



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.

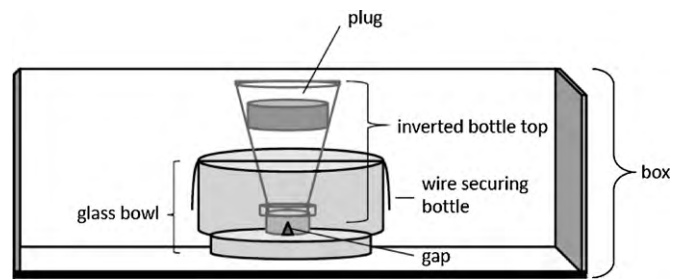


Fig. 1. Task apparatus. The gap was oriented towards the back of the box during the final part of the training phase and the colour discrimination and reversal tests. The apparatus was designed to exclude the 4 other avian species (*Carib grackles*, *Quiscalus lugubris*; Lesser-Antillean bullfinches, *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).

2.4. Habituation, training, and learning test procedure

All observations were made at a distance of 15 m from the task apparatus. If no territory owners appeared within 20 min of task presentation, the trial was aborted and another trial attempted at the same territory 4 h later on the same day, or the next day. A dove was considered to have habituated or to have passed a training or test level if it fed from the apparatus for three consecutive minutes. The experimenter then slowly approached the task in a straight line at a constant pace. At the moment the dove fled, the experimenter dropped a marker and measured the distance to the task apparatus to quantify the dove's tolerance to human proximity or 'tameness'. A dove failed a habituation, training or test level when it left the apparatus without having fed from it and did not return to the apparatus within the next 10 min. Habituation, training and test levels progressed according to the fastest learner in each dove pair, but all task interactions of both members were recorded.

2.5. Habituation phase

Before starting the training phase, each test subject was habituated to the test apparatus by allowing it to feed on mixed bird seed presented progressively more like the food presentation in the actual task apparatus: (1) mixed bird seed on a 30 cm × 10 cm × 2 cm wooden shelf; (2) seed in a glass bowl on the shelf; (3) the bowl with seed on top of the wooden apparatus box; (4) the bowl with seed inside the box. Once the test subject had passed these four levels, it was presented with the actual task apparatus and trained to gain access to the seed within.

2.6. Training phase

To raise doves' interest in the task apparatus, we preceded each trial of the training phase by presenting the bowl with seed inside the open box (habituation level 4). Once the test subject had fed for 3 min, we replaced the bowl with the task apparatus. As none of the test subjects discovered how to extract the seed from the bottle top when there was no seed available in the bowl holding the apparatus, we shaped the doves towards pecking the bottle rim gap by providing seed in front of it. Once the test subject learned to peck the gap without seed in the bowl, we turned the apparatus such that the gap was oriented towards the back of the box. In this way, the dove could only inspect the gap by entering the box and putting its head in between the bottle and the back of the box. This procedure was necessary for the colour discrimination and reversal learning tests (see Sections 2.7 and 2.8). For each task apparatus visit, we recorded the time at which the test subject entered and left the box, and duration of pecking the bottle top. We also recorded the durations of all territorial chases. Each dove's latency to learn to feed from the foraging apparatus was calculated by summing time spent in the box up to the moment it had pecked the gap oriented towards the back of the box, without seed presentation in the bowl, for 3 min.

2.7. Colour discrimination test

Before starting the colour discrimination test, we conducted a pre-test to establish test subjects' inherent colour preferences: we presented two copies of the learning task apparatus in two boxes, 1 green and the other white, positioned next to each other with 15 cm in between, and recorded the colour of the box entered first. We then started the actual discrimination test by presenting each test subject with four boxes simultaneously, two of each colour. Boxes of the colour entered first during the pre-test contained task apparatuses with sealed gaps, making them unrewarded, whereas boxes of the non-preferred colour contained the rewarded apparatuses (i.e. with open gaps). We recorded the time at which the

test subject entered and exited each of the boxes and measured the latency to access seed in one of the rewarded task apparatuses and the number and duration of visits to unrewarded task apparatuses if any such errors were made before the test subject made the correct choice. We also noted the trials in which the subject reached a criterion of immediate exploitation of the correct box, without errors or time delays (latency < 5 s). After the test subject had fed from a rewarded box for 3 min, we approached the boxes, measured flight initiation distance, and presented the four boxes again, but in a different order. The four boxes were thus presented next to each other five times in a row, each time in a different colour order (e.g. for trial 1, from left to right: green–white–white–green, trial 2: white–green–white–green). Colour orders were determined beforehand and held constant across all test subjects.

2.8. Reversal test

The rewarded colour was reversed for each dove pair, and the test was conducted in the same way as the colour discrimination test. However, in this test the four boxes were presented ten times in a row on each territory because two subjects who had acquired the learning criterion during the discrimination test (i.e. immediate exploitation of the correct box) had not reached the learning criterion by the 5th trial of the reversal test.

Depending on the pair tested, the total test procedure from habituation to reversal learning took between 8 and 32 days (mean ± SD = 21.33 ± 7.22 days). All habituation, training and learning trials were conducted between 6:00 and 18:00 h and were recorded with a Panasonic 3CCD camera to check data recorded manually during direct observations.

3. Analyses and results

We conducted our analyses in R version 2.8.1 using the functions 'glm.nb' (MASS library) and 'lme' (nlme library; R Development Core Team, 2008), and SPSS version 15.

3.1. General observations

Territorial Zenaida doves reliably visited our task apparatus and defended it against conspecifics. At least one member of the 12 targeted pairs interacted with the apparatus on 96% of all test days, while both members of these pairs appeared on 69% of all test days. Bullfinches tended to visit the apparatus before Zenaida doves, attracting territory owners to the food (Webster and Lefebvre, 2001), and were generally tolerated. Seed exploitation during the habituation and training phases by ground doves and neighbouring Zenaida doves or floaters was met with aggressive territorial chases. On average, territorial doves spent 9.77 ± 8.11% of their trial time chasing away conspecifics and ground dove intruders and 47.94 ± 15.56% interacting with the apparatus, with a mean of 0.86 ± 1.22 aggressive interruptions of foraging per trial.

3.2. Do Zenaida doves learn in the field?

At least one member of each territorial pair learned to feed from the apparatus and completed all trials for the two learning tests on each of the 12 territories, with the number of individuals that learned to feed from the apparatus and that participated in the learning tests increasing over tests (Table 1).

To assess whether doves required less time to extract seed across trials, which would suggest they learned to enter the correct colour box in the discrimination and reversal tests, we modeled 'latency to extract seed' as a function of 'trial number' and 'bird', using a negative binomial generalized linear model to accommodate the non-normal error structure of the data. 'Bird' was a fixed

Table 1
Total number of birds across the 12 targeted territories that finished each of the three learning phases, and the number of pairs in which birds learned to feed from the apparatus while scrounging from their mates' seed extractions.

Test	# of birds solving without scrounging	# pairs in which mate scrounges without solving	# pairs in which mate learns to solve after scrounging	# pairs in which mate does not participate	# pairs in which both mates solve/total # of pairs tested
Training phase	13	7	2	2	3/12
Colour discrimination	15	3	2	4	5/12
Reversal	18	0	1	5	7/12

Table 2
Results of negative binomial generalized linear models in R used to test whether trial number was a significant predictor of latency to extract seed in the discrimination test and first five trials of the reversal test, including 'bird' as a fixed effect to accommodate the repeated measures-structure of the data. Analyses were conducted on all solvers as well as first solvers only for both learning tests. Negative estimate values indicate that latencies to extract seed decreased across trials, suggesting that doves learned the colour-reward association.

Learning test	Sample size	Estimate \pm SE	Statistics	p-value
Discrimination: 5 trials				
All solvers	15	-1.077 ± 0.164	$Z_{1,72} = -6.566$	<0.001
First solvers only	12	-0.971 ± 0.117	$Z_{1,58} = -8.275$	<0.001
Reversal: first 5 trials				
All solvers	18	-0.530 ± 0.102	$Z_{1,80} = -5.181$	<0.001
First solvers only	12	-0.596 ± 0.171	$Z_{1,58} = -3.478$	<0.001

effect instead of a random effect because there is as yet no mixed effects version of the `glm.nb` function available in R (R Development Core Team, 2008). Inclusion of 'bird' as a fixed effect is more conservative than it would be as a random effect by using up more degrees of freedom. We ran `glm.nb` models on the five trials of the colour discrimination test and on only the first five trials of the reversal test to compare the effect of trial number in these two tests.

Individuals may become faster at accessing food from a rewarded box across trials by learning to switch more quickly from unrewarded to rewarded boxes, rather than by acquiring the intended colour-reward association. To assess this possibility, we transformed the abovementioned latencies into binomial scores where individuals that chose the rewarded box immediately were assigned a '1', and individuals that entered and/or pecked at an unrewarded apparatus during a trial before exploiting the rewarded box for three consecutive minutes were assigned a '0'. We then plotted the proportion of all doves that immediately chose the correct box for each discrimination and reversal learning trial. Doves were expected to perform below chance levels during the first few trials of the discrimination test, as the box of the colour that was not preferred by the test subject during a pre-test was rewarded first (see Section 2). However, if individuals acquired the colour-reward association, the proportion of doves choosing the correct box should increase to above chance levels across trials.

We found trial number to be a significant negative predictor of birds' latencies to extract seed in both the discrimination and reversal learning tests, for all solvers as well as the first solvers within each pair only (Table 2). This significant decrease in doves' latency to access seed from the correct box, together with an obvious increase in the proportion of birds choosing the correct box immediately (i.e. without entering an unrewarded box first) across both discrimination (linear regression slope estimate \pm SE = 0.192 ± 0.077 , $t_5 = 2.475$, $R^2 = 0.819$, $p = 0.090$; Fig. 2A) and reversal learning trials (linear regression slope estimate \pm SE = 0.047 ± 0.019 , $t_9 = 2.466$, $R^2 = 0.657$, $p = 0.039$; Fig. 2B) suggests that individuals acquired the colour-reward association.

3.3. Predictors of learning performance

3.3.1. Body condition

We operationally defined a bird's body condition as its residual on a regression of body mass against body size (Jakob et al., 1996). We expressed body size as the first two factors on a Principal

Components Analysis that included \log_{10} -transformed and standardized measures of wing length (mean of left and right wings), tail length, tarsus length (mean of left and right tarsus), bill length and bill width. We used the residuals of the regression of \log_{10} -transformed and standardized body weight against each bird's factor scores on body size Principal Components 1 and 2 as an index of body condition.

3.3.2. Tameness

We used a one-way ANOVA to test whether mean distance to flee from the experimenter differed significantly between individu-

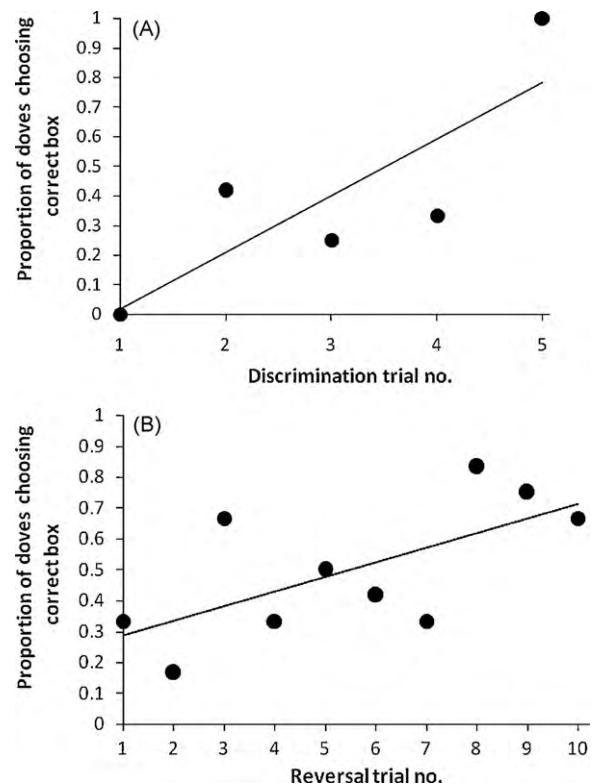


Fig. 2. Proportion of doves ($n = 12$) choosing the rewarded box immediately in (A) the discrimination test and (B) the reversal test.

als. We calculated the repeatability r of individuals' fleeing distance according to Lessells and Boag (1987). We used a linear mixed effects model to test whether birds' distance to flee changed across trials, including 'bird' as a random effect, 'test number' as a fixed effect and 'distance' as the response variable.

3.3.3. Territory disturbance

We gave each territory a score between 1 and 3 according to the intensity of human disturbance in the area, with '1' indicating hardly any disturbance and '3' indicating frequent disturbance. Our scores were confirmed by 4 independent observers familiar with the study area. We used Spearman rank correlation tests to explore whether intensity of human territory disturbance was correlated with mean experimenter approach distance at which birds fled or with learning performance.

3.3.4. Analysis

Effects of sex, body condition, time spent on territorial chases (excluding individuals with zero chase time), and tameness on latency to learn to feed from the apparatus during the training phase, and to extract seed during each of the two learning tests, were tested with multiple regressions. We used backward selection to obtain the minimally adequate model with a selection criterion of $\alpha = 0.05$. We included only the individual that was first to acquire seed from the apparatus on each territory ('first solver'), as on territories where both mates solved, data from the two individuals cannot be considered independent.

Neither sex nor body condition significantly predicted performance during the training phase and learning tests. In 6 of the 12 dove pairs that we tested, the first bird to finish training and to choose the correct box immediately in the discrimination and reversal tests was always the male of the pair, whereas in the remaining 6 pairs a female was the first to do so. Interestingly, both body condition and tameness of mates in each pair were strongly and positively correlated (body condition: $r = 0.783$, $n = 8$, $p = 0.022$; tameness: $r = 0.776$, $n = 11$, $p = 0.005$), so we used only the data for first solvers in our multiple regressions to avoid co-linearity problems. Body condition did not predict first solvers' latency to learn to feed from the apparatus (estimate \pm SE = -0.0715 ± 0.049 , $t_7 = -1.466$, $R^2 = 0.235$, $p = 0.186$) nor total time spent in unrewarded boxes during the colour discrimination (estimate \pm SE = -0.026 ± 0.096 , $t_7 = -0.269$, $R^2 = 0.010$; $p = 0.795$) or reversal tests (estimate \pm SE = -0.140 ± 0.157 , $t_7 = -0.891$, $R^2 = 0.102$; $p = 0.402$). However, tameness significantly predicted performance during the training phase: the bolder the dove was towards experimenter approach, the longer it took to learn to feed from the foraging apparatus (estimate \pm SE = -311.316 ± 85.862 , $t_{10} = -3.626$, $R^2 = 0.754$, $p = 0.005$; Fig. 3).

Tameness was not significantly correlated with the usual level of human disturbance on the territory ($r_s = -0.492$, $n = 12$, $p = 0.104$). However, doves on territories with higher human disturbance tended to be slower at learning to feed from the apparatus than doves on less disturbed territories ($r_s = 0.577$, $n = 12$, $p = 0.049$). Individuals differed significantly and consistently in tameness (repeatability r of mean tolerated approach distance = 0.77 , $F_{10,143} = 47.504$, $p < 0.001$), although our linear mixed effects model showed that experimenter approach distance decreased significantly as the number of times a bird was tested increased (estimate \pm SE = -0.098 ± 0.036 , $t_{142} = -2.719$, $p = 0.007$). Mean tolerated approach distance, in turn, was significantly predicted by dove body weight (estimate \pm SE = 0.137 ± 0.049 , $t_7 = 2.777$, $R^2 = 0.524$, $p = 0.027$), but not by dove body condition (estimate \pm SE = 2.320 ± 1.350 , $t_7 = 1.718$, $R^2 = 0.297$, $p = 0.129$).

Time spent on territorial chases did not predict the latency to learn to feed from the apparatus (estimate \pm SE = 0.012 ± 0.150 ,

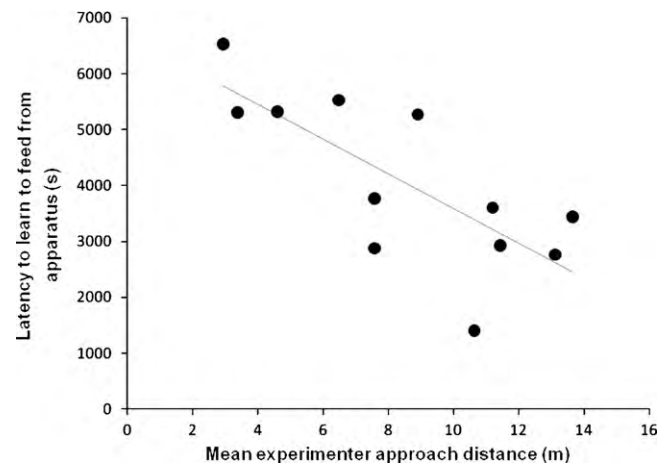


Fig. 3. The relationship between the mean distance of experimenter approach at which each of the twelve doves fled, and the time they took to learn to feed from the foraging apparatus.

$t_{10} = 0.077$, $R^2 < 0.001$, $p = 0.94$), nor total time spent in unrewarded tasks in the reversal learning test (estimate \pm SE = 0.423 ± 0.328 , $t_{10} = 1.287$, $R^2 = 0.142$, $p = 0.227$). However, time spent chasing intruders did significantly and negatively predict the time that territory owners spent in unrewarded tasks across the five trials of the colour discrimination test (estimate \pm SE = -0.403 ± 0.150 , $t_{10} = -2.683$, $R^2 = 0.419$, $p = 0.023$): individuals that displayed more aggression towards intruders spent less time in unrewarded tasks.

3.4. Learning performance across the three learning phases

Negative transfer from the discrimination to the reversal learning test would be suggested by individuals performing below chance levels in the first trials of the reversal learning test. In the first reversal learning trial, 8 out of 12 doves chose the incorrect box first (Chi-Square test $X^2_1 = 1.333$, $p = 0.248$), while in the second reversal learning trial, 10 out of 12 doves chose the incorrect box first ($X^2_1 = 5.333$, $p = 0.021$; see Fig. 2B), perhaps suggesting that the colour-reward association acquired during the previous day hampered doves in learning the reversed association.

The ranks of individuals' latencies to learn to feed from the apparatus and the slopes of their discrimination and reversal learning curves showed no significant correlation (Kendall's coefficient of concordance $W = 0.012$, $n = 12$, $X^2_2 = 0.298$, $p = 0.862$).

3.5. The effect of scrounging

Scrounging from the successful mate occurred on 9 of the 12 territories in the training phase, but decreased over the discrimination and reversal tests. Table 1 shows that mates scrounged without solving on 7 of the 12 territories in the training phase, but on only 1 of the 12 territories in the reversal test. In contrast, both mates learned to feed from the apparatus during the training phase on only 3 of the 12 territories, but this number increased to 7 pairs in the reversal test. The difference between the training phase and reversal learning test in solving without scrounging and scrounging without solving is significant ($X^2_1 = 1.98$, $p < 0.001$). Some of the mates that scrounged in the early trials of the training phase or a learning test eventually learned to feed from the apparatus in later trials. This occurred on 2 territories in the training phase, 2 territories in the discrimination test and 1 territory in the reversal test (Table 1). The mates that learned to feed from the apparatus after scrounging spent significantly more time interacting with the task apparatus and scrounging from their solving partners than mates that scrounged without ever learning to feed from the apparatus

(time spent interacting with task: $t_8 = 2.654$, $p = 0.029$; scrounging: $t_8 = 2.467$, $p = 0.039$).

4. Discussion

Our study shows that inter-individual differences in behavioural flexibility can be quantified in the field in a species where site fidelity and territorial defence allow repeated testing of focal individuals and exclusion of non-focal ones. At least one member of each targeted Zenaida dove pair was present in 96% of all test days, and both learning tests were completed on all territories. Thus, Zenaida doves, despite the fact that they are the slowest problem-solvers in the mixed species aggregation that feeds together in urbanized areas of Barbados (Webster and Lefebvre, 2001), yielded repeated measures on tests of discrimination and reversal learning in the field.

Latency to pass each of the learning phases was not predicted by sex, body condition, the number of territorial chases performed by the solver's mate or the time the latter spent scrounging, but it should be noted that our sample size was small and our negative findings on these points should thus be taken with caution. However, tameness towards humans was a significant predictor of performance during the training phase: tamer doves required more time to learn to feed from the foraging apparatus than did doves that were more inclined to flee upon experimenter approach. Our finding might be explained by the fact that doves are often fed by visitors of our field sites. Bolder individuals may be habituated to feed on easily accessible food provided by humans and may have focussed on the experimenter instead of the apparatus to gain a food reward, whereas individuals more fearful of human proximity may tend to look for food in other places, and performed better during the training phase as a result. In support of this explanation, we found that slower learners owned territories that were more often subject to regular human disturbance than the territories of faster learners.

Møller (2008) reported that urban bird populations have shorter flight distances when approached by humans than do rural populations, and that an urban population's flight distance decreases as the number of generations since urbanization increases. Our research on a semi-urbanized bird population shows that tameness is a highly repeatable and individual-specific trait. While comparative studies suggest that inter-specific differences in flight initiation distance may have important consequences for the distribution and abundance of species (Blumstein, 2006), our study suggests that within species, individuals' degree of tolerance to human proximity may be an important determinant of their tendency to exploit novel food sources.

While the territoriality of Zenaida doves offered advantages for this study, the fact that subjects often interrupted their interactions with the task to chase away intruders could have posed some problems. Overall, however, territory defence did not have a strong, systematic effect on individual differences in performance. Time spent on territorial chases did not predict the latency to learn to feed from the apparatus, nor total time spent in unrewarded tasks in the reversal learning test. The only significant effect we found was in the colour discrimination test, but in the opposite direction to the one we would have predicted: individuals that displayed more aggression towards intruders spent less time in unrewarded tasks, and were more efficient in solving the task as a result. Territorial aggression was thus not traded-off against learning performance in our study, as two of the three learning phases showed no significant relationship between the two variables and one test showed an effect in the opposite direction. However, the latter result should be treated with caution as, with our small sample size, it could have been found by chance.

Scrounging by the mate was frequent in the training phase, but decreased over successive tests. An indication that scrounging had a positive effect on learning performance lies in the difference between scroungers that later passed tests on their own and scroungers that did not: mates that learned to feed from the apparatus after scrounging spent significantly more time interacting with the apparatus and scrounging from their solving partners than mates that scrounged but never learned. As observed in Florida scrub-jays (Midford et al., 2000), keas (Gajdon et al., 2006), and wild meerkats (*Suricata suricatta*; Thornton and Malapert, 2009), scrounging might thus have facilitated learning to feed from the apparatus, by encouraging mates to spend more time interacting with the task. With regards to the non-solvers in this study, however, it should be noted that only a separate test of the scrounger in the absence of its successful mate can establish whether or not the scrounger has learned the task by observation, but never shown it when the producer was present (Giraldeau and Lefebvre, 1986, 1987; Lefebvre and Helder, 1997). This was not possible here, as our goal was to examine learning under normal field conditions. Had we removed producers, neighbouring doves would likely have moved in, as a previous study involving territory owners has suggested (Sol et al., 2005).

Experimenters who adopt the reversal learning paradigm in captivity usually present their animals with tens to hundreds of reversals (Macphail, 1982). However, authors of such papers have pointed out that interspecific differences in error rates are most pronounced in the first test session following each reversal (Warren, 1966; Gossette, 1968; Bond et al., 2007). In addition, Day et al. (1999) and Tebbich et al. (2010) showed that a predicted species difference in performance was achieved after a single reversal. Given these findings and the fact that in the field, opportunities to conduct learning tests are constrained by environmental conditions, test subject availability and feeding motivation, as well as experimental time constraints, we subjected the Zenaida doves to a single reversal test.

One surprising result of our study is the lack of correlations between learning rates in the three phases of the study. It would be profitable for future studies of reversal learning in the field to conduct enough trials in the discrimination test to ascertain that all individuals reached the same learning criterion of choosing above chance levels multiple times in a row, before allowing them to proceed to the reversal test. Perhaps not doing so caused the predicted negative transfer effect from the discrimination to the reversal learning phase to be relatively weak. Even so, individuals that performed well in the training phase did not necessarily do as well on the colour discrimination and reversal tests. This finding was unexpected because comparative studies have reported positive correlations between a variety of learning-associated behaviours, such as innovation, tool use, problem-solving and reversal learning across bird species (Lefebvre and Bolhuis, 2003). Within species, individual learning correlates positively with social learning in wild-caught, captive pigeons (*Columba livia*; Bouchard et al., 2007). However, a recent study on male satin bowerbirds (*Ptilonorhynchus violaceus*; Keagy et al., 2009) reported that birds' scores on two problem-solving tests conducted in the field were not correlated. The number of individuals available for testing can be limited in field studies such as Keagy et al.'s and ours, and our relatively small sample sizes may present part of the reason that we failed to find a significant correlation between test performances. In addition, perhaps significant correlations between performances on different tests are more likely to be found when individuals are tested in isolation in captivity, where one can influence motivation (e.g. through food deprivation) and control other factors. When conducted in the field, tests of behavioural flexibility provide data that may be more 'noisy', but render important insights into the effect of eco-

logical and social factors on the performance of the studied species as well.

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