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ARTICLE

Evaluating the novel-environment test for measurement of exploration by bird species

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Abstract Novel-environment tests are the most widespread experimental technique for characterizing exploration, yet detailed evaluation of their performance among species is lacking. We compared the test for eight bird species by combining three well-known metrics of behavior: movement frequency, proportion of features visited, and scanning. In both overall and species-level analysis of our multi-group principal component analysis, all three metrics loaded strongly and similarly on one principal component, explaining comparable ranges of variation. We conclude that novel-environment tests are a robust means of quantifying exploration and that scanning behavior may be an important but under-used metric for exploration behavior.

Keywords Exploratory behavior · Novel-environment test · Scanning behavior

Introduction

Exploration is an important means of assessing risks and rewards in the current environment (Mettke-Hofmann et al. 2006). For example, information gathered through exploratory activity is crucial in finding patchy resources or identifying potential risks in the surrounding habitat (Valone 1989; Dingemanse et al. 2004; Fletcher 2006; Forsman et al. 2009). For researchers to understand the ecological consequences of exploration behavior, metrics with high ecological validity and experimental reliability are required (Carter et al. 2013). To this end, most studies have used the "novel-environment" (or "open-field") test as a standardized method for quantifying exploratory variation within a population (Verbeek et al. 1994; De Pasille et al. 1995; Choleris et al. 2001; Dingemanse et al. 2002). The test is implemented by releasing individuals into a new (captive) environment for a specific period of time, observing their behavior, and then quantifying such variables as the number and/or frequency of location shifts, latency in exploring the features provided, or the proportion of the test arena visited (Dingemanse et al. 2002; Butler et al. 2012).

The two most commonly used metrics in novel-environment tests are measures of body positional change: movement frequency and number of features visited in the environment (Dingemanse and de Goede 2004; Both et al. 2005; Schuett and Dall 2009; Guillette et al. 2010; Mutzel et al. 2011). Indeed, movement and position shifts in novel-environment tests have repeatedly enabled prediction of spatial exploration in the wild (Herborn et al. 2010; van Overveld and Matthysen 2010; but see Minderman et al. 2010). We have not, however, encountered a critical rationale for the choice of these as the only two definitive metrics of exploration capability. We note, for example, that from a purely energetics perspective, locomotion could merely be an expression of species-specific activity, rather than targeted behavior, for example exploration (Renner 1990; Kelley 1993; Carter et al. 2012). Furthermore, scanning behavior has rarely been included when quantifying exploration behavior (Marchetti and Zehtindjiev 2009), despite evidence suggesting that visual scanning is a key aspect of avian exploration (Huang et al. 2012).

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Although exploration testing is extremely popular in animal biology, our understanding of exploration behavior is derived from a very small number of taxa. Most of our knowledge of how to measure exploration behavior comes from a small set of well-studied groups of model taxa, including species whose physiognomies are well-suited to the typical novel environmental enclosures that can be replicated in a laboratory or aviary (e.g. house mouse, Augustsson and Meyerson 2004; great tit, Groothuis and Carere 2005; guppy, Budaev 1997). For birds, only a small fraction of species ($n = 15$) have been subjected to novel-environment tests (Kluen and Brommer 2013; van Oers and Naguib 2013), and cross-species comparisons of exploration are quite rare (Mettke-Hofmann et al. 2009). Thus, concerning the exploration behavior of birds, it remains uncertain whether the same types of experimental settings and test procedures will be informative for a broader range of species (Hall 1994; Ryan 1996).

Here, we present a brief report of investigation of the broader applicability of novel-environment tests by focusing on three commonly used exploration metrics for eight avian species occurring in Florida, USA, including an exotic invasive species.

Materials and methods

Study species

We collected behavioral data in novel-environment tests for 8 species representing 7 distinct avian families: Carolina chickadee (*Poecile carolinensis*; CACH) and tufted titmouse (*Baeolophus bicolor*; TUTI) in the family Paridae, Carolina wren (*Thryothorus ludovicianus*; CAWR; Troglodytidae), Eastern towhee (*Pipilo erythrophthalmus*; EATO; Emberizidae), monk parakeet (*Myiopsitta monachus*; MOPA; Psittacidae), myrtle warbler (*Setophaga coronata*; MYWA; Parulidae), Northern cardinal (*Cardinalis cardinalis*; NOCA; Cardinalidae), and white-eyed vireo (*Vireo griseus*; WEVI; Vireonidae). These species were selected because:

1. they are abundant or available locally, and
2. they vary in many ecological traits that potentially affect their underlying exploratory activities, for example nesting site, foraging type and strata, social structure, and range size.

Sampling design

On the basis of a-priori power analysis (G*Power 3.1; Faul et al. 2007), 70–90 individuals were required to detect a 40–60 % effect size (expected interspecific variation based on preliminary data) with at least 80 % power for eight groups in an F test. Therefore, we sought to study at least ten individuals of each species in our sampling.

The monk parakeets we used ($n = 28$) were trapped in Southern Florida (Miami-Dade County), by placing nets over nest entrances at night (Tillman et al. 2004), and were housed in communal cages (1.8 × 1.2 × 1.2 m) within a roofed aviary at the USDA/APHIS National Wildlife Research Center Florida Field Station in Gainesville, USA. Individuals of the other 7 species ($n_{\mathrm{CACH}} = 10$, $n_{\mathrm{CAWR}} = 15$, $n_{\mathrm{EATO}} = 11$, $n_{\mathrm{MYWA}} = 10$, $n_{\mathrm{NOCA}} = 13$, $n_{\mathrm{TUTI}} = 16$, $n_{\mathrm{WEVI}} = 15$; all passerines) were captured at different locations in Florida, including the Ordway–Swisher Biological Station in Melrose (Putman County), the USDA/APHIS Florida Field Station (Alachua County), and 4 private yards in the city of Gainesville (Alachua County). To maximize genetic independence among sampled individuals of each species, juvenile (young of the year) birds were not used when more than one individual of each species was captured at a single trap site, and all trap sites were >2 km apart. Tests of all seven wild bird species were conducted under permit number 003-09WEC from the non-regulatory Animal Research Committee, Institute of Food and Agricultural Sciences Research Division, University of Florida, USA.

Testing protocol

Our design of novel-environment test cages (2 versions; Fig. 1) was a modification of that of Verbeek et al. (1994). Because the MOPA is regarded as an invasive pest in Florida (Avery et al. 2012), we used stationary cages (located inside a small aviary to prevent escapes) with wire mesh on three sides and a wooden door with a Plexiglass window on the 4th side (1.2 × 1.8 × 2.5 m). All MOPA tests were conducted onsite at the USDA/APHIS laboratory in accordance with USDA standard protocols for animal handling. Although Verbeek et al. (1994) housed individual birds overnight before conducting behavioral assays, in our study, to reduce captivity-induced stress (McCowan et al. 2015, Huang et al. 2012, Kluen et al. 2012, Mindernan et al. 2009) and because managers at some sites prohibited wildlife removal, wild caught passerines were subjected to novel-environment tests immediately at trapping sites. A portable novel environment cage was constructed from 3 cm diameter polyvinyl chloride (PVC) pipe draped with plastic bird netting and covered with white sheets (the sheets encouraged the birds to explore and eliminated the frantic escape behavior observed with mesh only around the enclosure; 3 × 3 × 2 m). To stimulate exploration, we placed 5–8 branches inside all test cages (Dingemanse et al. 2002). We assumed that all test individuals identified test arenas as novel habitat. For MOPA, the stationary novel environment cage had a different interior design

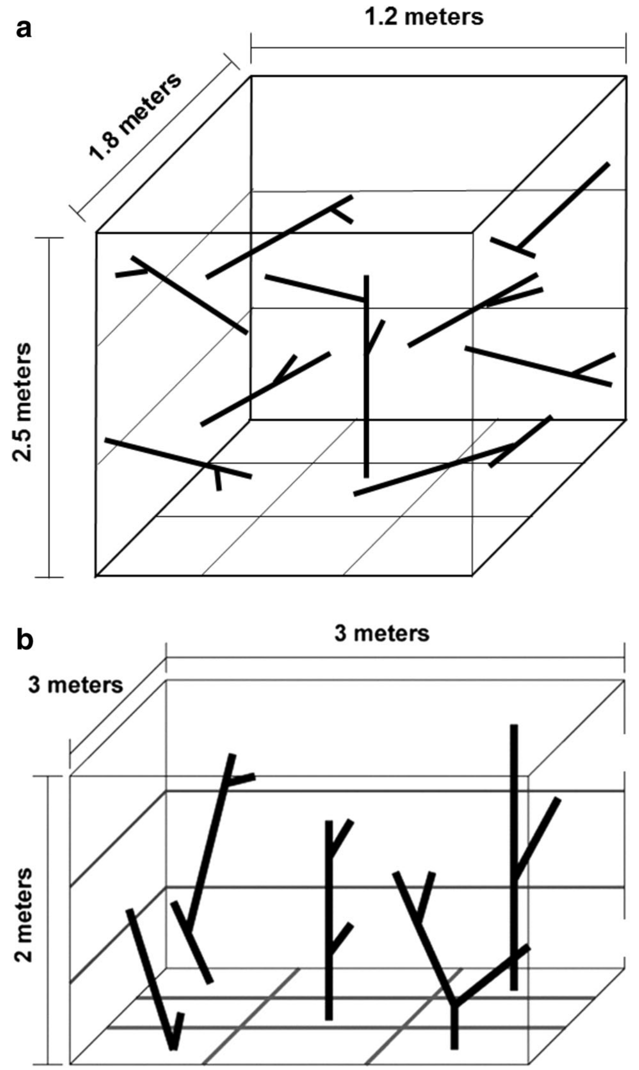

Fig. 1 Diagrams of the novel-environment test arenas. *Thick lines* represent branches and twigs. **a** The stationary experimental cages used inside an aviary for monk parakeet. **b** The portable experimental cage used at a field site for the other species

from that of their long-term housing cages and was located in a separate section of the facility to minimize habituation; all other birds were free-living and unmarked upon capture for this study.

Behavioral observations were conducted in May–June 2013 (MOPA) or in May 2009–February 2010 (other species). At the onset of each trial, individuals were transferred to their test locations in a small opaque carrier, and placed inside a darkened release cage. Birds were then introduced into the novel environment cage via a remotely triggered door after a 10-min acclimatization period (Kluen et al. 2012). Once released, birds were allowed to explore the cage for 10 min. The observation period was considered to be sufficient to capture the underlying exploratory activity, because equal or shorter durations were used in other studies (Herborn et al. 2010, Minderman et al. 2010). Behavior was recorded by use of digital video cameras and quantified by PH and KK. Immediately after testing, wild birds were released at the sites where they were captured, and MOPA were immediately moved back to their long-term holding pens.

Measuring exploration behavior

We used 3 behavioral measurements that describe exploration behavior:

1. movement frequency: the total number of flights and hops divided by the observation time;
2. proportion of features visited: the total number of perches and walls (including 4 sides and the ceiling) an individual contacted, divided by the total number of features in the test arena; and
3. scanning frequency: the number of head-only movements divided by the observation time.

Statistical analysis

We implemented a statistical data reduction and ordination technique called multiple group principal component analysis (MgPCA; Thorpe 1988). First, we used log and arcsine square-root transformations to normalize the data, then examined how behavioral output obtained from novel-environment tests was related across species by applying two levels of analysis (Krzanowski 1979; Abdi et al. 2013, Eslami et al. 2013).

1. *Overall analysis*, in which all individuals were considered together, irrespective of species; and
2. *Species-level analysis*, which grouped individuals of each species separately.

In both cases, we focused solely on significant principal components (PC) with Eigenvalues larger than 1.0 (Kaiser 1960). We calculated loadings for each variable on a given component by using correlation matrices, in accordance with Stevens (1992); variable loadings on a given PC that were less than 0.4 (absolute value) were considered non-significant. We obtained two sets of principal components scores for test individuals; one set from each PCA. The variation in species-level exploration scores is presented in boxplots and was compared by use of one way analysis of variance (ANOVA). All statistical analysis were conducted in R (Statistical Package, R. 2014). MgPCA was run in the package “multigroup” (Eslami et al. 2014), and figures were created by using the package “ggplot2” (Wickham 2009).

Results

Summary statistics of behavior measurement for each species are provided in Table 1.

Overall analysis

When considering all the species together (overall analysis), we obtained a single principal component (PC1) with an Eigenvalue >1 explaining 62 % of the total variation (Table 2). All 3 metrics contributed to PC1 with similar weights. According to PC1, individuals who moved frequently in the new environment tended to visit a greater volume of the test arena, and visually scanned their surroundings more often. We called this component "exploration".

Species-level analysis

The species-level analysis revealed the same pattern observed in the overall analysis; all metrics loaded similarly on PC1 for each species, with a consistent pattern across taxa (Table 2). The amount of variation explained by the exploration axis ranged between 40 and 76 %. It overlapped substantially among species. We did not observe any taxon-specific differences in exploration behavior ($F = 0.59$, df = 7, $p = 0.76$; Fig. 2).

Discussion

The novel-environment test has a long history of use; our results suggest it is also a universally applicable metric for assay of exploration behavior. On the basis of our analysis, exploration behavior in an unfamiliar environment was equally captured by all metrics, and was a combination of both active (locomotion shifts) and passive (scanning) means of obtaining information about the environment. Scanning is traditionally interpreted as part of "vigilance", an important survival mechanism that may be expressed in both familiar and novel environments (Lima and Dill 1990; Brown 1999; Caro 2005; Pascual et al. 2014). However, rather than forming a distinct behavioral trait, scanning a novel environment was as important as other traditionally considered aspects of exploration. This result demonstrated its importance in environmental information gathering. Indeed, recent evidence suggest that scanning behavior functions not only for predator detection but also as a form of monitoring of the environment (Gall and Fernández-Juricic 2010). It enables individuals to determine whether the visual landscape has changed over time by direct observation or visual tracking of heterospecific behavior (Moore et al. 2013; Fernández-Juricic et al. 2011; Gall and Fernández-Juricic 2010).

We found that the variation explained by exploratory activity was similar and the behavioral measures were of equal importance in exploration across taxa, even though the species investigated in this study were a diverse array of ecological and behavioral adaptations. For example, our dataset included species that are invasive (MOPA) and migratory (MYWA); altogether the species represented a broad array of foraging habits. Mettke-Hoffman et al. (2009) found that migrant species were less likely to visit features in the novel-environment chamber, potentially relying more on passive exploration. This tendency should be reflected by a negative relationship between scanning and locomotion shifts. However, in contrast with that finding, a positive correlation among all 3 metrics was observed for MYWA, as for the resident species. Similarly, invasive populations have been reported to be more active explorers (Cote 2010). Yet, as a successful invasive species, a positive relationship between active and passive exploration metrics was observed for MOPA, demonstrating the importance of considering several metrics in a design to study exploration.

Table 1 Summary statistics of behavior measurement for each species

Species	*n*	Movement frequency	Proportion of features visited	Scanning frequency
CACH	10	0.09 ± 0.02	0.23 ± 0.20	0.02 ± 0.003
CAWR	15	0.06 ± 0.04	0.26 ± 0.09	0.01 ± 0.003
EATO	11	0.07 ± 0.04	0.13 ± 0.13	0.01 ± 0.003
MOPA	28	0.03 ± 0.03	0.20 ± 0.10	0.50 ± 0.300
MYWA	10	0.04 ± 0.01	0.16 ± 0.06	0.01 ± 0.002
NOCA	13	0.06 ± 0.04	0.22 ± 0.12	0.02 ± 0.010
TUTI	16	0.07 ± 0.03	0.27 ± 0.12	0.01 ± 0.003
WEVI	15	0.04 ± 0.02	0.11 ± 0.06	0.12 ± 0.003

CACH = *Carolina chickadee*; CAWR = *Carolina wren*; *EATO* = *Eastern towhee*; MOPA = *Monk parakeet*; MYWA = *Myrtle warbler*; NOCA = *Northern cardinal*; TUTI = *Tufted titmouse*; and WEVI = *White-eyed vireo*. *n* sample size. Numbers under each measure represent mean ± standard deviation

Table 2 Factor loadings of the three behavior metrics on the extracted principle component (PC1) for the overall analysis and for the species-level analysis

PC1 *Exploration*

Species	Behavioral metrics loadings			% Variance	Eigenvalue
	Movement frequency	Features visited	Scanning frequency		
Overall analysis	0.60	0.60	0.53	62.0	1.7
Species-level analysis					
CACH	0.57	0.62	0.54	56.7	1.5
CAWR	0.62	0.60	0.51	67.9	1.9
EATO	0.54	0.58	0.61	69.2	1.9
MOPA	0.60	0.59	0.53	75.8	2.1
MYWA	0.57	0.69	0.45	50.6	1.4
NOCA	0.62	0.56	0.55	60.1	1.7
TUTI	0.59	0.58	0.56	76.4	2.2
WEVI	0.64	0.64	0.43	40.1	1.4

Overall analysis reflects the overall loadings; species-specific loadings are the results from species-level analysis. CACH = *Carolina chickadee*; CAWR = *Carolina wren*; EATO = *Eastern towhee*; MOPA = *Monk parakeet*; MYWA = *Myrtle warbler*; NOCA = *Northern cardinal*; TUTI = *Tufted titmouse*, and WEVI = *White-eyed vireo*

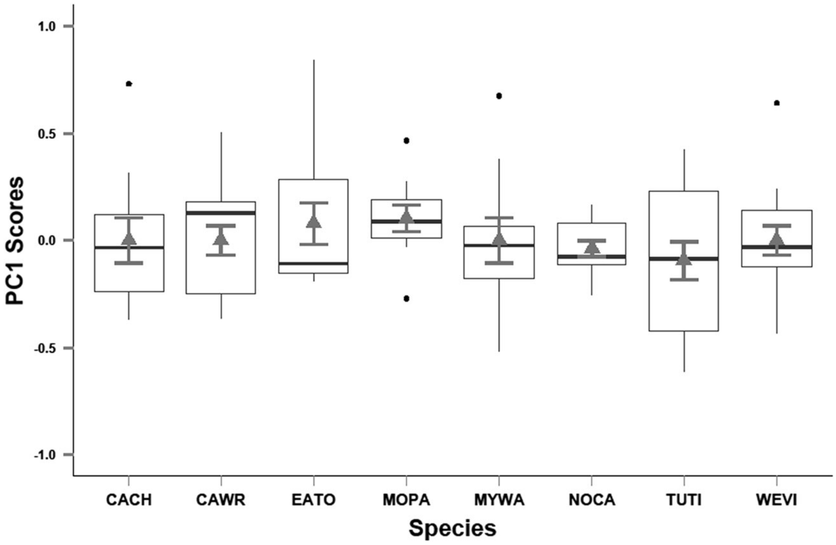

Fig. 2 Boxplots of PC1 for each species. Vertical axis includes composite, scaled scores from the species-level PCA. *Hedges* represent 25th and 75th percentiles, and *black horizontal line* depicts the median values. *Gray triangles* and *bars* show the mean and confidence intervals of PC scores for each species, respectively. *Black dots* represent outliers. CACH = *Carolina chickadee*; CAWR = -*Carolina wren*; EATO = *Eastern towhee*; MOPA = *Monk parakeet*; MYWA = *Myrtle warbler*; NOCA = *Northern cardinal*; TUTI = -*Tufted titmouse*, and WEVI = *White-eyed vireo*

Critical evaluation of the methodology used to elicit exploratory (or other) behavior must be accurate and carefully considered. This is especially important when the resulting descriptions of behavior form the basis for derivative investigations of, for example, the evolutionary and ecological mechanisms underlying behavior variation (Hall 1994; Ryan 1996; Richardson 2001; Møller 2010; Carrete and Tella 2011). Here, we substantially increased the number of bird species whose exploration behavior is now quantified (from 15 to 23 spp.). We also critically evaluated the performance of novel environment assays, to provide better information for future studies seeking to apply them to characterize exploration by diverse taxa. We conclude that:

1. the current use of novel-environment tests indeed captures the spatial investigation patterns of birds for broad taxonomic surveys of exploration behavior;
2. any one of the three measures used here could be used for reliable characterization of exploration, and, therefore,

3. scanning should be included among the robust metrics of exploration by birds.

Finally, we recognize that eight species is still few, and we encourage researchers to replicate this study design with a wider range of species to further eliminate uncertainty in designing tests of exploration for other species. We also propose future work to measure consistency of performance by conducting repeatability analysis when applying this study design. It should help us to obtain a broadened, comprehensive knowledge of the cross-species applicability of exploration assays.

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