



## Personality and body condition have additive effects on motivation to feed in Zebra Finches *Taeniopygia guttata*

MORGAN DAVID,<sup>1,2,\*†</sup> YANNICK AUCLAIR,<sup>1,†</sup> LUC-ALAIN GIRALDEAU<sup>2</sup> & FRANK CÉZILLY<sup>1</sup>

<sup>1</sup>Université de Bourgogne, Équipe Écologie Évolutive, UMR CNRS 6282 Biogéosciences, 6 boulevard Gabriel, 21000 Dijon, France

<sup>2</sup>Université du Québec à Montréal, Département des Sciences biologiques, Groupe de Recherche en Écologie Comportementale et Animale, CP 8888, Succursale Centre Ville, Montréal, H3C 3P8 QC, Canada

Several hypotheses have been proposed to account for the adaptive evolution of personality, defined as inter-individual differences in behaviour that are consistent over time and across situations. For instance, the ‘pace-of-life syndrome’ hypothesis suggests that personality evolved as a behavioural correlate of life-history trajectories that vary within populations. Thus, proactivity, corresponding to higher exploratory tendencies or higher boldness levels, has been linked to higher productivity or mortality rates. However, the extent to which proactivity is associated with a higher motivation to forage remains poorly understood. Moreover, although personality and its effects on foraging behaviour are usually considered to be independent of any motivational or nutritional state, few studies so far have challenged this. Here we show that personality traits, both individually or combined using a principal component analysis, and body condition have additive effects on latency to feed following food deprivation in the Zebra Finch *Taeniopygia guttata*, with personality accounting for 41% and body condition for about 20% of the total variation in latency to feed. In accordance with the pace-of-life syndrome hypothesis, latency to feed was negatively related to the degree of proactivity and positively related to body condition. Thus, proactive individuals and individuals in poorer condition were quicker to start feeding after a period of food deprivation. The absence of a significant interaction between personality and body condition further suggests that the effect of personality was independent of body condition. We discuss the relevance of our results in relation to the different factors influencing foraging in birds. Moreover, we place our results within a life-history framework by emphasizing the correlated evolution of life-history traits and personality.

**Keywords:** exploration, feeding latency, life-history trade-offs, pace-of-life syndrome hypothesis, principal component analysis, productivity.

A growing literature shows the importance of the concept of personality, defined as inter-individual

differences in behaviour that are consistent over time and across situations, in both captive and wild animal populations (Dingemanse *et al.* 2002, Montiglio *et al.* 2010, David *et al.* 2011a). These behavioural differences may evolve through both natural (Réale & Festa-Bianchet 2003) and sexual selection (Schuett *et al.* 2010). Several hypotheses, from the role of sexual selection (Schuett *et al.* 2010) to state-based differences (Dall *et al.* 2004), have been formulated to account for the evolution of personality within populations (Dingemanse &

\*Corresponding author.

Email: morgan.david@gmx.fr

<sup>†</sup>Present address: Centre for Ecology and Conservation, Biosciences, College of Life & Environmental Sciences, University of Exeter, Cornwall Campus, Penryn, Cornwall TR10 9EZ, UK.

<sup>‡</sup>Present address: University of Zürich-Irchel, Institute of Evolutionary Biology and Environmental Studies, c/o Animal Behaviour Group, Winterthurerstrasse 190, 8057 Zürich, Switzerland.

Wolf 2010). The 'pace-of-life syndrome' hypothesis proposes that personality evolved as a behavioural correlate of life-history strategies varying at the population level (Réale *et al.* 2010). Thus, proactivity, corresponding to higher exploratory tendencies or higher boldness, and associated with a high metabolic rate (Careau *et al.* 2010), high growth rates and a high productivity (Biro & Stamps 2008) may be constitutive of a fast pace-of-life (Réale *et al.* 2010). Conversely, a slower pace-of-life may be related to reactive behaviours, such as shyness, a low metabolic rate, low growth rates and low productivity (but see Adriaenssens & Johnsson 2009, 2011, David *et al.* 2011b). Several studies have successfully linked high exploration tendencies or risk-prone behaviour to fitness-related traits such as survivorship (Biro *et al.* 2004), social dominance (David *et al.* 2011a) or food intake (Ward *et al.* 2004). To date, however, few studies have examined whether proactivity is associated with a higher motivation to engage in foraging activity (Hallerman *et al.* 2007). Yet, a higher motivation to feed is expected to help proactive individuals acquire enough resources to sustain a high level of productivity.

Although personality and its effects on foraging behaviour are usually considered to be independent of individual variation in motivational or nutritional state (Réale *et al.* 2007, Bergmüller 2010), this assumption has not been challenged experimentally. This is surprising given the recent suggestion that personality and consistent individual variation in metabolic rate may be subject to correlated evolution (Careau *et al.* 2008, Biro & Stamps 2010). Indeed, it is intuitive to imagine that a consistently high or low resting metabolic rate is manifested, respectively, as higher or lower hunger levels, which in turn increases or decreases motivation to feed (Careau *et al.* 2008). Considering motivational and nutritional state is all the more important because several tests designed to assess personality involve a foraging task, such as the measurement of neophobia or risk-taking (e.g. David *et al.* 2011a). Despite this, few studies to date have controlled for the influence of nutritional state on the expression of personality traits. More precisely, little is known about whether personality and natural variation in body condition have additive or interactive effects on individual motivation and foraging behaviour.

We assess the joint effect of personality (David *et al.* 2011a) and body condition on the motivation

of captive Zebra Finches *Taeniopygia guttata* to feed after a period of food deprivation, assessed from the latency to forage. We expected birds with lower nutritional status (i.e. those in poorer condition) to be at higher risk of starvation and therefore to show higher hunger levels and to be more willing to feed. Latency to start feeding is commonly used to measure individual motivation or willingness to feed in birds (e.g. Lazarus 1979, Sundberg 1995, Seferta *et al.* 2001) and may thus represent an adequate behavioural test with which to evaluate the joint influence of personality and natural variation in body condition on foraging behaviour.

## METHODS

### Study subjects

Forty-one wild-type young adult female Zebra Finches, previously used in another study (David *et al.* 2011a), constituted our study sample. Only females were used, as the present study was part of a larger research programme on the influence of personality on female sexual behaviour (David & Cézilly 2011). Birds were kept in a single room and maintained in dyads in home cages (60 × 33 × 30 cm) for 10 days before the experiments started. Temperature was maintained at 22 ± 2° C and the photoperiod was 13 : 11 h light : dark (07:30–20:30 h), with a 30-min period of increasing light intensity in the morning and decreasing light intensity in the evening to imitate dawn and dusk. Each bird was identified by an orange numbered leg ring (size XF; AC Hughes, Hampton Hill, UK). Individuals were provisioned with millet seeds, cuttlefish bones and water *ad libitum*.

### Assessment of personality traits

Four principal, inter-related, personality traits previously identified in Zebra Finches (David *et al.* 2011a) were assessed twice with a 1-week interval at the rate of one trial per day for each bird. Trials were performed in the same room in which the colony was maintained to prevent stress due to social isolation. Birds were deprived of food for 1 h before each trial to standardize hunger levels (David *et al.* 2011a).

### Activity

Intrinsic activity was recorded in a cage similar to home cages (a familiar environment) where birds

were maintained. These cages contained four perches and two water dispensers. Birds were placed alone for 12 h in a home cage before the trial. We then recorded individual behaviour using a video camera (JVC Everio GZ-MG20, JVC France SAS, Carrières sur Seine, France) that had been placed 50 cm in front of the cage 1 h before the trial to avoid any novelty effect. We scored activity during consecutive periods of 5 s during a 10-min block. During each period, the bird was assigned a score of 1 if it moved between perches or the equivalent distance on the floor. Birds had no access to any food source when tested.

#### *Exploration tendencies*

Exploration tests are sometimes referred to as novel environment tests (Dingemanse *et al.* 2002). Individual exploratory tendencies were assessed in a large, unfamiliar cage (l × w × h: 140 × 140 × 70 cm) (David *et al.* 2011a) with opaque walls and a clear Plexiglas ceiling, containing five artificial trees (50 cm high) composed of four small branches each. A single bird was introduced into a small black box placed against one side of the apparatus. Experimenters then gently opened a trap from outside the room that enabled the individual to enter the apparatus. Again, birds had no access to any food source when tested. The cumulative number of movements between trees and between branches recorded during 1 h was taken as the exploration score (David *et al.* 2011a).

#### *Reaction to startle*

Also known as 'risk-taking behaviour' (van Oers *et al.* 2004), this test aims at assessing individual latency to resume feeding after having been threatened off the feeder. Birds were placed alone for 12 h in a cage similar to a home cage before the trial. The trial consisted of replacing the feeder within the home cage after the 1-h food-deprivation period. A small device, corresponding to two washers wedged between the feeder top and the trap door above it, was set up and linked with a thin thread to the experimenter outside the room. Pulling the thread caused the bird to fly off the feeder at the moment it came to feed. Then latency to resume feeding after this stressful event was considered as a measure of risk-taking behaviour (David *et al.* 2011a). Individuals resuming feeding early, i.e. more willing to take risks, thus had lower values.

#### *Neophobia*

This was defined as the tendency to approach the feeder and consume seeds from it (David *et al.* 2011a). As above, individuals were kept alone for 12 h before the trial, with a feeder placed in one side of the cage. Immediately before the trial, the bird was deprived of food for 1 h. Then, we replaced a feeder full of seeds in the cage, and added an unfamiliar object (a small bag in one trial and a football figurine in the other) 10 cm from it. We then video-recorded each bird's latency time to reach the feeder, the number of times it came to feed, the amount of time it fed, the latency time to perch near the feeder and the number of times it perched near the feeder. All these variables were reduced to a single synthetic value using a principal component analysis (David *et al.* 2011a) from which we derived individual scores. Highest neophobia scores corresponded to individuals spending more time feeding near the novel object (i.e. less neophobic birds).

#### **Motivation to feed**

Motivation to feed was assessed from the latency to start feeding after a 1-h food deprivation period. For the purpose of this test, birds were placed alone in a home cage the evening before the trial. Seed feeders were removed from the home cage for 1 h while a miniature video camera was placed 1 m in front of the cage in order for the birds to get used to it before the recording. After this period, a single feeder was gently replaced in its normal location at the furthest side of the cage. Individual behaviour was then observed through the video camera. Latency time to start feeding was then recorded for a maximum of 10 min. This test was performed in the middle of the session of behavioural trials, on the same day as the 'reaction to startle' test, and repeated twice with a 1-week interval to check for consistency.

#### **Morphometric measures**

All morphometric measurements were recorded 1 day before and 1 day after the behavioural trials. Tarsus length was measured with a digital calliper to the nearest 0.1 mm. Birds were weighed to the nearest 0.01 g with an electronic balance (OHAUS, Scout Pro SPU202, Ohaus Europe GmbH, Nänikon, Switzerland) at the same time of day for each bird. The two values were averaged

for each individual. We measured individual body condition as residuals of the linear regression of  $\log_{10}(\text{average weight})$  on  $\log_{10}(\text{average tarsus length})$  (Carrascal *et al.* 1998, Strong & Sherry 2000, Schamber *et al.* 2009, however see Merilä *et al.* 2001).

### Statistical analyses

Details of the consistency of personality traits can be found in David *et al.* (2011a). We here used the average of the two recorded values for each personality trait as our personality variables. As reaction to startle, neophobia, exploration tendencies and activity were previously found to be inter-related (David *et al.* 2011a), we computed a multivariate personality measure (hereafter termed the personality synthetic value) from a principal component analysis of these four traits. The first axis of this analysis explained 51.3% of the variance, with eigenvectors of each trait on this axis as follows: exploration tendencies, 0.46; activity, 0.53; neophobia, 0.52; reaction to startle, -0.50. Individuals defined by a high score were more active, more exploratory, less neophobic and more willing to take risks. They were therefore categorized as 'proactive', whereas individuals with low scores were less active, less exploratory, more neophobic, less willing to take risks and categorized as 'reactive' (Réale *et al.* 2007). Consistency of motivation to feed was assessed from the ANOVA intra-class correlation coefficient ( $R$ ) using Lessells and Boag's (1987) method. This procedure assesses the proportion of the total variance that is attributable to inter-individual variation vs. intra-individual variation. Thus, the more the total variance is generated by differences between individuals, the more the behaviour is repeatable within individuals. Data for one of the two trials were missing for two individuals due to technical problems. These birds were thus assigned a single value. Therefore, the repeatability of 'latency to start feeding' was estimated from 39 individuals. Mean latency to start feeding was otherwise calculated from the two trials and used thereafter. This latter variable was log-transformed to achieve normality. For each of the two trials, the influence of the time when trials were carried out (morning or afternoon) on latency to start feeding was tested using  $t$ -tests.

We performed separate multiple linear regression analyses to assess the influence of each personality trait and its interaction with body condition on

latency to start feeding. Moreover, we computed the Pearson's correlation coefficient to provide an effect size of the relationship between the two variables. Last, we ran a multiple regression analysis to test the joint effect of the personality synthetic value derived from the principal components analysis and body condition on latency to start feeding. All analyses were conducted using JMP 5.0.1 statistical software (SAS Institute, Cary, NC, USA).

### RESULTS

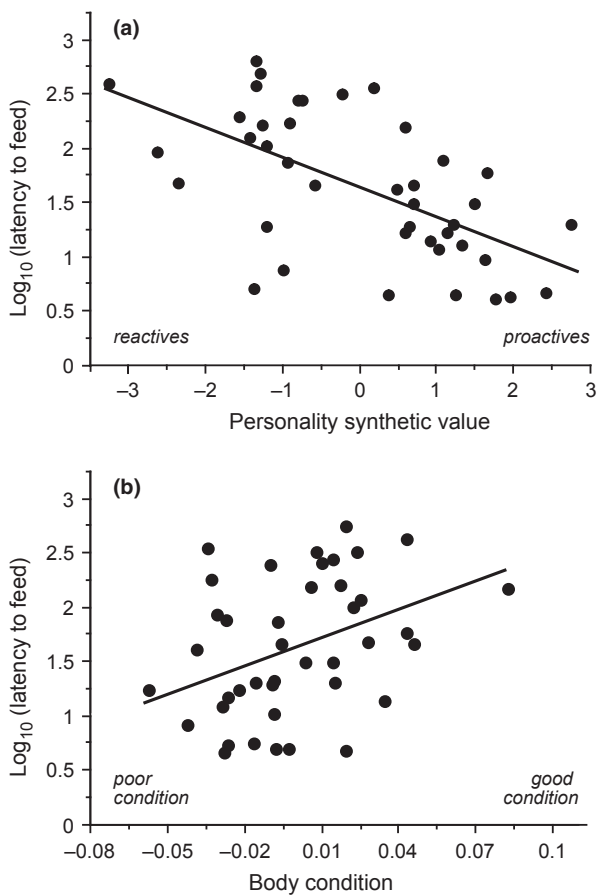
Latency to start feeding did not differ between the first and the second trial (paired  $t$ -test:  $t_{38} = -0.43$ ,  $P = 0.67$ ), was highly consistent between trials ( $R = 0.75$ ,  $P < 0.0001$ ,  $n = 39$ ) and did not depend on the time of the day when the trial was conducted (1st trial:  $t_{38.5} = 0.09$ ,  $P = 0.93$ ; 2nd trial:  $t_{37} = 0.57$ ,  $P = 0.57$ ). The median value of latency to start feeding, averaged across the two trials, was 45.5 s (interquartile range: 14.1–154.5 s.). All birds started feeding within the 10-min period.

Latency to start feeding was significantly influenced by neophobia (regression line slope  $b = -0.14$ ,  $F_{1,37} = 6.08$ ,  $P = 0.02$ ; Pearson's  $r = -0.34$ ), exploration tendencies ( $b = -0.32$ ,  $F_{1,37} = 7.22$ ,  $P = 0.01$ ;  $r = -0.39$ ), reaction to startle ( $b = 0.80$ ,  $F_{1,37} = 46.2$ ,  $P < 0.0001$ ;  $r = 0.76$ ) and activity ( $b = -0.64$ ,  $F_{1,37} = 4.23$ ,  $P = 0.05$ ;  $r = -0.24$ ). There was no significant interaction between body condition and any personality trait affecting latency to feed ( $P > 0.55$  for each model).

The multiple regression analysis revealed that both the personality synthetic value ( $b = -0.26$ ,  $R^2 = 0.41$ ,  $F_{1,37} = 25.0$ ,  $P < 0.0001$ ; Fig. 1a) and body condition ( $b = 7.72$ ,  $R^2 = 0.19$ ,  $F_{1,37} = 8.93$ ,  $P = 0.005$ ; Fig. 1b) affected latency to start feeding, but there was no significant interaction between the two predictor variables ( $F_{1,37} < 0.01$ ,  $P = 0.98$ ), indicating additive effects of body condition and personality. Thus, proactive individuals started feeding sooner than reactive ones after 1 h of food-deprivation. Similarly, individuals in poor condition started feeding sooner than individuals in good condition. The personality synthetic value was not related to body condition (Pearson's  $r < -0.01$ ,  $P = 0.99$ ,  $n = 41$ ).

### DISCUSSION

Birds in poorer body condition and those with more proactive behaviour (more active, exploratory,



**Figure 1.** (a) Significant regression of latency to start feeding on the personality synthetic value of female Zebra Finches. Proactive individuals started feeding sooner than reactive individuals. (b) Significant regression of latency to start feeding on body condition of female Zebra Finches. Body condition was computed as the residuals of the linear regression of body mass on tarsus length. Individuals in poorer condition started feeding sooner.

risk-taking and less neophobic) expressed a higher motivation to feed. Both neophobia and risk-taking were assessed in a feeding context and may themselves reflect differences in feeding motivation mediated by nutritional state. However, we also found a positive link between exploration and activity, assessed in a non-feeding context, and feeding motivation. We are therefore confident that the link between proactivity and motivation to feed is biologically meaningful and not biased by individual nutritional state. Moreover, personality was not related to body condition. These findings add to the recent literature linking feeding behaviour to personality (Biro & Booth 2009),

while emphasizing the role of personality on the outcome of behavioural tests. In Guppies *Poecilia reticulata*, for instance, unpredictable availability of food during early life leads individuals to adopt riskier behaviours (Chapman *et al.* 2010). In the present study, we found no significant interaction between body condition and personality on latency to start feeding, confirming one key assumption of personality studies (Réale *et al.* 2007, but see Schuett & Dall 2009). Indeed, personality appears to be independent of body condition in female Zebra Finches, indicating that its influence on foraging behaviour is independent of hunger levels or state.

Various studies have used motivation to feed to assess, for example, food value, variance-sensitive foraging, or the decisions underlying individual behaviour within the hiding/foraging trade-off (Martín *et al.* 2003). Our results indicate that, all else being equal, motivation to feed is independently affected by both personality and body condition. We therefore suggest that both should be taken into account when assessing inter-individual variation in feeding motivation, at least in Zebra Finches and possibly in other species. For example, it has been shown that Zebra Finches in poor condition had a higher feeding success in a scramble competition (David & Giraldeau 2012), perhaps simply because of their higher motivation to feed. However, a higher feeding success may not necessarily translate into an increase in condition or higher fitness, as Zebra Finches in poor condition might have a higher basal metabolic rate (Mathot *et al.* 2009, Mathot & Giraldeau 2010). Personality and body condition may also affect the foraging decision rules used by individuals. For example, lower profitability of foraging options are confounded with a lower motivation to feed, possibly related to personality, and may affect the conclusions of prey-choice studies (Krebs *et al.* 1977). Further work may then benefit from considering variation in personality and body condition when investigating the foraging decision rules used by animals (David *et al.* 2011b).

Similarly, the possibility exists that the assessment of personality in a feeding context may be confounded by differences in body condition. Indeed, these trials commonly involve the measurement of individual willingness to feed near a novel object or the latency to forage. Intuitively, individual behaviour within such trials could be affected by nutritional state, just as body condition

affected latency to start feeding in the present study. Thus, we might predict that individuals in poorer condition would be bolder in feeding near a novel object or quicker to resume feeding after a perturbation. Conversely, personality trials excluding any foraging might be more reliable as they excluded the possibility that willingness to forage drives behavioural performance. Despite this, we found that the expression of personality was not associated with body condition in the present sample. Yet, given the possible influence of condition of foraging behaviour, we feel that it is important to investigate the relationship between an index of nutritional state such as body condition, which can be standardized using a food-deprivation period, and personality measures when trials involve a foraging task.

Finally, in accordance with the 'pace-of-life syndrome' hypothesis (Careau *et al.* 2008, Réale *et al.* 2010), our results are consistent with the proposition by Biro and Stamps (2008) that inter-individual variation and within-individual consistency in personality may have co-evolved with differences in organisms' productivity (i.e. growth or fecundity), associated with differences in growth–mortality trade-offs within populations (Stamps 2007, Wolf *et al.* 2007). Several studies across taxa show a positive relationship between proactivity and food intake or growth (Biro & Stamps 2008). In the present study, motivation to feed was highly consistent, as were personality traits assessed from the present sample (see David *et al.* 2011a). Moreover, feeding motivation and personality were correlated. Taken together, these findings suggest that different individuals may adopt different and consistent life-history trajectories. Higher motivation to feed might then be a behavioural mechanism favouring higher, and possibly opportunistic, food intake in proactive individuals, and as a consequence may positively affect growth rate and productivity in general (Hallerman *et al.* 2007, Millot *et al.* 2008).

We thank Sébastien Motreuil for his assistance during bird care and device building, Elise Melloul for her assistance during the experiments, and Pete Biro, Wiebke Schuett, Simon Butler, Jeremy Wilson and an anonymous referee for useful comments on a previous draft. This work was funded by both a PhD grant provided to M.D. and a master honorific grant to Y.A. from the Conseil Régional de Bourgogne. Experiments in this study were performed in accordance with the University of Burgundy's procedures concerning animal ethics and the British Ornithologists' Union statement of ethics.

## REFERENCES

- Adriaenssens, B. & Johnsson, J.I.** 2009. Personality and life-history productivity: consistent or variable association? *Trends Ecol. Evol.* **24**: 179–180.
- Adriaenssens, B. & Johnsson, J.I.** 2011. Shy trout grow faster: exploring the links between personality and fitness-related traits in the wild. *Behav. Ecol.* **22**: 135–143.
- Bergmüller, R.** 2010. Animal personality and behavioural syndromes. In Kappeler, P. (ed.) *Animal Behaviour – Evolution and Mechanisms*: 587–621. Heidelberg: Springer.
- Biro, P.A. & Booth, D.J.** 2009. Extreme boldness precedes starvation mortality in six-lined trumpeter (*Pelates sexlineatus*). *Hydrobiologia* **635**: 395–398.
- Biro, P.A. & Stamps, J.A.** 2008. Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.* **23**: 361–368.
- Biro, P.A. & Stamps, J.A.** 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends Ecol. Evol.* **25**: 653–659.
- Biro, P.A., Abrahams, M.V., Post, J.R. & Parkinson, E.A.** 2004. Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proc. R. Soc. Lond. B* **271**: 2233–2237.
- Careau, V., Thomas, D., Humphries, M.M. & Réale, D.** 2008. Energy metabolism and animal personality. *Oikos* **117**: 641–653.
- Careau, V., Réale, D., Humphries, M.M. & Thomas, D.** 2010. The pace of life under artificial selection: personality, energy expenditure and longevity are correlated in domestic dogs. *Am. Nat.* **175**: 753–758.
- Carrascal, L.M., Senar, J.C., Mozetich, I., Uribe, F. & Doménech, J.** 1998. Interactions among environmental stress, body condition, nutritional status, and dominance in Great Tits. *Auk* **115**: 727–738.
- Chapman, B.B., Morrell, L.J. & Krause, J.** 2010. Unpredictability in food supply during early life influences boldness in fish. *Behav. Ecol.* **21**: 501–506.
- Dall, S.R.X., Houston, A.I. & McNamara, J.M.** 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* **7**: 734–739.
- David, M. & Cézilly, F.** 2011. Personality may confound common measures of mate-choice. *PLoS ONE* **6**(9): e24778.
- David, M. & Giraldeau, L.-A.** 2012. Zebra Finches in poor condition produce more and consume more food in a producer-scrounger game. *Behav. Ecol.* **23**: 174–180.
- David, M., Auclair, Y. & Cézilly, F.** 2011a. Personality predicts social dominance in female Zebra Finches, *Taeniopygia guttata*, in a feeding context. *Anim. Behav.* **81**: 219–224.
- David, M., Cézilly, F. & Giraldeau, L.-A.** 2011b. Personality affects Zebra Finch feeding success in a producer-scrounger game. *Anim. Behav.* **82**: 61–67.
- Dingemanse, N.J. & Wolf, M.** 2010. Recent models for adaptive personality differences: a review. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**: 3947–3958.
- Dingemanse, N.J., Both, C., Drent, P.J., van Oers, K. & van Noordwijk, A.J.** 2002. Repeatability and heritability of exploratory behaviour in Great Tits from the wild. *Anim. Behav.* **64**: 929–938.

- Hallerman, E.M., McLean, E. & Fleming, I.A. 2007. Effects of growth hormone transgenes on the behavior and welfare of aquacultured fishes: a review identifying research needs. *Appl. Anim. Behav. Sci.* **104**: 265–294.
- Krebs, J.R., Erichsen, J.T., Webber, M.I. & Charnov, E.L. 1977. Optimal prey-selection by the Great Tit (*Parus major*). *Anim. Behav.* **25**: 30–38.
- Lazarus, J. 1979. Flock size and behaviour in captive Red-billed Weaverbirds (*Quelea quelea*): implications for social facilitation and the functions of flocking. *Behaviour* **71**: 127–145.
- Lessells, C.M. & Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* **104**: 116–121.
- Martín, J., López, P. & Cooper, W.E. Jr 2003. When to come out from a refuge: balancing predation risk and foraging opportunities in an alpine lizard. *Ethology* **109**: 77–87.
- Mathot, K.J. & Giraldeau, L.-A. 2010. Family-related differences in social foraging tactic use in the zebra finch (*Taeniopygia guttata*). *Behav. Ecol. Sociobiol.* **64**: 1805–1811.
- Mathot, K.J., Godde, S., Careau, V., Thomas, D.W. & Giraldeau, L.-A. 2009. Testing dynamic variance-sensitive foraging using individual differences in basal metabolic rates of Zebra Finches. *Oikos* **118**: 545–552.
- Merilä, J., Kruuk, L.E.B. & Sheldon, B.C. 2001. Natural selection on the genetical component of variance in body condition in a wild bird population. *J. Evol. Biol.* **14**: 918–929.
- Millot, S., Begout, M.-L., Person-Le Ruyet, J., Breuil, G., Di-Poi, C., Fievet, J., Pineau, P., Roue, M. & Severe, A. 2008. Feed demand behavior in sea bass juveniles: effects on individual specific growth rate variation and health (inter-individual and inter-group variation). *Aquaculture* **274**: 87–95.
- Montiglio, P.O., Garant, D., Thomas, D. & Réale, D. 2010. Individual variation in temporal activity patterns in open-field tests. *Anim. Behav.* **80**: 905–912.
- van Oers, K., Drent, P.J., de Goede, P. & van Noordwijk, A.J. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proc. R. Soc. Lond. B* **271**: 65–73.
- Réale, D. & Festa-Bianchet, M. 2003. Predator-induced natural selection on temperament in bighorn ewes. *Anim. Behav.* **65**: 463–470.
- Réale, D., Reader, S.M., Sol, D., McDougall, P.T. & Dingemanse, N.J. 2007. Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**: 291–318.
- Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V. & Montiglio, P.O. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**: 4051–4063.
- Schamber, J.L., Esler, D. & Flint, P.L. 2009. Evaluating the validity of using unverified indices of body condition. *J. Avian Biol.* **40**: 49–56.
- Schuett, W. & Dall, S.R.X. 2009. Sex differences, social context and personality in Zebra Finches, *Taeniopygia guttata*. *Anim. Behav.* **77**: 1041–1050.
- Schuett, W., Tregenza, T. & Dall, S.R.X. 2010. Sexual selection and animal personality. *Biol. Rev.* **85**: 217–246.
- Seferta, A., Guay, P.J., Marzinotto, E. & Lefèbvre, L. 2001. Learning differences between feral pigeons and Zenaida doves: the role of neophobia and human proximity. *Ethology* **107**: 281–293.
- Stamps, J.A. 2007. Growth-mortality tradeoffs and ‘personality traits’ in animals. *Ecol. Lett.* **10**: 355–363.
- Strong, A.M. & Sherry, T.W. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *J. Anim. Ecol.* **69**: 883–895.
- Sundberg, J. 1995. Female Yellowhammers (*Emberiza citrinella*) prefer yellower males: a laboratory experiment. *Behav. Ecol. Sociobiol.* **37**: 275–282.
- Ward, A.J.W., Thomas, P., Hart, P.J.B. & Krause, J. 2004. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behav. Ecol. Sociobiol.* **55**: 561–568.
- Wolf, M., van Doorn, G.S., Leimar, O. & Weissing, F.J. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature* **447**: 581–584.

Received 4 October 2011;  
revision accepted 22 January 2012.  
Associate Editor: Simon Butler.