

Problem-solving performance is correlated with reproductive success in a wild bird population

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ARTICLE INFO

Article history:

Received 11 July 2012

Initial acceptance 14 August 2012

Final acceptance 14 September 2012

Available online 26 October 2012

MS. number: A12-00533R

Keywords:

behavioural plasticity

fitness component

great tit

individual variability

innovation

Parus major

problem solving

reproductive success

string-pulling task

Although interindividual variation in problem-solving ability is well documented, its relation to variation in fitness in the wild remains unclear. We investigated the relationship between performance on a problem-solving task and measures of reproductive success in a wild population of great tits, *Parus major*. We presented breeding pairs during the nestling provisioning period with a novel string-pulling task requiring the parents to remove an obstacle with their leg that temporarily blocked access to their nestbox. We found that nests where at least one parent solved the task had higher nestling survival until fledging than nests where both parents were nonsolvers. Furthermore, clutch size, hatching success and fledgling number were positively correlated with speed in solving the task. Our study suggests that natural selection may directly act on interindividual variation in problem-solving performance. In light of these results, the mechanisms maintaining between-individual variation in problem-solving performance in natural populations need further investigation.

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An animal's habitat varies in time and space, whether this happens more or less predictably from one season to the next, unpredictably during environmental perturbations, or gradually as a result of climate change. As a consequence, animals are sometimes faced with situations in which they have to deviate from their normal behavioural repertoire to solve unexpected problems. Differences among species and individuals in the ability to solve such problems can be experimentally assessed with novel tasks conducted in captivity (Overington et al. 2009a) and in the field (Morand-Ferron et al. 2011). These tasks routinely involve obstacle removal (Keagy et al. 2011), detouring (Boogert et al. 2011a) or string pulling (Seibt & Wickler 2006; Cole et al. 2011). Such tests are assumed to operationalize innovativeness (Webster & Lefebvre 2001), defined as the propensity to invent a new behaviour or to

flexibly adjust established behaviours to solve new problems (Reader & Laland 2003).

Although innovativeness is widespread in humans, many other animals, including nonhuman primates (Kummer & Goodall 1985) and other mammals (Patterson & Mann 2011), fish (Laland & Reader 1999) and birds (Sol et al. 2005a), are also known to innovate when faced with new situations. In birds, comparative studies have shown that innovation rate, measured for a large number of species (Lefebvre et al. 1997; Lefebvre 2011), is positively correlated with species introduction success (Sol et al. 2002), habitat generalism (Overington et al. 2011b), urbanization (Liker & Bokony 2009; Sol et al. 2011) and species richness (Nicolakakis et al. 2003; Sol et al. 2005b).

At the within-species level, differences among individuals in innovativeness, measured using problem-solving performance, have been well documented in a variety of avian taxa, such as Psittacidae (Funk & Matteson 2004), Falconidae (Biondi et al. 2008), Corvidae (Bluff et al. 2010) and Paridae (Cole et al. 2011), both in captivity (Boogert et al. 2008b; Overington et al. 2011a) and in the field (Gajdon et al. 2006; Keagy et al. 2009; Morand-Ferron et al.

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2011). Whereas the benefits of innovativeness have been well investigated at the species level, few studies have examined its fitness consequences at the individual level. Only four recent studies provide evidence for an indirect link between mating success and problem-solving ability (but see Boogert et al. 2011b for a review of sexual selection acting on other cognitive abilities). In the satin bowerbird, *Ptilonorhynchus violaceus*, males with better problem-solving ability in the field obtained more copulations (Keagy et al. 2009, 2011). In the siskin, *Carduelis spinus*, males with long yellow wing stripes, a secondary sexual trait used by females in mate selection, were faster problem solvers in captivity than males with shorter stripes (Mateos-Gonzalez et al. 2011). In captive zebra finches, *Taeniopygia guttata*, males that sang more complex songs, and thus, that were preferred by females, were faster in learning how to solve a novel foraging task (Boogert et al. 2008a). Finally, in song sparrows, *Melospiza melodia*, males with larger song repertoires, which have higher lifetime reproductive success in the field (Reid et al. 2005), required fewer trials to solve a detour-reaching task in captivity (Boogert et al. 2011a). Yet only one recent study has provided direct evidence for a positive link between problem-solving performance and reproductive output: in great tits, *Parus major*, females that solved a novel foraging task in captivity produced larger clutches and fledged more young in the wild than did nonsolvers (Cole et al. 2012). However, solvers were also more likely to desert their nests upon capture by experimenters than nonsolvers, suggesting a trade-off between the fitness benefits and costs of problem-solving performance (Cole et al. 2012).

In this study, we explored the potential correlation between individual performance on a novel nonforaging task and reproductive success in a natural great tit population. The great tit is known for its innovativeness, as reflected in particular by its many feeding innovations reported in nature (Overington et al. 2009b), its ability to take advantage of anthropogenic food sources in urban environments (Fisher & Hinde 1949) and its broad diet (Gosler 1993). The ability to solve problems might benefit individuals in several ways, for example by escaping new (e.g. invasive) predator species, adjusting to new constraints in changing habitats (e.g. limited nest site availability due to urbanization) or finding new food resources when the usual ones are scarce. Food availability is particularly important for many passerine birds in temperate regions, where rapid nestling growth involves high-protein food demands and reproductive output therefore strongly depends on food resources with limited availability (van Noordwijk et al. 1995; Naef-Daenzer & Keller 1999; Cresswell & McCleery 2003). Survival of young until recruitment is strongly associated with growth and body mass at fledging (e.g. Tinbergen & Boerlijst 1990; Linden et al. 1992; Monrós et al. 2002), and thus depends on parental foraging performance during the nestling period (e.g. Ens et al. 1992; Barba et al. 1995; Naef-Daenzer & Keller 1999; Schwagmeyer & Mock 2008). Better problem-solving abilities might allow individuals to reduce the risk of starvation for their young and maintain optimal body condition before, during and/or after the reproductive effort. We thus predicted that individuals showing better problem-solving performance should achieve higher reproductive success. Contrary to most previous problem-solving tests that use food as the source of motivation (but see Keagy et al. 2009, 2011), we assessed problem-solving performance during the nestling period in the field, using a string-pulling task that blocked access to the nest for 1 h during parental provisioning visits to the young. We measured reproductive success during one breeding season using several standard breeding parameters, as well as motivation (Keagy et al. 2009) and neophobia (Webster & Lefebvre 2001; Bouchard et al. 2007), which could potentially confound our measure of problem-solving performance (Greenberg 2003; Sol et al. 2011).

METHODS

Study Site, Population Monitoring and Measures of Reproductive Success

We carried out the study in a breeding population of great tits monitored on the island of Gotland, Sweden (57°10'N, 18°20'E) between April and June 2010. Great tits are small, socially monogamous passerines that readily breed in nestboxes. The female incubates alone, but both sexes care for the brood (Smith et al. 1988; Gosler 1993). We visited nestboxes at least every 2 days from the beginning of the breeding season onwards to determine the following measures of reproductive success: laying date, clutch size (from 6 to 12 eggs), hatching proportion (i.e. number of hatched young/number of eggs laid), brood size at day 14 and fledging proportion (i.e. number of fledged young/number of hatched young). We ringed young at day 9 after hatching and measured their tarsus length (to the nearest 0.1 mm) and body mass (to the nearest 0.1 g) at day 14. When chicks were 6–12 days old, we caught adults in the nestbox using a swing-door trap, ringed them if they were unringed, sexed them according to plumage characteristics (Svensson 1992) and measured their mass and tarsus length. Birds were caught, handled and ringed under a licence from the Stockholm Museum Ringing Center (license number 644:M03) and behavioural tests were conducted under a general licence from the Swedish Committee for Experiments on Animals for all experiments on the site (license number C 108/7).

Previous studies in different great tit populations revealed no brood parasitism and only a small percentage of extrapair young (3.5–8.6%; Verboven & Mateman 1997; Lubjuhn et al. 1999; Griffith et al. 2002). We therefore consider offspring number and body condition to be reliable measures of both male and female reproductive success in our study population.

Measurement of Problem-solving Performance

So far, most problem-solving tasks presented to birds have been motivated by food: to encourage participation in the test, the experimenter withholds food before testing or offers a preferred food item as a reward. In the wild, however, adult satiation cannot easily be manipulated. Using a food-motivated task could thus lead to low levels of response if natural food is abundant elsewhere in the environment or, if food is rare, it could affect offspring condition and/or survival depending on parental problem-solving success. Here, we measured problem-solving performance by developing a novel string-pulling task motivated by accessing the young during the peak of nestling food demand. This task featured a door placed in front of the entrance hole of the nestbox (Fig. 1). The door was by default closed, preventing the birds from entering and reaching their chicks. It could be opened by pulling a string placed below the door, and, once opened, birds could slip their body under the door to access their young. The door then closed behind them, but the birds could get out of the box by simply pushing the door open (Fig. 1). In this species, pulling behaviour can frequently be observed during foraging (e.g. lifting leaves or twigs) and nest building (e.g. collecting moss and hair material). However, great tits mainly pull using their beak, and very rarely pull using their legs only. Furthermore, the presence of an obstacle that would naturally and suddenly block the entrance of the nest cavity (e.g. following the fall of a branch) is an extremely unlikely event in this population. Over the past 10 years, no such natural blocking has been observed at the approximately 1500 boxes monitored each year, even though most of the forest study plots are unmanaged, with the presence of a lot of dead and broken trees and branches. Therefore, the novelty of the situation presented to great tits (removing an

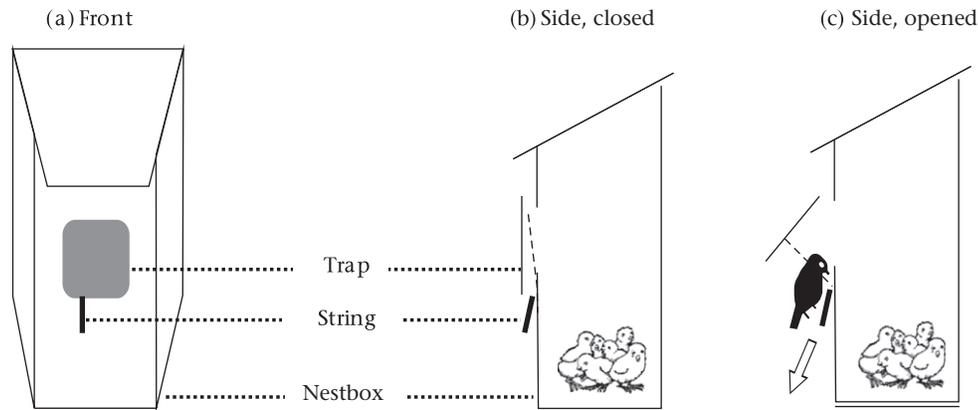


Figure 1. Views of the task used to measure problem-solving performance in great tits based on opening a door blocking the entrance to the nestbox. Birds had to pull the string to open the door and be able to slip under the door to enter the nestbox. The door then closed behind them. (a) Front view, door closed, (b) side view, door closed and (c) side view, door opened.

obstacle in front of the nestbox entrance) and the necessity to use a rarely used behaviour (pulling with a leg) to deal with it, make our task a good problem-solving task that requires innovative behaviour to be solved (Reader & Laland 2003).

Our task was performed during a period when, and involved a problem for which, the effects of parental performance on offspring survival and condition are likely to be crucial. To ensure maximal participation of parents, we carried out the problem-solving test during the peak of nestling food demand and parental visiting rate (i.e. when chicks were 6–10 days old and between 0800 and 1600 hours; Gosler 1993). We conducted the test only when chicks were satiated (e.g. not begging) at the beginning of the test, and the test lasted for 1 h only, to avoid possible direct negative effects of the test itself on chicks if parents were not able to solve the task (e.g. starvation). In this population, parents are often observed to take 1 h breaks in chick provisioning when food is abundant and chicks are satiated before resuming provisioning (B. Doligez, personal observation). We randomly selected breeding pairs to be tested and avoided any bias due to sampling since parents were caught after we measured their problem-solving performance (Biro & Dingemanse 2009). Great tits are highly territorial and aggressive towards conspecifics during reproduction (Gosler 1993), which therefore ensured that only the breeding pair of the focal nest tested tried to solve the task and enter the nestbox. To ensure that problem-solving trials were independent and to avoid social learning between tested pairs, we carried out the test on nests separated by at least 200 m from their nearest neighbours (Both & Visser 2000; Leal & Powell 2011). Just before attaching the task to the nestbox entrance, we installed a camouflaged video recorder at a distance of approximately 6 m in front of the nestbox and recorded the parents' behaviour for 60 min. When neither parent was seen during this period, the trial was cancelled and carried out once again on the next day. All the movements and interactions of each parent with the nestbox and the task were subsequently scored from video recordings by a single observer who was blind to the measures of reproductive success. We observed no desertion or total reproductive failure after the test was conducted.

For each tested parent, we first recorded whether the individual succeeded in solving the task (i.e. opened the door and entered into the nestbox at least up to its shoulders; results were unchanged when we used other parts of the body, such as head only or entire body, to define when the task was solved). Birds that failed to enter were considered nonsolvers. For birds that succeeded in solving the task (i.e. entering the nestbox), we recorded the latency to enter

into the nestbox as the time elapsed between the first contact of the bird with the string (i.e. that caused a movement of the door) and the bird's entry into the nestbox. Results were qualitatively similar when measuring latency as the time elapsed from the first contact with the task instead of the string. When individuals left the box after contacting the string and then returned within the same trial, we excluded the time spent away from the box from this latency (i.e. the latency only accounted for the time spent trying to enter the nestbox).

Neophobia and Motivation Levels

Personality traits can interfere with the process of innovation (Greenberg 2003). For instance, animals that avoid novel stimuli have been found to show longer problem-solving latencies than less neophobic ones (Bouchard et al. 2007; Sol et al. 2011). This potentially confounding effect on problem-solving performance should therefore be controlled for. Because the door and string were novel on the day of the test, we used the time between landing on the nestbox and first contact with the door or string as a measure of neophobia for each individual, including the time away from the nestbox after first landing.

Problem-solving performance measured as the latency to remove an obstacle in front of the nestbox entrance could reflect a difference in motivation to access the young, for example, associated with the number of chicks in the nestbox (Smith et al. 1988). We controlled for the effect of this potentially confounding variable in two ways. First, when chicks were 5 days old, we recorded chick-provisioning rates of the pair as the total number of visits to the nest during 1 h. Because provisioning rate depends on brood size, it should represent the motivation of the parents to enter the nest, and thus to solve the problem. Second, we also computed the number of times each parent contacted the two task areas directly relevant to solving the problem (i.e. the trapdoor and the string, Fig. 1) divided by the total number of times other areas (top, front, corners and sides of the box) were contacted during the problem-solving test. This measure should reflect the persistence of the parent in trying to solve the problem (Overington et al. 2011a), and thus its motivation.

Statistical Analyses

Because we could not measure latency for nonsolvers, we used the performance of the solver as the performance of the pair composed of one solver and one nonsolver. For the pairs where

both parents were solvers, we considered the solving latency of the fastest parent only. In both cases, this relies on the assumption that the most successful parent drives the success of the pair. However, to test for the robustness of our results with respect to the measure for pairs with two solvers, we repeated the analyses considering the two pairs that had two solving parents in alternative ways: (1) we excluded these two pairs, keeping only the 16 single-solver pairs, (2) we used the average latency of the two parents and (3) we used the latency of the first parent that solved the task, instead of the fastest, to avoid possible social learning from the partner (see [Supplementary Material](#)).

We analysed the relationship between problem-solving performance and reproductive success at the nest level. Because problem-solving latency could not be determined for the eight nonsolver pairs, we conducted two different statistical analyses. First, we compared measures of breeding success between nests where at least one parent solved the task and those where both parents were nonsolvers. Then we tested for a relation between measures of breeding success and problem-solving latencies in nests where at least one parent solved the task. We analysed binary variables (hatching and fledging proportion) using generalized linear models (GLM) with binomial error and logit link function (χ^2 tests). We analysed continuous variables (laying date, clutch size, fledging number, provisioning rate) using linear models and, for offspring body mass, a linear mixed model including brood identity as a random factor to account for common rearing environment and parental effects on siblings (F tests).

All initial models included as explanatory variables the measure of the problem-solving performance of the pair (either a binary variable: solver versus nonsolver pairs, or a continuous variable: latency to enter). Because breeding success can be measured at different stages throughout the breeding process, and each measure at a given stage depends on the preceding measure (i.e. clutch size depends on laying date: [Perrins & McCleery 1989](#); brood size depends on clutch size, etc.), we used a sequential approach to investigate the influence of problem-solving performance on success at each breeding stage independently from preceding ones. To do so, we included some of the dependent variables as covariates in the models analysing subsequent independent variables: (1) laying date when analysing clutch size (or hatching date when analysing offspring body mass) and (2) clutch size when analysing brood size (or brood size at day 14 when analysing offspring body mass). This allowed us to characterize the cumulative relations between problem-solving performance and measures of breeding success over stage. In addition, we included as covariates (3) the body condition of both parents (defined as the ratio of body mass to tarsus length) in all analyses, (4) the tarsus length when analysing offspring body mass and (5) provisioning rate when analysing measures of reproductive success after day 5. The age of the parents (yearling versus older), which is known to affect breeding success, was not included in the models because age assessment was uncertain in the field. Given that age is highly correlated with laying date in this population (B. Doligez, unpublished data), as well as in other populations ([Perrins & McCleery 1985](#)), we included laying date as a covariate in all models to partially control for age effects. Including the sex of the parent with the highest problem-solving performance (or highest activity around the nestbox if both parents were nonsolvers) as a covariate showed that sex had no influence on the results; we therefore did not retain this factor in the analyses. Sample sizes varied among analyses because one female could not be captured and feeding rate was not available for four nests. We did not test for interactions between explanatory variables because of our small sample size and the fact that we had no a priori hypotheses to justify them.

We tested whether interindividual variation in the degree of neophobia could influence the variation of problem-solving performance by examining the relationship between these two variables at the individual level. We first compared neophobia between solvers and nonsolvers. In a second analysis, we tested for a relation between neophobia and latency to open in solvers only. For both analyses we used linear mixed models with neophobia as the dependent variable and nest as a random factor to control for the nonindependence of the two pair members. The models also included the sex of the individual, its interaction with the measure of individual problem-solving performance and the age of the brood when measuring neophobia and performance. Again, sample sizes varied among analyses because the measure of neophobia was missing for three of the nonsolvers.

Finally, we investigated the potentially confounding effect of motivation by testing whether parental provisioning rate per nest was related to between-pair variation in problem-solving performance (either as a binary factor: solving versus nonsolving pairs, or as a continuous variable: latency among solving pairs), using parental provisioning rate as the dependent variable and including laying date, clutch size and the body condition of both parents as covariates. We also tested whether the persistence score was related to interindividual variation in problem-solving performance, using persistence score as the dependent variable, the age of the brood on the day of the test as a covariate and nest as a random factor when comparing solvers versus nonsolvers, to account for the nonindependence of both parents (this did not apply to the latency since only one parent was a solver in most pairs).

We performed all analyses using SAS version 9.1 (SAS Institute, Cary, NC, U.S.A.). We removed nonsignificant variables using a stepwise backward selection procedure. We tested the residuals of linear models for normality and homoscedasticity. Overdispersion was checked for generalized linear models and we corrected chi-square tests into F tests (and corresponding P values) when (small) overdispersion occurred, which is why we report sometimes chi-square tests and sometimes F tests for our GLMs. All tests were two tailed.

RESULTS

Eighteen out of 26 tested pairs solved the task, and among these solver pairs, only one parent succeeded in 16 pairs, while both parents did in the remaining two pairs. Of the 45 individuals that were tested, 40.4% were successful solvers ($N = 20$), including 50% of each sex ($N = 10$ females and $N = 10$ males; $\chi^2_1 < 0.01$, $P > 0.99$). Furthermore, among solving individuals, the latency to solve did not differ between males and females ($F_{1,18} = -0.673$, $P = 0.509$; mean latency \pm SE: males: 205.10 ± 536.51 s; females: 89.80 ± 74.58 s).

Problem-solving Performance and Reproductive Success

Nests where at least one parent solved the task had a significantly higher proportion of chicks surviving until fledging than nests where both parents were nonsolvers ($\chi^2_1 = 5.92$, $P = 0.015$; [Fig. 2](#)). This result accounted for the effect of clutch size as a covariate in the same model (hatching success decreased with increasing clutch size: $\chi^2_1 = 4.28$, $P = 0.038$). No significant difference was observed between solvers and nonsolvers for laying date ($F_{1,24} = 2.58$, $P = 0.121$), clutch size ($F_{1,24} = 1.46$, $P = 0.239$), proportion of eggs that hatched ($F_{1,23} = 0.06$, $P = 0.807$), fledging number ($F_{1,18} = 0.01$, $P = 0.909$, with clutch size, $F_{1,18} = 6.67$, $P = 0.019$, and provisioning rate, $F_{1,18} = 4.90$, $P = 0.040$, as significant covariates in the same model) and offspring body condition

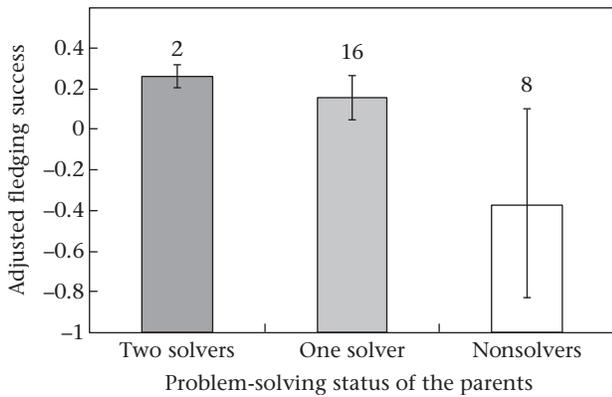


Figure 2. Mean offspring survival until fledging \pm SE (adjusted for clutch size) depending on the problem-solving status of the pair: nests where both parents solved the task (two solvers), nests where one parent solved the task (one solver), and nests where both parents failed to solve the task (nonsolvers). Numbers above bars indicate sample sizes. Grouping the nests where both parents solved the task and those where only one parent solved the task did not significantly change the value of fledging success for the solving category.

(i.e. body mass corrected for tarsus length, $F_{1,152} < 0.01$, $P = 0.960$, with brood size at day 14, $F_{1,152} = 5.31$, $P = 0.022$, as a significant covariate in the same model). The absence of a significant difference in clutch size, hatching rate and fledging number between solvers and nonsolvers, despite higher nestling survival rate for solvers, was probably due to the low statistical power to detect differences because of the limited sample size. The difference in fledging number between solvers and nonsolvers was indeed higher than the difference in clutch size (relative fledging number and clutch size for solvers and nonsolvers: 1.18 ± 0.84 and 0.69 ± 0.58 , respectively), as expected from a higher nestling survival rate, but these differences remained nonsignificant due to large associated standard errors. Furthermore, because clutch size was accounted for in the analysis of fledging number, we compared fledging number between solvers and nonsolvers independently from earlier breeding stages, and thus a higher nestling survival rate may not translate into a higher fledging number once clutch size is accounted for.

Among solvers pairs, the fastest pairs to solve the task laid significantly more eggs per clutch than the slowest solver pairs ($F_{1,15} = 5.21$, $P = 0.037$; Fig. 3a), with a trend in male body condition ($F_{1,15} = 3.91$, $P = 0.067$), which was thus included as a covariate in the same model: 100 s increase in latency to solve corresponded to a decrease in clutch size of 1.1 ± 0.5 eggs. The fastest pairs also hatched a higher proportion of eggs ($F_{1,14} = 4.85$, $P = 0.045$; partial regression coefficient \pm SE: -0.011 ± 0.005 ; Fig. 3b), with female body condition as a significant covariate in the same model ($F_{1,14} = 5.85$, $P = 0.030$). Finally, fast problem solvers fledged significantly more young than slow solvers ($F_{1,11} = 24.45$, $P = 0.0004$; partial regression coefficient \pm SE: -0.017 ± 0.003 ; Fig. 3c), with clutch size ($F_{1,11} = 14.34$, $P = 0.003$) and parental provisioning rate ($F_{1,11} = 7.90$, $P = 0.017$) as significant covariates in the same model. The relationship between latency to solve and number of fledged chicks remained significant ($F_{1,16} = 6.93$, $P = 0.018$) when latency was the only predictor in the model (excluding clutch size and parental provisioning rate as covariates). Solving latency was not related to laying date ($F_{1,16} = 2.05$, $P = 0.172$) or offspring body condition (i.e. body mass corrected for tarsus length; $F_{1,109} = 0.24$, $P = 0.624$), with male body condition ($F_{1,109} = 6.48$, $P = 0.012$) and hatching date ($F_{1,109} = 8.02$, $P = 0.005$) as significant covariates in the same model. The proportion of chicks that survived from hatching to fledging was not related to solving latency ($\chi^2_1 = 0.12$, $P = 0.731$).

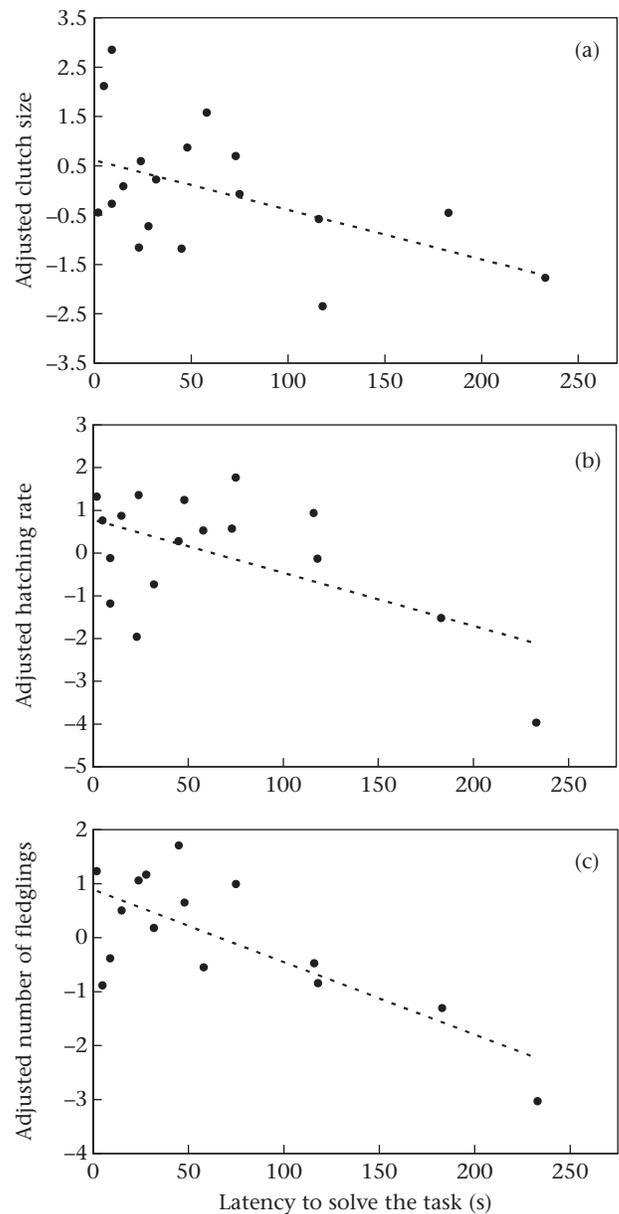


Figure 3. Measures of reproductive success depending on problem-solving latency (i.e. increasing latency to enter indicates worse performance) in nests where at least one parent solved the task: (a) clutch size (adjusted for male body condition), (b) hatching rate (adjusted for female body condition) and (c) fledging number (adjusted for clutch size and provisioning rate).

Our results are robust to the measures used to assess the performance of the pair in cases where the two parents were solvers: most results were unchanged when considering different measures for the two concerned pairs (see [Supplementary Material](#)).

Problem-solving Performance and Levels of Neophobia and Motivation

The level of neophobia differed between solvers and nonsolvers ($F_{1,15} = 5.22$, $P = 0.037$): solvers were less neophobic than nonsolvers (mean level \pm SE: solvers: 9.80 ± 4.08 ; nonsolvers: 22.50 ± 3.92). The level of neophobia did not differ between fast and slow solvers, although there was a tendency for neophobia to

decrease with increasing latency ($F_{1,17} = 3.91$, $P = 0.064$; partial regression coefficient \pm SE: -0.073 ± 0.037). Importantly, results remained qualitatively unchanged when the latency to solve the task was corrected for the level of neophobia (by including neophobia as an additional covariate in models exploring measures of reproductive success; results not detailed here).

The provisioning rate of solvers (29.7 ± 3.8 feeds/h) was higher than that of nonsolvers (16.9 ± 5.5 feeds/h), but the difference was not statistically significant ($F_{1,20} = 3.72$, $P = 0.068$). Among solvers, problem-solving latency was not related to parental provisioning rate ($F_{1,11} < 0.01$, $P = 0.972$, with clutch size as a covariate in the same model, $F_{1,12} = 4.58$, $P = 0.053$). After the first contact with the string, solvers also showed higher persistence than nonsolvers ($F_{1,18} = 28.50$, $P < 0.0001$). However, latency to solve was not related to persistence ($F_{1,18} = 0.29$, $P = 0.271$).

DISCUSSION

Our results suggest a significant positive relationship between problem-solving performance and reproductive success in our study population of great tits, at least in the short term. Pairs where at least one parent solved the task fledged a higher proportion of their clutch than did pairs where no parent solved the task. Furthermore, nests where parents were faster at solving the task laid and hatched more eggs and fledged more offspring than nests where parents were slower at solving the task. Because each measure of breeding success was analysed while accounting for preceding measures, our results suggest that the influence of problem-solving performance is cumulative over these different stages of the breeding event. Our study therefore supports the hypothesis that natural selection might be operating on problem-solving performance in great tits in the wild.

Although more relations appeared significant when considering solving latency for solvers than when distinguishing solvers from nonsolvers (i.e. continuous versus binary measure of problem-solving performance), these results should be interpreted with caution. While the relationships between measures of breeding success and latency might be dependent on the few pairs that took longest to solve the problem, the ‘nonsolver’ category may include both birds that tried but could not solve and birds that might eventually have solved had they tried harder, sooner or longer. Nevertheless, the fact that both the analyses of latencies and solver versus nonsolver categories showed a significant and positive relationship between problem-solving performance and different measures of reproductive success suggests that our findings are robust. Furthermore, the similarity between our results and those of Cole et al. (2012), while using different novel problems (opening a trap door versus solving a foraging task) in different contexts (field versus captivity, and spring versus winter), further strengthens the evidence for a positive relationship between problem-solving performance and reproductive success in great tits.

Although it is tempting to conclude that better problem-solving performance causes higher reproductive success, we cannot exclude the possibility that the positive relationship between reproductive success and problem-solving performance might be a consequence, rather than a cause, of the higher motivation of parents to feed more successful and/or larger broods (Smith et al. 1988; Garcia-Navas & Sanz 2010). Parents with more chicks could have been more motivated to enter the nestbox, and thus could have been more prone to contact the door and pulled the string harder. Pair provisioning rates and individual persistence scores in manipulating the task should reflect both chick demand and parental motivation to feed their chicks. Because problem-solving latency was not related to these two measures of motivation and

because the relation between fledgling number and problem-solving latency remained significant even when provisioning rate was accounted for in the model, our results suggest that latency to solve reflects problem-solving performance rather than merely motivation. Furthermore, even though almost all birds succeeded in making the door move by pecking the string, some of them did not peck or pull at the right place to open the door. Therefore, the parents' motivation to feed their brood does not seem to have generated the observed relationship between problem-solving performance and breeding success. An experimental brood size manipulation would be necessary to address this issue explicitly (i.e. to confirm the causality of the relation between parental problem-solving ability and breeding success). Furthermore, parents may trade the quantity and quality of food items brought to the nestlings (Garcia-Navas & Sanz 2010). A recent study on house sparrows, *Passer domesticus*, showed that the size of the food items provided by parents was a better predictor of reproductive success than chick-provisioning frequency (Schwagmeyer & Mock 2008). Moreover, males and females could differ in their provisioning strategies (Smith et al. 1988). In our study, we measured provisioning rate at the level of the pair, not the individual parent. Further studies should examine each parent's provisioning strategy in more detail to assess the link between an individual's problem-solving ability and the size or type of the food items it brings to feed chicks.

Finally, the potential role of stress as a mediator of the relationship between reproductive success and problem-solving ability needs to be explored. Parents showing a high level of stress in response to the presence of the novel task may have been unable to solve it and also achieved lower breeding success. However, the task itself is unlikely to have generated a sufficiently high level of stress to affect breeding success directly, because of its short duration over the course of the breeding cycle (1 h) and because problem-solving performance was also related to measures of breeding success before the test, namely clutch size and hatching success. Instead, the stress response to the task and the associated success (or failure) in solving the task may have revealed parental variation in the general ability to handle stressful situations, which is likely to have affected the final breeding success. Furthermore, because provisioning rate decreased during the test, chick begging intensity may have increased over the course of the test, eliciting an increasing stress response from the parents that may have been proportional to the number of chicks and thus affected the parents' ability to solve the task. Although we found no difference in the parents' motivation to open the door (i.e. the individual persistence score), chick begging intensity, parental stress hormone levels and other factors known to affect parents' motivation to feed the chicks (i.e. plumage or beak coloration: Heeb et al. 2003; Tanner & Richner 2008) should be investigated to better understand the role of motivation and stress in the performance to solve the task. This, however, goes beyond the scope of the present study.

For natural selection on a trait to take place, three conditions are required: (1) there must be variation among individuals for the trait, (2) this variation must be linked to variation in individual fitness, and (3) this variation must be heritable (Fairbairn & Reeves 2001). Between-individual variation in innovative ability is well documented, while evidence for its association with fitness is limited to the current study and that of Cole et al. (2012) on great tits. Heritability of many cognitive traits has been shown in nonhuman species, but evidence comes mainly from domesticated animals, mostly rodents, tested in captivity (Plomin & Spinath 2002), as well as from selection experiments in insects (Mery & Kawecki 2004). Exploration behaviour, a correlate of problem-solving in other birds (carib grackles, *Quiscalus lugubris*: Overington et al. 2011b; Indian mynahs, *Acridotheres tristis*: Sol

et al. 2011), has been shown to be heritable in wild great tits (Dingemanse et al. 2002). In this species, boldness is also correlated with speed in searching for new food sources when familiar sites are experimentally decreased, which is a measure of feeding flexibility (van Overveld & Matthyssen 2010). Investigating the heritability of innovative ability and cognition is an obvious next step.

If problem-solving performance is found to be heritable, and thus the three conditions for the evolution of innovative ability are met, the processes maintaining high levels of between-individual variation in this trait need to be explored, in particular, the costs and benefits of increased innovative ability in relation to spatio-temporal variation of the environment. As far as costs are concerned, innovativeness at the interspecific level is associated with a bigger brain (Timmermans et al. 2000), increased vulnerability during the prolonged period of development associated with larger brains (Iwaniuk & Nelson 2003) and increased exposure to a wider variety of parasites and microbes (Garamszegi et al. 2007; Vas et al. 2011). At the intraspecific level, problem-solving performance can be associated with higher nest desertion following capture by experimenters (Cole et al. 2012), suggesting a potential link between innovativeness and sensitivity to nest disturbance and predation risk (Cole et al. 2012). Thus, although there is now evidence that problem-solving performance, a measure of innovativeness, is correlated with reproductive benefits, its potential costs remain to be investigated.

Acknowledgments

We thank S. E. Overington, A. Desrochers, B. Angers, D. Cheney and two anonymous referees for constructive comments on the manuscript. For help with field work, we are grateful to A. Colas, N. Deleva, F. Desray, A. Edme, J. Haquet, P. Rosa and more particularly F. Théron for help in designing the task, and T. Borderie for help with video-recording analysis. We thank L. Gustafsson for giving access to the site. This work was supported by a Fonds de Recherche du Québec (FQRNT) Team Grant to F.D., L.-A. Giraldeau and L.L., a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery grant to L.L., and by the Centre National de la Recherche Scientifique (CNRS) via an International Program for Scientific Cooperation (PICS) grant and a Projet Exploratoire/Premier Soutien (PEPS) grant to B.D.

Supplementary Material

Supplementary material for this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2012.10.005>.

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