abilities, by affecting an individual's behavioral plasticity, may determine which species will thrive in urban environments, and which ones will not.

Three different mechanisms have been proposed to explain changes in behavior in response to the urban environment (see López-Sepulcre and Kokko 2012; Sol et al. 2014). First, selection may favor less risk-averse individuals in urban environments (adaptation mechanism). Second, individuals may directly change their behavior in response to the urban environment (behavioral plasticity mechanism). Finally, the urban environment may filter individuals, so that only those with the proper behavior may colonize cities (sorting/filtering mechanism). The role of adaptation has been demonstrated in some rare cases. For example, Mueller et al. (2013) revealed consistent genetic divergence between urban and rural populations of the blackbird *Turdus merula* in a polymorphic locus of SERT, a candidate gene that is linked to harm avoidance behavior.

In contrast, the two other mechanisms (behavioral plasticity and sorting/filtering) are more difficult to demonstrate directly. Some evidence that birds with relatively larger brains are better able to exploit urban environments suggests that behavioral plasticity may favor settlement in cities (Møller 2009; Maklakov et al. 2011), though this result is inconsistent across studies (Kark et al. 2007; Sol et al. 2014). Because relative brain size is a correlate but not a direct measure of behavioral plasticity (e.g., innovativeness, Timmermans et al. 2000) and cognition, these discrepancies are difficult to interpret. In addition, behavioral plasticity could just be one strategy among others that favor colonization of a given urban environment, explaining the difficulty of detecting consistent trends at a global scale (Sol et al. 2014). Direct tests are needed to better understand the potential effect of behavioral plasticity on urbanization.

Here, we aim at testing, within an assemblage of birds displaying opportunistic foraging behaviors, whether variation in innovativeness between species predicts variation in risk-taking behavior across environments. We used the avian feeding innovation database initiated by Lefebvre and colleagues (Lefebvre et al. 1997, 1998; Timmermans et al. 2000; Overington et al. 2009) to compare feeding innovation rates with risk-taking behaviors in birds occurring in differently urbanized areas of Barbados. Barbados birds have been extensively investigated for their behavior, innovativeness and cognition (e.g., Webster and Lefebvre 2001; Morand-Ferron and Lefebvre 2007; Overington et al. 2009; Ducatez et al. 2014), and recently, differences in problem-solving abilities (a proxy of innovativeness; Griffin and Guez 2014) were demonstrated between urban and rural individuals of *L. barbadensis* (Audet et al. 2016). Intense anthropogenic modification of the original environment on the island of Barbados provides birds with many novel habitats and food sources. Both innovative (e.g., members of the Icteridae (Carib grackles *Quiscalus lugubris* and Shiny cowbirds *Molothrus bonariensis*) and Tyrannidae families (gray kingbirds *Tyrannus dominicensis*)) and non-innovative (e.g., members of the Columbidae family: Zenaida dove *Zenaida aurita* and Common ground-dove *Columbina passerina*) species occur in urbanized areas in Barbados, favoring an investigation of how differences in innovativeness can affect behavioral changes in response to urbanization.

Using field experiments on wild birds, we measured risk-taking behaviors in two experiments: flight initiation distance (FID) and response to novel objects (neophobia). FID, the distance at which an individual approached by a predator initiates flight (Blumstein 2003), is a proxy of boldness (reaction to a risky situation, Réale et al. 2007) and tolerance to disturbance (Blumstein 2006), and is expected to affect innovation opportunities, especially in urban environments. Bolder and more tolerant species/individuals are likely to invest more time in exploring such opportunities than warier ones. In addition, FID is also known to vary within species with urbanization, urban populations tending to have shorter FID (Møller 2008a, b, c; Samia et al. 2015a). However, to our knowledge, the association between FID and innovativeness has never been tested. Neophobia is known to vary with urbanization (e.g., Echeverría and Vassallo 2008; Audet et al. 2016) and is associated with an individual's and a species' propensity to innovate and solve new problems (Greenberg and Mettke-Hofmann 2001; Webster and Lefebvre 2001; Greenberg 2003; Overington et al. 2011).

We measured FID in urban and rural areas around the island. In a separate experiment, we assessed neophobia by habituating birds to feeders and measuring the effect of introducing a novel object close to the feeder on their latency to feed after disturbance. We predicted that experience with anthropogenic food sources and exposure to humans would be one key variable affecting novelty responses in our birds. We thus selected study sites differing in their proximity to anthropogenic food sources to test for small-scale variation in behavior.

Flight initiation distance

Study area

The data were collected from February to May 2012. A total of 212 FIDs were opportunistically induced and recorded in both urban and rural landscapes of nine regions, in St James, St Thomas, St Peter, Christ Church and St Philip parishes, covering the west, south and center of the island. Nine species participated in this experiment: *C. passerina*, *Z. aurita, L. barbadensis*, *M. bonariensis*, *Q. lugubris, T. dominicensis*, as well as red-necked pigeons *Patagioenas squamosus,* black-faced grassquits *Tiaris bicolor* and bananaquits *Coereba flaveola.* For each site, we estimated the distance to the closest anthropogenic food source (picnic area, restaurant terrace) measured as a continuous variable. This variable does not convey the entire spectrum of variation in avian contact with humans and of familiarity with anthropogenic food. Variables such as the amount of anthropogenic food available in a given radius around each site might be more relevant, but we did not have access to such data. Alternatively, considering the density of food sources in a given area might seem more appropriate. This variable is, however, difficult to establish, and does not necessarily provide a better estimate of anthropogenic food availability: terraces' size, food types and human attendance strongly vary across places. We thus decided to consider the distance to the closest anthropogenic food source as a cue of avian contact with humans and of familiarity with anthropogenic food. We also determined whether the site was an urban or rural one. Following Møller (2010), we defined urban areas as built-up areas with continuous buildings, interspersed by roads and city parks, and rural areas as open farmland, forests or other habitats with scattered, non-continuous houses and farms. In most cases, we recorded the FID of a maximum of one or two individuals per species per site. In some trials, a maximum of 5 different birds per species were recorded, when it was possible to assess that these birds were different individuals (e.g., via morphological differences).

Experimental procedure

To measure flight initiation distances, we followed a protocol similar to the one described in Blumstein (2006) and Møller (2008a, b, c). After locating a bird, the observer (SD) moved at a constant walking speed toward the individual. At the same time, he recorded the number of steps (1 step being approximately equal to 1 m). Both the FID (distance from the observer to the bird when it first took flight) and the starting distance (distance from where the observer started walking toward the bird) were recorded. The starting distance is known to affect the FID (Blumstein 2006) and was thus included in the analyses. The birds' height above ground was recorded to the nearest meter to estimate Euclidian distance (square root of the sum of the squared horizontal distance and the squared height above ground level).

Analyses

To test whether FID varied with species and environment, we used linear mixed models with FID (continuous) as response variable, and starting distance (continuous), species, and either urbanization (binary variable, urban vs rural) or distance to anthropogenic food (continuous) as explanatory variables. To test whether variation in FID was better predicted by urbanization or distance to anthropogenic food, we thus built one model including one or the other of these variables, and then compared their AIC. To test whether the environmental effect on FID varied across species, we also included the interaction effects between species and urbanization (or distance to the anthropogenic food). Site was included as a random effect. FID was log-transformed to meet normality assumptions. We used Tukey HSD tests for post hoc comparisons.

We also tested whether variation in FID and changes in FID across environments were predicted by innovation rate. The innovation data for the species were drawn from an extended version of the feeding innovation database initiated by Lefebvre and colleagues (Lefebvre et al. 1997, 1998, 2016; Timmermans et al. 2000). This database relies on exhaustive coverage of available volumes from 100 regional ornithology journals published between 1944 and 2014 [see details in Lefebvre et al. (1997), Overington et al. (2009), Lefebvre et al. (2016)], covering North America, western Europe, Australia, New Zealand, the Indian sub-continent, southern Africa and the Neotropics. Innovation reports are included in the database if they contain words such as 'novel,' 'opportunistic,' 'first description,' 'not noted before' and 'unusual' (see examples in Lefebvre et al. 2016). Because the number of innovations recorded by ornithologists is usually higher for more intensely studied species (Sol et al. 2005; Overington et al. 2009, 2011), we initially aimed at correcting innovation frequencies by research effort, estimated as the number of papers published for the species between 1978 and 2008, according to the online version of the Zoological Record (Ducatez and Lefebvre 2014). However, in our subset of species, research effort did not significantly affect innovation rate ($p = 0.359$) so we did not keep research effort in the analyses.

To test whether innovation rate predicted a species FID and the effect of urbanization (or distance to anthropogenic food) on FID, innovation was included in a second run of the analyses, replacing species identity with its innovation rate (continuous) as a fixed effect in the model, and adding species identity as a random effect nested within site. We also included phylogeny [from Jetz et al. (2012)] as a random effect in a phylogenetic linear mixed model with Markov chain Monte Carlo (MCMC) techniques using the R package MCMCglmm (Hadfield 2010), the results of which are shown in the supplementary material only given the fact that our results were identical with or without phylogenetic corrections. Because body mass is a major predictor of tolerance of human disturbance (Samia et al. 2015a, b), we initially included it (from Dunning 2008 and our own data on *L. barbadensis*) in the models to make sure that it did not confound any effect of innovation. We removed it in the final models as it was never significant (pMCMC > 0.223). All analyses were lead using R 3.2.3 (R Development Team 2008).

Results

The model with the best AIC was the one where the environment was measured by urbanization (rural vs urban site) instead of distance to the closest anthropogenic food source (ΔAIC = 8). We thus only consider this model in the rest of the analysis. FID was significantly explained by all fixed effects, including the interaction between species and urbanization (Table 1). Over the main effect of species, FID was higher in rural sites (Fig. 1). At the level of particular species, the post hoc comparison was significant in *Z. aurita* only (Tukey HSD: $p < 0.001$, other $p > 0.730$). In rural areas, *Z. aurita* had a significantly higher FID than *L. barbadensis* ($p = 0.027$) and *C. flaveola* ($p = 0.036$), and in urban areas, *P. squamosus* had a higher FID than *L. barbadensis* ($p = 0.038$). All other interspecies comparisons were not significant (Tukey HSD tests: all $p > 0.078$).

After including innovation rate instead of species identity as a fixed effect and adding species identity as a random effect nested in the site, we found that the interaction between urbanization and innovation rate significantly affected FID (Table 2). Analyzing separately the effects of innovation on FID in rural and urban area, we found that innovation rate significantly explained FID variation in rural ($p = 0.028$) but not urban areas ($p = 0.589$): species with a higher rate of innovation had a smaller FID in rural, but not urban, areas (Fig. 1). This result remained similar when phylogeny was included as a random factor (see Supplementary Material).

Experiment 2: boldness and neophobia

Study area

The study was carried out in and around Holetown, St James, Barbados, between April and June 2012. We chose six sites, three located close to anthropogenic food sources (within 60 m of either picnic areas or restaurant terraces) and three located farther from these sources (more than 250 m away). Distances between sites were >200 m, to decrease the probability of repeated sampling of territorial birds. Because the 6 sites sampled in experiment 2 were relatively close from each other, we could not objectively segregate them into urban and rural sites, as was done in experiment 1. Instead, we assessed the extent of urbanization around each site to test whether landscape structure was a better predictor of birds' behavior than the distance to the closest anthropogenic food sources. To that aim, we used the percentage of anthropogenic structures in a 1 and 5 ha circle around the experimental point. The maximum distance between two different sites was 1.2 km.

Experimental procedure

We compared the responses of individuals during trials when one novel object was placed near a feeder (treatment) with those of individuals in control trials without the novel object near the feeder (control). We established one feeding station per site that consisted of a 20-cm-diameter PVC dish. The feeders were not removed during the experiment and were replenished with 1 kg of a mixture of seeds every day during 7 days prior to the experiment, to habituate the birds.

The experiment consisted of three 120 min sessions, one per day, made on three consecutive days. Twenty minutes

Table 1 Effects of environmental variables and species on flight initiation distance and on birds' behavior during control and novel object trials in Barbados birds

Response variable	Explanatory variable	*df*	*F*	*p*
Flight initiation distance	Starting distance	1, 185	16.853	<0.001
	Species	8, 185	2.758	0.007
	Urbanization	1, 8	13.46	0.006
	Species × urbanization	8, 185	3.019	0.003
Latency to feed after disturbance	Trial type	1, 520	16.968	<0.001
	Distance to anthropogenic food	1, 4	11.212	0.029
	Species	4, 520	55.950	<0.001
	Species × trial type	4, 520	4.245	0.002
	Species × distance to anthropogenic food	4, 520	12.181	<0.001

Site was included as a random effect in all models

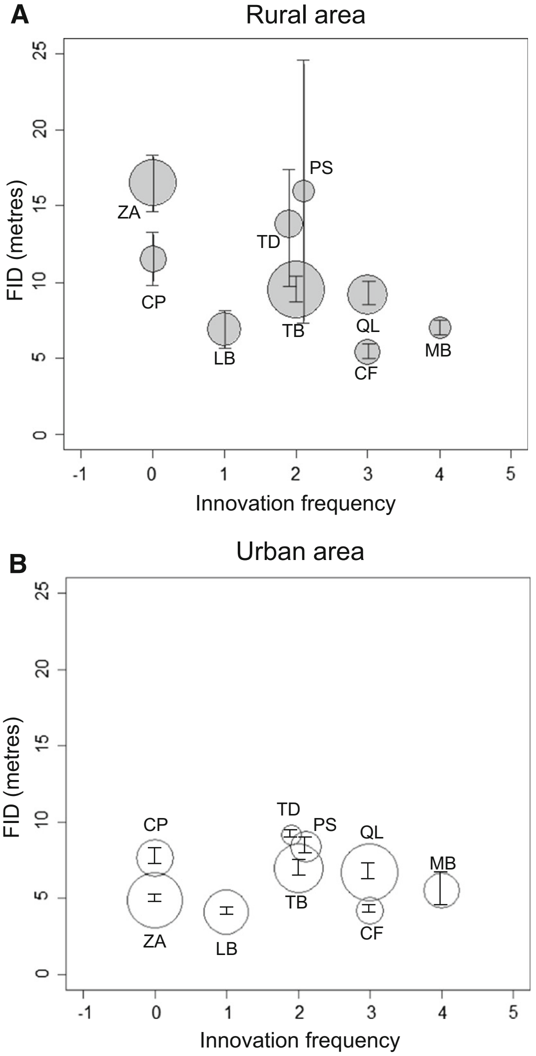

Fig. 1 Effect of innovation rate on FID measured in urban (**a**) and rural (**b**) areas in Barbados birds. *Each circle* represents one species, and circles are sized proportionally to sample size, ranging from three FID observations (e.g., in rural area, *Molothrus bonariensis* with four innovations) to 30 FID observations (e.g., in urban area, *Quiscalus lugubris* with three innovations). Mean ± SE are given. *CF Coereba flaveola*, *CP Columbina passerina*, *MB Molothrus bonariensis*, *LB Loxigilla barbadensis*, *PS Patagioenas squamata*, *QL Quiscalus lugubris*, *TB Tiaris bicolor*, *TD Tyrannus dominicanus*, *ZA Zenaida aurita*

before a session started, the observer replenished the feeder. We then alternated three 20 min control trials with three 20 min treatment trials. We thus conducted three sessions of six trials (three controls and three treatments) per site, yielding a total of 18 trials per site (nine controls and nine treatments). A control trial involved rotating the food dish and touching the food, while a novel object trial involved rotating the dish, touching the food and placing the new object(s) near the feeder. The order of control and novel object trials was random for each site and session number, but changed from 1 day to the other, and control and treatment trials were always alternated. The objects included: two vertical yellow plastic sticks (12 cm height) positioned on each side of the dish (1 cm from the dish), a colorful plastic ball (4 cm diameter), and three colorful plastic balls (4 cm diameter; different colors from the unique ball) positioned around the dish, at equal distance from each other. The novel objects were positioned 2 cm from the edge of the dish, and each object was used once per session, and presented to the birds a total of three times (once per day, in a random order). The objects were chosen to be unfamiliar to the birds, and sufficiently different to avoid a habituation to the novel objects because of similarities between them. Previous experiments in captivity with two species (*L. barbadensis* and *Q. lugubris*) confirmed their sensitivity to these objects (note that the individuals observed at the feeder were different from the ones used in captivity). The use of one vs three colorful bowls allowed us to expose the birds to different types of new objects: the first colorful ball, displayed alone, was of particularly bright and vivid color, but its position on only one side of the dish made it possible for birds to feed from the other side of the dish without approaching the new object too closely. In contrast, the three balls were less vivid, but placed all around the feeder, so that the birds had to get closer to the objects if they wanted to feed. Finally, the two yellow plastic sticks were intermediate in both how vivid their coloration was and the fact that they were on each side of the feeder, so that birds had to approach them more closely than the single ball, but less so than the three balls. We initially conducted analyses including the type of object as a covariable, but it only tended (not significantly, results not shown) to affect the latency to return to the feeder so we did not consider this effect in the analyses presented here.

Sessions were recorded (audio and video) for subsequent analyses in the laboratory. The camera was positioned 5 m away from the feeder, while the observer, visible, was 30 m away. For each trial, we recorded the time of arrival to the feeder of the first individual of each species (in seconds). Note that since individuals were not marked, we were not able to identify each individual, and we thus recorded the arrival of the first individual of each species. If, for a given species, no individual visited the feeder within the 20 min limit of a trial, it was attributed a score of 1201 (20 min + 1 s). Boldness differences between sites and species can be assessed by latency to return to the feeder on control trials, while neophobia per se is the difference between latency to return to the feeder during control and novel object trials.

Analyses

We first tested whether birds were still habituating to the feeder during the observations. We used linear mixed

Table 2 Effects of environmental variables and innovation rate on flight initiation distance, and on birds' behavior during control and novel object trials in Barbados birds

Response variable	Explanatory variable	*df*	*F*	*p*
Flight initiation distance	Starting distance	1, 147	12.995	<0.001
	Innovation rate	1, 52	0.347	0.558
	Urbanization	1, 8	13.807	0.006
	Innovation rate × urbanization	1, 52	5.068	0.029
Latency to feed after disturbance	Distance to anthropogenic food	1, 4	11.206	0.029
	Trial type	1, 507	18.709	<0.001
	Innovation rate	1, 23	8.631	0.007
	Innovation rate × trial type	1, 507	4.805	0.029

Species identity nested in site was included as a random effect in all models

models considering latency to feed after disturbance as response variable, with the session number (day 1, 2 or 3), trial number within a session (1, 2 or 3) and trial type (control or novel object) as explanatory variables, as well as their interactions with species. Site was included as a random effect.

We then used latency to feed as the response variable, and as explanatory variables, we included species, environments (close vs far from anthropogenic food sources, or urbanization) and trial type (novel object vs control), as well as all interactions (including the triple interaction between the three explanatory variables). Site was included as a random effect. Latency to feed after disturbance was log-transformed to meet the models' assumptions. We first ran four models with each of the four environmental variables (binary or continuous distance to anthropogenic food sources, urbanization within circles of 1 or 5 ha) using maximum likelihood and compared their AIC to select the environmental variable that best explained our data. We then chose the model with the lowest AIC and ran it again with restricted maximum likelihood to interpret the model's output, as advised in Zuur et al. (2009). As we found significant interaction effects showing that species differed in their responses to the trial type and/or to the environment, we then built one model per species to investigate in details these species differences.

To test whether behavioral scores and behavioral changes between environments were predicted by species innovation rate, we conducted all the analyses a second time, including species innovation rate instead of species identity as a fixed effect in the model, and adding species identity as a random effect nested in site.

Results

Five species (*C. passerina*, *L. barbadensis*, *M. bonariensis*, *Q. lugubris* and *Z. aurita*) out of the nine seen in Experiment 1 visited the feeders during most of the trials and were included in the analyses. *C. passerina* did not visit the feeders on sites that were far from anthropogenic food sources. *P. squamosus* also occasionally visited the feeders (for two trials in total), but too rarely to be included in the analyses. We did not detect any habituation effect on control or new object trials. Indeed, the effect of session number or trial number (within a session) and the interaction effects between species and session or trial number did not significantly affect the latency to feed (all $p > 0.174$). We thus considered all trials together and did not include session or trial number in our analyses.

The latencies to feed during the control and the new object trials were better explained by the distance to the closest anthropogenic food source (especially when using the binary variable describing this distance) than by extent of urbanization, as illustrated by the AIC differences between models including these different variables (see Supplementary Material). For simplicity, we thus focus on the results from models including the binary variable defining sites as either close or away from anthropogenic food (hereafter called *distance to anthropogenic food*) rather than the extent of urbanization.

The latency to feed after disturbance was significantly longer in presence of a new object ($F_{1,520} = 16.800$, $p < 0.001$, Table 2) and higher on sites away from anthropogenic food sources ($F_{1,4} = 16.381$, $p = 0.0155$). The effects of the type of trial and distance to anthropogenic food were, however, species dependent, as illustrated by the significant interactions between species and trial type ($F_{1,520} = 4.230$, $p = 0.022$) and between species and distance to anthropogenic food ($F_{1,520} = 12.138$, $p < 0.001$, Table 1). In contrast, the interaction between the distance to anthropogenic food and the trial type was not significant ($F_{1,519} = 0.714$, $p = 0.399$) and this interaction effect was removed from the main model. Similarly, the triple interaction effect between distance to anthropogenic food, trial type and species was not significant ($F_{4,515} = 0.907$, $p = 0.459$) and was subsequently removed from the model.

We then built separate models for each of the five species in order to investigate which species were more affected by the presence of a new object and by the distance to anthropogenic food. These models included the latency to feed after disturbance as response variable, both trial type and distance to anthropogenic food as explanatory variables, and site as a random effect. We initially also included the interaction between trial type and distance to anthropogenic food to test for differences in new object effects across environments, but then removed it from all models as it was never significant (all $p > 0.110$). The presence of a new object increased the latency to feed after disturbance in *Q. lugubris*, *Z. aurita* and *M. bonariensis* (all $p < 0.001$, see Table 2) but had no effect in *L. barbadensis* or *C. passerina* ($p = 0.402$ and 0.298). Similarly, the latency to feed after a disturbance was significantly higher in sites close as opposed to away from anthropogenic food in the same three species (though the effect was marginally significant in *M. bonariensis*, $p = 0.062$, Table 2), but did not differ between the two types of sites in *L. barbadensis* ($p = 0.317$; *C. passerina* did not visit feeders on sites away from anthropogenic food).

Including innovation rate instead of species identity as a fixed effect and adding species identity as a random effect nested in the site, we found that overall, innovative species came earlier to the feeder than less innovative species (Fig. 2), and innovation rate and its interaction with the type of trial significantly affected the latency to feed after disturbance ($p = 0.0029$; none of the other interaction effects was significant: all other $p > 0.275$; Table 2). Innovative species indeed tended to be more sensitive to the presence of a new object (Fig. 1), as illustrated by the stronger effect of trial type on latency to feed after disturbance in more innovative species such as *Q. lugubris* and *M. bonariensis* (see details for each species in Table 3). Overall, innovation rate thus predicted the latency to feed after disturbance and the reaction to the presence of a novel object, but did not predict the effect of distance to anthropogenic food on these variables. In Experiment 1, our analyses could separate the effects of phylogeny and innovation rate, but this was impossible in Experiment 2, as only five of the nine species from Experiment 1 were attracted to the sites where we ran the second experiment. In these five species, variation in innovation is tightly coupled with variation in phylogeny, as the two species without innovations are both Columbiformes (*Z. aurita* and *C. passerina*), while the three species with innovations are all passerines from the Emberizoidea superfamily (*Q. lugubris, M. bonariensis* and *L. barbadensis*).

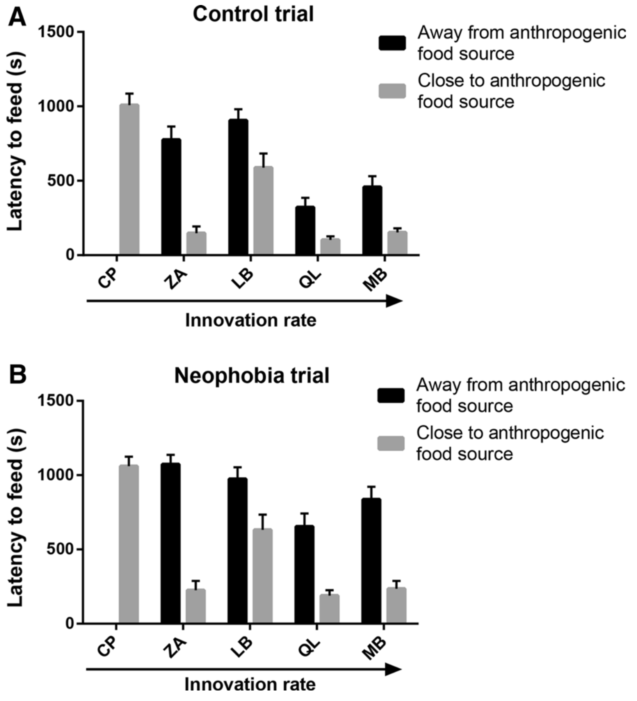

Fig. 2 Effect of innovation rate on latency to return to the feeder after disturbance in control (**a**) and novel object (**b**) trials at sites that are close or away from an anthropogenic food source. Mean ± SE are given. Species labels as in Fig. 1

Discussion

Our results show that risk-taking behaviors are affected by urbanization in Barbados birds, even at a very small scale involving a few hundred meters. Urban birds showed a shorter flight initiation distance than rural ones, and birds tested near anthropogenic food sources were faster to return to a feeder after a disturbance than were birds tested farther away. The interaction of these effects with innovation rate and species identity was more complex. Innovative species had a shorter FID than non-innovative ones in rural areas only and returned faster to the feeder after a disturbance when no novel object was placed next to the food. As the innovation database we used here contains only reports from specialized ornithology journals, some cases that were published in more generalist journals (e.g., *Animal Behaviour*, *Philosophical Transactions of the Royal Society B*) were not included in our analyses. Our results are thus conservative, as the addition of these cases for *Q. lugubris* and *L. barbadensis* [see Lefebvre et al. (2016)] would only increase the association between innovation and FID in rural birds. The effect of the novel object was strongest at sites that were farther from anthropogenic food sources, but restricted to only three of the species, *Q. lugubris*, *M. bonariensis* and *Z. aurita*.

Our data offer partial confirmation of results from previous work on several of the species studied here. The generally smaller FID’s and greater boldness of Passerines like *Q. lugubris, M. bonariensis* and *L. barbadensis* compared to Columbids like *Z. aurita* and *C. passerina* confirm the trends reported by Webster and Lefebvre (2001), who had also found that differences in problem solving in the

Table 3 Effects of environmental variables on each species' behavior during control and novel object trials

Species	Explanatory variable	Estimate	*df*	*F*	*p*	Innovation rate
Zenaida aurita	Trial type	**0.452 ± 0.193**	**101**	**5.493**	**0.021**	0
	Distance to anthropogenic food	**−2.123 ± 0.400**	**4**	**28.202**	**0.006**	
Columbina passerina	Trial type	0.122 ± 0.117	100	1.095	0.298	0
	Distance to anthropogenic food	−0.398 ± 0.397	4	1	0.374	
Loxigilla barbadensis	Trial type	−0.159 ± 0.189	100	0.702	0.402	1
	Distance to anthropogenic food	−0.799 ± 0.700	4	1.303	0.317	
Quiscalus lugubris	Trial type	**0.849 ± 0.182**	**101**	**21.54**	**<0.001**	3
	Distance to anthropogenic food	**−1.200 ± 0.398**	**4**	**9.078**	**0.039**	
Molothrus bonariensis	Trial type	**0.433 ± 0.178**	**101**	**5.892**	**0.017**	4
	Distance to anthropogenic food	−1.322 ± 0.514	4	6.604	0.062	

Site was included as a random effect in all models. Trials without new object were taken as reference, so that a positive effect of the variable trial type shows an increase in latency to feed in presence of a new object. Sites away from anthropogenic food were taken as reference, so that a negative effect of this variable shows a lower latency to feed after disturbance in sites close to anthropogenic food (as opposed to sites away from anthropogenic food)

Bold values are the significant variables ($p < 0.05$)

field and in captivity between the five species mirrored the differences in innovativeness that we used here as a basis for our predictions. The generally smaller FID's and greater boldness of birds more familiar with humans (urban sites in Experiment 1, sites closer to anthropogenic food sources in Experiment 2) also support the findings of Audet et al. (2016), who reported that urban *L. barbadensis* were bolder and better problem solvers than rural conspecifics. Our results are also in line with those of Samia et al. (2015a, b), who found that species with a relatively larger brain (a correlate of innovation rate) tolerate a closer approach before initiating flight than those with smaller brains.

As is the case in many studies [see discussion in Audet et al. (2016)], the neophobia test produced inconsistent results: in the present study, as in that of Webster and Lefebvre (2000), *L. barbadensis* showed no difference in return latencies with and without a novel object. In Audet et al. (2016), urban *L. barbadensis* actually showed more neophobia than rural ones despite their better problem solving and greater boldness. Local differences in *L. barbadensis* behavior may play a role here, as the birds from both this study and that of Webster and Lefebvre (2000) were from the same highly urbanized area in St James, while those studied by Audet et al. (2016) also came from other parts of the island that were much more distant from each other. Beyond this possible effect, the role of neophobia in responses to new problems and new habitats remains to be clarified, as Griffin and Guez (2014) conclude in their review.

If the main effects of urbanization seem to have clear consequences for risk-taking behaviors in our two experiments, increasing boldness and reducing flight distances, the interactions with innovation rate suggest a more complicated picture. Previous studies on the relationship between innovativeness and urbanization yielded mixed results: Kark et al. (2007) found no association between the two in Jerusalem, nor did Clucas and Marzluff (2015) in Seattle. In Berlin, however, both Meffert and Dziock (2013) and Clucas and Marzluff (2015) report that more urbanized species tend to have high innovation rates. In these studies, different species could be present at sites with different degrees of urbanization, but in our study, the same species (with the exception of *C. passerina* at sites that were far from anthropogenic food sources) were present in differently urbanized areas. This allowed us to examine the behaviors that covary with urbanization without the confounding effect of species composition. Unfortunately, this approach yielded contradictory results. The idea that innovative species become urbanized via lower FID's and lower neophobia is not supported by our data: the interaction effects of innovativeness and urbanization were significant in both experiments, but in the *opposite* direction to that predicted by this simple hypothesis. FID varied with innovativeness in rural sites *only*, not urban ones, and innovative species avoided novel objects *more* than non-innovative ones, with no interaction effect of distance from an anthropogenic food source. The results on FID suggest that innovative species might only need to slightly change their behavior when settling in urban environments, whereas the change is more drastic for less innovative ones. In turn, the fact that innovative birds returned later to novel objects supports Sol's (2015) suggestion that, in certain contexts, reducing the potential costs of innovativeness might lead to more persistent sampling and less impulsive decision-making. Alternatively, the fact that our sampled sites have a relatively high degree of urbanization (though these sites differed in the distance from anthropogenic food source) may explain why innovativeness did not explain variation in neophobia across environments. Measuring neophobia in rural environments would allow discarding or validating this hypothesis.

Three potential limitations of our study need to be mentioned. In Experiment 2, phylogeny is confounded with innovativeness, as among the five species that visited the feeder, the most innovative were three Emberizoid Passerines (see Lefebvre et al. 2016, for an analysis on this clade) and the two species with zero innovations were Columbidae. Secondly, we measured the latency to feed after disturbance of the first individual of each species that came to our feeder, so our results may reflect variation in each species' maximum boldness, rather than mean boldness. Differences among individuals of each species visiting the feeder may have affected the probability of observing a particularly bold one for stochastic reasons. This is particularly important in gregarious species like *Q. lugubris* and *M. bonariensis*, where the number of individuals coming to the feeder is much higher than it is in territorial species like *Z. aurita* and *L. barbadensis*. In the absence of density estimations for each site, this effect cannot be ruled out. Finally, the measures of latency to feed after disturbance were made in a natural context, where we could not control for the presence of other species on the feeder. More than one species commonly occurred at the feeders, and the presence of individuals from another species may affect the decision to visit the feeder. The latency to feed after disturbance thus likely results from a combination of a species intrinsic behavior, and from the influence of other species presence/absence on the decision to visit the feeder.

Our study adds to a robust literature showing higher boldness (FID and latency to feed after a disturbance) in urbanized birds, but a more mixed literature on neophobia and innovation. Some of these mixed results may be due to local variation in species composition, urbanization history, human behavior and habitat structure. Such local effects might be strong in studies examining limited sets of species in restricted areas like Barbados (our experiments), Mar del Plata (Echeverría and Vassallo 2008), the Argentinian Pampas (Echeverría et al. 2006), Jerusalem (Kark et al. 2007), Seattle (Clucas and Marzluff 2015), or Berlin (Meffert and Dziock 2013; Clucas and Marzluff 2015). Global studies of the type done by Sol and colleagues (e.g., Sol et al. 2005, 2012, 2014) may be needed to factor out variation due to local effects and achieve a comprehensive understanding of the relationships between urbanization, novelty responses and innovation.

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Conflict of interest

Ethical Approval Research on birds of Barbados is conducted with permission from the McGill University Animal Care Committee (Protocol 2013-7140) and the Natural Heritage Department of the Barbados Ministry of Environment and Drainage.

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