

Geographic variation in the repeatability of a personality trait

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Animal personalities are interindividual behavioral differences that are consistent across time or contexts. Increasing research is revealing the adaptive significance of personalities, although the mechanisms driving this variation remain largely unknown. A possible source of variation in personality traits is interpopulational differences in the strength of selection acting upon them. The response to selection can be measured indirectly via the behavior's repeatability, as repeatability generally sets an upper limit to trait heritability. However, no information currently exists on geographic variation in personality repeatability. We therefore quantified repeatability in exploratory behavior, a common personality trait, over multiple trials for 3 populations of rufous-collared sparrow (*Zonotrichia capensis*), focusing on 3 specific measures (exploration speed, diversity of perches visited, and number of hops). We also asked how differences in repeatability of these 3 measures affect other aspects of exploration, such as the temporal consistency of intercorrelations between the measures. Exploration speed was highly repeatable across all populations, whereas diversity was only repeatable in 2 of 3 populations and hopping behavior not at all. These differences in repeatability lead to temporal variation in the correlation matrices of the 3 exploration measures. Finally, only trial number influenced interindividual variability in exploration, whereas population identity, experimental conditions (i.e., conducting the novel environment assay under laboratory or field conditions), and time since capture all had no effect. Our findings highlight the complexity of using measures of behavioral consistency as a definition of personalities and emphasize the value of quantifying interpopulational patterns of trait repeatability. *Key words:* animal personalities, exploratory behavior, novel environment experiment, repeatability, *Zonotrichia capensis*. [*Behav Ecol*]

Animals often differ consistently among individuals in certain behaviors. When these differences persist temporally or across different contexts, they are labeled animal personalities, behavioral syndromes, or coping strategies (Sih, Bell, and Johnson 2004; Sih, Bell, Johnson, and Ziemba 2004; Bell 2007). These rank-order differences between individuals are often consistent across a range of behaviors (e.g., exploratory behavior, aggressiveness, boldness) such that the overall personality of an individual can be defined by a suite of intercorrelated behaviors (e.g., passive/submissive or active/aggressive individuals). Personalities are typically population specific (Bell 2007), and it is now known that correlations between behaviors can be adaptive and represent different strategies to cope with the local environmental pressures (Sih et al. 2003; Dingemans et al. 2004; Bell 2005; Bell and Sih 2007; Dochtermann and Jenkins 2007). Although personalities have traditionally been quantified in single populations, increasing research is targeting interpopulational differences in personalities with the realization that the selective pressures acting on certain behavioral combinations may differ among populations depending on local environ-

mental constraints. For example, Dingemans et al. (2007) showed that, across 12 populations of three-spined stickleback (*Gasterosteus aculeatus*), high predation pressures can select for the coupling of certain behaviors, resulting in interpopulational differences in personalities based on the occurrence of predators.

An important step in understanding the strength and evolutionary consequences of natural selection acting upon personalities is to document behavioral variability among individuals and consistency within individuals. Repeatability is a measure commonly used for such purposes, reflecting the amount of interindividual variation in a trait relative to the total phenotypic variation (i.e., the sum of interindividual and intraindividual variation: Lessells and Boag 1987). The repeatability of a trait will thus be high if individuals behave consistently (low intraindividual variability) or large variation between individuals exists (high interindividual variability). Moreover, repeatability can also predict the upper limit for the heritability of a trait because it includes both genetic and environmental sources of variation, whereas heritability includes only interindividual genetic differences (Lessells and Boag 1987; Dohm 2002). However, inter- and intraindividual variability of a trait can arise both due to labile environmental factors that promote phenotypic plasticity and fixed genetic differences between individuals (Falconer and Mackay 1996). If genetic and environmental differences exist between populations, geographic variation in the repeatability of traits may therefore also occur. Understanding these population-level differences in repeatability will provide important insights on the effects of selective pressures acting on personality traits and the

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causes of personality differences between populations. To date, no studies have found population differences in the repeatability measures for a personality trait.

Exploratory behavior is one behavioral trait that commonly forms parts of animal personalities. This behavior describes the process of collecting information about the immediate surroundings as individuals move through the environment and has been shown to have strong fitness consequences across diverse taxa (Dingemanse et al. 2003, 2007; Avni and Eilam 2008; Pruitt et al. 2008). Avian exploratory behavior, which is often coupled with aggressive and risk-taking behavior in personalities (Groothuis and Carere 2005), has been linked to overwinter survival rates, extrapair mating patterns, dispersal patterns, and the ability to find food resources (Dingemanse et al. 2003, 2004; van Oers et al. 2008; Herborn et al. 2010). Recently, Minderman et al. (2009) reported moderate repeatability in various measures of exploratory behavior in a single population of starling (*Sturnus vulgaris*). Similarly, Dingemanse et al. (2002) documented repeatability in exploratory behavior in 2 great tit (*Parus major*) populations and found this trait to be both highly repeatable and heritable. Although repeatability was estimated across different populations in this latter study, no interpopulation differences were found. It therefore remains uncertain whether repeatability in exploratory behavior can vary between populations and what the underlying causes of such variation may be.

Here, we quantify geographic variation in the repeatability of exploratory behavior in a bird species to understand the mechanisms that may control interpopulational and interindividual differences in animal personalities. Under laboratory conditions, we quantified the exploratory behavior, across multiple trials, of rufous-collared sparrows (*Zonotrichia capensis*) that originated from 3 different populations. This sparrow is a common species found throughout the entire central and south Americas in a vast range of habitats (Ridgley and Tudor 1989). We also explored which factors can influence our estimates of exploratory behavior, such as location of origin (i.e., geographic variation), time spent in captivity, and familiarity with the experimental apparatus. Finally, we measured exploration in the novel environment apparatus in both laboratory and field conditions to document whether the experimental protocol can influence estimates of exploratory behavior in birds.

MATERIALS AND METHODS

Study sites

We conducted novel environment experiments on rufous-collared sparrows from 3 Chilean populations—Copiapó, Santiago, and Llanquihue. Copiapó (lat 27°18'S, long 70°25'W) is situated in an arid environment with little rainfall and relatively high temperatures (mean maximum temperature: 15.7 °C and annual precipitation: 11.2 mm). Santiago (lat 33°31'S, long 70°50'W) is also located in an arid environment but experiences higher rainfall and lower temperatures (mean maximum temperature: 13.8 °C and annual precipitation: 337.4 mm). In sharp contrast, Llanquihue (lat 41°16'S, long 73°00'W) experiences both high rainfall and low temperatures (mean maximum temperature: 9.4 °C and annual precipitation: 3112 mm). To further understand environmental differences between the 3 populations, we estimated primary productivity via the de Martone aridity index (DMi) calculated via $DMi = \frac{P}{T+10}$, where P and T represent monthly precipitation (millimeters) and average monthly temperature (degree Celsius), respectively (Cavieres and Sabat 2008). The annual mean and variance of this index are low (i.e., low productivity) in hot dry deserts and high (i.e., high productivity) in cool wet

areas. In addition, it has previously been shown that this index is strongly related to energy expenditure and osmoregulatory physiology in rufous-collared sparrows (Cavieres and Sabat 2008; Sabat et al. 2009). Our calculations demonstrated a north–south increase in primary productivity from Copiapó ($DMi - \bar{X} = 0.04$, $\sigma^2 = 0.004$) through to Santiago ($DMi - \bar{X} = 1.44$, $\sigma^2 = 2.75$) and Llanquihue ($DMi - \bar{X} = 14.28$, $\sigma^2 = 63.46$). Climatic data were obtained from 1) www.meteochile.cl, 2) el Centro de Información de Recursos Naturales, Chile, and 3) Di Castri and Hajek (1976).

Laboratory-based study

Individuals were captured passively with mist nets from the 3 field sites between April and May 2009 and housed under laboratory conditions at the Facultad de Ciencias, Universidad de Chile in Santiago, Chile. Sixteen individuals were captured from Copiapó, 19 from Santiago, and 22 from Llanquihue. The sexes of these individuals are unknown due to the difficulty in sexing this species via morphometrics during the non-breeding season. The sparrows were housed together in plastic mesh cages measuring 100 × 100 × 100 cm (up to 4 individuals per cage) and provided with seed and water ad libitum. Temperature and photoperiod were maintained at 22 ± 2 °C and 12:12 h light:dark, respectively. These laboratory conditions differed to varying degrees from the ecological conditions experienced during April and May at each site but were always warmer with longer light periods (mean temperature for April/May—Copiapó: 15.4/13.3 °C, Santiago: 13.6/10.4 °C, and Llanquihue: 9.7/7.9 °C and photoperiod range for April/May: Copiapó: 11.9–11.0 h, Santiago: 11.7–10.1 h, and Llanquihue: 11.6–9.4 h). Individuals were allowed to settle in the laboratory for at least 3 days before the exploration assays (mean time before first trial—Copiapó: 3.0 ± 0.0 days, Santiago: 10.6 ± 0.9 days, and Llanquihue: 23.5 ± 1.8 days). Although the 3 populations differed significantly in mean time elapsed between capture and time of the first trial (Kruskal–Wallis: $Z = 43.95$, degrees of freedom [df] = 2, $P < 0.001$), our analyses show that time since capture does not affect exploratory behavior (see RESULTS). The exploration behavior of each individual was quantified twice (mean time elapsed between first and second trial—Copiapó: 25.0 ± 0.0 days, Santiago: 10.7 ± 0.5 days, and Llanquihue: 13.4 ± 1.0 days).

Exploration behavior was quantified via novel environment experiments in a large field-portable cage (270 cm length × 150 cm width × 150 cm height) constructed of polyvinyl chloride poles and semitransparent black shading cloth. Five wooden perches (80 cm in length and 2 cm in diameter) were hung throughout the cage at varying heights (between 50 and 110 cm above ground). One perch was placed diagonally in the opposite corner at each far end of the cage and the remaining 3 spaced at regular intervals (70 cm apart) along the long axis of the cage. The cage was placed in a fixed position within the laboratory.

Before each trial, the subject was placed in a small holding cage (30 cm length × 25 cm width × 39 cm height) in a corner of the experimental cage and covered with a cloth during a 5-min acclimatization period. Each experimental trial lasted 10 minutes. At the commencement of the experimental period, the cloth was removed and the door of the holding cage was opened. An observer, hidden from view but with full sight of the cage, dictated all the subjects' movements onto a digital voice recorder including 1) number and destination of flights and 2) number and destination of hops. Although the experimental cage was not acoustically isolated from the observer, all observations were dictated in a low voice volume to minimize any effects of observer presence on the exploratory

behavior of subjects. Flight and hop destination included both the perches and the walls of the cage. We also distinguished between cases where the birds landed on the front and back ends of the 2 side walls. This resulted in 11 areas of the cage where the birds regularly perched (5 wooden perches and 6 wall regions). At the termination of each trial, sparrows were recaptured within the cage using a butterfly net and returned to the housing.

To quantify variation in the exploratory behavior during the trial, we calculated 3 variables: 1) proportion of hops during the trial relative to the total number of all movements (i.e., all hops and flights), 2) exploration diversity and 3) exploration speed. Exploration diversity was quantified via the Shannon's diversity index, via $H = -\sum p_i \ln p_i$ where p represents the total number of times perch i was visited, expressed as a proportion of the total number of perch visits throughout the trial. Finally, exploration speed was calculated by summing the distances traveled between perches (when an individual hopped along the same perch or on the same wall, travel distance was estimated at 10 cm). Dividing the total distance covered during the trial by the duration of the trial period provided exploration speed (i.e., meters per minute). Individuals were assumed to be more thorough explorers when they hopped more frequently, explored more slowly, and visited a higher diversity of perches during the trial.

Field-based study

In addition to quantifying exploration in the laboratory-based study, we were also interested in the effect of housing birds in captivity for an extended period on their exploratory behavior. We therefore also quantified exploration of sparrows from Santiago at the source population immediately after capture to allow a comparison with exploratory behavior of the same population that had been held in captivity. Field-based experiments occurred in August 2008. Individuals used for the field-based study were not used for the laboratory-based study to avoid familiarity with the cage confounding our results. We passively captured 12 individuals in mist nets and fitted each with a unique combination of colored leg rings. Upon capture, each individual was introduced into the novel environment cage for a 10-min period as previously described. All birds were released at the site of capture at the termination of the trial. The cage was placed in a fixed position within the study site.

Statistical analysis

All data were tested for normal distributions and transformed where necessary. Nonparametric tests were used where transformations did not improve normality. Repeatability of exploratory behavior was estimated following Lessells and Boag (1987), where repeatability is given by $r = \frac{S_A^2}{S_W^2 + S_A^2}$ (S_A is the among-groups variance component and S_W is the within-group variance component). However, low repeatability in a given behavior can either result from high intraindividual variability between trials or low interindividual variability. Therefore, to understand which sources of variation drive differences in repeatability between populations, we also calculated the intraindividual and interindividual coefficients of variation for each behavior, where $CV = \frac{\text{Standard deviation}}{\text{Mean}}$. Intraindividual CVs were obtained by calculating the CV for each individual (via the mean and standard deviation of the 2 trials) and taking the average for each behavior and population. Interindividual CVs were calculated by averaging the values of each individual and behavior and subsequently calculating the mean and standard deviation within each population.

To compare differences in intraindividual CVs within behaviors, but across populations, we conducted general linear models, incorporating population as a fixed effect. Differences in interindividual CVs between populations were calculated following Feltz and Miller (1996) who present calculations for a general statistic that tests the hypothesis that the CVs for k populations, with unequal sample sizes, are the same. P values could not be assigned exact values in this latter test because statistical tables were used. In all other tests, exact P values are quoted.

In order to investigate the factors that influence interindividual variation in exploratory behavior, we used general linear mixed models. Each measure of exploratory behavior was included separately as a dependant variable. Time since capture (in days), trial number (first or second trial—a measure of familiarity with the experimental cage), and location of origin were included as fixed factors. As we included each individual twice in the analysis (i.e., for both the first and the second trials), we also included individual identity as a random factor to avoid pseudoreplication biasing our results. Models had either normal errors with identity link (exploration diversity) or Poisson errors with logarithm link (proportion of hops and exploration speed). A set of models were created, consisting of all possible combinations of the fixed factors as main effects and as interactions. We then used Akaike's Information Criteria (AIC; Akaike 1974) to select the most parsimonious statistical model. AIC is calculated as the model deviance plus twice the number of estimable parameters of the model (Burnham and Anderson 1998). The model resulting in the lowest AIC was considered the most parsimonious model, and competing models with differences in AIC values of more than 2 were considered significantly different. However, when the AIC values for 2 competing models differed by less than 2, we chose the model with the least number of parameters as the best-fitting model (Quinn and Keough 2002). The AIC values for the top 8 candidate models for each behavior (i.e., those with the lowest AIC values) are presented as Supplementary Material. Generalized linear mixed models were conducted using Genstat 11.0 and all other analyses in SPSS 15.0 and Systat 12.0. Data are presented as means \pm standard error.

RESULTS

Characteristics of exploratory behavior

During the novel environment experiments, the rufous-collared sparrows displayed large variability in their responses upon release into the novel environment cage. Individuals typically flew and hopped throughout the cage, moving between both the wooden perches and the mesh walls (mean number of movements to perches = 20.0 ± 4.1 movements and mean number of movements to walls = 20.2 ± 4.9 movements; $n = 57$ trials). On average, the sparrows utilized 3.2 ± 0.2 of the 11 available surfaces to perch on ($n = 57$ trials, range = 1–10 perches utilized), and although they typically only remained stationary on each perch for a few seconds, some individuals stayed stationary on a single perch for the majority of the trial (mean time spent stationary on a perch = 13.3 ± 1.2 s, $n = 2490$, range = 0.5–592 s). There was no difference in the number of times each individual hopped or flew during the trials (mean number of flights throughout trial: 33.1 ± 4.4 flights; hops: 34.4 ± 4.5 hops; Wilcoxon-signed rank test: $Z = -0.940$, $n = 57$, $P = 0.347$).

Repeatability in exploratory behavior

The repeatability of exploratory behavior varied between the 3 populations (Table 1; Figure 1). Proportion of hops was not

Table 1

Differences between populations in repeatability (r) of exploratory behavior by rufous-collared sparrows during 2 novel environment experiment trials

Population	Proportion of hops			Exploration diversity			Exploration speed		
	r	F	P	r	F	P	r	F	P
Copiapó	0.549	3.458	0.084	0.932	28.731	<0.001	0.909	21.029	<0.001
Santiago	0.604	4.048	0.061	0.906	20.327	<0.001	0.840	11.536	0.003
Llanquihue	-0.202	0.664	0.423	-0.170	0.709	0.410	0.829	10.687	0.004
	Intraindividual CV	Interindividual CV		Intraindividual CV	Interindividual CV		Intraindividual CV	Interindividual CV	
Copiapó	75.6	70.2		35.4	43.1		71.2	132.1	
Santiago	69.7	72.8		48.5	53.1		53.4	113.1	
Llanquihue	65.5	44.1		65.8	35.6		64.0	98.9	
Z statistic	0.249	3.017		5.320	1.745		1.951	0.349	
P value	0.883	<0.25		0.070	<0.50		0.377	<0.90	

Intraindividual and interindividual coefficients of variation in the measures allow the comparison of repeatability between behaviors. See main text for further explanations of how repeatability and coefficients of variation were calculated.

repeatable between trials for any population. In contrast, exploration diversity was highly repeatable between trials for Copiapó and Santiago but not Llanquihue. Finally, exploration speed was highly repeatable for all 3 populations. Differences in the repeatability of exploration diversity may be related to higher intraindividual variation of birds from Llanquihue rather than lower interindividual variation in this population. Interindividual variation in exploration diversity was similar between populations (Table 1). In contrast, differences in intraindividual variation between populations approached significance with individuals from Llanquihue tending to be less consistent in exploration diversity between trials than those from Copiapó ($Z = -1.953$, $df = 1$, $P = 0.051$) and Santiago ($Z = -1.936$, $df = 1$, $P = 0.053$). There were no interpopulational differences in neither interindividual nor intraindividual coefficients of variation for exploration speed (Table 1).

Intercorrelations amongst measures of exploratory behavior

The correlation matrices between the 3 measures of exploratory behavior showed high variability between both populations and trials (Table 2). First, we found differences between populations in the correlation matrices. For example, during the first trial, a negative relationship existed between proportion of hops and exploration speed and proportion of hops and diversity but only for individuals from Copiapó. In contrast, exploration speed during trial 1 was positively correlated with diversity in all 3 populations. Second, the correlation matrices showed some variation between trials for certain populations. For example, the negative correlation between proportion of hops and diversity in Copiapó did not exist during the second trial, whereas the positive correlation between diversity and exploration speed in Llanquihue was also lost during the second trial.

Sources of variation in exploratory behavior

The factors influencing variation in exploratory behavior depended on what measure of exploration was used. First, the most parsimonious model describing variation in proportion of hops only included location of origin (Table 3 and Supplementary Table 1). Individuals from Llanquihue hopped the most often, whereas those from Santiago hopped the least. However, these patterns became nonsignificant when only data from the first trials were used (see below). The most parsimonious model describing variation in exploration diversity included location of origin, trial number, and

the interaction between the 2 terms, although the effect of location was not significant (Table 3 and Supplement 1). The effects of each factor indicate that the sparrows visited a higher diversity of perches during the second trial. However, the interaction between trial number and location of origin indicated that the effect of trial number on exploration diversity was highest for Llanquihue and lowest for Santiago. Similarly, the most parsimonious model for exploration speed included trial number, location, and the interaction between the 2 terms (Table 3 and Supplement 1), although again the effect of location was not significant. Individuals tended to explore faster during the second trial, and this effect was greatest for the birds from Copiapó and least for birds from Santiago.

Our AIC-based analyses revealed that time since capture was never an important determinant of exploratory behavior in our study species but that location of origin and trial number was. However, our estimates of population-wide differences in exploratory behavior, using the AIC analysis, are likely to be influenced by the fact that the extent of intertrial variation in exploratory behavior varied between populations. These patterns were therefore explored in more detail. Figure 2 reveals that there were marked differences between the populations in how the 3 measures varied between trials. First, only individuals from Llanquihue increased their hopping frequency during the second trial (paired t -test: $t = -2.35$, $df = 21$, $P = 0.029$), whereas those from Copiapó and Santiago did not change their hopping behavior between trials (Copiapó paired t -test: $t = 1.01$; $df = 16$; $P = 0.327$ and Santiago paired t -test: $t = -0.284$; $df = 18$; $P = 0.779$; Figure 2a). Second, individuals from both Copiapó and Llanquihue, but not Santiago, increased the diversity of perches visited during the second trial (Copiapó paired t -test: $t = -6.02$; $df = 16$; $P < 0.001$; Llanquihue paired t -test: $t = -5.433$; $df = 21$; $P < 0.001$; and Santiago paired t -test: $t = 1.621$; $df = 18$; $P = 0.122$; Figure 2b). Lastly, individuals from both Copiapó and Llanquihue, but not Santiago, increased their speed of exploration during the second trial (Copiapó paired t -test: $t = -3.60$; $df = 16$; $P = 0.002$; Llanquihue paired t -test: $t = -2.878$; $df = 21$; $P = 0.009$; and Santiago paired t -test: $t = 0.432$; $df = 18$; $P = 0.671$; Figure 2c). Due to these differences, we conducted analyses including only data from the first trials in order to obtain better estimates of interpopulational differences in exploratory behavior. The 3 populations did not differ in their frequency of hopping ($F_{2,55} = 0.110$, $P = 0.284$) during the first trial (although interpopulational differences were detected during the second trial; $F_{2,55} = 4.676$, $P = 0.013$). Likewise, no differences were found between populations in the mean diversity of perches visited during trial 1

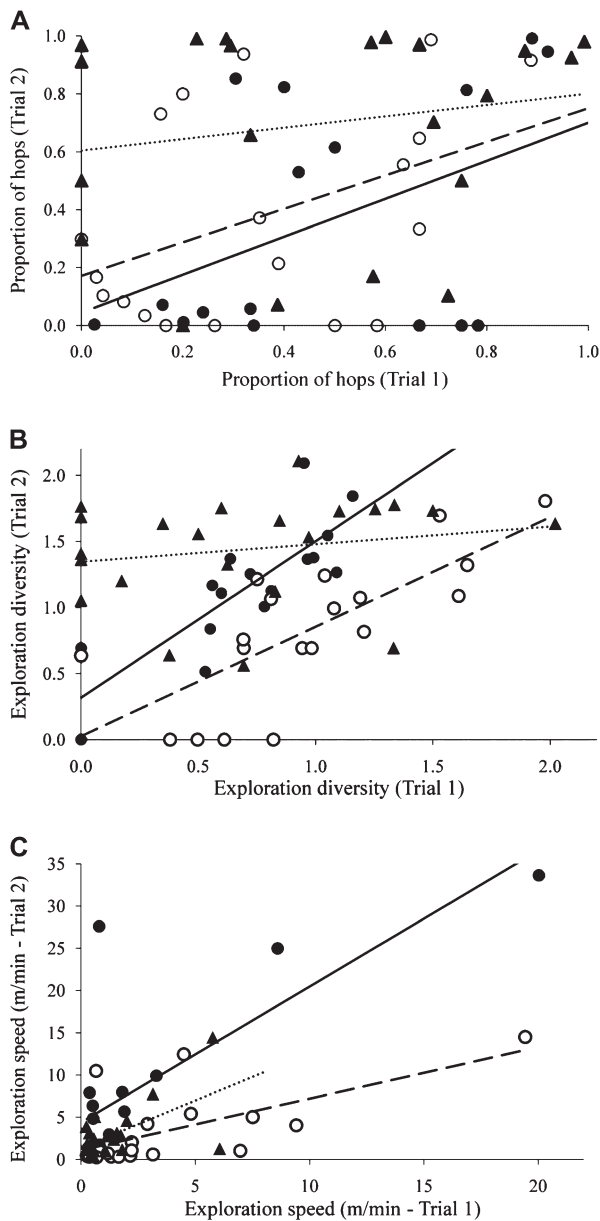


Figure 1
Interpopulational differences in the repeatability of a) proportion of hops, b) exploration diversity and c) exploration speed of rufous-collared sparrows between trials of the novel environment experiments. Individuals from Copiapó are represented by filled circles and solid line, Santiago by open circles and dashed line and Llanquihue by filled triangles and dotted line.

($F_{2,55} = 2.142$, $P = 0.127$), although differences were again detected during the second trial ($F_{2,55} = 8.237$, $P = 0.001$). Finally, no differences were found in exploration speed between populations ($F_{2,55} = 1.946$, $P = 0.153$), although, as with proportion of hops and diversity, differences were detected during the second trial ($F_{2,55} = 5.169$, $P = 0.009$).

A comparison of exploration behavior of individuals from Santiago quantified under different conditions revealed that the behavior of individuals measured under field conditions did not differ significantly from those measured in the laboratory (proportion of hops—field: 0.21 ± 0.06 , laboratory: 0.35 ± 0.06 ; $F_{1,31} = 2.415$, $P = 0.130$; exploration diversity—field: 0.99 ± 0.14 , laboratory: 1.02 ± 0.11 ; $F_{1,31} = 0.019$,

$P = 0.890$; exploration speed—field: 4.8 ± 1.1 m/min, laboratory: 3.8 ± 1.0 m/min; $F_{1,31} = 0.432$, $P = 0.516$).

DISCUSSION

We have shown here that variation in the diverse aspects of exploratory behavior quantified here (i.e., repeatability, behavioral intercorrelations, and causes of interindividual differences) is complex, occurring both temporally and geographically. First, our 3 measures of exploration (proportion of hops during the exploration trial, exploration diversity, and exploration speed) tended to be highly repeatable between trials (with repeatability estimates of up to 0.93), suggesting that within-individual variation in certain measures of exploration is much lower than between-individual variation. Such rank-order consistency of interindividual differences in behavior is characteristic of personality traits (Bell 2007), when behavioral consistency is maintained either temporally or across different contexts. Exploration speed was highly repeatable across trials for all 3 populations, whereas exploration diversity was only repeatable in Copiapó and Santiago. In contrast, the proportion of hops was never repeatable. Second, the intercorrelations between our 3 measures of exploratory behavior did not display any predictable consistency between neither populations nor trials, with most behavioral intercorrelations not being maintained between trials and little consistency between populations. In addition, we show that few factors explained interindividual variation in exploratory behavior. First, neither the conditions under which exploration was quantified (i.e., under field or laboratory conditions) nor time spent in captivity affected our estimates of exploration, justifying the use of temporarily captive birds to estimate exploration under field conditions, at least for rufous-collared sparrows (see also Herborn et al. 2010). However, our data revealed that individuals from some populations appeared to habituate to the experimental enclosure between trials—individuals from Llanquihue hopped more during the second trial and individuals from both Llanquihue and Copiapó explored faster and visited a higher diversity of perches during the second trial. Similar changes in exploration between trials have been reported in other bird species (e.g., Dingemanse et al. 2002; Minderman et al. 2009) and may reflect a reduction in anxiety with increased familiarization with the novel environment apparatus. Once habituation was taken into account, we found no interpopulational differences in exploratory behavior. Finally, we have identified a novel measure to estimate exploration, exploration diversity, which has been thus far ignored by other researchers. Exploration diversity would intuitively be a reliable indicator of true exploratory tendency as an individual in an unknown environment (or indeed a known environment where the location of available food sources are unknown) would benefit from exploring a greater diversity of areas rather than only exploring a subset of the available area. Overall, the marked variation existing in the different aspects of exploratory behavior provides new insights into the complexity of personality consistency across both space and time.

Our data reveal that variation in exploratory behavior within and between the 3 populations of sparrows quantified is complex and, currently, difficult to explain. However, the various levels of exploratory behavior that we quantified provide some insights into the causes and consequences of such variation. First, the underlying cause of the lack of repeatability of our measures of exploration in certain populations was the relatively high intraindividual variation (i.e., low individual consistency between trials) compared with interindividual variation (i.e., variation between individuals within populations). For example, although intraindividual variation between trials

Table 2

Correlation matrices for the 3 measures used to describe exploratory behavior of 3 populations of rufous-collared sparrows during novel environment experiments

Population	Proportion of hops					Exploration diversity				
	Trial 1		Trial 2		Intertrial <i>z</i> , <i>P</i>	Trial 1		Trial 2		Intertrial <i>z</i> , <i>P</i>
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	
Exploration diversity										
Copiapó	-0.681	0.003	0.172	0.509	-2.56, 0.01					
Santiago	-0.421	0.072	-0.307	0.201	-3.72, 0.71					
Llanquihue	0.060	0.790	0.574	0.005	-1.83, 0.07					
Exploration speed										
Copiapó	-0.651	0.005	-0.641	0.006	-0.04, 0.97	0.641	0.006	0.277	0.282	1.34, 0.18
Santiago	-0.211	0.387	-0.112	0.648	-0.29, 0.77	0.537	0.018	0.614	0.005	-0.33, 0.74
Llanquihue	0.319	0.148	0.035	0.887	0.91, 0.36	0.758	<0.001	0.252	0.257	2.26, 0.02

For all tests, $n = 16$ for Copiapó, $n = 19$ for Santiago, and $n = 22$ for Llanquihue. *P* values highlighted in bold correspond to statistically significant results. Because exploratory behavior can vary between trials (see RESULTS), we calculated separate matrices for trials 1 and 2. Probability of finding 8 statistically significant tests (with $P \leq 0.018$) of 18 due to chance alone (calculated via a Bernoulli process: Moran 2003): $P < 0.001$. "Intertrial" refers to differences in correlation coefficients between 2 aspects of exploratory behavior between trials. Probability of finding 2 statistically significant tests (with $P \leq 0.02$) of 9 due to chance alone: $P = 0.013$.

was relatively high for both exploration speed and proportion of hops, differences in interindividual variation for these behaviors (high for exploration speed and low for proportion of hops) resulted in only the former, and not the latter, displaying high repeatability estimates. Likewise, exploration diversity was repeatable in Copiapó and Santiago but not in Llanquihue due to the population differences in intraindividual consistency (i.e., high in Copiapó and Santiago but low in Llanquihue).

These differences in repeatability estimates in turn may result in variation in other aspects of exploratory behavior observed in this species. First, during the first trial for individuals from Copiapó, the 3 exploratory measures were highly intercorrelated, with faster exploring individuals hopping less (probably because hopping individuals cover less distance per unit time) and visiting a higher diversity of perches (probably because more active individuals have a greater opportunity to visit a high number of perches within the trial period), whereas proportion of hops was negatively

correlated with diversity. However, only the positive relationship between exploration speed and diversity was maintained during the second trial, a possible consequence of only these 2 measures being repeatable between trials for this population. Interestingly for this population, although both exploration speed and diversity were repeatable between trials, both increased during the second trial. This suggests that although individuals change their behavior between trials, they do so in a consistent way and maintain the rank-order differences between individuals. In contrast to Copiapó, the only behavioral intercorrelations of individuals from Santiago were between exploration speed and diversity. These measures were positively related during both trials, although no habituation effects were detected. Again, these intercorrelations appear to be maintained due to the fact that only exploration speed and diversity were repeatable in this population. However, it remains unknown why individuals from this population did not habituate to the novel environment apparatus during trials. Lastly, only exploration speed was repeatable for

Table 3

Sources of interindividual variation in 3 measures of exploratory behavior of rufous-collared sparrows during novel environment experiments

Factor	Effect	Wald	<i>P</i>
Proportion of hops ^a			
Constant	-0.848 ± 0.149		
Location (Copiapó/Santiago/Llanquihue)	0.000/-0.191/0.300	6.88	0.039
Exploration diversity ^b			
Constant	0.916 ± 0.102		
Location (Copiapó/Santiago/Llanquihue)	0.000/-0.015/0.154	2.04	0.367
Trial number	0.495 ± 0.117	35.44	<0.001
Location × trial number (Copiapó/Santiago/Llanquihue)	0.000/-0.632/0.246	34.86	<0.001
Exploration speed ^c			
Constant	1.308 ± 0.242		
Location (Copiapó/Santiago/Llanquihue)	0.000/-0.373/-0.664	6.16	0.054
Trial number	1.305 ± 0.186	30.22	<0.001
Location × trial number (Copiapó/Santiago/Llanquihue)	0.000/-1.411/-0.559	29.62	<0.001

Results are from GLMMs including individual identity as a random factor and location of origin, time since capture, and trial number as fixed factors. The most parsimonious model explaining variation in each measure was selected via the Akaike's information criterion (see main text for explanation and Supplement 1 for list of most parsimonious models for each test).

^a Random effect = 0.157 ± 0.082.

^b Random effect = 0.118 ± 0.035.

^c Random effect = 0.788 ± 0.19.

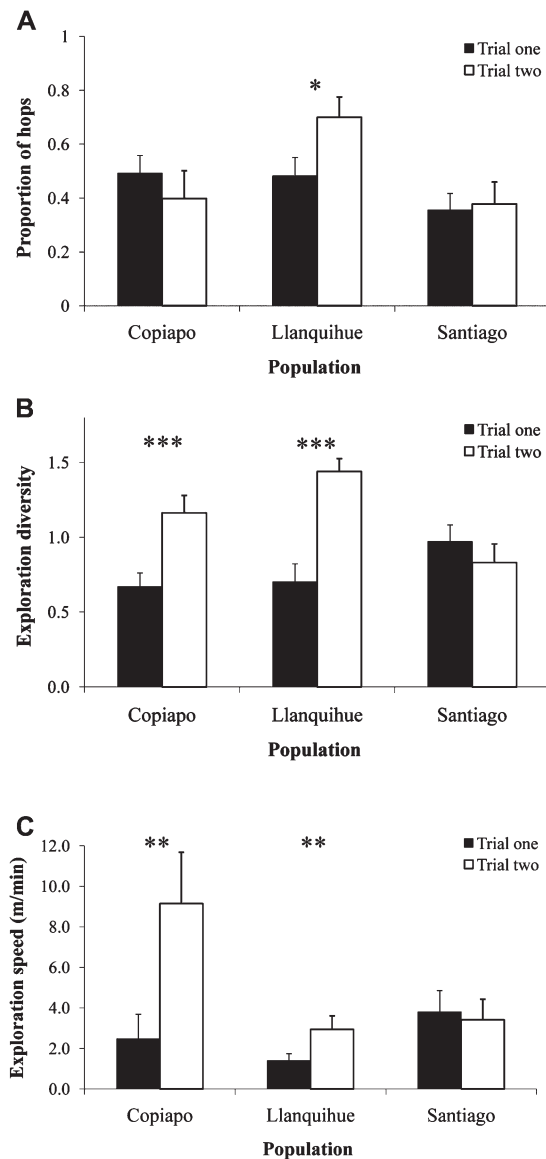


Figure 2
Variation between populations in inter-trial differences in a) proportion of hops, b) exploration diversity and c) exploration speed of rufous-collared sparrows during novel environment experiments. Black bars represent means (plus standard errors) of the first trial and white bars represent means (plus standard errors) of the second trial.

individuals from Llanquihue. The fact that only one measure was repeatable within this population seemed to be reflected in the lack of consistency of behavioral intercorrelations between trials: During the first trial, only a positive relationship between exploration speed and diversity was detected, whereas during the second trial, only a positive relationship between proportion of hops and diversity existed.

A somewhat surprising finding of our study was that we detected no geographic variation in our 3 estimates of exploratory behavior, despite the sharp ecological differences between the 3 study populations. Therefore, individuals from Copiapó and Santiago, which originate from arid environments with low primary productivity, displayed the same exploratory tendencies as those from Llanquihue, where the habitat is much wetter with a much higher primary productivity. Our measure of primary productivity (using the DMi) is

an appropriate estimate of the environmental pressures that may be experienced by the sparrows in each population, as this index is known to correlate with physiological measures related to environmental stress in this species (Cavieres and Sabat 2008; Sabat et al. 2009). Our data therefore suggest that the magnitude of exploration behavior is an inflexible characteristic of this species, which is unaffected by local environmental conditions. However, a greater number of populations need to be sampled in order to confirm this pattern. In addition, it is not currently possible to predict how exploratory behavior should vary across the geographic distribution of this species as it remains unknown what the selective advantage of more thorough exploratory behavior in this species is. In other species, the consequences of more thorough exploratory abilities are diverse. For example, in great tits, exploratory behavior has been linked to overwinter survival rates, extrapair mating patterns, and dispersal patterns (Dingemanse et al. 2003, 2004; van Oers et al. 2008), whereas in blue tits (*Cyanistes caeruleus*), exploration tendency under captive conditions is known to correlate with an individual's ability to find new feeding stations in the field (Herborn et al. 2010).

Despite not detecting any population differences in exploratory behavior, our findings that the repeatability of different aspects of exploratory behavior vary between populations suggests that individuals from different populations specialize in different strategies when exploring. In addition, as repeatability in a behavior generally sets an upper limit to heritability of the trait (Lessells and Boag 1987; Dohm 2002), our data suggest that the heritability of the 3 measures of exploration vary markedly between populations. For example, exploration speed and diversity may be under stronger selection in Copiapó and Santiago, whereas only exploration speed may be selected for sparrows from Llanquihue. Our data also suggest that the heritability of exploration speed and diversity is much higher than that of hopping behavior. However, population and behavioral differences in repeatability may also have arisen solely due to the influences of labile environmental effects (Falconer and Mackay 1996).

Although the individuals used in this study originated from environments with vastly different natural conditions, all were housed in laboratory conditions with the same light and temperature cycles. Compared with the ecological conditions at the site of capture, individuals from Llanquihue experienced relatively warmer conditions in the laboratory, with longer days, than those captured in Copiapó. The possibility therefore arises that these population differences in the relative ecological and laboratory conditions could account for some of the interpopulation variation we observed. However, our findings that exploratory behavior was not affected by assay conditions (i.e., laboratory vs. field) nor by time spent in captivity suggests that variation in exploration is not sensitive to slight differences in temperature and light cycles experienced under laboratory conditions. Likewise, although the individuals were housed in variable numbers in the laboratory cages (sometimes 3 individuals per cage but usually 4), this is unlikely to add significant variation to our estimates of exploratory behavior given both the low variation in bird density within the cages and the apparent robustness of exploratory behavior toward variation in housing conditions.

Dingemanse et al. (2002) have previously demonstrated moderately high repeatability estimates for exploration across 2 populations of great tits with estimates ranging from 0.27 to 0.66. Although repeatability estimates for exploratory behavior were calculated for the 2 study populations, no interpopulation differences were detected. Similarly, Minderman et al. (2009) reported exploration estimates ranging between 0.31 and 0.40 in a single population of starlings. In addition to the advances of these earlier studies on repeatability in avian

exploration, we have shown here that estimates of repeatability can also differ between populations. In addition, intercorrelations between different estimates of exploratory behavior can also vary across populations.

Our findings therefore have important implications for both our current understanding of the selective pressures acting on animal personalities and on the practicalities of future personality research. First, personalities are typically defined as behaviors that are consistent across either time (i.e., high repeatability between trials) or contexts (Bell 2007). An underlying assumption of personality research is that behavioral consistency does not vary between populations. Our findings contradict this view and highlight how, based on the above definition, certain behaviors may be described as personalities in some populations (e.g., exploration diversity in Copiapó) but not in others (e.g., exploration diversity in Llanquihue). Future studies would therefore benefit from obtaining repeatability estimates from a range of populations for a given species to assist in making general conclusions concerning the nature of personalities. In addition, geographic variation in the repeatability of individual personality traits could account for some of the differences between populations in personality intercorrelations (e.g., between exploratory behavior, boldness, and aggression: Bell 2005; Dingemanse et al. 2007; Herczeg and Merila 2009). Our results also highlight the fact that the choice of measures used to describe a behavior (e.g., hopping behavior, exploration speed, and diversity to describe exploration in the current study) can have significant implications on whether or not a behavior is regarded as a personality as determined by its repeatability (see also Bell et al. 2009; Minderman et al. 2009). Finally, we have shown that although the magnitude of exploration may not vary between populations, variation can still exist in the exploration strategies adopted within each population (based on behavioral intercorrelations and repeatability estimates). Although the low number of populations sampled means that we are unable to conclusively identify the precise factors affecting population differences in behavioral repeatability and exploratory behavior, our data convincingly demonstrate that interpopulation variation in exploratory behavior is indeed possible.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

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