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Feeding innovations in a nested phylogeny of Neotropical passerines

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Several studies on cognition, molecular phylogenetics and taxonomic diversity independently suggest that Darwin's finches are part of a larger clade of speciose, flexible birds, the family *Thraupidae*, a member of the New World nine-primaried oscine superfamily *Emberizoidea*. Here, we first present a new, previously unpublished, dataset of feeding innovations covering the Neotropical region and compare the stem clades of Darwin's finches to other neotropical clades at the levels of the subfamily, family and superfamily/order. Both in terms of raw frequency as well as rates corrected for research effort and phylogeny, the family *Thraupidae* and superfamily *Emberizoidea* show high levels of innovation, supporting the idea that adaptive radiations are favoured when the ancestral stem species were flexible. Second, we discuss examples of innovation and problem-solving in two opportunistic and tame Emberizoid species, the Barbados bullfinch *Loxigilla barbadensis* and the Carib grackle *Quiscalus lugubris fortirostris* in Barbados. We review studies on these two species and argue that a comparison of *L. barbadensis* with its closest, but very shy and conservative local relative, the black-faced grassquit *Tiaris bicolor*, might provide key insights into the evolutionary divergence of cognition.

1. A nested phylogeny of flexible new world birds

The superfamily *Emberizoidea*, also known as New World nine-primaried oscines [1], includes the families *Emberizidae*, *Icteridae*, *Parulidae* and *Cardinalidae*, as well as *Thraupidae*, whose most famous members are Darwin's finches. The superfamily accounts for almost 8% of all birds (832 species, [2]) and has evolved a broad range of morphologies and feeding adaptations that have allowed it to radiate throughout the New World, parts of the Old World (buntings) and to colonize outlying islands in the Pacific (Galápagos finches, Cocos finch) and Atlantic oceans (Tristan da Cunha finches, Gough finch) [3]. The diversification rate of the superfamily, based on statistical comparisons [4] and molecular estimates of divergence time from common ancestors [1], is higher than that of other clades, with the families *Icteridae* (grackles, cowbirds and New World blackbirds) and *Thraupidae* (collectively referred to as tanagers) contributing most of the effect.

The family *Thraupidae* in particular has a 40% higher diversification rate than its most closely related clades, five times higher than that of the *Neoaves* mean and an order of magnitude higher than the vertebrate average [1]. Recent revisions of *Thraupidae* molecular phylogeny [5] have led to the incorporation into this family of many species previously classified [6] as *Emberizidae*. This includes Darwin's finches, as well as several Caribbean bullfinch and grassquit genera, plus the bananaquit *Coereba flaveola* that had earlier been considered the sole member of the *Coeribidae*. This revision makes tanagers the second largest family of birds, representing 12% of the Neotropical avifauna (371 species, [5]).

Within *Thraupidae*, the subfamily *Coeribinae*, to which Darwin's finches belong, shows a range of trait variation (for example, bill dimensions) that is much higher than that of other subfamilies with similar ages and levels of sequence divergence [7]. Because of this range of trait variation, the high diversification rate, and the ability to disperse from South and Central America to islands in the Caribbean as well as the Pacific and Atlantic oceans, Burns and co-authors [5] go as far as suggesting that the *Coeribinae* might have intrinsic evolvability, i.e. a greater propensity for dispersal than other lineages, a greater capability of colonizing islands and a developmental-genetic architecture that includes a

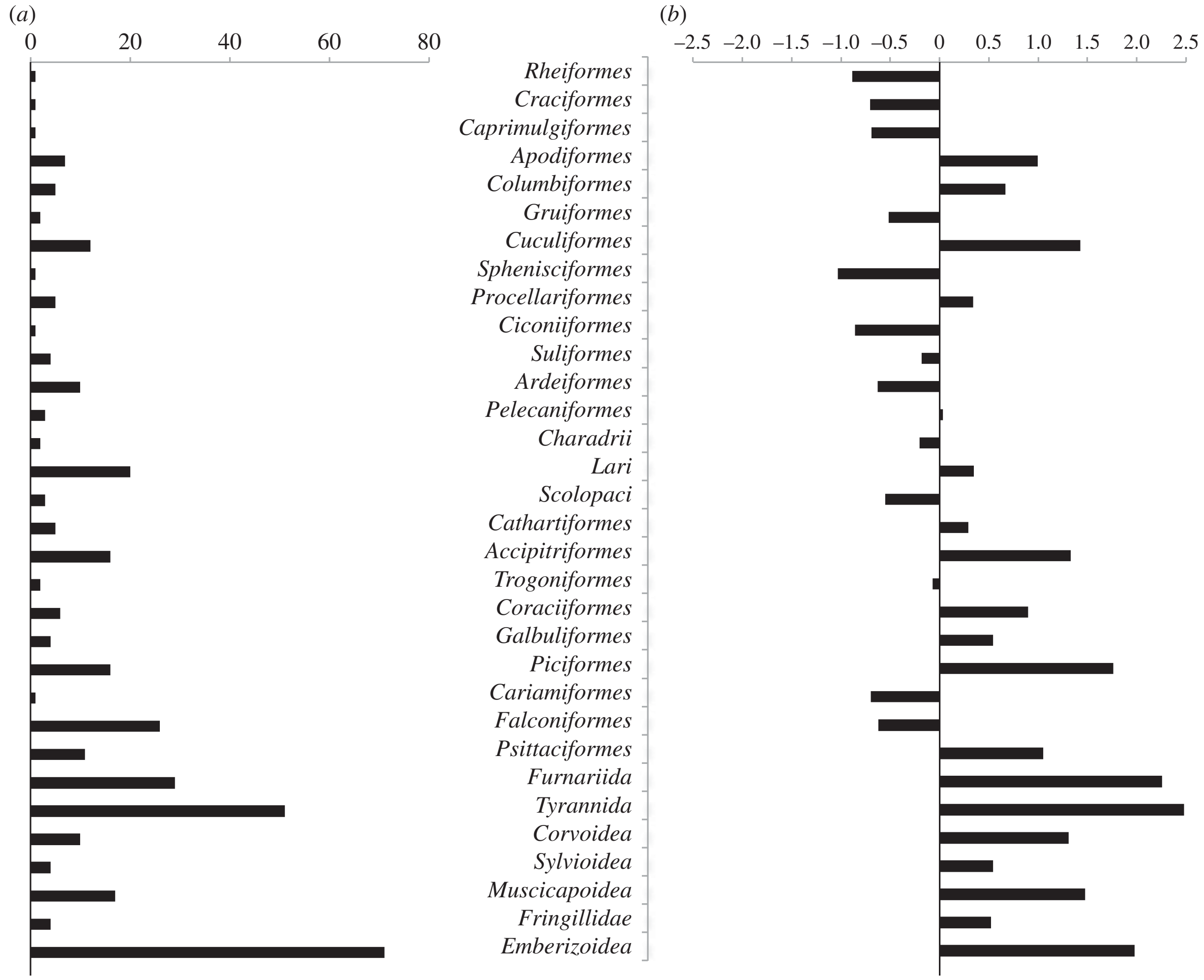

Figure 1. Frequency (*a*) and rate (*b*) residuals of frequency corrected by research effort and phylogeny of feeding innovations in Neotropical orders, suborders, infraorders and superfamilies.

greater variety of regulatory genes leading to a higher degree of phenotypic variation in key traits (see also [7,8]). For example, different lineages of Darwin's finches and endemic Caribbean bullfinches show both variation and convergence in the genetic system guiding the bone and cartilage development that determines beak size and shape [8,9]. Chaves *et al.* [10] contrast the large morphological variation seen in Darwin's finches with the lack of variation observed in the yellow warblers that have also colonized the Galápagos and Cocos islands; similar to Burns *et al.* [5,7], they also raise the possibility of differences in evolvability between the clades.

Independently of this literature on molecular phylogenetics and developmental genetics, Tebbich *et al.* [11] applied West-Eberhard's [12] concept of 'the flexible stem' in discussing both the speciosity and cognitive abilities of Darwin's finches. In her 2003 book, West-Eberhard [12] had proposed that adaptive radiations may be favoured when an exceptionally flexible stem species colonizes a new environment. In comparing the tool-using woodpecker finch *Camarhynchus pallidus* and its non-tool-using sister species, the small tree finch *Camarhynchus parvulus*, Tebbich *et al.* [11] found no evidence that the former had an adaptively specialized form of physical cognition that differed from its non-tool-using relative. Tebbich *et al.* [11] proposed that innovativeness might be phylogenetically primitive in the clade and that flexibility within the founding population of the Galápagos had led to the development of new behaviours to exploit the new foods and new habitats the colonizers found there. Given genetic variation, selection had then, over time, led to several cases of genetic accommodation.

What is striking about this 'flexible stem hypothesis' is its similarity to the conclusions arrived at by the analysis of molecular diversification and phenotypic variation: the highly innovative, tool-using woodpecker finch shares key traits with the whole, speciose, clade of Darwin's finches, who share these traits with their relatives in the whole *Coeribinae* subfamily, the whole tanager family and several branches of the *Emberizoidea* superfamily. In other words, high innovativeness, high phenotypic variation and high diversification rates might be shared traits of a nested phylogeny that goes from the species to the superfamily. The 'flexible stem' might thus be ancient.

Our paper addresses this possibility in two ways, combining a phylogenetic analysis of a new, previously unpublished, dataset of innovations from the Neotropical region and a discussion of innovations and problem-solving in two well-studied Emberizoid species from Barbados. The new Neotropical innovation database is given in its entirety in the electronic supplementary material, table S1. If the flexible stem hypothesis applies to Darwin's finches, we predict that the nested clades (subfamily *Coeribinae*, family *Thraupidae*, superfamily *Emberizoidea)* that lead to Darwin's finches should show high innovation frequencies. To do this, we draw on the same method used for previous innovation databases (birds: North America and the British Isles: [13]; Australia and New

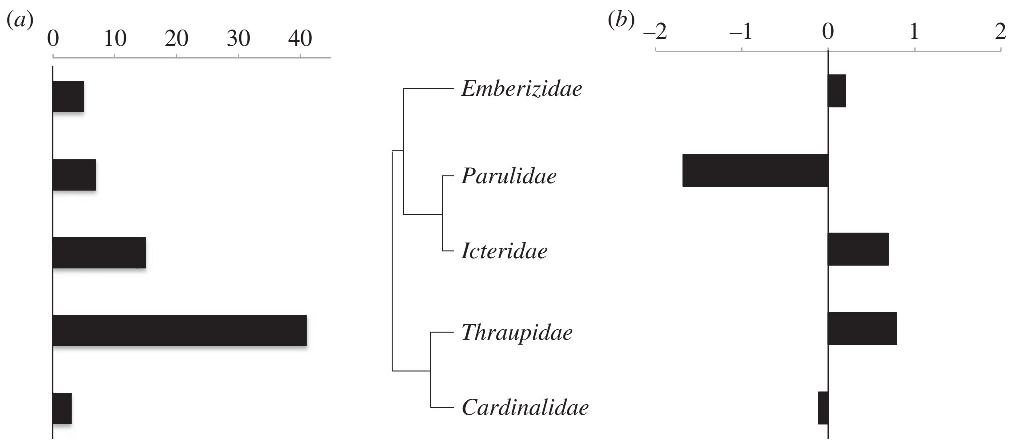

Figure 2. Frequency (*a*) and rate (*b*) residuals of frequency corrected by research effort and phylogeny of feeding innovations in families of the superfamily Emberizoidea. The phylogenetic tree is adapted from [1].

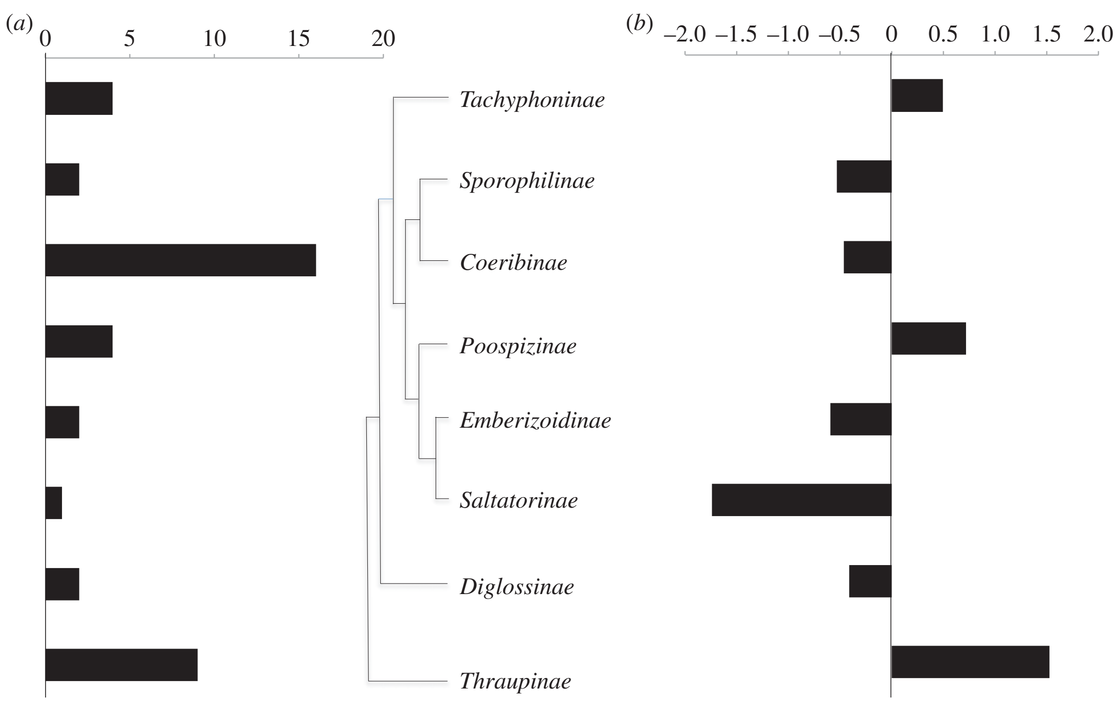

Figure 3. Frequency (*a*) and rate (*b*) residuals of frequency corrected by research effort and phylogeny of feeding innovations in subfamilies of the family Thraupidae. The phylogenetic tree is adapted from [5].

Zealand: [14]; Western Europe and the Indian subcontinent: [15]; primates: [16]): an exhaustive search of the short notes of as many local specialized journals as we could consult. The second part of our paper reviews field and experimental data on innovativeness in one of the Darwin's finches closest relatives, the endemic Barbados bullfinch *Loxigilla barbadensis*. We also extend our discussion of field and experimental data to the most innovative genus within *Emberizoidea*, the grackle genus *Quiscalus*, in particular the highly opportunistic species that feeds with *L. barbadensis* in the wild, the Carib grackle *Q. lugubris fortirostris*.

2. Comparative analyses of feeding innovations in Neotropical birds

We exhaustively searched the short notes of all Neotropical ornithology journals available to us online at McGill (37 journals from Mexico to Chile; see the electronic supplementary material S1 for details of the methods) for key words mentioning opportunism (112 cases; note that a given case may contain several key words), 'not' or 'never' or 'un-' recorded behaviours (111 cases), 'first' reports (56 cases), 'new' and 'novel' (44 cases) or 'unusual '(9 cases) observations that 'depart' from the usual behaviour (30 cases) or have been seen 'only' in 'other' species or 'other' foods (42 cases) or are 'learned' (5 cases). As in previous databases, we used the judgement of the author of the primary observation as a criterion for inclusion, as Neotropical ornithologists know their study species better than we do.

We found 352 innovations in 256 species. The entire database is given in the electronic supplementary material, table S1. Innovations ranged from simple opportunistic feeding on a newly available food source (often insects) to the more spectacular cases of an Antarctic skua (*Stercorarius antarcticus*) and a blackish cinclodes (*Cinclodes antarcticus*) drinking blood from a wound on an elephant seal (*Mirounga leonina*), tool use in the shiny cowbird (*Molothrus bonariensis)* and the yellow-rumped marshbird *(Pseudoleistes guirahuro)* and baiting fish with bread in the rufescent tiger heron (*Tigrisoma lineatum*), a behaviour normally reported in the striated heron (*Butorides striata)* and other heron species (see review in [17]).

Figures 1–3 present phylogenetic diagrams of innovation rate per clade at three taxonomic levels: *Emberizoidea* against other superfamilies and orders (figure 1), *Thraupidae* against other nine-primaried oscine families (figure 2) and *Coeribinae* against other Thraupid subfamilies (figure 3). In these diagrams, taxa are placed according to their phylogenetic proximity, and innovation rates (part (*b*) of each figure) are calculated as residuals of Phylogenetic Generalized Least-Squares (PGLS) regressions of innovation frequency (part (*a*) of each figure) against research effort (taken from [18]) per clade, which is an important confounding variable of innovation frequency ($p = 0.058–0.0003$ in this dataset depending on the taxonomic level; see the electronic supplementary material S1). Clades where no innovations were found are not included in the analyses, as the absence of innovations might mean either that birds of these clades are not innovative or that whatever innovations they might show were not observable for geographical or research effort reasons (research effort on 2217 of avian species worldwide is zero [18]). The phylogenetic signal was high at the superfamily and subfamily levels (Pagel's λ estimated by maximum likelihood = 0.934 and 1), but null at the family level (Pagel's $\lambda = 0$), suggesting that variation in innovativeness between families is independent of phylogeny.

As is evident in part (*a*) of each figure, the nested phylogeny that goes from *Emberizoidea* to *Coeribinae* reveals high innovation frequencies at all three taxonomic levels. When frequencies are regressed against research effort and common ancestry controlled in the PGLS, however, only the higher two phylogenetic levels, the superfamily and the family, reveal high innovation rates for the nested clades that include Darwin's finches. At the highest taxonomic level (figure 1), *Emberizoidea* have the largest number of innovations (71, figure 1*a*), as well as positive phylogenetically corrected residuals (figure 1*b*) that are only slightly smaller than those of the two sub-oscine infraorders *Tyrannida* (tyrant flycatchers) and *Furnarida* (ovenbirds*)*. As in other parts of the world [19], *Piciformes* (in the neotropics, toucans as well as woodpeckers), gulls (suborder *Lari*) and raptors (*Falconiformes* and *Accipitriformes*) show high innovation frequencies (figure 1*a*). Caracaras are the species group with the highest number of innovations, 18, the genus *Milvago* (eight innovations) and *Caracara plancus* (seven innovations) providing the largest share (see the electronic supplementary material, table S1). As is the case in other innovation databases [19], shorebirds (suborders *Scolopaci* and *Charadrii*) and doves (*Columbiformes*) show low innovation frequencies. Ratites and *Galloanserae* also show either zero or very low innovation rates: ducks and landfowl are absent from figure 1 because they show no innovations, while the greater rhea registers the only known ratite innovation worldwide, with the presence of fish in faeces supporting an observation of consumption of fish at the margins of a reservoir [20].

Several passerine clades show high innovation rates, in particular the sub-oscine infraorders *Tyrannida* and *Furnarida*. Surprisingly, corvids (*Corvoidea*) do not dominate the

Figure 4. Feeding innovations in Carib grackles in Barbados. (*a*) Dunking dog pellets in water at the Bellairs Research Institute. (*b*) Stealing a pellet from a dunking bird. (*c*) Eating fish remains at the Payne's Bay fish market.

database in the way they do in all other parts of the world [19] and rank 12th and 9th, respectively, in terms of innovation frequency and phylogenetically corrected residual rate in the Neotropics. The two dietary categories that are the source of many innovations in other parts of the world, predation and carrion feeding, seem to be rare in South American Corvids [21]. Instead, Lopes *et al.* [21] highlight the fact that two Thraupid species show corvid-like ingestion of meat remains on cattle skin drying in the sun.

At the level of families within nine-primaried oscines, *Thraupidae* rank first with 56% of the innovations in the clade (41 of 71; figure 2*a*). *Icteridae* (grackles, cowbirds and allies) rank second on both the left and right part of figure 2. Within *Thraupidae*, the subfamily *Coeribinae* ranks highest in terms of innovation frequency (16, figure 3*a*), but falls behind other subfamilies when research effort, elevated by the many studies on Darwin's finches, is factored in with the PGLS (figure 3*b*). As in

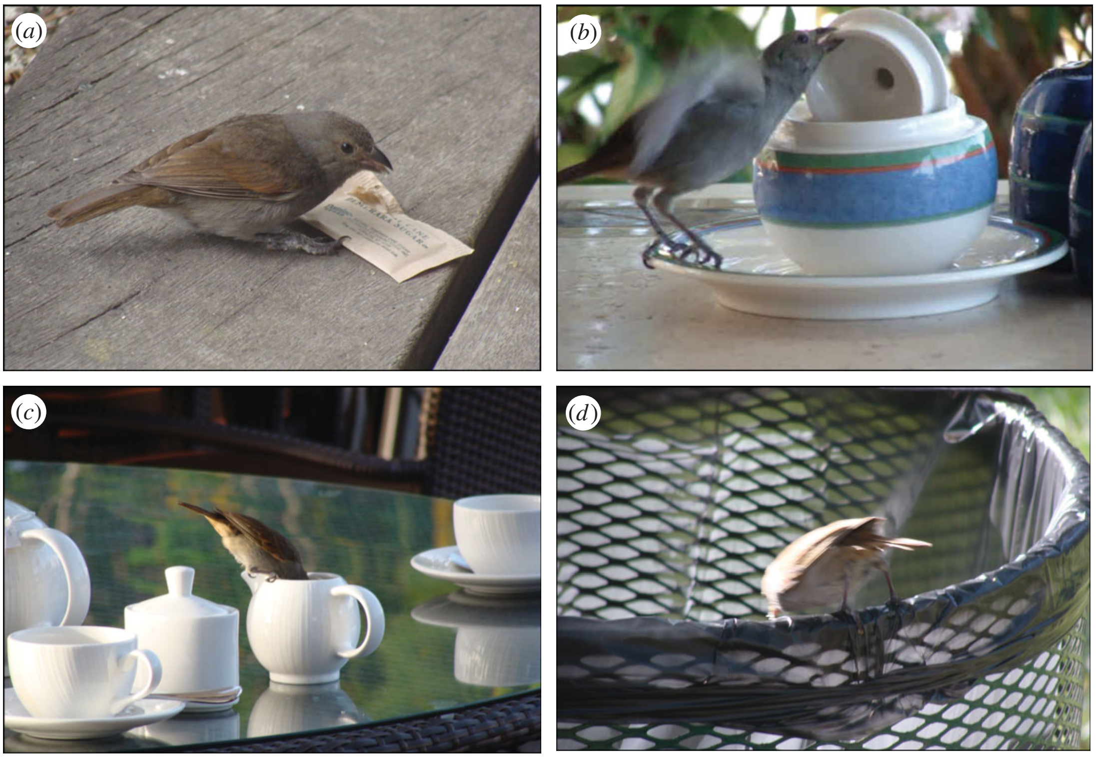

Figure 5. Feeding innovations and opportunistic feeding in Barbados bullfinches in the field. (*a*) Opening sugar packets at a restaurant. (*b*) Lifting the lid on a bowl of sugar (see also the electronic supplementary material, movie S1). (*c*) Drinking cream from a jug on a restaurant table (see also the electronic supplementary material movie S2). (*d*) Foraging inside a garbage can.

other innovation databases [13–15,19], our focus on low impact factor regional ornithology journals might have underestimated innovation rates in taxa where the most spectacular cases are reported in higher impact factor journals, which are included in research effort, but not in innovation frequency. We are currently estimating the effects of this limitation on our worldwide database. Owing to this possible limitation, the family level provides more robust support of the flexible stem hypothesis than the subfamily level.

3. A review of innovativeness and problem-solving in *Loxigilla barbadensis* and *Quiscalus lugubris fortirostris*

The neotropical innovation database clearly supports the flexible stem hypothesis at all three taxonomic levels when innovativeness is measured as uncorrected frequencies, and at the levels of the family and superfamily when innovation frequencies are corrected for research effort and phylogenetic signal. Beyond the comparison of innovation rates in the wild, however, a more complete understanding of innovativeness requires experimental assays that can be transferred to captivity. Problem-solving tasks, especially those that involve the removal of obstacles blocking access to food, have proved useful for this [22]. It was both Darwin's finch innovativeness in the wild and their strong performance in problem-solving tasks [23–27] that led Tebbich *et al.* [11] to apply the flexible stem hypothesis to this clade. If our innovation data suggest that the stem is at the level of the family and superfamily, we should be able to identify other innovative *Thraupidae* and New World nine-primaried oscines that also show enhanced problem-solving abilities.

The island of Barbados hosts two Emberizoid species that are good candidates, the endemic bullfinch *Loxigilla barbadensis*, and the Carib grackle *Quiscalus lugubris fortirostris*. Both species are dietary generalists. Barbados shares many of the features that facilitate innovative behaviour in finches of the Galápagos: tameness owing to a historically low level of predation, wide niches owing to low levels of competition from a paucity of avian species, and limited resources owing to small island size. Barbados lacks the dryness extremes that make the Galápagos a particularly challenging environment, but it has an additional feature that favours behavioural plasticity: intense anthropogenic modification of the original environment, providing birds with many novel habitats and food sources as a result of urbanization and agriculture.

Several studies in the field and in captivity have documented the opportunism, innovativeness and problem-solving abilities of *L. barbadensis* and *Q. lugubris fortirostris*. We briefly review them here. In the field, Carib grackles take dry food pellets from dog bowls and soften them by dipping them in water ([28]; figure 4*a*). Some individuals steal the dunked pellets when they are dropped in water by a conspecific (figure 4*b*), and the frequency of dunking is determined by social (flock size, theft) and energetic (distance to water, consumption time of dunked versus dry food) costs and benefits [28–30]. The relationship between dunking and stealing follows the frequency-dependent payoffs of a producer–scrounger game [30]. Barbados grackles have been seen foraging for dead insects under the windshield wipers of parked cars, as well as passing bread and rice to a begging juvenile through the wire mesh of its cage during captive experiments [31]. Grackles were also observed several times eating fish remains at the Payne's Bay fish market (St-James; figure 4*c*). This behaviour is typical of cattle egrets in Barbados (Oistins and Bridgetown fish markets) and elsewhere, but has not been seen before or described in *Q. lugubris*. The Carib grackle is not the only innovative *Quiscalus* species: in North America, the genus totals 19

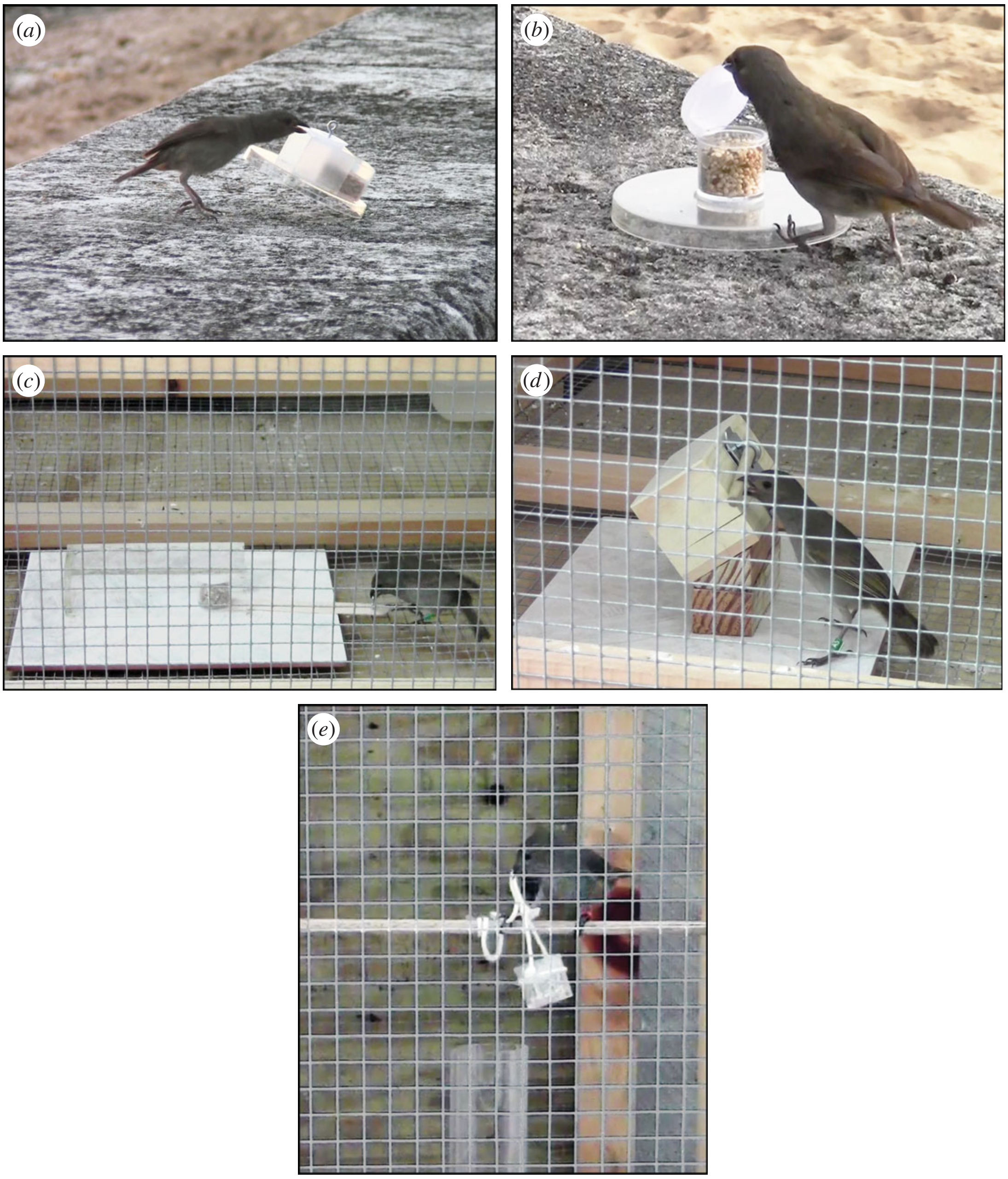

Figure 6. Problem-solving in Barbados bullfinches. (*a*) Opening a box containing seed in the field. (*b*) Lifting the lid on a cylinder containing seed in the field. (*c*) In captivity, pulling a stick out of a tunnel to open a cylinder containing seed. (*d*) Opening the three-step chest task (see also the electronic supplementary material, movie S3). (*e*) String pulling.

innovations [19], making it the second most innovative Passerine genus after *Corvus* in that part of the world.

In field experiments, bullfinches and grackles were the fastest of five tested species (*Molothrus bonariensis*, *Zenaida aurita* and *Columbina passerina* were the others) to open a problem-solving apparatus [32]. Bullfinches and grackles were also the least neophobic of the five species. Bullfinches further proved bolder than bananaquits *Coereba flaveola* in experiments where dishes of dissolved sugar were offered in the field [33]. Barbados bullfinches take and pierce packets of refined sugar from restaurant tables ([34,35]; figure 5*a*). Investigations of this behaviour provide the first direct evidence of the independent emergence of the same behavioural innovation in different individuals in different places [35]. Barbados bullfinches open the lids of sugar jars (figure 5*b* and electronic supplementary material, movie S1), steal cream from jugs on terraces (figure 5*c* and electronic supplementary material, movie S2) and reach for food in deep trash bins (figure 5*d*). Untrained individuals readily solve obstacle removal tasks in the wild (figure 6*a*,*b*). In captivity, both bullfinches and grackles perform well on problem-solving tasks like the two-step 'tunnel task' ([36]; figure 6*c*), where birds have to pull a stick out of a transparent tunnel to gain access to a plastic container and then flip a lid to obtain the reward, or the three-step 'chest task' (figure 6*d* and electronic supplementary material, movie S3), where the birds have to displace a wooden stick to unlock a metal latch, then push or pull to open the latch and finally push the base of the box to open it. Finally, both Barbados bullfinches and Carib grackles spontaneously solve the string-pulling test (J. N. Audet, S. Ducatez and L. Lefebvre 2016, unpublished data; figure 6*e*), which is considered by some to involve an understanding of cause–effect relationships [37–39].

The ease with which Carib grackles and Barbados bullfinches can be tested in captivity has provided insights into differences in problem-solving between individuals and populations. At the population level, Barbados bullfinches from urbanized areas perform better in problem-solving tasks compared with rural individuals [36]; urban bullfinches are also bolder and have a stronger immune response than rural ones. At the individual level, Carib grackles that responded to movements of the obstacle by redirecting their probes from the centre of the apparatus to its edges were more successful at solving the problem [40]. Interestingly, individual differences in grackle obstacle removal performance are *negatively* correlated with discrimination learning performance: birds that are fast at obstacle removal are also fast at making discrimination choices, good or bad, making more errors in the process and thus reaching the learning criterion later [41]. This surprising negative relationship between tasks can be reconciled as a coherent individual strategy that favours different aspects of a single speed–accuracy trade-off [42], where better problem-solvers rapidly interact with a variety of stimuli that lead to obstacle removal [40], but also to higher error rates in situations where wrong choices are penalized.

One of the most intriguing opportunities offered by Emberizoid variation in innovativeness in Barbados is the sharp difference between *L. barbadensis* and its closest phylogenetic relative on the island [2,5,7], the black-faced grassquit *Tiaris bicolor*, a granivorous species that eats small seeds. Barbados bullfinches are extremely tame, neophilic and opportunistic, but grassquits, by contrast, do not approach novel patches of provisioned seed or anthropogenic sources of food [43]. Both *L. barbadensis* and *T. bicolor* are territorial in Barbados and both feed on seeds in similar environments, but the sharp difference in their opportunism, if associated with differences in problem-solving [42], might yield important insights into the evolution of cognitive divergence between species otherwise matched for phylogeny, sociality and diet.

Galápagos finches does not characterize Lesser Antillean passerines in general [44], but rapid speciation does seem to have characterized the divergence of *L. barbadensis* from the *Loxigilla noctis* stem found on nearby islands [45]. Intriguingly, one of the key traits that differentiates *L. barbadensis* from *L. noctis* is shared with Barbados populations of *Q. lugubris fortirostris*: the two species have evolved monomorphic plumage in Barbados, while populations on other islands are sexually dimorphic. However, monomorphic plumage has evolved in different directions in the two species: *L. barbadensis* males have lost the black and red plumage that *L. noctis* shows on other islands and converged on the female's brown coloration, while *Q. lugubris fortirostris* females have lost the brown plumage they show on other islands and converged on the male's black.

The Emberizoids of Barbados, in particular *L. barbadensis* owing to its close phylogenetic proximity with Darwin's finches, offer a unique opportunity to study the flexible stem. Barbados is more accessible and less ecologically fragile than the Galápagos. Many avian species are extremely tame there and adapt well to captive testing, and are thus ideal models to investigate variation in innovativeness, and more generally, cognition in wild birds. By combining experimental studies of wild birds kept in captivity for short periods of time and large-scale comparative analyses quantifying innovative behaviours in the wild, we provide strong support for the flexible stem hypothesis. The high innovativeness and problem-solving abilities of *Emberizoidea* are likely to have been a major driver of the high diversification rate, adaptive radiation and colonization abilities observed in this superfamily. High innovativeness is associated with high colonization success across the entire class of birds [46] and the combination of the two might also have been a factor in the planetary radiation of the genus *Homo* [47].

4. Conclusion

Our study provides clear evidence for high innovativeness at all levels of the nested phylogeny leading to Darwin's finches, with the family level providing the most robust results on both innovation frequency and rate corrected for research effort. This supports the suggestions independently derived from research on cognition [11], molecular phylogenetics [5,7,8] and taxonomic diversity [4] that the higher stems from which Darwin's finches descend are also flexible. Observations and experiments in the field, as well as studies done in captivity, show that members of the *Emberizoidea* superfamily in Barbados are good model species for the experimental study of innovativeness and problem-solving. The high level of evolutionary radiation that accompanies behavioural plasticity in

Ethics. 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.

Authors' contributions. L.L. collated the innovation dataset and wrote §§1 and 2. S.D. and L.L. conducted the statistical analyses of the innovation data. J.-N.A., S.D. and L.L. wrote §3. J.-N.A. and S.D. conducted the experiments featured in the videos.

Competing interests. We have no competing interests.

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