Habitat urbanization and stress response are primary predictors of personality variation in northern cardinals (*Cardinalis cardinalis*)

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Abstract

Behavioral traits that vary consistently among individuals across different contexts are often termed as 'personality traits,' while the correlated suite formed by those traits is called a 'behavioral syndrome'. Both personality trait and behavioral syndrome are potentially responsive to animal 'states', defined as strategically relevant individual features affecting the cost-and-benefit trade-offs of behavioral actions. Both extrinsic 'states' (e.g. urban versus rural habitats), and intrinsic 'states' (e.g. sex), may shape among-individual variation in personality traits, as well as behavioral syndromes. Here, we used northern cardinals sampled from four locations to examine the effect of habitat type (urban versus rural, an extrinsic state), stress hormone corticosterone (CORT) parameters, body weight and sex (intrinsic states) on personality traits and behavioral syndrome variation. We used behavioral trials to measure five personality traits. Using principal component analysis to quantify personality traits first, followed by general linear mixed models, we found that habitat type, CORT at capture and 2-day CORT response affected some personality traits, while body weight and sex did not. Cardinals inhabiting more urbanized areas had lower CORT metabolite levels at capture and were more neophilic, less neophobic and also less aggressive than their rural conspecifics. Using structural equation modeling to construct behavioral syndromes formed by our selected personality traits, we found that urban and rural cardinals varied in the models representing syndrome structure. When utilizing the shared syndrome structural model to examine the effects of states, habitat type and 2-day CORT response appear to affect syndrome variation in a coordinated, not hierarchical, manner.

Key words: behavioral syndrome, state-dependent theory, structural equation modeling, urbanization, corticosterone

Introduction

Urbanization poses many challenges to wildlife (Chace and Walsh, 2006) that affects multiple abiotic and biotic environmental factors (Shochat et al. 2004; Reis, López-Iborra, and Pinheiro 2012; Stracey and Robinson 2012). Although some alterations, such as warmer microclimate or anthropogenic food resources may be beneficial (Marzluff 2001; Marzluff et al. 2008),

other changes such as increased invasive competitors and anthropogenic noises can be harmful (Strasser and Heath 2013). In any case, animals in urban areas often face multiple novel stressors not present in the native habitat, with behavior often being the first response to such changes. Thus, understanding the key components affecting behavior is critical, particularly considering the rapid changes occurring due to anthropogenic

effects (Tuomainen and Candolin 2011; Wong and Candolin 2015).

However, it has become clear that the range of behavioral plasticity in individuals and populations may be more limited than originally thought (Sih, Kats, and Maurer 2003; Sih, Bell, and Johnson, 2004; Duckworth 2010), which may limit responses to environmental change. The concept 'behavioral syndrome' describes the consistent individual variation across ecological context and over time (Sih, Bell, and Johnson 2004; Bell 2007). Although a 'personality trait' is often defined through quantifiable behavioral axes that reflect functionally different biological dimensions (i.e. aggressive-docile or bold-shy; Réale et al. 2007), with a suite of correlated personality traits (e.g. more aggressive individuals are also bolder; Sih, Bell, and Johnson 2004) being defined as a 'behavioral type' at the individual level and 'behavioral syndrome' at the population level. In other words, animals may respond to the world in a 'package' manner that is not always well adapted for all situations (Sih, Kats, and Maurer 2003; David et al. 2004; Sih, Bell, and Johnson 2004; Duckworth 2010).

The variation of personality traits within and among populations has the potential to affect both ecological and evolutionary dynamics. For instance, in *Anolis sagrei* lizards, urban individuals are more tolerant of humans, less aggressive, bolder after a predator simulation and spend more time exploring new environments; this urban behavioral syndrome is associated with foraging niche change correlated with the presence of an invasive predator lizard *Leiocephalus carinatus*, suggesting that differences in personality traits facilitate the adaptation of animals under novel selective regimes caused by anthropogenic activities (Lapiedra et al. 2017). Moreover, studies have also shown that variation in behavioral types can have fitness consequences due to trade-offs associated with the behavioral syndrome structure (Sih, Bell, and Johnson et al. 2004, Smith and Blumstein 2008); e.g. Trinidadian guppies (*Poecilia reticulata*) possessing a more proactive (more active, explorative and bolder) behavioral type along the Activity-Boldness-Exploration syndrome had higher fitness (greater survival) when facing predators (Smith and Blumstein 2010). Attempts to understand why and how such individual variation persists through time under selection has therefore led to a rapid growth of studies addressing proximate and ultimate questions of behavioral syndrome, with new theoretical models providing adaptive links with general ecology (Dingemanse and Wolf 2010; Sih et al. 2015; Bell 2017). A key area in this array of studies is how personality traits vary in response to different states (i.e. environmental condition or metabolic rate; Sih et al. 2015), and ultimately how behavioral syndrome is shaped by or limits the environments where organisms occur.

'State', defined as strategically relevant individual features affecting the cost-and-benefit trade-offs of behavioral actions (Houston and McNamara 1999, Wolf and Weissing 2010), has the potential to determine individual differences in personality traits and behavioral types. It is thus not surprising then that state-dependent theory has become popular for the emergence and maintenance of behavioral syndromes (Sih et al. 2015). States can either be intrinsic (e.g. metabolic rate, plasma hormone levels or body mass; Kluen, Siitari, and Brommer, 2014; Dosmann, Brooks, and Mateo 2015; Krams et al. 2017) or extrinsic (e.g. physical or social environment; Bell and Sih 2007; Rudin, Tomkins, and Simmons 2018). Although an intrinsic state may be enough to generate a state-behavior feedback loop that leads to consistent individual variation through direct determination of an individual's condition and its behavioral response (Biro and Stamps 2008; Wolf and Weissing 2010; Sih et al. 2015), extrinsic state variables are equally important as environment shapes selective pressures that may act on personality variation (Réale et al. 2007; Brydges et al. 2008; Le Coeur et al. 2015). A single state variable may be enough to generate the state-behavior feedback loop (Rodin 1985; Kishida et al. 2011), yet state variables also may work in concert to shape consistent individual variation (Sih et al. 2015; Roy and Bhat 2018).

Investigating the effect of urbanization, as an extrinsic state, on not only single personality traits but also the behavioral syndromes is important, given ongoing threats to wildlife due to the expansion of human population, and that the associated behavioral alterations may shed light on how animals cope under such a regime (Shochat et al. 2006; Wong and Candolin 2015). Although urban–rural variation in single personality traits has been well-documented in multiple species (Sol, Lapiedra, and González-Lagos 2013), thus far only a few studies have examined more than one personality trait along an urban–rural gradient (but see Evans, Boudreau, and Hyman 2010; Scales, Hyman, and Hughes 2011; Sol et al. 2011; Bókony, 2012 ; Miranda et al. 2013). To date, single personality trait studies often suggest a shift toward the more proactive end of a given personality trait in urban animals that possibly derives from the needs to deal with human disturbance or to exploit novel resources (i.e. more aggressive, explorative, bolder; Boon, Réale, and Boutin 2007; Biondi, Bó, and Vassallo 2010; Lin et al. 2012). Interestingly, even when correlated personality traits shift in similar directions, breakdown of the formed syndrome has been observed (Evans, Boudreau, and Hyman 2010; Scales, Hyman, and Hughes 2011), suggesting that indeed the relationship among personality traits is also a subject that can be altered by urbanization (Bókony et al. 2012).

Importantly, urbanization is an extrinsic state that may potentially affect several intrinsic states. For example, urban individuals are expected to have reduced body mass due to greater population density and overexploitation of resources associated with high food predictability and low mortality (Shochat 2004); urban house sparrows (*Passer domesticus*) are indeed leaner than their rural conspecifics (Liker et al. 2008). To achieve a more mechanistic perspective of urban ecology, we really need to consider how those intrinsic state variables fit into the picture of behavioral variation patterns under the influence of urbanization. Such studies should not only help to improve our understanding of how personality variation arises and is maintained within and between populations, but also provides another angle to evaluate the impact of human-induced environmental change on wildlife populations and the implications for their long-term persistence in such environments.

In this study, we used a comprehensive, multivariate approach with northern cardinals (*Cardinalis cardinalis*) sampled from four locations (two urban and two rural) during the non-breeding season to investigate the effect of states on both personality traits and behavioral syndrome variation. The five personality traits we selected (all commonly measured and reported in the literature) were quantified using principal component analyses (PCAs) of all the behavioral measurements collected in each assay (Groothuis and Carere 2005; Réale et al. 2007; Carere, Caramaschi, and Fawcett 2010; Conrad et al. 2011; Herborn et al. 2010; Miranda et al. 2013; Dall and Griffith 2014; Huang, Kimball, and St. Mary 2018). Behavioral syndromes were then constructed through structural equation modeling (SEM) using the personality components obtained from the PCA. The states we selected include urban or rural (an extrinsic state), stress hormone corticosterone (CORT) parameters, sex and

body weight (three potentially important intrinsic states). With its link to the hypothalamic-pituitary-adrenal (HPA) axis, CORT is associated with behavioral responses in animals and expected to be an underlying mechanism for individual variation (Cockrem 2007; Romero and Butler 2007; Koolhaas et al. 2010; Schoech, Rensel, and Heiss 2011). Sex was selected because selection can vary between the sexes and generate different patterns of behavioral correlation (Schuett and Dall 2009; Fresneau, Kluen, and Brommer 2014). We also measured body weight, a commonly used indicator for future reproductive success (Clark 1994; Dowling and Godin 2002) that has been shown to be important to the expression of behavioral variation (Clark 1994; Sih et al. 2015). Overall, we predicted to see effects from at least some of our selected states on both personality and behavioral syndrome variation. Moreover, given that most of our intrinsic states could be affected by the extrinsic state (Rising and Somers 1989; Anderson et al 1993; Shochat 2004; Partecke, Schwabl, and Gwinner 2006; Liker et al. 2008; Fokidis, Orchinik, and Deviche 2009; Atwell et al. 2012), correlating or even hierarchical relationships among influential states affecting animal personality was also expected.

Methods

Sampling design and quantification of habitat urbanization

The study was conducted in north central Florida, USA during the non-breeding seasons across 2013–2015, including February 2013, September 2013 to February 2014, and September 2014 to February 2015. In total, 80 after-hatching-year (AHY) northern cardinals were sampled from two paired urban–rural sites: (i) an urban location, Gainesville (29°65′ N, 82°32′ W), and a rural location, Austin Cary Forest (29°75′ N, 82°21′ W) in Alachua County; and (ii) an urban location, Ocala (29°18′ N, 82°14′ W) and a rural location at a private farm (29°44′ N, 82°24′ W) in Marion County. We separated hatching-year (HY) and AHY individuals by both plumage and beak patterns; as a mixture of faded brown juvenile feathers and fresh reddish or red feathers, as well as dusky patches around beak, is often noted for HY birds (Piranga 2015). These two sites are separated by about 65 km. In contrast, paired urban and rural locations within a site are separated by 20–30 km. The adult dispersal range of northern cardinal is about 40 km (Dow and Scott 1971). Thus, if we found significant variation between habitats, rather than between sites, it would suggest that the differences were due to environmental variation, as predicted.

We only used passive mist netting to capture our birds because other capture methods may be biased with respect to personality (Carter, Goldizen, and Heinsohn 2012). All our sampling points within the two urban locations (five each) were private backyards along the edge of roads or buildings. The 10 rural sampling points were randomly selected inside the accessible woods around Austin Cary Forest and the private farm (5 each).

In order to quantify urbanization level, we measured the vehicle road density (km per km^2) and concrete density within 500-m centered on each sampling point (Myczko et al. 2014) using the ArcGIS online program by Esri based on satellite images (World Imagery, Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Gemapping, Aerogrid, IGN, IGP, swisstopo and the GIS User Community). Descriptive statistics for the two locations were summarized in Table 1. Multivariate analysis of variance (ANOVA) indicated that there was a significant difference in both landscape features between urban and

Table 1: Mean ± SE of road density and concrete density for each location

Location	Type	Sampling points	Road density	Concrete density
Gainesville	Urban	5	11.2 ± 2.3	362.8 ± 48.7
Austin Cary Forest	Rural	5	2.8 ± 0.7	13.8 ± 7.5
Ocala	Urban	5	10.4 ± 4.3	319.4 ± 60.1
Farm	Rural	5	2.8 ± 0.4	17.8 ± 4.2

rural sites ($F_{6,30} = 19.525$, $P < 0.001$). A post hoc Tukey test showed that the urban locations (Gainesville and Ocala) differed significantly from the two rural locations (Austin Cary Forest and the private farm); the differences between locations within a habitat type were not significant (all $P > 0.33$).

Handling protocol and behavioral trials

As a sexually dimorphic species, the sex of individual northern cardinals can be identified by sight; the body weight for each bird was measured and recorded at capture. Individuals were then transported to the USDA/APHIS National Wildlife Research Center Florida Field Station in Gainesville, FL. They were housed individually in $1 \times 0.8 \times 2$ m observation rooms; perching branches, ad libitum food (mixed seed, mealworms and chopped fruit) and clean water were provided. We refreshed food and water daily at 8:00 am. During the 8-day captivity period, individuals were run through five behavioral trials that are commonly used to characterize personality traits in birds. The five personality traits were selected because they are commonly used in urban–rural comparison studies. We have already demonstrated that these behavioral measurements are repeatable within an individual northern cardinal (Huang, Kimball, and St. Mary 2018). Moreover, exploratory factor analysis showed that measurements from different trials formed distinct clusters corresponding to the trial-specific personality traits (Huang, Kimball, and St. Mary 2018).

Birds were tested either in their $1 \times 1 \times 3$ m housing room or the two outdoor aviaries containing five perches inside: small ($2 \times 2 \times 3$ m) and large ($9 \times 6 \times 3$ m). Within 1 h after the end of testing, all birds were released at their capture points, unless weather conditions did not permit an immediate release; no bird died during the testing period. All behavioral trials were run between 8:00 and 11:30 am. Trials were always conducted in the same order (Fig. 1). We did not expect an influence on responses caused by trial order; though, by using the same order for all birds, the influence, if any, should equally affect all individuals and hence not influence our final results. All trials were recorded with a digital video recorder for later behavioral quantification. The order of behavioral trials was (Fig. 1):

i. 'Novel environment test'. The number of movements (hops and flights), the frequency of scanning behavior, and the proportion of space visited (both perches and ground) during the 10-min observation in the small aviary right upon arrival were used to quantify the personality trait Exploration (exploration of new environments; Verbeek, Drent, and Wiepkema 1994; Dingemanse et al. 2002; Herborn et al. 2010; Minderman et al. 2010; Huang, Sieving, and St. Mary 2012; Miranda 2017).

ii. 'Novel object test in a foraging context'. The difference in latency and frequency for a bird to approach within 50 cm
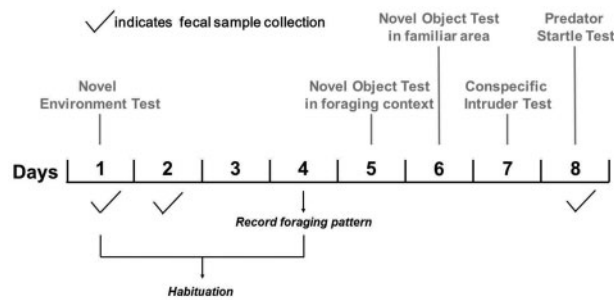
Figure 1: Order and timing of behavioral trials and fecal sample collection while in captivity (modified from Huang, Kimball, and St. Mary 2018).

of the food bowl, latency and frequency to feed, and proportion of time spent within 50 cm of the food bowl as well as feeding with and without the presence of the novel object we provided (a cat toy ball) within an hour were used to quantify the trait Neophobia (novelty avoidance; Greenberg 1983; Mettke-Hofmann, Winkler, and Leisler 2002; Feenders, Klaus, and Bateson 2011; Kerman et al. 2016; Miranda 2017).

iii. 'Novel object test in a familiar area'. The latency and frequency for an individual to approach within 50 cm of a novel object (a parakeet spinning bells toy, which replaced the food bowl), as well as the proportion of time spent within the close range to inspect the object were recorded for an hour to quantify the trait Neophilia (attraction to novelty; Mettke-Hofmann, Winkler, and Leisler 2002; Greenberg 2003; Feenders, Klaus, and Bateson 2011; Andersson, Laikre, and Bergvall 2014; Miranda 2017). Given that the toys used in the Neophobia and Neophilia trials were presented to an individual once only for the corresponding test, and that the individuals did not have visual access to the other housing rooms, we believe it is safe to assume these were novel objects.

iv. 'Conspecific intruder test'. The latency and the frequency to approach the conspecific wood-carved, sex-specific decoy model within 50 cm, as well as the proportion of time spent within this range during the 30-min observation period were used to quantify the personality trait Aggression (attack or other aggressive interactions or displays; Schlinger 1987; Duckworth 2006; Duckworth and Badyaev 2007; Scales, Hyman, and Hughes 2011; Miranda 2017). The painting of the wood-carved decoy mimicked the pattern of living northern cardinals, though we did not measure reflectance on the decoy. A 3-min playback song randomly selected from local recordings was presented together with the decoy inside the housing room to mimic a possible encounter in the wild (Scales, Hyman, and Hughes 2011).

v. 'Predator startle test'. Activities (hop and flight numbers) during the 'Before,' 'During' and 'After' stages of an encounter with a tufted titmouse (*Baeolophus bicolor*) seet call together with a life-size Cooper's hawk (*Accipiter cooperii*) silhouette fly-over across the top of the large aviary were recorded. Cardinals are known to tune to this alarm call indicating an actively attacking predator nearby (Huang, Sieving, and St. Mary 2012). Differences in the During-Before and After-Before activity, as well as the 'freezing time' once the individuals got startled, were used to quantify Boldness trait (exposure to risk; Klump and Curio 1983; Miller, Garner, and Mench 2006; Huang, Sieving, and St. Mary 2012; Miranda 2017).

For our two novel object tests and the conspecific intruder test, some individuals not only approached within close range, but also took direct action toward the stimulus we provided (i.e. contacted the parakeet toy during the novel object test in a familiar area). The proportion of individuals taking such actions was from 3.8% to 52.5%, depending on tests. In order to include such individual differences, we calculated the 'latency score' for each individual as:

$$\frac{\text{Approaching latency}}{\text{Observation Duration}} \times \left(\frac{\text{Direct action latency} - \text{Approaching latency}}{\text{Observation Duration} - \text{Approaching latency}}\right).$$

If no direct action was taken at the end of the observation time, then we treated the portion of the equation inside the parenthesis as 1. Therefore, higher latency score indicated slower responses.

Scoring personality traits of northern cardinals

We took a multiple measures reduction approach to generate a 'score' for the corresponding personality trait (Dingemanse et al. 2007; Wilson et al. 2010). We first normalized measurement data through arcsine square-root or log transformation, as appropriate, for each behavioral trial. For each of the five behavioral trials, we then performed PCAs of behavioral measurements collected from our 80 cardinals during a behavioral trial. For each PCA, extracted principal components (PCs) with Eigenvalues > 1.0 were deemed to be significant (Kaiser 1960), and kept as the score(s) for the personality trait defined by that particular behavioral trial. Critical behavioral measurements (with a variable absolute loading value > 0.70 on the PC(s) of its associated behavioral trial; Stevens 2009) for each personality trait were summarized in Table 2. All PCAs were performed using PASW Statistics 18.0 (SPSS Inc. 2009).

Profiling CORT parameters

Wet feces were collected at three time points throughout the behavioral trials period: the capture day, the second day, and the eighth day in captivity (Fig. 1). Once captured, before transporting to the housing area, birds were placed in a standard bird bag immediately for 5 min; the bird bag was lined with a paper bag for dropping collection (Garamszegi, 2012). For the two remaining samples (taken on Days 2 and 8), droppings were collected between 8:00 and 8:30 am after daily refreshment of food and water; to obtain these samples, a paper sheet was positioned on the bottom of each cage for collection (Carere et al. 2003). We then transferred five dropping pools with similar amount and appearance into an empty plastic tube previously filled with 95% ethanol and immediately put into a freezer. Samples were later transported (no longer than 2 h) to the lab in an insulated cooler and stored at −20°C until the day of extraction (Carere et al. 2003; Garamszegi et al. 2012).

For CORT metabolite extraction, we followed the procedures in Möstl, Rettenbacher, and Palme (2005) and Touma and Palme (2005). Metabolites were then measured via CORT Enzyme-Linked Immunosorbant Assay (ELISA) Kit following the manufacturer's instructions (Enzo Life Sciences Inc., Farmingdale, NY, USA). There are several different fecal metabolites that can be formed from cortisol and CORT (Teskey-Gerstl et al. 2000). Cross reactivity to some of those compounds in the assay kit we used was: CORT (100%), deoxycorticosterone (28.6%), progesterone

Table 2: Eigenvalues and % variance explained by common PCs for each location (followed Huang, Kimball, and St. Mary 2018)

Personality trait	Critical behavioral measurement (loading value)	Eigenvalue	% of variance explained	↑plaineinterpretation
Exploration	Movement number (0.998)	1.711	57.042	More explorative
	Proportion of space explored (0.742)			
Neophobia	Latency score difference (0.992)	1.258	25.151	More neophobic
Neophilia	Latency score (0.941)	1.472	49.266	Less neophilic
	Approaching frequency (−0.759)			
Aggression	Latency score (−0.953)	1.519	50.622	More aggressive
	Approaching frequency (0.745)			
Boldness	Freezing time (0.997)	1.094	36.455	Less bold

(1.7%), tetrahydrocorticosterone (0.28%), aldosterone (0.18%), testosterone (0.13%), cortisol (0.046%), pregnenolone (< 0.03%), ß-estradiol (< 0.03%), cortisone (< 0.03%) and 11-dehydrocorticosterone acetate (< 0.03%). The minimum detectable level of CORT metabolites was 0.027 ng/ml according to the manufacturer's manual. Assessment of parallelism was conducted by comparing the curve from diluted samples to the standard curve provided as recommended (Möstl, Rettenbacher, and Palme 2005); three serial dilutions of six randomly selected fecal samples yielded displacement parallel to the standard CORT curve ($P = 0.370$), thus indicating that the kit indeed measured metabolites in northern cardinals correctly. We also tested whether there is intra- and/or inter-assay biases by checking the coefficient of variation of CORT standards (Möstl, Rettenbacher, and Palme 2005). The coefficient of variation from the five CORT standards of known concentration that we included when running the ELISA kit was 8% for inter-assay, and 0.8% to 4.1% for intra-assay. We also biologically validated the measurements (Touma and Palme 2005); we detected a significant increase in CORT metabolites within the same individual before and after the capture plus 1-day in captivity ($P < 0.001$), independent of whether the bird was a female or male, where the bird was sampled, or variation in the capture date and time.

Using this non-invasive approach to measure CORT metabolite levels is commonly accepted since exogenous CORT levels in cloacal fluid correlates with those in plasma (Hiebert et al. 2000; Goymann, Möstl, and Gwinner 2002; Stöwe et al. 2010; Legagneux et al. 2011; Herring, Ackerman, and Herzog 2012). CORT metabolite levels in feces does not elevate for 2–12 h after capture (Ludders et al. 2001; Washburn et al. 2003). Given that we checked our mist nets every 10 min and kept the initial processing to under 30 min, our CORT metabolite levels at capture highly possibly reflected the baseline level of an individual. Samples collected from the second day were considered to reflect stressed levels after experiencing capture and captivity, whereas the eighth day samples were considered to reflect stressed levels after all the behavioral trials. We termed changes in CORT metabolite level between second day and the capture day as 2-day CORT response, and between eighth day and the capture day as 8-day CORT response (Dickens, Earle, and Romero 2009). Out of the 80 birds we sampled, 67 individuals produced enough fecal samples in every collection time point and thus could be included in the full analysis. There were 18, 17, 17 and 15 birds from Gainesville, Austin Cary Forest, Ocala and the private farm, respectively.

Statistical analyses of the effects of state

First, we applied general linear mixed model (GLMM) via PASW Statistics 18.0 (SPSS Inc. 2009) to evaluate the effect of our selected states on personality traits (Boon, Réale, and Boutin 2007; Verhulst, 2016). Personality scores generated from PCA for each personality trait were treated as dependent variables. Predictor variables included habitat type, CORT metabolite level at capture, 2-day CORT response, 8-day CORT response, sex, body weight and the following pairwise interactions: habitat type * (weight, CORT at capture, 2-day CORT response and 8-day CORT response), as the impact of those intrinsic states may depend on the level of the extrinsic state. Sampling location was treated as a random variable. Bonferroni correction was applied to adjust significant P-values. Backward elimination of least significant variables was used to obtain the minimum adequate model; the model that passed the goodness-of-fit test containing the minimum number of significant predictors (Boon, Réale, and Boutin 2007).

We then applied SEM (Dingemanse et al. 2010; Fargallo et al. 2014) to construct the behavioral syndrome structure among our personality traits. We first constructed all possible models of syndrome structure formed by at least two of our personality traits (since by definition a 'behavioral syndrome' happens only when at least two personality traits show a behavioral correlation). In all cases, behavioral syndrome was treated as our latent variable and personality traits were observed variables. We then checked each model's fit through three commonly applied criteria in SEM analysis: (i) Chi-square test that evaluates the level of discrepancy between the sample and fitted covariance matrices of a model (Bentler and Bonnett 1980; Hu and Bentler 1999); a non-significant result suggests negligible differences. (ii) Goodness-of-fit index (GFI) that checks the variances and covariances accounted for by a model to examine how closely that model can replicate the observed covariance matrix (Hu and Bentler 1999). (iii) Root means square error of approximation (RMSEA) that tests how well a model fits the population's covariance matrix (Sugawara and MaCallum 1993). We deemed a model with a non-significant P-value for a Chi-square test, a GFI value > 0.9, and a RMSEA value < 0.5 as a good fit (Schermelleh-Engel, Moosbrugger, and Müller 2003; Arbuckle 2014). For all models with good fit, we then applied Akaike information criterion (AIC) for model selection. The model with lowest AIC score, which also accounts for variation in complexity, was considered as the best model. However, if the difference between AIC values (ΔAIC) of a model and the best model was < 2, we considered the two models equally good (Ruppert, Wand, and Carrol 2003; Marzerolle 2006) and further discussed both of them. Only models that had a significantly better AIC than the independent, null model (i.e. no relationships) were further processed through model selection.

We used SEM again with the syndromes identified above, as well as influential states for personality traits identified from GLMM, to construct models reflecting possible correlating or hierarchical structures to test alternative state-syndrome

relationship(s). The three criteria used for model fit evaluation, as well as the AIC/ΔAIC for model selection, were also applied here to identify the best model(s) describing the relationship between the behavioral syndrome(s) and the state(s).

If the identified model(s) suggested that either categorical variable (habitat type or sex) was important, we further tested whether the syndrome structure varied between groups by constructing and comparing within-group syndrome structural models (Bókony et al. 2012). If a shared syndrome structure was detected between categories, we further applied multigroup analysis to test whether the structural weights of personality traits composing the behavioral syndromes differed between groups (Arbuckle 2014; Fargallo et al. 2014). To compare the structural weights, C_{min}, the minimum value of discrepancy calculated by maximum likelihood estimation was used. With degrees of freedom equal to the difference between the degrees of freedom of the two competing models (e.g. the urban model and the rural model), C_{min} has an approximate chi-square distribution that can be used to test the significance of dissimilarity between models (Arbuckle 2014; Fargallo et al. 2014). All the SEMs were performed using AMOS 23.0 (Arbuckle 2014).

Results

Effects of states on personality trait variation

Five personality traits Exploration, Neophobia, Neophilia, Aggression and Boldness were scored from the corresponding behavioral trials (Huang, Kimball, and St. Mary 2018). Exploration indicated the space an individual explored inside the novel aviary. Neophobia suggested how much an individual's daily routine feeding was disrupted by the presence of a novel object. Neophilia scored how long it takes for a bird to approach and investigate a novel object. Aggression demonstrated how fast an individual approached and confronted a conspecific intruder. Boldness revealed how long an individual took to recover from the startle state induced by a nearby predator. Although Neophilia and Neophobia may seem two sides of the same coin, studies suggest that these may actually belong to different behavioral dimensions: the need to exploit potential opportunities or the need to avoid novel risk (Greenberg and Mettke-Hofmann 2001; Mettke-Hofmann, Winkler, and Leisler 2002; Herborn et al. 2010; Huang, Kimball, and St. Mary 2018). Eigenvalue and percentage of variance explained by each personality score, the PC obtained, was summarized in Table 2.

GLMM revealed that habitat type and CORT metabolite level at capture were the two significant predictors for the personality traits Neophilia and Aggression (Table 3). The personality trait Neophobia differed somewhat; while habitat type remained as a significant predictor of variation, it was 2-day CORT response, instead of CORT at capture, that remained in the minimum adequate model for this trait. Even after Bonferroni correction, most predictors remained significant, with CORT metabolite levels at capture for Aggression as the only exception. In the case of the personality traits Exploration and Boldness, none of the states we tested were significant predictors of variation.

Overall, estimated β coefficients from the GLMM suggested that higher CORT metabolite level at capture and more acute 2-day CORT response were linked to more reactive behavioral types (more neophobic but less neophilic and aggressive; Table 3). Urban northern cardinals were in general less influenced by the presence of something unfamiliar (less neophobic; ANOVA, $F_{66,1} = 7.961$, $P = 0.006$). They also approached and investigated a novel object more quickly (more neophilic; ANOVA $F_{66,1} = 13.035$, $P = 0.001$) but took longer to confront a conspecific model (less aggressive; ANOVA $F_{66,1} = 4.212$, $P = 0.044$) than rural birds.

Effects of states on behavioral syndrome variation

First, we compared 26 possible models that could be constructed using 2 or more (of our 5) personality traits to identify the behavioral syndrome structure of northern cardinals. The best model was the one comprised of Exploration, Neophobia, Neophilia and Boldness (Fig. 2; AIC = 19.477, no other competitive models with ΔAIC< 2 were found). Based on the standardized effects of personality traits on the syndrome, Exploration had the greatest contribution to the behavioral syndrome, followed by Boldness, Neophilia and Neophobia; animals that were more exploratory were also more bold and neophilic, however these animals were less neophobic. Thus, overall, it can be described as a reactive (less explorative, shyer, less neophilic and more neophobic)—proactive (more explorative, bolder, more neophilic and less neophobic) continuum.

Second, we compared the 29 possible models built using the identified behavioral syndrome above, habitat type, CORT metabolite level at capture and 2-day CORT response (the states showing an effect on personality traits in the GLMM), with all possible correlating or hierarchical relationships considered (Supplementary Fig. S1), to investigate the effect of those states on behavioral syndrome. The best model was the one in which habitat type and 2-day CORT response (Model 7, Supplementary Fig. S1) affected syndrome independently. Nevertheless, a competitive model with ΔAIC = 0.36 (Table 4) was also observed. This model was nearly identical to the previous one, with the exception that an additional correlation between habitat type and 2-day CORT response was included (Model 8, Supplementary Fig. S1). In other words, we cannot completely rule out the possibility that the two states work coordinately. Indeed, a following ANOVA analysis revealed that urban

Table 3: Effects of each state, the predictor variable, in the minimum adequate models for personality trait Neophobia, Neophilia and Aggression

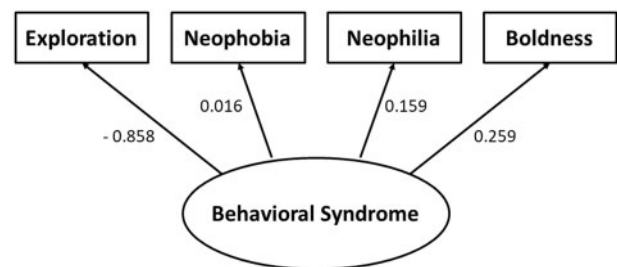| Personality trait	Effect	$F_{64, 1}$	P-value	β
Neophobia	Habitat type	6.201	0.015	−0.558
	2-day CORT response	7.935	0.006	0.061
Neophilia	Habitat type	4.299	0.020	−0.581
	CORT level at capture	5.975	0.022	0.048
Aggression	Habitat type	6.822	0.011	−0.628
	CORT level at capture	4.140	0.046	−0.094

Figure 2: The best behavioral syndrome structural model for overall northern cardinals. Numbers next to the arrows are standardized effects underlying behavioral syndrome structure on personality traits.

Table 4: AIC scores, estimated weights and *P*-values for the two competitive models addressing state-syndrome relationship

Model	AIC	Direction	Weight	P-value
Habitat type, 2-day CORT response → syndrome	36.323	Habitat type → syndrome	−0.579	0.003
		2-day CORT response → syndrome	0.041	0.012
Habitat type < > 2-day CORT response → syndrome	36.683	Habitat type ↔ 2-day CORT response	−0.402	0.010
		Habitat type → syndrome	−0.579	0.002
		2-day CORT response → syndrome	0.041	0.010

Table 5: AIC scores of competitive models for urban and rural northern cardinals

Habitat type	Rank	Constructing personality trait	AIC
Urban	1	Exploration, Neophobia, Neophilia and Aggression	16.166
	2	Exploration, Neophilia, Aggression and Boldness	16.753
	3	Exploration, Neophobia, Neophilia and Boldness	18.015
Rural	1	Exploration, Neophobia, Aggression and Boldness	17.458
	2	Exploration, Neophobia, Neophilia and Aggression	18.028
	3	Exploration, Neophobia, Neophilia and Boldness	18.232

northern cardinals had significantly lower CORT metabolite levels than rural conspecifics (*P*-value = 0.014). Noticeably, in these two equally good models, the 2-day CORT response was always greater in animals with more reactive personalities (Table 4), which was the same pattern we observed for individual personality traits (Table 3).

Last but not least, given that the categorical variable habitat type was a predictor in the state-syndrome SEM analyses, we further examined how the syndrome structure differed between habitats. To determine whether the syndrome structure was constructed differently, we redid our earlier analysis using the 26 models of various combinations of personality traits, but this time separately for urban and rural birds. We found that while both habitats had three equally good syndrome models, the order and the composition varied between habitat types (Table 5). Best model for urban birds was constructed with Exploration, Neophobia, Neophilia and Aggression (Fig. 3A); while the best rural syndrome model involved Exploration, Neophobia, Aggression and Boldness (Fig. 3B). In other words, a divergence in behavioral syndromes was observed for urban and rural northern cardinals, given that Boldness replaced Neophilia in the behavioral syndrome of rural birds. Second, we applied multigroup comparison to the shared competitive model (ranked in the third place for both urban and rural datasets) to see whether there was an urban–rural difference in standardized effects of personality traits involved. The result suggested that the urban and rural birds did not differ in the structural weights of the four personality traits constructing this shared competitive model (df = 3, C_{min} = 1.556, *P*-value = 0.669).

Discussion

We found that habitat type (whether birds were urban or rural; an extrinsic state), as well as two stress hormone parameters (CORT metabolite level at capture and 2-day CORT response; intrinsic states) had significant effects on personality trait variation in northern cardinals and, indeed, influenced behavioral syndrome structure. CORT metabolite level at capture had a significant influence on the personality traits Neophilia (how long it takes to approach and inspect a novel object), while 2-day CORT response affected Neophobia (how much the daily feeding affected by the presence of a novel object). Urban versus rural

was a strong predictor of not only those two personality traits but also of Aggression. Urban cardinals were more neophilic, less neophobic, yet also less aggressive when compared with their rural conspecifics; they also had a consistently attenuated CORT metabolite level at all the three time points in our CORT sampling.

Moreover, habitat type and 2-day CORT response were also the states that influenced the behavioral syndrome. Although a hierarchical relationship between the two states was not suggested, the competitive model included a correlation between the two. Further examination suggested that rural and urban northern cardinals varied in their behavioral syndromes, with different personality traits involved in the construction of syndrome structural models.

Urban–rural variation in animal personality

Based on our results, urban cardinals were less neophobic, more neophilic but also less aggressive than their rural conspecifics. Although the urban syndrome involved Exploration, Neophobia, Neophilia and Aggression, the rural syndrome was constructed by Exploration, Neophobia, Aggression and Boldness instead, suggesting a possible urban–rural divergence of correlated behavioral traits (Table 6). Thus, our results suggest that, in the case of cardinals, urban birds are proactive whereas rural birds are shyer and more reactive. In most respects these results mirror urban–rural comparisons of other species.

Increased intraspecific Aggression has long been described as a 'urban wildlife syndrome' (Warren et al. 2006) in a variety of species (Cooke 1980; Gliwicz, Goszczynski, and Luniak 1994; Smith and Engeman 2002; Parker and Nilon 2008; Evans, Boudreau, and Hyman 2010; Scales, Hyman, and Hughes 2011; Galbreath et al. 2014). It has been proposed that the increased population density and clumped resource distribution in urban habitats (Prange, Gehrt, and Wiggers 2004; Warren et al. 2006; Parker and Nilon 2008) generating higher agonistic encounter rates (Macdonald et al. 2004; Foltz et al. 2015) are the reasons for such a change. However, we detected less aggression in urban northern cardinals. Given that we did not survey population densities across sampling locations, it is hard to conclude whether urban population densities might be lower for
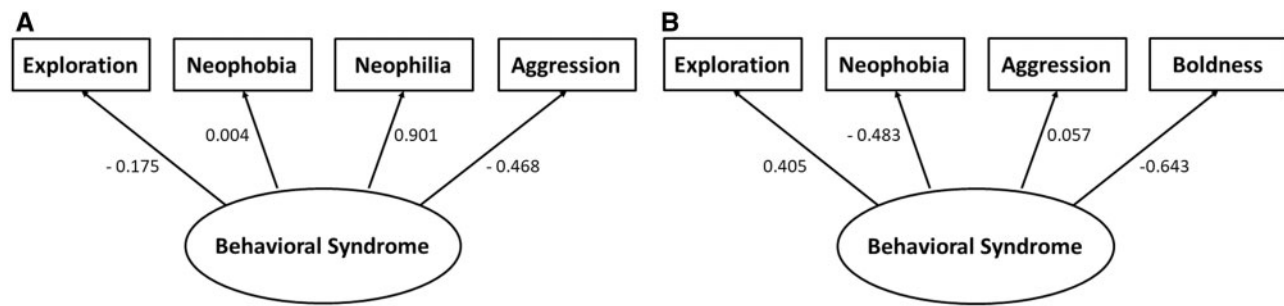
Figure 3: The best behavioral syndrome structural models for (**A**) urban and (**B**) rural northern cardinals. Numbers next to the arrows are standardized effects underlying behavioral syndrome structure on personality traits.

Table 6: Summary of detected behavioral and hormonal variation between northern cardinals inhibiting in urban and rural habitats

Habitat type	Urban	Rural
Behavioral type	Less neophobic	More neophobic
	More neophilic	Less neophilic
	Less aggressive	More aggressive
Syndrome structure	Exploration	Exploration
	Neophobia	Neophobia
	Neophilia	Neophilia
	Aggression	Boldness
CORT parameter	Lower CORT level at capture	Higher CORT level at capture
	Lower stressed CORT level	Higher stressed CORT level

northern cardinals in Florida. Moreover, we restricted our study to the non-breeding season, while aggression in general elevates in breeding season (Galbreath et al. 2014).

Alternatively, our results may indicate that northern cardinals are highly tolerant to urbanization. In Merrian's kangaroo rats (*Dipodomys merriami*), a lack of urban–rural aggression variation was also noted, and the ability of this rodent to live under a wide range of conditions was suggested to be the reason (Hurtado and Mabry 2017). The result may also reflect the age of population or the resource competitiveness in the study area. As urban areas expand, high initial aggression of new populations occupying those habitats may eventually lessen due to the cost of aggression and the need to coexist with higher densities of heterospecifics in urbanized environments (Duckworth 2008; Charmantier et al. 2017). In addition, if a consistent high food base exists, as is the situation in many urbanized environments (Shochat et al. 2006), selection from resource competition may be relaxed allowing less aggressive, less competitive individuals to survive (Shochat 2004; Anderies, Katti, and Shochat 2007; Hasegawa et al. 2014). We cannot rule out those possibilities with the information we have.

Human-induced environmental changes pose numerous conditions that animals are unlikely to have encountered before, and thus the ability to adjust to those constant novel challenges can be critical for surviving in an urban environment (Tuomainen and Candolin 2011; Candolin and Wong 2012; Sih 2013; Shanahan et al. 2014). Being less averse to novel objects (more neophilic and/or less neophobic), as we observed in our urban birds, can be beneficial because it increases the likelihood an individual might approach novel environmental features or food resources, which may be a first step in adapting to a new world (Greenberg 1983; Greenberg and Mettke-Hofmann 2001). Benefits may also arise from correlated abilities, such as innovation. Response to novelty is known to predict problem-solving ability in several bird species (Webster and Lefebvre 2001; Biondi, Bó, and Vassallo 2010; Overington et al. 2011; Sol et al. 2011; Tebbich, Stankewitz, and Teschke 2012). As urban habitats present many novel conditions, selection may favor more innovative individuals (Brosnan and Hopper 2014).

Noticeably, this pattern between urbanization and response to novelty is consistent with some (Sol et al. 2011; Tryjanowski et al. 2016) but not all other studies in birds (Atwell et al. 2012; Miranda et al. 2013), even though all of these studies measured Neophobia and Neophilia similarly. On one hand, it may suggest that there is no unique way to be an urban dweller (Sol, Lapiedra, and González-Lagos 2013). For instance, northern cardinals rely on understory vegetation for nesting sites in both urban and rural habitats (Leston and Rodewald 2006), whereas European blackbirds living in urban areas use anthropogenic structures for nesting while their rural conspecifics nest in dense understory (Partecke, Schwabl, and Gwinner 2006). Such differences in reproductive ecologies may lead to different coping styles in response to urbanization. Indeed, species-specific patterns of survival and relative habitat use in urban landscapes have been documented (Whittaker and Marzluff 2009; Kralj-Fišer, Hebets, and Kuntner 2017). On the other hand, the inconsistent patterns may reflect different population dynamics. It has been suggested that while reduced Neophobia and increased Neophilia may be beneficial during the colonization of urban areas, persisting in these habitats might necessitate more cautious behavior, which results in a reduced affinity for novelty (Bókony et al. 2012; Sol, Lapiedra, and González-Lagos 2013; Candler and Bernal 2015). In other words, not only species-specific characters but also different population dynamics may contribute to the inconsistency across studies.

As we observed divergent sets of competitive models between urban and rural northern cardinals, the differences in the distribution of personality trait values may ultimately contribute to the evolution of a distinct habitat-specific behavioral syndrome. The replacement of Neophilia by Boldness in rural behavioral syndrome may either suggest that rural birds takes longer to recover from an experience with a flying predator, and/or that urban birds have a greater means to exploit novel resources. Both can be particularly adaptive under their different scenarios, with rural birds possibly more exposed to the tested predator type (Stracey and Robinson 2012) and urban birds having more exposure to novel stimuli (Tuomainen and Candolin 2011; Candolin and Wong 2012; Sih 2013; Shanahan et al. 2014).

Stress hormone, animal personality and urbanization

Among our intrinsic states, two stress hormone parameters, CORT metabolite level at capture and 2-day CORT response, significantly explained between-individual variations in three personality traits and the behavioral syndrome. Greater CORT metabolite level or response predicted a more reactive (less neophilic and more neophobic) northern cardinal personality.

The HPA axis, one of the main mediators of an individual's physiological stress response that ends with the secretion of glucocorticoid hormones, such as CORT in birds, has long been proposed as a possible mechanism underlying individual variation in animal personality (Cockrem 2007; Aubin-Horth, Deschênes, and Cloutier 2012). Elevated glucocorticoid levels play a role in the initiation of a number of behaviors such as vigilance or escape, and thus are crucial for facilitating the 'fight-or-flight' responses that prepare individuals to fight or flee when facing stressors (Romero and Butler 2007; Schoech, Rensel, and Heiss 2011). Based on evidence collected from selective lines of several studies using captive animals, a more reactive behavioral type is related with a more acute HPA axis activity and/or greater glucocorticoids release relative to a more proactive type (Korte et al. 1997; van Hierden et al. 2002; Carere et al. 2003; Veenema et al. 2003; Albert et al. 2008; David et al. 2009; Stöwe et al. 2010). For instance, in two artificially selected lines of great tits (*Parus major*), less aggressive but more cautious birds exhibit higher CORT levels for both baseline (Stöwe et al. 2010) and stressed (Carere et al. 2003) situations than the more aggressive individuals.

Our observed pattern in northern cardinals that greater CORT metabolite level at capture and 2-day CORT response indicate more reactive personality fits with those previous findings from captive animals (Korte et al. 1997; van Hierden et al. 2002; Carere et al. 2003; Veenema et al. 2003; Albert et al. 2008; David et al. 2009; Stöwe et al. 2010). In other studies utilizing wild-caught animals, individuals with more reactive personality also expressed higher glucocorticoid hormonal levels (Schoech, 2009 ; Aubin-Horth, Deschênes, and Cloutier 2012; but see Garamszegi et al. 2012). For instance, in dark-eye juncos (*Junco hyemalis*), stressed CORT level negatively predicted a bird's exploratory style; animals with higher stressed CORT levels were shyer and slower explorers (Atwell et al. 2012). Therefore, together with those studies, our results suggest that the hypothesis that individual stress hormone response determines behavioral type variation may hold true in both captive and wild animals.

Noticeably, however, while our studies indicate that the proactive behavioral response (i.e. less neophobic and more neophilic) of urban northern cardinals may be attributed to their lower CORT metabolite levels, the trend may not be universal based on other studies characterizing differences in stress hormone function between urban and non-urban populations (Partecke, Schwabl, and Gwinner 2006; Bonier et al. 2007; Fokidis, Orchinik, and Deviche 2009; Zhang et al. 2011; Atwell et al. 2012; Davies et al. 2013; Miranda et al. 2013). Thus far, no consistent pattern has been observed; both baseline and stressed CORT levels have been reported to be higher, lower or similar in urban versus non-urban animals depending on species, sex and life history stage (Bonier 2012). The allostatic load (the energy demands that increase over time when an individual is exposed to repeated or chronic stress) experienced by an animal may differ from species to species (Bonier 2012); for instance, wild-caught animals respond to chronic captive stress in a highly species-specific way (Fischer and Romero 2018). The

fact that physiology and behavior may respond to stress on different timescales (Gormally et al. 2019) also makes the situation more complicated. Overall, to fully elucidate general endocrine responses to urbanization, interdisciplinary approaches replicated across environments and species will be needed (Bonier 2012; Gormally et al. 2019).

Conclusion

In sum, our findings demonstrated a behavior-hormone covariation along urban–rural gradient (Table 6). Habitat type was found to have an effect on personality traits and behavioral syndrome in northern cardinals, with stress hormone parameters predicting trait variation and providing a possible underlying explanation. Along with several other studies, our results suggest that urban environments may favor individuals that have an affinity for novelty, a feature often linked to innovation. Moreover, the sets of competitive behavioral syndrome models constructed by personality traits differed between urban and rural habitat, implying that the behavioral syndrome could also be diverging. In other words, the environmental selection pressures arising from urbanization may work not only on single personality traits, but also the intercorrelated structure among them. Variation in phenotypic traits between urban and rural habitats can reflect either phenotypic plasticity or genetic variation. Further research incorporating population-level features, such as population dynamics or natal dispersal choices, and genetic structures is thus recommended to understand how this variation arises. The impact of urbanization is complicated, so investigation of the involvement of intrinsic and extrinsic states (either additive or interactive) to understand urban–rural personality variation, as our study did, should be extended to a wider variety of species so that we may begin to identify the underlying mechanisms aside from the complexity caused by population history or species-specific requirements. With the continued expansion of human population, urbanization poses immense threats to the wildlife, and hence the knowledge gained can be truly useful for understanding the longer term implications for wildlife corresponding with our own population distribution.

Supplementary data

Supplementary data are available at *JUECOL* online.

Data Availability

The authors confirm that the data supporting the findings of this study are available within the supplementary materials.

Conflict of interest statement. None declared

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