



A migratory sparrow has personality in winter that is independent of other traits

Theadora A. Block ^{a,*}, Rachel Star ^a, Daizaburo Shizuka ^b, Alexis S. Chainé ^{c,d}, Bruce E. Lyon ^a

^a Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, U.S.A.

^b School of Biological Sciences, University of Nebraska-Lincoln, NE, U.S.A.

^c Station d'Ecologie Théorique et Expérimentale du CNRS (UMR5321), Evolutionary Ecology Group, Moulis, France

^d Institute for Advanced Studies in Toulouse, Toulouse School of Economics, Toulouse, France

ARTICLE INFO

Article history:

Received 22 September 2020

Initial acceptance 7 January 2021

Final acceptance 21 April 2021

Available online 14 July 2021

MS. number: A20-00711R

Keywords:

badge of status

bird

golden-crowned sparrow

life-history

personality

repeatability

social dominance

vocalization

winter ecology

Small birds in winter face trade-offs between predation risk and foraging, and alternate life-history strategies may arise from these trade-offs. Animal personality shows similarities with alternative life-history strategies, and using a life-history context to understand personality can provide valuable insights. Golden-crowned sparrows, *Zonotrichia atricapilla*, a small migratory bird, have a complex winter social system with high site-fidelity, long-term social associations between individuals and competition mediated by badges of status. We asked whether golden-crowned sparrows show personalities during winter, whether these personalities were consistent over 3 years and whether they correlated with social and morphological traits. We found that golden-crowned sparrows had highly repeatable behaviours, as measured in captive behavioural assessments, constituting personalities consistent within one season and over time for up to 3 years, a time span that covers the average life span of the sparrows. While long-term repeatability was present, it varied considerably among different behaviours and time spans, and length of time between measures did not predict the magnitude of repeatability. Two movement-based aspects of sparrow personality were independent of the traits we measured (dominance, badges of status, size and age). However, nonsong vocalizations (a repeatable aspect of personality) correlated with wing length and gold badge size in some years. Because personality did not strongly link to the social traits we measured, sparrow personality could represent a separate axis of variation that might connect with other winter life-history parameters such as foraging, predation response or survival.

© 2021 The Authors. Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

One of the main life-history trade-offs that animals face in winter is between foraging and survival (McNamara & Houston, 1987; McNamara, Houston, & Lima, 1994). Small birds, in particular, face many difficulties surviving winter conditions due to challenges of keeping warm combined with limited fat reserves – they must forage to avoid starvation, but in doing so, they increase the risk of predation (Houston, McNamara, & Hutchinson, 1993; Lima, 1986; McNamara et al., 1994). Known as the small-bird-in-winter paradigm (Roth, Lima, & Vetter, 2006), this was proposed as one reason why birds form groups in winter (Caraco, Martindale, & Pulliam, 1980). Forming groups can protect individuals from predation so that birds can spend more time foraging and less time

scanning for predators (Lima, 1987) despite increased competition for resources within groups. The trade-off between foraging and predation can manifest on multiple levels, from general selection pressures on decisions like when to forage or join a group to how individuals respond to risk, and can lead to a variety of optimal solutions.

Alternative life-history strategies have been studied mostly in the context of reproduction (Dominey, 1984; Lyon & Eadie, 2008; Taborsky, Oliveira, & Brockmann, 2008), but there is some evidence that alternative life-history strategies occur in other parts of the life cycle. In wintering pied wagtails, *Motacilla alba*, some birds defend territories while others live in flocks (Davies, 1976). Other examples of alternative nonbreeding strategies have been found in partial migration tactics, which have been shown in pied avocets, *Recurvirostra avosetta*, and European robins, *Erithacus rubecula* (Adriaensen & Dhont, 1990; Chambon et al., 2019).

* Corresponding author.

E-mail address: tablock@ucsc.edu (T. A. Block).

Considerable variation seen in social traits during the nonbreeding season could be indicative of alternative strategies. For birds that form social groups in winter, competition between individuals for access to food can be mediated by signals of status or social recognition (Chaine, Shizuka, Block, Zhang, & Lyon, 2018). Previous studies suggest that variation in social dominance signalled by badges of status could favour alternative foraging strategies, such as producers versus scroungers (Barta & Giraldeau, 1998) or sheep and shepherds (Rohwer & Ewald, 1981). For example, Harris' sparrows, *Zonotrichia querula*, flock in winter and use variation in the size of their black chest patches (Rohwer, 1975) as badges of status that predict an individual's dominance. Rohwer (1982) further theorized that this variation in plumage and social dominance in Harris' sparrows could reflect alternative winter strategies with trade-offs between dominance and food finding.

In many ways, animal personalities can mirror the patterns of alternative life-history strategies (Réale et al., 2010; Stamps, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007). Behaviours associated with alternative life-history strategies are often consistent within individuals but differ across individuals (Brockmann, 2001), and animal 'personalities' also consist of specific behaviours that vary among individuals but are consistent for a given individual (e.g. boldness, exploration, neophobia). If dominant and subordinate individuals use different foraging mechanisms like producers versus scroungers, dominant individuals may be bolder in general, so dominance would potentially correlate with a bold–shy axis of personality. Indeed, personality types have been found to correlate with foraging and survival (Bubac et al., 2018; Cote, Dreiss, & Clobert, 2008; Dingemanse, Both, Drent, & Tinbergen, 2004; Patrick & Weimerskirch, 2014) and other life-history traits such as growth or the timing of reproduction (Hall et al., 2015; Montiglio, Garant, Bergeron, Messier, & Réale, 2014; Niemelä, Vainikka, Hedrick, & Kortet, 2011).

The interplay between personality, dominance and foraging strategy can vary within the same species. For example, in captivity, shy barnacle geese, *Branta leucopsis*, act as scroungers and bold geese as producers, but personality does not correlate with dominance (Kurvers et al., 2009). In contrast, in the wild, less dominant geese (smaller and younger) are more explorative and act as producers, while dominants (larger and older) then displace them at the feeding sites (Stahl, Tolsma, Loonen, & Drent, 2001). Life-history traits and strategies may also vary with age and sex, both of which can be correlated with personality (Biro & Stamps, 2008; Dammhahn, Dingemanse, Niemelä, & Réale, 2018; Johnson et al., 2017). Connecting personality to other traits such as dominance, age, sex and morphology can reveal whether, and how, personality may be part of a winter alternative strategy.

By definition, personalities are behaviours that are consistent over time, but we currently do not have expectations for how long personalities should be stable. In theory, personality could be stable for a particular season, for one or multiple years, or over the animals' entire life. While it is important to determine the consistency of behaviour over shorter time frames, we also need to measure the stability of these behaviours over longer periods of an animal's life span. If personality is a component of life-history strategies, then the time span of the particular tactics an individual adopts should determine the time span of stable personalities. For example, if the life-history tactic is age dependent, personality should reflect those changes and we might expect to see consistent behaviours varying across age classes. Alternatively, if the life-history tactics are fixed for life, personality should also be consistent across all years. Finally, if life-history tactics change across years, e.g. based on condition, personality should track these changes accordingly.

Despite clear links between personality and fitness in some study systems (Biro & Stamps, 2008; Bubac et al., 2018; Costanzo et al., 2018; Dingemanse et al., 2004; Dingemanse & Réale, 2005; Hall et al., 2015; Stein, Trapp, & Bell, 2016), personality is usually measured in captive conditions that are removed from the life-history contexts in which it is favoured. Therefore, it is necessary to understand the relevance of the experimentally determined personalities by linking them to important behavioural and ecological aspects of an animal's life in the wild (Archard & Braithwaite, 2010; Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013; Dingemanse et al., 2004).

We examine the occurrence and consistency of personality traits in a migratory bird, the golden-crowned sparrow, *Zonotrichia atricapilla*, during winter. We investigate whether personality correlates with behaviours and social traits that could be part of alternative winter social strategies such as producers versus scroungers (Barta & Giraldeau, 1998). Golden-crowned sparrows vary widely in several traits that are likely important to survival, such as plumage and dominance. Golden-crowned sparrows have plumage crown patches with two outer black stripes that flank a central gold patch. Experiments confirm that the variable black and gold crown patches function as badges of status that determine social dominance in contests over food (Chaine et al., 2011, 2013). However, whether the birds pay attention to the badges depends on social context: unfamiliar sparrows rely mostly on the badges of status to settle contests while familiar birds can rely on individual recognition (Chaine et al., 2018).

Golden-crowned sparrows live in highly stable, complex winter social groups (Shizuka et al., 2014), and individuals within these groups vary in social measures that could also potentially reflect different wintering strategies. The sparrows form flocks during winter and forage in fission–fusion groups, and these flocks are subsets of larger communities of 3–17 birds (Shizuka et al., 2014). These communities have organized social structure due to social preferences among individual birds; social structure is not an incidental by-product of overlapping space use. Overall, communities are relatively stable, and if a sparrow returns to the wintering ground across winters, it nearly always returns to the same community (Shizuka et al., 2014). As part of this remarkable fidelity, some sparrows socialize with the same individuals in the same area for multiple years (Shizuka et al., 2014). Theory suggests that stable social systems such as those seen in golden-crowned sparrows are particularly amenable for the evolution of personality (Wolf & Krause, 2014; Wolf & Weissing, 2010).

Migratory birds face different challenges compared to residents (Mettke-Hofmann, Ebert, Schmidt, Steiger, & Stieb, 2005), and much of the bird personality research is on resident year-round species (van Oers & Naguib, 2013). The migratory aspect of the sparrows' lives emphasizes the importance of studying their behaviours over multiple years, as they deal with both social stability within a season and significant social changes and turnover over years (Shizuka et al., 2014). The social and geographical differences that come with breeding and wintering in different areas could mean that personality and other traits shift over time due to these seasonal changes. If migrant birds have stable personality types year-round, there could be trade-offs in fitness between seasons. For example, if bolder birds have higher reproductive success during the summer, they might face a trade-off with lower survival during winter.

Here, we ask whether golden-crowned sparrows show personalities in winter and, if so, whether personality correlates with social and morphological traits. If personality correlates with one or more of the key social traits we assess, it could reflect the occurrence of alternative winter life-history strategies in these birds. To address this, we ask three questions. First, do golden-crowned

sparrows have experimentally determined repeatable behaviours (personality traits) within one season? Second, if so, are these behaviours repeatable across multiple years? Third, does personality correlate with dominance, badge of status, age or size?

METHODS

Field Methods

We studied wintering golden-crowned sparrows at the University of California Santa Cruz Arboretum. These migratory sparrows breed in Alaska and western Canada and are on the wintering grounds from late September through to the end of April. We gathered all field data and ran aviary trials during three winter seasons. Season 1 spanned September 2014–May 2015, Season 2 spanned September 2015–May 2016 and Season 3 spanned September 2016–May 2017. Subsequently, we will refer to each field season by the year in which it began: 2014, 2015 and 2016.

We caught golden-crowned sparrows with baited Potter traps and mist nets. Each captured bird was banded with a U.S. Geological Survey metal band and a unique combination of colour bands to enable individual identification in the field. For all birds (new unbanded and returning banded individuals), we measured body mass (g), length of the tarsus (mm), culmen (mm) and flattened wing length (mm), and collected a blood sample from the ulnar vein for sexing. Birds were sexed by amplifying the *CHD* gene on the Z and W sex chromosomes (Griffiths, Double, Orr, & Dawson, 1998) following methods described in Chaine et al. (2011).

Personality Trials

We conducted behavioural trials during banding sessions after the birds were banded and before they were measured to minimize handling time ([dataset] Block, Star, Shizuka, Chaine, & Lyon, 2020). We kept birds in bird bags in a quiet environment and started the trials by the order in which we caught the birds. In each assessment, the bird was placed in one of two 1.2 m³ outdoor aviaries in a natural, shaded environment and videorecorded for 5 min with no observer present. Each cage had woodchips covering the ground, chicken wire walls with mosquito mesh covering the internal sides and four natural wooden perches fixed on each corner of the cage floor. From the videos, we extracted the following eight behaviours that have been shown to be relevant in other avian studies (Dingemanse, 2002; Dingemanse et al., 2004; Kluen, Kuhn, Kempenaers, & Brommer, 2012; van Oers 2004): the number of quadrants used, number of perches used, perch bouts (number of times birds hopped onto a perch), number of perch turns (a 180° rotation on a perch), number of flights, latency to land after release into the cage, number of nonsong vocalizations (call notes) and number of hops in 2 min. All measures from the video were counted over 5 min, except for the number of hops, which were counted over 2 min (timing began 1 min after we released the bird into the cage to give birds time to acclimate to the new environment). We also measured two additional behaviours with an 'escape test' and a 'bag test'. For the escape test, we placed each bird in a cardboard box (22.86 × 31.12 × 24.13 cm) with a small door (12.7 × 12.7 cm) opened after 1 min of acclimation to the box environment (Sasaki et al., 2018). We positioned the box on the ground outdoors near vegetation, with the small door opening on ground level. An observer hidden behind the box opened the door and timed how long the bird took to leave the box (in seconds); the test was capped at 300 s. The bag test was conducted before we banded the bird. The bird was placed in a cloth bird bag, hung on a clothesline and videorecorded for 1 min with no observer present (Montiglio, Garant, Pelletier, & Réale, 2012). Later, the number of

times the bird moved distinctly in the bag over 1 min was counted from the video recording. Two observers extracted a set of the same videos to calibrate counts and then they extracted all video data. The observers were blind to the sex, age and social status of the birds. We performed personality trials for the following numbers of individuals per year: 2014, *N* = 148; 2015, *N* = 143; 2016, *N* = 100. No trials were conducted after 1 March.

On a subset of birds (*N* = 25), we conducted repeated trials at least 1 month after the initial trial within the 2014 season to first identify which behaviours we would consider 'personality'. We measured the repeatability of the 10 extracted behaviours (detailed above) and retained all behaviours with repeatability >25%. This revealed six repeatable behaviours that we then used as a measure of personality for all three seasons. To ask which traits correlated with personality, we condensed the six behaviours in a principal component analysis (PCA) to form a composite measure of a bird's personality.

Potential Correlates with Personality

We measured several social and morphological traits, described in the sections below, to determine whether personality was correlated with other golden-crowned sparrow winter traits ([dataset] Block et al., 2020). All of these morphological traits are stable within a winter season. Badge size (size of a plumage patch) does not change as birds do not moult their plumage feathers in the winter season; they start moulting their badges shortly before leaving on spring migration and after we had finished collecting data on 1 April (Norment, Hendricks, & Santonocito, 2020). Mass is also consistent both within years and across years (Block, 2021), similar to other passerines during winter (Broggi, Hohtola, Koivula, Orell, & Nilsson, 2009).

Age

We characterized an individual's age as one of two standard avian age class categories: hatch-year (HY), which refers to birds in their first year of life, and after hatch-year (AHY), any age after year 1. Previously banded birds are necessarily AHY, but ambiguity in age exists for unbanded birds captured for the first time. To estimate age classes of newly captured birds, we used a modified version of Colwell's (1999) method to determine age class using rank scores for crown plumage. The size of the crown patches can increase over an individual's lifetime, but there is often a large change between the HY and AHY, and all HY birds have relatively smaller and duller plumage patches (Lyon et al., 2021). Crown features are an imperfect indicator of age, but plumage nevertheless improves the accuracy of ageing over the assumption that all unbanded birds are HY birds.

Badges of Status

To measure the plumage traits that function as badges of status, we took digital photographs of birds' crowns (photos focused on the top of the head, level with a ruler for size reference) during banding and extracted the size of the black and gold patches (mm²). We used Adobe Photoshop to isolate each colour patch and converted the number of pixels to mm² using a standardized method from Chaine et al. (2011).

Dominance Assay

We determined social dominance by observing interactions between birds over access to seed at regular prebaited feeding stations. We observed social interactions from at least 10 m away

and counted the interactions following methods from [Chaine et al. \(2011\)](#): fight, supplant, chase and avoid. Fights occurred when birds made physical contact, while supplants occurred when one bird rapidly replaced another at the seed pile. During chases, the bird that initiated the chase was considered the winner, while the bird that fled was the loser. Avoidance took place when the loser waited nearby but did not approach a bird feeding at the pile. We recognized this as a dominance interaction because the converse does not happen: dominant birds do not wait for a subordinate to leave the food, but rather chase or supplant them. We only included interactions with a clear winner and loser and used these data to calculate dominance scores (Elo rating; see [Statistical Methods](#)). We used dominance data from before 1 April of each season to calculate Elo ratings. After April, birds begin moulting their crown plumage to prepare for migration to the breeding grounds, and their behaviour may alter due to changing physiology. We calculated dominance for the following numbers of individuals per year: 2014, $N = 91$; 2015, $N = 94$; 2016, $N = 61$.

Ethical Note

All methods were approved by the Institutional Animal Care and Use Committee of the University of California, Santa Cruz, and the committee for animal research welfare and ethical treatment (Animal Welfare Permit Number Lyonb1808 to B. Lyon). All research and bird handling complied with Federal and California State regulations under permits to B. Lyon. All bird capturing and handling was done in good weather conditions (dry, not too cold). We minimized stress by keeping birds in single bird bags and handled birds as little as required. All personality trials were conducted between 0800 hours and 1400 hours. Birds were kept for the minimum amount of time necessary to perform the personality trials and banding, and generally released no longer than 2 h after capture. Personality trials occurred by the order in which birds were caught, so any impact of stress should be random rather than producing any particular response pattern. We monitored birds for stress, looking for well-known signs such as crown feather erection or lack of responsiveness. All birds appeared to suffer no lasting stress after release and were seen behaving normally in the field afterward.

Statistical Methods

We calculated repeatability for the experimentally measured behaviours across different timescales: within seasons (within years) and across multiple seasons (across years). Following [Nakagawa and Schielzeth \(2010\)](#), we used the rptR package (v.0.9.22) to calculate all repeatability measures ([Nakagawa & Schielzeth, 2010](#); [Stoffel, Nakagawa, & Schielzeth, 2017](#)). We report link-scale repeatability values, with confidence intervals calculated via bootstrapping (1000 iterations), and likelihood ratio test (LRT) P values. Link-scale repeatability measures the consistency of an individual's behaviour relative to variation among all individuals in the population ([Nakagawa & Schielzeth, 2010](#)). All numeric fixed effects in the models were scaled and zero-centred.

For our within-year repeatability calculations, we used repeated trials within 2014. We included single trials (i.e. birds measured just once) in the models along with the repeated trials ($N = 25$ repeats, $N = 125$ total), as this represents the amount of variation for all birds sampled that year ([Nakagawa & Schielzeth, 2010](#)). Within-year repeatability modelling had individual identity as a random effect in Poisson-distributed generalized linear mixed models (GLMMs). We could not estimate repeatabilities for perch bouts and number of quadrants because models did not converge. Hence, we did not include these two behaviours in [Fig. 1](#) (see [Results](#)).

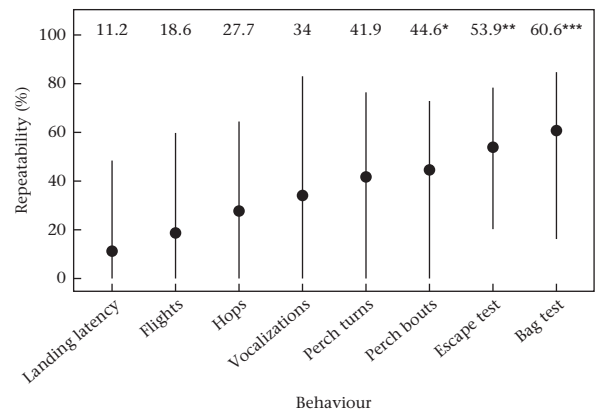


Figure 1. Within-year repeatability of golden-crowned sparrow behaviours during the 2014–2015 season. We dropped two behaviours, landing latency and flights, and used the six most repeatable behaviours ($>25\%$) in a principal component analysis to define golden-crowned sparrow personality. Error bars show 95% confidence intervals. Asterisks indicate the following LRT P values: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

We used within-year repeatability measures to determine which behaviours to include in our estimate of personality. As we only wanted to focus on consistent behaviours, we selected repeatable behaviours ($R > 0.25$) to then integrate into a PCA using all years of data. For any individuals with multiple trials within a season, we used only the first trial to avoid violating any assumptions of PCA that are skewed with repeated trials ([Budaev, 2010](#); [Dingemanse & Wright, 2020](#)). We retained principal components (PCs) with an eigen score >1 . All PC scores were scaled and zero-centred. We used the global loading scores to calculate individual PC scores for the duplicate trials in 2014. PCA was conducted in the base R stats package using Singular Value Decomposition without rotation ([R Core Team, 2019](#)). We found three PCs, but the number of vocalizations was the main component loading for PC 3, so we used the raw data instead of PC 3 (see details in the [Results](#) and the [Appendix, Tables A1 and A2](#)).

We calculated across-year repeatability for personality behaviours following the same procedure as within-year repeatability. We included all single trials when calculating the repeatability to account for all variation present in the sampled population. We analysed repeatability over four time periods: 2014–2015 ($N = 35$ repeats, $N = 148$ total), 2015–2016 ($N = 14$ repeats, $N = 118$ total), 2014 and 2016 ($N = 14$ repeats, $N = 169$ total), and birds present in all 3 years ($N = 9$ repeats, $N = 195$ total). We considered these four time period contrasts as each timescale provides a better understanding of how consistent the behaviours were over time and whether any consistency depended on the specific years analysed. Some of the time periods showed 0% repeatabilities for several behaviours, but as was the case for some within-year repeatabilities, these are not true zeros; rather, the models did not converge (see [Results, Fig. 2](#)).

To see whether repeatability changed over time and across different years, we ran separate models for the three components of personality (PC 1, PC 2, vocalizations). Each model included all years of data and had the repeatability of each response variable with time since first trial as a fixed effect and individual identity as a random effect. We used linear mixed models to predict PC 1 and PC 2, while the vocalization model was a Poisson GLMM ($N = 249$ total, $N = 195$ unique individuals). Time since first trial was in units of years: 0, 1 or 2. Therefore, for an individual tested only in 2014, the value would be 0; if a bird was tested in 2014, 2015 and 2016, it would be 0 in 2014, 1 in 2015 and 2 in 2016.

We determined each bird's dominance score via Elo rating. Elo rating calculates dominance scores based on the sequence of

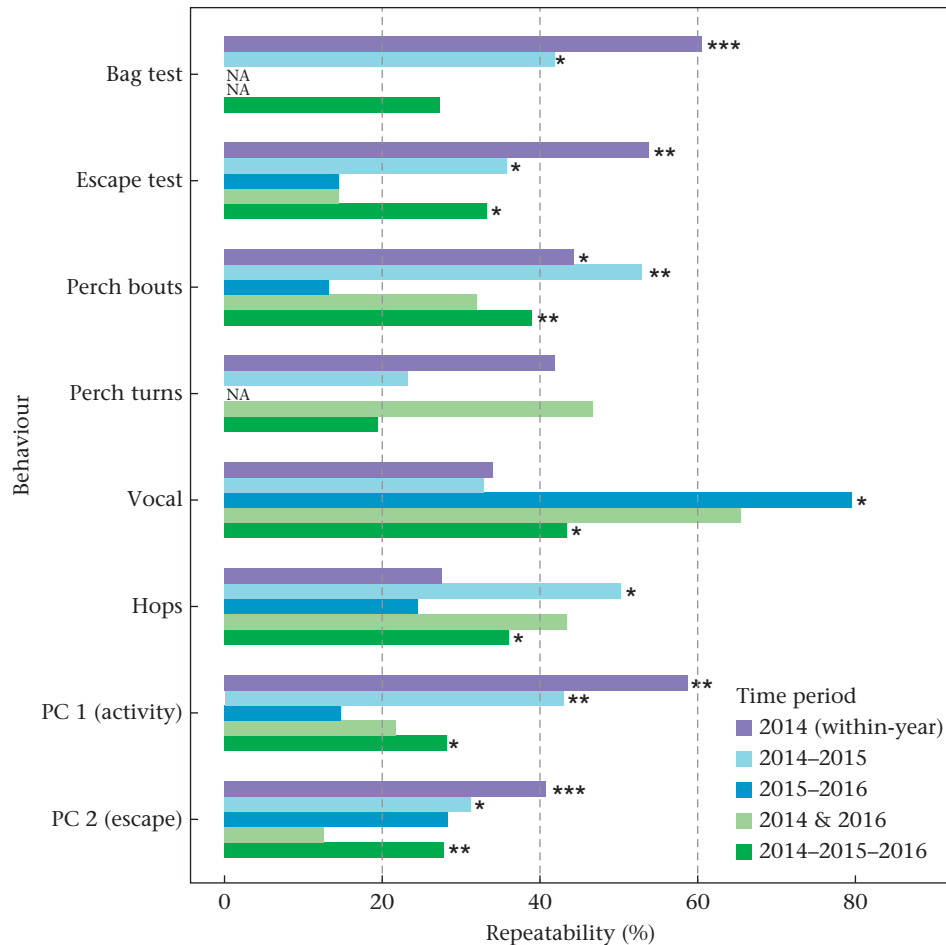


Figure 2. A comparison for the repeatability of behaviours, including assessments within years (2014) and across multiple years. For the long-term repeatability, we show all pairwise combinations of years. This comprises both raw behaviours (only considering behaviours with initial repeatability >25%) and principal components PC 1 (activity axis) and PC 2 (escape axis). An NA indicates that repeatability estimates were not obtained because models with those behaviours failed to converge. Statistically significant repeatable behaviours are denoted by: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

observed interactions between dyads and awards points based on winning or losing the interaction. The number of points awarded depends on the probability of each individual winning the interaction – e.g. an individual with a high score has a higher probability of winning an interaction against an individual with a low score and so gains fewer points than if an individual with a low score wins an interaction against a high-scoring individual. Each individual started with a baseline score of 1000. The parameter k , which determines the speed of points changing after each interaction, was set to 100. We followed methods from Neumann and Kulik (2014) and calculated dominance scores with the EloRating package (v.0.46.11).

To investigate connections between personality and other social and morphological traits, we determined whether personality correlated with black and gold crown size, wing length, dominance score, sex and age class. We made models for several time periods, first examining global patterns (all 3 years combined), then looking at individual years. We had included the day of the year as a factor but it had no effect, so we removed it from the models. Sample sizes for individual models are smaller than the total sample of birds because we did not have all measurements for all birds, so using all factors in the same model decreased the sample size due to nonoverlapping data. The final sample sizes in the global personality correlation models were $N = 144$ total samples and $N = 114$ unique individuals, and by year; 2014: $N = 60$, 2015: $N = 42$, and 2016:

$N = 42$. For the global models including all years, we used linear mixed effect models (package lme4, v.1.2-21) with individual identity as a random effect and the previous factors listed as fixed effects for personality PCs (Bates, Mächler, Bolker, & Walker, 2015). We did not include year as a random effect as it accounted for almost no variation in the multi-year models. Reported R^2 values for all mixed effect models are marginal R^2 , which indicates how much variation the fixed effects account for in the model (Nakagawa & Schielzeth, 2012). Vocalizations were modelled similarly to the other PCs, but with Poisson GLMMs. In separate models by year, we did not include individual as a random effect as we used one personality trial for each bird. We used linear models for the PC models in each year separately and report adjusted R^2 . We used GLMMs with Poisson distributions for vocalizations and report Nagelkerke's R^2 . All non-categorical fixed effects were scaled and zero-centred in the models. We checked all models for heteroscedasticity by visual inspection and ensured that models had low collinearity by measuring variance inflation factors (VIF calculated with the car package, v.3.0-3), where VIF values were <5 for all models (Fox & Weisberg, 2019). For all 2015 models, VIF values were elevated, so we removed the factor with the largest VIF value, wing length (for correlation matrices, see Appendix, Table A3). After this removal, the model collinearity decreased and all VIF values were <5 .

All statistical analysis was performed in R v.3.6.2 ([dataset] Block et al., 2020; R Core Team, 2019).

RESULTS

Within-year Repeatability (2014)

Six of the 10 behaviours we measured in 2014 had >25% within-season repeatability (Fig. 1). We used these six repeatable behaviours to define personality behaviours for golden-crowned sparrows for all years. These behaviours included hops, vocalizations, perch turns, perch bouts, escape test and bag test. While these behaviours had high repeatability estimates, the confidence intervals were large, so only three were statistically significant. The large confidence intervals are due to the limited sample size combined with non-normal distributions, which can be problematic for using bootstrapping to construct confidence intervals accurately. Additionally, bootstrapped confidence intervals are larger than more traditional conversions to Fisher's *Z* as those tend to underestimate the degree of confidence (Nakagawa & Schielzeth, 2010). Hence, we mostly focus on the magnitude of the repeatability.

Principal Component Summary of Personality Traits

We found three main principal components, which explained 75% of the variation: PC 1, an activity axis, PC 2, an escape response axis, and PC 3, a vocalization axis. PC 1 accounted for 39% of the overall variation in the behaviours we measured, PC 2 explained 19% of the variation and PC 3 explained 17% (Appendix, Table A1). PC 1 summarized movement and activity with the primary factor loadings of perch bouts, perch turns and hops (Appendix, Table A2). A higher PC 1 score represented increased activity and movement. PC 2's main factor loadings were escape time and bag test: as escape time increased, bag movements decreased. With a higher PC 2 score, the sparrows tended to stay still and stay put, while a lower PC 2 score meant that birds escaped the box more quickly and were more active in the bag (Appendix, Table A2). PC 3 mainly comprised the number of times a bird vocalized (Appendix, Table A2). As a single factor was the main factor loading, we used the raw vocalization behaviour for analysis instead of PC 3.

Across-year Repeatability

We found that the individual behaviours and the three PCA behavioural measures were repeatable across years (Fig. 2). We examined four different across-year comparisons: 2014–2015, 2015–2016, 2014–2015–2016, and 2014 and 2016 (i.e. no data from 2015). The comparisons thus include three different combinations of two seasons of samples (two with a 2-year span and one with a 3-year span) and one comparison with 3 years of samples. Some behaviours that were highly repeatable within one season showed both lower and higher repeatabilities over longer periods (Fig. 2). Interestingly, the degree of repeatability within a season was unrelated to a behaviour's repeatability across years. For example, the bag test score was the most highly repeatable behaviour within one season (60.2%), yet never had similarly high across-year repeatability values (all time contrasts had <42% repeatability). Some of the other behaviour–time contrasts also had repeatability that varied considerably – e.g. vocalizations, which leapt from 32.8% in 2014–2015 to 79.5% in 2015–2016 (Fig. 2).

We analysed whether the length of time (in years) since the first trial affected repeatability. The amount of time from the first behavioural trial had no effect on repeatability, so the length of time between measurements did not influence behavioural consistency (PC 1: $\beta = 0.04$, $SE = 0.15$, $P = 0.76$, $R^2 = 0$; PC 2: $\beta = 0.09$, $SE = 0.10$, $P = 0.38$, $R^2 = 0.003$; vocalizations: $\beta = 1.01$, $SE = 0.20$, $P = 0.96$, $R^2 = 0$). Additionally, time since the first trial accounted

for very little to none of the variation in the models (see R^2 values above).

Personality Correlates

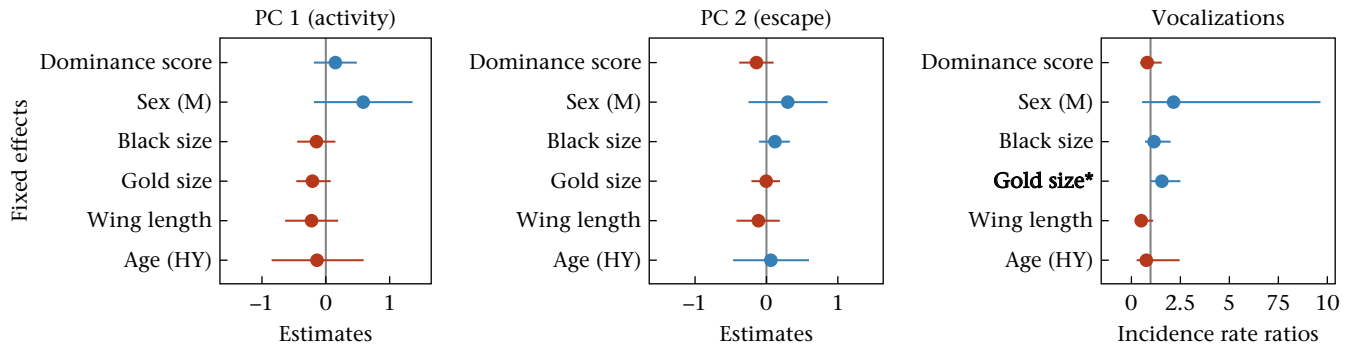
No traits correlated with PC 1 or PC 2 when examining all years together (PC 1: $R^2 = 0.042$, PC 2: $R^2 = 0.025$; Fig. 3a). Gold badge size increased somewhat with vocalizations, but this was a weak correlation as reflected in the low R^2 value ($\beta = 0.47$, $SE = 0.23$, $P = 0.05$, $R^2 = 0.056$; Fig. 3a). Given the considerable variation in the consistency of behaviours between years, we also examined each year separately. Similar to the global model, no traits correlated with personality in 2014 (PC 1: $R^2 = 0.033$; PC 2: $R^2 = 0$; vocalizations: $R^2 = 0.16$; Fig. 3b). In 2015, vocalizations increased with gold badge size ($\beta = 0.70$, $SE = 0.27$, $P = 0.010$, $R^2 = 0.416$; Fig. 3c), but none of the traits correlated with PC 1 or PC 2 (PC 1: $R^2 = 0$; PC 2: $R^2 = 0$; Fig. 3c). In 2016, males were more active than females (PC 1: $\beta = 2.12$, $SE = 0.93$, $P = 0.029$, $R^2 = 0.059$; Fig. 3d), and birds with longer wings vocalized less (vocalizations: $\beta = -1.03$, $SE = 0.33$, $P = 0.002$, $R^2 = 0.52$; Fig. 3d). However, in 2016 the model for PC 1 explained very little of the variation (low R^2), so we do not consider sex to be important in explaining the PC 1 axis of the birds' personalities.

DISCUSSION

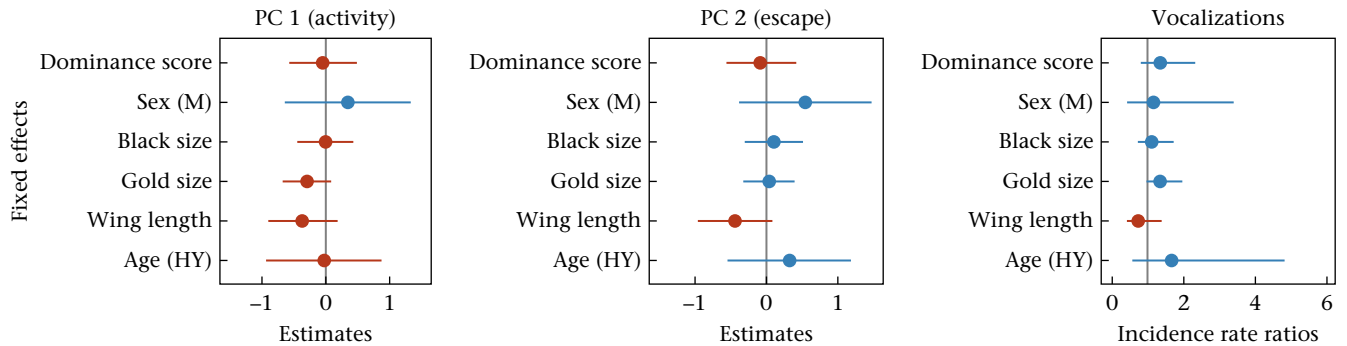
Our experiments revealed that golden-crowned sparrows have highly repeatable behaviours – i.e. personalities – within a winter season. These behaviours also showed varying degrees of consistency over multiple years. However, these personalities did not show any strong correlations with dominance score, sex or age, contrary to expectation if personality were connected to winter alternative behavioural strategies. Thus, these behavioural traits may represent a separate axis of variation among individuals important in migratory birds' winter ecology.

Two of the PC axes that resulted from condensing the top six most repeatable behaviours are similar to those found in other animal personality studies. Our first PC axis (PC 1), termed the 'activity axis', describes the movement level in the cage, which we considered to represent exploratory behaviour. Exploratory behaviours often align on a fast–slow exploration continuum and have been found to relate to foraging (Aplin, Farine, Mann, & Sheldon, 2014; Kurvers et al., 2009; Patrick & Weimerskirch, 2014; Tan, Chang, & Tan, 2018; Verbeek, Drent, & Wiepkema, 1994) and risk taking (Cole & Quinn, 2014; Dammhahn & Almeling, 2012; Garamszegi, Eens, & Török, 2008; van Oers, Drent, de Goede, & van Noordwijk, 2004). Our second PC axis (PC 2) summarizes escape response, with measures from the bag and escape tests correlating strongly. Both of these variables could be viewed in the context of predation risk; birds that escaped more quickly or showed more movements in the bird bags may be more reactive and quicker to flee from predators. Escape response could also be tied to a stress response – birds with different personalities respond differently to stress and predation (and often the two are intertwined). This escape response could be seen as boldness and fall along the 'shy–bold' continuum, a common spectrum of individual differences in animal behaviour across taxa. Additionally, escape response has been found to correlate with a genetic polymorphism in blue tits, *Cyanistes caeruleus*, suggesting a genetic basis (Kluen et al., 2012). The axes of fast–slow and shy–bold can correlate with each other (e.g. exploration and neophobia), forming 'behavioural types' in some systems (David, Auclair, & Cézilly, 2011; Hall et al., 2015; Montiglio et al., 2012). However, as these behaviours were on orthogonal PC axes, they were clearly not correlated,

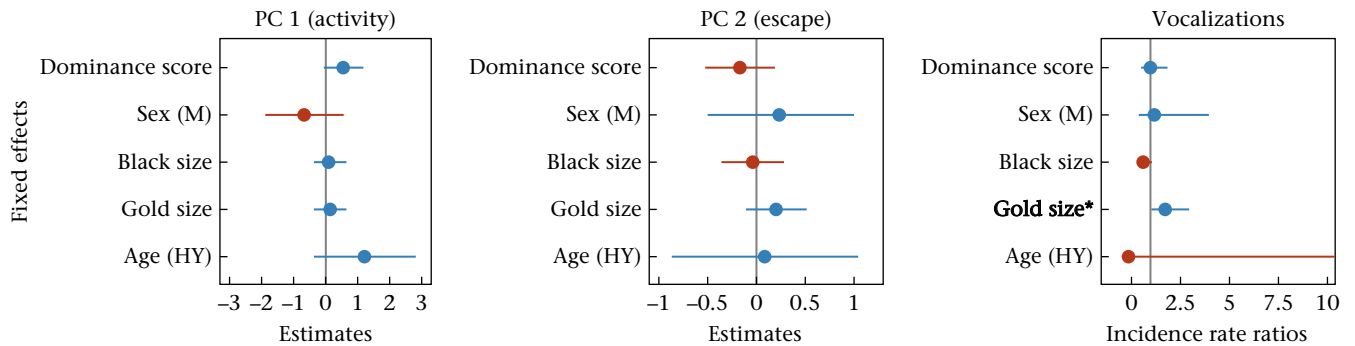
(a) Global (2014, 2015, 2016)



(b) 2014



(c) 2015



(d) 2016

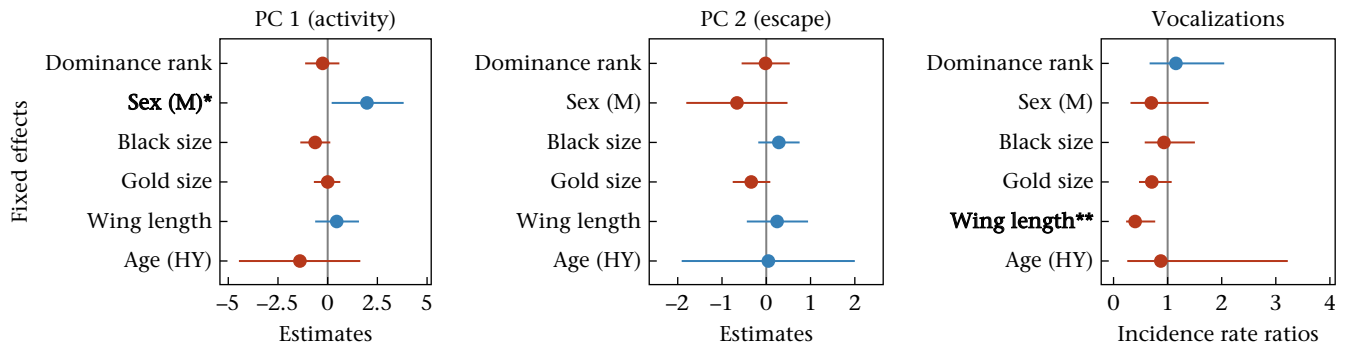


Figure 3. Results from models showing the relationships between personality axes and other traits for all years: (a) 2014, 2015, 2016; (b) 2014; (c) 2015; (d) 2016. Blue indicates positive correlations (circles right of the horizontal line), and red indicates negative correlations (circles left of the horizontal line). Circles show the effect size values, and lines show 95% confidence intervals. Incidence rate ratios are backtransformed estimates to compare effect sizes to principal components PC 1 (activity) and PC 2 (escape), as vocalization models were in a Poisson distribution. Statistically significant values as indicated: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

consistent with results of other studies (David et al., 2011; Favati, Leimar, & Løvlie, 2014; Herborn et al., 2010).

For vocalizations, we used the raw data rather than a PC axis because the third PC axis (PC 3) consisted mostly of the number of nonsong vocalizations during cage exploration. Studies rarely include nonsong vocalizations in personality assays, but we found they were sufficiently repeatable within years to meet our criteria for personality behaviour. One other study examined vocalizations in the nonbreeding season and found that black-capped chickadees, *Poecile atricapillus*, had repeatable songs and vocalizations that correlated with exploration in response to a stressful situation, but not during a control assessment (Guillette & Sturdy, 2011). More studies have focused on song response during breeding; for example, more exploratory great tits responded differently to simulated territory intrusions than nonexplorative individuals, and the direction of response varied in different populations (Amy, Sprau, de Goede, & Naguib, 2010; Jacobs et al., 2014; Naguib, Kazek, Schaper, van Oers, & Visser, 2010). Vocalizations during winter can serve different functions than for territory defence and mate attraction (Sorensen, Jenni-Eiermann, & Spottiswoode, 2016). Golden-crowned sparrow nonsong winter vocalizations could have several functions: maintaining contact and cohesion within a flock, establishing social dominance or functioning as alarm calls. If calls are used as warnings, we may be detecting vocalizations as individually consistent responses to a stressful situation, whether that is being in a new environment like a cage or needing to escape from a predator.

Our study was unusual for the length of time over which we assessed personality, as we measured behaviour repeatability both within 1 year and up to 3 years. Golden-crowned sparrows live for approximately 2–3 years (Norment et al., 2020), so measuring repeatability over 3 years covers most of their life span. Less than 10% of previous studies examined repeatability over more than 1 year (Bell, Hankison, & Laskowski, 2009). The high repeatabilities we observed within years indicate stable personalities in golden-crowned sparrows within a single winter season. Similar patterns of high within-year (or shorter-term) repeatability are common in personality studies (Bell, 2007; Sih et al., 2004, 2015). However, sparrow personalities were often repeatable for up to 3 years and, importantly, the strength of repeatability measures were unrelated to the time between the first and second assessments. The fact that repeatabilities did not diminish with time interval is surprising as multiple studies have found that consistency tends to decrease over longer periods for many behaviours (see Bell et al., 2009 for a review). Additionally, the time span over which repeatability is maintained can vary substantially among behaviours (Bell et al., 2009). For example, David, Auclair, and Cézilly (2012) found that exploratory behaviour in captive zebra finches, *Taeniopygia guttata*, was repeatable over both short (~1 week) and moderate (~7 months) time spans, but struggling behaviour was only repeatable over the short term.

On average, golden-crowned sparrows have consistent personality traits during winter for much of their lives, but the variability present across years indicates that personality behaviours may change in response to external factors such as the physical or social environment. For instance, the behaviour assessed with the bag test showed very high within-season repeatability with lower repeatability over multiple years, which could reflect changes due to years having different environmental pressures. In some species, individuals' personalities change depending on the season (Carter, Goldizen, & Heinsohn, 2012), while those of other species react to changes in the environment (Herborn, Heidinger, Alexander, & Arnold, 2014; Nicolaus, Tinbergen, Ubels, Both, & Dingemanse, 2016) or social situations (Marchetti & Drent, 2000; van Oers, Klunder, & Drent, 2005). One mechanism for behavioural

plasticity is personality types varying in their response to environmental factors. For example, more exploratory individuals could have more plastic responses (Dall, Houston, & McNamara, 2004; Dingemanse, Kazem, Réale, & Wright, 2010; Sih et al., 2015). In our study, the magnitude of repeatability varied across years and behaviours, so personality behaviours could be changing in reaction to external factors. Some may be responding to year-to-year changes in the environment, while others could be responding to predation pressure or climate. This pattern of behavioural change is similar to the pattern of plumage trait changes in lark buntings, *Calamospiza melanocorys*, where male traits can change asynchronously across years, potentially due to a combination of local and broad factors (Chaine & Lyon, 2015). One puzzling pattern of change was that several behaviours had higher consistency across years than within a season. We do not have a biological explanation for this, and it could be an artefact of different sample sizes across timescales.

Altering external conditions could differentially affect the fitness of individuals based on their personality or experience level (Dammhahn & Almeling, 2012). For example, in North American red squirrels, *Tamiasciurus hudsonicus*, the associations between different personality traits and lifetime offspring production for males depends on whether or not males experience a year with a strong resource pulse (Haines et al., 2020). Recognizing behavioural changes over time and contexts will help us make sense of the temporal patterns of consistency versus flexibility. Indeed, understanding how personality and/or fitness payoffs change over time can help future studies shed more light on how selection maintains personalities (Dingemanse et al., 2012; Dingemanse & de Goede, 2004; Mathot, Wright, Kempenaers, & Dingemanse, 2012; Sih et al., 2015).

We focused on personality in the context of sociality as previous research suggested that sparrows might have alternative wintering strategies related to dominance and plumage badges of status (Rohwer & Ewald, 1981; Chaine et al., 2011, 2013). However, our study did not provide support for this idea based on the personality traits we measured. Neither activity (PC 1) nor escape behaviour (PC 2) correlated with any social or morphological traits we measured. Although the vocalization axis did increase with gold badge size in 2015 and decrease with wing length in 2016, these patterns were limited to single years, suggesting that they were not robust. While we also observed a weak relationship between vocalizations and gold badge size in the global model, this pattern was driven by the 2015 relationship. Thus, the three axes of personality we identified seem to be independent of variation in morphology or traits related to dominance.

In golden-crowned sparrows, the mechanism for dominance can change depending on the social context, which may require more flexible behavioural responses (Chaine et al., 2018), potentially explaining the lack of correlation between personality and dominance. Personality has correlated with dominance in a number of species (David et al., 2011; Dingemanse & de Goede, 2004; Kurvers et al., 2009), but the patterns of correlation vary across species, even closely related ones. For example, personality predicted dominance in mountain chickadees, *Poecile gambeli* (Fox, Ladage, Roth, & Pravosudov, 2009), but not in black-capped chickadees (Devost, Jones, Cauchoux, Montreuil-Spencer, & Morand-Ferron, 2016). One possible explanation for the variable connection between personality and dominance is that the patterns and mechanisms of social dominance likely depend on the specific details of social organization. Both dominance and social organization vary among species and can even change within species across space and time.

A valuable next step is determining whether personality traits in winter could be relevant to other contexts necessary for winter

survival that we did not assess, such as foraging, risk response or other environmental factors. The small-bird-in-winter paradigm (Roth et al., 2006) stresses the critical importance of the trade-off between survival and foraging in winter (Houston et al., 1993; Lima, 1986; McNamara & Houston, 1987). Bird-eating raptors are common at our study site and are likely important drivers of the sparrows' winter ecology and behaviour. While the small-bird-in-winter paradigm focuses on group size and foraging behaviour as key aspects of survival, variation among individuals in these trade-offs could select for variation in how the individuals react to foraging and predation situations that might be aligned with personality traits such as boldness. Along with different risk responses, personality measures have predicted variation in foraging behaviour (Kurvers et al., 2009; Wilson & Coleman, 1993; Wilson & McLaughlin, 2007). For example, black-browed albatross, *Thalassarche melanophrys*, individuals varied in foraging patterns based on personality type, and personality correlated with reproductive success in some years depending on the quality and availability of food (Patrick & Weimerskirch, 2014). The trade-offs between survival and foraging in winter could be a factor maintaining adaptive variation in individual behaviour.

Conclusion

Golden-crowned sparrows have personality traits in winter, but these consistent behaviours are independent of the morphological and social traits we measured. We did not find evidence connecting personality to stable alternative winter strategies, as the degree of repeatability varied across years. Whether birds are migratory or resident could have a considerable impact on the links between personality and other traits, and selection on personalities in migratory birds may occur during the breeding season, rather than in winter. Not only are migrants undergoing seasonal change but also large geographical change. Therefore, migrant bird behaviours may face different selection pressures than resident bird behaviours. Golden-crowned sparrow personality traits may be under selection during the breeding season or in other winter contexts like foraging or predation avoidance.

Author Contributions

T.A.B, A.S.C, B.E.L and D.S. designed the research. T.A.B, B.E.L and R.A.S performed the fieldwork. T.A.B and R.A.S extracted all video data. T.A.B performed the analysis with help from A.S.C and D.S. T.A.B wrote the manuscript with input and revisions from B.E.L, A.S.C and D.S.

Declaration of Interest

We declare that we have no conflicts of interest.

Acknowledgments

Special thanks to Jenny Anderson, Inger Marie and many volunteers for help with fieldwork. Much gratitude to Bob Montgomerie for statistical advice. Many thanks to Zack Mikalonis for proof reading and Carla Sette for coding help. We thank the University of California, Santa Cruz Arboretum for logistic support. We also thank the anonymous referees for their comments improving the paper. A U.S. National Science Foundation (NSF) Graduate Research Fellowship supported T.A.B and an NSF CAREER grant (NSF IOS-1750606) and a National Geographic, United States grant (WW-R012-17) supported D.S and the research. A.S.C was supported by the Laboratoire d'Excellence (LABEX), France entitled

TULIP (ANR-10-LABX-41) and IAST, France through ANR grant ANR-17-EURE-0010 (Investissements d'Avenir program).

References

- Adriansen, F., & Dhont, A. A. (1990). Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. *Journal of Animal Ecology*, 59, 1077–1090.
- Amy, M., Sprau, P., de Goede, P., & Nguib, M. (2010). Effects of personality on territory defence in communication networks: A playback experiment with radio-tagged great tits. *Proceedings of the Royal Society B*, 277, 3685–3692.
- Aplin, L. M., Farine, D. R., Mann, R. P., & Sheldon, B. C. (2014). Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B*, 281, 20141016.
- Archard, G. A., & Braithwaite, V. A. (2010). The importance of wild populations in studies of animal temperament. *Journal of Zoology*, 281, 149–160.
- Barta, Z., & Giraldeau, L.-A. (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: A phenotype-limited producing–scrounging game. *Behavioral Ecology and Sociobiology*, 42, 217–223.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.
- Bell, A. M. (2007). Animal personalities. *Nature*, 447, 539–540.
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, 77, 771–783.
- Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23, 361–368.
- Block, T. A. (2021). *Demographic and social influences on the winter ecology of a migratory songbird, the golden-crowned sparrow (Zonotrichia atricapilla)* (Doctoral thesis). Santa Cruz, CA: University of California Santa Cruz.
- Block, T. A., Star, R., Shizuka, D., Chaine, A. S., & Lyon, B. E. (2020). A migratory sparrow has personality in winter that is independent of other traits. *Dryad*. <https://doi.org/10.7291/D1B37D>
- Brockmann, H. J. (2001). The evolution of alternative strategies and tactics. *Advances in the Study of Animal Behavior*, 30, 1–51.
- Broggi, J., Hohtola, E., Koivula, K., Orell, M., & Nilsson, J.-Å. (2009). Long-term repeatability of winter basal metabolic rate and mass in a wild passerine. *Functional Ecology*, 23, 768–773.
- Bubac, C. M., Coltman, D. W., Bowen, W. D., Lidgard, D. C., Lang, S. L. C., & Heyer, C. E. (2018). Repeatability and reproductive consequences of boldness in female gray seals. *Behavioral Ecology and Sociobiology*, 72, 1–12.
- Budaev, S. V. (2010). Using principal components and factor analysis in animal behaviour research: Caveats and guidelines. *Ethology*, 116, 472–480.
- Caraco, T., Martindale, S., & Pulliam, H. R. (1980). Avian flocking in the presence of a predator. *Nature*, 285, 400–401.
- Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlshaw, G., & Heinsohn, R. (2013). Animal personality: What are behavioural ecologists measuring? *Biological Reviews*, 88, 465–475.
- Carter, A. J., Goldizen, A., & Heinsohn, R. (2012). Personality and plasticity: Temporal behavioral reaction norms in a lizard, the Nambian rock agama. *Animal Behaviour*, 84, 471–477.
- Chaine, A. S., & Lyon, B. E. (2015). Signal architecture: Temporal variability and individual consistency of multiple sexually selected signals. *Functional Ecology*, 29, 1178–1188.
- Chaine, A. S., Roth, A. M., Shizuka, D., & Lyon, B. E. (2013). Experimental confirmation that avian plumage traits function as multiple status signals in winter contests. *Animal Behaviour*, 86, 409–415.
- Chaine, A. S., Shizuka, D., Block, T. A., Zhang, L., & Lyon, B. E. (2018). Manipulating badges of status only fools strangers. *Ecology Letters*, 21, 1477–1485.
- Chaine, A. S., Tjerner, K. A., Shizuka, D., & Lyon, B. E. (2011). Sparrows use multiple status signals in winter social flocks. *Animal Behaviour*, 81, 447–453.
- Chambon, R., Gélinaud, G., Paillisson, J.-M., Lemesle, J.-C., Ysnel, F., & Dugravot, S. (2019). The first winter influences lifetime wintering decisions in a partially migrant bird. *Animal Behaviour*, 149, 23–32.
- Cole, E. F., & Quinn, J. L. (2014). Shy birds play it safe: Personality in captivity predicts risk responsiveness during reproduction in the wild. *Biology Letters*, 10, 20140178.
- Colwell, R. R. (1999). Age-specific crown variation in basic-plumaged golden-crowned sparrows. *North American Bander*, 24, 1–5.
- Costanzo, A., Romano, A., Ambrosini, R., Parolini, M., Rubolini, D., Caprioli, M., et al. (2018). Barn swallow antipredator behavior covaries with melanic coloration and predicts survival. *Behavioral Ecology*, 23, 987–989.
- Cote, J., Dreiss, A., & Clobert, J. (2008). Social personality trait and fitness. *Proceedings of the Royal Society B*, 275, 2851–2858.
- 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, 734–739.
- Dammhahn, M., & Almeling, L. (2012). Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness. *Animal Behaviour*, 84, 1131–1139.
- Dammhahn, M., Dingemanse, N. J., Niemelä, P. T., & Réale, D. (2018). Pace-of-life syndromes: A framework for the adaptive integration of behaviour, physiology and life history. *Behavioral Ecology and Sociobiology*, 62, 1–8.

- David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour*, 81, 219–224.
- David, M., Auclair, Y., & Cézilly, F. (2012). Assessing short- and long-term repeatability and stability of personality in captive zebra finches using longitudinal data. *Ethology*, 118, 932–942.
- Davies, N. B. (1976). Food, flocking and territorial behaviour of the pied wagtail (*Motacilla alba yarrellii* Gould) in winter. *Journal of Animal Ecology*, 45, 235–253.
- Devost, I., Jones, T. B., Cauchoix, M., Montreuil-Spencer, C., & Morand-Ferron, J. (2016). Personality does not predict social dominance in wild groups of black-capped chickadees. *Animal Behaviour*, 122, 67–76.
- Dingemanse, N. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, 64(6), 929–938. <https://doi.org/10.1006/anbe.2002.2006>
- Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society B*, 271, 847–852.
- Dingemanse, N. J., Bouwman, K. M., van de Pol, M., van Overveld, T., Patrick, S. C., Matthysen, E., et al. (2012). Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*. *Journal of Animal Ecology*, 81, 116–126.
- Dingemanse, N. J., & de Goede, P. (2004). The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology*, 15, 1023–1030.
- Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25, 81–89.
- Dingemanse, N. J., & Réale, D. (2005). Natural selection and animal personality. *Beyond Behavior*, 149, 1159–1184.
- Dingemanse, N. J., & Wright, J. (2020). Criteria for acceptable studies of animal personality and behavioural syndromes. *Ethology*, 126, 865–869.
- Dominey, W. J. (1984). Alternative mating tactics and evolutionarily stable strategies. *American Zoologist*, 24, 385–396.
- Favati, A., Leimar, O., & Løvlie, H. (2014). Personality predicts social dominance in male domestic fowl. *PLoS One*, 9, Article e103535. <https://doi.org/10.1371/journal.pone.0103535>
- Fox, R. A., Ladage, L. D., Roth, T. C. I., & Pravosudov, V. V. (2009). Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*. *Animal Behaviour*, 77, 1441–1448.
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Thousand Oaks, CA: Sage.
- Garamszegi, L. Z., Eens, M., & Török, J. (2008). Birds reveal their personality when singing. *PLoS One*, 3, e2647. <https://doi.org/10.1371/journal.pone.0002647>
- Griffiths, R., Double, M. C., Orr, K., & Dawson, R. (1998). A DNA test to sex most birds. *Molecular Ecology*, 7, 1071–1075.
- Guillette, L. M., & Sturdy, C. B. (2011). Individual differences and repeatability in vocal production: Stress-induced calling exposes a songbird's personality. *Naturwissenschaften*, 98, 977–981.
- Haines, J. A., Nason, S. E., Skurdal, A. M. M., Bouchier, T., Boutin, S., Taylor, R. W., et al. (2020). Sex- and context-specific associations between personality and a measure of fitness but no link with life history traits. *Animal Behaviour*, 167, 23–39.
- Hall, M. L., van Asten, T., Katsis, A. C., Dingemanse, N. J., Magrath, M. J. L., & Mulder, R. A. (2015). Animal personality and pace-of-life syndromes: Do fast-exploring fairy-wrens die young? *Frontiers in Ecology and Evolution*, 3, 1–14. <https://doi.org/10.3389/fevo.2015.00028>
- Herborn, K. A., Heidinger, B. J., Alexander, L., & Arnold, K. E. (2014). Personality predicts behavioral flexibility in a fluctuating, natural environment. *Behavioral Ecology*, 25, 1374–1379.
- Herborn, K. A., Macleod, R., Miles, W. T. S., Schofield, A. N. B., Alexander, L., & Arnold, K. E. (2010). Personality in captivity reflects personality in the wild. *Animal Behaviour*, 79, 835–843.
- Houston, A. I., McNamara, J. M., & Hutchinson, J. M. C. (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society B*, 341, 375–397.
- Jacobs, C. G. C., van Overveld, T., Careau, V., Mathysen, E., Adriaenssens, F., & Slabbekoorn, H. (2014). Personality-dependent response to field playback in great tits: Slow explorers can be strong responders. *Animal Behaviour*, 90, 65–71.
- Johnson, K. V. A., Aplin, L. M., Cole, E. F., Farine, D. R., Firth, J. A., Patrick, S. C., et al. (2017). Male great tits assort by personality during the breeding season. *Animal Behaviour*, 128, 21–32.
- Klue, E., Kuhn, S., Kempenaers, B., & Brommer, J. E. (2012). A simple cage test captures intrinsic differences in aspects of personality across individuals in a passerine bird. *Animal Behaviour*, 84, 279–287.
- Kurvers, R. H. J. M., Prins, H. H. T., van Wieren, S. E., van Oers, K., Nolet, B. A., & Ydenberg, R. C. (2009). The effect of personality on social foraging: Shy barnacle geese scrounge more. *Proceedings of the Royal Society B*, 277, 601–608.
- Lima, S. L. (1986). Predation risk and unpredictable feeding conditions: Determinants of body-mass in birds. *Ecology*, 67, 377–385.
- Lima, S. L. (1987). Vigilance while feeding and its relation to the risk of predation. *Journal of Theoretical Biology*, 124, 303–316.
- Lyon, B. E., & Eadie, J. M. (2008). Conspecific brood parasitism in birds: A life-history perspective. *Annual Review of Ecology, Evolution and Systematics*, 39, 343–363.
- Lyon, B. E., Shizuka, D., Block, T. A., Anderson, J., Laursen, I. M., & Chaine, A. S. (2021). *Delayed winter plumage maturation in a migratory songbird*. Manuscript in preparation.
- Marchetti, C., & Drent, P. J. (2000). Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour*, 60, 131–140.
- Mathot, K. J., Wright, J., Kempenaers, B., & Dingemanse, N. J. (2012). Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos*, 121, 1009–1020.
- McNamara, J. M., & Houston, A. I. (1987). Starvation and predation as factors limiting population size. *Ecology*, 68, 1515–1519.
- McNamara, J. M., Houston, A. I., & Lima, S. L. (1994). Foraging routines of small birds in winter: A theoretical investigation. *Journal of Avian Biology*, 25, 287–302.
- Mettke-Hofmann, C., Ebert, C., Schmidt, T., Steiger, S., & Stieb, S. (2005). Personality traits in resident and migratory warbler species. *Behaviour*, 142, 1357–1375.
- Montiglio, P.-O., Garant, D., Bergeron, P., Messier, G. D., & Réale, D. (2014). Pulsed resources and the coupling between life-history strategies and exploration patterns in eastern chipmunks (*Tamias striatus*). *Journal of Animal Ecology*, 83, 720–728.
- Montiglio, P.-O., Garant, D., Pelletier, F., & Réale, D. (2012). Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, 84, 1071–1079.
- Naguib, M., Kazek, A., Schaper, S. V., van Oers, K., & Visser, M. E. (2010). Singing activity reveals personality traits in great tits. *Ethology*, 116, 763–769.
- Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, 85, 935–956.
- Nakagawa, S., & Schielzeth, H. (2012). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.
- Neumann, C., & Kulik, L. (2014). *EloRating: Animal dominance hierarchies by Elo-rating* (R Package version 0.43) <https://rdr.io/cran/EloRating/>.
- Nicolaus, M., Tinbergen, J. M., Ubels, R., Both, C., & Dingemanse, N. J. (2016). Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecology Letters*, 19, 478–486.
- Niemelä, P. T., Vainikka, A., Hedrick, A. V., & Kortet, R. (2011). Integrating behaviour with life history: Boldness of the field cricket, *Gryllus integer*, during ontogeny. *Functional Ecology*, 26, 450–456.
- Normant, C. J., Hendricks, P., & Santonocito, R. (2020). Golden-crowned sparrow (*Zonotrichia atricapilla*) (Version 1.0). In A. F. Poole, & F. B. Gill (Eds.), *Birds of the world online*. Ithaca, NY: Cornell Lab of Ornithology <https://birdsoftheworld.org/>.
- Patrick, S. C., & Weimerskirch, H. (2014). Personality, foraging and fitness consequences in a long-lived seabird. *PLoS One*, 9(2), Article e87269. <https://doi.org/10.1371/journal.pone.0087269>
- R Core Team. (2019). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B*, 365, 4051–4063.
- Rohwer, S. (1975). The social significance of avian winter plumage variability. *Evolution*, 29, 596–610.
- Rohwer, S. (1982). The evolution of reliable and unreliable badges of fighting ability. *American Zoologist*, 22, 531–546.
- Rohwer, S., & Ewald, P. W. (1981). The cost of dominance and advantage of subordination in a badge signaling system. *Evolution*, 35, 441–454.
- Roth, T. C. I., Lima, S. L., & Vetter, W. E. (2006). Determinants of predation risk in small wintering birds: The hawk's perspective. *Behavioral Ecology and Sociobiology*, 60, 195–204.
- Sasaki, T., Mann, R. P., Warren, K. N., Herbert, T., Wilson, T., & Biro, D. (2018). Personality and the collective: Bold homing pigeons occupy higher leadership ranks in flocks. *Philosophical Transactions of the Royal Society B*, 373, 1–8.
- Shizuka, D., Chaine, A. S., Anderson, J., Johnson, O., Laursen, I. M., & Lyon, B. E. (2014). Across-year social stability shapes network structure in wintering migrant sparrows. *Ecology Letters*, 17, 998–1007.
- Sih, A., Bell, A. M., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19, 372–378.
- Sih, A., Mathot, K. J., Moirón, M., Montiglio, P.-O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state-behaviour feedbacks: A review and guide for empiricists. *Trends in Ecology & Evolution*, 30, 50–60.
- Sorensen, M. C., Jenni-Eiermann, S., & Spottiswoode, C. N. (2016). Why do migratory birds sing on their tropical wintering grounds? *The American Naturalist*, 187, 1–12.
- Stahl, J., Tolsma, P. H., Loonen, M. J., & Drent, R. H. (2001). Subordinates explore but dominants profit: Resource competition in high Arctic barnacle goose flocks. *Animal Behaviour*, 61, 257–264.
- Stamps, J. A. (2007). Growth-mortality trade-offs and 'personality traits' in animals. *Ecology Letters*, 10, 355–363.
- Stein, L. R., Trapp, R. M., & Bell, A. M. (2016). Do reproduction and parenting influence personality traits? Insights from threespine stickleback. *Animal Behaviour*, 112, 247–254.

- Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8, 1639–1644.
- Taborsky, M., Oliveira, R. F., & Brockmann, H. J. (2008). The evolution of alternative reproductive tactics: Concepts and questions. In M. Taborsky, R. F. Oliveira, & H. J. Brockmann (Eds.), *Alternative reproductive tactics* (pp. 1–21). Cambridge, U.K.: Cambridge University Press.
- Tan, M. K., Chang, C.-C., & Tan, H. T. W. (2018). Shy herbivores forage more efficiently than bold ones regardless of information-processing overload. *Behavioural Processes*, 149, 52–58.
- van Oers, K., Drent, P. J., de Goede, P., & van Noordwijk, A. J. (2004). Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal Society B*, 271, 65–73.
- van Oers, K., Klunder, M., & Drent, P. J. (2005). Context dependence of personalities: Risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology*, 16, 716–723.
- van Oers, K., & Naguib, M. (2013). Avian personalities. In C. Carere, & D. Maestripieri (Eds.), *Animal personalities: behavior, physiology, and evolution* (pp. 66–95). Chicago, IL: University of Chicago Press.
- Verbeek, M. E. M., Drent, P. J., & Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behavior of male great tits. *Animal Behaviour*, 48, 1113–1121.
- Wilson, D. S., & Coleman, K. (1993). Shy–bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Psychological Bulletin*, 107, 250–260.
- Wilson, A. D. M., & McLaughlin, R. L. (2007). Behavioural syndromes in brook charr, *Salvelinus fontinalis*: Prey-search in the field corresponds with space use in novel laboratory situations. *Animal Behaviour*, 74, 689–698.
- Wolf, M., & Krause, J. (2014). Why personality differences matter for social functioning and social structure. *Trends in Ecology & Evolution*, 29, 306–308.
- Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447, 581–584.
- Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B*, 365, 3959–3968.

Appendix

Table A1

Eigenvalues for each principal component (PC), showing the percentage of variance and cumulative variance

	Eigenvalue	Variance (%)	Cumulative variance (%)
PC 1	2.34	38.95	38.95
PC 2	1.16	19.28	58.22
PC 3	1.01	16.74	74.97
PC 4	0.84	13.94	88.90
PC 5	0.52	8.59	97.49
PC 6	0.15	2.51	100

PC 1, PC 2 and PC 3 were selected as they all had eigenvalues >1.

Table A2

Component loadings for each personality measure in all principal components (PCs)

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Hops	0.53	−0.03	−0.08	0.06	0.80	−0.27
Vocalizations	0.03	0.11	−0.99	0.04	−0.12	−0.01
Perch turns	0.57	0.16	0.11	−0.06	−0.55	−0.58
Perch bouts	0.61	0.08	0.03	−0.08	−0.14	0.77
Escape test	−0.06	0.70	0.01	0.70	0.04	0.05
Bag test	0.13	−0.68	−0.03	0.71	−0.16	0.01

Values over 0.5 are shown in bold for PC 1, PC 2 and PC 3, as these had the strongest influence on each PC. The component loadings were calculated from $N = 249$ personality trials from 2014, 2015 and 2016.

Table A3

Correlation matrices for each year of data (2014, 2015, 2016) and all 3 years combined

	Dominance	Black size	Gold size	Wing length
All years correlation matrix				
Dominance				
Black size	0.45***			
Gold size	0.20*	0.33***		
Wing length	0.51***	0.50***	0.40***	
2014 Correlation matrix				
Dominance				
Black size	0.61***			
Gold size	0.30*	0.40**		
Wing length	0.43***	0.32*	0.39**	
2015 Correlation matrix				
Dominance				
Black size	0.37*			
Gold size	0.18	0.41**		
Wing length	0.48***	0.65***	0.58***	
2016 Correlation matrix				
Dominance				
Black size	0.33*			
Gold size	0.10	0.17		
Wing length	0.70***	0.50***	0.27	

Wing length correlated with all other traits strongly in 2015, so to avoid collinearity issues within the 2015 models, we removed wing length. We used Pearson correlations and listwise deletion for any missing values. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.