



## A field test of behavioural flexibility in Zenaida doves (*Zenaida aurita*)

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### ABSTRACT

Animals' ability to adjust their behaviour when environmental conditions change can increase their likelihood of survival. Although such behavioural flexibility is regularly observed in the field, it has proven difficult to systematically quantify and predict inter-individual differences in free-living animals. We presented 24 Zenaida doves (*Zenaida aurita*) on 12 territories with two learning tests in their natural habitat in Barbados. The dove pairs showed high site fidelity and territoriality, allowing us to test individuals repeatedly while accounting for the effects of territorial chases and pair bonds on our learning measures. We used a foraging apparatus that enabled Zenaida doves to access seed, yet excluded other species, and measured doves' performance on colour discrimination and reversal learning tests. We found that (1) doves on all 12 territories passed the two tests; (2) mates within a pair were consistently solvers or scroungers; (3) sex, body condition and territorial chases did not consistently affect learning rates; (4) tameness was a significant negative predictor of learning to feed from the foraging apparatus and (5) scrounging within pairs seemed to facilitate learning. Our study presents a method to quantify intraspecific differences in behavioural flexibility in the field and relate these to individuals' physical and social traits.

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### 1. Introduction

The ability to adjust behaviour when environmental conditions change can increase an individual's likelihood of survival. For example, young cactus finches (*Geospiza conirostris*) that acquired the foraging skills necessary to exploit unfamiliar food sources in a time of severe drought were more likely to survive than juveniles that stuck with typical wet-season foraging behaviour (Grant and Grant, 1989). Apart from a few illustrative cases, however, intraspecific differences in behavioural flexibility have proven difficult to quantify in the field, as no systematic measures existed until relatively recently.

In contrast, behavioural flexibility has long been a standard term in psychology and neuroscience, where it is often quantified using a subject's performance on tests of reversal learning (e.g. Fellows and Farah, 2003; Izquierdo et al., 2007; Haluk and Floresco, 2009). In the traditional reversal learning paradigm, an animal is presented with two stimuli simultaneously, where one is associated with a reward and the other is not. After the animal has achieved a certain learning criterion, or after it has experienced a predetermined number of trials, the reinforcement value of the two stimuli is reversed. Animals

often make several errors in the first reversal trials (a phenomenon known as negative transfer), but improve over successive reversals until performance asymptotes.

Despite its usefulness as a measure of flexibility, reversal learning has never, to our knowledge, been assessed in the field. Instead, field measures of flexibility have centered on novel problem-solving tasks (Webster and Lefebvre, 2001) and frequency counts of innovative feeding in the wild (Lefebvre et al., 1997; Overington et al., 2009). One drawback of the latter approach is that foraging innovations in less cognitively advanced species might be too rare to be practically used as a quantitative measure of inter-individual differences in behavioural flexibility (Overington et al., 2009). In addition, organisms may not need to deviate from established behavioural routines to solve novel problems or to acquire new stimulus–response associations in stable environmental conditions and times of plenty (Tebbich et al., 2010).

A difficulty associated with presenting a novel foraging task to measure behavioural flexibility in the field, is that dominant individuals may monopolize the task and prevent conspecifics from accessing it. This is what happened in the New Zealand wild mountain parrot, or kea (*Nestor notabilis*), when presented with butter inside a tube attached to a pole, a food reward requiring innovative behaviour to access (Gajdon et al., 2004). In free-living Florida scrub-jays (*Aphelocoma coerulescens*), the presence of dominant breeding males inhibited task performance by subordinate helpers at the nest, who would only perform when the dominant adults had left the vicinity of the task (Midford et al., 2000). Social dominance

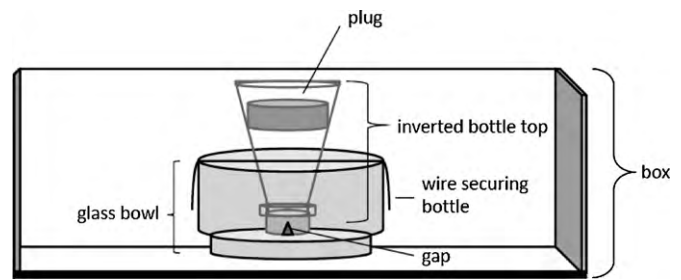
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did not prevent keas from attempting to open the lids of rubbish bins, but this mechanical task appeared to be too challenging to solve for most keas (Gajdon et al., 2006). When a foraging task is too difficult to solve, or the food reward too large for the solving conspecific to monopolize, individuals in gregarious species may opt to scrounge from the solvers' food rewards instead of attempting to solve the task themselves (Giraldeau and Lefebvre, 1987; Gajdon et al., 2006). A final problem with measuring behavioural flexibility is that it ideally involves measures of individuals' performance on more than one trial (Deaner et al., 2006; Tebbich et al., 2010). Although it is easy to measure animals repeatedly in captivity, free-living subjects come and go as they wish. Following a cohort of focal individuals over a controlled series of repeated trials may thus be difficult because some of them may be absent on given trials.

In this paper, we bridge the gap between measures of behavioural flexibility in the field and in captivity by conducting tests of discrimination and reversal learning in free-living birds. To circumvent the abovementioned problems, we conducted our learning tests on a tame territorial animal with high site fidelity, the Zenaida dove (*Zenaida aurita*) of Barbados. The Zenaida dove is a monogamous columbid species endemic to the Caribbean islands. In most areas of Barbados, Zenaida doves defend stable year-round territories, feed on the ground, are very tame around humans and readily approach provisioned feeding sites that contain a novel apparatus (Webster and Lefebvre, 2001). In addition, the doves form stable pair bonds and both members of the pair aggressively chase intruders attempting to feed on the territory (Lefebvre, 1996; Sol et al., 2005). Zenaida doves are thus very likely to interact with a learning apparatus in conditions that are easy to observe, as well as to provide repeated measures on their territory. We trained free-living Zenaida doves to feed from a novel apparatus that was subsequently used for a discrimination test (which colour cue identifies the apparatus with accessible seed) and a reversal test (changing the colour cue that identifies which apparatus has accessible seed).

We first describe the conditions under which learning in Zenaida doves occurred, with particular reference to the roles of pair bonds and territorial aggression. We then test whether sex, aggression, scrounging, body condition or tameness can predict individuals' performance during training and the two learning tests. Previous studies on free-living birds have suggested that males may be more inclined to solve a foraging task than females (e.g. in keas: Gajdon et al., 2006; and in New Caledonian crows *Corvus moneduloides*: Bluff et al., 2010) and to aggressively exclude mates from experimental food sources (e.g. in New Zealand robins *Petroica australis*: Steer and Burns, 2008). We therefore expected that in Zenaida doves, males would be the first within each pair to interact with the apparatus during training trials and to choose the correct apparatus consistently in both of the learning tests presented on the pair's territory. The role scrounging may play in acquiring a task solution is difficult to predict: while captive experiments on feral pigeons showed that scrounging prevented learning of a foraging task solution (Giraldeau and Lefebvre, 1987), recent avian field studies suggest that scrounging might facilitate learning (e.g. Midford et al., 2000; Gajdon et al., 2006). Whether scrounging from mates within free-living pairs facilitates or inhibits learning has not yet been tested. Finally, tolerance of human proximity, or tameness, predicted differences in latency to feed from an experimental food source in the field when comparing different species: tamer feral pigeons (*Columba livia*) were faster to feed than less tame Zenaida doves (Seferta et al., 2001). However, individual differences in tameness have, to our knowledge, not been related to learning performance in the field. We predicted that tamer Zenaida doves would be faster at solving our learning tasks than individuals less tolerant of human proximity.



**Fig. 1.** Task apparatus. The gap was oriented towards the back of the box during the final part of the training phase and the colour discrimination and reversal tests. The apparatus was designed to exclude the 4 other avian species (*Carib grackles*, *Quiscalus lugubris*; Lesser-Antillean bullfinches, *Loxigilla noctis*; Common ground doves, *Columbina passerina*; Shiny cowbirds, *Molothrus bonariensis*) that normally compete with Zenaida doves for food in mixed species aggregations (Dolman et al., 1996). Dimensions: glass bowl: 11.8 cm diameter, 7.0 cm high; plug: 5.0 cm diameter, 1.4 cm high; wooden box: 34.2 cm × 15.2 cm × 11.8 cm high.

## 2. Materials and methods

### 2.1. Zenaida doves

We studied adult male and female Zenaida doves at the Bellairs Research Institute of McGill University and the adjacent grounds of Folkestone Park and St-James Church (Holetown, Saint James Parish, 13.19°N; -59.64°W). Between March 1st and June 20th, 2006, we caught 85 doves in walk-in traps baited with seed, and banded each individual with a unique colour combination of four plastic leg bands (A.C. Hughes, Hampton Hill, U.K.). For each bird, we measured left and right tarsus and wing length, tail length, bill length and width. Tarsus and bill measurements were conducted with a digital calliper (precision: ±0.01 mm) and wings and tail with a ruler (precision: ±0.05 mm). Heavily damaged tails were excluded. Individuals were weighted with a digital pocket scale (precision: ±0.1 g). A small blood sample (40 µl twice) was also collected by puncturing the brachial vein for molecular sex identification (Monceau, 2009). Once morphological measurements and blood samples were taken, doves were released at their site of capture. Many of the doves we banded were not resighted again, possibly because they were floaters in search of a territory (Sol et al., 2005). Two pairs of territorial doves were used for pilot studies and tests of another 6 pairs were aborted as the doves did not interact with the task apparatus regularly enough. This left us with 24 birds making up 12 pairs. For all 24 test subjects, molecular gender assignment confirmed behavioural sexing from field observations.

### 2.2. Learning tests

Each pair of doves on the 12 territories was allowed to habituate to the test apparatus before learning tests were started, to prevent individuals' object neophobia from interfering with learning test performance (Boogert et al., 2008). The same test apparatus was used for all learning phases presented to each pair in the same order: (a) training phase; (b) colour discrimination test; and (c) colour reversal test.

### 2.3. Test apparatus

The test apparatus consisted of the top 10 cm of a plastic bottle placed upside-down in a glass bowl and secured to the bowl with a metal wire. The bottle was filled with mixed bird seed and covered with a plug to prevent other bird species from eating the seed. Doves could access the seed by pecking at a small triangular gap cut in the rim of the bottle opening. This apparatus was positioned in an open wooden box (i.e. missing top and front; see Fig. 1).

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