



Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context

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Although personality has been defined as a suite of correlated behaviours, most studies of animal personality actually consider correlations between a few traits. We examined the repeatability and correlational structure of five potential personality traits (activity, neophobia, exploratory tendencies, risk-taking behaviour and obstinacy), in female zebra finches. In addition, we assessed to what extent personality influenced social dominance in a feeding context in this gregarious species. All personality traits were found to be highly repeatable within individuals. In addition, except for obstinacy, all of them were related to each other, thus defining a behavioural syndrome. Social dominance was predicted by personality, with proactive individuals being more likely to be dominant. Our results suggest that personality can be considered as a new static factor influencing within-group hierarchies. We finally discuss these results in terms of the consequences for the evolution of personalities and the need to take several traits into account to provide full descriptions of individual personality.

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Consistent individual differences in behaviour across various contexts and situations are of increasing interest to behavioural ecologists (Sih et al. 2004a; Réale et al. 2007). Several studies have shown that individual variation in personality can have fitness consequences (reviewed in Smith & Blumstein 2008). For instance, survival between two breeding seasons is related to personality in female red squirrels, *Tamiasciurus hudsonicus* (Boon et al. 2008), whereas the influence of personality on survival varies according to population density in the common lizard, *Lacerta vivipara* (Cote et al. 2008). Reproductive fitness can also be influenced by personality, as shown by recent evidence in fish (Wilson et al. 2010a), birds (van Oers et al. 2008) and mammals (Réale et al. 2009). In addition, individual variation in personality can be repeatable (Quinn et al. 2009; Wilson & Godin 2009) and linked to genetic variation (van Oers et al. 2004a, b; Fidler et al. 2007), suggesting that variation in personality can be exposed to natural selection.

Assessing the ecological relevance of personality, both between and within species (Uher 2008), however, requires that personality be assessed in some standardized way. Although personality has been defined as a suite of correlated behaviours expressed either within a given behavioural context or across different contexts (Sih et al. 2004b), in practice most studies of animal personality consider correlations between a few traits, focusing eventually on only two aspects of personality such as, for instance, exploration and risk taking (Brodin 2009; Harcourt et al. 2009; but see Wilson et al. 2010b). This is in strong contrast to studies of personality in human beings, where personality is assessed from patterns of covariation of traits belonging to several broad factors (McCrae et al. 1998; Uher 2008). Recent studies of human personality, however, suggest that measuring only a few personality traits might be insufficient to predict complex behaviours (Paunonen et al. 2003; Ashton & Lee 2007; de Vries et al. 2009). In particular, using a larger number of factors is recommended to reduce error in behaviour prediction and increase accuracy in behaviour explanation (Paunonen & Ashton 2001), particularly in the case of relatively complex behaviours, which can be considered multidimensional and multidetermined (Paunonen et al. 2003).

Although various constraints can limit the number of personality dimensions that can be quantified using free-ranging individuals,

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experiments with captive individuals may allow a deeper consideration of the multidimensional nature of personality. The present study was precisely designed to investigate consistent differences in personality between individuals, while considering simultaneously several dimensions of personality. To that end, we quantified a series of traits previously used to estimate personality in birds in a nonsocial context, and assessed the correlational structure between those traits. We then investigated to what extent variation in personality was a predictor of dominance status (Fox et al. 2009), a character known to have a strong influence on fitness in socially living organisms (Ellis 1995; Koivula et al. 1996; Mennill et al. 2004), and to be potentially influenced by personality in the wild (Dingemanse et al. 2004; Fox et al. 2009). Following the 'life history productivity' hypothesis (Biro & Stamps 2008), according to which some individuals express a personality enabling them to sustain a high productivity, we predicted that such proactive individuals should have preferential access to food through dominance. We chose the zebra finch as our model organism as it is a highly social bird species that is regularly used in experimental studies of behaviour (Zann 1996), including personality (Martins et al. 2007; Schuett & Dall 2009).

METHODS

Biological Model

We used 42 wild-type and virgin, but sexually mature, female zebra finches, purchased from a reliable local supplier. Only females were used, as the present study was part of a larger research programme on the influence of personality on female sexual behaviour. Birds were kept in a single experimental room and maintained in individual cages (60 × 33 cm and 30 cm high), containing four perches at different heights and four feeders with food and water. Room temperature was maintained at 22 ± 2 °C and the photoperiod was 13:11 h light:dark (0730–2030 hours), with a 30 min period simulating dawn and dusk through increasing and decreasing light intensity in the morning and evening. Each individual was identified by an orange numbered ring (A. C. Hughes, Hampton Hill, U.K., size XF). Birds were provisioned with millet seeds, cuttlebones and water ad libitum. Vegetables were only given outside of the experimental periods. Birds were not given any additional vitamins. One bird looking ill and showing little activity was permanently removed from the experiment, reducing our sample size to 41 individuals. The bird seemed unable to cope with a new stressful situation, but recovered after being isolated and provided with vitamins. At the end of the experiment, birds were kept in groups of two to be used in subsequent studies. The experimental procedures were in agreement with the ethical requirements of the Université de Bourgogne.

Personality Traits

Each of the following traits was assessed twice for each individual at a 1-week interval.

Exploratory tendencies

In line with previous studies of exploratory behaviour in birds (Dingemanse et al. 2002; Drent et al. 2003; van Oers et al. 2004a), individual exploratory tendencies were assessed in a large, unfamiliar cage (140 × 140 cm and 70 cm high) with opaque walls and a Plexiglas ceiling, containing five artificial trees, each composed of four small branches. Birds were deprived of food for 1 h before being introduced into the cage in a black box placed against a small sliding door on one side of the apparatus. The experimenters then gently opened the door with a pulley system from outside the

room. From that moment, individual behaviour inside the apparatus was recorded for 1 h, using a video camera (JVC Everio GZ-MG20) placed 1 m above the cage. During the analysis, the experimenters recorded the number of movements between trees and between branches of a single tree. The cumulative number of movements was subsequently taken as a measure of exploratory tendencies.

Neophobia

Neophobia was assessed using the novel object test procedure (Boogert et al. 2006; Spencer & Verhulst 2007; Tobler & Sandell 2007). After 1 h of food deprivation, an unfamiliar object was introduced within the cage 10 cm from the single feeder. We used a different object (a small bag or a soccer figurine) on the first and second trial to avoid habituation, with the order of presentation being randomly chosen for each bird. Individual behaviour was then videorecorded for 15 min. The experimenters recorded latency to perch within 15 cm of the feeder, latency to reach the feeder and take seeds, the number of times the birds came to feed, the number of times they perched near the feeder, and the amount of time spent feeding (s). Mean values were calculated from both trials for each measure and a principal components analysis (PCA) was performed on all measures to synthesize them into a single value of neophobia (first axis explained 71.92% of variance; eigenvectors: latency to perch near the feeder: -0.42; number of times on the perch: 0.46; latency to reach the feeder: -0.46; number of feeding events: 0.48; time spent feeding: 0.41). Neophobia score was then negatively related to the actual degree of neophobia, with low values characterizing neophobic individuals. For convenience, we reversed neophobia scores for subsequent analysis, such that higher values corresponded to neophobic individuals. Owing to an accident, the behavioural measures recorded in the 'small bag' conditions were missing for one individual, reducing our sample size to 40 individuals when testing the influence of the type of object on neophobia. For this particular individual, we then only considered the behavioural measures in front of the soccer figurine for the neophobia test.

Activity

Intrinsic activity was videorecorded in individual home cages immediately before the neophobia test. Birds were deprived of food for 1 h before each trial, and had no access to any food source during it. Following the time-sampling technique (Martin & Bateson 1993), the experimenters assigned a score of 1 if the birds had moved between two perches or an equivalent distance on the floor during the last 5 s. As activity was assessed for 10 min, individuals could then receive a maximal score of 120. If they stayed still, birds were assigned a score of zero.

Startle test

Startle tests classically assess latency to resume foraging after a stressful event (Martins et al. 2007). Birds were deprived of food for 1 h before the trial, after which the feeder was reintroduced into the cage with two washers wedged between the feeder top and the trap door above it, connected with a thin thread to the outside of the room. The experimenters then gently pulled the thread when the individual started feeding, creating vibrations on the feeder and a brief sound, which successfully frightened the bird off the feeder. Latency to resume foraging after that startle was then recorded live with a stopwatch and a miniature video camera placed 1 m in front of the cage and linked to a monitor outside the room. Individuals were given a latency time of 601 s if they failed to resume foraging at the feeder within 10 min. For convenience, 'reaction to startle' scores were reversed for subsequent analyses, such that birds taking longer to resume foraging obtained lower scores.

Struggle rate or obstinacy

The intensity of individual struggling after catching is commonly assessed in studies of personality in mammals (Réale et al. 2000; Boon et al. 2007; Martin & Réale 2008), although, to our knowledge, such a test has never been used with birds. Individuals were caught and put on a flat surface below a small landing net (20 × 15 cm). The time needed to catch the bird in the home cage and the numbers of hops and escape attempts under the net were recorded for 30 s. All manipulations were done by M.D. Struggle rate was considered as a measure of individual obstinacy.

Aggressiveness and social dominance

Aggressiveness and social dominance were both assessed in seven groups of six individuals wearing different colour rings (light grey, light yellow, orange, black, blue and purple; Animalerie Nation, France) to allow individual identification. Individuals were randomly allocated to the groups. Groups were maintained in large cages (100 × 50 cm and 50 cm high) for 10 days before the tests, allowing individuals to interact freely. Birds were deprived of food for 1 h before trials to enhance motivation to feed. Social dominance was assessed through the access order to a single feeder (Boogert et al. 2006; Val-Laillet et al. 2008), the monopolization of resources and aggressiveness, as previously done in other species (Duckworth et al. 2004; Boogert et al. 2006). Within-group interactions were then recorded twice on 2 consecutive days in a feeding context. Individuals were deprived of food for 1 h before each trial. The experimenters then placed a single feeder, allowing only one bird to feed at a time, at the extreme side of the cage. Trials were videorecorded for 15 min with a miniature camera (Typhoon Easycam) following the introduction of the feeder. Interactions at the feeder mainly consisted of chases and displacements. Pecking was rare, and no bird was injured in the course of the trials. During the analysis, the experimenters measured the access order to the feeder, such that the first bird to reach the feeder was given a score of 1, the second was given a score of 2, and so on until score 6. The number of agonistic interactions (displacement from the feeder and its surroundings) and identities of birds involved, the number of times at the feeder and the total time spent feeding were also recorded. Thus, access order to the feeder, number of aggressive acts, time spent at the feeder and number of times at the feeder were all separately used to assess social dominance. We assumed that the birds reaching the feeder first, spending more time at the feeder and showing a high level of aggressiveness were the dominant birds (Boogert et al. 2006).

Morphometric Measures

All morphometric measures were taken twice on two different days by Y.A. Values were then averaged for each bird. 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). We determined a body condition index (BCI) corresponding to residuals calculated from the linear regression of log (weight) on log (tarsus length). Measures were significantly repeatable: tarsus length: $r = 0.73$, $P < 0.0001$; weight: $r = 0.98$, $P < 0.0001$.

Data Analysis

Consistency in personality was assessed by calculating behaviour repeatability between the two trials, using Lessells & Boag's (1987) method. For each personality trait, mean values were calculated from both trials and used thereafter. The existence of a behavioural syndrome was then assessed from the correlations between personality traits. As multiple correlations were

performed to test the relationships between personality traits, it was necessary to control for type I errors. Hence, as an alternative to Bonferroni correction (see Moran 2003; Nakagawa 2004), we relied on the procedure introduced by Benjamini & Hochberg (1995), which is similar to Bonferroni's, but also reduces type II errors by controlling for the false discovery rate (Verhoeven et al. 2005). All analyses were conducted using JMP 5.0.1 statistical software (SAS Institute, Cary, NC, U.S.A.). Only two-tailed tests were used. Variables were log, square-root or arcsine square-root transformed to reach normality when needed.

RESULTS

Evidence for a Behavioural Syndrome

Personality traits were highly consistent between successive trials (neophobia: $R = 0.43$, $F_{40,80} = 2.51$, $P = 0.002$; activity: $R = 0.40$, $F_{40,80} = 2.15$, $P = 0.004$; exploration: $R = 0.81$, $F_{40,80} = 9.67$, $P < 0.0001$; reaction to startle: $R = 0.37$, $F_{40,80} = 2.19$, $P = 0.009$; obstinacy: $R = 0.43$, $F_{40,80} = 2.48$, $P = 0.002$). During the neophobia tests, birds took longer to perch within 15 cm of the feeder (paired t test: $t_{39} = -2.71$, $P = 0.010$) and to reach the feeder ($t_{39} = -2.82$, $P = 0.001$) when facing the small bag than when facing the soccer figurine. Relationships between personality traits enabled us to define a 'behavioural syndrome' within our study group (Table 1, Fig. 1). Only obstinacy was not related to any other trait. A PCA was thus performed on all traits, except obstinacy, to reduce individual personality to a single value hereafter called the personality synthetic value. The first axis explained 51.26% of variance. Eigenvectors of each personality trait on the axis are as follow: exploration: 0.46; activity: 0.53; neophobia: 0.52; reaction to startle: -0.50. The frequency distribution of the personality synthetic values is shown in Fig. 2. Individuals defined by a high value were more exploratory, active, bolder and quicker to resume feeding after the startle. Within the continuum of personality synthetic values, they were therefore categorized as 'proactive', whereas individuals possessing lower values were categorized as 'reactive' (Réale et al. 2007).

Influence of Personality on Aggressiveness and Social Dominance

The medians for the personality synthetic value did not differ significantly between all groups ($\chi^2_6 = 8.43$, $P = 0.208$), and variances were homogeneous (Levene's test: $F_{6,34} = 1.63$, $P = 0.169$). Ring colour had no effect on access order to feeder ($\chi^2_5 = 2.07$, $N = 41$, $P = 0.840$), initiated aggressive acts ($\chi^2_5 = 4.56$, $P = 0.472$), received aggressive acts ($\chi^2_5 = 4.29$, $P = 0.508$), number of times at the feeder ($\chi^2_5 = 3.53$, $P = 0.620$) or total time spent feeding ($\chi^2_5 = 3.61$, $P = 0.606$). Traits defining dominance were highly consistent between trials (access order to feeder: $R = 0.61$,

Table 1
Correlations between each personality trait

Behaviour pairs	Pearson r	P
Activity – reaction to startle	0.29	0.063
Activity – exploration	0.42	0.006*
Activity – neophobia	-0.41	0.007*
Activity – obstinacy	0.11	0.481
Exploration – reaction to startle	0.28	0.077
Exploration – neophobia	0.23	0.146
Exploration – obstinacy	0.07	0.657
Neophobia – reaction to startle	-0.46	0.003*
Neophobia – obstinacy	0.22	0.165
Reaction to startle – obstinacy	0.17	0.292

Asterisks indicate correlations remaining significant after Benjamini & Hochberg's (1995) correction (black arrows in Fig. 1).

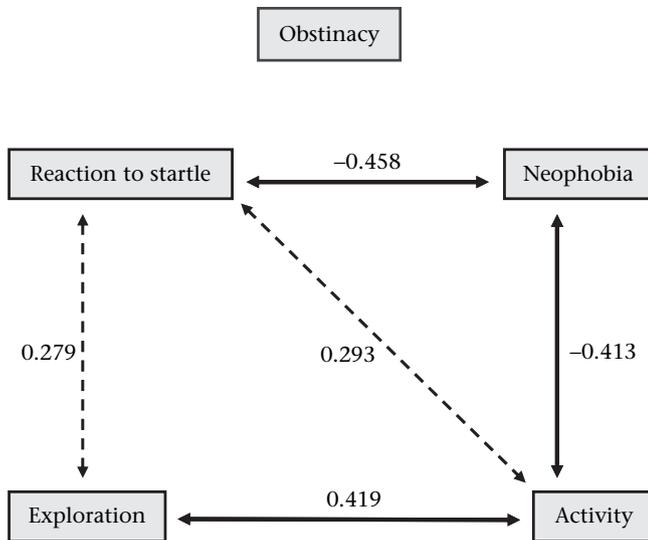


Figure 1. Relationships between personality traits defining the behavioural syndrome in our population. Black arrows indicate correlations remaining significant after Benjamini & Hochberg's (1995) correction (see Methods), whereas dashed arrows indicate marginally significant correlations ($P < 0.10$). Pearson correlation coefficients are indicated above each link.

$F_{40,75} = 4.11$, $P < 0.0001$; total time spent feeding: $R = 0.41$, $F_{40,75} = 2.39$, $P = 0.005$; number of initiated aggressive acts: $R = 0.53$, $F_{40,75} = 3.28$, $P = 0.0003$; number of times at the feeder: $R = 0.65$, $F_{40,75} = 4.76$, $P < 0.0001$). The personality synthetic value moderately but significantly predicted access order to feeder ($R^2 = 0.13$, $N = 41$, $P = 0.021$; Fig. 3), total time spent feeding ($R^2 = 0.20$, $N = 41$, $P = 0.004$; Fig. 4) and number of times at the feeder ($R^2 = 0.12$, $N = 41$, $P = 0.027$), but not initiated aggressive acts ($R^2 = 0.03$, $N = 41$, $P = 0.251$). Hence, proactive females were more likely to be dominant. Taking each of the seven groups of six birds separately, we observed the same trends in four groups for the relationship between access order to feeder and personality, in six groups for the total time spent feeding, and in five groups for the number of times at the feeder. To assess again the overall consistency of the relationship, we combined probabilities from a series of separate Spearman correlation tests performed within each group (Sokal & Rohlf 1995). Both 'time spent feeding' and 'number of times at the feeder' were significantly related to the personality synthetic value ($P = 0.048$ for both, one-tailed tests), whereas 'access order to feeder' was not ($P = 0.200$).

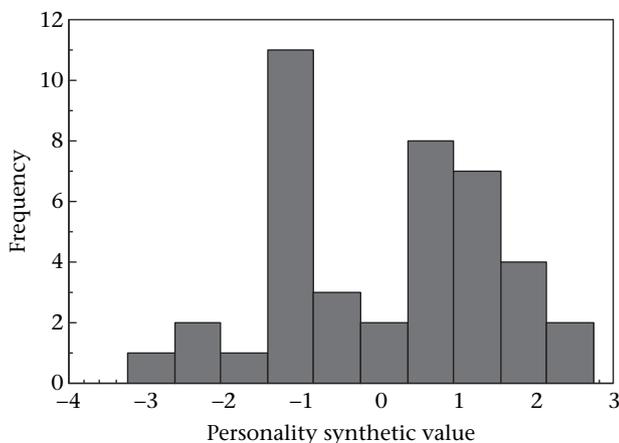


Figure 2. Frequency distribution of the personality synthetic values in our sample.

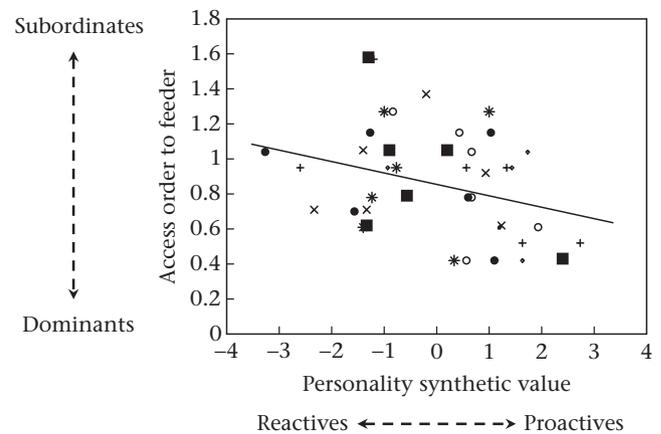


Figure 3. Influence of personality on access order to feeder. The Y axis was arcsine square-root transformed to reach normality. The personality synthetic value was obtained through a PCA on activity, exploration, reaction to startle and neophobic behaviours. Each symbol corresponds to individuals from the same group.

Body condition had no effect on access order to feeder ($R^2 = 0.003$, $N = 41$, $P = 0.733$), total time spent feeding ($R^2 = 0.005$, $N = 41$, $P = 0.666$), number of times at the feeder ($R^2 = 0.002$, $N = 41$, $P = 0.806$), initiated aggressive acts ($R^2 = 0.001$, $N = 41$, $P = 0.869$) or personality synthetic value ($R^2 < 0.001$, $N = 41$, $P = 0.986$).

DISCUSSION

Four of five personality traits were correlated within a wide behavioural syndrome in the present study, and proactive individuals were more likely to be dominant during within-group competition. Although some relationships were only marginally significant, neophobia, activity, exploration and reaction to startle showed substantial correlations, enabling us to sort individuals on a continuum from proactive (explorative, quicker to resume foraging, less neophobic and active birds) to reactive ones (less explorative, longer to resume foraging, neophobic and less active birds). However, one trait, obstinacy, defined as the intensity of escape behaviour in a stressful and threatening situation, was not related to any other. Although we may have expected a priori that such a behavioural reaction would be related to the other traits, with obstinate individuals being quicker to resume foraging and more active for instance, this was clearly not the case. Even though

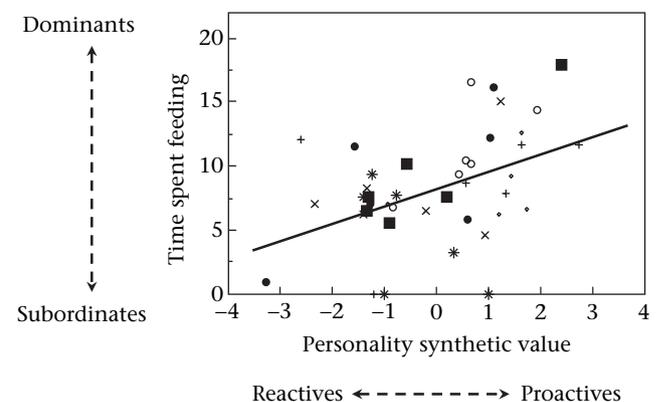


Figure 4. Influence of personality on total time spent feeding. The Y axis was square-root transformed to reach normality. The personality synthetic value was obtained through a PCA on activity, exploration, reaction to startle and neophobic behaviours. Each symbol corresponds to individuals from the same group.

the consequences of obstinacy in terms of survival have never been experimentally challenged, there is little doubt that the escape behaviour that the birds showed has important consequences, as an antipredator behaviour or in an intraspecific competition context. This suggests that its measurement is both meaningful and relevant when investigating personality, especially when it could not have been predicted by the other traits, as is the case in our study. Taken together, these statements argue in favour of the need to assess a wide range of traits to provide a full account of individual personality, as is commonly done in humans (Paunonen et al. 2003; Ashton & Lee 2007; de Vries et al. 2009).

Personality has already been found to influence many components of individual behaviour such as learning (Boogert et al. 2006), mating (Wilson et al. 2010a) or antipredator behaviour (Jones & Godin 2010). In this study, we showed that personality predicted social dominance in a feeding context, a strong predictor of fitness in gregarious bird species (Schubert et al. 2008; but see Verhulst & Salomons 2004). Hence, proactive individuals were more likely to be dominants and spent more time feeding whereas reactive ones tended to be subordinates. Although we only used females in our experiment, we would not expect to obtain different results in mixed or male groups, as zebra finches are gregarious not territorial birds (Zann 1996). We would expect dominance to be mainly beneficial during interference competition for food in flocks, irrespective of the sex of the birds involved. In addition, both male and female groups show substantial between-individual aggressiveness (Adkins-Regan & Robinson 1993; M. David, unpublished data).

Our results make sense in relation to the 'life history productivity' hypothesis (Biro & Stamps 2008), according to which proactive individuals express behaviours enabling them to sustain a high productivity, associated with a high metabolic rate (Careau et al. 2008). It follows that proactivity should be related to preferential access to feeding resources, which can be achieved through dominance. In this study, subordinate birds could have reached the feeder after dominant ones, but this was not systematically the case. This suggests that the fact that subordinates spent less time feeding most likely resulted from lower energetic needs rather than from the monopolization of resources by dominants.

Although similar results were found in a population of great tits, *Parus major* (Dingemanse & de Goede 2004), the direction of the relationship between personality and dominance seems to vary between studies and across species. Whereas proactive birds were found to be dominant in the present study, the opposite was observed in a population of mountain chickadees, *Parus gambeli* (Fox et al. 2009), and in another study on great tits (Verbeek et al. 1999). Those results lead to the question of why the consequences of personality for dominance vary across studies. One possibility is that the relationship between the two variables is context dependent, even within a single population (Dingemanse & de Goede 2004). External factors such as the social organization or the ecology of the species may also explain why individuals of the same personality do not get the same dominance status across species. For instance, Dingemanse & de Goede (2004) argued that territoriality mediated the relationship in a complex way. Consequences of personality are likely to differ as a function of the way individuals compete for food or territory. Unfortunately, few studies have investigated the relationship between personality and competition outcomes (but see Höjesjö et al. 2004). However, one could expect proactive individuals to outcompete reactive ones, especially when the intensity of competition by interaction is high. On the other hand, reactive individuals should not have less success when competition is low, all other things being equal. These simple predictions have the benefit of providing theoretical ground for both intra- and interspecific studies, as well as ultimately bringing insight to how competition may play a role in the differential

success of personalities. Finally, the relationship between personality and dominance has been shown to fluctuate among species (Fox et al. 2009; present study). Such discrepancies offer interesting opportunities to understand which role the ecology of a given species can play in the processes leading to the establishment of within-group dominance hierarchies.

Overall, our study suggests a multifactorial origin of dominance relationships in zebra finches. Dominance hierarchies are commonly considered as being determined by either individual abilities ('prior attributes' hypothesis) or social interaction between group members ('social dynamics' hypothesis; Chase et al. 2002). While one process may be predominant over the other, as in cleaning gobies, *Elacatinus prochilos* (Whiteman & Côté 2004), evidence shows that both may contribute to the establishment of hierarchies (Chase et al. 2002; Valderrábano-Ibarra et al. 2007), which is likely to be the case in our study. Our results indicate that variation in personality explains 13% of total variation in dominance status in our zebra finch population. If we consider that dominance is determined by both 'prior attributes' and 'social dynamics', it means that personality (a 'prior attribute') accounts for more than 13% of the variation explained by static factors only, making it an important predictor of dominance in our biological model. Future research may address the importance of individual personality in shaping hierarchies within groups, by comparing species with contrasted social organizations.

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