BEHAVIORAL TYPES AND SYNDROMES IN THE NEOTROPICAL PASSERINE BLUE-BLACK GRASSQUIT (*Volatinia jacarina*)

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ABSTRACT

Recent studies focusing on animal personality have been limited to model species found mainly in temperate regions. Selection pressures upon tropical species differ markedly from those of temperate regions (*e.g.,* higher predation, prolonged breeding seasons) and may influence the evolution of behavioral syndromes. We investigated animal personality using a Neotropical bird model *Volatinia jacarina* and tested for the presence of behavioral types and a context-general behavioral syndrome. Birds were captured in the field, held in captivity and tested for three different behaviors: feeding, exploration and sexual receptivity of females within two contextual conditions. Birds showed different behavioral types for exploration behavior, but not for feeding behavior. Besides, birds showed no context-general syndrome. We conclude that the blue-black grassquit does not follow any model predicting a long-term association between different behaviors, such as genetic models predicting syndromes.

Keywords: animal personalities; birds.

INTRODUCTION

Studies of animal personality have attracted increasing interest in the last decade, and recent empirical research has shown that personality attributes appear to be heritable and may involve many aspects of life history (Réale *et al*. 2007). Moreover, they can affect mating strategies and reproductive success, predation rates, and dispersion patterns (Dall *et al.* 2004, Sih *et al.* 2004, Dingemanse & Réale 2005, Carter *et al.* 2010, Møller 2010, Schuett *et al.* 2010). In the last few years a new approach in the study of animal personalities has emerged, focusing on the ecological consequences of personality for individuals. This approach attempts to evaluate the correlations that sometimes occur between different measured behaviors, as well as the proximal mechanisms that underlie such variations and correlations. Additionally, the study of model species, such as rodents or birds, is currently considered useful for the further understanding of human personalities (Gosling 2001).

Ecological studies of animal personalities focus mainly on two relevant issues: behavioral types and behavioral syndromes. Behavioral types (or tendencies) are most analogous to human personalities, and refer to consistent differences in behavior shown by individuals across multiple situations (*e.g.,* Digman 1990, Gosling 2001, Sih *et al.* 2004, Bell 2010). For instance, birds may consistently differ in the way they explore their environment or deal with challenges, with some showing greater boldness and aggression (Groothuis & Carere 2005). On the other hand, behavioral syndromes are correlations of different behavioral types across two or more contexts. In a given species or population, more aggressive individuals may exhibit this tendency in varied contexts. When mating, for instance, they may be bolder or more promiscuous, and when foraging they may feed more voraciously. Although positive correlations have frequently been reported for context-general behavioral syndromes (Bell 2010, Smith & Blumstein 2010), the lack of such correlations has also been documented (*e.g.,* Herczeg *et al.* 2009, Nyqvist *et al.* 2013).

The importance of animal personalities has been demonstrated in a variety of species and behaviors. For example, *Parus major* shows different individual

exploration patterns (Dingemanse *et al.* 2013). This raises the possibility that some bolder individuals are the ones that usually colonize new environments, as shown by Møller (2010) for a variety of bird species. Different behavioral types of *P. major* have also been demonstrated to respond differently to selection pressures. In resource-poor winter years, males with a lower exploration behavior had higher fitness; in resource-rich winter years, males with a higher exploration rate had higher fitness. Interestingly, the pattern for females was always the opposite (see Dingemanse & Réale 2005). Bold lizards *Agama planiceps* usually feed more, but also suffer higher predation (Carter *et al.* 2010). In an environment with poor food resources, bold individuals must have an advantage, but shy individuals will perform better in an environment with high predator abundance. Similarly, more aggressive spider individuals may have an advantage early in life, if food is scarce. But this aggressive behavior may 'spill over' to adulthood and prevent some females from mating, since they might attack every single potential partner (Arnqvist & Henriksson 1997, Johnson 2001). All these examples demonstrate the importance of animal personalities in ecological and evolutionary contexts. Such differences in behavior may be under selection and different behavioral types could have an advantage in different environments.

Given these occasionally unpredictable or contradictory results from studies of behavioral syndromes, many questions have emerged, providing fertile ground for further empirical studies. It is unclear, for instance, why all behavioral types in a population are maintained and why they do not evolve to a unique optimal level. One possibility in this regard is that environmental variability selects for different behavioral types, which allows for the coexistence of many personalities (Mangel & Stamps 2001). However, most studies are carried out within limited climatic or geographic areas and this logistic limitation may bias the generality or scope of the concept. Thus, before a unified theory for behavioral syndromes emerges, it remains necessary to test empirically the existence of individual behavioral consistencies in as many taxonomic categories as possible, across different contexts, and to examine the environmental conditions that exert stronger or more relaxed selective pressures

upon such traits. Species-specific natural history characteristics may be important in such considerations.

Behavioral types and syndromes have been examined more often in temperate species, which are exposed to different selective pressures when compared with tropical species. It is plausible to assume that behaviors can evolve to be more or less flexible in response to such different environments. In this study we tested for the presence of behavioral types and a context-general behavioral syndrome using the blue-black grassquit (*Volatinia jacarina*), a fairly well studied Neotropical passerine (reviewed in Macedo *et al.* 2012). This species is exposed to a broad range of environmental conditions in the Tropics, as its geographic range extends from approximately 30º N in Mexico to 35º S in Argentina (Sick 2001). Despite the variability in climatic conditions that occurs over such a broad range, the species is subjected to a fairly homogeneous photoperiod and relatively benign temperatures through the year in comparison to birds that inhabit extremely seasonal areas in temperate regions. Additionally, selection pressures upon this species that could also be important in the context of behavioral syndromes involve the more prolonged breeding periods, very high nest predation, and repeated nesting attempts, all traits emblematic of tropical birds (see Roper *et al.* 2010), and in sharp contrast to conditions experienced by birds in temperate regions. Our main objective was to investigate the potential of a behavioral syndrome in this Neotropical species. We asked two questions: (a) does the blue-black grassquit exhibit distinctive behaviors in the contexts presented? And (b) do these behaviors correlate with each other?

MATERIAL AND METHODS

Study species

The blue-black grassquit is a granivorous passerine, endemic of Neotropical regions, and common from Mexico to northern Argentina and Chile, where it inhabits open and altered habitats (Sick 2001). The species is partially migratory in parts of its range (Sigrist 2009), and in the breeding season males defend

small, aggregated territories and perform a conspicuous motor display that consists of short and fast vertical flights, resembling leaps, while exposing white underwing patches. Such leaps are performed synchronously with a short vocalization (Webber 1985, Sigrist 2009). Within its range, populations of this bird are either resident (*e.g.,* parts of the Amazon) or migrate to other regions in the Neotropics.

To examine the behavioral types that might be expressed in the blue-black grassquit we selected three contexts that we felt could be inter-related due to their possible dependence upon a general level of activity of the birds, as proposed by Bell (2010). These behavioral contexts were (1) foraging, (2) exploration of the environment, and (3) sexual behavior of females. Blue-black grassquits migrate into central Brazil (presumably from the Amazon region in northern South America) at the end of October and males aggressively demarcate small territories in aggregated clusters (Webber 1985, Almeida & Macedo 2001). In this circumstance, successful birds should be those with bold, exploratory behavior, which establish and vigorously defend territories in seed-rich habitat patches. Blue-black grassquits also have extremely high rates of extrapair copulation, which suggest that females actively seek males outside of the pair-bond for mating (Carvalho *et al.* 2006; Macedo *et al.* 2012; Manica *et al. in press*).

Collection and housing of captive birds

Between the breeding seasons of 2007 and 2009, 32 adult birds (16 males and 16 females) were captured with mist nests in the Fazenda Água Limpa (FAL), an ecological reserve owned by the Universidade de Brasília (UnB). The birds were maintained together until the end of the experiments in 2012, in two enclosures (2.0 m x 2.0 m x 2.5 m) within an outdoor aviary in the UnB campus and provided with an *ad libitum* diet of a mixture of seeds (green, red and yellow millet and birdseed) and water. Every bird was given a unique combination of bands. The 32 individuals were randomly divided into four groups of eight birds (four males and four females). Capture, aviary maintenance, and banding procedures were authorized by CEMAVE (license no. 1301/2) and Instituto Brasileiro do Meio

Ambiente e dos Recursos Naturais Renováveis (IBAMA license no. 17765-1).

Experimental design

We examined three behavioral contexts in 32 individual birds: (a) foraging; (b) exploration of environment; and (c) sexual context of females. To test for the presence of personalities, we assessed the behavior of each individual in two separate conditions within the foraging and exploration of environment behavioral contexts. For the foraging context the conditions were *hungry* and *satiated*; for the exploration of the environment the conditions were *novel* and *familiar*. In each of the two conditions we expected that personalities would be expressed similarly. Since this species does not breed successfully in captivity, we could not pair males and females, so for the sexual context, the conditions applied to *socially unpaired* females only and we did not test for behavioral types.

Our experimental design took into consideration the possibility that past experiences may cause changes in behavioral responses (Stamps & Groothuis 2010). Thus, to avoid this bias, the order of the experiments was different for each of the four groups, so that every experimental group trial both preceded and followed every other alternative experimental group trial (Table 1), as proposed by Dochtermann (2010). Moreover, since one of our goals was to assess the existence of long term syndromes, we did not measure all three behaviors in consecutive time periods; instead, experiments were separated by a time interval of up to six months.

Behavioral trials

Foraging context: To experimentally assess foraging activity in the *hungry* condition, we deprived each individual of food for 10 h (0600-1600 h), after which the bird was given unlimited food for 10 min. This period was chosen based on pilot studies that demonstrated that these birds can usually sustain a 10h food restriction and recover after being fed. With a 0.01g precision scale we weighed the food container before and after the birds fed. This allowed an accurate

measurement of the amount of food ingested by individuals, which served as an indicator of foraging activity. One week after this experiment, the same individuals were submitted to the same procedure; however, this time they were in the *satiated* condition, as they were not submitted to the food deprivation period. Therefore, we assessed foraging behavior in two distinct conditions: *hungry* and *satiated*.

Table 1. Order in which experiments were performed for the four groups of blue-black grassquits (*Volatinia jacarina*) used to test for the presence of personalities.

Group	Order	Experiment		
Group 1	1	Feeding	Exploration	Sexual context
Group 2	2	Sexual context	Feeding	Exploration
Group 3	3	Exploration	Feeding	Sexual context
Group 4	4	Sexual context	Exploration	Feeding

Exploration of environment context: The manipulation for environment exploration was conducted in a small triangular-shaped compartment of the aviary, with each side measuring approximately 2 m. This area was completely covered with cloth, preventing the birds in the aviary of seeing the area inside. Within this area we placed artificial vegetation to function as perches to be explored by the birds. The compartment area was represented by a map that allowed us to plot each individual´s movements. The birds were observed from outside the aviary, through a metal grid that obscured their view of the observer, but the lighting inside the compartment allowed the birds to explore the environment easily and was enough for the observer to see the birds clearly. Before the experiment, the birds were acclimated inside a closed box in the center of the compartment for 5 min, after which the box cover was lifted with a pulley from outside the aviary. The exact placement and timing of the bird´s movements were recorded during a 15 min trial. Three variables were measured for each bird: total linear distance travelled (m), latency (min) to emerge from the box, and the number of flights performed (independent of the distance explored). Distance and number of flights were measured by taking notes on the map by hand and the latency to leave the box was measured using a hand chronometer. After the 15 min experiment, the same protocol was performed again with the same individual. The bird was recaptured, placed in the box for 5 min before the same exploration trial took place. We chose to repeat the protocol right after the first trial so the birds could not 'forget' the environment. Since both trials subjected the birds to the same potential for stress induced by capture and handling, we are confident that they were equivalent, except for the novelty effect, allowing the comparison of how birds responded to a novel environment relative to a known environment. This design enabled us to check if there was a novelty effect of the environment on the exploration behavior exhibited by the birds (*i.e.,* if the birds showed different exploratory behaviors between the first and second trials), and the separation of the experiments in two distinct conditions: *novel* environment and *familiar* environment.

Sexual context: The experiments involving sexual behavior were performed only with females. Each female was placed in a cage (2.5 m x 1.2 m x 0.6 m) that was visually, though not acoustically, isolated by two metal plates from a neighboring cage in which there was a male. After a 5 min period of acclimatization, we removed one of the plates. Birds were then filmed for 10 min. After this period, the other plate was removed to establish visual contact between the birds, and the behavior of the male and female was filmed for another 10 min. This design controlled for any effect on female behavior due to the removal of the metal divider between the cages, since the female was exposed to that effect both before and after being able to see the male. We recorded the amount of time females spent at distances of 10-40 cm from the stimulus male cage. Female response to

the male stimulus (*i.e.,* percentage of time spent close to the male) was used as a measure of female propensity to engage in sexual behavior when she was *socially unpaired*. We expected that females that spent more time closer to males (higher propensity to engage in sexual behavior) would be those with higher exploratory and feeding behaviors (*i.e.,* showing positive associations between time in proximity to males and exploration and food ingestion), since feeding, exploration and sexual behaviors are energetically costly, and thus, possibly correlated (Careau *et al.* 2008, Bell 2010, Biro & Stamps 2010, Wolf & Weissing 2010, Conrad 2011).

Statistical analysis

To check if the variables collected in the exploration experiment (linear distance traveled, number of flights and latency to leave the box) were related to each other, we performed a principal component analysis (PCA) with those variables (*novel* and *familiar* environments).

To test for the presence of personalities (behavioral types), we built behavioral reaction norm models with constant slopes (Dingemanse *et al.* 2009). Reaction norms are mixed-models in which the response variable is a measure of behavioral activity, the predictor variable is a range of environmental conditions and the random variables are each individual. The range of environmental conditions does not have to be a continuous variable and the model is still powerful if it is categorical (Dingemanse *et al.* 2009). Simulations have shown that two environmental conditions (as in this study) are sufficient for a good estimation of the model parameters (Dingemanse & Dochtermann 2013). The response variables included the behaviors measured (*i.e.,* amount of food ingested and exploration activity) and the predictor variables were the two conditions in which each experiment was conducted. For the exploration context this included the *novel* and *familiar* environments, and for the foraging context this included the *hungry* and *satiated* conditions. In both models the independent variable was mean-centered, so that different intercepts would indicate different average behavioral activities between the two conditions (Dingemanse *et al.* 2009). Since

males are the ones who establish territories in this species, while females are thought to monitor male sexual displays, it is possible that males and females have different exploration tendencies. To control for this possible effect, we included 'sex' as a fixed effect in the behavioral reaction norm for exploration behavior. We used the restricted maximum likelihood approach for model fitting. Fixed effects were tested with the Walt statistics and random effects were tested by likelihood ratio tests (Snijders & Bosker 1999, Faraway 2006).

To test for the presence of the exploration/feeding behavioral syndromes, a simple regression was performed with the exploration activity as the response variable and using foraging behavior as a predictor variable. We used a Spearman correlation to test for the presence of a behavioral syndrome for female propensity to engage in sexual behavior and foraging. A correlation between sexual behavior and exploration was not performed due to the small sample size for the test (N = 3). This happened mainly as a result of mortality of some individuals during the period of the study.

We used multiple imputations to deal with missing data whenever possible, since this procedure is considered much more powerful than listwise deletion, even though the latter is the default method of all statistical softwares (Sinharay *et al.* 2001, Schafer & Graham 2002, Graham 2009). Assessments of normality and homoscedasticity were performed graphically and all tests were performed in R version 3.1.0 (R Development Core Team, 2008).

RESULTS

Foraging context

For the hungry condition, birds typically ate voraciously for a few minutes and then stopped eating for the rest of the trial. For the satiated condition, birds ate much less and, sometimes, did not eat at all. There was a significant fixed effect in the foraging mixed model (Walt's t = 7.27, p < 0.01), indicating that animals in the *hungry* condition ate more than animals in the *satiated* condition (hungry condition: mean = 0.23 ± 0.11 g, satiated condition: mean = 0.03

± 0.05 g). This indicates that the trial was long enough to measure the amount of food resources needed by individuals. The random effect was not significant (Likelihood Ratio < 0.01, p = 0.99), indicating that there was no variation in the average amount of food eaten by the birds (Table 2).

Table 2. GLMM final model for two behaviors of *Volatinia jacarina*. Random effects were always 'individual', so a significant random effect would indicate the presence of distinct behavior types for that behavior. *LR= Likelihood Ratio.

	Fixed effects		**Random effects**	
	Food ingested		**Individual**	
Foraging	**β (± SE)**	**p**	**LR**	**p**
	0.215 (± 0.030)	< 0.001	< 0.01	0.99
	Environment		**Individual**	
	β (± SE)	**p**	**LR***	**p**
Exploration	0.76 (± 0.20)	0.002	6.85	0.009
	Sex			
	β (± SE)	**p**		
	0.43 (± 0.43)	0.33		

Exploration of environment context

We found that the first principal component explained 74.6% of the total variance in the data and was strongly and negatively correlated with the number of flights and distance traveled by the bird (r = -0.91 and r = -0.94, respectively), and positively correlated with the latency to leave the box (r = 0.72). These results indicate that numerous flights and a long distance traveled characterize highly explorative animals, while a long latency to leave the box characterizes low exploratory behavior. The first principal component was thus used as an inverse measure of the exploration activity by the birds.

The mixed model performed with the exploration data also showed a significant effect of the environment, showing that when birds were faced with a novel environment they showed higher exploration than when the environment was familiar (PC1: novel = -0.25 ± 1.04, familiar = 0.51 ± 0.76, Walt's t = 3.72, p < 0.01). This difference was also evident during our observations, because the birds in the first trial typically explored the novel environment until coming to rest on a perch for the remainder of that trial. In the second trial, the birds usually flew directly to that same perch, without exploring the environment again. The sex of the animal did not influence its exploration behavior (PC1: males = -0.05 ± 0.87, females = 0.39 ± 1.09). Unlike the foraging model, the exploration one showed a significant random effect (Likelihood Ratio = 7, p < 0.01), indicating that there is strong variation in the average exploration rate of animals (*i.e.,* there are different personalities).

Sexual behavior context

In the sexual behavior experiments, all females were clearly influenced by the presence of a male in the neighboring cage, spending a significantly higher percentage of time within 10 cm of the males when there was no visual barrier between them (with visual contact: 0.3% ± 0.27, without visual contact: 0.06% ± 0.12, Wilcoxon Z = 2.20, p = 0.028). The amount of time females spent closer than 10 cm

relative to the male was used to determine the existence of a propensity to engage in sexual behavior.

Behavioral syndromes

We did not find a significant correlation between the feeding rate after 10h of food restriction of animals and their exploration rate in a novel environment. In other words, the birds did not exhibit a behavioral syndrome in the context of exploration/foraging (r = 0.075, p = 0.35). We did not find a propensity to engage in sexual behavior/foraging syndrome (Spearman correlation: r = -0.20, p > 0.05), *i.e.,* females that spent more time in close proximity to males did not consume greater amounts of food.

DISCUSSION

Our study shows that individuals exhibit personality in exploration of environments but not in foraging contexts. Thus, some individuals have a higher average exploration rate, but the same was not true for feeding behavior. This illustrates the fact that individual differences in personality (*i.e.,* differences in average behavioral expression) can exist in some behavioral categories but not in others. Considering the blue-black grassquits, personality was expressed for environment exploration, but not for feeding behavior. As for behavioral syndromes, our data indicate that for this species, the behaviors we studied are not linked.

Individual differences in exploration behavior have been studied in other bird species and appear to be heritable in some (Dingemanse *et al.* 2003) and for some species can also predict patterns of migration (Møller 2010). Our study species is migratory (Sigrist 2009) and defends small aggregated territories during the breeding season (Almeida & Macedo 2001). Since males maintain the same territories for the entire breeding season, and commonly perform their displays using the same perches (L. T. Manica, personal communication), the exploratory behavior measured may be more important during migration and territory establishment. In the great tit *Parus major*, highly explorative birds in captivity dispersed greater distances in nature (Dingemanse *et al.* 2003). More exploratory

blue-black grassquit males may be able to more quickly find and establish good quality territories when arriving at their breeding site.

This study is not the first to document a lack of relationship between two or more different behaviors (Herczeg *et al.* 2009, Nyqvist *et al.* 2013). Moreover, most studies that were able to find such relationships measured behaviors over a very short period, biasing the results towards a significant relationship between behavioral activities (Nyqvist 2012), since behavioral syndromes might be state dependent (Dall *et al.* 2004). At any given time, the state of an individual depends on its energy reserves, territory quality, and risk of predation, for example. Individuals should thus control all their important behaviors based on their current state. This gives rise to a variety of syndromes, but behaviors can be decoupled if measured at two different points in time, when the state of the animal has changed. We measured different behaviors in very distinct time periods, with intervals of up to six months. Even if the blue-black grassquit shows any state-dependent syndrome in the short term, it is not repeatable over longer periods and we found no evidence of a long-term syndrome mechanism (*e.g.,* syndromes driven by genetic differences; Weber 1992, Drent *et al.* 2003). This shows the importance of measuring behaviors over a longer period, if the objective is to test for the presence of time-consistent differences in behavior.

Another hypothesis commonly evoked to explain suites of correlated behaviors is the metabolic rate hypothesis (Careau *et al.* 2008, Biro & Stamps 2010). According to this hypothesis, energetically costly behaviors depend on the basal metabolic rate of an individual, and therefore are all correlated with each other. Since the amount of food ingested is usually a good predictor of the basal metabolic rate (Careau *et al.* 2008), our study provides a good test of this hypothesis. We can conclude that the blue-black grassquit does not conform to the metabolic rate hypothesis, since the amount of food ingested by the birds did not predict either of the two expensive behaviors tested.

In summary, the Neotropical blue-black grassquit shows individual differences in behavior (*i.e.,* personalities) for only one of three behaviors studied

here (environment exploration). There seems to be no link between the three different behaviors over the long term, excluding any strong genetic effects mediating the interaction between different behaviors. This study contributes to the understanding of behavioral types and syndromes, and it is unique in the sense that it focused on a tropical species and was conducted over an extended period. More studies in the tropical region are needed to compare behavioral traits with species from both temperate and tropical regions and understand how suites of correlated behaviors vary over different climatic regimes.

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REFERENCES

Almeida, J. B., & Macedo, R. H. 2001. Lek-like mating system of the monogamous blue-black grassquit. The Auk, 118(2), 404–411.

Arnqvist, G., & Henriksson, S. 1997. Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. Evolutionary Ecology, 11(03), 255–273.

Bell, A. M. 2010. Future directions in behavioural syndromes research. Proceedings of the Royal Society B, 274(1611), 755–761.

Biro, P. A., & Stamps, J. A. 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends in Ecology and Evolution, 25(11), 653–659.

Careau, V., Thomas, D., Humphries, M. M., & Réale, D. 2008. Energy metabolism and animal personality. Oikos, 117(05), 641–653.

Carter, A. J., Goldizen, A. W., & Tromp, S. A. 2010. Agamas exhibit behavioral syndromes: bolder males bask and feed more but may suffer higher predation. Behavioral Ecology, 21, 655–661.

Carvalho, C. B. V, Macedo, R. H., & Graves, J. A. 2006. Breeding strategies of a socially monogamous neotropical passerine: extra-pair fertilizations, behavior, and morphology. The Condor, 108(3), 579–590.

Conrad, J. L., Weinersmith, K. L., Brodin, T., Saltz, J. B., & Sih, A. 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. Journal of Fish Biology, 78(02), 395–435.

Dall, S. R. X., Houston, A. I., & McNamara, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecology Letters, 7(08), 734–739.

Digman, J. M. 1990. Personality structure: emergence of the five-factor model. Annual Review of Psychology, 41(01), 417–440.

Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. 2003. Natal dispersal and personalities in great tits (*Parus major*). Proceedings of the Royal Society of London B, 270(1516), 741–747.

Dingamanse, N. J., & Dochtermann, N. A. 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. Journal of Animal Ecology, 82(1), 39–54.

Dingamanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. 2009. Behavioural reaction norms: animal personality meets individual plasticity. Trends in Ecology and Evolution, 25(2), 81–89.

Dingemanse, N. J., & Réale, D. 2005. Natural selection and animal personality. Behaviour, 142(9–10), 1159–1184.

Dochtermann, N. A. 2010. Behavioral syndromes: carryover effects, false discovery rates, and a priori hypotheses. Behavioral Ecology, 21(3), 437–439.

Faraway, J. J. 2006. Extending linear models with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models. Boca Raton, FL: Chapman and Hall/CRC: p. 331.

Gosling, S. D. 2001. From mice to men: what can we learn about personality from animal research? Psychological Bulletin, 127(1), 45–86.

Graham, J. W. 2009. Missing data analysis: making it work in the real world. Annual Review of Psychology, 60, 549–576.

Groothuis, T. G. G., & Carere, C. 2005. Avian personalities: characterization and epigenesis. Neuroscience & Biobehavioral Reviews, 29(1), 137–150.

Herczeg, G., Gonda, A., & Merilä, J. 2009. Predation mediated population divergence in complex behaviour of nine-spined stickleback (*Pungitius pungitius*). Journal of Evolutionary Biology, 22(03), 544–552.

Johnson, C. D. 2001. Sexual cannibalism in fishing spiders (*Dolomedes triton*): an evaluation of two explanations for female aggression towards potential mates. Animal Behaviour, 61(05), 905–914.

Macedo, R. H., Manica, L., & Dias, R. I. 2012. Conspicuous sexual signals in a socially monogamous passarine: the case of neotropical Blue-black Grassquits. Journal of Ornithology, 153(Suppl 1), S15–S22.

Mangel, M., & Stamps, J. 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. Evolutionary Ecology Research, 3(05), 583–593.

Manica, L. T., Graves, J. A., Macedo, R. H. In press. Multimodal flight display of a Neotropical songbird predicts social pairing but not extrapair mating success. Behavioral Ecology and Sociobiology.

Møller, A. P. 2010. Interspecific variation in fear responses predicts urbanization in birds. Behavioral Ecology, 21,

365–371.

Nyqvist, M. J., Gozlan, R. E., Coucherousset, J., Britton, R. J. 2013. Absence of a context-general behavioural syndrome in a solitary predator. Ethology, 119(02), 156–166.

R Development Core Team (2008). R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews, 82(02), 291–318.

Roper, J. J., Sullivan, K. A., & Ricklefs, R. E. 2010. Avoid nest predation when predation rates are low, and other lessons: testing the tropical-temperate nest predation paradigm. Oikos, 119(04), 719–729.

Schafer, J. L., & Graham, J. W. 2002. Missing data: our review of the state of the art. Psychological Methods, 7(02), 147–177.

Schuett, W., Tregenza, T., & Dall, S. R. X. 2010. Sexual selection and animal personality. Biological Reviews, 85(02), 271–246.

Sick, H. 2001. Ornitologia Brasileira. 3rd ed. Rio de Janeiro: Nova Fronteira: p. 912.

Sigrist, T. 2009. Avifauna brasileira: the Avis Brasilis field guide to the birds of Brazil. Vol 2. Vinhedo, SP: Avis Brasilis Editora: p. 1080.

Sih, A., Bell, A., & Johnson, J. C. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology and Evolution, 19(7), 372–378.

Smith, B. R., & Blumstein, D. T. 2010. Behavioral types as predictors of survival in Trinidadian guppies (*Poecilia reticulata*). Behavioral Ecology, 21, 919–926.

Sinharay, S., Stern, H. S., & Russel, D. 2001. The use of multiple imputations for the analysis of missing data. Psychological Methods, 6(4), 317–329.

Snijders, T. A. B., & Bosker, R. J. 1999. Multilevel analysis: an introduction to basic and advanced multilevel modeling. Trowbridge, Wiltshire: SAGE Publications: p. 266.

Stamps, J. A., & Groothuis, T. G. G. 2010. Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. Philosophical Transactions of the Royal Society B., 365(1560), 4029–4041.

Weber, K. E. 1992. How small are the smallest selectable domains of form? Genetics, 130(2), 345–353.

Webber, T. 1985. Songs, displays, and other behavior at a courtship gathering of blue-black grassquits. The Condor, 87(04), 543–546.

Wolf, M., & Weissing, F. J. 2010. An explanatory framework for adaptive personality differences. Philosophical Transactions of the Royal Society B, 365(1560), 3959–3968.