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Personality in captivity reflects personality in the wild

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To investigate the ecological significance of personality, researchers generally measure behavioural traits in captivity. Whether behaviour in captivity is analogous to behaviour in the wild, however, is seldom tested. We compared individual behaviour between captivity and the wild in blue tits, *Cyanistes caeruleus*. Over two winters, 125 blue tits were briefly brought into captivity to measure exploratory tendency and neophobia using variants of standard personality assays. Each was then released, fitted with a passive integrated transponder. Using an electronic monitoring system, we then recorded individuals' use of feeders as they foraged in the wild. We used variation in the discovery of new feeders to score 91 birds for exploratory tendency in the wild. At eight permanent feeding stations, 78 birds were assayed for neophobia in the wild. Behavioural variation in the captive personality trials was independent of permanent (e.g. sex) and nonpermanent (e.g. condition or weather) sources of between-individual variation at capture. Individual exploratory tendency and neophobia were consistent and repeatable in captivity, and analogous traits were repeatable in the wild; thus all constituted personality traits in the blue tit. Exploratory tendency and neophobia were not correlated with each other, in either the captive or the wild context. Therefore they are independent traits in blue tits, in contrast to many species. Finally, exploratory tendency and neophobia measured in captivity positively predicted the analogous traits measured in the wild. Reflecting differences in the use of feeding opportunities, personality in captivity therefore revealed relevant differences in foraging behaviour between individuals.

Confronted with the same environmental or behavioural stimuli, even within a homogeneous captive environment, individuals of the same species often differ markedly in their behaviour (Verbeek et al. 1996; Gosling 2001). Notable axes of variation are aggression (aggressive–passive; Huntingford 1976), activity (active–inactive; Sih et al. 1992), sociality (sociable–antisocial; Cote & Clobert 2007), exploratory tendency (fast–slow explorer; Verbeek et al. 1994) and risk responsiveness (risk-prone–risk-averse, neophobic–neophilic or bold–shy; Clark & Ehlinger 1987; Wilson et al. 1993; van Oers et al. 2004).Where differences in behaviour between individuals are stable across a range of situations or contexts, we refer to this variation as 'personality' (Gosling 2001). Heritability in personality traits (Dingemanse et al. 2002; Drent et al. 2003; van Oers et al. 2004) and differences in fitness or survival between personality types (Fraser et al. 2001; Dingemanse et al. 2004; Bell 2005) suggest that personality may reflect ecologically significant variation between individuals.

Few studies have measured personality in the wild (but see Coleman & Wilson 1998; Réale et al. 2000; Réale & Festa-Bianchet 2003; Briffa et al. 2008; Hollander et al. 2008). To investigate the ecological significance of personality, researchers generally measure behaviour in captivity and compare the distribution or fitness of individuals in the wild thereafter (Dingemanse et al. 2004; Bell 2005). Studying behaviour in captivity has numerous advantages, notably allowing researchers to control the conditions under which all individuals are tested (Campbell et al. 2009). However, classifying personality in captivity may be misleading for two reasons. First, behaviour changes as wild individuals adapt to the captive environment (Butler et al. 2006). Where there are systematic differences in the rate of acclimation between personality types, therefore, testing in captivity may exaggerate or even generate behavioural differences between personality types. For example, risk-averse or 'shy' individuals take longer to recover from handling or capture stress and also to eat in a novel environment

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than risk-prone or 'bold' individuals (Wilson et al. 1993; van Oers et al. 2004, 2005). As food is usually withdrawn prior to personality trials and often returned within trials to stimulate behaviour, residual stress, hunger or condition may then motivate shy but not bold individuals to a greater extent in captivity than in the wild. Therefore, it is important to test whether behavioural differences between personality types extend beyond the captive environment.

Second, classifying behaviour in captivity may be misleading because behaviour is often highly context specific. Isolation from the appropriate context may suppress or subvert personality traits in captivity. For example, studies carried out in captivity, in artificially constructed group dominance interactions, found an overall negative correlation between rank and exploratory tendency in great tits, *Parus major*, with fast explorers generally at the bottom of dominance hierarchies (Verbeek et al. 1999). However in the wild, this relationship is only negative between nonterritorial juvenile males, and in contests between territorial males on neutral ground, fast explorers dominate slow explorers (Dingemanse & De Goede 2004). Indeed, within their own territory, males were dominant regardless of personality, so the absence of a territorial context in captivity may limit our ability to predict the ecological significance of captive personality traits. Another important contextual difference may be social isolation in captivity, as numerous studies suggest individuals modify their risk-taking behaviour in relation to the presence and identity of conspecifics (van Oers et al. 2005; Boogert et al. 2006; Stöwe et al. 2006; Apfelbeck & Raess 2008; Pike et al. 2008). The relationship between different behavioural traits may also be context dependent. Bell & Sih (2007), for example found that aggression and risk taking in a predator-naïve population of sticklebacks, *Gasterosteus aculeatus*, were correlated only after exposure to a predator, suggesting that the absence of the predator–prey context affects captive personality trait estimates. Without comparing behaviour in captivity to behaviour in the wild, therefore, it is impossible to assess whether or indeed which personality traits directly contribute to fitness differences observed between personality types.

We investigated individual variation in exploratory tendency and neophobia (risk responsiveness towards novel objects) in a population of blue tits, *Cyanistes caeruleus*. To measure this variation, we used variants of two classic behavioural assays in captivity and developed versions of these for use in the wild: Verbeek et al.'s (1994) exploration test and Greenberg's (1983) novel object test. Verbeek et al.'s (1994) exploration test assigns exploratory tendency by movement in a novel captive environment. While it is difficult to quantify movement per se in the wild, we may compare the movement of individuals by their presence at certain targets. Dingemanse et al. (2003), for example, have used the distance between the origin and endpoint of postnatal dispersal as a measure of differences in dispersal behaviour in the great tit. Here, we used presence or absence at new feeding sites, introduced within a network of established feeding stations, as a measure of exploratory tendency during foraging. Greenberg's (1983) novel object test assigns 'neophobia', the aversion to the unfamiliar, by the latency to return to a known resource, for example a food bowl or nest site, in the presence of a novel object (see also van Oers et al. 2004, 2005). The novel object appears to generate a motivational conflict between the desire to obtain the resource and the desire to avoid any unknown risks associated with the novel object (Richard et al. 2008). This test is often used in the wild, where novel objects are introduced to familiar feeding sites, but usually for unmarked individuals (Webster & Lefebvre 2000, 2001; Echeverría et al. 2006). In variants of these established tests, exploratory tendency and neophobia in species from a variety of taxa are often, but not universally, correlated (Clark & Ehlinger 1987; Wilson et al. 1993; but see Coleman & Wilson 1998; Mettke-Hofmann et al. 2002). Our aims were threefold: first, to determine whether variation between individuals in these trials was repeatable, and hence whether exploratory tendency and neophobia constitute personality traits in the blue tit; second, as trait correlations may differ between contexts, to assess whether neophobia and exploratory tendency are themselves correlated in either captivity or the wild; and third, to compare exploratory tendency and neophobia measured in captivity with the analogous traits measured in the wild for the same, marked individuals.

METHODS

Studies were conducted between 2007 and 2009 in oak-dominated woodland on the east bank of Loch Lomond, U.K. (56°08′N, 4°37′W). In October 2007, we first established eight feeding stations at approximately 500 m intervals. These feeding stations were removed at the end of February 2008 and reinstalled in the same positions between October 2008 and February 2009. Each feeding station consisted of two tubular Defender feeders (35 cm height, 7 cm diameter) hung above one another from a bracket on an oak trunk, at approximately 2 m and 3 m above ground level, respectively. The feeders were stocked with peanut granules, and covered with a tube of grey laminated paper to disguise cues about the amount of food available. There was one small feeding hole, so only one bird could feed at a time. We attached a wooden rectangular perch (8 cm × 5 cm) under this hole, onto which we laid flat a rectangular metal hoop antenna (8 cm × 5 cm; Trovan, www.trovan.com). Between November and February, we captured birds as they approached the feeding stations, using mist nets. We mist-netted three times at each feeding station in the 2007–2008 season, and twice in the 2008–2009 season, generally between dawn and noon, to ensure equal disturbance at each site. We trapped 125 blue tits over this time (4–17 per site in 2007–2008, 2–10 per site in 2008–2009) for captive personality trait testing. On first capture, each bird was fitted with a unique passively integrated transponder ('PIT' tag; 11.5 mm × 2.1 mm, <0.1 g, Trovan Unique) attached to a plastic leg ring with Araldite glue (as in Macleod et al. 2005). The PIT tag weighs less than 1% of the body mass of a blue tit and hence is unlikely to affect individual behaviour. On entering the electromagnetic field generated within the antenna loop, the PIT tag produces an amplitude-modulated code signal. Using an electronic monitoring system (Trovan LID665) we were able to identify individual birds as they used the feeders, from which we derived our measures of personality traits in the wild. In 2007–2008, wild exploration trials were carried out between 1 and 28 February 2008 and wild neophobia trials between 19 December 2007 and 28 February 2008. In 2008–2009, both trials ran between 11 January and 28 February 2009. A total of 91 birds were detected at feeders in the wild: 61 in 2007–2008 and 30 in 2008–2009.

Personality Trials in Captivity

Birds arrived in captivity generally between 1000 and 1200 hours, within 15 min journey time from their capture site. They were housed indoors, at a temperature of 17 ± 1 °C and, to conduct all tests within the captive period while standardizing captive conditions across birds, we used a longer than natural 12:12 h light:dark regime. Each bird was housed individually in a cage measuring 150 × 50 cm and 50 cm high. Peanut granules, Haiths' Prosecto insectivorous mix and water were provided ad libitum, along with around 10 *Tenebrio molitor* and two *Galleria mellonella* larvae per day. All birds were observed eating within 10 min of arrival in captivity. They were then left undisturbed for a minimum of 2 h. An exploration trial was run after this period, followed by a further 1 h without disturbance. Neophobia trials ran between

1300 and 1700 hours on day 1 and were repeated between 0800 and 1100 hours on day 2. Following trials on day 2 in 2007–2008, we took a blood sample from the brachial vein of up to 110 μl, some of which was used for molecular sexing, and then released each bird at its site of capture at least 1 h before sunset. In 2008–2009, after blood sampling they were kept undisturbed in captivity for a further night, and released after a second exploration trial on the morning of day 3.

Exploratory Tendency in Captivity

The exploration trial was conducted within what would become the home cage of the focal bird. Each cage contained six perches, three in each half, that were covered with plastic plant vines to increase habitat complexity. The cage bottom was lined with white paper. On arrival into captivity, the bird was introduced to one side of the cage only, selected at random; the other was blocked off by an opaque metal divider. We anticipated that the 2 h in the cage prior to testing would create a 'familiar' and, behind the divider, a 'novel' environment. To assay exploratory tendency and not neophobia, the arrangement of plastic plants and perches was the same in each cage half, so that the novel environment was novel only in that it was unexplored. Prior to the trial, the food bowl and any spilt food were removed from the cage to motivate birds towards foraging activity. After 30 min, the water bowl was also removed. After a further 30 min, the observer removed the cage divider, stepped behind a screen, and observed the focal bird through a small hole for 10 min. Unlike other exploration trials (e.g. Verbeek et al. 1994), individuals had the option of remaining within the familiar environment. We allowed this option to help distinguish activity associated with exploration from activity associated with escape behaviours in the novel environment, as the birds had been in captivity for only a short period prior to testing (Mettke-Hofmann et al. 2009). A movement was defined as a hop or flight between two perches and/or the floor, the cage wall or the front and rear of the cage. The number of movements in each side of the cage was recorded, with the endpoint of each movement defining the side of the cage: novel or familiar. After the test, food and water were returned and the bird was allowed free access to the entire cage.

In 2008–2009, birds underwent a second exploration trial, on day 3. On arrival into captivity, birds were randomly allotted to a cage lined with either white paper (as in 2007–2008) or brown paper. The arrangement and size of perches and artificial plant material were similar between these cage types, but different leaf shapes were used in the brown- and white-lined cages. Our aim was to create two similar but distinct environments and, when we controlled for cage order and bird identity, there was no difference in activity (linear mixed-effects model, LME: $F_{1,43} = 0.01$, $P = 0.89$) or exploration ($F_{1,43} = 0.09$, $P = 0.63$) between brown- and white-lined cage types. Trials were conducted as in 2007–2008 for days 1 and 2. After collecting a blood sample on day 2 (when birds in 2007–2008 were released), we then moved each bird to one half of a new home cage, of the other cage type. They were left undisturbed until the following morning, when exploration trials began 1 h after the lights were switched on.

We accounted for differences in overall activity level between birds by deducting the number of movements in the familiar environment from the number in the novel environment. This residual activity in the novel environment from the first exploration trial was our measure of exploratory tendency. We used the number of movements in the trial rather than latency to enter the novel environment (as used in Verbeek et al. 1994) because here 56 birds entered then exited immediately as the divider was removed, and this appeared to reflect an escape or startle response towards the removal of the divider rather than exploration (K. Herborn, personal observation). To investigate whether activity in general or activity specifically in the novel environment then correlated with captive neophobia or with exploration in the wild, we conducted separate analyses using the total number of movements in the first exploration trial as a measure of activity during the captive exploration trial. Four birds were excluded from the first exploration trial because of accidental disturbance immediately prior to testing, and three (including one of the above) from the second exploration trial. Exploratory tendency (Shapiro–Wilks test: $W_{120} = 0.94$, $P < 0.0001$) and activity during the exploration trial ($W_{120} = 0.95$, $P < 0.0001$) were leptokurtic in their distributions.

Neophobia in Captivity

The neophobia trial had two phases: a novel object phase and a disturbance control phase. Each bird took part in one replicate of the neophobia trial on day 1 and another (with a different novel object) on day 2. Food and water were removed for 30 min prior to each phase. In the novel object phase, the observer then returned the food bowl with one of two novel objects placed inside. The objects were a luminous pink plastic frog and a half of a purple rubber ball, of similar size (approximately 4 cm diameter and 4 cm height). The latency to approach the familiar food bowl was recorded. The object was then removed and the water returned.

Independent of differences in response towards a novel object, individuals may also differ in their motivation to feed, or their response to disturbance by the observer returning the food bowl to the cage (van Oers et al. 2005). To control for this, we also measured latency to feed by the same procedure but without a novel object, returning the familiar food bowl only. This disturbance control phase was performed either 1 h before or 1 h after each novel object phase. The order of novel object and disturbance control phases was randomized on each day. One bird was excluded from one replicate of the disturbance control phase because of a disruption during the replicate. Of 79 birds, one bird did not approach within 10 min in either phase, and was excluded from analyses. A further three birds did not approach during the novel object phase, one bird during the disturbance control phase, nine birds in only one replicate of the novel object phase and three in only one replicate of the disturbance control phase. Birds that participated in both replicates performed consistently between day 1 and day 2 in disturbance control (LME with order of trials as a random effect: $F_{1,117} = 3.27$, $P < 0.0001$) and novel object phases ($F_{1,106} = 2.3$, $P < 0.0001$) so a mean was calculated per phase per individual. Birds that approached the food bowl in only one replicate of a phase were given the latency of that replicate rather than a mean.

Neophobia was defined as the latency to feed in the presence of a novel object. In the wild neophobia trials (see below), birds were not disturbed as the novel object was introduced, that is, pure neophobia was measured. Therefore, to discount the effect of disturbance from neophobia in captivity, we deducted mean latency in the control disturbance phase from mean latency in the novel object phase. Consequently, the four birds that did not approach in either replicate of one phase were also excluded from the analyses. Mean neophobia had a leptokurtic distribution (Shapiro–Wilks test: $W_{78} = 0.89$, $P < 0.0001$).

Between-individual Sources of Variation

To measure repeatability of behaviour in captivity accurately, and hence define personality traits, we must first identify covariance between behaviour and permanent (e.g. sex) or non-permanent (e.g. condition) differences between individuals that may also generate consistent individual differences in behaviour.

Permanent variables (that would not change within a field season) were wing length, age and sex. Wing length was used as a measure of overall body size; it was not measured in one bird. Age (juvenile/adult) was determined from plumage traits (Jenni & Winkler 1994); there were 67 juveniles and 58 adults. Sex was determined using a molecular technique from a blood sample taken at the end of day 2 in captivity (Arnold et al. 2007); there were 32 females and 86 males, and seven birds were not sexed. While dominance in Parids is highly context specific (Dingemanse & De Goede 2004), in general smaller, juvenile and female Parids are subordinate at feeders. As such, they may be more likely to take risks during foraging, and hence be faster to explore or less neophobic than larger birds, adults or males, respectively.

Nonpermanent variables were a combination of morphometric and environmental variables collated at capture. Morphometric measures reflecting an individual's current state were body mass and condition. Condition was calculated as the residual of body mass at capture regressed on tarsus length (Lindeń et al. 1992); a condition measure was not obtained in one bird. Environmental variables that would affect foraging opportunity immediately prior to entering captivity were daylength, rainfall (mm) and minimum and maximum temperature for the day of, and day prior to, capture. Weather data were collated from Meteorological Office records for Glasgow Bishopton (www.metoffice.gov.uk). Together, these variables may affect an individual's perceived starvation risk at capture, and hence may have short-term effects on individual behaviour in captivity.

Personality Trials in the Wild

Exploratory tendency in the wild

In the wild exploration trial, birds were scored for whether or not they discovered new feeders installed within the study site. In each of nine consecutive replicates in 2007–2008, and 16 consecutive replicates in 2008–2009, a new feeder was installed an average of 160 m (range 110–260 m) from one of the eight established feeding stations. To avoid influencing concurrent neophobia trials, it was located such that the two closest feeding stations were not currently under experimental manipulation. The feeder was positioned 1.5 m from the nearest mature oak on a pole 1.5 m high. The location was otherwise selected at random, but in 2008–2009 chosen such that each permanent feeding station was closest to the new feeder on two occasions during the season, about a month apart; an arrangement used in the calculation of repeatability of wild exploratory tendency (see Statistical methods). It was installed before sunrise, left undisturbed for 3 days, and then removed after sunset. We used PIT tag records from established feeding stations to deduce which individuals were identifiable (i.e. had not lost their PIT tags) in the wild during a replicate. As birds were added to the study as the season progressed, replication was uneven between individuals. For each replicate in which a bird participated, it was scored 0 or 1 for discovering the new feeder, from PIT tag records. Ninety-one birds were detected in the wild and were included in on average 10 replicates of this trial (range 2–16). Exploratory tendency was then defined by the number of new feeders an individual did discover relative to the number it could have discovered (i.e. the number of replicates in which it participated).

Difference in site coverage by individuals may have affected the probability that they discovered new feeders, so at the end of the field season we used PIT tag records to deduce which permanent feeders each bird had used. On average, birds used 1.8 of the eight permanent feeding stations (range 1–4). To account for differences in the distance birds would have to travel to discover each new feeder, we then calculated the distance between the nearest of these permanent feeders and the position of the new feeder in each replicate for each bird. These variables were included in the analyses of wild exploratory tendency (see Statistical methods).

Neophobia in the wild

In the wild neophobia trial, birds were scored for the latency to return to an established feeding station following introduction of a 'novel object': a colourful feeder cover, substituted for the familiar grey cover. Installed at least 3 months prior to the study, the eight 'familiar' feeding stations, each with two tubular feeders with grey covers, were analogous to the familiar food bowl in the captive trials. In 2007–2008, for 3 days prior to an experimental manipulation, we used PIT tag records to establish which individuals used and hence were familiar with the grey feeders at a given site. On the fourth day, between 1200 and 1630 hours (but on one occasion at 1830 hours), one of the grey covers was replaced with a coloured cover (blue, green, red or yellow). This cover was left on for 3 or 4 days and then the grey cover was returned. In 2008–2009, the coloured cover was left on for 1 day, starting between 1200 and 1500 hours, so in both years PIT tag data were censored at 24 h after presentation of the coloured feeder cover. In each year we repeated this process four times at each site a minimum of 10 days apart, twice modifying the upper feeder and twice the lower feeder. The four colours were presented in a different order and combination of positions (upper or lower) at each site. Using a subset of data from 2007 to 2008, we compared the number of PIT tag records in the first hour after introduction of the novel cover to the mean of the same hour in the 3 previous control days, and found a significant reduction in use of the novel feeder relative to the control (paired Mann–Whitney U test: $U = -2.34$, $N_1 = N_2 = 24$, $P = 0.03$). Therefore, at the population level, the novel feeder cover elicited a neophobic response.

After introduction of a novel cover, for each bird, we used PIT tag records to count the visits to the control feeder before the first visit to the novel feeder. The PIT tag readers recorded the time a bird was first detected on the feeder and then whether it was still present at 2 s intervals until not detected. As such, a visit was defined as a record separated from previous or subsequent records by more than 3 s. Birds that used the novel coloured feeder first, that is, immediately on returning to the feeding station, were given a count of zero. Birds that encountered the same colour at more than one site were included only in their first experience of that colour.

A limitation of our method is that we do not know whether a long latency to use the novel feeder reflected aversion to the feeder or simply absence from a site. Therefore we calculated the average foraging bout length using PIT tag records from experimental periods in 2007–2008 as follows: the median interval between an individual's feeding station visits was 2 min, with an upper interquartile limit of 14 min. A feeding bout was then defined as a period of feeding station use bounded by periods of 14 min or more with no records of that bird. Using this definition, across birds the median feeding bout length at a feeding station was 42 min. Birds that took longer than our average feeding bout of 42 min to use a novel feeder after first returning to a feeding station were assumed to have left the site and were excluded from that replicate. Compared to birds taking under 42 min, these excluded birds were not particularly neophobic (or neophilic) in captivity (Mann–Whitney U test: $U = 330$, $N_1 = 167$, $N_2 = 57$, $P = 0.22$). Under this criterion, we obtained wild neophobia scores from 78 birds, 53 from 2007 to 2008 and 25 from 2008 to 2009, with an average of two replicates per bird (range 1–4). Of these 78 birds, 75 had a captive neophobia score.

Ethical Note

Work was done under licence of the U.K. Home Office and subject to ethical review by the Waltham Centre for Pet Nutrition and the University of Glasgow. Captive studies were completed and

feeders removed 2 months before the first record of nest building in the area. While we routinely weighed the birds prior to release to ensure they had not lost more than 10% body mass in captivity, there was on average a body mass gain ($2.97 \pm 7.3\%$). Following release at the site of capture, 108 of the 125 birds were later recorded using the feeders or retrapped in the area. Permission for holding birds in captivity and for using PIT tags was obtained from Scottish Natural Heritage and the British Trust for Ornithology, respectively.

Statistical Methods

Analyses were carried out using R 2.9.1 (R Development Core Team 2009). There were no differences in behavioural data between years so data were pooled across years.

Defining personality traits in captivity

We first determined whether permanent (sex, age and wing length) or nonpermanent (body mass or condition, and weather and daylength) between-individual variation at capture explained a significant proportion of variation in behaviour in each captive personality trial replicate. We could not normalize the residuals of general linear models (GLMs) using captive personality traits as the dependent variable, nor the distribution of the traits themselves, so we used nonparametric Mann–Whitney *U* tests or Kendall rank sum correlations. We applied a Bonferonni correction for multiple comparisons, with a *P* value of less than 0.004 for significance.

Consistency across days was analysed using a mixed model, with trial order as a random effect. We then calculated repeatability of captive personality measures using the mean squares from an analysis of variance, with the repeated measures of neophobia or exploratory tendency as the dependent variable and individual identity as the independent variable, following Lessells & Boag (1987). Repeatability is the proportion of variation in a trait that is explained by differences between individuals; thus larger values reflect greater within-individual consistency.

Defining personality traits in the wild

Personality traits were measured repeatedly in the wild (up to 16 replicates of the exploration trial and up to four replicates of the neophobia trial per individual). In all analyses using wild data, therefore, we accounted for repeated measures by using generalized linear mixed models (GLMMs), with a wild personality trait as the dependent variable and individual identity as a random factor. Wild exploratory tendency was binary (discovered versus not discovered) and wild neophobia a count (visits to the control feeder); thus GLMMs used either a binomial or Poisson error structure, respectively. In this and all subsequent analyses of wild personality traits, we also included two variables with each wild personality trait to control for experimental variation between replicates. First, in the exploration trial, feeder discovery may depend on the distance between an individual's nearest permanent feeding station and a given new feeder. Similarly, feeder discovery may be affected by the number of permanent feeding stations an individual used (i.e. their coverage of the study site). Therefore, distance and the number of sites used were included as covariates in all analyses of wild exploratory tendency. Second, in the neophobia trial, the latency to approach a novel feeder may depend on colour or height biases. Therefore feeder colour and feeder position (upper or lower) were included as fixed main effects and an interaction (colour $\times$ position) in all analyses of wild neophobia.

Analyses of repeatability used only birds that participated in more than one replicate of a trial. Repeatability of wild personality traits was calculated using the variance component estimates for individual identity from these GLMMs, following Lessells & Boag (1987; see also Quinn & Cresswell 2005). The significance of repeatability estimates was determined using a likelihood ratio (LRT) chi-square test between the GLMM including individual identity and a GLMM excluding individual identity.

In the exploration trial, variation in feeder discovery was low, with only 47 of 91 birds discovering any new feeders. As such, high repeatability would be misleading, resulting from all individuals scoring mostly '0's rather than consistent individual variation (i.e. between birds with mostly '1's and birds with mostly '0's). Feeder discovery (and hence behavioural variation) was highest among individuals using the closest permanent feeding station to the new feeder within a given replicate. In 2008–2009, we conducted two replicates of the exploration trial within the vicinity of each permanent feeding station, around a month apart (see Exploratory tendency in the wild). To analyse repeatability, therefore, we limited the data for each 2008–2009 replicate to birds that were using the nearest permanent feeding station and that participated in both replicates at that permanent feeding station. Permanent feeding station identity was then included in the GLMM as a fixed effect and repeatability calculated using the variance component from individual identity nested within permanent feeding station as a random factor.

Correlations between traits

For analyses on captive traits, we performed a Kendall rank sum correlation. For analysis of wild traits, we constructed a GLMM with wild neophobia as the dependent variable. To generate a single measure of wild exploratory tendency per bird for the independent variable, which accounted for unequal replication between individuals, we created a two-vector variable with the number of feeders an individual discovered over the number of replicates in which it took part as the binomial denominator. To generate a single measure of distance between new and permanent feeding stations per individual, we took the mean distance across replicates. Along with feeder colour and position, the number of sites an individual used and this mean distance were included in the GLMM, as covariates. To test the significance of wild exploratory tendency as an explanation for variation in wild neophobia, we performed an LRT chi-square test between the GLMM including wild exploratory tendency and a GLMM excluding wild exploratory tendency.

Correlations between captive and wild personality traits

GLMMs were similar to those used when calculating repeatability of wild traits (see above). We tested whether captive personality measures explained a significant proportion of variation in wild behaviour by adding the analogous captive personality measure to these GLMMs as an independent variable, and performing an LRT chi-square test between the GLMM including and a GLMM excluding that independent variable.

RESULTS

Definition of the Captive Exploration Trait

We observed considerable behavioural variation among birds during the 10 min trials. The number of movements ranged from zero to 605 (novel side: median = 132, interquartile range, IQR = 123; familiar side: median = 113, IQR = 118). In the second trial, birds were significantly more active (paired Mann–Whitney *U* test: $U = 151$, $N_1 = N_2 = 45$, $P < 0.0001$). However, exploratory tendency (activity in the novel environment minus activity in the familiar environment) did not differ between trials (paired Mann–Whitney *U* test: $U = 501$, $N_1 = N_2 = 45$, $P = 0.95$).

Exploration scores did not differ between sexes or ages, (all $P > 0.42$); therefore data were pooled to analyse other sources of between-individual variation. With the Bonferroni correction threshold P value of 0.004, all other morphometric and environmental variables were nonsignificant. Therefore consistency and repeatability of these traits were calculated on actual scores. When we controlled for trial order, exploratory tendency (LME: $F_{1,43}$ 1.7, $P = 0.04$) and activity in the exploration trial ($F_{1,43} = 3.39$, $P = 0.0001$) were consistent across replicates. Exploratory tendency across day 1 and day 3 (ANOVA: $F_{1,43} = 1.71$, $r = 0.27$, $P = 0.04$) and activity during the exploration trials ($F_{1,43} = 2.56$, $r = 0.42$, $P = 0.001$) were significantly repeatable.

Definition of the Captive Neophobia Trait

We observed considerable individual variation during the 10 min trials. Latencies to return to the food bowl in the novel object phase (median = 23 s, IQR = 95.8 s) or disturbance phase (median = 9 s, IQR = 32 s) varied between 1 and 590 s. Mean latency in the novel object phase was significantly greater than in the disturbance phase, indicating that the presence of the novel object modified behaviour (paired Mann–Whitney U test: $U = 5023$, $N_1 = N_2 = 120$, $P = 0.0006$).

Neophobia scores did not differ between sexes or ages (all $P > 0.11$); therefore data were pooled to analyse other sources of between-individual variation. As with the exploration score, all other morphometric and environmental variables were nonsignificant (all $P > 0.1$). Therefore consistency and repeatability of this trait were calculated on actual scores. When we controlled for trial order, the neophobia score (novel object phase latency minus disturbance phase latency) calculated for each day was consistent across days (LME: $F_{1,103} = 1.77$, $P = 0.002$). Neophobia across day 1 and day 2 was significantly repeatable (ANOVA: $F_{1,103} = 1.77$, $r = 0.28$, $P = 0.002$).

Definition of Wild Personality Traits

In the wild exploration trial, individual discovery of feeders across two replicates within the vicinity of a given permanent feeding station was near significantly repeatable (i.e. individuals generally found both or neither feeder; GLMM: LRT: $\chi^2 = 5.29$, $N = 23$ birds, $r = 0.16$, $P = 0.07$,). In the wild neophobia trial, individual latency to approach the novel feeder was significantly repeatable (GLMM: LRT: $\chi^2 = 126.83$, $N = 43$ birds, $r = 0.55$, $P < 0.0001$).

Correlations between Traits within Contexts

In captivity, neophobia did not correlate with exploratory tendency (Kendall rank correlation: tau = −0.62, $N = 115$, $P = 0.54$; Fig. 1a) or activity in the captive exploration trial (Kendall rank correlation: tau = −0.74, $N = 115$, $P = 0.46$). Similarly, in the wild, the proportion of feeders discovered in the exploration trial did not predict an individual's neophobia (GLMM: LRT: $\chi^2 = 0.66$, $N = 78$ birds, $P = 0.72$; Fig. 1b).

Correlations between Captive and Wild Measures

Wild exploratory tendency had a significant positive relationship with captive exploratory tendency (GLMM: LRT: $\chi^2 = 3.889$, $N = 91$ birds, $P = 0.04$; Fig. 2a). There was no relationship between activity during the captive exploration trial and wild exploratory tendency (GLMM: LRT: $\chi^2 = 0.002$, $N = 91$ birds, $P = 0.97$; Fig. 2b). Therefore, the relationship between captive and wild traits relates specifically to activity in the novel environment, that is, exploratory tendency. Wild neophobia had a significant positive relationship with captive neophobia (GLMM: LRT: $\chi^2 = 48.28$, $N = 75$, $P < 0.0001$; Fig. 2c).

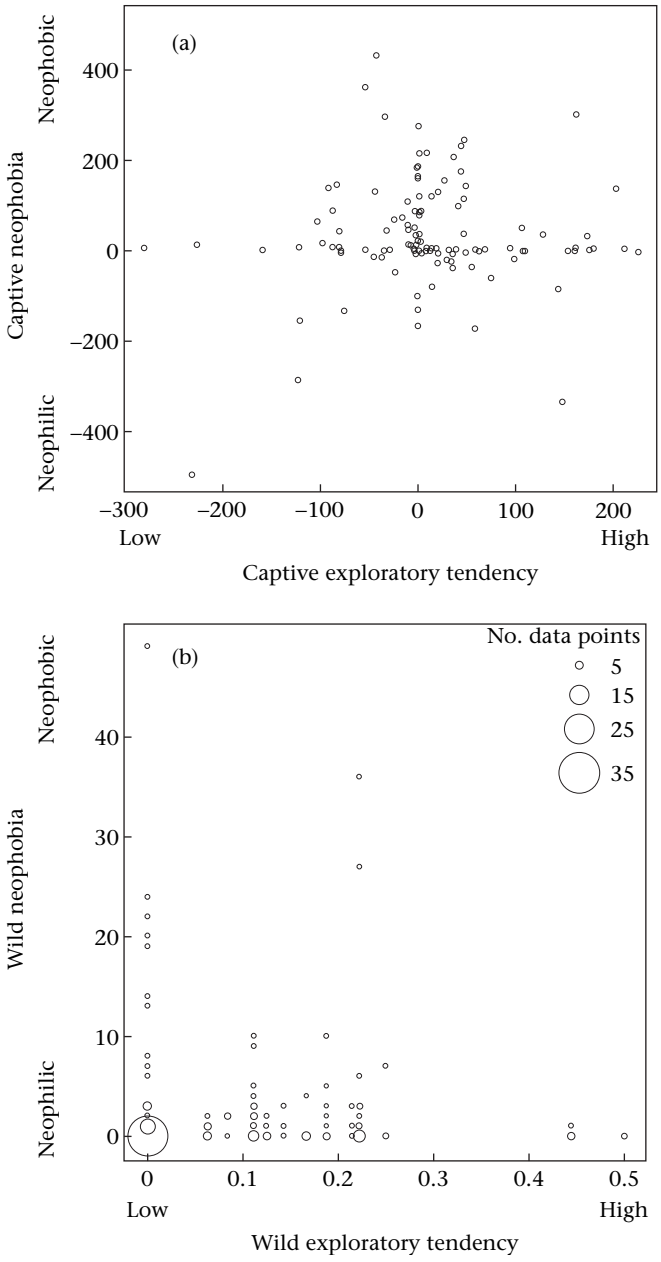

Figure 1. (a) Plot of captive exploratory tendency (no. of movements in novel environment minus no. of movements in familiar environment) and captive neophobia (mean novel object phase latency minus mean disturbance control phase latency). $N = 115$ birds. (b) Plot of wild exploratory tendency (proportion of feeders discovered) and wild neophobia (no. of visits to familiar feeder before first visit to novel feeder); individuals are represented one to four times and where multiple data points occur on the same point this is indicated by the point size. $N = 78$ birds.

DISCUSSION

In this study, we showed that personality traits measured in captivity were a reflection of behavioural differences between individuals foraging in the wild. First, variation between blue tits in exploratory tendency and neophobia were repeatable in captivity, and analogous traits repeatable in the wild. Second, captive

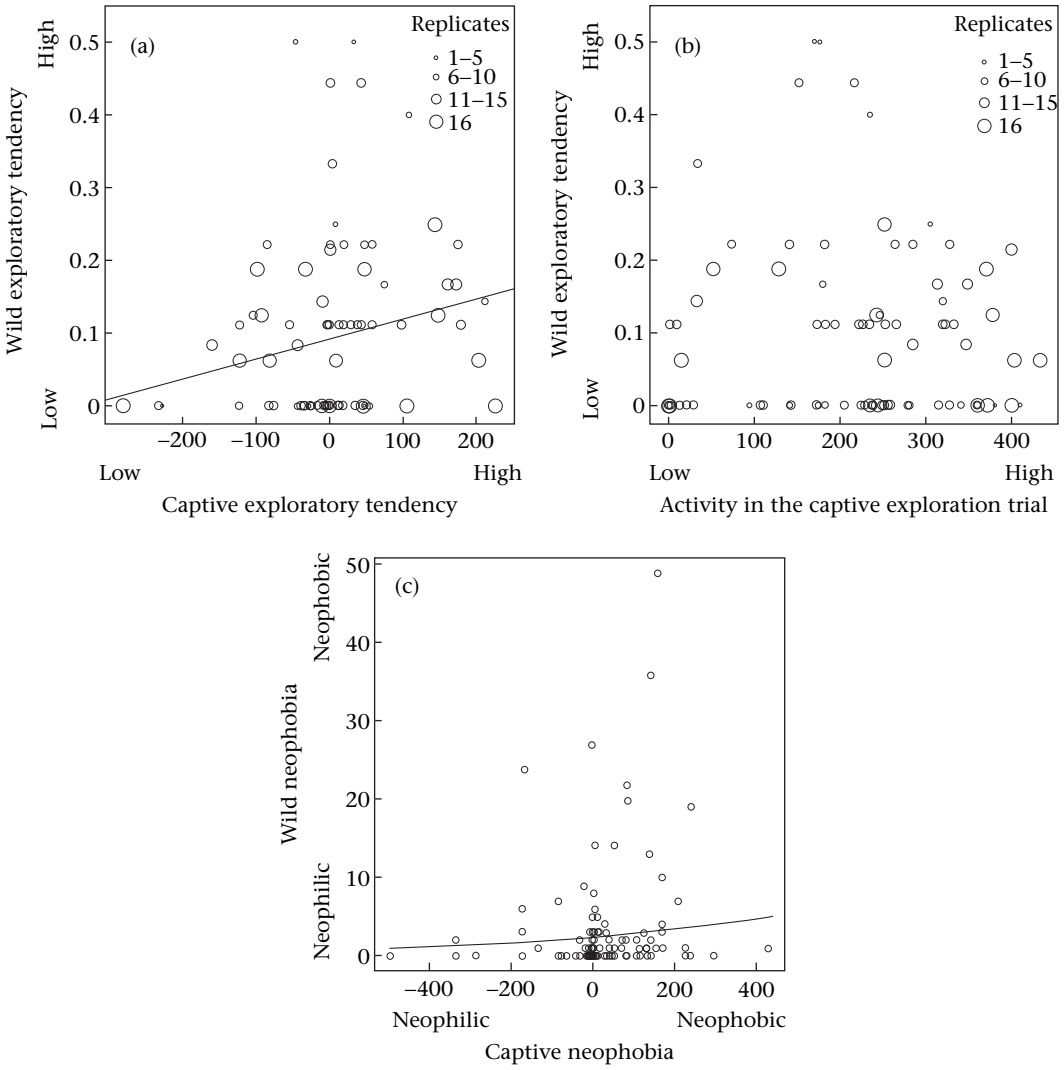

Figure 2. (a) Relationship between captive exploratory tendency (no. of movements in novel environment minus no. of movements in familiar environment) and wild exploratory tendency (proportion of feeders discovered). The line is fitted from a linear regression; no. of replicates of the wild exploration trial per bird is indicated by the point size. $N = 91$ birds. (b) Plot of activity in the captive exploration trial (no. of movements in novel environment plus no. of movements in familiar environment) and wild exploratory tendency (proportion of feeders discovered); no. of replicates of the wild exploration trial per bird is indicated by the point size. $N = 91$ birds. (c) Relationship between captive neophobia (mean novel object phase latency minus mean disturbance control phase latency) and wild neophobia (no. of visits to familiar feeder before first visit to novel feeder), the line is fitted from a Poisson regression; individuals are represented one to four times. $N = 75$ birds.

measures of exploratory tendency and neophobia were not correlated within individuals, and this was also true of the analogous wild traits. Finally, captive measures of exploratory tendency and neophobia then predicted the analogous wild measures of these traits. Birds that were relatively exploratory in captivity were also more likely to find new feeders in the wild and vice versa. Similarly, an individual's neophobia measured in captivity correlated positively with its latency to approach novel colour feeders in the wild. As our wild measures of personality relate to differences in the use of feeding opportunities, the traits we have measured in captivity appear to represent ecologically relevant differences between individuals.

While many studies have used behaviour in captivity to explain differences in fitness observed between individuals in the wild, few have directly compared behaviour between captivity and the wild, as we have done. Referring to captive studies on great tits for example, Dingemanse et al. (2004) suggested that lower survival of slow than fast-exploring females in food-poor winters relates to differences in propensity to capitalize upon patchily distributed food. In captive studies, fast-exploring great tits are quicker to form foraging routines, more aggressive, and more likely to use social cues than slow explorers: all attributes that support monopolization of clumped resources (Verbeek et al. 1994, 1996; Marchetti & Drent 2000). From captive studies, it appears likely that exploratory tendency also reflects differences between individuals in information gathering: when returned to formerly novel environments, search behaviour is often then directed towards locations or cues that were associated with food during the preceding novel environment trials (Mettke-Hofmann & Gwinner 2004). Our findings complement these captive observations as, here, exploratory tendency in captivity appeared to be connected to the ability or propensity to seek out new feeding sites in the wild. In particular, the absence of correlation between activity during the exploration trial and feeder discovery in the wild suggests that it was attention to the novel environment specifically, where new information may be gathered, rather than activity per se that affected feeder discovery.

We also demonstrated that neophobia measured in captivity reflected differences in neophobia in the wild. Neophobia in

free-living birds is associated with reactions to other novel foraging situations, for example dietary conservatism towards new food types or propensity to innovate to obtain food in a novel foraging task (Webster & Lefebvre 2001; Thomas et al. 2003). As such, the ecological significance of neophobia may be as a measure of propensity to approach and hence learn about new feeding opportunities. However, if exposure to the novel object elicits a physiological stress response, that is, a release of the stress hormone corticosterone, it may also be a measure of response to stressors in general. Whether novel objects elicit a physiological stress response, however, has so far been tested only in Japanese quail, *Coturnix japonica*, which do show an elevation in corticosterone (Richard et al. 2008), and starlings, *Sturnus vulgaris*, which do not (compared to a disturbance control; Apfelbeck & Raess 2008). That great tits (Groothuis & Carere 2005) and the blue tits in our study exhibit a behavioural aversion towards novel objects suggests the object may cause a stress response. Indeed, in great tits, individual corticosterone responses derived from a handling trial predict behavioural responses in novel object trials, suggesting similar physiological mechanisms may underlie the responses to handling and novel objects (Groothuis & Carere 2005). However, stereotypical stress behaviours are not necessarily evidence of physiological stress; for example, blue tits disturbed at the nest prior to trapping exhibit aggressive behaviour and alarm-call, yet show no greater corticosterone response than birds trapped unawares (Müller et al. 2006). Therefore, we should be cautious of assuming neophobia is a measure of response to stressors in general. To assess the ecological significance of our neophobia trait, future work should be addressed both at investigating whether the novel object trial elicits a physiological stress response, and also at comparing neophobia with measures of risk responsiveness towards different potential stressors.

That we did not find a correlation between exploratory tendency and neophobia in our population of blue tits, either in captivity or in the wild, was surprising. Exploratory tendency and neophobia or risk taking are positively correlated in species from a variety of taxa, and in the closely related great tit this appears to be under genetic control (van Oers et al. 2005). In these species, neophobia and exploratory tendency may be two measures of a single approach–avoidance trait, with risk-prone, fast-exploring or 'proactive' individuals at one extreme and risk-averse, slow-exploring or 'reactive' individuals at the other. In other words, Verbeek et al.'s (1994) novel environment trial and Greenberg's (1983) novel object trial may be regarded as approach–avoidance in a novel and a familiar environment, respectively (Clark & Ehlinger 1987; Wilson et al. 1993; Johnson & Sih 2007). Although our captive methods differ slightly from those used by Verbeek et al. (1994), the lack of a proactive–reactive personality trait is unlikely to be an artefact of methodology, as we have tested a small sample of great tits using our protocol and found the correlation anticipated (K.A. Herborn & K.E. Arnold, unpublished data). While the contrast to great tits is surprising, divergences in trait correlations between closely related species (e.g. Mettke-Hofmann et al. 2002; Mettke-Hofmann & Gwinner 2004) and even populations of the same species (Bell & Sih 2007; Dingemanse et al. 2007) can be explained by different selection pressures. Consequently, we suggest the traits we have assayed in the blue tit are distinct, and hence the ecological significance of each trait should be considered independently.

Differences between individuals, such as body condition or weather at capture, did not explain a significant proportion of the variation in captive behaviour. This contradicted our prediction that variables increasing starvation risk, such as short daylength and poor weather (and hence reduced recent foraging opportunity) would lessen neophobia or increase propensity to explore in the short term. In the wild, Parids modify behaviour rapidly in response to environmental conditions, for example attuning foraging behaviour and hence body fat to changes in starvation and predation risk (Macleod et al. 2005). That behaviour in the captive personality trials was consistent between the first and subsequent days in captivity suggests blue tits may equally adjust their perception of starvation risk rapidly to the conditions and food availability in the captive environment. The absence of state effects is consistent with previous work on wild great tits (Hollander et al. 2008), and encouraging for studies seeking to compare personality between individuals drawn from different times or environments.

In conclusion, personality measures drawn in captivity revealed differences between individuals in their natural foraging behaviour. In directly comparing individuals between captivity and the wild, this study on blue tits joins the few similar in situ versus ex situ studies of personality (birds: Hollander et al. 2008; fish: Wilson & McLaughlin 2007; Coleman & Wilson 1998; Brown et al. 2005; molluscs: Briffa et al. 2008). As such, it is an important validation of research based purely on captive measures of personality. Moreover, it lends weight to the growing evidence that wild animals have personality traits that are expressed consistently across contexts.

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