

Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*

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(Accepted: 12 January 2005)

Summary

Animal ‘personalities’ or behavioural syndromes can be defined as individual differences in suites of correlated behaviours. Using chaffinches *Fringilla coelebs* temporarily held in captivity, we determined the extent to which activity level (AL), the behavioural response to a stressful situation (BRSS) and two anti-predation risk behaviours when exposed to a model predator were inter-correlated within individuals. We assayed AL and BRSS when the chaffinches were first put in an experimental room. Subsequently we recorded their initial response (freeze or escape) to the sudden appearance of a model hawk, in addition to their latency to resume activity afterwards as a measure of cautiousness (‘latency’). Each bird was assayed in two situations that differed in the risk level posed and in the assumed optimal response required to minimize predation risk: (1) high risk, when the hawk flew directly over the chaffinch and the assumed optimal response was to escape; and (2) low risk, when the model hawk flew 2 m to the side of the chaffinch and, since the bird was not being targeted, the assumed optimal response was to freeze in order to avoid attracting attention. All of the variables had relatively high repeatabilities and were inter-correlated, providing strong evidence for a behavioural syndrome. Though propensity to freeze was much greater in the low risk treatment, AL was negatively correlated with freezing behaviour in both risk treatments, and therefore there was a ‘behavioural carryover’ across situations. While hypoactive individuals were more likely to freeze in the low risk treatment, and were therefore assumed to be better able to assess risk compared to hyperactive individuals, some hypoactive individuals also froze in the high risk situation when it was assumed to be inappropriate to do so. Despite this apparently maladaptive behaviour in the high risk situation, overall hypoactive individuals showed a greater degree of behavioural plasticity across treatments compared to hyperactives. Taken together our results support the hypothesis of differential predation risk among personality types. We discuss the implications of our results for current interest in personalities, and for predation risk and group-living theories.

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Keywords: personality, behavioural correlation, anti-predation behaviour, stress, activity level, behavioural plasticity, coping style, freeze behaviour, cryptic behaviour.

Introduction

Behavioural syndromes, coping strategies or personalities have been identified in fish, amphibians, reptiles, birds, cephalopods and many other taxa, including humans (Mather & Anderson, 1993; Wilson et al., 1994; Boissy, 1995; Koolhaas et al., 1999; Gosling, 2001; Sih et al., 2004). They are defined as individual differences in suites of inter-correlated behaviours. Evidence from wild populations suggests that behavioural syndromes are inherited (Réale et al., 2000; Dingemanse et al., 2002) and artificial selection on specific personality types in captivity results in the evolution of multiple behaviours (van Oers et al., 2004). Furthermore, measures of different behavioural phenotypes used to assay personality are repeatable within situations over time (Dingemanse et al., 2002; van Oers et al., 2004) and can be limited in plasticity across situations (Sih et al., 2003). This means that some individuals do not necessarily make the optimal response in a given situation, even though over an individual's lifetime limited plasticity can still be an adaptive strategy (Dall et al., 2004; Sih et al., 2004). Behavioural syndromes may prove to be fundamentally important in explaining behavioural variation and population level processes because they mean that expected frequencies of one behavioural phenotype in a population can be predicted only on the basis of measured selection for (1) all other correlated phenotypes and (2) each phenotype in all meaningful situations (Roff, 1997; Merilä & Sheldon, 2001; Sih et al., 2004). In this paper we test whether an individual's behaviour during a simulated attack by a predator, a novel scenario in personality research, is correlated to other behavioural phenotypes that have been used to assay animal personalities.

One commonly studied behavioural syndrome is the 'proactive-reactive axis'. This encompasses correlations between exploratory behaviour, activity level, aggression, responses to novel situations and fearfulness (Hessing et al., 1994; Verbeek et al., 1994; Koolhaas et al., 1999; Benus, 2001; Dingemanse et al., 2002). In some situations proactive individuals are faster explorers (Verbeek et al., 1994), better foragers (Marchetti & Drent, 2000), relatively dominant (Verbeek et al., 1996, 1999), bolder when faced with novel situations (Verbeek et al., 1994), and disperse further (Fraser et al.,

2001; Dingemanse et al., 2003; Krackow, 2003), while reactive individuals are the opposite. In other situations, however, the exact opposite is the case (e.g., Coleman & Wilson, 1998; Marchetti & Drent, 2000; Dingemanse & de Goede, 2004) and this context dependence is thought to partly explain why selection on exploratory behaviour and other similar behavioural traits (Réale et al., 2000; Dingemanse et al., 2004; Höjesjö et al., 2004) fluctuates greatly and sometimes reverses completely from year to year in the wild.

Predation is one of the main suspected mechanisms behind differential selection patterns amongst personality types (Dingemanse & Réale, 2005; Sih et al., 2004). The arsenal of anti-predation behaviours available to prey is extensive (Caro, 2005) and yet the extent to which such behaviours are linked to personality is almost entirely unexplored. Moreover existing research on this topic is biased towards fish (Huntingford, 1976, 1982; Magurran & Seghers, 1994; Ward et al., 2004; Magnhagen & Staffan, 2005) though a few studies have been on amphibians (Sih, 1992), insects (Hedrick, 2000), lizards (López et al., 2005) and bovids (Réale et al., 2000; Réale & Festa-Bianchet, 2003). Two general conclusions can be drawn from these studies. The first is that bold or 'geared up' individuals show a tendency to take apparently greater risks in the presence of predators, either through remaining highly active (Sih et al., 2003; Ward et al., 2004; Bell, 2005), or by having a higher tendency to inspect predators (Huntingford, 1976, 1982) which is generally thought to deter predators from attack (Godin & Davis, 1995; Brown & Dreier, 2002; but see Dugatkin, 1992). The second, albeit weaker, conclusion is that this correlation might well lead to direct fitness costs in the form of higher predation (Dugatkin, 1992; Réale & Festa-Bianchet, 2003; Sih et al., 2003). However, the direction of selection appears to be system dependent and more studies are needed to determine whether any general patterns exist.

Studies that have provided evidence for a correlation between personality type and predation-linked fitness have relied primarily on comparisons of survival estimates in the presence and absence of predators. With the possible exception of Sih et al. (2003), who showed that geared up or hyperactive salamander larvae were less likely to use cover in the presence of predators (at the same time as suffering high predation), researchers have yet to demonstrate exactly why personality correlates with predation risk, a question that can only be answered by observing prey behaviour during attacks, the point at which any differential fitness costs or benefits arise. Individual prey are known to vary how they respond to predators upon attack and this

affects their probability of survival (Cresswell, 1993, 1994; Caro, 1995). This forms the basis of our first working hypothesis, that response to an attacking predator is likely to covary with personality type. Though several studies have looked at cautiousness post-attack (Ward et al., 2004; Bell, 2005), to our knowledge none have examined behaviour at the moment the attack occurred. In addition to providing a mechanistic understanding of observed fitness, such an approach has consequences for our understanding of perceived individual risk within groups and therefore for the evolution of group living.

We tested whether anti-predation behaviour in response to a moving model predator was influenced by personality as indicated by standard assays of activity level (AL), a behavioural trait which on its own can indicate personality type. First we tested whether there were consistent individual differences in several behavioural phenotypes across trials, i.e., whether they were repeatable. Second we explored the extent to which AL, a behavioural response to a stressful situation, propensity to use freezing behaviour when attacked and cautiousness post-attack (latency to resume activity or latency) were inter-correlated. Third, we looked for evidence of limited behavioural plasticity in these traits when assayed in different situations. We assumed that when there was a low risk of being seen by a predator that appeared suddenly, the optimal response was to freeze in order to avoid attracting attention; when there was a high risk of being seen, we assumed the optimal response was to escape. Finally, we tested whether individual differences in behavioural plasticity across treatments could be explained by personality types.

Methods

General

Thirty-seven chaffinches were caught under license to English Nature during January and February 2004, and kept in captivity for a maximum of two weeks at the Wytham Field Laboratory, Oxford. This system has been used for several years to study predation risk management (Cresswell et al., 2003; Whittingham et al., 2004). On capture birds were aged, sexed and wing-measured (see Svensson, 1984). Twenty-four of the birds were male (14 adult, 10 first winter) and 13 female (3 adult and 10 first-winter). Chaffinches

were housed individually in standard small-bird keeping cages. Lighting followed the natural cycle and included 30 minutes of twilight in the mornings and evenings. Birds were fed wild birdseed mixture ad libitum and water. Room temperature was maintained between 10 and 15°C throughout the course of the experiment.

Trials were conducted between 1000 and 1700 h (mean 13.36 ± 0.17 SE). AL and anti-predation behaviours were assayed during the same trial for each bird and this was repeated over three different trials. Before each trial, birds were food deprived for 2-3 hours (depending on conditions) to encourage them to settle and feed during trials. Before each trial the bird was caught by hand in a temporarily darkened room and was transferred in a bird bag from its keeping cage to an experimental cage within 5 minutes. The time elapsed between when the bird was caught by hand and returned to its keeping cage, at which point food and water were restored, was usually less than 30 minutes for each experiment. The experimental cage was cubic ($0.5 \times 0.5 \times 0.5$ m), made of wire and placed over an artificial stubble substrate, the latter simulating the primary feeding habitat of chaffinches wintering on farmland in the UK (UK Biodiversity Steering Group, 1998). Two hundred canary grass (*Phalaris canariensis* L.) seeds were scattered evenly over the 0.5 m^2 basal area of the cage to encourage the birds to forage. This relatively high density was at the upper end of the natural range found in their usual habitats and ensured that foraging behaviour was not limited by food availability. The substrate was constructed using straws fixed to a wooden board (1×1 m) at a density of 60 straws m^{-1} , with 12.5 cm between rows. The 3 cm high stubble allowed chaffinches, standing 4-6 cm high at eye-level, good all-round visibility and yet provided some cover which we expected would encourage chaffinches to freeze. Behaviour of chaffinches was watched remotely from an adjacent room on a monitor attached to a video camera (C in Figure 1) with which the entire trial was recorded for later analysis.

Behavioural assessment

Once released into the experimental cage, birds invariably flew back and forth until the experimenter left the room. ALs were recorded from the video tapes for 20 seconds one minute after the experimenter's departure. ALs were defined by the number of times the bird crossed a row or made a short flight.

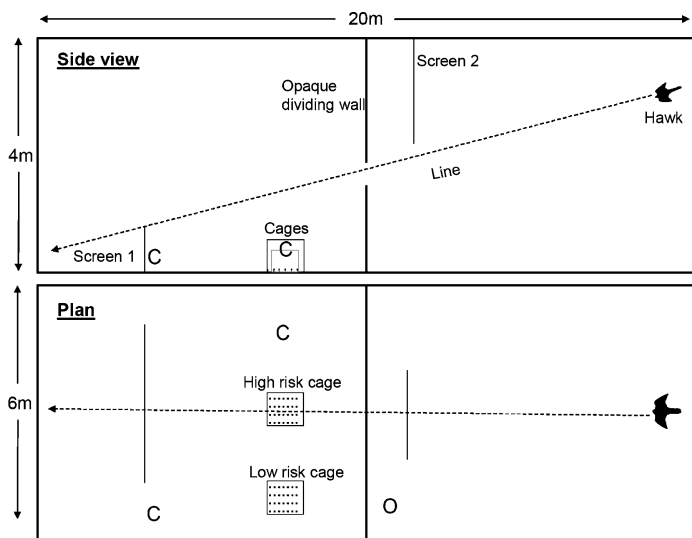


Figure 1. Side view and plan of experimental setup. Lines in cages represent artificial stubble. C and O denote positions of cameras and monitor (observation point) respectively. Approximate dimensions shown; not drawn to scale.

We recorded the number of times a row of straws was crossed, rather than the number of steps, because the distance travelled by an individual step varied, though birds could move between rows in a single determined hop. A flight was defined as a single movement between two points punctuated by more than an instantaneous pause and typically involved the bird flying from the ground to the cage, or vice versa.

Our AL measure was similar to the 'exploration scores in a novel environment' used in other studies (e.g., Dingemanse & de Goede, 2004). The experimental conditions differed in our study in that birds were handled directly by the experimenter and were retained in a relatively small experimental cage. Birds were therefore probably under more stress during our assays, though captive birds are likely to experience heightened stress whatever the experimental condition. To aid interpretation of our ALs and to provide an estimate of another behavioural phenotype, we also classified birds according to whether they showed an apparent behavioural response to the stress of being placed in a cage (BRSS), whilst acknowledging the limitations of such a subjective assessment. Some activity movements during the 20 second periods were associated primarily with foraging, pecking or apparent exploration, during which time birds subjectively seemed to be relatively calm, generally

making no attempt to escape from the cage. Other movements seemed to indicate stress because they were stereotypic and were often apparently associated with birds attempting to escape from the cage. Initially BRSS was quantified on a 5 point scale from 0 (no response) to 4 (high response) but in practice birds either clearly showed a response as listed above or they did not, so these values were converted into a two level factor.

To see if AL or BRSS changed with time elapsed since the experimenter had left the experimental room, chaffinches were assayed again 40 seconds before the hawk was released. The hawk was released approximately 3 minutes after first being put in the cage, the exact time depending on whether the bird was on the ground and not on the cage walls. We assume this slight variation in hawk release time did not affect subsequent chaffinch behaviour. Estimates from the second assays are denoted as AL2 and BRSS2 to distinguish them from first assay estimates, AL1 and BRSS1, during the same trial. AL(s) and BRSS(s) refer to the general case(s). Unless stated otherwise, all reference to AL is in terms of a continuous variable. When referring to individuals that were relatively active or inactive, for brevity we used the terms hyperactives and hypoactives respectively, which we suspect is largely equivalent to the terms bold/shy, fast/slow and geared-up/geared-down individuals used elsewhere.

Experimental treatment

Each bird was exposed to a flying model sparrowhawk, the main avian predator of passerines in Eurasia (Newton, 1986), in each of three different trials. Previous work with this system showed that chaffinches can distinguish between the model hawk and a similar sized harmless species because they reacted more quickly to the hawk and were more vigilant afterwards (Cresswell, Quinn et al., unpubl.). During trials a single chaffinch was put in cages placed in either one of two positions: (1) the high risk position, when the hawk flew 1 m directly over the bird or (2) the low risk position (when the hawk flew along the same path as in 1 but the bird was in a different cage 2 m to the side of the high risk cage). Additionally, a bird was either alone in the experimental room or was partnered with another bird in the opposite position in a separate cage, again simulating another level of risk. This experimental setup, therefore, gave four different treatments: (1) high risk alone; (2) low risk alone; (3) high risk with non-targeted partner; (4) low risk with

targeted partner. All birds were given treatments 1 and 2. They were also given treatment 3 or 4, but not both to limit time spent in captivity and the effects of habituation. The order in which birds were tested in low and high risk situations was randomised. After initial analyses, it became clear that being in a pair had no effect in any of the analyses. This may have been partly because of low sample size. In hindsight we also felt that the scenario was not realistic enough to represent a rigorous test of whether risk assessment was affected by the presence of other birds because birds were in different cages. For the sake of clarity, these trials are not considered further in this paper.

We used a commercial taxidermic sparrowhawk set in an attacking glide posture (wings flat and held slightly back). From an initial height of 3.5 m, the model slid down a 19 m line (after the remote release of a holding pin) and always passed directly over the cage in the targeted position, finishing at ground level 4 m behind the cage, at which point the hawk became invisible to the bird by means of a screen. The model therefore initially aimed for the targeted position up to the point at which it past directly over the cage. Thereafter even though the hawk was no longer in view, from the chaffinch's viewpoint there remained the possibility that the hawk was still nearby. A blind placed in front of the cage ensured that the model first became visible to chaffinches only when it was within approximately 1.5 m of the bird in the high risk cage and within about 2.5 of the low risk cage. The speed at which the hawk travelled was not measured in this experiment but mean speed was 13.5 ± 0.19 SE km h⁻¹ ($N = 30$) in another experiment that used the same set-up (C. Devereux, pers. comm.). 'White noise' recorded from an un-tuned radio was played on a tape recorder in the experimental room throughout the experiment to limit the effect of the slight noise made by the hawk as it travelled down the line. We did not habituate birds to the noise beforehand and assume this had no affect on the interpretation of these results.

Chaffinch responses to the appearance of the sparrowhawk were recorded and classified as one of the following: (1) escape response, when the bird tried to fly away, (2) freezing, where the bird remained almost or entirely motionless, though usually making slight eye or head movements, (3) tracking, where the chaffinch stayed on the ground and tracked the flight path of the sparrowhawk until it went out of view, spinning on a vertical axis as it did so, (4) hop, run, walk or any other discrete movement followed immediately by freezing. In analyses, all responses were classified as either escape

(1) or 'freeze' behaviour (2-4), both of which are typical avian anti-predator responses (Shalter, 1979). Thereafter birds were left in the cages until they began moving around or feeding again. If birds did neither of the two within a set amount of time, the trial was ended and latency to resume activity was conservatively set at the maximum for that treatment. In most cases this was within 15 minutes but a few trials were terminated earlier for logistical reasons.

Latency to resume activity (latency), i.e., foraging or moving, was taken from video recordings of the trials as a measure of cautiousness during the post-hawk period. The trial bird was said to have begun foraging when it made two definite pecks for seeds. It was said to be moving again when it took two definite steps, hops or flights, each separated in time by no more than 5 seconds. Birds that initially landed on the side of the cage would shift their positions slightly (ca 1-2 cm) from time to time. From watching a gradual lowering of the body prior to these shifts, it seemed that these were caused by muscle strain and so these movements were ignored. Similarly if birds landed on the side of the cage and not on the ground following their initial response to the model hawk, but then shortly after dropped to the ground and remained in a freeze state for longer than an arbitrary 5 second period, this preceding movement was also ignored. Birds that remained in the freeze state varied in the numbers of minor body movements. Some showed absolutely no movement whatsoever while others would look from side to side with inconspicuous head-movements, occasionally shifting the orientation of their bodies. All of these movements were ignored for the sake of this analysis and represent a different scale of freezing behaviour.

Analysis

Repeatabilities of most variables were calculated following (Lessells & Boag, 1987). Though repeatabilities are normally calculated for measures repeated in a similar situation, they were also calculated for latency in low and high risk situation because there was no difference in latency between the treatments (see below). For BRSS1 data, which consisted of 1's (stressed) or 0's (not stressed) and which therefore were not normally distributed, repeatability was calculated using a generalized linear mixed model (GLMM) expressing the individual variance component as a proportion of total variance. GLMMs provide exact variance component estimates, as recommended

by Lessells & Boag (1987), and do not use mean square estimates alone. All analyses were done using a GLMM in which individual was specified as a random effect (GENSTAT version 6.2; VSN Intl., 2003). The analysis of whether chaffinches froze was undertaken with a logistic binary regression GLMM, while the analysis of latency was done with a normal error GLMM and $\text{Log}_{10} + 1$ transformed. AL1 and AL2 were $\text{Ln} + 1$ transformed. To determine whether there was a link between AL and individual differences in behavioural plasticity across treatments, we initially tested the significance of the 3-way interaction between AL, treatment and individual, and examined reaction norms (plots of response probability from the model against treatment for each individual). For reasons of power (see results), we also did a logistic regression of whether individuals changed their behaviour between treatments on the mean of the two treatment AL1s.

All errors approximated to a normal distribution where appropriate. The significance of all variables in GLMMs was tested using the Wald statistic ($\text{deviance} \div \text{df}$) which approximates to a Chi-squared distribution. Instead of providing slopes for individual lines or treatment levels within factors, GENSTAT provides differences in parameter estimates with reference to the first level. For a factor with two levels, the parameter for the first level is set to 0 and the given parameter states how the second level differs from the first, while the associated SE is for this difference. For an interaction between a covariate and factor, while the parameter (B) provided for the covariate alone is equivalent to the slope for the first level interaction term, parameters shown for subsequent terms are expressed as differences with respect to the first level parameter and here are also denoted by B. Significant effects in models are often represented graphically using raw data or by using residuals after controlling for other effects in the model. To look at the variation only in the plane of the factor and variate of interest, the "RGRAPH" procedure provided by GENSTAT was used. If all effects in the model are displayed in the graph, this procedure simply plots the raw data. If, on the other hand, adjustment has to be made for other effects in the model, adjusted response values (the partial residuals) are plotted, and are calculated by adding residuals to predictions produced for all observations. The line that is then drawn through these points using a least squares approach indicates the true effect.

We considered several potentially confounding variables in the models. Chaffinches are strongly sexually dimorphic and in experimental tests, model males placed on the tops of bushes were three times as likely as model

females to be attacked by wild sparrowhawks (Götmark, 1993), though the authors felt the effect was likely to be less pronounced when on the ground (Götmark & Hohlfalt, 1995). Nevertheless, we expected on this basis that females might show a higher propensity to freeze because of their more cryptic plumage. Similarly in all analysis we controlled for habituation to trials by including trial order, and state dependent effects by including time of day, days since 1 January for seasonal effects (Houston et al., 1993) and relative body mass (e.g., Cresswell, 1998).

Results

Repeatability

Repeatability estimates showed that there was significant individual variation for first and second activity level estimates (AL1 and AL2; Table 1). There was also significant individual variation for the first behavioural response to stress assay (BRSS1) but not for the second (BRSS2; Table 1); the non-significance of the second arose because the probability of an individual showing a behavioural response to stress was 0.24 during the first compared to only 0.06 during the second assay in which there was therefore little variation (logistic binary regression GLMM; $W = 16.30$, $df = 1$, $p < 0.001$; logit means \pm SE for first and second assays were -1.18 ± 0.23 and -2.74 ± 0.06). There was no difference in latency between treatments (see below) and repeatability was 0.39 (Table 1). AL, BRSS and latency were therefore all repeatable behavioural phenotypes.

Behavioural phenotypic correlations

AL1 was higher in birds that showed a behavioural response to stress (mean $\ln AL1 + 1 \pm SE$ for non-stressed and stressed respectively, based on BRSS1: 0.88 ± 0.11 and 2.36 ± 0.15 ; $W = 100.10$, $p < 0.001$; normal error GLMM). None of the other controlling variables tested had significant effects on AL1 in the first assay (mass, sex, age, time of day, days since 1 January; all p values > 0.12). There was no difference in AL1 and AL2 across both trials ($W = 0.92$, $df = 1$, $p = 0.34$; GLMM on $\ln AL + 1$; means \pm SE, 1.26 ± 0.12 and 1.15 ± 0.12) which is in contrast to the result given above that the probability of a behavioural response to stress was 0.24 in the first assay

Table 1. Means, phenotypic variance V_p and repeatability (r) for different behavioural phenotypes assayed. F and p statistics are given for the ANOVA upon which r was based ($df = 1$ and 73 for all). AL1 and AL2 are activity levels during first and second assay. BRSS1 and BRSS2 are behavioural responses to stressful situation during first and second assays.

Phenotype	Mean \pm SE	V_p	$r \pm$ SE	F	p
Ln AL1 + 1	1.26	1.1	0.49 ± 0.13	2.91	<0.001
Ln AL2 + 1	1.15	0.99	0.38 ± 0.14	2.21	0.009
BRSS1	0.31	0.22	0.44 ± 0.13	2.59	0.002
BRSS2	0.15	0.13	0.05 ± 0.17	1.11	0.375
Log (Latency + 1)	0.6	0.24	0.39 ± 0.14	2.3	0.007

but only 0.06 in the second. Together these results suggest that individuals with high activity levels and that showed a high BRSS1 during the first assay continued to be more active several minutes later during the second assay, even though BRSS2 was then less pronounced.

Hyperactives were less likely to freeze when the hawk appeared than were hypoactives (Table 2; Figure 2a, b). Similarly birds that showed a behavioural response to stress during the first assay (BRSS1) were also less likely to freeze ($W = 4.10$, $p = 0.041$) but this effect was overridden by AL1 when both were in the same model. Neither AL2 nor BRSS2 were correlated to freezing behaviour (Table 2).

Chaffinches remained in the freeze state for an average of 5.88 ± 0.89 SE minutes (range 0.0-18.05; $N = 37$, based on means of individual mean latencies) after the hawk had been released. Latency was negatively correlated to AL1 controlling for other state dependent effects (Table 3; Figure 3). Latency also varied according to BRSS1 (mean of $\text{Log}_{10} + 1$ latencies, 0.68 ± 0.07 SE and 0.42 ± 0.10 SE, response and no response respectively; $W = 4.87$, $p = 0.027$; means) but BRSS1 dropped out of the model when AL1 was included. While BRSS2 had no effect ($W = 2.38$, $p = 0.123$) on latency, AL2 provided a marginally stronger effect than AL1 ($W = 13.48$, $p < 0.001$, slope = -0.144 ± 0.039 SE).

Freezing behaviour correlated to latency (minimal model, $W = 4.55$, $p = 0.033$, $df = 1$; Figure 4a, b) while both treatment and mass remained in the model with similar effects to those shown in Table 2; statistics for non-significant effects are excluded here but were very similar to those shown in

Table 2. Correlates of freezing behaviour among chaffinches when exposed to a model hawk. Results are from a logistic binary regression GLMM with individual as a random effect and all other variables as fixed effects. Statistics for non-significant terms are taken from the point at which the terms dropped out of the model in a backwards deletion procedure. For factorial effects, standard errors of the differences between levels are given (see methods). Abbreviated names as in Table 1.

	<i>W</i>	df	<i>p</i>	<i>B</i> ± SE
<i>Significant effects</i>				
Constant	n/a	n/a	n/a	-2.44 ± 0.642
Risk treatment	15.93	1	<0.001	3.03 ± 0.76
Ln (AL1 + 1) ¹	4.76	1	0.029	-0.88 ± 0.40
Ln mass per unit length (g mm ⁻¹)	4.39	1	0.036	-14.37 ± 6.86
<i>Non-significant effects</i>				
Risk treatment × AL1	0.01	1	0.915	0.11 ± 1.02
Ln days since 1 January	1.69	1	0.193	0.65 ± 0.50
Ln time of day	0.27	1	0.602	1.91 ± 3.67
Sex	0.12	1	0.727	0.34 ± 0.97
BRSS1 ¹	0.00	1	0.951	-0.10 ± 1.68
Age	0.00	1	0.987	-0.02 ± 0.90

AL2 had no effect ($W = 0.03$, $p = 0.874$) if switched with AL1 in model. BRSS2 also had no effect if switched with BRSS1 in model ($W < 0.01$, $p = 0.993$).

Table 2. In summary, therefore, AL, BRSS, freezing behaviour and latency were all inter-correlated (Figure 5).

Risk treatment and behavioural plasticity

Freezing behaviour was strongly influenced by treatment (Table 2). Chaffinches responded by freezing 57% of the time when in the low risk position ($N = 37$) but only 11% of the time when in the high risk position ($N = 37$). The relationship between AL and freezing behaviour was the same in both high and low risk treatments (Risk Level × AL was NS, Table 2, Figure 2). Therefore, although the propensity to freeze differed greatly between treatments, the difference between behavioural types in their tendency to do so carried over across the two situations. In other words, hyperactives were less likely to freeze in the low risk situation and never froze in the high risk situation, while hypoactives were more likely to freeze in the low risk situation, though a few individuals also froze in the high risk situation.

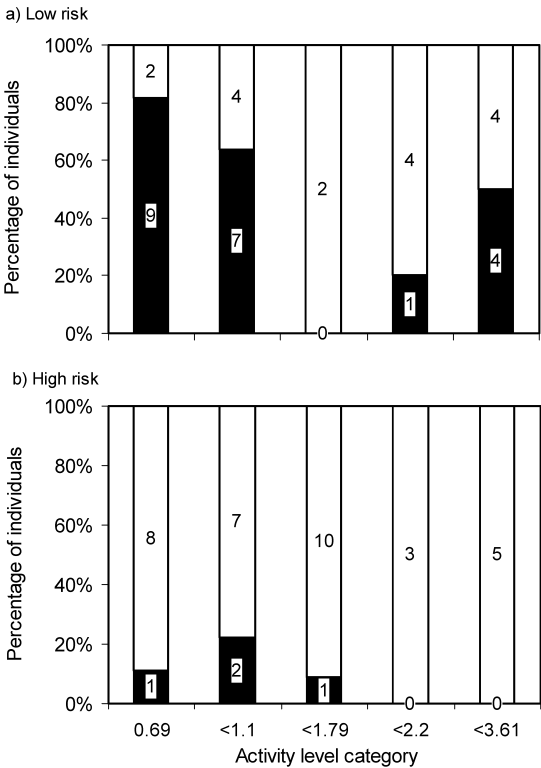


Figure 2. Behavioural responses to the sudden appearance of a hawk in relation to activity level (Ln AL1+1) in (a) low risk and (b) high risk treatments. ■ = freeze; □ = fly. Statistical analysis shown in Table 2 and number of trials shown in bars. Categories derived with equal percentiles.

To determine whether individuals differed in the plasticity of their response between treatments, and if this in turn were dependent on their AL, the Treatment \times AL \times Individual interaction was tested but fell short of significance ($W = 2.51$, $p = 0.113$, $df = 1$, GLMM with all three possible 2-way interactions also in the model). This non-significance was likely due to insufficient power and two arguments support this. First, plotting the fitted values from the 3-way interaction model in the form of reaction norms for each individual, and classifying individuals into relatively hyperactive and hypoactive categories on the basis of mean AL's between assays, showed there was a clear tendency for the reaction norms of hypoactives to be steeper indicating greater plasticity in response between treatments (Figure 6). Second, a similar analysis but in a form more appropriate to the sample size

Table 3. Correlates of latency to resume activity ($\text{Log}_{10} + 1$ transformed) in chaffinches. Results are from a normal error GLMM with individual as a random effect and all other variables as fixed effects. Statistics for non-significant terms are taken from the point at which the variable dropped out of the model in a backwards deletion procedure. Parameter estimates (B) are shown with standard errors. For factorial effects, average standard error of the differences between the levels are given.

	<i>W</i>	<i>df</i>	<i>p</i>	<i>B</i> \pm <i>SE</i>
<i>Significant terms</i>				
Constant	n/a	n/a	n/a	0.601 ± 0.058
Ln AL1 + 1	5.95	1	0.015	-0.125 ± 0.051
Ln days since 1 January	10.00	1	0.002	-0.229 ± 0.072
<i>Non-significant terms</i>				
Ln time of day	2.16	1	0.142	0.660 ± 0.449
Risk treatment	1.66	1	0.198	-0.110 ± 0.085
Ln mass per unit length (g mm^{-1})	0.76	1	0.382	-0.686 ± 0.786
Age	0.09	1	0.770	-0.035 ± 0.119
Sex	0.03	1	0.867	0.025 ± 0.151
BRSS1	0.51	1	0.473	-0.109 ± 0.152
Ln AL1 + 1 \times risk treatment	1.69	1	0.193	0.117 ± 0.090

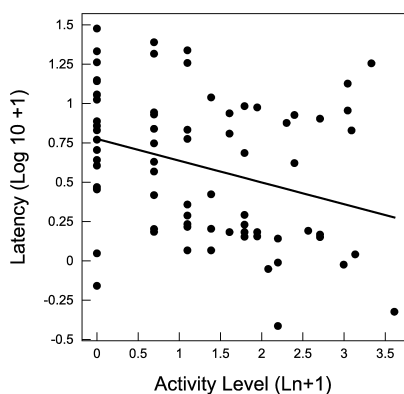


Figure 3. Correlation between latency to resume activity (post-hawk cautiousness) and activity level (AL1; statistics in Table 2). Values of latency based on partial residuals (see methods).

showed a highly significant effect. Of the 37 chaffinches tested in both treatments, 17 showed a ‘plastic’ response (fly in high risk, freeze in low risk) and

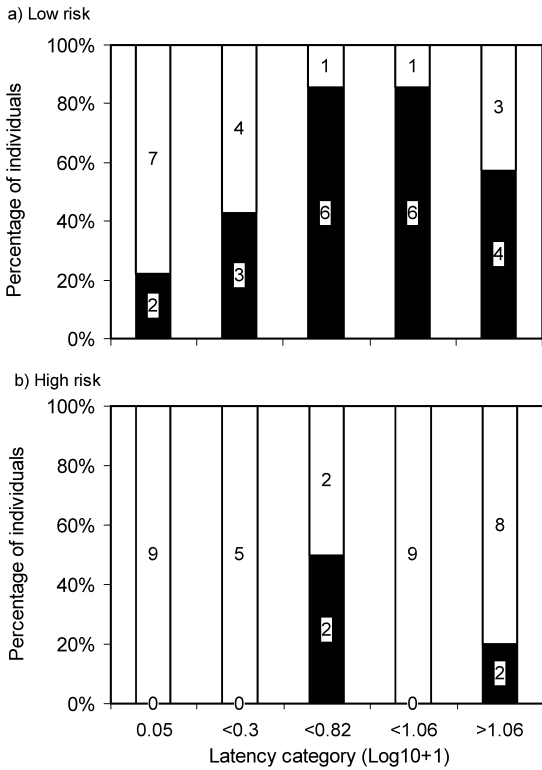


Figure 4. Behavioural responses to the sudden appearance of a hawk relative to post-hawk cautiousness ($\text{Log}_{10} \text{ latency} + 1$) in (a) low risk and (b) high risk treatments. ■ = freeze; □ = fly. Statistical analysis given in text. Number of trials shown in bars. Categories derived with equal percentiles.

20 showed the same response in both treatments (either fly in high and low risk, $N = 16$, or freeze in both, $N = 4$). The probability of showing a plastic response was strongly and negatively correlated to activity level (AL1) averaged across two treatments for each individual (Figure 7). Note that this response mirrors that for the low risk treatment alone (Figure 2a), which is predicted by the fact that essentially all individuals behaved the same way in the high risk treatment (Figure 2b).

Treatment had no significant effect on latency and therefore there was no difference in plasticity between personality types with respect to this behavioural phenotype.

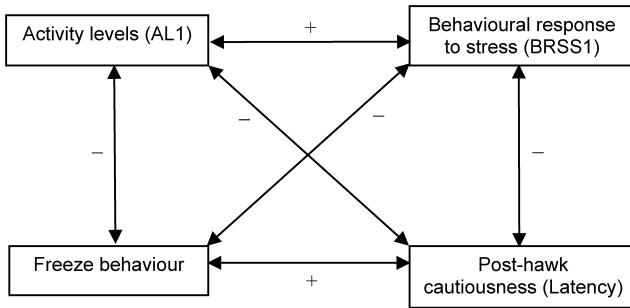


Figure 5. Summary of correlations in the behavioural syndrome. All correlations were significant, though not all independently.

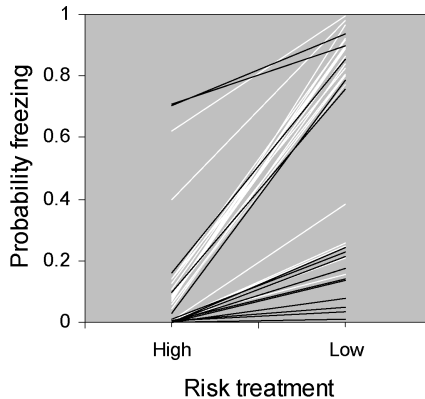


Figure 6. Individual reaction norms using fitted probabilities from a GLMM with $AL \times TR \times \text{individual}$ interaction ($p = 0.11$; see results). Hypoactives (light lines) were more plastic in their response than hyperactives (dark lines). Each line represents an individual's reaction norm and links the two predicted probabilities from the model of a single individual. Hyperactive and hypoactive categories were separated using the mid-point in the range in activity levels (individual ALIs averaged across treatments).

Discussion

Personality, predation risk and behavioural plasticity

Activity level, behavioural response to a stressful situation, latency to resume activity post-hawk release and freezing behaviour were all inter-correlated (Figures 2-5). The first three of these all showed similar or higher repeatability (0.49, 0.44-0.57 and 0.39 respectively) compared to similar variables in other studies (e.g., 0.27-0.66 for exploratory behaviour, Dingemanse et al., 2002; 0.26 for risk taking, van Oers et al., 2004). Taken together, the high

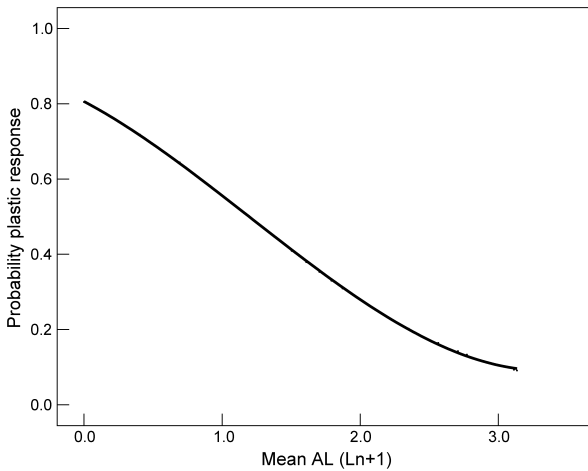


Figure 7. Relationship between the probability of individual chaffinches displaying a plastic response across treatments and their mean activity level scores (ALs averaged across treatments) (logistic regression, $W = 6.77$, $p = 0.009$, $B = -1.185 \pm 0.456$, $N = 37$). Fitted values shown.

level of inter-correlation between all variables and their associated repeatabilities are good evidence for a behavioural syndrome, which suggests that anti-predation behaviour is phenotypically correlated to personality. To our knowledge this is the first study to show this in a taxum other than fish (cited above) or reptiles (Lopéz et al., 2005). The specific context of the result is also novel because, although several studies have considered anti-predation behaviour pre-attack (Huntingford, 1976, 1982) (Godin & Davis, 1995), cautiousness post-attack (Ward et al., 2004; Bell, 2005) or have inferred fitness costs linked to predation (Brown & Dreier, 2002; Sih et al., 2003), none have examined behaviour at the moment of attack.

The hypothesis of differential predation risk amongst personality types is supported by the negative correlation between activity level and latency to resume activity post-hawk (Figure 3). This agrees with the findings of other studies which suggest that bold or relatively active individuals take greater risks in the presence of predators (Huntingford, 1976, 1982; Sih et al., 2003; Ward et al., 2004; Bell, 2005) or after having been startled (Erhard & Mendl, 1999; van Oers et al., 2004). However, drawing a similar conclusion from the negative correlation between activity level and freezing behaviour is dependent on the assumption that freezing was optimal in the low risk situation (Figure 2). We argue this assumption is likely to be true

given that the hawk was not flying directly at the chaffinches and that flying would have drawn the hawk's attention which otherwise would have been oblivious to the chaffinch's presence. Hypoactives were therefore able to assess that the risk of being seen and then caught by the hawk was lower by freezing in the low risk situation than if they escaped. Nevertheless there are alternative explanations for this apparent differential risk sensitivity which we cannot discount. One is that, given hypoactives are generally thought to be more reactive to their surroundings (Wilson et al., 1994; Sih et al., 2004), they realised that escape was impossible in the cage. Our result would then indicate greater reactivity to the presence of the cages rather than risk sensitivity to the proximity of the hawks, and it might be further predicted that the negative correlation would have disappeared if the birds had not been in cages. Against this, almost all birds escaped in the high risk situation, which effectively acted as a control for these other effects, though an interaction between reactivity to the cage and risk level cannot be discounted. Another alternative explanation is that, rather than there being an inherent difference in risk taking behaviour between personalities, hypoactives were slower at detecting or reacting to predators. By the time chaffinches had identified the risk, freezing then became a better option than escaping late relative to hyperactives. At first this explanation might seem unlikely on the grounds that sparrowhawks are highly manoeuvrable, can travel at 25 ms^{-1} (Hilton et al., 1999), and therefore that the proximity of the hawk to the chaffinch in our experimental room would have overridden any advantage a split second would have given to hyperactives. However, even slight delays in escape responses are thought to have consequences for predation risk when the threat is real (Hilton et al., 1999; Quinn & Cresswell, 2005). Furthermore, previous work on our system, albeit with a different setup, showed that slower and hence poorer foragers were indeed slower responding to a model hawk (Cresswell et al., 2003), though it was not tested whether this was due to differences in detection ability or response strategy. Clearly, the precise mechanisms behind differences in freezing behaviour between personalities in our system require further clarification.

While the greater tendency to freeze may have benefited hypoactives in the low risk situation, their tendency to also freeze in the high risk situation may have been suboptimal (Figure 2). Again this interpretation depends on the assumption that escaping was the best option. For example, hypoactive individuals may have been able to assess that the stuffed hawk was not

real, that they were safe in the enclosed cage or that escape was impossible given the close proximity of the hawk when it first appeared and that freezing was still most appropriate. Clearly without actual fitness measures, any further discussion concerning which behaviour was optimal in either situation represents unwarranted speculation. However, our data provides more convincing evidence of differential predation risk amongst personality types when the propensity to freeze is considered across the two situations. Figures 6 and 7 show that hypoactive individuals displayed greater behavioural plasticity in their response to an attacking predator while, in contrast, hyperactives were more stereotypic in their response. We equate this general pattern of greater behavioural plasticity amongst hypoactives to the term 'reactivity' in the reactive-proactive axis (Benus et al., 1990; Koolhaas et al., 1997; Sih et al., 2004). Assuming that greater behavioural plasticity is the preferred state, this result further supports the hypothesis of differential predation risk among animal personalities (Sih et al., 2003; Dingemanse et al., 2004).

The behavioural response to a stressful situation was also correlated to anti-predation behaviour and activity level. Personality has been shown by others to be correlated with physiological measures of stress such as temperature and breathing rate (Carere et al., 2003; Carere & van Oers, 2004). The effects of stress on hormone levels among different personality types, and on resulting behavioural patterns or pathological effects are more complex (Koolhaas et al., 1997, 1999; Sih et al., 2004) and largely beyond the scope of this discussion. Two points can be made at this stage. The first is that the link between stress related hormones and risk assessment under threat of predation risk deserves further study. Birds were clearly under stress in our system but are also likely to be stressed in the wild, for example when exposed to interference competition that results from living in groups, when conflicts arise with conspecifics (Carere et al., 2001, 2003), or when under physiological stress due to hunger. Individual differences in personality are sometimes more pronounced in a stressful situation (Suomi, 2004), which may exacerbate individual risk. Incidentally, this may explain why only the first AL score, when chaffinches were likely to be most stressed, was correlated to freezing behaviour. Though one study has examined corticosterone responses to model predators in a single situation (Cockrem & Silverin, 2002), the extent to which these and other hormonal responses vary between situations and provide proximate explanations for subsequent differences in individual behaviour should prove to be a fruitful avenue of research.

General theoretical implications

Our results, and those concerned with personality theory generally, have important implications for group living theory. The dilution effect (Foster & Treherne, 1981) assumes that all individuals are at equal risk when attacked by a predator. However there is considerable evidence for differential predation risk amongst individuals in groups (Krause & Ruxton, 2002) and it is likely that at least some of these individual differences are linked to personality. This could arise, for example, because relatively safe positions (Hamilton, 1971; Krause, 1994) are more likely to be occupied by cautious individuals, though it could equally be argued that bold individuals parasitize shy individuals by occupying the safest position because they tend to be more dominant. In terms of an animal in the selfish herd (Hamilton, 1971), bold individuals might achieve small 'domains of danger' at the expense of shy individuals. One study on fish in captivity found the former to be the case in their system because bold individuals occupied the front positions within shoals (Ward et al., 2004). Since other studies on captive fish suggest the front positions are at greater risk of predation, this work supports the hypothesis of higher predation risk amongst bold individuals living in groups. Similarly, whether an individual avoids being killed when an attack occurs is partly dependent on whether they make an appropriate escape response (Cresswell, 1993); if hypoactive individuals are more risk sensitive, they may then be more likely to make an appropriate escape response and less likely to make mistakes, either in groups or when alone. From an ecological perspective, predation rates may also be dependent on the relative frequency of different personality types in the population since predation rates are known to vary with prey vulnerability (e.g., Quinn & Cresswell, 2004).

As for predation risk theory generally, differential predation among personalities critically affects our understanding of the trade-off between the risks of starvation and predation (Stephens & Krebs, 1986). Traditionally, theory assumes that, apart from state dependent (e.g., mass and experience) and status (e.g., sex and age) effects, variation in whether individuals can behave optimally in a given situation is explained by individual 'ability' or 'quality' (Goss-Custard, 1996; Newton, 1998; Cresswell, 2001). The theory of personalities, however, suggests that variability can also be caused by differences in genetically inherited, correlated traits adopted by individuals throughout their lives, and that these have limited plasticity which imposes

limitations on the animal's ability to achieve any given optimum. In the case of the chaffinches in this study, then, hyperactives might be seen as investing relatively little in anti-predation behaviour, not because they cannot afford to, but because their personality somehow constrains them from doing otherwise for reasons that are adaptive in the long term (Stephens & Krebs, 1986; Dall et al., 2004; Sih et al., 2004). The converse applies for hypoactives. It follows that some of the variation in apparent individual quality could in fact be explained by personalities. The facts that mass — a typical state dependent variable — and activity level had independent effects on freezing behaviour in our system (Table 1) illustrates that the two phenomena can operate simultaneously and are not mutually exclusive. The relative importance of both effects remains largely unexplored. Finally, though most personality research has focused on the behaviour of individuals as prey or in a non-predation context, predators also have personalities (Riechert & Hedrick, 1993), which has intriguing implications for understanding and predicting the outcome of predator-prey interactions.

Acknowledgements

J. Quinn was supported by a Leverhulme Trust Research Fellowship, and W. Cresswell by a Royal Society University Research Fellowship and a Leverhulme Research Grant. We thank M. Denny, K. Jones, J. Howe and M. Whittingham for help catching chaffinches, D. Wilson for technical support, D. Garant and Anne Charmantier for statistical advice and discussion, C. Devereux for providing hawk speeds and B. Sheldon for helpful discussion. We thank A. Bell for stimulating discussion. Thorough review by Niels Dingemanse and an anonymous referee improved the paper.

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