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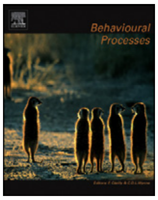

Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*

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ABSTRACT

Individual variation in exploratory behaviour has been demonstrated in a diverse array of animal species. Understanding the evolutionary antecedents and ecological consequences of this variation is an active research area within animal behaviour. Here we investigate whether different exploration styles exhibited by black-capped chickadees (*Poecile atricapillus*) in a novel environment are related to how quickly these birds learn an acoustic discrimination task. We found that birds that readily enter a novel environment learn an acoustic discrimination task faster than birds that do not readily enter a novel environment. This result contrasts with previous work suggesting no correlation between exploration style and learning a spatial or associative task in great tits (*Parus major*), a close relative of the black-capped chickadee.

Darwin wrote about emotion in human and nonhuman animals as early as 1872 (Wilson, 2005). The experimental study of individual differences in animal temperament, and how temperament interacts with learning, dates back at least to Pavlov's work with conditioned reflexes in dogs (1927). In another classic early study, Hall (1934) measured the defecation and urination rate of rats in an open field to assess individual differences in emotionality, and validated his findings with behavioural assays involving eating in a novel setting. In addition to studying individual differences in emotionality, open field studies have also been used to assess related personality traits such as fearfulness and exploration (Gosling, 2001). With these and other historical accounts of personality, there is a continuing, and perhaps growing, interest in the study of personality traits in nonhuman animals (for a thorough review see Gosling, 2001).

To date, individual variation in exploratory behaviour represents one of the best-studied personality characteristics in nonhuman animals (e.g., Verbeek et al., 1994; Sih et al., 2004a,b; Dingemanse and Réale, 2005; Groothuis and Carere, 2005; Réale et al., 2007; Sih and Bell, 2008). Individual variation in this trait may represent a life-history strategy trade off between growth and mortality maintained by frequency- or habitat-dependent selection (Wilson et al., 1994; Stamps, 2007; Biro and Stamps, 2008; Wolf et al., 2007, 2008). If exploration is a component of a broader life-history strategy, then we ought to find correlations with individual variation in other behavioural and physiological traits at the population level, such as the observation that faster explorers also tend to be bolder and more aggressive (a behavioural syndrome *sensu* Sih et al., 2004a).

The relationship between personality characteristics and individual variation in cognitive ability has received limited attention in animals (Koolhaas et al., 1999; Moreira et al., 2004; Øverli et al., 2007; Sih and Bell, 2008). However, exploratory style is one personality characteristic that is related to learning speed in specific tasks. This relationship is supported by evidence from several, diverse species and learning tasks. Sneddon (2003) found that rainbow trout which are more willing to venture into an unprotected open area acquired a classical conditioning task more quickly than shyer trout. Guppies that are more willing to inspect predators, an index of boldness, learn associative tasks faster than guppies that are less willing to inspect predators (Dugatkin and Alfieri, 2003). Rhesus macaques that avoid novel food in their home environment are more difficult to train to perform instrumental learning tasks like retrieving food from an experimenter for positive reinforcement or learning to touch a goal object for a food reward (Coleman et al., 2005). Similarly, trait anxiety may reduce cognitive performance in nonhuman primates in certain tasks (Toxopeus et al., 2005). Finally, fast and slow exploring great tits do not differ significantly in their speed of acquisition in either associative learning or spatial memory tasks, although fast explorers demonstrated better retention (unpublished data cited in: Groothuis and Carere, 2005).

Great tits (*Parus major*) are one of the best-studied models of animal personality. Wild-caught, hand-reared, male great tits

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show consistent individual differences in exploratory behaviour, approach to a novel object, aggression, and dominance behaviour (Verbeek et al., 1994, 1996, 1999). Birds that explored a novel environment, or approached a novel object more readily were also more likely to return to a location where food had previously been available, while birds that were slow to explore a novel environment or approach a novel object altered their foraging habits more rapidly when food locations varied (Verbeek et al., 1994). Field work has expanded these findings in natural populations (e.g., Dingemanse et al., 2004) demonstrating that personality may influence individual fitness through mate choice, extrapair behaviour (Van Oers et al., 2008), natal dispersal (Dingemanse et al., 2003), and nest defence (Hollander et al., 2008).

All studies, of which we are aware, that have explicitly examined the relationship between learning ability and personality characteristics involve either associative (i.e., classical or Pavlovian conditioning) or spatial memory tasks (but see Coleman et al., 2005). Here we investigate the relationship between individual variation in exploratory behaviour and the acquisition of an instrumental note-type discrimination task in wild-caught black-capped chickadees (*Poecile atricapillus*), a North-American relative of the great tit. Our instrumental conditioning paradigm requires animals to respond to S+ (rewarded) stimuli and withhold responding to S− (non-rewarded) stimuli belonging to different note-type categories from their namesake *chick-a-dee* call. The goal of the present study is to examine the association between an individual's learning speed and their exploratory behaviour in a novel environment.

1. Methods

1.1. Subjects

Twenty-four adult black-capped chickadees were trained in an acoustic discrimination task in 2007 or 2008. Nineteen of these birds (12 males, 7 females) were captured from sites around Edmonton, Alberta (53°30′N, 113°W) in 2006 and 2007. The remaining birds (1 male, 4 females) were captured in Alberta at the Barrier Lake Field Station (51°02′N, 115°03′W) in 2004 and 2006. Of the initial 24 birds, 22 birds were available to test in the novel environment task. All birds were adults when captured and were naïve to all experimental procedures. Sex was determined by DNA analysis.

1.2. Apparatus

A detailed description of the instrumental discrimination apparatus can be found in Sturdy and Weisman (2006). In brief, birds lived and worked in a modified budgerigar cage (30 cm × 40 cm × 40 cm) that had several perches, grit cup, cuttle bone, water tube, an opening in one side to allow access to the food hopper and plastic mesh suspended from the bottom so that birds could not eat spilled food. A request perch with an infrared beam was situated 5 cm from the opening to the food hopper; another infrared beam spanned the entrance to the food hopper. A speaker which broadcast stimuli was at perch height next to the food hopper on the outside of the cage. This apparatus was housed in a ventilated sound attenuating chamber.

The novel environment room (3.15 m × 2.0 m × 2.87 m) housed five artificial trees. The artificial trees consisted of a 2 cm × 2 cm 'trunk' that was 1.4 m high. There were four 1 cm diameter 'branches' that extended 20 cm from the trunk. Two upper branches were 5 cm from the top of the trunk, and other two branches were 20 cm lower and perpendicular to the top branches (following Verbeek et al., 1994). In one corner of the room was a false wall with a 35 cm × 24 cm opening behind which the bird is placed in home cage (30 cm × 40 cm × 40 cm). Each session was recorded via a wireless camera so behavioural data could be scored at a later date.

1.3. Stimulus preparation

A detailed description of stimulus preparation can be found in Charrier et al. (2005). Briefly, notes were taken from high-quality recordings of black-capped chickadee *chick-a-dee* calls. Twenty exemplars each, of three note types (i.e., A, B, C) were recorded, one call per track, to a CDR for discriminative stimuli in the instrumental discrimination task.

1.4. Instrumental discrimination task

1.4.1. Nondifferential training

Once a bird had learned to use the request perch and food hopper to obtain food, nondifferential training began. To start a trial, a bird had to wait on the request perch, thus breaking an infrared beam, for a randomly selected interval of between 900 and 1100 ms. Following this, a note from the pool of 20 notes (10 each of two note types) was randomly selected from the pool and played (between about 70 and 80 dB SPL (A)). If the bird left the request perch before the note had finished playing, the trial terminated and a 30 s inter-trial interval (ITI) with the houselights off ensued (termed a zap). This was to train birds to remain on the perch and attend to each stimulus in its entirety before making a response. If the bird remained on the perch until the note was played in its entirety and then flew to the feeder within 1 s from the termination of the stimulus, it was given 1 s access to food followed by a 30 s ITI, with the houselights on. If the bird listened to the entire note, left the request perch within 1 s of stimulus termination but did not enter the feeder, the trial ended after 1 s. If the bird listened to the entire call note and remained on the request perch, the trial ended after 1 s and a 60 s ITI followed, with the houselights on. We used nondifferential training to train birds to create high, uniform, responding to all training stimuli that would be used in the initial acquisition phase of the experiment, and to train the birds to listen to each stimulus in its entirety while also training them to leave the request perch after each stimulus was played (see Charrier et al., 2005 for details). This step also ensured that birds approached all stimuli prior to discrimination training, thus eliminating any bias that neophobia may have imposed on initial acquisition performance. The criteria to complete nondifferential training was 6–500 trial blocks with over 60% responding to all stimuli, and no more that 3% difference in response to future S+ and S− exemplars.

1.4.2. Discrimination acquisition

For detailed description of acoustic discrimination and transfer training procedure refer to Charrier et al. (2005). In this phase, breaking the infrared beam in the food hopper after food-rewarded (S+) notes resulted in 1 s access to food whereas visits to the feeder following non-rewarded (S−) notes resulted in a 30 s ITI with the houselights extinguished and no food access. All other procedures from nondifferential training (e.g., random selection of notes, remaining on the perch until stimulus completion, etc.) remained in effect during discrimination training.

Discrimination training (i.e., acquisition) was initiated immediately following nondifferential training. Birds were trained on one of six discrimination tasks: birds learned to discriminate between either A and B notes (A S+ and B S− or A S− and B S+), B and C notes (B S+ and C S− or B S− and C S+) or A and C notes (A S+ and C S− or A S− and C S+) of the *chick-a-dee* call. In this way, we tested a more general ability of note type discrimination, to increase the generalizability of our findings, rather than focusing on one or two particular discriminations.