

Problem-solving and learning in Carib grackles: individuals show a consistent speed–accuracy trade-off

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Abstract The generation and maintenance of within-population variation in cognitive abilities remain poorly understood. Recent theories propose that this variation might reflect the existence of consistent cognitive strategies distributed along a slow–fast continuum influenced by shyness. The slow–fast continuum might be reflected in the well-known speed–accuracy trade-off, where animals cannot simultaneously maximise the speed and the accuracy with which they perform a task. We test this idea on 49 wild-caught Carib grackles (*Quiscalus lugubris*), a tame opportunistic generalist Icterid bird in Barbados. Grackles that are fast at solving novel problems involving obstacle removal to reach visible food perform consistently over two different tasks, spend more time per trial attending to both tasks, and are those that show more shyness in a pretest. However, they are also the individuals that make more errors in a colour discrimination task requiring no new motor act. Our data reconcile some of the mixed positive and negative correlations reported in the comparative literature on cognitive tasks, suggesting that a speed–accuracy trade-off could lead to negative correlations between tasks favouring speed and tasks favouring accuracy, but still reveal consistent strategies based on stable individual differences.

Keywords Cognition · Problem-solving · Innovation · Discrimination learning · Speed–accuracy trade-off · Cognitive styles

Introduction

Variation in cognitive abilities has mainly been investigated at the species level, with some studies focusing on adaptive specializations (Shettleworth 2010) and others identifying domain general abilities common to different tasks (Deaner et al. 2006; Reader et al. 2011; see, however, Amici et al. 2012). Beyond such interspecific differences, recent studies show that variation in cognitive performance is also widespread *within* species (Seibt and Wickler 2006; Boogert et al. 2008a; Titulaer et al. 2012), raising questions about the evolutionary mechanisms responsible for both the generation and maintenance of such individual variation. Cognition, i.e. the mechanisms by which animals acquire, process, store and act on information from the environment (Shettleworth 2010), is expected to be inherently costly to build and maintain (Laughlin et al. 1998; Dukas 1999; Isler and Van Schaik 2009; Burns et al. 2011; Cole et al. 2012). Individual variation in cognitive abilities may thus reflect differences of investment in cognition relative to other energetically costly, non-cognitive, traits. For instance, in guppies (*Poecilia reticulata*), artificial selection on brain size (a correlate of many cognitive abilities) is traded off against reproductive performance in males (Kotrschal et al. 2013). In *Drosophila*, lines of flies selected for improved learning abilities (measured as the ability to associate an odour with an aversive mechanical shock) show a lowered competitive ability of their larvae when food was scarce (Mery and Kawecki 2003); inversely, larvae selected for their competitive ability on a

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limited food supply show poorer learning (Kolss and Kawecki 2008).

Within cognition itself, studies vary in the type of relationship found between different tasks. Some show positive correlations between performance on different cognitive measures, while others show negative correlations or do not detect any significant relationship. As with correlations between species, a positive association between individual differences on several cognitive measures is often interpreted as evidence for domain general processes, as Banerjee et al. (2009) conclude from the consistent individual differences they found across eleven tasks in cotton-top tamarins (*Saguinus oedipus*), or as Matzel et al. (2003) conclude from a similar pattern observed across five tasks in laboratory mice (*Mus musculus*). Positive correlations across individuals have also been obtained between individual problem-solving and social-learning in pigeons (*Columba livia*, Bouchard et al. 2007), between problem-solving and asocial-learning in European starlings (*Sturnus vulgaris*, Boogert et al. 2008b), as well as between cognitive abilities that are often thought to belong to different modules, such as song complexity and problem-solving in zebra finches (*Taeniopygia guttata*, Boogert et al. 2008a), song complexity and detour-reaching in song sparrows (*Melospiza melodia*, Boogert et al. 2011) and song complexity and spatial memory in European starlings (Farrell et al. 2011). Negative relationships between individual differences in cognitive measures can indicate trade-offs between the measures, while a lack of significant correlations can mean they are independent of each other. Sewall et al. (2013) report that song sparrows with wider song repertoires make more errors in a spatial task. Keagy et al. (2009, 2011) find little association between obstacle removal, song repertoire size and different measures of bower repair in bowerbirds (*Ptilonorhynchus violaceus*), while Boogert et al. (2011) report mostly non-significant correlations between problem-solving, colour discrimination, reversal and detour-reaching in song sparrows. Similarly, Locurto et al. (2003) did not find correlations between scores at five problem-solving tasks performed on laboratory mice.

Sih and Del Giudice (2012) have recently proposed that inter-individual variation in cognitive measures, as well as relationships between cognitive scores, might be associated with a continuum of cognitive strategies. They suggest that some individuals might be consistently slower than others in their response to a cognitive challenge. Speed is one of the main dimensions identified in recent work on behavioural syndromes (i.e. suites of correlated behaviours reflecting between-individual consistency in behaviour across multiple situations, Sih et al. 2004). Studies on birds, most notably great tits, have identified fast and slow individuals that differ in the speed with which they explore

a new environment (Verbeek et al. 1994). The fast versus slow dimension is heritable (Drent et al. 2003) and may correspond to different adaptive peaks that are selected in alternation in fluctuating environmental conditions (Dingemanse et al. 2004). The fast versus slow dimension affects dispersal (Dingemanse et al. 2003), dominance (Dingemanse and de Goede 2004), mate choice (Both et al. 2005) and extra-pair paternity (van Oers et al. 2008).

This slow–fast continuum might also be behind individual differences in performances across different cognitive tasks, as already suggested by associations between personality traits and learning efficiency in tits (Exnerova et al. 2010; Titulaer et al. 2012) and chickadees (Guillette et al. 2011). More specifically, personality traits such as shyness and neophobia, which are strongly associated with this slow–fast continuum (shy and neophobic individuals being usually on the slow part of this continuum), are known to strongly affect individual responses to cognitive challenges (Sih and Del Giudice 2012; Sol et al. 2012). The so-called speed–accuracy trade-off, a perceptual and motor constraint in which animals cannot simultaneously achieve high levels of speed and high levels of accuracy, has been demonstrated in a wide range of organisms from humans (Wickelgren 1977) to mice (Abraham et al. 2004) to guppies (Burns and Rodd 2008), bees (Chittka et al. 2003) and ants (Franks et al. 2003). Its importance in generating and maintaining variation in responses to cognitive challenges remains poorly understood, however, especially in birds, despite the fact that birds are a model taxon in the study of inter-individual variation in cognition.

This trade-off can be expected to affect performance on problem-solving or discrimination-learning tasks (Sih and Del Giudice 2012). Under the speed–accuracy trade-off hypothesis, fast individuals should quickly interact with any new task they are exposed to, but with poor accuracy. In a problem-solving task involving novel motor acts, fast individuals might be successful earlier because they are fast at interacting with the task and at producing a large number of trials and errors. However, because of their poor accuracy, they are expected to need more time interacting with the task before solving it, as compared to more accurate individuals. Fast individuals should thus succeed earlier (i.e. after a lower total amount of time being exposed to the task), but spend more time directly interacting with the task. In a colour discrimination task, where no new motor act is required, individuals that are fast at choosing a colour should be more likely to make errors than individuals that wait longer and make more accurate choices (see for instance Chittka et al. 2003).

In this paper, we use wild-caught Carib grackles, a tame and omnivorous opportunistic species living in Barbados (Webster and Lefebvre 2001; Griffin and Galef 2005; Morand-Ferron et al. 2004; Overington et al. 2011) to test

whether the speed–accuracy trade-off could explain individual differences in problem-solving and discrimination learning. We compare performance in two problem-solving tasks where a novel motor act needs to be performed to access visible food and one discrimination-learning task where individuals only need to choose the correct colour cue identifying a food container they know how to open. In the problem-solving tasks, birds have to switch from motor acts directed at visible food to those directed at movable parts of the apparatus. In a task of this type, grackles generally require some time to approach the apparatus, then peck at the part of the apparatus where food is visible, then move away, to return a few seconds later and either repeat their pecking towards the visible food or start directing pecks at other parts of the apparatus, eventually producing a movement in the appropriate part of the apparatus and concentrating more and more on that movable part. In terms of speed at solving the task, fast individuals tend to be those that are also fast at approaching the apparatus (Webster and Lefebvre 2001), as well as fast and persistent at switching from the part of the apparatus where food is visible to the part that moves and leads to displacement of the obstacle (Overington et al. 2011). In this paper, we show that fast solvers are also those that spend a larger amount of time in each trial interacting with the apparatus.

If rapid solving of a motor task is a stable trait that depends on the slow–fast continuum, we predict that individuals should show positive correlations in their performance on the two problem-solving tasks, as well as positive correlations with their shyness and neophobia scores. If birds show a speed–accuracy trade-off, we predict that fast problem solvers should also be fast at choosing colours in the discrimination task, but make more colour choice errors. This also implies that there should be a negative correlation between performance in the two problem-solving tasks and performance in the discrimination task.

Materials and methods

Bird housing

We captured forty-nine grackles (40 males and 9 females) between March and June 2012 and between February and April 2013, in baited (with dog pellets) walk-in traps (1 × 0.55 × 0.55 m) on the grounds of the Bellairs Research Institute of McGill University, St. James, Barbados. For each capture event, the trap was continuously watched from a distance of 25 m until grackles fed in it, then manually sprung. As the birds were kept in captivity on their capture site (i.e. at the Bellairs Research Institute),

there was no transportation between capture and captivity sites, and birds were transferred from the trap to their captivity cage within 5 min of capture. Upon capture, we weighed and measured each individual and banded it with a unique combination of coloured aluminium bands (A.C. Hughes Ltd., UK). All birds were sexed based on morphological and behavioural observations. This method was validated by Overington et al. (2011) and is as accurate as molecular sexing. Body condition was estimated as the residual of the log-regression of body mass against wing length (measured as unflattened wing chord length to the nearest 0.5 mm using a raised-edge ruler). Birds were housed in individual wood and wire mesh cages (2.63 × 1.52 × 1.10 m) with four wooden perches, in an outdoor aviary where up to four birds were kept at any one time. The aviary was in the shade, 25 m from the capture area, with temperature and noise conditions identical to those experienced by wild individuals (i.e. 24–28 °C). Cages were separated from each other by opaque plastic sheets so that subjects were visually but not acoustically isolated from each other. Birds were given ad libitum access to water throughout the experimental period. Food (soaked dog pellets, a favoured food of Carib grackles; Morand-Ferron et al. 2004) was provided ad libitum for the first day in captivity, and for at least 3 h after testing on days where we conducted experiments. Overnight food deprivation began on the third day in captivity, as detailed below.

The five phases (shyness, neophobia, lid removal, stick-pulling, colour discrimination) of our experiments were carried out in succession on days 2–5 following capture. The amount of food given as reward for each of the five phases was constant (1/6 soaked dog pellet) in order to maintain a similar hunger level in all birds. We chose to keep the order of the phases constant (as in Seferta et al. 2001; Webster and Lefebvre 2001; Overington et al. 2011) because in wild-caught birds, a gradual habituation to captivity could produce a spurious negative association between tests if order was counterbalanced or randomised (Bell 2013, Guy Beauchamp, personal communication). Birds habituating to captivity and testing would on average do better on day 2 than day 1, whatever the task given on each day; if tasks 1 and 2 are given to one bird on days 1 and 2, respectively, and to another bird on days 2 and 1, respectively, the simple effect of habituation might create an artificial negative relationship between performance on the two tasks. The tasks we used also built on the mastery of successive motor acts: task 1 required grackles to remove a lid from a cylinder containing visible food, task 2 to pull the cylinder out of a tunnel, and task 3 to discriminate the colour that indicates which of two lid-covered, opaque cylinders contain food.

Birds were kept for a maximum of 8 days to complete other behavioural measurements (not shown here), then

released at their site of capture. All cages were entirely disinfected after each release and before each capture. Supplementary food (dog pellets) was provided at the release site during the 2 days following each release, and several of our experimental birds were observed successfully nesting and raising young within weeks of their release (and as much as 1 year later), suggesting that captivity had no negative effects for the birds over the short or long term. All experiments and captures were conducted according to Animal Use Protocol 2012–7140, approved by the McGill University Animal Care Committee, and permit 8434/56 from the Natural Heritage Department of the Barbados Ministry of Environment and Drainage.

Shyness

Shyness was measured on the second day of captivity, around 15:00. Birds were food-deprived 1 h before testing, and we recorded their latency to eat from their food dish after it had been replaced by the experimenter (see Overington et al. 2011). Maximum time allowed was 20 min, and birds that did not eat during this period were given a score of 1,201 s (i.e. 20 min + 1 s). Immediately after, the experimenter removed and replaced the food dish of each bird six times successively in order to habituate the birds to experimenter disturbance. Additionally, latency to feed after disturbance was assessed the same way on the following days of behavioural testing, immediately before the cognitive tasks.

Neophobia

In the morning of the third day in captivity, we measured the latency for individuals to eat when a novel object was placed beside their food dish. After overnight food deprivation, birds were first given a dish containing their usual food. As a control, we measured the time each bird needed to feed after introducing the food in the cage. In a second trial that took place 1 min after the control trial, we placed the novel object (a colourful mug that birds were unlikely to be familiar with) beside the food dish and recorded the latency to feed. For both trials, the maximum time allowed was 5 min. As some individuals did not eat during the control trial, the food was removed from the cage at the end of the trial, the experimenter waited 2 min, and another control trial was started. This was repeated until the bird ate within 5 min in a control trial. Six birds needed two trials before eating, and one ate at the fourth control trial. Neophobia was measured as the time difference between the latency to feed with the new object and the latency to feed at the control trial occurring before the novel object trial.

Problem-solving task 1: Lid removal on a transparent cylinder

In the next two tests, birds had to remove an obstacle to reach food by performing a motor act. They did this without prior exposure and, if they succeeded within ten trials, without shaping. We use the term problem-solving rather than learning here because we are only interested in the first successful opening (not improvement from reinforcement over successive openings), and we presume our wild-caught birds have not faced an identical motor task before. The first problem-solving task consisted of a transparent PVC cylinder (diameter = 3 cm, height = 5 cm) fixed to the middle of a petri dish, over which we placed a white plastic lid (3.4 cm diameter; see Fig. 1a). The visible food reward (1/6 soaked dog pellet) was placed inside the cylinder. To solve the task, a bird had to flip the lid off the cylinder to gain access to the food (Supplementary Material 1a). A bird accessing food once was considered as successful. The task was first presented with the lid placed on top of the cylinder, and each individual was allowed a maximum of 10 trials of 5 min each with 10 min between two trials on the third and fourth days of captivity to solve the task before starting the ‘shaping’ phase, if unsuccessful. For each trial, we recorded the amount of time an individual spent interacting with the task, i.e. the time not contacting the apparatus was subtracted from the maximum 5 min allowed or until the lid was removed. This allowed us to calculate, for each individual, the average time spent interacting with the task per trial within the 10 first trials or until success.

For individuals that were unsuccessful after 10 trials, we used a shaping procedure to progressively lead the subject towards success. At level 1, an opened cylinder was presented, with the lid placed next to it; at level 2, the cylinder was half covered by the lid; at level 3, the cylinder was totally covered by the lid (as during the first 10 trials). When the bird managed to reach the food once, it passed to the next level of difficulty, whereas two successive failures at the same level returned it to the previous level on the next trial. As an estimate of performance on this task, we used the number of 5-min trials before success (adding the number of shaping trials to the 10 first trials for individuals unsuccessful after 10 trials). After a success, each bird was exposed six more times to the task, and as all birds were able to access the food on these six consecutive times, we only consider the number of 5-min trials before the first success as indicator of performance.

Problem-solving task 2: Stick-pulling out of a tunnel

The next task required a different motor act, pulling on a stick to bring out of a semi-transparent box, a cylinder

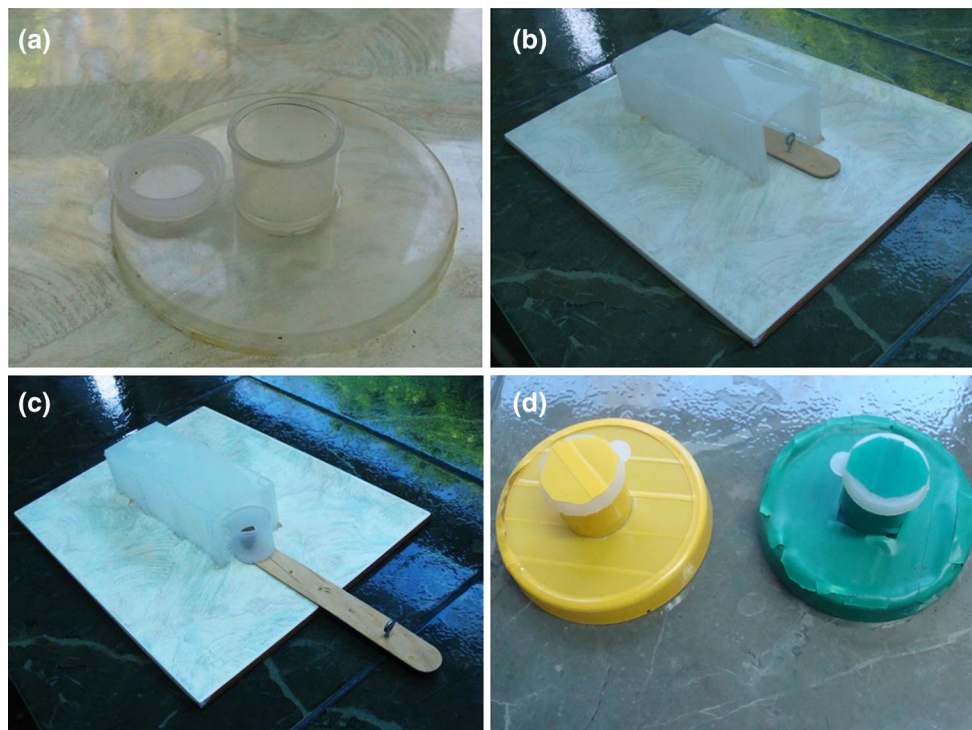


Fig. 1 Tasks used to measure cognitive skills in Carib grackles: **a** lid-removal task with the lid placed near the cylinder; **b** stick-pulling task with the wooden stick inside the tunnel; **c** stick-pulling task with the

wooden stick outside of the tunnel; **d** colour discrimination-learning tasks with lids placed on the cylinders (*yellow task on the left, green task on the right*)

containing a food reward. The apparatus consisted of a semi-transparent PVC ‘tunnel’ box opened on one end ($13 \times 4 \times 3.5$ cm, see Fig. 1b, c). An uncovered transparent cylinder (2 cm diameter, 3 cm height) containing the food reward was glued at the extremity of a wooden stick (17×1 cm) equipped with a metal O-ring (acting as a handle) on the other end. This stick assembly was introduced inside the tunnel so that the transparent cylinder touched the closed end of the tunnel. To solve the task, a bird had to pull the wooden stick out of the tunnel to gain access to the reward (Supplementary Material 1b).

Each individual was allowed a maximum of 10 trials of 5 min each with 10 min between two trials on the fourth and fifth days of captivity to solve the task. At each trial, we recorded the amount of time an individual spent interacting with the task, i.e. the time not contacting the apparatus was subtracted from the maximum 5 min allowed or until the stick was pulled out of the tunnel. This allowed us to calculate, for each individual, the average time spent interacting with the task per trial within the 10 trials or until success. For individuals unsuccessful after the 10 first trials, we then followed a shaping procedure similar to the one used for the lid removal task, with three different levels; at level 1, the stick was pulled out of the tunnel, with the cylinder right in front of the tunnel opening, so that the bird only needed to reach the reward inside the

cylinder; at level 2, the stick was inserted halfway in the tunnel, the cylinder with the reward being 5 cm from the tunnel opening, so that the bird had to lightly pull the stick to access the reward; at level 3, the stick was pushed into the other end of the tunnel, as in the 10 first trials. In total, each individual was allowed a maximum of 30 trials (10 trials + 20 shaping trials), and birds that failed to solve the task after 30 trials were given a score of 31. We used the number of trials before success (adding the number of shaping trials to the 10 first trials for individuals unsuccessful after 10 trials) as an estimate of performance at the stick-pulling task. After a success, each bird was exposed six more times to the task, and since all birds were able to access the food on these six consecutive times, we only consider the number of 5-min trials before the first success as indicator of performance.

Colour discrimination learning

In the previous two tasks, individual variation in the tendency to peck off a lid or pull on a stick to obtain food could drive performance differences in the first ten trials. In the next task, we eliminated initial individual differences in motor performance by shaping all birds to the same fast, reliable level of lid-flipping before testing started. Success or failure in this task now only depended on choosing the

correct colour that identified a lid with food. The test apparatus consisted of two lid-covered cylinders (same as lid removal task) covered with different colours of electric tape (yellow or green, see Fig. 1d). Contrary to the lid removal task, the birds could not detect the presence of food inside the cylinders because of the opaque tape, but could associate a colour with the presence of a reward. At the start of the discrimination-learning session, each individual was first exposed to the two opened cylinders until it had eaten the food from both. The same procedure was then repeated, but with the lids on top of the cylinders, to make sure that each individual was able to easily open the two lids. A ‘colour choice’ trial was then made, where the bird was allowed to flip the lid and eat from only one cylinder (once the bird had flipped one lid and eaten the reward, the experimenter immediately intervened and removed the two cylinders before the bird had a chance to try the second one), and the colour of the cylinder chosen by the bird was considered as its preferred colour. The other colour thus became the rewarded one in order to control for initial colour preference. On each trial, the two cylinders were introduced simultaneously inside the cage and placed at a distance of 30 cm from each other. The bird was given up to 5 min to remove one of the lids and obtain the reward. If the bird removed the correct lid, it was allowed to eat the food the cylinder contained (1/6 soaked dog pellet), after which the apparatus was removed from the aviary and a new trial with two covered cylinders was again presented after an inter-trial interval of 60 s. If the bird chose the wrong coloured cylinder, the experimenter immediately intervened and removed the two cylinders before the bird had a chance to try the second one, a new trial being started again after a 60 s interval. The location of the rewarded cylinder was switched at each trial. As a measure of discrimination colour-learning performance, we used the number of trials needed by each bird to visit (i.e. flip the lid and feed) the rewarded (initially not preferred) colour seven times in succession. We also measured the time between the introduction of the apparatus in the cage and the opening of one of the cylinders and averaged it over the total number of trials before success to estimate the average time before colour choice. Discrimination colour-learning was measured on the fourth or fifth day of captivity, after the stick-pulling trials.

Analyses

Effects of shyness, neophobia and body condition on time variables and numbers of trials to success in the three tasks

For each cognitive variable (i.e. trials to success for lid removal, stick-pulling and discrimination learning, average time spent interacting with the task for lid removal and stick-

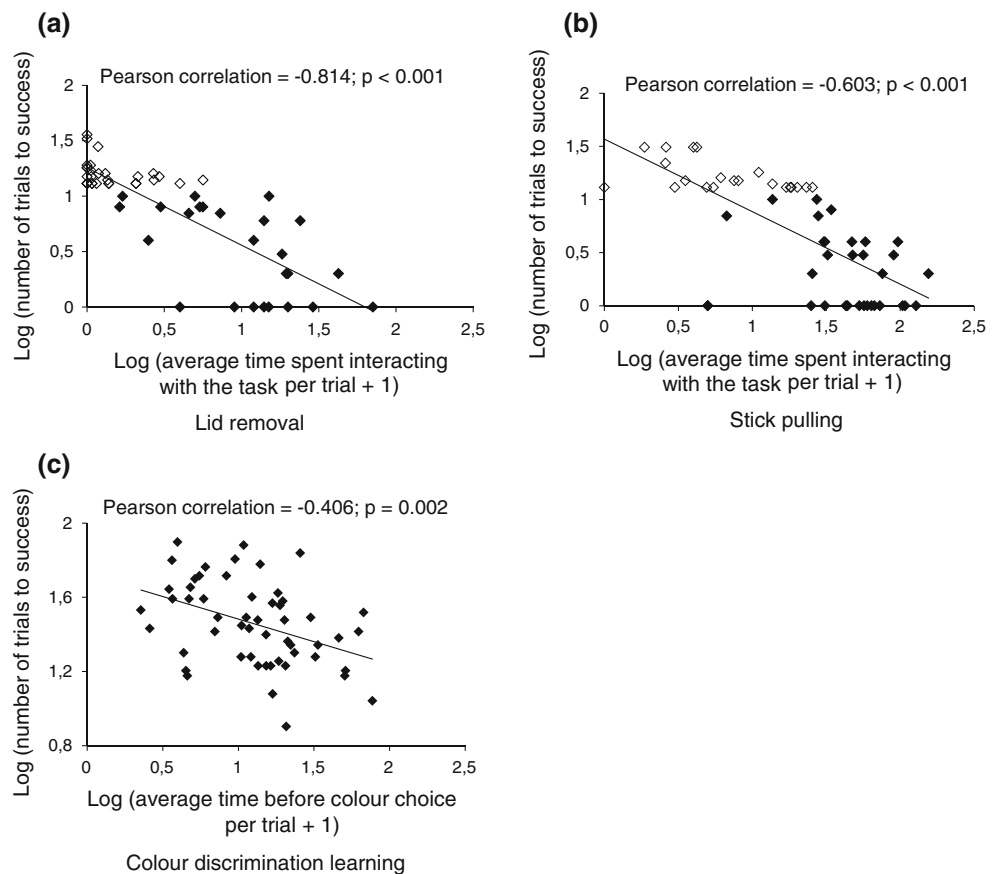
pulling, average time before choosing a colour at discrimination learning), we built a GLM model with the cognitive score as response variable, and shyness, neophobia, as well as body condition, sex and year (2012 or 2013, considered as a random effect) as explanatory variables. Latency to feed after disturbance (measured on day 2) was used as an estimate of initial shyness. In addition, we measured the shyness before all cognitive tests as latency to feed after a disturbance and included it in the models. We then selected the best model using backward selection. Only variables with $p < 0.05$ were kept in the final models.

Correlations between time variables and number of trials before success

We used Pearson correlations to test for associations (1) between time variables and number of trials before success within each task, (2) among time variables at the three tasks and (3) among numbers of trials before success at the three tasks. Since inter-individual differences in shyness, neophobia or body condition could be associated with any of the tested correlations, we built linear models with one of the cognitive performances included as response variable, and the other as explanatory variable, and included as covariable any of the shyness, neophobia, sex or body condition variables found to significantly affect time or numbers of trials to success. The best model was selected using backward selection, and only variables with $p < 0.05$ were kept in the final model. The time variables and the number of trials to success at the three tasks were log-transformed to achieve normality and homoscedasticity.

Finally, we carried out a canonical correlation analysis (CCA) to test for a general association between the birds’ responses to the discrimination-learning task on one side and problem-solving tasks on the other. CCA determines whether two sets of variables (i.e. the variables describing birds’ behaviour during discrimination-learning tasks, number of trials before success and average time before choosing a colour, and the variables describing birds’ behaviour during problem-solving tasks, number of trials before success and average time spent interacting with the task at obstacle removal and stick-pulling tasks) are related. This analysis creates pairs of canonical variates that explain the relationship between the two sets of variables. For each pair of canonical variates, we can then determine the contribution of each variable to the opposite canonical variate. Thus, we can determine the strength and direction of relationships between each variable and the opposite set of variables (Tabachnik and Fidell 2012). All dependent variables were normally distributed after log-transformation. All analyses were conducted using R 3.01.

Fig. 2 Relationships between the number of trials to success in the three tasks and the time spent interacting with the task (a, b) or the time before choosing a colour (c). Lines represent the linear regressions between each pair of variables. a, b Closed data points illustrate individuals successful within the 10 first trials; open data points illustrate individuals that were unsuccessful in the first 10 trials and hence shaped starting on the eleventh trial (see text for details). The average time spent interacting with the lid removal and stick-pulling tasks were calculated over the 10 first trials (see text for details)



Results

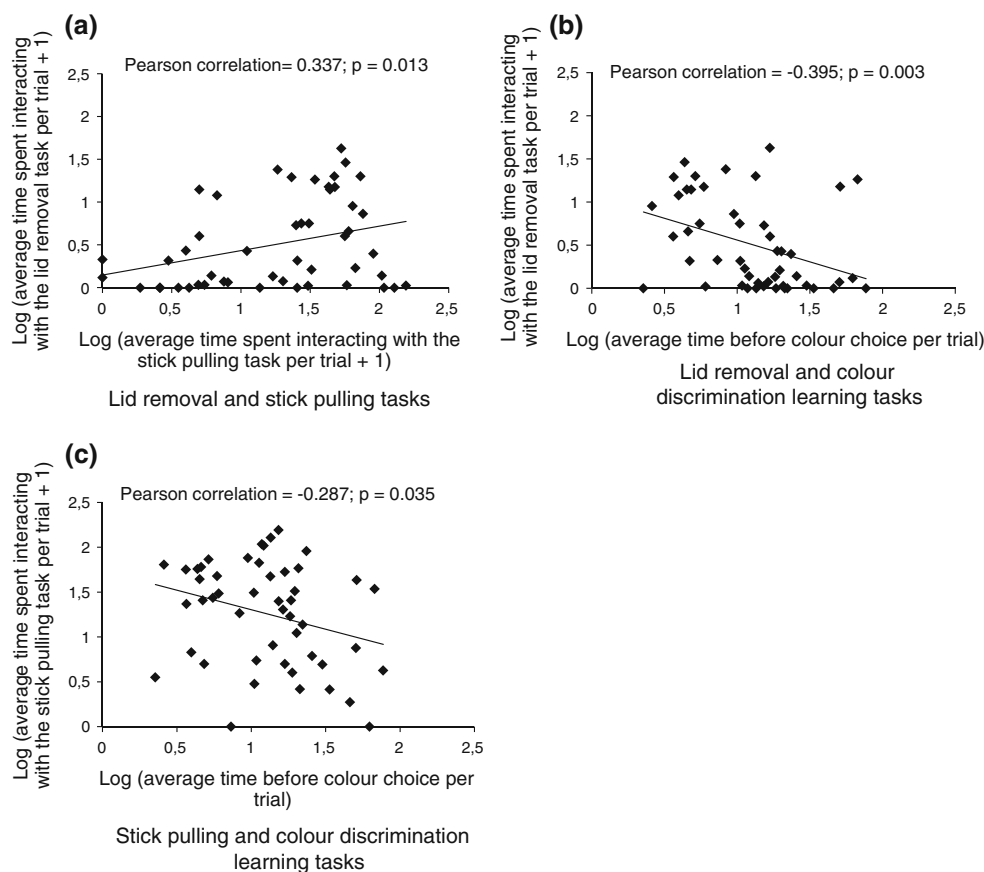
Twenty-one individuals needed shaping to succeed at the lid removal, and thirty at the stick-pulling task. We found that birds that solved the tasks faster spent more time interacting with them during each 5-min trial: the number of 5-min trials to success was negatively correlated with the average time per trial spent interacting with the lid removal (Pearson correlation = -0.814 ; $p < 0.001$, Fig. 2a) and stick-pulling tasks (Pearson correlation = -0.603 ; $p < 0.001$, Fig. 2b). For the discrimination task, we found that birds that are fast at choosing a colour make more errors than individuals that wait a longer time before choosing: the number of trials until the completion of seven consecutive successful learning trials was negatively correlated with the average time before colour choice (Pearson correlation = -0.406 ; $p = 0.002$, Fig. 2c).

As predicted, shyness was associated with problem-solving success and time spent interacting with the apparatus, but only for the first task, lid removal (trials to success: estimate = 0.298 ± 0.109 ; $t = 2.731$; $p = 0.009$; time spent interacting: estimate = -0.362 ± 0.156 ; $t = -2.326$; $p = 0.024$). Shyness was not significantly associated with either success or time in the stick-pulling or colour discrimination tasks, nor, somewhat surprisingly,

was neophobia associated with performance on any of the tasks (all $p > 0.312$). Body condition affected both the number of trials before success (estimate = 0.078 ± 0.038 ; $t = 2.075$; $p = 0.044$) and the time spent interacting with the apparatus (estimate = -0.150 ± 0.054 ; $t = -2.783$; $p = 0.008$) on the lid removal task, but not the stick-pulling or colour discrimination tasks. Despite these effects, the negative relationship between trials to success and time spent interacting with the lid removal task remained significant after taking into account shyness and body condition (Pearson correlation = -0.754 ; $p < 0.001$), using the residuals of the multiple regression of each of these two variables against shyness and body condition. None of the other explanatory variables affected the number of trials before success or the time interacting with the task at lid removal (all $p > 0.334$). None of the explanatory variables were associated with variables describing the birds' behaviour in the stick-pulling and colour discrimination tasks (all $p > 0.122$). Including the 2012 versus 2013 field season as a random variable did not improve any of the models (likelihood ratio tests: all $p > 0.432$).

If individuals behave consistently across tasks, we expected performance on the two problem-solving tasks to be positively correlated, both at the level of time spent

Fig. 3 Relationships between the time spent interacting with the lid removal and stick-pulling tasks (a), as well as the time before choice in the colour discrimination task (b, c). Lines represent the linear regressions between each pair of variables. The average time spent interacting with the lid removal and stick-pulling tasks were calculated over the 10 first trials only



interacting with the apparatus and trials to success. As predicted, individuals that spent more time interacting with the lid removal task also spent more time interacting with the stick-pulling task: the average time per trial spent interacting with the task was positively correlated between the stick-pulling and lid removal problems (Pearson correlation = 0.337; $p = 0.013$, Fig. 3a). This effect was still significant after considering the effects of shyness and body condition on the lid removal task (estimate = 0.318 ± 0.106 ; $t = 3.011$; $p = 0.004$). Similarly, the number of 5-min trials before success at the lid removal and stick-pulling tasks was positively correlated (Pearson correlation = 0.378; $p = 0.005$, Fig. 4a). This relationship was still significant after considering the effects of shyness and body condition on the lid removal task (estimate = 0.318 ± 0.106 ; $t = 3.011$; $p = 0.004$).

Under the speed-accuracy trade-off hypothesis, we expected birds that are slower at novel motor act performance to make fewer discrimination errors. Negative correlations were thus expected, first between the time spent interacting with problem-solving tasks and the time before colour choice, and second between the number of trials to success at problem-solving tasks and the number of trials to success at discrimination task. As expected, the average time before colour choice in the discrimination task was

negatively correlated with the average time spent interacting with the task for both the lid removal (Pearson correlation = -0.395 ; $p = 0.003$, Fig. 3b) and stick-pulling tasks (Pearson correlation = -0.287 ; $p = 0.035$, Fig. 3c). The relationship between the average time spent interacting with the lid removal task and the time before colour choice was still significant after considering the effects of shyness and body condition (estimate = -0.549 ± 0.163 ; $t = -3.367$; $p = 0.002$). Individuals that spent more time before choosing a colour thus also spent less time per trial interacting with the lid removal and stick-pulling tasks. We also found a negative correlation between the number of trials to success at the lid removal and learning tasks (Pearson correlation = -0.367 ; $p = 0.006$; Fig. 4b), a relationship that remained after taking the effects of shyness and body condition into account (estimate = -0.585 ± 0.256 ; $t = -2.286$; $p = 0.027$). Individuals that needed fewer trials to solve the lid removal task thus needed more trials to succeed at the colour-learning task. In contrast, the number of trials before success in the stick-pulling and colour-learning tasks were not significantly correlated (Pearson correlation = 0.196; $p = 0.179$, Fig. 4c).

In all these analyses, we considered the number of trials to success as a continuous variable. However, birds that

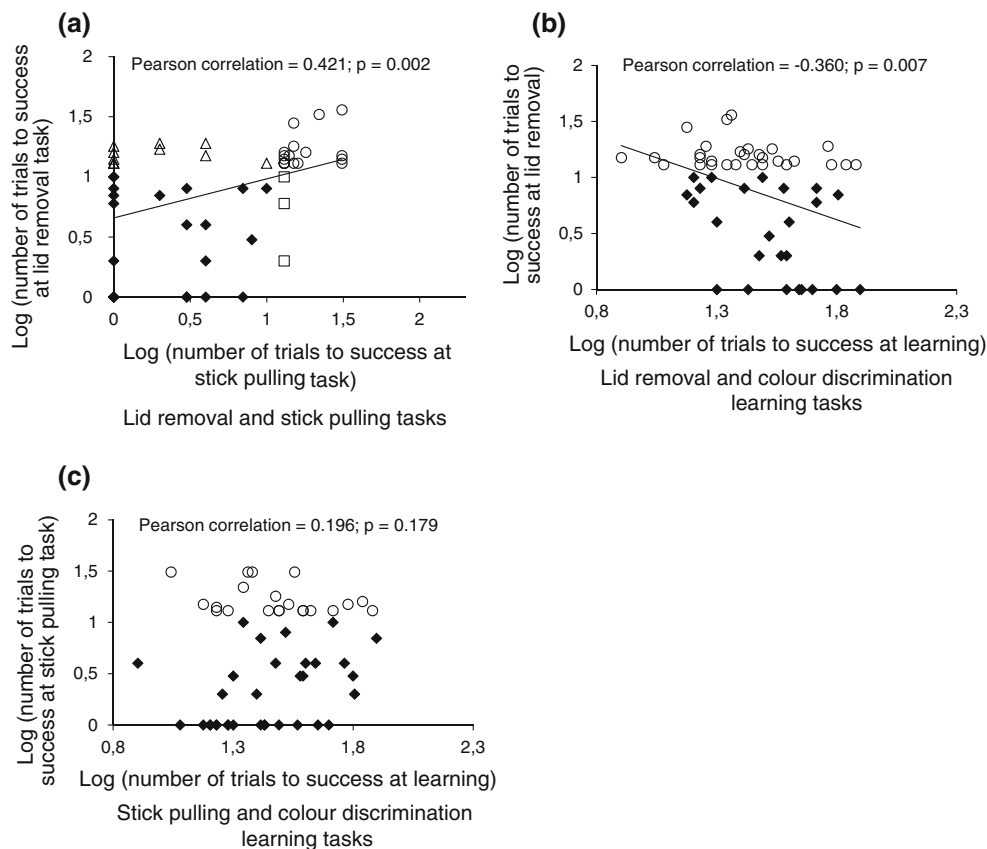


Fig. 4 Relationships between the number of trials to success at the lid removal, stick-pulling and colour discrimination tasks. *Lines* represent the linear regressions between each pair of variables. **a** *Closed diamonds* illustrate individuals successful at both the lid removal and stick-pulling tasks within the 10 first trials, *open triangles* illustrate individuals successful at the stick-pulling, but not the lid removal task within the 10 first trials, *open squares* illustrate individuals successful at the lid removal, but not the stick-pulling tasks within the 10 first trials, and *open circles* illustrate individuals

unsuccessful at both the lid removal and stick-pulling tasks within the 10 first trials. **b** *Closed diamonds* illustrate individuals successful within the 10 first trials at the lid removal task; *open circles* illustrate individuals unsuccessful after 10 trials and thus shaped from the eleventh trial on (see text for details). **c** *Closed diamonds* illustrate individuals successful within the 10 first trials at the stick-pulling task; *open circles* illustrate individuals unsuccessful after 10 trials and thus shaped from the eleventh trial on (see text for details)

needed more than 10 trials to succeed in the lid removal and stick-pulling tasks were shaped after their tenth unsuccessful trial (as illustrated by the open and closed data points in Fig. 2a, b). We thus redid the analyses, comparing individuals that were successful within the first 10 trials and individuals that were not (and thus shaped starting on trial 11). Comparisons of these two groups yielded the same results as the continuous GLM models presented above (see Supplementary Material 2), with the sole exception that successful and unsuccessful individuals at the lid removal task did not differ significantly in the numbers of trials to success at discrimination colour-learning (Wilcoxon test: $p = 0.120$).

Finally, we conducted a CCA to test for a general association between birds' behaviour at discrimination learning and at problem-solving. The two canonical correlations were 0.42 and 0.39 and were both statistically significant ($p = 0.023$ and 0.042 ; see Supplementary

Material 3 (SM3) for details). The first canonical axis was most strongly influenced by a negative correlation between the number of trials to success at stick-pulling and the time before choosing a colour at discrimination learning (SM3). The second canonical axis was positively correlated with the number of trials to success at obstacle removal, and negatively with the number of trials to success at discrimination learning (SM3). These results confirm that individuals that are slower at solving problems (and interact less with the problem-solving tasks) are the same ones who are taking a long time to choose a colour and also make fewer errors at discrimination learning.

Discussion

Taken together, our results support the idea that 'fast' versus 'slow' cognitive strategies underlie differences in

performance across cognitive challenges (Sih and Del Giudice 2012). We found that latency to solve two obstacle removal problems was positively correlated in a sample of 49 wild-caught Carib grackles, but that performance on these obstacle removal problems was negatively correlated with trials to criterion in a colour discrimination task. These results suggest that the production of novel motor acts in the lid removal and stick-pulling tasks tap into the same processes, but that colour discrimination learning depends on different mechanisms. Despite this difference, the time invested by individuals in each of the three tasks suggests a consistent strategy: grackles that waited longer before choosing a colour in the discrimination task made fewer errors and thus reached the learning criterion faster, but these individuals in turn spent less time per trial interacting with the two obstacle removal problems and thus solved them later. Variation between individuals appeared to be linear (see figures), suggesting the existence of a continuum rather than discrete cognitive styles. Nonetheless, separating individuals into two groups according to whether or not they needed shaping at the problem-solving tasks yielded results that were very similar to the linear approach.

When several cognitive measures are taken on a set of animals, results vary from positive correlations across tests to negative ones to non-significant ones. Features of the tests can have a strong influence on these results. In our case, the two problem-solving tasks featured similar sensory and motor requirements: focusing away from the part of the apparatus where food was visible and using the beak to interact with another part of the apparatus that gave motor feedback by moving. Overington et al. (2011) showed in Carib grackles that the initial attempts to solve an obstacle removal task involve a series of pecks at the transparent part of the container in the area where the food is visible. It is only after repeated failure of these pecks that grackles peck elsewhere and discover the part of the apparatus that moves and can eventually be removed. It is the increasing focus on the moving part of the task that distinguishes grackle solvers from non-solvers in Overington et al.'s study. The same motor patterns are required in our study, and the fastest solvers are the ones that spend more time interacting with the apparatus. In the colour discrimination task, birds do not have to switch from motor acts directed at visible food to those directed at moving parts of the apparatus. They have had extensive training at fast (within 2 s) and errorless (on six consecutive trials) lid-flipping, and there is no visible food to attract inefficient pecks. The only thing to learn is the colour that identifies cylinders with food. It is here that individuals that spent less time interacting with the lid removal and stick-pulling tasks and solved them later (and/or needed shaping on them) are more accurate and make fewer discrimination

errors. In tasks where a hungry individual tries to find a novel motor route to food, standing back and waiting are associated with reduced success. In a task where the motor route to food is known and only errors in choosing the correct colour produce a delay in feeding, the slower birds in the problem-solving tasks have a higher discrimination success.

Shyness and neophobia are known to strongly affect individual responses to cognitive challenges (Sih and Del Giudice 2012; Sol et al. 2012). Here, we found that shyness only affected an individual's behaviour and performance in the first task we presented, the lid removal task: shy individuals spent less time interacting with the task and needed more trials to solve it. This effect is consistent with the expectation that shy individuals will adopt a slow behavioural strategy (Sih and del Giudice 2012), thus interacting less with the task and solving it later. The absence of a neophobia effect on any of our tasks seems surprising, as this trait is expected to affect cognitive performance (Greenberg and Mettke-Hofmann 2001) and has been shown to do so in a previous study involving Carib grackle problem-solving (Overington et al. 2011; Webster and Lefebvre 2001). This could be because we measured neophobia here as the difference between the latency to feed with and without a new object, in order to eliminate any shyness (which should slow approach to both conditions) effect from our estimate. In contrast, Overington et al. (2011) used only the latency to feed next to the novel object. The fact that the effect of shyness does not extend to the stick-pulling and colour discrimination tasks might be a consequence of habituation to the captivity and testing conditions, as these two tests were performed after the lid removal test on the fourth and fifth days following capture. Similarly, body condition (as measured on the day of capture) only affected behaviour and performance at the lid removal task, as body condition differences between birds in the wild are expected to decrease in captivity due to abundant feeding. Individuals in poorer condition spent more time interacting with the lid removal task and succeeded faster, which is conceivably tied to the fact that individuals in poorer condition are expected to take more risks to obtain food rewards. This evidence for habituation to captivity suggests that counterbalancing test order might have produced the spurious negative correlations between tasks identified by Bell (2013) and Guy Beauchamp (personal communication). The negative relationship we did find between performance on the problem-solving and colour discrimination tasks is all the more convincing given that the constant task order we gave all birds carries a risk of producing a spurious positive one.

Sih and Del Giudice (2012) have proposed that the trade-off between speed and accuracy might interact with individual differences in impulsivity, persistence and risk

or loss aversion to affect performance on cognitive problems. Our results are a first step in supporting this view (see also Griffin et al. 2013) and suggest that beyond the correlations, positive or negative, in performance measures on cognitive tests, individual differences in the way animals approach problems and respond to the costs of different errors are crucial. The literature on both humans (Tom et al. 2007) and non-humans (e.g. Lakshminaryanan et al. 2008) suggests that the benefit of a success is not valued along the same scale as the cost of an error. Individuals might respond in different ways to this asymmetry, with some being more cautious and focused on accuracy, while others favouring speed. The inevitable trade-off between the two extremes might be one of the factors that maintain variation between individuals, which might otherwise be puzzling in a theoretical context where abilities are always thought to be maximised.

Our results suggest that considering variation in performance at cognitive tasks in terms of cognitive strategy rather than cognitive ability per se might bring new insights into how variation in cognition is generated and maintained. Indeed, as pointed out by Chittka et al. (2009), during cognition experiments, animals are interested in getting the reward, but not necessarily in being good at the task. Similarly, when confronted with cognitive challenges in the wild, individuals are expected to adopt optimal strategies with regards to their phenotype and environment rather than excel at the task they are exposed to. We may thus expect individuals to be selected for their cognitive strategy in a given biotic and abiotic context as opposed to their cognitive abilities per se. In this framework, there is a need to better understand whether the variation in cognitive strategies evidenced in this study has a genetic basis and could thus be the target of natural selection, or whether it is mainly determined by environmental factors such as developmental conditions, or by individuals' experience.

Recently, Réale et al. (2010) proposed to incorporate behavioural strategies within the classical 'pace-of-life-syndrome', which originates from the concept of *r* and *K* selection (MacArthur and Wilson 1967; Pianka 1970; Reznick et al. 2002). Relying on empirical and theoretical data, they hypothesise that the slow–fast continuum (or reactive–proactive continuum, Koolhaas et al. 1999; Sih et al. 2004) characterising behavioural syndromes is part of the 'pace of life syndrome', where, for instance, bolder, more aggressive and more explorative individuals also reproduce faster and have shorter development time and shorter lifetime (Réale et al. 2010). Combining the views of Réale et al. (2010) and Sih and del Giudice (2012), we may expect variation in cognitive strategies to be associated with life history strategies, slow and accurate individuals eventually evolving slow life history strategies, and conversely. Adopting a more integrated approach, including

detailed studies of (genetic) covariances between cognitive, behavioural and life history traits might help us understand the constraints and adaptive mechanisms affecting cognition evolution.

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References

- Abraham NM, Spors H, Carleton A, Margrie TW, Kuner T, Schaefer AR (2004) Maintaining accuracy at the expense of speed: stimulus similarity defines odor discrimination time in mice. *Neuron* 44:865–876. doi:10.1016/j.neuron.2004.11.017
- Amici F, Barney B, Johnson VE, Call J, Aureli F (2012) A modular mind? A test using individual data from seven primate species. *PLoS ONE* 7(12):e51918
- Banerjee K, Chabris CF, Johnson VE, Lee JJ, Tsao F, Hauser MD (2009) General intelligence in another primate: individual differences across cognitive task performance in a New World monkey (*Saguinus oedipus*). *PLoS ONE* 4:e5883
- Bell A (2013) Randomized or fixed order for studies of behavioral syndromes? *Behav Ecol* 24:16–20. doi:10.1093/beheco/ars148
- Boogert NJ, Giraldeau LA, Lefebvre L (2008a) Song complexity correlates with learning ability in zebra finch males. *Anim Behav* 76:1735–1741. doi:10.1016/j.anbehav.2008.08.009
- Boogert NJ, Reader SM, Hoppitt W, Laland KN (2008b) The origin and spread of innovations in starlings. *Anim Behav* 75:1509–1518
- Boogert NJ, Anderson RC, Peters S, Searcy WA, Nowicki S (2011) Song repertoire size in male song sparrows correlates with detour reaching, but not with other cognitive measures. *Anim Behav* 81:1209–1216. doi:10.1016/j.anbehav.2011.03.004
- Both C, Dingemanse NJ, Drent PJ, Tinbergen JM (2005) Pairs of extreme avian personalities have highest reproductive success. *J Anim Ecol* 74:667–674. doi:10.1111/j.1365-2656.2005.00962x
- Bouchard J, Goodyer W, Lefebvre L (2007) Social learning and innovation are positively correlated in pigeons (*Columba livia*). *Anim Cogn* 10:259–266
- Burns JG, Rodd FH (2008) Hastiness, brain size and predation regime affect the performance of wild guppies in a spatial memory task. *Anim Behav* 76:911–922. doi:10.1016/j.anbehav.2008.02.017
- Burns JG, Foucaud J, Mery F (2011) Costs of memory: lessons from 'mini' brains. *Proc R Soc B* 278:923–929. doi:10.1098/rspb.2010.2488
- Chittka L, Dyer AG, Dornhaus A (2003) Bees trade off foraging speed for accuracy. *Nature* 424:388
- Chittka L, Skorupski P, Raine NE (2009) Speed–accuracy trade-offs in animal decision making. *Trends Ecol Evol* 24:400–407. doi:10.1016/j.tree.2009.02.010
- Cole EF, Morand-Ferron J, Hinks A, Quinn JL (2012) Cognitive ability influences reproductive life history variation in the wild. *Curr Biol* 22:1808–1812
- Deaner RO, van Schaik CP, Johnson VE (2006) Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. *Evol Psychol* 4:149–196
- Dingemanse NJ, de Goede P (2004) The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behav Ecol* 15:1023–1030. doi:10.1093/beheco/arh115

- Dingemanse NJ, Both C, van Noordwijk AJ, Rutten AL, Drent PL (2003) Natal dispersal and personalities in great tits (*Parus major*). *Proc R Soc B* 270:741–747. doi:10.1098/rspb.2002.2300
- Dingemanse NJ, Both C, Drent PJ, Tinbergen JM (2004) Fitness consequences of avian personalities in a fluctuating environment. *Proc R Soc B* 271:847–852
- Drent PJ, van Oers K, van Noordwijk AJ (2003) Realized heritability of personalities in the great tit (*Parus major*). *Proc R Soc B* 270:45–51
- Dukas R (1999) Cost of memory: ideas and predictions. *J Theor Biol* 197:41–50
- Exnerová A, Svádová KH, Fucíková E, Drent PJ, Stys P (2010) Personality matters: individual variation in reactions of naive bird predators to aposematic prey. *Proc R Soc B* 277:723–728. doi:10.1086/285892
- Farrell TM, Weaver K, An YS, MacDougall-Shackleton SA (2011) Song bout length is indicative of spatial learning in European starlings. *Behav Ecol* 23:101–111. doi:10.1093/beheco/arr162
- Franks NR, Dornhaus A, Fitwsimmons JP, Stevens M (2003) Speed versus accuracy in collective decision making. *Proc R Soc B* 270:2457–2463. doi:10.1098/rspb.2003.2527
- Greenberg R, Mettke-Hofmann C (2001) Ecological aspects of neophobia and neophilia in birds. *Curr Ornithol* 16:119–178
- Griffin AS, Galef BG (2005) Social learning about predators: does timing matter? *Anim Behav* 69:669–678. doi:10.1016/j.anbehav.2004.02.020
- Griffin AS, Guez D, Lermite F, Patience M (2013) Tracking changing environments: innovators are fast, but not flexible learners. *PLoS ONE* 8:e84907. doi:10.1371/journal.pone.0084907
- Guillette LM, Reddon AR, Hoeschele M, Sturdy CB (2011) Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. *Proc R Soc B* 278:767–773. doi:10.1098/rspb.2010.1669
- Isler K, Van Schaik CP (2009) The expensive brain: a framework for explaining evolutionary changes in brain size. *J Hum Evol* 57:392–400
- Keagy J, Savard JF, Borgia G (2009) Male satin bowerbird problem-solving ability predicts mating success. *Anim Behav* 78:809–817. doi:10.1016/j.anbehav.2009.07.011
- Keagy J, Savard JF, Borgia G (2011) Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds *Ptilonorhynchus violaceus*. *Anim Behav* 81:1063–1070. doi:10.1016/j.anbehav.2011.02.018
- Kolss M, Kawecki TJ (2008) Reduced learning ability as a consequence of evolutionary adaptation to nutritional stress in *Drosophila melanogaster*. *Ecol Entomol* 33:583–588
- Koolhaas JM, Korte SM, de Boer SF, van Dervegt BJ, van Reenen CG, Hopster H, de Jong IC, Ruis MAW, Blokhuis HJ (1999) Coping style in animals: current status in behavior and stress-physiology. *Neurosci Biobehav Rev* 23:925–935
- Kotschal A, Rogell B, Bundsen A, Svensson B, Zajitschek S, Brännström I, Immler S, Maklakov AA, Kolm N (2013) Artificial selection on relative brain size in the guppy reveals costs and benefits of evolving a larger brain. *Curr Biol* 23:1–4
- Lakshminaryanan V, Chen MK, Santos LR (2008) Endowment effect in capuchin monkeys. *Philos Trans R Soc B* 363:3837–3844. doi:10.1098/rstb.20080149
- Laughlin SB, de Ryuter van Steveninck RR, Anderson JC (1998) The metabolic cost of neural information. *Nat Neurosci* 1:36–40
- Locurto C, Fortin E, Sullivan R (2003) The structure of individual differences in heterogeneous stock mice across problem types and motivational systems. *Genes Brain Behav* 2:40–55
- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton
- Matzel LD, Han YR, Grossman H, Karnik MS, Patel D, Scott N, Specht SM, Gandhi CC (2003) Individual differences in the expression of a “general” learning ability in mice. *J Neurosci* 23:6423–6433
- Mery F, Kawecki TJ (2003) A fitness cost of learning ability in *Drosophila melanogaster*. *Proc R Soc B* 270:2465–2469. doi:10.1098/rspb.2003.2548
- Morand-Ferron J, Lefebvre L, Sol D, Reader SM, Elvin S (2004) Dunking behaviour in Carib grackles. *Anim Behav* 68:1267–1274
- Overington SE, Cauchard L, Côté KA, Lefebvre L (2011) Innovative foraging behavior in birds: what characterizes and innovator? *Behav Proc* 87:274–285
- Pianka ER (1970) On r- and K-selection. *Am Nat* 104:592–597
- Reader SM, Hager Y, Laland KN (2011) The evolution of primate general and cultural intelligence. *Philos Trans R Soc B* 366:1017–1027
- Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio PO (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos Trans R Soc B* 365:4051–4063. doi:10.1098/rstb.20100208
- Reznick D, Bryant MJ, Bashey F (2002) r- and K selection revisited: the role of population regulation in life history evolution. *Ecology* 83:1509–1520. doi:10.1890/0012-9658(2002)083[1509:RAKSRT]2.0.CO;2
- Seferta A, Guay PJ, Marzinotto E, Lefebvre L (2001) Learning differences between feral pigeons and zenaida doves: the role of neophobia and human proximity. *Ethology* 107:281–293
- Seibt U, Wickler W (2006) Individuality in problem solving: string pulling in two *Carduelis* species (Aves: Passeriformes). *Ethology* 112:493–502
- Sewall KB, Peters S, Nowicki S (2013) Potential trade-off between vocal ornamentation and spatial ability in a songbird. *Biol Lett* 9:20130344. doi:10.1098/rsb.12013.0344
- Shettleworth SJ (2010) Cognition, evolution, and behaviour, 2nd edn. Oxford University Press, Oxford
- Sih A, del Giudice M (2012) Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philos Trans R Soc B* 367:2762–2772. doi:10.1098/rstb.20120216
- Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol* 19:372–378. doi:10.1016/j.tree.200404.009
- Sol D, Griffin A, Bartomeus I (2012) Innovative behaviours in invasive common mynas: creativity, motivation or emotional responses? *Anim Behav* 83:179–188
- Tabachnik BG, Fidell LS (2012) Using multivariate statistics, 6th edn. Pearson, Boston
- Titulaer M, van Oers K, Naguib M (2012) Personality affects learning performance in difficult tasks in a sex-dependent way. *Anim Behav* 83:723–730
- Tom SM, Fox CR, Trepel C, Poldrack RA (2007) The neural basis of loss aversion in decision-making under risk. *Science* 315:515–518. doi:10.1126/science.1134239
- Van Oers K, Drent PJ, Dingemanse NJ, Kempenaers B (2008) Personality is associated with extra pair paternity in great tits *Parus major*. *Anim Behav* 76:555–563. doi:10.1016/j.anbehav.2008.03.011
- Verbeek MEM, Drent PJ, Wiepkema PR (1994) Consistent individual differences in early exploratory behaviour of male great tits. *Anim Behav* 48:113–1121. doi:10.1006/ambe.1994.1344
- Webster S, Lefebvre L (2001) Problem-solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Anim Behav* 62:23–32
- Wickelgren WA (1977) Speed–accuracy trade off and information-processing dynamics. *Acta Psychol* 41:67–85. doi:10.1016/0001-6918(77)90012-9