

Original Article

# Who are the innovators? A field experiment with 2 passerine species

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Ecological and evolutionary drivers of innovativeness among species are relatively well studied, but the significance of similar variation within species is much less well understood. Using automated foraging devices, we conducted the first large-scale study of novel problem-solving performance in a wild bird population to test whether variation in innovativeness can be explained by inherent individual differences and by factors related to the “necessity drives innovation” hypothesis. We detected 20145 visits by 236 great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) and found consistent individual differences in the propensity to solve and in the time spent at devices between successive solutions in the field. Although individuals that were successful in a similar version of the task in captivity solved 3 times faster in the wild than those that were unsuccessful in captivity, success in captivity did not predict success in the wild. Thus, innovative propensity varies among individuals but it is also context dependent. Juveniles were more likely to solve the problem in the wild than adults, supporting the necessity drives innovation hypothesis. We found no evidence for social learning at problem-solving devices in the wild. The consistent individual differences in novel problem-solving performance we report suggest that innovativeness may be of adaptive significance within our population. Our results also suggest that selection for innovativeness may occur primarily among juveniles. **Key words:** age differences, innovation, personality, problem solving, social learning, state. [*Behav Ecol* 22:1241–1248 (2011)]

## INTRODUCTION

Innovation—solving a novel problem or finding a new solution to an old one—is a process by which individuals can broaden their behavioral repertoire (Kummer and Goodall 1985) and is therefore an important aspect of behavioral plasticity (Reader and Laland 2003). The propensity to innovate can have important ecological and evolutionary implications. For instance, innovative bird taxa are more likely to survive when introduced to novel environments (Sol et al. 2005) and show a greater number of species per taxon, suggesting a link between innovativeness and speciation rates (Nicolakakis et al. 2003).

Despite the potential importance of innovation in population responses to anthropogenic perturbations and its central role in the appearance of local traditions and culture, conceptual and empirical work on innovation is still in its infancy (Ramsey et al. 2007). One important challenge in the field is judging the novelty of the behavior against the established repertoire of an individual or a population. An extensive study by Van Schaik et al. (2006) on wild orangutans established that 3000 observation hours were required to obtain a stable inventory of the population's behavioral variants. Detailed knowledge of this kind is rarely available. An alternative approach is to examine the success and efficiency of individuals presented with a novel problem, most often in the foraging context (e.g., Frigaszy and Visalberghi 1990; Laland and Reader 1999a; but see Keagy et al. 2009). Studies using this “novel problem” approach reveal a significant amount of

interspecific variation in problem-solving performance, with species that are generally more dependent on manipulative foraging and less neophobic being better at solving novel tasks (Webster and Lefebvre 2001; Day et al. 2003; Seibt and Wickler 2006).

In addition to interspecific variation, it is generally recognized that individuals differ in their propensity to innovate, but the evolutionary significance of this variation is poorly understood (Reader 2003). We suggest that this is for 3 main reasons. First, most studies have scrutinized isolated individuals in captivity (but see Biro et al. 2003; Gajdon et al. 2006; Keagy et al. 2009; Boogert et al. 2010), where conditions are unlikely to reflect realized innovation rates in natural social and environmental conditions (Morand-Ferron et al. 2004). Because the cross-contextual consistency of individual innovative tendencies has rarely been assessed (Pfeffer et al. 2002), it is generally unknown whether results from the lab can be used to draw general conclusions on individual variation in innovativeness in a natural selective environment. Second, evaluating consistency of individual differences in the propensity to innovate is essential when assessing whether the observed phenotypic variation is likely to have an additive genetic basis and therefore to be of evolutionary significance (Roff 1997; Bell et al. 2009). Whether individuals consistently differ in their propensity to innovate has never been measured explicitly under natural conditions (Bell et al. 2009). The third reason is that, over and above inherent individual differences, it remains unclear what factors (e.g., sex, age, and dominance rank) influence the propensity to innovate (Reader 2003). Not only would these factors lead to heterogeneous selection on innovativeness within the population, they could also influence how novel behaviors spread through the population via social learning (Laland 2004; Van de Waal et al. 2010).

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The “necessity drives innovation” hypothesis states that innovation occurs predominantly when established behaviors are unsuccessful. It therefore predicts a negative relationship between competitive ability and innovativeness because good competitors enjoy better access to limiting resources (Laland and Reader 1999a, 1999b; Reader and Laland 2003). Although this relationship has been demonstrated in wild primates (Reader and Laland 2001) and male guppies (Laland and Reader 1999b), other studies have found no relationship (Gajdon et al. 2006; Bouchard et al. 2007) or even a positive relationship between social dominance and innovativeness (Boogert et al. 2006). Juveniles are expected to innovate more frequently than adults because they are usually subordinate and show a greater propensity to explore new objects (Greenberg and Mettke-Hofmann 2001; Biro et al. 2003; Biondi et al. 2010). Contrary to this prediction, a review on wild primates (Reader and Laland 2001), as well as a study on captive families of callitrichid monkeys (Kendal et al. 2005), found adults to be more innovative than juveniles. Although small and food-deprived guppies could find a novel food source more quickly than larger and well-fed conspecifics (Laland and Reader 1999b), recent avian studies report no effect of body condition (Boogert et al. 2010; Overington 2010; Cole et al. 2011) or motivation (Keagy et al. 2009) on problem-solving success. Empirical tests thus provide conflicting evidence for the necessity drives innovation hypothesis.

Here, we use the novel problem approach to explore individual variation in innovative problem solving among mixed-species flocks of wild passerines and compared the consistency of individual performance in the wild and in captivity for great tits (*Parus major*). We also include data from the wild for the closely related blue tit (*Cyanistes caeruleus*). We follow captive studies using the novel problem approach and operationally define innovators as those individuals that solved the problem and noninnovators as individuals not solving the problem. Previous work on great tits from our population shows that innovative problem-solving performance in captivity differs consistently between individuals, that these differences are maintained over time spans of up to a year and across different types of novel foraging problems, and are unrelated to other personality traits, including neophobia and exploration behavior (Cole et al. 2011; Cole EF, Quinn JL unpublished data). Great tits and blue tits form the core of winter mixed-species flocks in Wytham (Hinde 1952) and are ideal models for the study of innovative problem solving for several reasons. First, they are known to spontaneously innovate at high rates in the wild (Fisher and Hinde 1949; Estók et al. 2009; Overington et al. 2009). Second, great and blue tits born or breeding in Wytham are fitted with a unique passive integrated transponder (PIT) tag, allowing the behavior of large numbers of marked individuals to be remotely monitored in the field. Finally, social dominance hierarchies have been well studied in these species, enabling a test of the necessity drives innovation hypothesis: great tits are dominant over other tit species (Hinde 1952); males are dominant over females, and within sexes adults are dominant over juveniles (Saitou 1979; Barluenga et al. 2000); larger individuals are dominant over smaller ones (Garnett 1981; Maynard-Smith and Harper 1988; Barluenga et al. 2000); and individuals closer to their breeding territory are usually dominant over those breeding further away (Brian 1949; Drent 1983; De Laet 1984). Moreover, subordinate individuals face a greater risk of starvation and are therefore known to carry a larger amount of body reserves than dominant individuals (Gosler 1996; Gosler and Carruthers 1999).

We tested the following predictions: 1) individuals differ consistently in the probability of solving a novel foraging problem in the wild; 2) individual problem-solving performance

in captivity predicts performance in the wild; lack of an effect would suggest plasticity in the propensity to innovate depending on the environmental conditions. If innovation is indeed driven by necessity, we also predict: 3) subordinate individuals—blue versus great tits, females versus males, juveniles versus adults, smaller individuals, and individuals further away their breeding territory—to show increased use of problem-solving devices, be more likely to solve the problem and reach their first solution more quickly than dominant individuals; and 4) a positive relationship between body reserves and problem solving in the field. Finally, 5) we examine the possibility that the solution to this novel foraging problem was learned socially by examining whether innovations occurring later in the course of our field experiments were characterized by increased efficiency (Boogert et al. 2008), assuming that the amount of social information potentially available to naive individuals in the wild increased with the number of successful innovators and therefore with time.

## MATERIALS AND METHODS

### Study site and general protocol

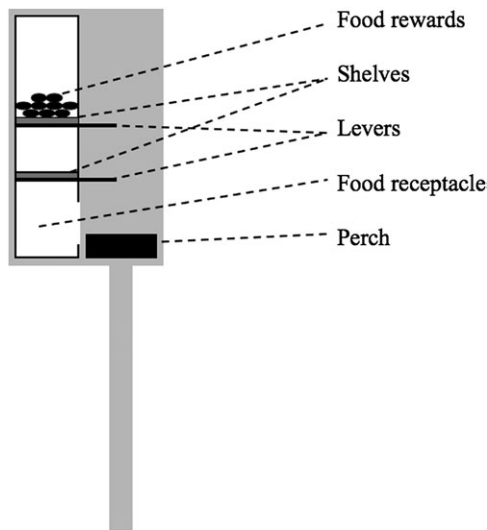
The study took place in Wytham Woods (lat 51°46'N, long 1°20'W), Oxfordshire, UK, from 2 February to 15 March 2010. Five locations in different areas of the Woods were chosen so as to maximize the distances, and minimize the differences, between the locations (i.e., presence of an open area with dense cover nearby). A multiaccess feeder filled with black husked sunflower seeds was installed at a location 5–7 days prior to catching to increase the local density of birds. We then used mist nets to consecutively catch 2–3 batches of 5–16 great tits over 3 days; all birds were caught under ringing licenses from the British Trust for Ornithology. Birds were aged (adult or juvenile if less than 1 year old) and sexed based on plumage (Svensson 1992). We recorded wing length, mass, and fat score (Gosler 1996) for all individuals caught. Fat score is inversely related to individual quality (Gosler and Carruthers 1999) and is correlated across seasons within individuals (Gosler and Harper 2000). All unringed individuals were fitted with a unique metal leg-ring and unique PIT tag (Core RFID Ltd Warrington, UK) which was attached to a celluloid split color leg-ring. Birds were transported singly in bird bags to the nearby John Krebs field station, where they were housed in individual cages, and isolated visually but not acoustically from each other. We examined individual performance on an overnight lever-pulling task and released birds at their point of capture 24–48 h later (see below for details). Two days after releasing the last batch of birds at a location, we installed 6 automated lever-pulling devices and ran field observations for 5–7 days before removing the devices and proceeding to the next location.

### Captive assays

The general procedure in captivity was similar to that detailed in Cole et al. (2011). One hour before lights-off on the day of catching, each lever-pulling device was baited with 4 waxmoth larvae (*Pyrallis farinalis*). These devices were made of a vertical perspex column, and a single shelf held in place by a lever, which had to be removed by the bird to gain access to the reward. Lever-pulling success (yes or no) was assessed at 08:00 h on the next day, that is, 2 h after sunrise. Around 15:00 h, individuals were released at their point of capture.

### Field observations

We used 6 automated lever-pulling devices (Figure 1; see also Supplementary Material), each installed on a 1.5 m wooden



**Figure 1**

Schematic depiction of a lever-pulling device used in the field (not to scale). The device (left) was made up of a transparent perspex tube and 2 shelves held by metallic sticks. The perch (right) was equipped with a PIT tag reader. Both components were connected to a battery-operated logger from which the data could be exported and saved using a laptop. Each device was baited with 30 sunflower seeds sitting on the top shelf; both sticks had to be pulled in either order, to release the 30 seeds in the bottom compartment where they could be collected by birds.

pole planted in the ground, 1–4 m from tree cover. We assumed the use of many devices per location reduced the probability of monopolization by dominant individuals (Drea 2006; Boogert et al. 2008). Each device was made from a transparent perspex tube and 2 shelves held by metallic levers. These devices required the same type of solution as the task in captivity, that is, pulling a lever out, which caused the food to fall from a shelf into a receptacle where it was available for consumption. The automated devices, however, required 2 levers to be removed in either order before accessing food, compared with one lever in the captive task. The second lever allowed us to examine acquisition of double lever-pulling behavior as an additional measure of problem-solving propensity that can be used to compare the behavior of captive solvers versus nonsolvers in the wild. Once pulled out, the levers had to be replaced by the experimenter, thereby preventing individuals from pulling levers on a device depleted of its rewards. The timing of the removal of each lever was automatically recorded by a battery-operated data logger. A PIT reader located in the perch, 2 cm away from the perspex lever-pulling device, recorded the timing and duration of visits by marked individuals. The perch was small enough so that only one bird could sit on it at a time.

After installation, we baited each device with 30 sunflower seeds and left the site. Sunflower seeds were also provided in a standard multiaccess feeder installed at each location 5–7 days before capture and after each daily observation period; birds should therefore be familiar with this food type. We checked the devices every 40 min and rebaited those that had been successfully opened with 30 sunflower seeds, leaving the other devices untouched. We ran this protocol for approximately 6 h per day between 10:00 and 17:00 h, 5–7 days per location, depending on weather conditions (no observations under rain or snow). The devices were left at the site for the whole duration of the experiment in order to minimize disturbance at experimental locations and reduce neophobia responses by the birds.

We used 86 min of video footage recorded at 3 locations to check 1) the rate of error in attributing solving events to PIT-tagged versus non-PIT individuals; 2) the rate of nondetection of PIT-tagged individuals; and 3) the duration of detection gaps when a PIT-tagged bird was still present at the device but stopped being detected, for instance when a bird hopped on other parts of the device than the perch but then returned to the perch without leaving the device. The percentage of visits by PIT-tagged individuals was 70.4% ( $N = 100$  of 142 visits by PIT and non-PIT birds). All 9 levers pulled out during these 86 min were properly attributed to PIT versus non-PIT individuals. The rate of nondetection was 13 of 99 visits (13.1%), but all of these except one (3 s) were for visits shorter than 2 s, suggesting that nondetection had a very low probability of leading to nonattribution of a solving event to a PIT-tagged bird. Maximal gap in detection records within a same visit by an individual was 12 s (mean  $\pm$  standard deviation =  $6.71 \pm 2.64$ ). We therefore defined a “visit” as a collection of detections separated by less than 12 s. We defined an “attempt” as a visit made to a baited device, which could be solved (i.e., with 1 or 2 levers to be removed before obtaining the food reward). We defined a successful “solving event” as an attempt leading to the device being opened, with 30 sunflower seeds becoming freely available to any bird for each solution.

The species, sex, age (adult or juvenile), and wing length (used here as a measure of body size; Gosler et al. 1998) of all marked individuals was recorded when they were initially ringed; sex and wing length of individuals ringed as nestlings and not caught as adults were therefore not available. Nest-box coordinates (Wilkin et al. 2006) were used to calculate a linear distance between breeding territory and the experimental location used by PIT-tagged individuals. We used Wytham coordinates for nest-boxes occupied in the 2010 breeding season, or in 2009 if the bird had not been recorded in 2010. For Wytham breeders detected at 2 ( $N = 5$ ) or at 3 experimental locations ( $N = 1$ ), we used the last location to calculate distance from territory.

### Statistical analyses

When examining which variables predicted whether an attempt would lead to solving or not, we used a generalized linear mixed-model (GLMM with Laplace approximation, family = binomial with logit link, package “lme4”) (Bolker et al. 2008). We included random factors for “location” and “individual” to control for nonindependence of data points collected at the same location and to take into account pseudoreplication caused by including several attempts per individual (Bolker et al. 2008). We also used a binomial GLMM including a random factor for location when analyzing the characteristics of birds that solved at least once in the field versus those that never solved. There was no overdispersion in the GLMMs (Crawley 2007). We used a linear mixed-model (LMM; package “nlme”) including a random factor for location when examining determinants of the total number of visits to devices (log-transformed) and latency to first solution by successful individuals (log-transformed number of seconds spent at baited devices before first solution,  $N = 33$ ). In order to examine the significance of individual differences in behavior, we compared models differing only in the presence or absence of a random intercept for individual using likelihood ratio tests (Pinheiro and Bates 2000; Bolker et al. 2008). For these tests, we provide information on the proportion of variance accounted for by individual differences in behavior (repeatability; Nakagawa and Schielzeth 2010). All analyses were conducted in R version 2.9.2 for Mac (R Development Core Team 2010).



Table 1

**Predictors of individual problem solving success (0 or 1) when visiting a baited device under natural conditions in Wytham Woods**

Attempt leads to solving or not

	Estimate $\pm$ SE	Z	P
Device state	0.30 $\pm$ 0.16	1.88	0.060
Duration of visit	0.06 $\pm$ 0.01	5.15	<0.001
Time of day	-0.03 $\pm$ 0.04	-0.76	0.449
Previous attempts	0.05 $\pm$ 0.01	7.33	<0.001

Analyses are from a GLMM of 4775 attempts by 197 individual great and blue tits (family = binomial, link = logit). "Location" and "individual" were included as random effects.

Device state is 1 or 2 (reference) levers to pull for the device to be solved, Duration of visit in seconds, Time of day to the closest hours, Previous attempts are the number of visits to baited devices by this individual before the current attempt.

## RESULTS

### Problem solving in the wild

We detected 20145 visits by 236 PIT-tagged birds (173 great tits and 63 blue tits) over 31 days of observation. The number of visits by individual birds to the devices ranged from 1 to 750 (median = 38, mean  $\pm$  standard error [SE] = 83.5  $\pm$  7.0). We recorded a total of 313 solving events over 4775 attempts (proportion of successful attempts = 6.6%). Forty-three individuals (18.0%) removed at least one lever, and 33 (13.8%) solved the device either by pulling the second lever or both levers within a visit. Even when restricting the dataset to the 117 birds that visited the device as frequently as the solver with the smallest number of visits (42 visits for a total duration of 99.5 s spent at devices), the proportion of successful individuals was still quite low, with only 28.2% of birds solving 1–61 times (median = 4, mean  $\pm$  SE = 9.5  $\pm$  2.4).

The probability of success increased with duration of attempt and number of previous attempts and tended to be higher when only one lever remained to be pulled out rather than 2 but was independent of time of day (Table 1). Controlling for these effects, there were significant individual differences in problem-solving success among birds that visited devices at least once while they were baited (repeatability = 0.86; Likelihood ratio test:  $\chi^2 = 333.9$ , degrees of freedom [df] = 1,  $P < 0.001$ ). Successful individuals were consistent in the time they needed to reach each successive solution (repeatability = 0.34; Likelihood ratio test:  $\chi^2 = 30.4$ , df = 1,  $P < 0.001$ ), and this time decreased over successive solving events (LMM:  $F_{1,302} = 32.0$ ,  $P < 0.001$ ).

### Problem solving in captivity versus in the wild

We assayed and released a total of 177 great tits near the 5 experimental locations. Among these birds, 96 (54.2%) were subsequently detected at devices in the wild. The probability of detection of captive solvers (40/68 = 58.8%) did not differ from that of captive nonsolvers (56/109 = 51.4%) (chi-square test:  $\chi^2 = 0.15$ , df = 1,  $P = 0.700$ ). Among the 36 captive solvers that made at least one attempt in the wild, 8 (22.2%) also solved in the wild versus 11 of 52 (21.1%) for nonsolvers, suggesting captive solvers were no more likely to solve than captive nonsolvers (chi-square test:  $\chi^2 = 0.01$ , df = 1,  $P = 0.905$ ). Including individuals assayed in 2009 according to the same captive protocol and now exhibiting one or more problem solving attempts in the field ( $N = 9$ , total = 97) did

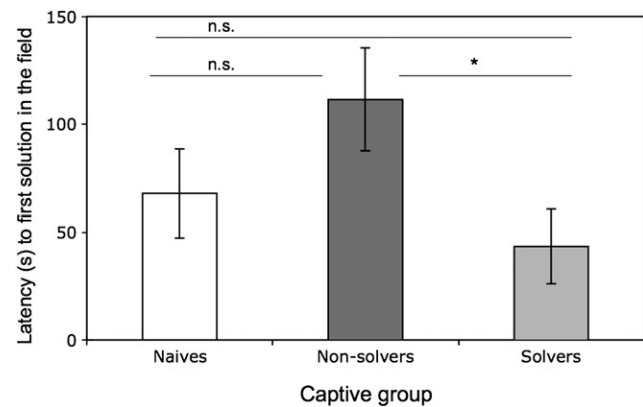


Figure 2

Latency to first solution in the field in relation to captivity group: naives ( $N = 13$ ), captive nonsolvers ( $N = 13$ ), and captive solvers ( $N = 7$ ). Latency was defined as the mean  $\pm$  SE number of seconds spent at baited devices before an individual's first solving event in the field. "n.s." indicates no significant difference in Tukey post hoc comparisons, whereas the "\*" indicates  $P < 0.05$ .

not change this conclusion (chi-square test:  $\chi^2 = 0.03$ , df = 1,  $P = 0.865$ ). Captive solvers and nonsolvers did not differ in total number of visits (2 groups  $t$ -test:  $t = 0.31$ , df = 94,  $P = 0.761$ ), mean duration of attempts (2 groups  $t$ -test:  $t = -0.94$ , df = 86,  $P = 0.353$ ), total number of levers pulled out (2 groups  $t$ -test:  $t = -0.05$ , df = 94,  $P = 0.960$ ), or percent successful attempts in the wild (Mann-Whitney test:  $U = 917$ ,  $n = 88$ ,  $P = 0.823$ ).

However, among successful individuals in the wild, captive solvers reached their first solution 3 times faster than captive nonsolvers; neither of these 2 groups differed significantly from naive birds, that is, not taken into captivity in 2010 (Figure 2; Analysis of variance:  $F_{2,30} = 5.56$ ,  $P = 0.009$ ; Tukey post hoc comparisons: solvers vs. nonsolvers:  $P = 0.007$ ; solvers vs. naive:  $P = 0.245$ ; nonsolvers vs. naive:  $P = 0.142$ ). Among individuals that pulled out at least one lever in the wild, a similar proportion of captive solvers (6/10 = 60%) and nonsolvers (8/15 = 53.3%) were capable of pulling both levers in one attempt (chi-square test:  $\chi^2 = 0.11$ , df = 1,  $P = 0.742$ ).

### Individual determinants of problem solving in the wild

We found no effect of species, sex, or wing length on the total number of visits to problem-solving devices in the field; however, juveniles visited the devices more often than adult birds (Table 2). This was not due to juveniles using the devices earlier in the season, or visiting devices faster than adults at each location (date of first visit: LMM:  $F_{1,170} = 1.38$ ,  $P = 0.242$ ; order for first visit within a location: LMM:  $F_{1,170} = 2.07$ ,  $P = 0.152$ ). There was no effect of species, sex, or wing length on the probability of solving the problem at least once in the field, but there was a tendency for juveniles to be more likely to solve than adults ( $P = 0.069$ ; Table 2; Figure 3). An additional analysis excluding other non-significant terms suggested a slightly stronger effect (Figure 3c; GLMM: Wald test:  $z = 2.03$ ,  $P = 0.042$ ). The higher problem-solving success of juveniles was not due to increased efficiency as the observed age-class effect disappeared when controlling for total duration of attempts (GLMM: Wald test: age class:  $z = 0.62$ ,  $P = 0.537$ ; attempts:  $z = 4.96$ ,  $P < 0.001$ ). Instead juveniles seemed more perseverant than adults because they engaged in longer unsuccessful attempts (mean  $\pm$  SE = 4.12  $\pm$  0.17 s

**Table 2**

**Predictors of (a) total number of visits (log-transformed) and (b) overall solving success (binary response) by individual great and blue tits under natural conditions in Wytham Woods**

	(a) Total number of visits				(b) Solved at least once or not			
	Estimate $\pm$ SE	F	P		Estimate $\pm$ SE	Z	P	
Species	$-1.32 \pm 1.24$	1.14	0.287		$-1.70 \pm 2.06$	$-0.83$	0.408	
Sex	$0.10 \pm 0.37$	0.08	0.782		$0.39 \pm 0.57$	0.68	0.500	
Age	$1.62 \pm 0.32$	26.0	<0.001		$1.17 \pm 0.65$	1.81	0.069*	
Wing length	$0.007 \pm 0.10$	0.01	<0.942		$-0.02 \pm 0.14$	$-0.17$	0.867	

Estimates and their standard error as well as value of the statistic and statistical significance were generated from LMM and GLMM models, respectively ( $n = 176$ ,  $df = 1, 167$ ). Each model included a random effect for “location.” Species is *Cyanistes caeruleus* or *Parus major* (reference set to zero), Sex is female or male (reference set to zero), Age is juvenile or adult (reference set to zero).

\* $P = 0.042$  when Age was included in a reduced model on its own.

vs.  $2.73 \pm 0.31$  s, respectively; LMM:  $F_{1,193} = 18.04$ ,  $P < 0.001$ ). Individuals visiting devices located closer to their breeding territory did not use them more often (LMM:  $F_{1,103} = 0.17$ ,  $P = 0.680$ ) and were no more likely to solve the problem (GLMM: Wald test:  $z = 1.19$ ,  $P = 0.233$ ) than birds further away from their territory. Fat score at capture did not predict total number of visits to the devices (LMM:  $F_{1,85} = 0.12$ ,  $P = 0.730$ ) or problem-solving success in great tits (GLMM: Wald test:  $z = -0.95$ ,  $P = 0.344$ ).

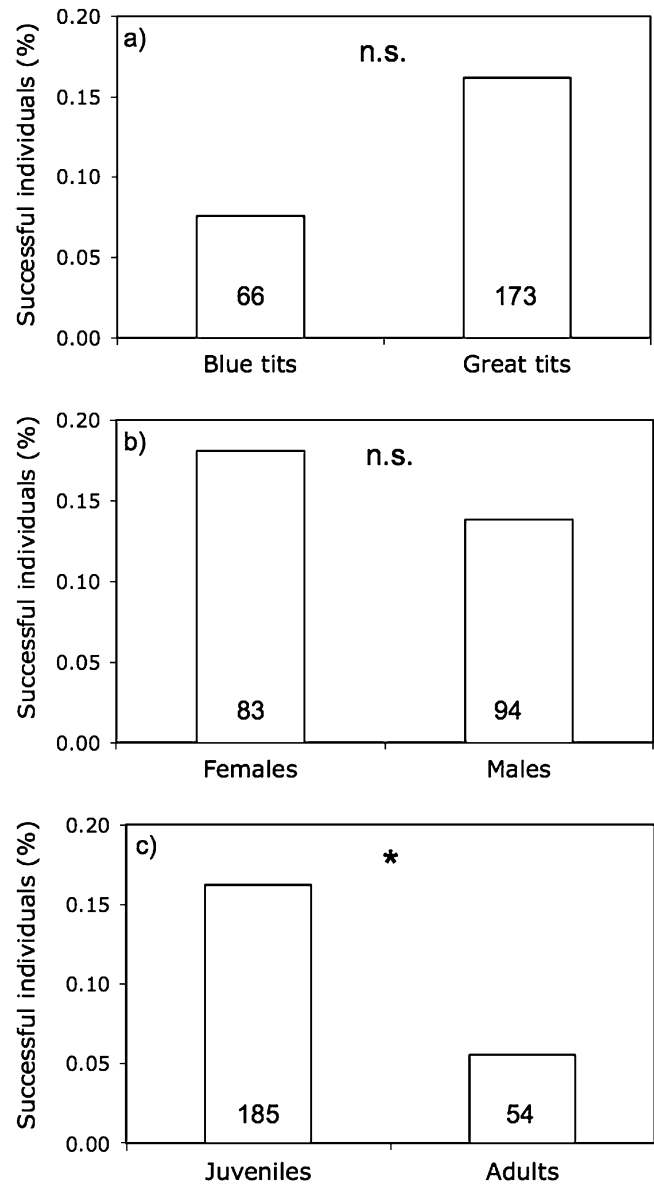
Controlling for captivity group (Figure 2: captive solvers, captive nonsolvers, or naive birds), the latency to the first solution by great tits in the field did not depend on sex (LMM:  $F_{1,20} = 0.07$ ,  $P = 0.793$ ), wing length (LMM:  $F_{1,20} = 0.03$ ,  $P = 0.870$ ), or fat score (LMM:  $F_{1,10} = 0.97$ ,  $P = 0.349$ ). The numbers of blue tit solvers ( $N = 5$ ), adult solvers ( $N = 3$ ), and the number of solvers with known distance from their breeding territory ( $N = 12$ ) were too low to examine the effect of these variables on latency to the first solution in the field.

### Social learning in the wild?

The date of initial contact with a problem-solving device in the field did not predict latency to first solution (within locations: LMM:  $F_{1,27} = 0.01$ ,  $P = 0.919$ ; over all locations: linear regression:  $F_{1,31} = 0.13$ ,  $P = 0.721$ ), suggesting that individuals that had potentially more time to acquire social information were not more efficient innovators. Moreover, the latency to first solution did not decrease with an increasing number of first solutions being recorded at a location (in fact this latency increased: LMM:  $F_{1,27} = 8.6$ ,  $P = 0.007$ ), suggesting that the innovation process was not influenced by the potential accumulation of social information in the local population.

### DISCUSSION

Our automated lever-pulling devices allowed us to conduct the first large-scale empirical investigation of individual differences and cross-contextual consistency in problem-solving performance in a wild bird population. Despite the very high number of attempts, only a small proportion of individuals solved the problem, suggesting it was a nontrivial task for tits. The probability that a bird solved the problem increased over successive attempts and the time spent trying to open baited

**Figure 3**

Percentage of individuals that solved the problem at least once in the field according to (a) species, (b) sex, and (c) age class. Numbers in bars indicate sample size for each category. “n.s.” indicates no significant difference in a GLMM on problem-solving success, whereas the “\*” indicates  $P < 0.05$ .

devices decreased between successive solutions, demonstrating increased individual performance over time: Birds were learning the solution. However, we found no evidence for social learning of the solution in the field. Individuals differed consistently in the probability of solving the task at each attempt, and in the time spent at devices between successive solving events, pointing to quantitative sources of variation in performance on this task in the wild; an additive genetic basis to at least part of this variation would suggest our measure of innovative problem solving is the target of natural selection. Recent studies on behavioral variation have emphasized the importance of measuring consistency when drawing conclusions about the evolutionary significance of behavioral variation under natural conditions (Dingemanse and Réale 2005; Oers et al. 2005; Sih and Bell 2008). Two studies have

examined performance of marked individuals on different tasks in the field and report nonsignificant correlations in problem-solving performance (Keagy et al. 2009; Boogert et al. 2010). However, to our knowledge, our study is the first to explicitly assess cross-contextual and temporal within-task consistency in innovative problem solving under natural conditions.

The propensity to solve in captivity did not predict the propensity to do so in the wild, which contrasts with the consistency reported previously in this population for a similar task in captivity, both across sessions and years (Cole et al. 2011). Moreover, a similar proportion of captive solvers and nonsolvers was capable of pulling both levers during the same attempt in the field. This lack of cross-contextual consistency is surprising considering that both tasks required birds to pull out lever(s) to access food. Indeed, captive solvers innovated 3 times faster in the wild than captive nonsolvers, suggesting that they benefited from their recent experience with a task requiring similar motor actions and/or that they were inherently better at solving problems. The use of an innovative food-processing technique in individual Carib grackles (*Quiscalus lugubris*) also did not correlate between the isolated captive context and the natural social context (Morand-Ferron et al. 2004). Differential individual tendencies to scrounge (Beauchamp 2001; Giraldeau and Dubois 2008; Kurvers et al. 2009) and/or differential responses to predation risk (Quinn and Cresswell 2005; Rieucou et al. 2010) or to the social context (Magnhagen and Staffan 2005; Stöwe et al. 2006; Piyapong et al. 2010) in nature could result in weak cross-contextual consistency if these tendencies are uncorrelated with innovativeness in captivity. Scrounging was indeed observed in the field, as each reward consisted of 30 seeds while a bird could carry only one seed at a time. Although scrounging was not an option when none of the devices were solved or when rewards were depleted, previous visits providing scrounging opportunities might have led to exclusive investment in this alternative tactic by some individuals (Giraldeau and Caraco 2000). It is also possible that captive solvers suffered interference or invested more than captive nonsolvers in antipredatory or social vigilance while attempting to solve the problem, although we did not detect a difference in mean duration of attempts between these 2 groups.

We report significant individual differences in the probability of solving a novel problem in a wild population (reviewed in Reader 2003). These individual differences could not be explained by species, sex, body size, distance to breeding territory, or fat score. It is possible that these variables would have had an impact if socially dominant individuals could monopolize the devices (Fragaszy and Visalberghi 1990; Gajdon et al. 2004), which we tried to avoid by providing 6 devices at each location. However, we found juveniles to be more likely than adults to solve the problem at least once in the field; a similar, but weak effect, was also observed in our captive assays (Cole et al. 2011). This effect was unlikely to be due to a difference in physical strength, as juveniles in their first winter are as heavy and large as adult great tits (Gosler 1993). Because the difference in innovativeness between juveniles and adults in the field disappeared when controlling for total duration of attempts, and because juveniles used devices more frequently and engaged in longer unsuccessful attempts than adults, we conclude that juveniles are more innovative because they make greater use of alternative food sources and are more perseverant rather than because they have better technical or cognitive abilities. A similar finding was observed in captive caracaras (*Milvago chimago*) presented with a novel problem: Although juveniles opened more lids for food in total, once controlling for effort they were no more efficient than adults

(Biondi et al. 2010). Few studies have examined individual differences in innovative problem solving in the wild, but those that have done so report no age effect (Keagy et al. 2009), or they report increased success in adults (Gajdon et al. 2006). Our findings, along with those from Biro et al. (2003), bring support to the necessity drives innovation hypothesis, which predicts increased innovation rates in poor competitors and therefore in juveniles compared with adults (Laland and Reader 1999a, 1999b; Reader and Laland 2003).

Socially mediated learning by captive nonsolvers in the wild could have led to reduced individual consistency across contexts; however, we found no evidence for social learning in the wild. Contrary to results obtained for starlings (*Sturnus vulgaris*; Boogert et al. 2008), individual tits contacting the task later during the course of our trials were no more efficient at solving than those that contacted the task earlier in the trial. Moreover, the latency to the first solution in the field did not decrease with an increase in the number of innovations recorded at a location and therefore with a potential increase in the number of demonstrators to learn from. Social information should have been readily available to naive observers in our system because devices were installed near and facing protective tree cover heavily used by birds. Previous research has shown that great tits can engage in observational learning in captivity (Marchetti and Drent 2000) and use local enhancement for locating patchily distributed food sources in the wild (Sasvari 1992). It is possible that tits used mainly local enhancement rather than observational learning at our devices, which might have increased their efficiency at finding the devices but not their efficiency at solving the problem. Examining novel problem-solving performance of individuals in isolation and in captive groups as well as in the wild when birds are territorial during the breeding season (Gosler 1993) should provide a better understanding of social influences on the expression of innovative propensities in this system.

In conclusion, our observations suggest substantial plasticity in innovativeness across captive and natural environments. In the wild, the probability of solving the task and the time spent at baited devices between each solving event were repeatable within individuals; these consistent individual differences suggest that innovativeness could be the target of natural selection in our population (Roff 1997; Bell et al. 2009). Juveniles were more likely to solve a novel foraging problem than adults, lending support to the necessity drives innovation hypothesis, and therefore suggesting that selection on innovativeness is likely to occur primarily among juveniles. The novel system described has provided new insight into the sources of variation underlying the propensity to innovate under natural conditions, which we hope will encourage further research on the evolutionary ecology of innovativeness.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

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