



Invited Review

Spatial personalities: a meta-analysis of consistent individual differences in spatial behavior

Erica F. Stuber,^{a,b,c,e} Ben S. Carlson,^{b,c} and Brett R. Jesmer^{b,c,d}

^aU.S. Geological Survey Utah Cooperative Fish and Wildlife Research Unit, Department of Wildland Resources, 5230 Old Main Hill, Utah State University, Logan, Utah, 84322, USA, ^bCenter for Biodiversity and Global Change, Yale University, 165 Prospect St., New Haven, CT 06520, USA,

^cDepartment of Ecology and Evolutionary Biology, Yale University, 165 Prospect St., New Haven, CT 06520, USA, and ^dDepartment of Fish and Wildlife Conservation, Virginia Tech, 310 West Campus Drive, Blacksburg, VA 24061, USA

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Individual variation in behavior, particularly consistent among-individual differences (i.e., personality), has important ecological and evolutionary implications for population and community dynamics, trait divergence, and patterns of speciation. Nevertheless, individual variation in spatial behaviors, such as home range behavior, movement characteristics, or habitat use has yet to be incorporated into the concepts or methodologies of ecology and evolutionary biology. To evaluate evidence for the existence of consistent among-individual differences in spatial behavior – which we refer to as “spatial personality” – we performed a meta-analysis of 200 repeatability estimates of home range size, movement metrics, and habitat use. We found that the existence of spatial personality is a general phenomenon, with consistently high repeatability (r) across classes of spatial behavior ($r = 0.67$ – 0.82), taxa ($r = 0.31$ – 0.79), and time between repeated measurements ($r = 0.54$ – 0.74). These results suggest: 1) repeatable spatial behavior may either be a cause or consequence of the environment experienced and lead to spatial personalities that may limit the ability of individuals to behaviorally adapt to changing landscapes; 2) interactions between spatial phenotypes and environmental conditions could result in differential reproduction, survival, and dispersal, suggesting that among-individual variation may facilitate population-level adaptation; 3) spatial patterns of species' distributions and spatial population dynamics may be better understood by shifting from a mean field analytical approach towards methods that account for spatial personalities and their associated fitness and ecological dynamics.

Key words: GPS tracking, habitat use, home range, intraspecific variation, movement ecology, repeatability.

INTRODUCTION

Spatial behaviors such as home range behavior, movement characteristics, and habitat use influence fitness by mediating environmental, intra- and inter-specific interactions (Fontaine and Martin 2006; Morales et al. 2010; Sommer and Schmitz 2020). Consequently, spatial behaviors influence population and community dynamics (Tilman 1994; Hanski 1998; Letcher et al. 1998; Clobert et al. 2009; Milles et al. 2020). Concurrently, traits that vary within and among individuals, such as morphology, physiology, cognition, competitive ability, and reproductive potential influence the expression of spatial behavior (Robinson et al. 1996;

Austin et al. 2004; Campioni et al. 2013; Schirmer et al. 2020). Although ecologists have historically held the view that behavioral variation represents noise around an adaptive population mean, studies investigating consistent individual differences are overturning this perception (Bennett 1987; Wilson 1998; Williams 2008; Wolf and McNamara 2012; Moiron et al. 2020). The degree to which individuals vary in the spatial behaviors that shape fitness (Gauzere et al. 2020), and the composition of behavioral phenotypes represented within and among populations (Kot et al. 1996; Morales et al. 2010) will, in part, determine the ability of species to adapt to environmental change. Thus, understanding the scope and role of intraspecific variation in spatial behaviors will advance our ability to conserve species and their habitats in the face of unprecedented environmental change.

Address correspondence to Erica F. Stuber. E-mail: efstuber@gmail.com.

Animal personality is defined as consistent among-individual differences in behavior across ecological contexts or time (Dall et al. 2004; Caspi et al. 2005; Réale et al. 2007). Animal personality research focuses on describing and understanding intraspecific variation in labile traits and has highlighted the ubiquity of consistent among-individual differences across a suite of behaviors and taxa (Gosling 2001; Sih et al. 2004; Pennisi 2016). Stemming from its foundations in psychology, the majority of animal personality studies focus on five personality dimensions: exploration, boldness, activity, aggression, and sociality, which have been linked to variation in reproduction and survival (e.g., Moiron et al. 2020). Originally, Allport and Odbert (1936) outlined approximately 4500 words relating to personal behavior, from which Cattell et al. (1943) statistically reduced to 16 traits, and Fiske (1949) further reduced to the five factor model of personality in psychology. Although behavioral ecologists studying animal personality began by quantifying traits qualitatively similar to those accepted in human psychology, ecologists have since adopted a broader definition of personality, wherein any behavior that consistently differs among individuals can be termed personality (Roche et al. 2016). We adopt this broader definition and investigate whether spatial behaviors are a form of personality.

Spatial ecology has largely ignored intraspecific variation in favor of mean-field approaches (Morales et al. 2010), although intraspecific variation is broadly acknowledged throughout behavioral ecology, evolutionary biology, and the social sciences. Mean-field approaches have likely been favored because it is currently unknown whether individuals consistently differ in their spatial behaviors, or whether population-mean values of spatial behaviors represent individual-specific optima. Recent developments in the area of resource selection analysis, however, have demonstrated that individual differences in resource selection behavior exist (Leclerc et al. 2016; Bastille-Rousseau and Wittemyer 2019), and can lead to biased estimates of environmental relationships (Muff et al. 2020). For example, individual differences in the direction, magnitude, and variance of selection coefficients (Gillies et al. 2006; Hebblewhite and Merrill 2008) may cause population averages to be inaccurate descriptions of population-level resource use (*sensu* Tinker et al. 2008; Bastille-Rousseau and Wittemyer 2019). Concerns related to individual variation confounding population-level inference are relevant to many areas of spatial ecology, such as metapopulation theory. The existence of spatial personality may lead to metapopulations or populations that are spatially structured by behavioral type, which has eco-evolutionary consequences (Wolf and Weissing 2012). Consequently, interactions between spatial personality and the environment can affect metapopulation dynamics and persistence (Cote et al. 2010; Sih et al. 2012). For example, in spatially structured populations, where sub-populations systematically differ in the spatial behaviors exhibited by individuals, there is potential for habitat loss or the development of ecological traps to lead to selective loss of behavioral phenotypes, and reduced genetic diversity (e.g., Wilson 1998; Clobert et al. 2009; Robertson and Chalfoun 2016). Concurrently, such consistent individual differences in habitat use may increase population niche width, thereby reducing intraspecific competition and increasing habitat overlap with other species (Bolnick et al. 2011; Jesmer et al. 2020). If spatial personality in movement (e.g., mobility, dispersal), habitat use, or home range behavior is a common phenomenon, taking a mean-field approach toward spatial behavior may hinder our ability to accurately estimate population and community dynamics

and implement successful conservation strategies (McDougall et al. 2006; Smith and Blumstein 2013; Merrick and Koprowski 2017).

Personality in movement, habitat use, and the size and location of home ranges may be interrelated (i.e., part of a behavioral syndrome) and shaped by factors including the environment, genetic makeup, and social context. Further, while mobile species may have access to an array of environmental conditions in heterogeneous landscapes, decisions regarding how to move and use space may be influenced by competitive interactions, territoriality, site fidelity, and environmental preferences, which may be personality traits themselves, as well as other intrinsic factors including morphology and physiology (Wolf and Weissing 2010). For example, site fidelity—a widespread ecological phenomenon wherein individuals occupy the same home range or seasonal range year after year or season after season (Switzer 1993; Morrison et al. 2021)—may lead to apparent consistent habitat selection over time. Alternatively, particular environmental preferences may lead to site fidelity when preferred environmental conditions are located and returned to. In either case, site fidelity or environmental preferences may lead to among-individual differences in movement behaviors, such as levels of tortuosity or sinuosity (i.e., first passage time; Fauchald and Tveraa 2003), which may be shaped by the conditions associated with each particular site. Nevertheless, and despite site fidelity, several authors have demonstrated that home range size, movement behaviors, and habitat selection indeed vary among individuals in a population even after controlling for among-individual variation in habitat availability (Leclerc et al. 2016; Hertel et al. 2019; Bastille-Rousseau and Wittemyer 2019). Because spatial behaviors play a role in shaping individual fitness and population dynamics, such intraspecific variation in spatial phenotype presents a novel lens through which ecologists and evolutionary biologists can gain insight into how populations respond to environmental change.

Identifying the existence of spatial personalities would open up new avenues for investigating population-level response to environmental change. In accordance with natural selection, species should evolve specific spatial behaviors in response to biotic and abiotic pressures (Fahrig 2007). If spatial personalities are genetically or culturally inherited like other personality traits (Dochtermann et al. 2015; Jesmer et al. 2018; Whitehead et al. 2019), the existence of spatial personalities may provide the raw material for natural selection to act upon and may therefore represent a source of rapid behavioral adaptation. In contrast, inheritance of spatial personality may conserve behavior across generations and decouple behavior from local environmental conditions, thereby limiting a population's ability to adapt to environmental change (Keith and Bull 2017). Thus, spatial personalities may shape several underlying ecological processes that facilitate or hinder the ability of populations to adapt to environmental change and represent a potentially valuable avenue for future research.

Advances in animal tracking technologies and statistical methods over the past two decades have resulted in a marked increase in tools for studying animal behavior and have spurred a dramatic increase in knowledge regarding the spatial behavior of individuals (Kays et al. 2015). The growing number of estimates regarding the degree to which among-individual variation in spatial behavior is consistent over time or context (i.e., repeatability; Nakagawa and Schielzeth 2010) provides an opportunity to evaluate whether there is widespread evidence for the existence of spatial personality. Such an evaluation provides a first step in determining whether mean field approaches in ecological studies require reevaluation and

whether studying individual variation in space use may be useful for advancing understanding of the adaptive capacity of wildlife in the Anthropocene. We performed a meta-analysis of repeatability in spatial behaviors, accounting for confounding factors proposed from previous personality studies, and evaluated whether spatial behaviors constitute a dimension of animal personality. We then discuss how considering spatial personality, rather than assuming all individuals act as exchangeable units (i.e., the mean field assumption), might impact our understanding of population and community ecology.

METHODS

Meta-analysis dataset assembly: behavioral repeatability estimates and potential confounding variables

Whether a trait is considered personality is commonly assessed using intra-class correlation coefficients (ICC), or repeatability estimates (Nakagawa and Schielzeth 2010). To compile ICC and repeatability estimates, we conducted a literature review via Web of Science using search terms related to personality and spatial phenotypes (see Supplementary Text S1 for search terms). We gathered all matching indexed English-language articles published between January 2001 (coinciding with Gosling’s (2001) seminal animal personality publication) and April 2019.

We used the following criteria to filter the initial data set, first screening by title, keywords, and abstract, and subsequently screening full content: 1) the studies collected repeated measures of individual-level spatial traits (e.g., repeated measurements related to estimates of individuals’ home range, habitat use, and movement metrics; not measured in a group setting; see below for expanded descriptions), 2) studies were limited to those considering non-domesticated vertebrates, and 3) studies presented estimates of repeatability or its components (i.e., variance components from mixed-effects models from which repeatability can be derived). We identified a total of 1194 publications between 2001 and 2019 (Supplementary Figure S1), of which 41 publications met our filtering criteria, yielding 200 estimates of repeatability of behaviors related to home range, habitat use, and movement (Supplementary Figure S2; see Table 1 for sample sizes in each behavior category and summaries across confounding variables). Most of the initial 1,095 excluded studies were either human trials, or presented repeatability estimates in the context of mechanical quality assurance. Most records rejected during full text review did not meet either our data requirements (i.e., did not provide estimates of repeatability, including many home range studies), or our requirement

that behavior be measured in a non-social context (e.g., we did not accept repeatability estimates of position within a school of fish under control and predation risk contexts). See “Categorizing measured phenotypes as home range-, habitat use, or movement-related” section below for examples of the types of studies that met our filtering criteria.

Previous work has identified potential methodological and ecological covariates that may influence estimates of repeatability. To ensure that inference regarding the presence of spatial personality was not confounded by covariates, we also extracted information from the 41 published studies that met our filtering criteria regarding study taxa, location of data collection (laboratory vs free-living conditions), duration of time elapsed between replicate measurements of behavior (timescale), sample size of number of individuals analyzed, sample size of number of replicate measurements collected per individual, age of individuals assayed (e.g., juvenile, adult), and whether repeated measurements of behaviors were collected specifically during different ecological contexts (e.g., nest building vs. incubation periods) or over time.

Variables related to study design (i.e., sample size, and number of replicates, data collection location, context, and time between replicates) influence the ability to accurately estimate repeatability (e.g., Dingemanse and Dochtermann 2013). Repeatability may be biased if repeated measurements are taken too close together in time (i.e., longer amounts of time between observations results in greater independence among measurements). The extent of this bias depends on the temporal autocorrelation of the environment relative to the resampling timescale and is important if the focal behavior is influenced directly by the environmental gradient. While we could not investigate the potential for environmental sampling bias in published estimates of repeatability, we attempted to account for potential bias by including time between repeated measurements as a covariate (see Discussion for further detail).

Both animal age (i.e., adult, juvenile, mixed, not reported) and taxa (i.e., amphibian, avian, fish, mammal, reptile) may either be confounding variables or drivers of variation in repeatability estimates. Repeatability has been hypothesized to systematically vary with age through multiple mechanisms including experience, age-dependent directional or stabilizing selection, age-dependent gene expression and physiology, developmental plasticity, senescence, and behavioral canalization with predictions and evidence supporting relationships in both directions (Bell et al. 2009; Brommer and Glass 2015; Araya-Ajoy and Dingemanse 2017; Kok et al. 2019). Although there is likely also sampling bias associated with taxa of study (Bell et al. 2009), repeatability of phenotype may also vary across taxa because of taxa-specific variation in characteristics

Table 1

Summary of the data from within the three behavioral classes included in our analyses. Repeatability estimates were extracted based on literature review, targeting estimated repeatability of behaviors falling within three broad behavior categories: home range, habitat use, and movement. $N_{studies}$ represents the number of publications, $N_{effect\ sizes}$ represents the number of repeatability estimates of spatial behaviors reported, $N_{species}$ represents the number of unique study species, $N_{individuals}$ represents the median number of individuals sampled, and $k_{repeats}$ represents the median number of repeated measures per individual. Interquartile range (IQR) represents the range between the 75th and 25th quartiles. Because the actual time interval between repeated measurements was inconsistently reported in publications, we generalized the time between repeated measures into categories: not reported, hours, days, weeks, months, years, and variable; we present the mode of the assumed interval

Behavior category	$N_{studies}$	$N_{effect\ sizes}$	$N_{species}$	$N_{individuals}$ median (IQR)	$k_{repeats}$ (IQR)	Interval mode (range)
Home range	5	15	5	11 (16)	3.8 (8.8)	Year (day–ear)
Movement	25	86	25	20 (15)	6.2 (7.7)	Day (hour–year)
Use characteristics	26	99	27	26 (22.5)	2.7 (4.65)	Year (day–year)

such as sensitivity to environmental conditions (e.g., ectotherms versus endotherms), variation in flexibility of the nervous system (e.g., invertebrates versus vertebrates) or hypothalamic-pituitary-adrenal axis, cognitive ability, strength of selection on traits, and pace of life syndrome (Cauchoix et al. 2018; Royaute et al. 2018; Schoenemann and Bonier 2018; Dochtermann et al. 2019).

Categorizing measured phenotypes as home range-, habitat use-, or movement-related

While our literature search examined manuscripts for published repeatability measurements from behaviors related to individuals' space use, and movement patterns, these types of behaviors can be quantified in many ways. For example, "movement" is not a singular concept, that can be fully quantified by a single, standardized measurement. Average step length, speed, and direction are all ways of describing aspects of movement patterns more generally, and studies presenting estimates of repeatability of movement behavior may quantify some or all of these phenotypes. In addition to investigating mean repeatability across all repeatability estimates of spatial behaviors extracted from our literature review, we further categorized repeatability estimates of diverse behavioral traits into three broad categories (i.e., home range, habitat use, or movement) based on the basic geospatial element (i.e., points, vectors, polygons) underlying the published data.

We classified repeatability estimates of behaviors based on point data describing individuals' spatial location, or environmental attributes associated with individuals' location into the "habitat use" category. Studies presenting repeatability estimates falling in this category could relate to repeatability in nest site selection, for example. Repeatability estimates of behaviors that were based on underlying vector data (e.g., movement paths between sequential locations), where step length, direction, or travel speed, for example, were classified as movement-related behaviors, and generally came from studies collecting GPS-based location and time information. Finally, repeatability estimates related to behaviors quantified based on polygon-type data were classified into the home range category. Studies presenting estimates of home range repeatability typically collected GPS-type location information from individuals over time, and summarized the area of space use (i.e., using kernel-density estimation, or minimum convex polygons) during multiple ecologically or biologically relevant sampling frames (e.g., repeatability of winter home range size, repeatability of night-time home range). These broad behavioral groups represent the majority of spatial phenotypes published in animal spatial ecology. Of the 200 published estimates of behavioral repeatability identified from our literature search, we classified 15 as home range, 99 as habitat use characteristics, and 86 as movement. Variation in traits within these three categories has previously been demonstrated to be linked with vital rates, inter-specific interactions, and population and community-level processes (Milles et al. 2020; Sommer and Schmitz 2020; Webber et al. 2020). Both the original behavior as extracted from the literature, and each behavior re-classified into our three broad categories (i.e., home range, habitat use, movement) are presented with the data (see Stuber et al. 2021).

Studies falling within our habitat use characteristics category broadly reflected repeatability of site use for breeding, foraging, and migration stopover. These studies investigated the elevation, habitat type, or latitude and longitude coordinates of locations used by individuals based on resource selection functions of use versus non-use sites or environmental gradient-based analyses. The habitat use

characteristics category also contained studies investigating the repeatability of residence time in foraging patches, timing of migration events, and number of stops used during migration.

Many studies meeting the filtering criteria of our literature search quantified repeatability of a wide variety of movement metrics that we generalized into a single, broad category entitled movement characteristics. For example, published repeatability of distance traveled, number of movements made, mean velocity, activity, mean straightness and bearing of step segments, exercise performance, and frequency of switching between active and inactive states, were all considered to represent movement-related traits.

Home range size is defined as the amount of area needed by an individual to gather resources so that it may survive and reproduce (Burt 1943). The size of the area encompassed by the utilization distribution during a given observation period (e.g., months or years) has been traditionally used to estimate home range size (Noonan et al. 2019). As the studies included in our meta-analysis exclusively presented estimates of the repeatability of home range size within a designated time period (i.e., we found no estimates of the repeatability of home range shape), we hereafter refer to home range characteristics as home range size. Studies included in our meta-analysis derived repeated measures of home range size from individuals' 50% or 95% utilization distributions (i.e., spatiotemporal distributions of locations visited by an individual during periods of range residency) during multiple sampling seasons (e.g., quantified home range size of sampled individuals during the breeding seasons for each of 3 subsequent years). The majority of studies (3 out of 4) quantified individuals' home range size using kernel-based estimators, while a single study used bridge-based methods.

Repeatability and standardization

For studies where variance components were reported, we calculated repeatability as the intra-class correlation coefficient (ICC) by dividing the among-individual variance by the total variance following (Nakagawa and Schielzeth 2010). Repeatability estimates presented in figures rather than text were extracted using Web Plot Digitizer (<https://automeris.io/WebPlotDigitizer/>). For meta-analysis, we calculated standardized effect sizes and sampling variances of repeatability (r and ICC) using Fisher's Z -transformation (McGraw and Wong 1996). The Z -transformation is commonly used in meta-analysis because repeatability estimates, for example derived from correlation-based analysis or mixed-effects models, have different possible ranges and are often not normally distributed (Nakagawa and Schielzeth 2010). Back transformations are presented for interpretation on the original scale (ICC; Fisher 1992).

Meta-analysis and meta-regressions

We conducted multi-level meta-analyses using standardized repeatability effect size (Fisher's Z -transformed) as the response variable. Meta-analysis was performed in R (version 4.0.5; R Core Team 2019) using the package metafor (Viechtbauer 2010; function rma.mv). We ran three different types of models. First, we ran a standard meta-analytic model (intercept-only model) to estimate the grand mean effect size of repeatability. Next, we repeated the intercept-only model but subset the data by generalized behavior class (i.e., one model each for home range size, movement metrics, and habitat use characteristics). Finally, we estimated meta-regressions using the full dataset with added covariates (i.e., taxa, behavior class, sample size, average replicates per individual, and life stage). Continuous

covariates were mean-centered. All models included a random effect for study ID, to account for published studies that reported separate repeatability estimates for multiple spatial behaviors, and extracted effect size ID nested within study ID. Because there were 42 species, from 37 taxonomic families, and 23 taxonomic orders, we included a random effect of taxonomic order to account for potential shared effects of taxonomic relatedness (i.e., there were very few repeated measures at the species and family levels independent of the “study ID” random effect). The variance associated with taxonomic order in the full meta-regression was estimated as 0.00. Because estimating the random effect of order substantially reduces the degrees of freedom associated with estimating taxa effects (i.e., with the $dfs = \text{“contain”}$ correction), we subsequently removed it from the model to better estimate the intercepts of each taxa.

We calculated coefficients' confidence intervals based on the t -distribution, and the degrees of freedom were corrected based on the random effects structure by specifying the $dfs = \text{“contain”}$ argument. To quantify the variation across estimates within studies, we calculated meta-analysis heterogeneity (I^2) as among-study variance divided by total variance (Higgins and Thompson 2002; Nakagawa and Santos 2012). We visually inspected funnel plots to assess the potential for publication bias (Nakagawa and Santos 2012).

RESULTS

Meta-analysis data

Of our literature review, only 41 studies met our filtering criteria for inclusion in the meta-analysis. Sample sizes were quite skewed within categorical covariates investigated here, as well as within the three broad behavior categories. For example, the majority of repeatability estimates were calculated from bird species (54%), and

based on free-living (91%), adult (58.5%) individuals (Table 2). Most repeatability estimates were for behaviors categorized as describing habitat use characteristics (49.5%), and movement patterns (43%), while estimates of home range size repeatability represented only 7.5% of extracted effect sizes with no representation of amphibians or reptiles. Although home range size is relatively well-studied in spatial ecology, and repeated measurements of individuals' home range are not uncommon, our literature review highlighted that studies including repeated measures of home range size rarely calculated repeatability, or presented estimates of variance components. This observation highlights the need for a broader uptake of the presentation of variance component estimates as a standard “best practice” of mixed-effects models. In addition to increasing the potential sample size for this or similar meta-analyses of repeatability estimates, standard presentation of all variance component estimates from mixed-effects models would allow a more complete investigation of variance structures beyond repeatability among studies of different populations or species which sample size did not allow for here (Dochtermann and Royauté 2019; Royauté and Dochtermann 2021). The majority of avian studies quantified repeatability in behaviors related to habitat use characteristics (58% of effects), while the majority of studies of fish quantified repeatability in behaviors related to movement patterns (52%).

Repeatability of spatial behavior

While individual repeatability estimates from single studies were often associated with relatively high uncertainty (Supplementary Figure S3), our meta-analysis of all 200 repeatability estimates highlighted high mean repeatability across all studies, with much smaller uncertainty around the mean (back-transformed overall ICC mean: 0.67; 95% CI: 0.55, 0.76; Figure 1). Furthermore, repeatability was consistently high across each spatial behavior class,

Table 2

Meta-regression estimates of relationships between confounding variables and repeatability estimates (Fisher's Z-transformed (Z_r)) of three classes of spatial behaviors, and for each taxa. We present coefficient estimates and their associated 95% confidence intervals. Taxa represent intercept estimates, and all other coefficients represent differences from the intercept reference categories. Reference categories for the intercepts are home range size (N_{studies} : 5; N_{effects} : 15; N_{species} : 5), adult individuals (N_{studies} : 23; N_{effects} : 117; N_{species} : 24), measured on a daily timescale (N_{studies} : 13; N_{effects} : 58; N_{species} : 14), in free-living conditions (N_{studies} : 36; N_{effects} : 182; N_{species} : 36), where replicate measures were taken in multiple ecological or environmental contexts rather than over time alone (N_{studies} : 6; N_{effects} : 23; N_{species} : 6). Timescale refers to the amount of time elapsed between replicate measurements. Sample sizes related to the number of studies, repeatability effect sizes extracted, and species represented are given for categorical variables

	β	CI lower	CI upper	N_{studies}	N_{effects}	N_{species}
Amphibian	1.57	0.06	3.08	2	10	2
Avian	1.35	0.78	1.92	17	108	17
Fish	1.58	0.80	2.36	11	50	11
Mammal	1.56	0.83	2.29	4	14	4
Reptile	1.60	0.84	2.35	7	18	7
Juvenile	-0.56	-1.52	0.41	4	16	4
Mixed ages	0.03	-0.47	0.53	5	18	5
Age not reported	0.49	0.21	0.76	9	49	9
Data collection in lab	-0.43	-1.20	0.34	4	16	4
Data collection mixed	-0.10	-1.48	1.29	1	2	1
Hours timescale	-0.07	-0.71	0.57	1	1	1
Months timescale	-0.64	-1.14	-0.15	6	16	6
Weeks timescale	-0.20	-0.70	0.31	7	27	7
Years timescale	-0.23	-0.61	0.15	14	88	14
Variable timescale	-0.50	-1.04	0.03	3	8	3
Sample size	-0.002	-0.005	-0.0002	—	—	—
Mean replicates per individual	0.005	0.0002	0.01	—	—	—
Temporal measurement context	-0.60	-1.08	-0.12	36	177	36
Movement	0.11	-0.11	0.32	24	86	25
Use characteristics	0.15	-0.04	0.35	24	99	27

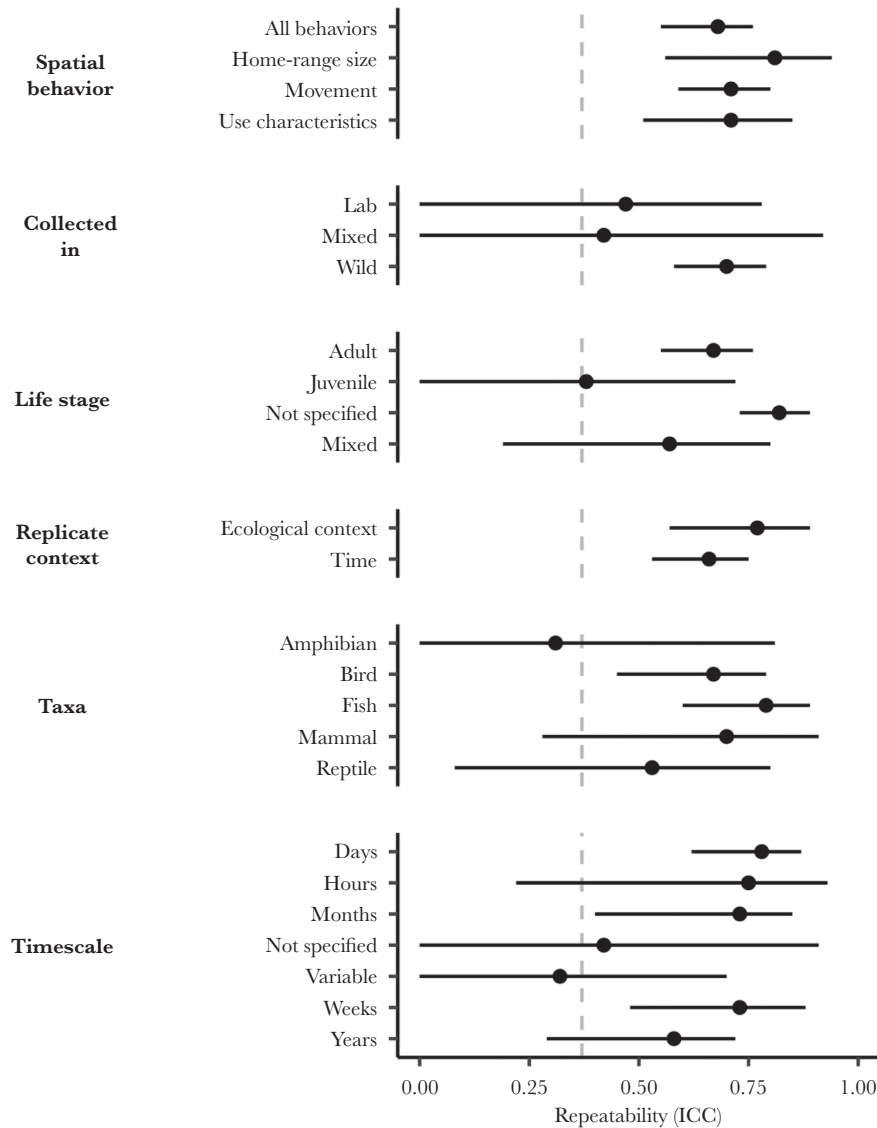


Figure 1

Meta-regression mean estimates of repeatability of spatial behaviors in different subgroups of analysis based on random effects models. All estimates were back-transformed from Fisher's Z-transformation (Z_r) into intra-class correlation coefficients (ICCs). We present point estimates with their associated 95% confidence intervals. The top section shows the grand mean meta-analytic estimate of repeatability across all spatial behaviors, and generalized behavior classes (i.e., home range size, movement characteristics and habitat use characteristics) without accounting for covariates. All other sections depict mean repeatability estimates for categorical variables which were based on models including the focal variable alone (e.g., we ran a model including only taxa as a covariate to generate the mean repeatability estimates for amphibians, birds, fish, mammals, and reptiles). The reference line (dashed, vertical) is shown at 0.37, the previously estimated meta-analytic mean across a broad suite of behaviors (i.e., not only spatial behaviors; from Bell et al. 2009). Sample sizes (number of studies, effect sizes extracted, and species) associated with categorical estimates are presented in Table 2.

with home range size displaying the highest average repeatability (ICC mean [95% CI], home range size: 0.82 [0.56, 0.94], movement characteristics: 0.71 [0.59, 0.80], use characteristics: 0.72 [0.51, 0.85]; Figure 1). We detected high total heterogeneities for all models indicating strong among-study variation in repeatability estimates (I^2 overall: 93%; use characteristics: 97%; movement: 89%; home range: 79%).

Effects of confounding variables on estimates of repeatability

In our analysis, seven covariates explained 43% of the variation in estimated repeatability across all studies (Table 2). Sample size

(number of individuals tested) was negatively related to repeatability across all three behavior classes. Conversely, repeatability increased with increasing mean number of replicate measurements per individual (Table 2). On average, repeatability was highest when measured in the wild, and when repeated measurements were taken across separate environmental or ecological contexts, rather than over time. Compared with replicates measured after hours to months had elapsed, repeatability estimates were on average lower when the time between replications was across years. The majority of repeated measures were re-collected on a yearly or monthly resampling basis (52% of estimates), although 29% were collected with a daily resampling timescale (59% of which were movement

behaviors). Estimates of repeatability were higher in adults compared with juveniles, and highest in fish and lowest in amphibians. Mean repeatability estimates within categorical variables are presented in Figure 1.

Publication bias

We constructed funnel plots based on standard errors and observed effect sizes to examine the potential for publication bias in repeatability estimates (see Supplementary Figure S4; Sterne and Egger 2001; Marks-Anglin and Chen 2020; Marks-Anglin et al. 2021). Possible publication bias may exist in studies of use characteristics with small sample size, where observed estimates skew positive. This is consistent with the “file drawer problem” (e.g., publication bias against small effects or negative results; Csada et al. 1996), although small sample size studies make up the minority of studies included here (50th quantile (i.e., median) sample size: 26; 10th quantile: 6; 5th quantile: 4). Estimates from movement characteristic and use characteristic studies with relatively large sample size skewed smaller than average, while studies of use characteristics with moderate sample size skewed higher than average.

DISCUSSION

Our meta-analysis indicates that the phenomenon of spatial personalities (i.e., consistent among-individual differences in spatial behavior) can be found across vertebrate taxa. We found high repeatability in three general classes of spatial behavior, which encompass most spatial behaviors measured in animal spatial ecology: home-ranging behavior, movement, and habitat use. Although some variation in repeatability estimates could be explained by factors including taxa, sample size, and number of and time elapsed between replicate observations, repeatability remained high after accounting for these factors. Compared to the average repeatability of a broad suite of behaviors ($r = 0.37$; Bell et al. 2009), the repeatability of spatial behaviors was high ($r = 0.67$) and consistent across subgroups including taxa, time elapsed between repeated measurements, and life stage. While repeatability suggests potential limits to individual plasticity, if spatial personalities are adequately variable and heritable (Dochtermann et al. 2015), selection for spatial phenotypes in heterogeneous landscapes could drive the evolution of spatial personalities and shape the spatial structuring of populations under environmental change.

The existence of consistently high repeatability in spatial behavior calls into question the validity of the mean field assumption (i.e., the expectation that all individuals have similar trait values or that variation is unimportant), an assumption implicit in the many theories and statistical approaches of population and community ecology (Bolnick et al. 2011; Violle et al. 2012). Considering spatial personalities may therefore alter our understanding of population and community processes, ecosystem structure, and function and lead to different conservation and management strategies (Holtmann et al. 2017). For example, if spatial personalities stem from individual variability in perceived predation risk (i.e., landscape of fear; Schmitz et al. 1997; Quinn et al. 2012), behaviorally mediated trophic cascades may only play out for subsets of individuals within populations or only for certain populations across a species' range, a situation not commonly considered in traditional studies of trophic interactions (Sommer and Schmitz 2020). Additionally, resource selection models that account for spatial personalities may predict important differences in patterns of nutrient, propagule, parasite, and pathogen

flows at both small (e.g., habitat patches) and large (e.g., migratory stopover sites and seasonal ranges) scales, compared with models ignoring personality (Bauer and Hoyer 2014; Schmitz et al. 2018; McInturf et al. 2019). Furthermore, among-individual variation in spatial behavior may drive among-individual heterogeneity in pathogen transmission and structure contact transmission at the population level (VanderWaal and Ezenwa 2016; Sah et al. 2018) mediated by individuals' space use and other personality traits (Boyer et al. 2010). The ability of individuals to plastically respond to changes in resource availability is increasingly important to consider as landscapes become more fragmented (Spiegel et al. 2017), which might act as a selective pressure that favors particular spatial personalities, with downstream effects on nutrient, propagule, and pathogen flows.

Evidence for spatial personality also provides support for the Niche Variation Hypothesis (Van Valen 1965; Bolnick et al. 2003; Ravnigne et al. 2009), whereby variation in the niches occupied by individuals can impact population dynamics and stability by influencing intra- and inter-specific interactions (Milles et al. 2020; Schirmer et al. 2020). Consistent individual differences in home range characteristics and the types of environments used by individuals can mediate the degree of intraspecific conflict, mating opportunities, and disease and parasite transmission depending on how habitat is spatially structured (Martin and Martin 2007; McLoughlin et al. 2000; Riordan et al. 2011; Sanchez and Hudgens 2015). Interdisciplinary efforts attempting to tease apart consistent individual differences in space use and interaction networks (Albery et al. 2021a, 2021b) will therefore provide inroads to understanding the independent contributions of niche variation and ecological networks to intra- and inter-specific interaction patterns that generalize across systems (White et al. 2018).

Repeatability is expected to vary across taxa and age due to either biological and ecological mechanisms (e.g., sensitivity to the environment, cognitive ability, experience, developmental plasticity), or structural biases in sampling design (e.g., certain behaviors are only expressed and measured in adults, or certain behaviors are oversampled in specific taxa). Although we did not find evidence supporting systematic differences in repeatability between ectotherms and endotherms, repeatability did vary across taxa (Figure 1) and we found evidence that as age increased (i.e., juvenile vs adult, a potential proxy for experience; Petelle et al. 2013; Reader 2015), repeatability increased (Figure 1, Table 2). As individuals gain more experience in a given environment (e.g., in terms of efficiency of use, predation risk, quality of resources, and competition; Merkle et al. 2014; Jesmer et al. 2018), they are more likely to demonstrate optimal behavioral responses as indicated by reduced within-individual variance, which is one avenue by which high repeatability may arise (Dochtermann and Dingemans 2013). However, our sample was skewed towards fish and avian species, and adults (only 8% of repeatability estimates were based on juvenile individuals). Additionally, we cannot rule out the influence of sampling bias in time between replicate measurements, which systematically varied between birds and fishes and is a confounder of repeatability estimates (birds' majority: years, fishes' majority: days; Figure 1). Further research is needed to resolve equivocal findings from observational studies and meta-analyses, and establish ecological differences in repeatability across taxa and other drivers of variation in repeatability including age.

Consistent between-individual differences in behavior may arise from genetic variation, developmental effects (i.e., epigenetics),

consistent differences in the environments experienced by individuals (i.e., repeatable environmental effects), or biased measurement error (Niemelä and Dingemanse 2017). Although repeatability itself does not indicate the mechanisms by which consistent differences arise, the literature on animal personality typically focusses on intrinsic individual differences (e.g., developmental or genetic differences; Niemelä and Dingemanse 2017). Repeatability in spatial behavior may pose an interesting estimation problem as it may be impacted by the environmental conditions individuals experience. For example, movement paths may be more tortuous for individuals occupying dense shrub habitat, compared to individuals occupying open grassland habitat. Consider if path tortuosity (i.e., the departure of a path from straightness) was measured in two subsequent hours for individual A in dense shrubs, and in two subsequent hours for individual B in open grassland. We may incorrectly conclude high repeatability due to consistent individual differences, but in reality our repeated measures were non-independent and due to biased sampling. Our literature review suggests that approximately half of the studies included here accounted for potential spatial or environmental confounding effects when estimating repeatability. Post hoc analyses of these studies highlight a reduction of 0.09 in mean repeatability when considering studies with and without adjusting for possible confounding variables ($r = 0.74$, $r = 0.65$, respectively). And while our sample size was too small to be conclusive for laboratory-based studies, the estimate of mean repeatability of behaviors when assayed in laboratory conditions (i.e., where environment is controlled by the experimenter) was 0.47. Taken together, these results suggest that while the environment experienced by the individual plays a role in shaping the expression of spatial behavior in the wild, there is scope for differences to arise from intrinsic mechanisms in addition to consistent differences in the environments individuals experience.

As in our path tortuosity example, repeatability estimates may be upwardly biased if environmental conditions themselves influence focal behaviors. Such bias is expected to occur if repeated measures of behavior were collected under very similar environmental conditions that systematically varied among individuals (Wilson 2018). This estimation bias can be avoided by conducting translocation experiments, environment manipulations, or by increasing the time between repeated measures such that individuals have the opportunity to sample other environments (Niemelä and Dingemanse 2017; Hertel et al. 2020). Reassuringly, the majority of studies reviewed in our study were conducted on highly mobile species, with substantial amounts of time between repeated measurements (i.e., months to years between measurements), meaning individuals had the opportunity to use and experience heterogeneous environments. In contrast to environmental sampling bias stemming from insufficient time elapsed between replicate measurements, replicate measurements of territorial or site-faithful individuals may result in consistent among-individual variation in environmental associations (Switzer 1993; Morrison et al. 2021). Nevertheless, territorial behavior and site fidelity are behavioral choices that arise from competitive outcomes, social status, or individual-specific preferences determined by heritable traits (e.g., Davis and Stamps 2004; Liu et al. 2018). Removing such relevant sources of intrinsic between-individual variation, for example by the inclusion of habitat-related fixed effects when habitat preference is a heritable trait, may induce a downward bias in repeatability estimates (Wilson 2018). Disentangling the ecological and biological independence of consistent among-individual differences in movement and home range characteristics from consistent differences in environmental preferences would enable exploration of how

spatial traits might co-evolve through correlated selection (Araya-Ajoy and Dingemanse 2014).

Understanding how behavior mediates the link between environmental conditions and population dynamics is necessary for effective conservation and management (Kareiva and Wennergren 1995; Smith and Blumstein 2013). Similar to how population ecology has benefitted from the development of stage-structured population models for age- and size-structured populations, we believe population and community ecology may benefit from considering spatial personality (e.g., by developing behavior-structured population models). We suggest that investigations into the heritability of spatial personality traits (Stooper et al. 2012) and the potential evolutionary consequences of spatial personality may lead to new insights regarding the interplay between animal behavior and population and community dynamics.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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