



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

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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

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