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The Tale of the Finch: Adaptive Radiation and Behavioural Flexibility

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Abstract

Darwin's finches are a classic example of adaptive radiation. The ecological diversity of the Galápagos in part explains that radiation, but the fact that other founder species did not radiate suggests that other factors are also important. One hypothesis attempting to identify the extra factor is the flexible stem hypothesis, connecting individual adaptability to species richness. According to this hypothesis the ancestral finches were flexible and therefore able to adapt to the new and harsh environment they encountered by exploiting new food types and developing new foraging techniques. Phenotypic variation was initially mediated by learning, but genetic accommodation entrenched differences and supplemented them with morphological adaptations. This process subsequently led to diversification and speciation of the Darwin's finches. Their current behaviour is consistent with this hypothesis as these birds utilise unusual resources by extraordinary means. In this paper we identify cognitive capacities on which flexibility and innovation depend. The flexible stem hypothesis predicts that we will find high levels of these capacities in all species of Darwin's finches (not just those using innovative techniques). Here, we test that prediction and find that while most of our data are in line the flexible stem hypothesis, some are in tension with it.

Keywords

flexible stem hypothesis; innovation; tool-use; phenotypic plasticity; adaptive radiation

Introduction

The fauna of the Galápagos Islands is one of the standard examples of evolution's two signatures: diversity and adaptation. There can hardly be a textbook on evolution that does not shelter somewhere within its pages a diagram of Darwin's finch beaks showing their divergent functions and morphology. However, morphological variation is not the only readily observed instance of evolutionary change in this species group: the birds illustrate the plasticity of behaviour, too. As we shall see, Darwin's finches have evolved a raft of innovative foraging capacities. However, Galápagos is not just a laboratory of phenotypic evolution. It is also a laboratory of speciation, and in particular, of adaptive radiation. "Darwin's finches" are a poster example of adaptive radiation (Schluter 2000). Fourteen

endemic species are now spread over the islands (Grant & Grant 2008) and occupy different niches, but they are one of the few lineages to have diversified. Among the mammals, only the rice rats have diversified, and of the seven reptile lineages that colonised the islands, four have diversified (Parent *et al.* 2008). Of the thirty land bird species that are resident on the Galápagos Islands, twenty-five are endemic but apart from the Darwin's finches, only the mockingbirds (*Nesomimus sp.*) have diversified (into four species). Why have just a few Galápagos stem lineages given rise to a crown of distinct species?

In this paper, we assess candidate explanations of the finch radiation. These explanations have a common pattern. All invoke the ecological mosaic — the fragmentation of the habitat into islands— and the special climatic conditions of the Galápagos as central factors in explaining radiation. Many of the islands are subject to severe seasonal and annual fluctuation in rainfall. In irregular intervals they are strongly influenced by the El Niño phenomenon, for the years that follow El Niño events have little or no rainfall, and in these dry years, finch populations crash, especially those of low-lying areas (Grant 1980). The ecological conditions vary from island to island, and the larger islands offer a disparate array of vegetation zones along an altitudinal gradient. Intense intraspecific competition in geographically restricted and fluctuating habitats creates an ecological push for behavioural divergence and the invention of new foraging techniques. Moreover, prior to the adaptive radiation of the initial colonising species, the complex ecological mosaic of the larger islands was not exploited by a disparate array of species (Grant 1986). If the fauna was low in diversity, then alongside intensively exploited resources, there would be those that were rarely or inefficiently exploited.. The first tool-using woodpecker finch was not in competition with woodpeckers, nor the sharp-beaked ground finch with tickbirds. This under-utilisation creates an ecological pull, and diverging feeding specialisations can then lead to speciation (Morse 1980, Grant 1986).

However, most lineages that arrived at the islands did not radiate. So could ecological fragmentation be a sufficient explanation of finch radiation? Perhaps. As Richard Lewontin (1982) and more recently the niche construction theorists have made clear, the extent to which a landscape is ecologically fragmented does not depend just on the objective features of the physical environment and the extent to which these vary over space and time. It also depends on how a population interacts with its environment (*Odling-Smee et al. 2003*). The heterogeneity of the Galápagos Islands depends on how the birds experience their world. So perhaps the islands were ecologically fragmented for the finches, but not, say, for the endemic hawk (*Buteo galapagoensis*); the Galápagos dove (*Zenaida galapagoensis*), or other endemics. So, arguably, the simplest idea in explaining radiation is ecological drive: ecological fragmentation drove finch radiation but not that of other endemics, since only the finches experienced the islands as a set of different habitats. Even this model implicitly presumes that there is something about the finch lineage that explains why they, but not the other small land birds, experience the islands as a set of different habitats.

The distinction between the finch lineage and other endemic birds is not absolute. Also the Mockingbirds have radiated to some degree. They differ in several morphological characters such as plumage colour, size and proportions, but these are minor variations upon a basic mockingbird plan, they less pronounced in comparison with the diversity of the finches (Grant 1986). But the yellow warbler (*Dendroica petechia*), the Galápagos flycatcher (*Myiarchus magnirostris*) and the Vermillion flycatcher (*Pyrocephalus rubinus*) did not radiate, although they are small insectivores, like the warbler finch, which is the oldest of the Darwin's finches (Grant & Grant 2008). Likewise, they are songbirds with large brains in relation to their body size (Rehkamper *et al.* 1991). Prima facie, these birds should also experience the different islands as different habitats, offering different opportunities. There does seem to be something special about the finches.

Two other hypotheses do not deny the central role of the special ecological conditions of the Galápagos Islands but combine it with some specific feature of the finch lineage; they are two-factor theories of radiation. West-Eberhard (2003) has argued that adaptive radiations depend on individual phenotypic plasticity: they occur when an exceptionally adaptable stem species encounters a new environment. A similar idea (known as behavioural drive) has been defended in Wyles *et al.* (1983) and Wilson (1985). There is some general evidence that favours a connection between individual flexibility and species richness. Nicolakakis *et al.* (2003), Sol *et al.* (2003) and Sol *et al.* (2005) have recently shown that behavioural flexibility and brain size predicts species and subspecies richness in birds. As a measure of flexibility, they used innovation rate, a frequency count of the number of opportunistic, novel or unusual feeding techniques displayed by avian orders and parvorders. In a very recent study, Overington *et al.* (2009) showed that the diversity of technical innovations in birds explained the greatest proportion of variance in brain size, indicating that innovativeness is related to enhanced cognitive abilities. However, such correlational studies cannot reveal the direction of causation.

We will focus on evidence about the finches, in particular, in assessing the argument that behavioural flexibility and innovation has been a driving factor in the evolution and radiation of Darwin's finches (see Grant & Grant, 2008; Price 2008; West-Eberhard 2003), and compare it to other hypotheses. Some data supports the FSH, but some is in tension with it.

The early arrival hypothesis

As noted above, one alternative to the flexible stem hypothesis is simply time. Darwin's finches may have arrived earliest, and encountered no competitors (Lack 1947). They had plenty of opportunity to occupy and adapt to different niches. The later arrivals of hawks (Bolmer *et al.* 2006) and yellow warblers (Browne *et al.* 2008) are in line with this hypothesis. Moreover, mockingbirds probably arrived at around the same time as Darwin's finches (Arbogast *et al.* 2006), and they too have diversified, though only into four species. However, the first arrival hypothesis does not explain why the diversification of Darwin's finches was slow at the beginning and rapid only recently, when the environments on the Galápagos Islands changed (Grant & Grant 2008). Grant & Grant (2008) suggest that adaptive radiation of the Darwin's finches was linked with a change in climate and increased habitat diversity. But if the finch radiation was relatively late and triggered by ecological change, we need to explain why late-arrivals like the yellow warbler did not radiate, too. If finch radiation is recent, early arrival drops out as an explanatory factor. It explains radiation only if the early migrants seized the opportunity to occupy vacant niche space before others arrived.

Genetic variability is another potential difference between the finches and the other, less diverse endemics. Darwin's finches show relatively high levels of diversity at the major histocompatibility complex, indicating that ancestral Darwin's finches arrived in a moderately large flock or several smaller ones (Vincek *et al.* 1996, Grant & Grant 2008). It is therefore conceivable that the evolutionary options of the other endemics were constrained by smaller founder populations. Although possible, it is hard to see how to test this idea (except, perhaps, by comparisons with other island radiations). The flexible stem hypothesis is, however, testable, and it will be our main focus.

The flexible stem hypothesis

In a little more detail, the FSH goes as follows: The foundation populations of the Galápagos endemics were exposed to a novel package of physical stressors, risks and opportunities. In response to this new environment, some birds developed new behaviours:

they learned to tolerate unfamiliar substrates while foraging and to exploit new foods which helped them to persist on the inhospitable islands (Grant & Grant 2008; Price 2008). According to this model, initially these changes are not evolutionary: no new genes have appeared and the frequencies of existing genes have not changed since the initial sampling of the founding population. But as time passes and these new environmental conditions persist, selection will change the genetic make-up of the population. For example, on predator-free islands where bolder foraging is advantageous, there will be positive selection for genetic differences that lead some birds to learn that they can afford to be bold more quickly than others. The same will be true of other genetic variants that accentuate, enhance or accelerate adaptive learned responses to the new environment.

In this model then, environmental change results in an initial response mediated by mechanisms of adaptive phenotypic plasticity. But many populations will have relevant pre-existing genetic variation, and sex, recombination and mutation will generate further variation. So when change persists, there is likely to be some form of genetic accommodation to the new phenotype. The adjustment may be nothing more than a faster and more reliable development of that novel phenotype (as in the Baldwin Effect, see Weber & Depew, 2003). However, the Baldwin Effect is just one special case of genetic accommodation in which the learned response becomes increasingly less dependent on specific experience. Genetic accommodation might also involve enhancing or modifying the response: for example, a change in foraging target may select for modification in beak size or shape, and thus accommodation may involve morphological changes that reinforce behavioural ones. The sharp-beaked finches of Wolf Island may be such a case. Only on this island finches have learned to drink blood by pecking seabird chicks, and this population has the sharpest and pointiest beaks (Price 2008; Schluter & Grant, 1984).

If West-Eberhard's model is right, individual phenotypic plasticity sets the stage for evolutionary change within the lineage. By this token, we find adaptive radiation in Darwin's finches rather than in other lineages, because individual finches were more adaptable than the members of other founder populations. We must imagine that flexibility allowed finches to respond to environmental variation by adapting differently to different habitats and to the resources available within them. These differences would initially have been merely behavioural, upheld by common mechanisms of learning, but later, genetic accommodation would have entrenched some behavioural differences and supplemented them with morphological differences, as morphology co-evolved with behaviour. In this model, differences that are dependent on learning appear first, to be followed by genetic and morphological differentiation and ultimately by isolation and speciation. The model is therefore a version of the "niche construction" approach to evolution. According to this theory, agents respond to their environment and in doing so, they alter the selective regime. That altered regime then results in further evolutionary change (Odling-Smee *et al.* 2003; Laland 2008). In this case, learning results in new foraging regimes, which in turn results in selection for genetic variations. This makes the new foraging mode more efficient, more reliably acquired, or both.

Innovative foraging in Darwin's finches

Darwin's finches do seem to be impressively flexible, for the different species show striking capacities for innovative foraging. For example, the woodpecker finch (*Cactospiza pallida*) uses twigs or cactus spines to extract arthropods from tree holes (Eibl-Eibesfeldt & Sielman, 1962), and an anecdotal observations of this behaviour also exist for the mangrove finch (*Cactospiza heliobatis*) (Curio & Kramer, 1964). The sharp-beaked ground finches (*Geospiza difficilis*) is also known as the "vampire finches", because these birds, as noted above, peck at the developing feathers of sea birds, thus drawing blood which they then

drink (Bowman & Billeb, 1965). Still more impressively, these small birds are able to break the eggs of boobies. These eggs are more than twice as heavy as their attackers (an egg weight around 55g; the finch only 20g). To break them, the bird braces its beak against the ground and kicks at the egg with both feet to push it over a ledge or against a rock (Schluter 1984). Two other ground finches, the small ground finch (*Geospiza fuliginosa*) and the large cactus finch (*Geospiza conirostris*), are known to search for invertebrates by using similar methods to move stones, thus exposing arthropods sheltering beneath (DeBenedictis 1966). The small and the medium ground finch (*Geospiza fortis*) glean ticks from iguanas and tortoises (MacFarland & Reeder, 1974) and even feed on the afterbirth of sea lions (Grant & Grant, 2008). The medium ground finch and large cactus finch capture spiders in the spider's own web by hauling in the silk thread, using a foot to hold each loop (Grant & Grant, 2008). Finally, the sharp-beaked ground finch and the small ground finch scavenge on decaying fish, seabird eggs and their dead young, as well as undigested faecal remains from sea birds (Bowman & Billeb, 1965). The only other birds on the Galápagos with similar feeding innovations are the mockingbirds, and they have also diversified. For example, two of the four mockingbird species drink blood from wounded sea lions, iguanas, or injured boobies—they may even inflict these wounds on iguanas while removing ticks. Mockingbirds also feed on faecal remains, on the placentas of sea lions and on carrion, and have even been observed to remove morsels from the teeth of sleeping seas lions (Curry & Anderson, 1987).

Genetic assimilation

In the FSH model, the connection between individual adaptive plasticity and lineage-level species richness depends on genetic assimilation entrenching initial divergent responses. This aspect of the model remains speculative, but perhaps plausible for three reasons. First, learning followed by assimilation is an efficient search procedure. A number of novel foraging techniques could arise from relatively simple behavioural modifications of existing practices. Scavenging, feeding on afterbirth and on faecal remains is unusual for passerines, but does not require the invention of new morphologies or behaviours. Likewise, the blood drinking of the sharp beaked ground finch could be a natural extension of foraging for invertebrates: a misdirected or inadvertently strong peck might well be rewarded with blood, and eventually the accident becomes a habit. Even the use of spider webs in foraging could be attributed to a reinforced accident since many passerines are known to use spider webs in nest construction. It is certainly possible that these one-step changes are the result of a genetic change initiating a new developmental pathway that then leads to a new behaviour. But innovation based on learning followed by reinforcement is more probable than a genetic switch from one hard-wired routine to another, for learning-based exploration searches the local space of foraging options much more efficiently than random mutations (Hinton & Nowlan, 1987; Ancel 1999). A population capable of fast trial-and-error learning will explore the space of options more efficiently, for each bird can explore more than one option (Weber & Depew, 2003). A behaviour can persist through learning alone, but if the new resources that an innovation secures are both important and lasting, there will be subsequent selection for genetic changes, thus making the acquisition of the new technique more reliable.

Second, some of the more complex foraging novelties of Darwin's finches seem most unlikely to be a single genetic switch away from foraging using only one's own morphology. This is the case with the tool-use of woodpecker finches and the egg breaking of sharp-beaked ground finches. Such complex behavioural adaptations, like complex morphological adaptations, are typically assembled one step at a time (Dawkins 1996). Eva Jablonka and her collaborators have developed an “assimilate and stretch” model to explain the evolution of such complex behaviours (Avital & Jablonka, 2000; Jablonka & Lamb, 2005). In the model, the behaviour under genetic control is a behavioural baseline—a platform upon

which learning can build. In an iterative process spanning generations, learning and subsequent genetic assimilation of various components and refinements of the behaviour results in a more complex and adaptively fine-tuned form of the behaviour.

A potential example of this process can be derived from woodpecker finch tool-use. This was first proposed by Bateson (2004) and later by Price (2008). The scenario is as follows. Current tool-use is complex: woodpecker finches shorten twigs or cactus spines if they are too long, and have been observed breaking off protruding twigs that would stop the finch inserting the tool into a tree holes. Imagine this tool-use as the product of a sequence of slight behavioural and genetic changes which fine-tuned the behaviour over time. At the beginning of the sequence, there was a crude, behaviourally limited form of tool-use by which only large, exposed insects could be extracted from shallow crevasses. Proto-woodpecker finches learned by way of an initial innovation, which then spread socially. Once this innovation was common within the population, it was partially genetically assimilated: some aspect of the behaviour, for example the stabbing motion or the size/weight of the twig to be used, no longer needed to be learned. This promoted faster acquisition of the primitive skill, thus freeing up the cognitive resources to add a further component. Perhaps they learned to select their tool more expertly or learned to shape it. As this component spread and was brought under genetic control, a new baseline competence was available as a platform for further improvement during that period of the bird's ontogeny when it is capable of learning through experimentation. A further improvement might be made, and thus the cycle iterates.

Finally, while the scenario above is indeed only a scenario, it fits with what is known of woodpecker finch learning and behaviour. The natural behaviour of the woodpecker finch suggests an underlying iteration of this kind: it is a complex behaviour that seems to have both a genetically fixed component but also components which are developed in ontogeny through individual learning (Tebbich et al. 2001). In an experimental study, Tebbich and her colleagues investigated intergenerational social learning in these birds by taking 6 broods from the wild, splitting them, and rearing half of the chicks with a tool-using model and the other half with one that did not use tools. It was found that although trial-and-error learning was important in improving efficiency, both groups learned to use tools. This suggests that the acquisition of tool-use depends on a very specific, genetically fixed learning disposition (Tebbich et al. 2001). So while the reliance on genetic assimilation is clearly a speculative component of the FSH, the model does not rely on intrinsically improbable events.

Predictions of the flexible stem hypothesis

The FSH identifies adaptability as the difference between the Darwin's finches and the warbler and the flycatchers. A crucial question, then, is whether we have direct evidence showing that the finches are indeed individually adaptable. Ideally, we would like comparative evidence about the behavioural flexibility of other small Galápagos passerines. We do not have such evidence in these species-poor lineages, (apart from novelty responses), however we can provide data on Darwin's finches, as we have used the finch group as a model system in studying the evolution of behavioural flexibility and its relation to cognition. The West-Eberhard model predicts a high baseline for learning capacities across the whole Darwin's finch clade and that these are greater than other comparable groups. However, one might argue that such a high baseline in learning abilities could also be a result of the special selective conditions on the Galápagos and not the legacy of a flexible ancestor. Yet, if the behavioural and cognitive preconditions of innovation are phylogenetically primitive, as the FSH assumes, they should be widely distributed through the crown species and we expect those species with typical foraging practices, not just innovative ones, to be adaptable learners. Thus, we predict that finches without special

feeding techniques should be as flexible as those with them, and that they also possess the essential cognitive mechanisms on which these novel techniques depend. These learning capacities need not be identical from species to species: genetic accommodation may have fine-tuned some particular learning trajectory (for example, increased sensitivity to some particular cue), or it may even have enhanced learning capacities in a specific domain. But the overall learning capacity across the group will be high in comparison to other small generalist birds with fairly short life expectancies. Of course, this test is not decisive. The original difference between the first finches and the other founding lineages might be masked by subsequent evolutionary change, especially since Galápagos lineages have been subject both to strong selection and the effects of small population size, as species suffer population crashes in bad years. Even so, all else being equal, we still expect to see the legacy of ancestral flexibility in living finches.

Components of flexibility

Though the impressive array of finch feeding behaviours provides *prima facie* support for the idea that this lineage is unusual in its behavioural flexibility, this conjecture needs to be tested. However, if we are to measure flexibility, an essential first step is to identify the components from which it is built. We suggest that the following capacities are important components of behavioural flexibility: (i) the seeking of novel information. This includes the willingness to approach novel objects, novel space or novel situations in order to explore them, although responses to new places, objects and individuals do not always co-vary (Boogert *et al.* 2006). The underlying mechanism that guides response to novelty is thought to be neophilia—the spontaneous attraction of an animal to a novel item or place (Thorpe 1956). Neophilia has obvious benefits like the discovery of new resources and of new patches of familiar resources or the development of new means of exploiting familiar resources. But it also can incur costs, such as increased risk of predation and thus, neophobia may have evolved to inhibit costly exploration (Greenberg & Mettke-Hofmann, 2001). We therefore expect flexible agents to seek novel information particularly in areas where the costs of exploration are low. (ii) To exploit novel opportunities, an agent must be able to learn about the affordances of a new object or situation, typically by some form of operant learning. Thus, we expect fast, effective learning by trial-and-error. (iii) Innovation does not require social learning. Nevertheless, the prospects of successful innovation are improved if an agent has the ability to learn affordances from others. (iv) In a fluctuating environment, flexible agents should readily react to changes and seek for alternative solutions to problems (Bond & Balda, 2007). Thus, the ability to inhibit previously successful responses is a factor that could enhance flexibility under changing conditions. (v) Agents are most flexible if they can apply what they have learned to a novel situation with the same underlying problem. Underlying mechanisms for this ability can reach from stimulus generalisation to insight. It is no coincidence that this list is identical to a list of Laland & Reader (2003) that analyses innovation, for flexibility is a precondition of innovation. Innovativeness can therefore be seen as an indicator of flexibility.

In this paper, we compare innovativeness, exploration, reversal learning, and operant learning in Darwin's finches to that of out-group bird species in order to test whether these components of flexibility are comparatively high, as predicted by the flexible stem hypothesis. Additionally, we compare physical cognition between tool-using woodpecker finches and the closely related, but non-tool-using, small tree finches. The aim is to investigate whether small tree finches possess some of the cognitive abilities necessary for tool-use, for that is what we expect if behavioural flexibility preceded the evolution of this special foraging technique.

These data were not collected in order to test these hypotheses, but were analysed post-hoc. Therefore, the evidence is patchy, as the number of species investigated varies and only the woodpecker finch has been studied in detail. However, overall, with some ambiguity, the data are in line with West-Eberhard's conjecture.

Methods

Innovativeness

We compared the number of unusual foraging behaviours reported in Darwin's finches (reviewed in Grant & Grant, 2008) with the number of feeding innovations reported for new world jays (Overington *et al.* 2009). Both sources list special typical behaviour and anecdotal observations of unusual or novel foraging techniques and/or feeding substrates. We chose this corvid sub-family, because in an analysis of 76 bird families, the corvids were found to have the most diverse innovation repertoire amongst passerines (Overington *et al.* 2009). Also, the new world jays have a similar number of genera (7 genera, 38 species) as the Darwin's finches (6 genera, 15 species including the Cocos finch) and are, like the Darwin's finches well-studied which reduces biases due to research efforts.

Study area, subjects and housing

The laboratory experiments on Darwin's finches were carried out at the Charles Darwin Research Station on Santa Cruz Island in the Galápagos Archipelago, from October 2007 - March 2008 and September 2008 - January 2009. We mist-netted a total of 18 woodpecker finches, 16 small tree finches and 8 medium ground finches and kept them individually in outdoor aviaries (200×100×200cm), that were visually separated. Aviaries were equipped with several natural perches and one experimental platform (40×20×50cm), where all experimental set ups were presented. The operant learning experiments on carrion crows (*Corvus corone*) were conducted by M. Scriba at the Max-Planck Institute for Ornithology in Seewiesen, Germany in August 2009.

Exploration in a field experiment

The data were collected between January and March 2000. We tested neophilia by placing three novel objects simultaneously in the finches' natural environment at 242 sample points on three different Islands (St Cruz, Floreana, Genovésa). The objects were: one white roller brush (length 14cm, diameter 6cm), one black, folded bicycle-tube (15×7cm) and a pair of white, flexible plastic tubes (20×1.5cm) bound together with string. We placed the objects on trees 5-7m and on bushes 1.5-2m above the ground in areas with low vegetation. We attracted finches by using a bird whistle. After one minute, the presence of Darwin's finches and other bird species within a radius of 10m around the objects was recorded. During 10-minute-trials, we recorded the mean time spent within a radius of 3m from the object. For each species, we calculated the proportion of individuals present that approached within 3m of the object during the experiment. However, calculating this proportion per sample point would often result in the value 0 or 1 because at many sample points only one individual per species was present at the start of the experiment. We therefore pooled the data from all sample points and calculated (per species) the ratio between the total number of individuals approaching within 3 m and the total number of individuals present within 10m. This resulted in a single percentage-value per species and island. For further details see (Tebbich *et al.* 2009).

Operant learning

The 18 woodpecker finches, 8 small tree finches, 8 medium ground finches and 8 carrion crows were presented with a box (3×2×2.3cm, for Darwin's finches and 10×14×13cm for

crows) containing a food reward. The box was closed on top with a hinged, transparent Perspex lid which overlapped one edge of the box. In order to obtain the food reward, birds had to push open the lid. They were tested twice a day and in a maximum of this in six experimental sessions, each lasting 25min. We measured success or failure to open the box and how many trials were needed to success.

Reversal learning

In this task, individuals are first trained in a discrimination task. Once they have learnt this discrimination, the reward contingencies are reversed. The test apparatus consisted of 2 white boxes (each 3×2×2.3cm) that were mounted 10 cm apart on a wooden base (20×20cm) and covered with coloured foam lids. A Perspex divider (29.5×21cm) between the boxes prevented the birds from removing the lid of the second feeder once they had made their initial decision. First, birds were trained to remove the lids. In the initial discrimination task, the 16 woodpecker finches, 8 small tree finches and 8 medium ground finches had to learn that of the two feeders with different coloured lids (blue and orange), only one, was rewarded. Once they had learned this colour-reward relationship, they moved on to the reversal phase in which the learning rule was reversed. Half of the birds were first rewarded with orange and the other with blue. We measured the number of trials needed and the number of errors made in attaining criterion (see below). We compared our data with the original data of a comparative study of Bond *et al.* (2007) (Table1). In this study 5 Pinyon Jays (*Gymnorhinus cyanocephalus*), 5 Western Scrub jays (*Aphelocoma californica*) and 5 Clark's nutcrackers (*Nucifraga columbiana*) were first trained in skinner box to gain a food reward by pecking a coloured, illuminated key. In the discrimination and reversal procedure they had to peck three times at one of two illuminated side keys (red or green) in order to obtain a food reward. For further details see Bond *et al.* (2007). We also present on reversal learning from study on pigeons (*Columba livia*) by Lissek *et al.* 2002) (Table1), but did not include them in the statistical comparison because we could not obtain the original data. Like the corvids the pigeons were tested in a skinner box. The pigeons had to peck once at on one of two illuminated keys to gain 3s access to food. The criterion to success was

Cane task

This test involved making a choice between two canes (12cm apart), each with a food reward placed either on the outside or the inside of the hook (figure 1a). Only pulling the cane with the food reward in line with its concave portion was rewarded. The canes rested on a rectangular base (15×24×1cm) which was covered with a low, transparent Perspex lid that was open at the front. Twelve woodpecker finches and 6 small tree finches were tested. The bird could see the configuration from above but could only gain access to the food once it had been pulled out from underneath the lid. The two canes were connected by a string, so pulling one cane caused the other to simultaneously withdraw into the apparatus. Thus if one cane was pulled past a certain point, the decision was irreversible.

Individuals that reached significance in the initial cane task were tested in a series of transfer tasks. These were variations of the initial task configuration that were designed to investigate step-wise how well the birds transferred their knowledge of the importance of contact to further configurations (figure. 1b-e).

Seesaw task

A seesaw platform was presented surrounded by a transparent box (figure 2a). Perching on one of the two levers tilted the seesaw towards the subject and caused the reward to roll towards it. During training, the seesaw platform was continuous, while for testing the surface was interrupted by a hole that was placed either centrally (figure 2b) or 2.5 cm off-centre (figure 2a). In order to obtain the reward, the bird had to hop onto the lever that

caused the food to roll down the continuous portion of the seesaw surface and out of the apparatus. Twelve woodpecker finches and 6 small tree finches were tested. Half the birds received the gap-central condition while the other half received the food-central condition. In the transfer task, the birds were presented with the alternative condition (figure 2b).

Criterion and testing procedure for reversal learning, seesaw task and cane task

Individuals were tested daily in two sessions of 10 trials in which the correct side was pseudo-randomised and counterbalanced right and left, so that there were five trials in each position per session. The number of trials in which the reward was presented consecutively on one side never exceeded 3, except in the case of a side bias correction procedure (see below). The birds were given a maximum of 140 trials in the discrimination/reversal-learning task, up to 160 trials in the seesaw task, up to 150 in the cane task and up to 30 trials in the cane transfer tasks. The criterion for passing a test was 7 consecutive correct trials or at least 8/10 correct trials in 2 consecutive sessions or in 1 session all 10 correct. In the comparative study on corvids (Bond *et al.* 2007) the birds received one block of 36 trials a day and in contrast to our study no correction trials for side biases (see below). The criterion for success in the discrimination and subsequent reversal was 90% correct in 3 successive sessions of 36 trials. To make the data more comparable we only included the number of sessions required to first achieve 90 % correct. Nevertheless, we cannot entirely exclude overtraining in the corvids as a factor in their slower reversal learning. In the comparative study on pigeons (Lissek *et al.* 2002) acquisition and reversal session lasted until the learning criterion of 15 correct responses in a row was reached, with session duration not to exceed 3 hr. Like the corvids the pigeons received no correction trials for side biases.

Correction procedure

If a bird developed a side bias, defined as 6 consecutive choices of one side during one session or over 2 sessions, in subsequent trials the reward was only presented on the non-preferred side until the subject chose that side and was rewarded. At that point we reverted back to the original randomised trial configuration. In the analysis, the correction trials were not treated differently from non-corrected trials.

Statistical methods

An extension of the Fisher's Exact Test to 2-by -K contingency tables (RxC-exact-exact-test) was used to test the species difference in number of individuals that reached the criterion in the operant task, the seesaw task and the cane task since this test can be used with small sample sizes, sparse, imbalanced, or heavily tied data (Fung & Lee, 1989). Species differences in exploration, the number of trials to reach criterion in the cane task, and post-hoc comparison, were assessed with Mann-Whitney U-Test. To test for differences within Darwin's finches and between species groups in reversal learning we used an analysis of variance (ANOVA).

Results

Innovativeness

In order to test whether Darwin's finches are indeed exceptionally innovative, we compared the number of unusual foraging behaviours reported in Darwin's finches with the number of feeding innovations reported in new world jays, which belong to an exceptionally innovative bird family (Overington *et al.* 2009). As predicted by the FSH, Darwin's finches had a significantly higher number of feeding innovations per species (median=1, range: 0-8) than the new world jays (median=0, range: 0-9, Mann-Whitney-U-Test, $U=183.5$, $P=0.011$)

Exploration

In a nearly predator-free environment like Galápagos, the costs of exploration are low and we therefore we expect little fear of novel situations (neophobia). Investment in exploration by Darwin's finches and the other terrestrial Galápagos bird species may depend only on the variable benefits of seeking novel information (neophilia). The FSH would therefore predict that Darwin's finches are more neophilic than other Galápagos bird species. In order to test these predictions we compared the reaction to novel objects of Darwin's finches with that of five other bird species from Galápagos in a field experiment. The comparison did not support our prediction: we found no significant difference between Darwin's finches and other Galápagos birds species in terms of the percentage of individuals that approached the novel object to within 3m (Darwin's finches: median %=39.5, range 11.1-67.6; other bird species: median=44.0, range 41.1-72.3; Mann-Whitney-U-Test: $U = 16.0$, $P = 0.117$).

Reversal learning: learning to inhibit a previously learned response

Reversal learning has been used to investigate behavioural flexibility in animals and humans. In this experiment flexibility is measured by the speed with which subjects learn that a previously successful strategy is no longer rewarded. We found no significant differences between woodpecker finches, small tree finches and medium ground finches in the initial discrimination phase (Table 1, ANOVA, $F_{2,29} = 2.508$, $P = 0.099$). In the subsequent reversal task we found no significant difference in the number of trials that the three species needed to reach the criterion (ANOVA, $F_{2,29} = 1.207$, $P = 0.314$). However, woodpecker finches did make significantly more errors than the small tree finches in attaining criterion in the reversal task (Mann-Whitney-U-Test, $U = 28.00$, $P = 0.027$). We attribute this to their extractive mode of foraging. Extractive foraging requires perseverance and perseverance in turn, requires that an agent continues with a behaviour, even when it is not rewarded. Fast reversal learning requires just the opposite.

Comparative data from other bird species indicate that these three Darwin's finch species are indeed unusually fast reversal learners. Unfortunately, no comparative data are available from small short-lived passerine species with a similar ecology. However, comparable data on visual discrimination and reversal learning are available from pigeons (Lissek *et al.* 2002) and three species of corvids (Bond *et al.* 2007) (Table 1). The corvid data are of special significance since corvids are large-brained birds, known for their feeding innovations and their extraordinary cognitive abilities across various domains (Emery & Clayton, 2004). Nevertheless, they took significantly more trials to reach criterion in the reversal phase of a comparable visual discrimination task (ANOVA, $F_{1,46} = 31.9$, $P < 0.001$). It is however possible that the speed of learning might be slower for animals tested in an operant box than for those tested in our experimental set-up. Furthermore, the 3 corvid species were not corrected for any side biases (see methods). Both factors could have affected the speed of learning in corvids but are unlikely to account for the substantial difference between the two groups.

Operant learning

The ability to solve a novel operant task differed significantly between the 4 tested species (RxC-exact-test: $\chi^2 = 7.94$, $P = 0.04$). Forty-four % of the woodpecker finches and 62.5% of the carrion crows were able to open a novel box with a transparent lid while none of the small tree finches and only 25% of the medium ground finches managed to do this in 6 experimental sessions (post-hoc comparisons RxC-exact-test: woodpecker finches versus small tree finches, $\chi^2 = 5.13$, $P = 0.03$; carrion crows versus small tree finches, $\chi^2 = 7.23$, $P = 0.02$; all other comparisons ns). The difference between the woodpecker finch and small tree finches can again, as in the reversal task, be attributed to the perseverance of woodpecker finches. Woodpecker finches made more contacts proportional to time tested

(median=2.3, range=1.0-25.2) than small tree finches (median=1.3, range=0.7-2.9; Mann-Whitney U-test: $U=28$, $P=0.013$).

These results show that the performance of woodpecker finches and medium tree finches in this operant task is similar to large brained corvids but also that problem solving can be influenced by other factors such as persistency. Further evidence showing that woodpecker finches are fast trial and error learners comes from a comparative study in which woodpecker finches performed similar to primates in series of problem solving tasks (Tebbich & Bshary 2004).

Physical Cognition in tool-using and non-tool-using Finches

It is not surprising that species with complex and distinctive, but species-typical behavioural adaptations, like tool-use, have evolved specific cognitive or learning strategies, since these explain the reliable acquisition of such unique foraging skills. However, according to the flexible stem hypothesis we also expect finches without these complex foraging routines to show a high learning baseline. One important line of experimental research supports this prediction: We ran a series of experiments, to compare the physical cognitive learning abilities of woodpecker finches and small tree finches and found no major difference in physical intelligence amongst these species.

Cane task

In the cane pulling task, there was no difference in the speed with which woodpecker finches (median trials to success=116.5, range 70-149, $N=8$) and small tree finches (median trials to success=106.5, range 76-140, $N=6$) learned to choose the correct configuration (Mann-Whitney U-test, $U=19$; $P=0.573$) nor was there a significant difference in the number of individuals of each species to attain criterion in the initial (woodpecker finches 8 out of 12 and all small tree finches, RxC-exact-test, $\chi^2=3.462$, $P=0.11$). Moreover, 3 small tree finches and 6 woodpecker finches were able to transfer their acquired knowledge to slightly different tasks (figure 1b).

Seesaw task

Individuals from both species were able to solve the seesaw task, but small tree finches outperformed woodpecker finches: 5 out of 6 small tree finches solved the initial task, but only 2 out of 12 woodpecker finches (RxC-exact-test, $\chi^2=7.481$, $P<0.012$). None of the tested birds passed the transfer task.

These results, showing little difference in physical cognitive intelligence between woodpecker finches and small tree finches, indicate that the capacities shared by the clade have been co-opted for the specific woodpecker finch niche—a finding which is consistent with the FSH. The results are inconsistent with the alternative hypothesis, namely that the capacity to solve physical problems evolved in the woodpecker finch in response to a specific ecological challenge.

A Brief Conclusion

Tebbich's and Teschke's experiments were not designed to test the flexible stem hypothesis, but rather to test hypotheses about the relationship between adaptive behaviour and cognitive mechanisms. Nevertheless, some of our results are in line with the FSH: We found that the Darwin's finch species show a high baseline in behavioural parameters that are plausible components of flexibility (i.e. reversal learning, operant learning and reported innovation rate). In these abilities, they rival and even outperform large-brained corvids. We also found that small tree finches, close relative of the tool-using woodpecker finches, seem

to possess the cognitive foundations for tool-use, which is in line with the idea that the preconditions of innovation are phylogenetically primitive. The data on exploration are in tension with the FHS: Darwin's finches were not more apt to explore than four other Galápagos bird species. We are aware that our data only provide preliminary evidence. A full test of the FSH would at the very least require the following:

- (i) The development of a more nuanced and empirically tractable break-down of the cognitive and behavioural capacities underlying flexibility and innovation. To more exhaustively test the FSH, we need to compare birds across a wide range of cognitive dimensions, not just a few.
- (ii) Extensive knowledge of the ontogeny of other special feeding techniques in Darwin's finches. The ontogeny of a capacity is clearly relevant to its potential for development, redeployment, and recombination with other elements of an animal's repertoire. As with other aspects of an agent's phenotype, the more modular a skill, the more freedom it has to vary independently of the rest of the agent's repertoire (Lewontin 1978), and the more it is a potential site of innovation. More knowledge in this area would allow a more competent assessment of the role of special feeding techniques in the evolution and adaptive radiation of Darwin's finches.
- (iii) Most obviously, we need a broader comparative base across the finch species, between the finch species and mockingbirds, and between these two diverse lineages and those endemics that have not diversified. Only a full comparative test can tell us whether (a) the finches collectively are more behaviourally flexible than other endemics, and (b) whether standard-model finches are as flexible as those with novel foraging methods.

Almost all scientific papers end with a clichéd remark on the need for further research. In this case, it is no cliché. That said, the FSH makes two central predictions: (i) the finches are more flexible than the endemics that did not radiate; (ii) flexibility in the finches is primitive; it preceded rather than evolved with innovation. The bottom line is that while we have very little data on the first prediction, the little that we have does not confirm it. We have much more data on the second, and this is confirmed.

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References

- Ancel LW. A quantitative model of the Simpson-Baldwin Effect. *J. theor. Biol.* 1999; 196:197–209. doi: 10.1006/jtbi.1998.0833. [PubMed: 9990740]
- Arbogast BS, Drovetski RL, Curry RL, Boag PT, Seutin G, Grant PR, Grant BR. The origin and diversification of Galápagos mockingbirds. *Evolution.* 2006; 60:370–382. doi:10.1111/j.0014-3820.2006.tb01113.x. [PubMed: 16610327]
- Avital, E.; Jablonka, E. *Animal traditions: behavioural inheritance in evolution.* Cambridge University Press; Cambridge, UK: 2000.

- Bateson P. The active role of behaviour in evolution. *Biol. Philos.* 2004; 19:283–298. doi: 10.1023/B:BIPH.000024468.12161.83.
- Bolmer JL, Kimball NK, Whiteman JH, Sarasola JH, Parker PG. Phylogeography of the Galápagos hawk (*Buteo galapagoensis*): A recent arrival to the Galápagos Islands. *Mol. Phylogenet. Evol.* 2006; 39:237–247. doi: 10.1016/j.ympev.2005.11.014. [PubMed: 16376110]
- Bond AB, Kamil AC, Balda RP. Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *J. Comp. Psychol.* 2007; 121:372–379. doi: 10.1037/0735-7036.121.4.372. [PubMed: 18085920]
- Boogert NJ, Reader S, Laland K. The relation between social rank, neophobia and individual learning. *Anim. Behav.* 2006; 72:1229–1239. doi: 10.1016/j.anbehav.2006.02.021.
- Bowman RI, Billee SL. Blood-eating in a Galápagos Finch. *The Living Bird.* 1965; 4:29–44.
- Browne RA, Collins EI, Anderson DJ. Genetic structure of the Galápagos population of the yellow warbler. *Condor.* 2008; 110:549–553. doi: 10.1525/cond.2008.8540.
- Curio E, Kramer P. Vom Mangrovenfinken (*Cactospiza heliobates* Snodgrass und Heller). *Z. Tierpsychol.* 1964; 21:223–234.
- Curry RL, Anderson DJ. Interisland variation in blood drinking by Galápagos mockingbirds. *Auk.* 1987; 104:517–521.
- Dawkins, R. *Climbing Mount Improbable.* W.W. Norton; New York, USA: 1996.
- DeBenedictis PA. The bill-brace feeding behaviour of the Galápagos finch *Geospiza conirostris*. *Condor.* 1966; 68:206–208.
- Eibl-Eibesfeldt I, Sielman H. Beobachtungen am Spechtfinken (Sclater und Salvin). *J. Orn.* 1962; 103:92–101.
- Emery NJ, Clayton SC. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science.* 2004; 306:1903–1907. doi: 10.1126/science.1098410. [PubMed: 15591194]
- Fung KP, Lee J. Extensions of Fisher Exact Test to 2-by -K Contingency Tables- A Computer Program in BASIC. *Comput. Meth. Prog. Bio.* 1989; 28:195–196.
- Grant, PR. *Ecology and evolution of Darwin's finches.* Princeton University Press; Princeton, USA: 1986.
- Grant PR, Grant RB. Annual variation in finch numbers, foraging and food supply on Isla Daphne Major, Galápagos. *Oecologia.* 1980; 46:55–62. doi: <http://dx.doi.org/10.1007/BF00346966>.
- Grant, PR.; Grant, RB. *How and why species multiply. The radiation of Darwin's finches.* Princeton University Press; Princeton, USA: 2008.
- Greenberg, R.; Mettke-Hofmann, C. Ecological aspects of neophobia and neophilia in birds. In: Nolan, V., Jr., editor. *Curr. Ornithol.* Vol. 16. Kluwer Academic / Plenum Publishers; New York, USA: 2001. p. 119-178.e. a.
- Hinton G, Nowlan S. How learning can guide evolution. *Complex Systems.* 1987; 1:495–502.
- Jablonka, E.; Lamb, M. *Evolution in four dimensions.* MIT Press; Cambridge, USA: 2005.
- Lack, D. *Darwin's finches.* Cambridge University Press; Cambridge, UK: 1947.
- Laland, K.; Reader, S. Animal innovation: an introduction. In: Reader, S.; Laland, K., editors. *Animal Innovation.* Oxford University Press; Oxford, UK: 2003. p. 3-35.
- Laland K. Exploring gene-culture interactions: insights from handedness, sexual selection and niche-construction case studies. *Phil. Trans. R. Soc. B.* 2008; 363:3577–3589. doi: 10.1098/rstb.2008.0132. [PubMed: 18799415]
- Lewontin RC. Adaptation. *Sci. Am.* 1978; 239:156–169.
- Lewontin, RC. Organism and environment. In: Plotkin, HC., editor. *Learning, development and culture.* Wiley; New York, USA: 1982. p. 151-170.
- Lissek S, Diekamp B, Güntürkün O. Impaired learning of a colour reversal task after NMDA receptor blockade in the pigeon (*Columba livia*) Associative Forebrain (Neostriatum Caudolaterale). *Behav. Neurosci.* 2002; 116:523–529. doi:10.1037//0735-7044.116.4.523. [PubMed: 12148920]
- MacFarland C, Reeder W. Cleaning symbiosis involving Galápagos tortoise and two species of Darwin's finches. *Z. Tierpsychol.* 1974; 34:464–483. [PubMed: 4454774]
- Morse, DH. *Behavioural mechanisms of ecology.* Harvard University Press; Cambridge, USA: 1980.

- Nicolakakis N, Sol D, Lefebvre L. Behavioural flexibility predicts species richness in birds, but not extinction risk. *Anim. Behav.* 2003; 65:445–452. doi:10.1006/anbe.2003.2085.
- Odling-Smee, F.J.; Laland, K.N.; Feldman, M.W. Niche construction: the neglected process in evolution. Princeton University Press; Princeton, USA: 2003.
- Overington SE, Morand-Ferron J, Boogert NJ, Lefebvre L. Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Anim. Behav.* 2009; 78:1001–1010. doi:10.1016/j.anbehav.2009.06.033.
- Parent CE, Caccone A, Petren K. Colonization and diversification of Galápagos terrestrial fauna: a phylogenetic and biogeographical synthesis. *Phil. Trans. R. Soc. B.* 2008; 363:3347–3361. doi: 10.1098/rstb.2008.0118. [PubMed: 18782729]
- Price, T. Speciation in Birds. Roberts & Company Publishers; Greenwood Village: 2008.
- Rehkämper G, Frahm HD, Zilles K. Quantitative development of brain and brain structures in birds (Galliformes and Passeriformes) compared to that in mammals (Insectivores and Primates). *Brain Behav. Evol.* 1991; 37:125–143. doi:10.1159/000114353. [PubMed: 2070254]
- Schluter D. Feeding correlates of breeding and social organization in two Galápagos finches. *Auk.* 1984; 101:59–68.
- Schluter, D. The ecology of adaptive radiation. Oxford University Press; New York, USA: 2000.
- Schluter D, Grant PR. Ecological correlates of morphological evolution in a Darwin's finch, *Geospiza difficilis*. *Evolution.* 1984; 38:856–869.
- Sol, D. Behavioural flexibility: a neglected issue in the ecological and evolutionary literature?. In: Reader, S.M.; Laland, K.N., editors. *Animal innovation*. Oxford University Press; Oxford, UK: 2003. p. 63–82.
- Sol D, Stirling DG, Lefebvre L. Behavioral drive or behavioral inhibition in evolution: subspecific diversification in Holarctic passerines. *Evolution.* 2005; 59:2669–2677. [PubMed: 16526513]
- Tebbich S, Bshary R. Cognitive abilities related to tool use in the woodpecker finch, *Cactospiza pallida*. *Anim. Behav.* 2004; 67:689–697. doi: 10.1016/j.anbehav.2003.08.003.
- Tebbich S, Fessl B, Blomqvist D. Exploration and ecology in Darwin's finches. *Evol. Ecol.* 2009; 23:591–605. doi:10.1007/s10682-008-9257-1.
- Tebbich S, Taborsky M, Fessl B, Blomqvist D. Do woodpecker finches acquire tool-use by social learning? *Proc. R. Soc. Lond. B.* 2001; 268:2189–2193. doi: doi 10.1098/rspb.2001.1738.
- Thorpe, W.H. Learning and instinct in animals. Methuen and Co. LTD; London, U.K.: 1956.
- Vincek V, O'Huigin C, Satta Y, Takahata N, Boag PT, Grant PR, Grant BR, Klein J. How large was the founding population of Darwin's finches? *Proc. R. Soc. Lond. B.* 1996; 264:111–118. doi: 10.1098/rspb.1997.0017.
- Weber, B.; Depew, D. Evolution and learning: the Baldwin effect reconsidered. MIT Press; Cambridge, USA: 2003.
- West-Eberhard, J. Developmental plasticity and evolution. Oxford University Press; Oxford, UK: 2003.
- Wyles JS, Kunkel JG, Wilson AC. Birds, behaviour and anatomical evolution. *Proc. Natl. Acad. Sci. USA.* 1983; 80:4394–4397. [PubMed: 6576345]
- Wilson AC. The molecular basis of evolution. *Sci. Am.* 1985; 253:148–158.

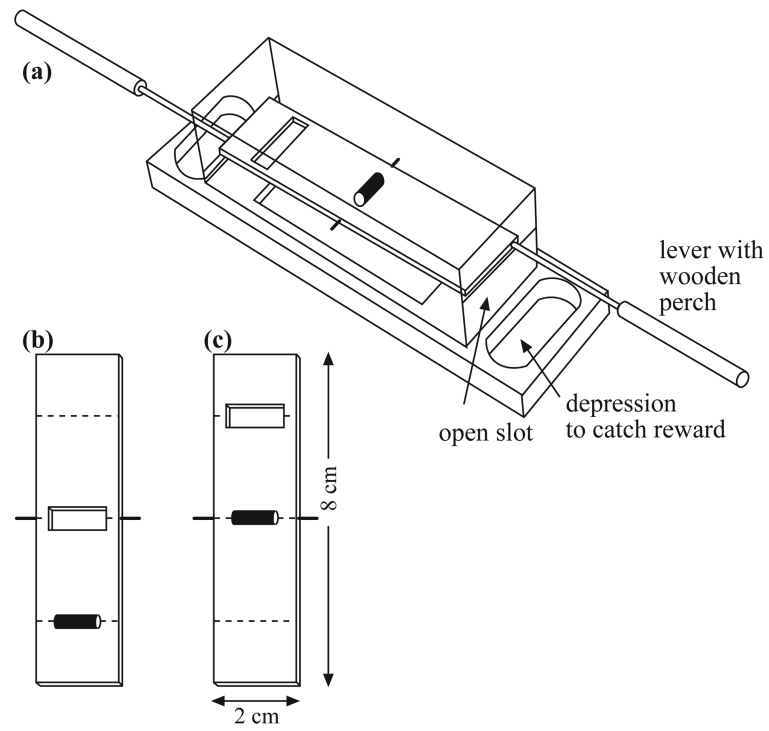


Figure 1.

(a) The cane task apparatus depicted in the initial test condition. (b)- (e) Transfer tasks 1-4.

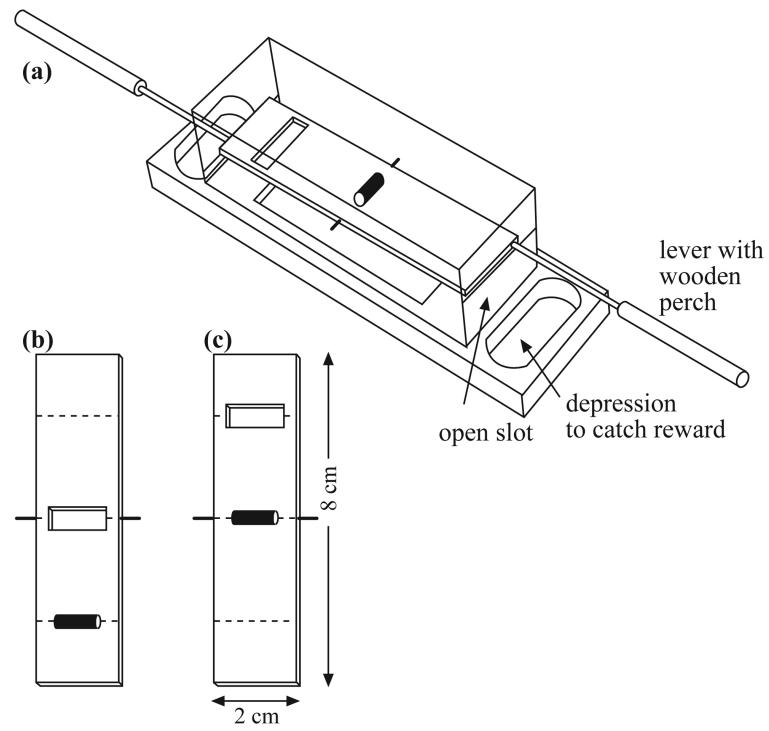


Figure 2.

(a) The seesaw task apparatus depicted in the food-central condition. (b) gap-central condition.

Table 1

Mean number of trials and mean number of errors (with standard errors) needed to reach a significant criterion in the discrimination and reversal phases of a visual discrimination task with pigeons, 3 corvid species and 3 species of Darwin's finches

Species	N	Disc	SE	Reversal	SE	Errors reversal	SE
Pigeon	8	40		168		99	
<i>Columba livia</i>							
Corvid species							
Pinyon jay	5	149,6	33,6	155,0	28,3		
<i>Gymnorhinus cyanocephalus</i>							
Western scrubjay	5	136,8	20,9	191,0	35,7		
<i>Aphelocoma californica</i>							
Clark's nutcracker	5	122,4	8,18	142,6	3,6		
<i>Nucifraga columbiana</i>							
Darwin's finch species							
Small tree finch	8	41,1	18,4	76,3	13,8	37,4	6,8
<i>Camarhynchus parvulus</i>							
Woodpecker finch	16	39,8	2,7	95,6	5,4	56,4	4,8
<i>Cactospiza pallida</i>							
Medium Ground finch	8	56,1	9,2	93,7	12,5	46,4	7,9
<i>Geospiza fortis</i>							