Report

Cognitive Ability Influences Reproductive Life History Variation in the Wild

Ella F. Cole,[1,3] Julie Morand-Ferron,[1,3] Amy E. Hinks,[1] and John L. Quinn[1,2,*]

[1]Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK
[2]School of Biology, Earth and Environmental Sciences, University College Cork, Cork, Ireland

Summary

Cognition has been studied intensively for several decades, but the evolutionary processes that shape individual variation in cognitive traits remain elusive [1–3]. For instance, the strength of selection on a cognitive trait has never been estimated in a natural population, and the possibility that positive links with life history variation [1–5] are mitigated by costs [6] or confounded by ecological factors remains unexplored in the wild. We assessed novel problem-solving performance in 468 wild great tits *Parus major* temporarily taken into captivity and subsequently followed up their reproductive performance in the wild. Problem-solver females produced larger clutches than nonsolvers. This benefit did not arise because solvers timed their breeding better, occupied better habitats, or compromised offspring quality or their own survival. Instead, foraging range size and day length were relatively small and short, respectively, for solvers, suggesting that they were more efficient at exploiting their environment. In contrast to the positive effect on clutch size, problem solvers deserted their nests more often, leading to little or no overall selection on problem-solving performance. Our results are consistent with the idea that variation in cognitive ability is shaped by contrasting effects on different life history traits directly linked to fitness [1, 3].

Results and Discussion

The ecological and evolutionary significance of cognition—defined as the mechanisms by which animals acquire, process, store, and act upon information from the environment [7]—is increasingly being studied in natural populations [4, 5, 8–10]. We used a wild population of great tits (*Parus major*) to examine life history correlates and the selective consequences of a simple cognitive trait, problem-solving performance (PSP, with two categories, "solver" and "nonsolver" [11]) (see Movies S1 and S2 available online). The great tit has long been an influential model species in the study of life history variation [12, 13]. Previously we demonstrated that individual great tits differ consistently in their propensity to solve novel, goal-oriented foraging problems, and that these differences persist for at least a year [11] and predict the efficiency with which similar problems are solved in the wild [14]. In our population, PSP is unrelated to a variety of motivation factors and personality traits, including hunger,

neophobia, and exploration behavior [11]. Video analysis of problem-solving attempts suggests that the solution involves operant conditioning mediated by a perceptual-motor feedback (see also [15, 16]) and does not depend on feeding motivation or activity levels (see Supplemental Information and Movies S1 and S2). Furthermore, PSP is correlated with string-pulling success [11], a task involving trial-and-error learning [15, 17, 18]. Our measure of PSP is therefore likely to reflect operant conditioning ability, though we note that other non-mutually exclusive cognitive processes, such as inhibitory control [19] or unexamined personality traits such as persistence [16, 19], could also explain some of the observed interindividual variation in PSP. Additionally, PSP is likely to reflect intrinsic variation in innovativeness [20, 21] because the tasks that birds were presented with had never been encountered previously.

First we tested whether clutch size, a trait that is intensively studied in many taxa, was higher for solvers than for nonsolvers. Typically clutch size is under positive selection but is moderated by the ability to provision nestlings [22] and counterselection for offspring condition and adult survival [23, 24]. Female great tits that solved the novel problem in captivity laid significantly larger clutches than nonsolvers when they were subsequently found breeding in the wild ($F_{1, 231} = 4.47$, p = 0.036, mean difference ± SE = 0.40 ± 0.189 eggs; Tables 1 and S1). The effect did not arise because PSP covaried with other traits known to influence clutch size, including the timing of breeding and habitat quality [25] (oak trees within 75 m of nest box) (Tables 1, S1, and S3). A link between PSP and clutch size was also found in males: although the effect was weak among all males (Tables 1 and S2), clutch sizes were larger in nests where both parents were solvers than in nests that included nonsolver parents ($F_{2, 115} = 5.13$, p = 0.007; Figure 1A), possibly because male great tits feed their partners during egg laying [26, 27]. These results provide the first evidence for a positive link between a cognitive trait and clutch size, one of the most important determinants of fecundity and reproductive fitness in birds.

We then asked whether solvers also produce more offspring and examined the possibility that apparent benefits of higher cognitive ability are traded off against costs associated with other reproductive life history traits [6]. Among those individuals that successfully reared young to fledging age, solver females indeed fledged more young than nonsolvers ($F_{1, 182} = 4.10$, p = 0.044; Figure 1B; Tables 1 and S1), although there was no effect of male PSP on the number of fledglings (Tables 1 and S2), and the number of parents that were solvers also had no effect (parental PSP was not present in the final model and dropped out of the model at $F_{1, 96} = 0.93$, p = 0.337). The condition of the larger number of fledglings in nests with solver females was not compromised: average fledgling mass was similar among broods from solver and nonsolver females ($F_{1, 188} = 0.52$, p = 0.473; PSP dropped from model in Table S1), and therefore their viability in the post-fledging period was unlikely to have been compromised. Similarly, parental viability was unaffected, because neither breeding female nor breeding male body condition differed between all solvers and nonsolvers that bred (Table S4) and

---

[3]These authors contributed equally to this work
*Correspondence: j.quinn@ucc.ie

Table 1. The Link between Problem-Solving Performance and Reproductive Life History Variation in Great Tits

	Lay Date	Clutch Size	Nest Success (1/0)	Number of Fledglings	Average Fledging Mass (g)	Number of Recruits
Female	n = 373	n = 368	n = 368	n = 307	n = 307	n = 368
PSP[a]	ns	(+)*	(−)*	(+)*	ns	ns
Lay date	x	(−)***	ns	(−)***	(−)***	ns
Disparity	x	(−)*	ns	(−)***	(−)***	ns
Habitat quality	ns	ns	ns	ns	ns	ns
Brood size	x	x	(+)***	x	x	x
Age[b]	(−)***	ns	ns	ns	ns	ns
Male	n = 308	n = 308	n = 308	n = 273	n = 273	n = 308
PSP[a]	ns	ns[c]	ns	ns	ns	ns
Lay date	ns	(−)**	ns	(−)***	(−)*	(−)**
Disparity	ns	(−)*	ns	(−)**	(−)**	ns
Habitat quality	ns	ns	(+)**	ns	ns	ns
Brood size	x	x	(+)***	x	x	x
Age[b]	ns	ns	ns	ns	ns	ns

Separate statistical models are shown for each trait for females (top) and males (bottom). Initial models included all fixed effects: problem-solving perfor-mance (PSP) (solver/nonsolver), age (first year/older), lay date (date first egg laid), disparity (difference in days between peak caterpillar abundance and when nestlings were 9 days old), habitat quality (oak density within 75 m of nest), and brood size, unless indicated by "x" in the table. Note that PSP for both partners was known for too few nests to allow an analysis with both sexes simultaneously. All models include the random terms bird identity and year. Model results are from either GLMMs (for nest success, binary error structure; for number of recruits, Poisson error structure) or LMMs (all other life history traits). (+), positive coefficient; (−), negative coefficient; ***p < 0.001; **p < 0.01; *p < 0.05; ns, p > 0.05. See Tables S1 and S2 for full model outputs and Experimental Procedures and Supplemental Experimental Procedures for more details.
[a]Nonsolver set to zero.
[b]First-year breeder set to zero.
[c]Last term removed from the model with p = 0.071.

there was no difference in adult survival among all solvers and nonsolvers that bred (Table S5). Thus, there was no evidence that the higher reproductive success achieved by solvers was traded off against fledgling condition or adult viability.

However, there was evidence for a trade-off with total brood viability, because the probability of fledging any young at all was lower for solver females than for nonsolvers ($W_1 = 6.22$, p = 0.013, n = 242; Tables 1 and S1; Figure 1B). This lower nest success among solvers was not caused by higher adult mortality during reproduction, because the nest success effect remained in a second analysis where the data were restricted to nests in which both partners were still alive post-breeding ($W_1 = 4.36$, p = 0.039, n = 134). Thus, solvers exhibited both larger clutch size and a higher probability of nest deser-tion than nonsolvers. These contrasting links with different life history traits may explain why we detected little or no direc-tional selection on PSP in either sex or in any of the four years (Table S6).

Next we examined possible mechanisms that could have led to the links between problem solving and the different life history traits. Cognitive processes are commonly hypothe-sized to improve fitness by increasing foraging efficiency or quality (e.g., [9, 27]), which we explored using a variety of approaches. First, automatic loggers (recording presence of parents) and cameras at the nest showed that when nestlings were 5 days old, working day length for solvers was shorter than for nonsolvers (mean difference ± SE = 13.40 ± 7.33 min; $F_{1, 38} = 5.54$, p = 0.024; Tables 2 and S7), not longer as might be expected given that solvers were provisioning more offspring. There was no significant difference in provi-sioning rate or the proportion of caterpillars provisioned (a measure of diet quality [28, 29]) between solvers and non-solvers (Tables 2 and S7); similarly, there was no difference in amount of time spent provisioning, provisioning rate, or diet quality when nestlings were 10–11 days old (Tables 2 and S8). Finally, radio tracking showed that home ranges

during provisioning were 65% smaller among solvers than among nonsolvers ($F_{1, 6} = 14.88$, p = 0.010; Figure 2). The smaller ranges were unlikely to be a result of gross differences in the quality of habitat used, because, in addition to the oak density analysis mentioned above, several measures of local habitat quality were similar for solvers and nonsolvers of both sexes (Table S3). Apparently problem solvers were able to produce more eggs and offspring without exhibiting higher provisioning rates, although the possibility remains that they foraged at higher rates on other days during the breeding period, or at times other than those when we recorded activity. For instance, the combined effect of male and female solving performance was more pronounced for clutch size than for fledgling number, so solvers may have had a behavioral advantage primarily during egg laying, when foraging condi-tions are much less favorable compared to the provisioning period [28, 29] and when foraging behavior is difficult to assess in the great tit. Alternatively, the shorter foraging distances and working days exhibited by solvers may have allowed solvers to be more nest attentive [30], helping them to optimize brood temperature especially in the morning and evening when temperatures are cold [31], to minimize predation risk through nest defense [32], and/or to reduce parasite load in chicks [33].

In birds, nest desertion is a common adaptive response to declining environmental conditions [34, 35]. Sixteen percent of nests were abandoned between the parent trapping (when nestlings were one week old) and when nestlings reached fledging weight (14 days old). Experimental data suggest that the majority of these desertions were likely to be a response to trapping. Trapping adults at the nest when nestlings were 7 days old caused higher desertion rates than postponing adult catching until nestlings were 10 days old (Z = 2.837, p = 0.005, n = 132; nests were assigned randomly to 7- or 10-day-old treatment groups; see Supplemental Experimental Procedures for further details). Until recently, adults were trap-ped when nestlings were 7 days old, but an increase in the
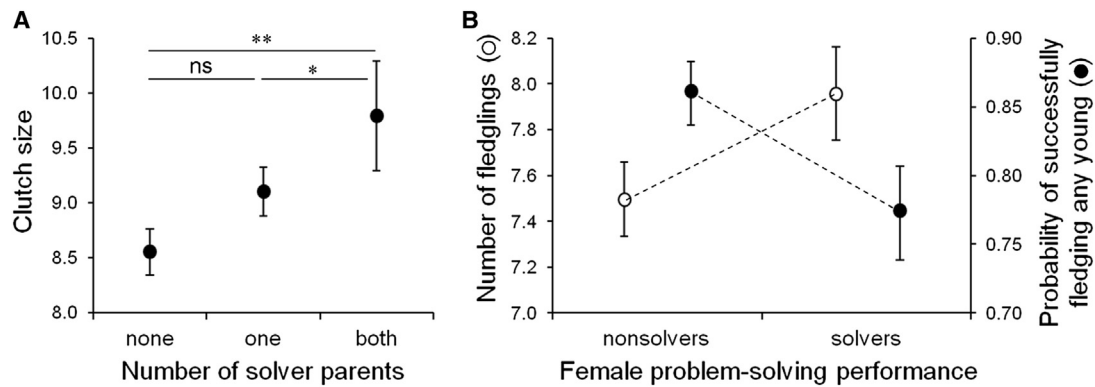
Figure 1. Problem-Solving Performance and Reproductive Performance in the Great Tit

(A) Clutch size varied with the number of solver parents at the nest. Analysis was restricted to nests where the problem-solving performance (PSP) of both parents was known (n = 136 pairs; both parents nonsolvers, n = 49; one solver parent, n = 65 [male only, n = 33; female only, n = 32]; two solver parents, n = 22). Clutch size was averaged across multiple individual breeding attempts for illustration. **p < 0.01; *p < 0.05; ns, p > 0.05.

(B) Number of fledglings and probability of fledging any offspring varied between solver and nonsolver females. Open circles indicate the average number of fledglings produced by nonsolver and solver females, based on nests where at least one nestling fledged (n = 214 individuals; nonsolvers, n = 132; solvers, n = 82). Where a female bred in successive years, fledgling number was averaged across breeding attempts for the sake of illustration. Black circles indicate the probability of fledging any young successfully from the nest. Plotted success data are back-transformed mean effects from a GLMM with a binomial error structure (n = 382 breeding attempts for 246 individuals; nonsolvers, n = 147; solvers, n = 99).
Error bars represent SEM.

population size in recent years has led to increased density-dependent desertion, and consequently adults are now trapped when nestlings are 10 days old (see Supplemental Experimental Procedures). Desertion following trapping and handling of birds is likely to mimic adaptive desertion following exposure to a natural predator [34, 35]. Previously we showed that the startle response, an antipredation behavior, tends to be more pronounced in solvers than in nonsolvers [36]. Problem solvers may generally be more sensitive to disturbance at the nest, and predation risk, than nonsolvers, though whether they have a stronger response to natural predation attempts remains to be tested.

Experiments on captive insect populations [2, 3] and common garden experiments [9, 10] suggest that adaptation to local environmental conditions can influence cognitive ability. Pioneering work on bumblebees (*Bombus terrestris*) [4] revealed a positive correlation between learning ability and a proxy for fitness, foraging efficiency among free-ranging colonies, and a study on male bowerbirds (*Ptilonorhynchus violaceus*) reported a correlation between problem-solving ability at the bower and mating success [5]. The results presented in this paper advance the field substantially for several reasons. First, they represent the first explicit investigation of links between cognitive ability and multiple life history traits determining reproductive fitness in a natural population; the selection coefficients presented are also the first estimates of natural selection for any cognitive trait in the wild. Second, the analyses control for the major ecological determinants of life history variation in the great tit, which has not been attempted previously. However, the possibility that unexamined correlates of PSP underlie the observed relationships remains until these links are assessed experimentally. Third, the higher desertion probability among solvers represents the first evidence from the wild for reproductive costs of elevated cognitive performance [6]. Previously we showed that problem solvers were less competitive at artificial feeders than nonsolvers [37]; though direct links to survival fitness were not tested, this illustrates that trade-offs with other unexplored traits may

also be important, as emphasized by the concept of behavioral syndromes [38]. Contrasting effects on fecundity and desertion highlight the importance of considering potential life history trade-offs when examining selection for cognition in natural environments. Ultimately, they offer a potential explanation for why variation in cognitive ability occurs within populations.

Experimental Procedures

Data Collection

Standardized assays of PSP were conducted on individually marked birds temporarily taken into captivity during winter (November to March) from Wytham Woods (51°46'N, 1°20'W), Oxfordshire UK, between 2007 and 2010. Birds were housed singly in wire cages (45 × 45 × 68 cm) and presented with a simple task, where a lever had to be removed from a device in order to obtain a food reward. Individuals were given three hours to solve this task and were classified as "solvers" or "nonsolvers" based on their performance (see [11] for full details). After being assayed, all individuals were subsequently released back into the wild, at the site of catching. In addition to these individuals, a further sample of birds was taken into captivity from February 27 to March 9, 2012, in order to examine the proximate mechanisms underlying individual variation in PSP. Specifically, we examined the hypothesis that the solution involves operant conditioning mediated through a perceptual-motor feedback. Videos of solving assays were analyzed to quantify feeding motivation and contacts with functional and nonfunctional parts of the problem-solving device (see Supplemental Experimental Procedures for full details). The protocols outlined were all subject to ethical review by the Department of Zoology (Oxford) ethical committee.

Over the four breeding seasons (2007–2010), 247 females and 221 males of known PSP bred in Wytham (n = 382 and n = 316 breeding attempts, respectively, including 152 breeding attempts where the PSP of both parents was known). Breeding attempts of all great tits in Wytham were monitored as part of a long-term study using 1,020 nest boxes (see [39]). Parents were trapped and identified at the nest when nestlings were approximately 7 days old. Laying date of the first egg, clutch size, brood size (number of young observed in the nest), fledgling number, fledgling mass, and nest success (failure or success, where a nest was classified as successful when at least one chick fledged successfully) were recorded during visits to nest boxes between April and June. Recruitment from each nesting attempt was established by recording how many fledglings bred in Wytham the following year (see [22]).

Table 2. Relationship between Problem-Solving Performance and Parental Provisioning Behavior in the Great Tit

	Working Day Length (Hours)	Provisioning Rate (Feedings/Hour, In Transformed)	Proportion of Prey Items = Caterpillars
5 Days	n = 44	n = 42	n = 42
PSP[a]	(−)*	ns	ns
Sex[b]	ns	(+)***	ns
Age[c]	ns	ns	(+)***
Lay date	ns	ns	(+)***
Disparity	ns	ns	ns
Habitat quality	ns	ns	ns
Brood size	ns	ns	ns
10–11 Days	n = 128	n = 106	n = 123
PSP[a]	ns	ns	ns
Sex[b]	(−)***	ns	(+)***
Age[c]	ns	ns	ns
Lay date	(+)**	(−)***	(+)*
Disparity	ns	(+)***	(−)***
Habitat quality	ns	ns	ns
Brood size	(+)*	ns	ns
Year[d]	(+)**	ns	ns

Relationship between parental provisioning behavior and parental PSP when nestling great tits were 5 days old during 2010 (top) and 10–11 days old during 2009 and 2010 (bottom). Separate statistical models are shown for each of the three provisioning variables. Each column represents a separate model; the final model included only significant terms. Fixed-effects definitions are as in Table 1; 10–11 day models also included year; nest identity was included as a random effect in all models. (+), positive coefficient; (−), negative coefficient; ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ns, $p > 0.05$. See Tables S7 and S8 for full model outputs and Experimental Procedures and Supplemental Experimental Procedures for further information.
[a]Nonsolver set to zero.
[b]Female set to zero.
[c]First-year breeder set to zero.
[d]2009 set to zero.

Individual provisioning behavior was recorded for birds of known PSP (usually only one parent per nest) using a combination of uniquely identifiable passive integrated transponder (PIT) tags detectable at nest boxes using PIT tag loggers, and video cameras (Handykam) attached to nest boxes during the 2009 and 2010 breeding seasons. Provisioning rate was estimated from video using the number of food items successfully delivered to the nest, divided by sample duration (1.5–3 hr). Video footage was also used to establish the proportion of caterpillars provisioned; caterpillars are a high-quality and preferred food source of *Parus* species [28, 29]. Working day length was calculated by subtracting, from 24 hr, the time elapsed between the last provisioning visit in the evening and the first feeding the following morning. In 2009, 11 adults for which PSP assays had previously been conducted were also radio tracked over 3 to 6 days (mean duration ± SD = 235 ± 61 min; range = 135–335 min) when nestlings were 8–13 days old in order to estimate home range size (see Supplemental Experimental Procedures for more details).

The hypothesis that the trapping protocol used in our population resulted in significant nest desertion was experimentally tested during the 2011 breeding season. This was done by comparing the rate of nest failure where adults were trapped using the normal trapping procedure to that where adults were not trapped until later in the nestling period, when increased brood value is likely to result in lower desertion rates. Nests were randomly assigned to one of two treatments, normal trapping (adults trapped when nestlings were 7 days old) or late trapping (adults trapped when nestlings were 10 days old). All broods were subsequently visited when 14 days old to determine whether the nest had failed, with failure being defined as no live nestlings remaining in the nest. "Late trapping" nests were also visited when nestlings were 7 days old, so that brood survival between 7 and 14 days old could be compared between treatments, and "normal trapping" nests were also visited at 10 days so that the total number of visits was equivalent for both treatments. The potential ethical issue associated with trapping became apparent only immediately before the 2011 breeding
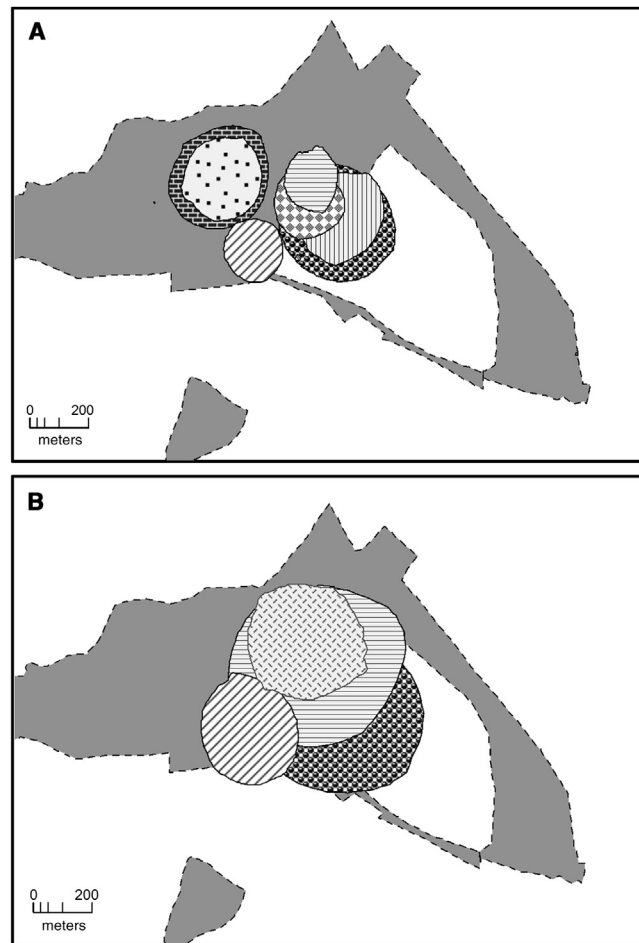

Figure 2. Home Range Sizes of Individual Great Tits When Provisioning Offspring

Harmonic mean-centered contour home ranges within part of Wytham Wood (gray area enclosed by dashed line). Individual nests within each panel are indicated by different patterns; nests in which both parents were tracked (n = 3 nests) are indicated by the same pattern across panels. White areas are farmland. Data are from n = 11 individuals from n = 8 nests.
(A) Solver great tits.
(B) Nonsolver great tits.

season; the experiment was conducted to test causality, and the trapping protocol has since been altered accordingly.

Data Analysis

Relationships between PSP and life history traits were tested using linear mixed models (LMMs) or generalized linear mixed models (GLMMs) containing the random factors year and bird identity (to account for multiple breeding attempts per individual), with males and females analyzed separately. The relationships between PSP and provisioning variables were analyzed using LMMs and GLMMs controlling for appropriate fixed and random effects (see Supplemental Experimental Procedures for more details). All final models were formed by backward stepwise removal of nonsignificant terms. Standardized directional selection coefficients (following methods from [40]) were estimated for fecundity (total number of young that fledged successfully) and recruitment. All analyses were carried out with GenStat v13.1 [41].

Supplemental Information

Supplemental Information includes eight tables, Supplemental Experimental Procedures, and two movies and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.07.051.

References

1. Dukas, R. (2004). Evolutionary biology of animal cognition. Annu. Rev. Ecol. Evol. Syst. *35*, 347–374.
2. Dukas, R. (2008). Evolutionary biology of insect learning. Annu. Rev. Entomol. *53*, 145–160.
3. Kawecki, T.J. (2010). Evolutionary ecology of learning: insights from fruit flies. Popul. Ecol. *52*, 15–25.
4. Raine, N.E., and Chittka, L. (2008). The correlation of learning speed and natural foraging success in bumble-bees. Proc. Biol. Sci. *275*, 803–808.
5. Keagy, J., Savard, J.-F., and Borgia, G. (2009). Male satin bowerbird problem-solving ability predicts mating success. Anim. Behav. *78*, 809–817.
6. Mery, F., and Kawecki, T.J. (2003). A fitness cost of learning ability in Drosophila melanogaster. Proc. Biol. Sci. *270*, 2465–2469.
7. Shettleworth, S.J. (2010). Cognition, Evolution, and Behavior, Second Edition (New York: Oxford University Press).
8. Pravosudov, V.V., and Clayton, N.S. (2002). A test of the adaptive specialization hypothesis: population differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile atricapilla*). Behav. Neurosci. *116*, 515–522.
9. Roth, T.C., LaDage, L.D., and Pravosudov, V.V. (2010). Learning capabilities enhanced in harsh environments: a common garden approach. Proc. Biol. Sci. *277*, 3187–3193.
10. Roth, T.C., 2nd, LaDage, L.D., Freas, C.A., and Pravosudov, V.V. (2012). Variation in memory and the hippocampus across populations from different climates: a common garden approach. Proc. Biol. Sci. *279*, 402–410.
11. Cole, E.F., Cram, D.L., and Quinn, J.L. (2011). Individual variation in spontaneous problem-solving performance among wild great tits. Anim. Behav. *81*, 491–498.
12. Perrins, C.M. (1965). Population fluctuations and clutch-size in the great tit, *Parus major* L. J. Anim. Ecol. *34*, 601–647.
13. Dhondt, A.A., Adriaensen, F., Matthysen, E., and Kempenaers, B. (1990). Nonadaptive clutch size in tits. Nature *348*, 723–725.
14. Morand-Ferron, J., Cole, E.F., Rawles, J.E.C., and Quinn, J.L. (2011). Who are the innovators? A field experiment with two passerine species. Behav. Ecol. *22*, 1241–1248.
15. Taylor, A.H., Medina, F.S., Holzhaider, J.C., Hearne, L.J., Hunt, G.R., and Gray, R.D. (2010). An investigation into the cognition behind spontaneous string pulling in New Caledonian crows. PLoS ONE *5*, e9345.
16. Overington, S.E., Cauchard, L., Côté, K.-A., and Lefebvre, L. (2011). Innovative foraging behaviour in birds: what characterizes an innovator? Behav. Processes *87*, 274–285.
17. Vince, M.A. (1956). 'String pulling' in birds. 1. Individual differences in wild adult great tits. Br. J. Anim. Behav. *4*, 111–112.
18. Seibt, U., and Wickler, W. (2006). Individuality in problem solving: string pulling in two carduelis species (Aves: Passeriformes). Ethology *112*, 493–502.
19. Thornton, A., and Samson, J. (2012). Innovative problem solving in wild meerkats. Anim. Behav. *83*, 1459–1468.
20. Webster, S.J., and Lefebvre, L. (2001). Problem solving and neophobia in a columbiform-passeriform assemblage in Barbados. Anim. Behav. *62*, 23–32.
21. Reader, S.M., and Laland, K.N. (2003). Animal Innovation (Oxford: Oxford University Press).
22. Pettifor, R.A., Perrins, C.M., and McCleery, R.H. (2001). The individual optimization of fitness: variation in reproductive output, including clutch size, mean nestling mass and offspring recruitment, in manipulated broods of great tits *Parus major*. J. Anim. Ecol. *70*, 62–79.
23. Williams, G.C. (1966). Natural selection, costs of reproduction and a refinement of Lack's principle. Am. Nat. *100*, 687–690.
24. Smith, C.C., and Fretwell, S.D. (1974). The optimal balance between size and number of offspring. Am. Nat. *108*, 499–506.
25. Wilkin, T.A., and Sheldon, B.C. (2009). Sex differences in the persistence of natal environmental effects on life histories. Curr. Biol. *19*, 1998–2002.
26. Gosler, A. (1993). The Great Tit (London: Hamlyn Press).
27. Boogert, N.J., Fawcett, T.W., and Lefebvre, L. (2011). Mate choice for cognitive traits: a review of the evidence in nonhuman vertebrates. Behav. Ecol. *22*, 447–459.
28. van Noordwijk, A.J., McCleery, R.H., and Perrins, C.M. (1995). Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. J. Anim. Ecol. *64*, 451–458.
29. Naef-Daenzer, L., Naef-Daenzer, B., and Nager, R.G. (2000). Prey selection and foraging performance of breeding great tits *Parus major* in relation to food availability. J. Avian Biol. *31*, 206–214.
30. Martin, T.E. (1987). Food as a limit on breeding birds: a life history perspective. Annu. Rev. Ecol. Syst. *18*, 453–487.
31. Sanz, J.J., and Tinbergen, J.M. (1999). Energy expenditure, nestling age, and brood size: an experimental study of parental behaviour in the great tit *Parus major*. Behav. Ecol. *10*, 598–606.
32. Greig-Smith, P.W. (1980). Parental investment in nest defence by stonechats (*Saxicola torquata*). Anim. Behav. *28*, 604–619.
33. Hurtrez-Bousses, S., Renaud, J., Blondel, J., Perret, P., and Galan, M.-J. (2000). Effects of ectoparasites of young on parents' behaviour in a Mediterranean population of blue tits. J. Avian Biol. *31*, 266–269.
34. Morton, M.L., Sockman, K.W., and Peterson, L.E. (1993). Nest predation in the mountain white-crowned sparrow. Condor *95*, 72–82.
35. Ackerman, J.T., Eadie, J.M., Yarris, G.S., Loughman, D.L., and McLandress, M.R. (2003). Cues for investment: nest desertion in response to partial clutch depredation in dabbling ducks. Anim. Behav. *66*, 871–883.
36. Dunn, J.C., Cole, E.F., and Quinn, J.L. (2011). Personality and parasites: sex-dependent associations between avian malaria infection and multiple behavioural traits. Behav. Ecol. Sociobiol. *65*, 1459–1471.
37. Cole, E.F., and Quinn, J.L. (2012). Personality and problem-solving performance explain competitive ability in the wild. Proc. Biol. Sci. *279*, 1168–1175.
38. Sih, A., Bell, A.M., Johnson, J.C., and Ziemba, R.E. (2004). Behavioral syndromes: an intergrative overeiw. Q. Rev. Biol. *79*, 241–277.
39. McCleery, R.H., Pettifor, R.A., Armbruster, P., Meyer, K., Sheldon, B.C., and Perrins, C.M. (2004). Components of variance underlying fitness in a natural population of the great tit *Parus major*. Am. Nat. *164*, E62–E72.
40. Lande, R., and Arnold, S. (1983). The measurement of selection on correlated characters. Evolution *37*, 1210–1226.
41. VSN International (2010). GenStat 13th Edition. VSN International Ltd., Oxford. http://www.vsni.co.uk/software/genstat.