Personality and behavioral syndromes in two *Peromyscus* species: presence, lack of state dependence, and lack of association with home range size

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Abstract

One common theme of adaptive hypotheses for the existence of stable individual differences in behavior (personality) or persistent correlations among behaviors (behavioral syndromes) is an association between intrinsic state (e.g., body size, mass, metabolism) and the behavioral traits of interest. Empiricists are tasked with assessing whether there is an association between intrinsic state and behavior, but the statistical methods to appropriately quantify the among-individual correlation between intrinsic state and behavior have only recently become widely known. We conducted a multiyear study in wild mice of two *Peromyscus* species (*Peromyscus leucopus noveboracensis* and *Peromyscus maniculatus gracilis*) to assess the existence of stable individual differences in four different behaviors (presence of animal personality, as assessed by quantifying repeatabilities) and one measure of intrinsic state (body mass), the degree of association between these four behaviors (presence of behavioral syndromes), and the association of these behavioral traits with body mass using multivariate methods that allowed us to estimate the within-individual (residual) component and the among-individual component. We used standardized behavioral tests to measure struggle time (time spent struggling when removed from the trap) and exploration time (time spent exploring a novel surface) and used open-field trials to measure whether or not an individual entered the open field plus the total time it spent active in the open field. In *P. leucopus*, we assessed whether coarse but quick methods of assessing animal personality (struggle or exploration time) correlate with behavior using more in-depth estimates obtained by open-field trials. Additionally, we tested the ecological relevance of our personality measures by assessing their association with home range size in *P. leucopus*. In both species, struggle time, exploration time, and body mass were significantly repeatable and there was a significant among-individual correlation between struggle time and exploration time. However, in both species, there was no evidence for an among-individual correlation between our measure of intrinsic state (body mass) and personality traits. In one species (*P. leucopus*), we found that individuals that spent more time struggling or exploring a novel surface were also more likely to emerge into an open field and spent more time being active in an open field, but these four behavioral measures were not associated with home range size. Our results suggest among-individual correlation among these different behaviors but no among-individual correlation between behavior and intrinsic state.

Significance statement

Over the past 15 years, it has become clear that nonhuman animals exhibit "personalities": some individuals consistently differ in their behavior, and there is limited flexibility in their behavior when they experience environmental change. Biologists have now

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been searching for why and how animal personalities exist and their ecological and evolutionary consequences. Some explanations have focused on how condition or "internal state" may cause variation in animal personalities. In this study, we show that two species of wild mice exhibit personalities and that their personality traits are associated with one another, in that mice that were less docile were also more active, exploratory, and bold. We then show that their personality traits were not linked with body mass, suggesting a lack of association between internal state and personality. Our results provide important insights into the causes of personality in nonhuman animals.

Keywords Animal personality, · Behavioral syndromes, · MCMCglmm, · Mice, · Pace-of-life

Introduction

The presence of individual differences in behavior and associations among behaviors in nonhuman animals has long been noted by behaviorists (reviewed by Wilson 1998; Gosling 2001). However, only relatively recently has it been widely recognized that these individual differences in behavior in nonhuman animals may be quite stable within individuals across contexts (i.e., personality in nonhuman animals exists: Réale et al. 2000; Gosling 2001) and that the association between different behaviors may be more inflexible than is traditionally thought (i.e., "behavioral syndromes" exist: Sih et al. 2004a). The presence of personality and behavioral syndromes in nonhuman animals may have important ecological and evolutionary implications (Sih et al. 2004a, 2012; Dingemanse and Réale 2005; Réale et al. 2007, 2010; Biro and Stamps 2008; Wolf and Weissing 2012). For example, different types of personality traits such as boldness, exploration, or general activity may be associated with survival and reproduction (Réale et al. 2003; Dingemanse et al. 2004; Boon et al. 2007; Niemelä et al. 2015; Lapiedra et al. 2018; Santicchia et al. 2018) or with other traits (dispersal, habitat and resource selection, seed dispersal, presence of disease/parasites, etc.) that could influence ecological processes (Wilson et al. 1993; Sol et al. 2002; Dingemanse et al. 2003; Dochtermann and Jenkins 2007; Duckworth and Badyaev 2007; Cote et al. 2010; Holtmann et al. 2017; Brehm et al. 2019; Feldman et al. 2019; Harris et al. 2020).

One of the challenges for both theoreticians and empiricists is to identify why animal personality and behavioral syndromes exist. Current explanations often adopt either an adaptive explanation or a constraints viewpoint. For example, the observation that some individuals consistently take more risks (or are bolder in the presence of risk) than others may reflect an adaptive response to low residual reproductive value (Wolf et al. 2007). Alternatively, consistent individual differences in behavior or persistent correlations among behaviors could reflect some pleiotropic mechanism (or developmental experience) that simultaneously influences multiple behaviors or that lessens the flexibility of a specific behavior across contexts (Koolhaas et al. 1999; Sih et al. 2004b; Duckworth 2010). For example, artificial selection on metabolism can produce a correlated response in suites of behavior, suggesting a shared mechanism constraining phenotypic variation (Maiti et al. 2019).

Adaptive explanations for the evolution of both stable individual differences in behavior and strong correlations among behavioral traits usually focus on either the state dependency of behavior or among-individual variation in intrinsic state as causing the emergence of animal personality traits or behavioral syndromes (Dingemanse and Wolf 2010; Houston 2010; Luttbeg and Sih 2010; Wolf and Weissing 2010; Sih et al. 2015). This is, of course, aligned with the long history of understanding the state dependency of behavior in behavioral ecology (Lima and Dill 1990; Houston and McNamara 1999). However, recent interest is based upon how differences in intrinsic state may cause stable individual differences across a wider diversity of behaviors than are often measured in animal personality research, such as boldness, exploration, activity, or aggression. There are a wide variety of both negative and positive feedback mechanisms that could cause adaptive covariation between intrinsic state and different behaviors (Luttbeg and Sih 2010; Sih et al. 2015), such as a feedback loop where individuals in poor condition are more willing to take risks to obtain resources. Other adaptive explanations focus less on these feedback loops and instead highlight how stable individual differences in behavior may be generated due to the adaptive integration of behavior with other intrinsic characteristics of the individual, such as their physiological, metabolic, and life history traits (Biro and Stamps 2008; Réale et al. 2010). For example, smaller individuals may exhibit both a "faster" pace-of-life and higher levels of risky behavior, boldness, or aggression (Réale et al. 2010).

Together, these different adaptive hypotheses about the evolution of animal personality and behavioral syndromes suggest some type of link between intrinsic state and behavior. This has provided a relatively simple way for empiricists to assess a key prediction/assumption of these models, that intrinsic state and behavior are linked. However, a recent study has highlighted a lack of empirical work appropriately documenting the association between intrinsic state and behavior. In a meta-analysis, Niemelä and Dingemanse (2018) showed that while measures of intrinsic state, such as body size or mass, were weakly positively correlated with different personality traits, they found that among-individual variation

in intrinsic state explained little of the variation in among-individual differences in behavior. In addition, Sih et al. (2015) found that although boldness may allow individuals to accrue more resources and increase their body size, the effect of body size on behavior may differ depending on the mechanism underlying the relationship. The meta-analysis by Niemelä and Dingemanse (2018) also highlighted a related issue when it comes to assessing the among-individual covariance between intrinsic state and personality traits, which is a lack of studies using more recently developed statistical approaches to characterize the association between intrinsic state and behavior. More than 10 years ago, Hadfield et al. (2010) emphasized the statistical limitations of estimating the association between trait values and fitness. Recently, Houslay and Wilson (2017) have amplified this view by describing more modern and appropriate statistical approaches in quantifying the among-individual covariance between behaviors, or between behaviors and measures of intrinsic state or fitness. Niemelä and Dingemanse (2018) highlighted how most studies that endeavor to measure among-individual covariances between behaviors and measures of intrinsic state have done so without directly estimating this relationship. A correlation between behavior and intrinsic state is not well established by the literature, with some studies finding support for such a correlation, others partial support, context-dependent support, no overall association, or correlations in the opposite direction. In light of these concerns, this study aimed to document whether there was an association between four different measures of behavior and a single measure of intrinsic state (body mass). Given that the association between intrinsic state and behavior can go in either direction (Sih et al. 2015), we did not make any strong predictions about the direction of the association between body mass and the behavioral traits we measured.

We conducted a multiyear study in wild mice of two *Peromyscus* species across multiple field sites to assess (1) the existence of stable individual differences in body mass and behavior (presence of animal personality as assessed by quantifying repeatabilities), (2) the degree of association between behaviors (presence of behavioral syndromes), and (3) the association of these behavioral traits with body mass as a measure of intrinsic state. The existence of individual differences in behavior has been well-documented in other muroid species, ranging from early demonstrations that the amount of time it took mice to travel a specific distance was highly repeatable within individuals (Dawson 1932) to a more sophisticated characterization of stable individual differences in the behavior of laboratory mice (Forkosh et al. 2019). We studied two different *Peromyscus* species (*P. leucopus noveboracensis* and *P. maniculatus gracilis*, hereafter *P. leucopus* and *P. maniculatus*) because they are a model system across many disciplines in biological research (Bedford and Hoekstra 2015); they are both common

throughout parts of Michigan and can coexist in the same forest stands (Myers et al. 2005, 2009); and they were part of a separate study examining ecological range expansion in *P. leucopus* (Baumgartner and Hoffman 2019; Moscarella et al. 2019). Previous studies in other *Peromyscus* species have also documented the presence of consistent individual differences in behavior (e.g., Careau et al. 2009, 2011; Wey et al. 2017; Brehm and Mortelliti 2018; Kalcounis-Rueppell et al. 2018), although we note that unlike some of the previous studies that used captive-bred individuals, we studied free-living mice exclusively.

We used four different measures of behavior: time spent struggling/moving after being removed from the trap ("struggle time"), time spent exploring a novel surface ("exploration time"), the likelihood that a mouse would emerge from a dark box into an open field ("emergence"), and overall activity inside of an open-field trial ("activity"). We note that we mostly refer to these behaviors as indicated to avoid applying judgments on what these behaviors may mean (Carter et al. 2013), although we also note that other studies may refer to struggle time as "docility," exploration time as "boldness" or "exploratory behavior," emergence into the open field as "boldness," and activity in the open-field trial as "exploratory behavior" or just "activity" (reviewed by Gosling 2001; Réale et al. 2007). For both species, we remeasured the struggle time, exploration time, and body mass every time a uniquely marked individual was captured. Additionally, for *P. leucopus* at one study site, we measured emergence and overall activity in the open field twice for the same individuals. We then used these data to quantify the repeatability of struggle time, exploration time, body mass, emergence, and activity.

The primary aim (as stated above) was to measure the among-individual correlations of behaviors and a measure of intrinsic state (body mass), using multivariate methods that allowed us to partition the within-individual (residual) component and the among-individual component. Secondarily, we wanted to assess some of the assumptions and possible limitations of field studies of animal personality. Due to limited sample sizes and few repeated measures of the same individuals, field studies of behavior may never achieve the sample sizes required to appropriately characterize both the within-individual (or residual) and among-individual association between two behaviors, or between a behavior and a measure of intrinsic state or fitness (Biro and Dingemanse 2009; Dingemanse et al. 2012; Garamszegi and Herczeg 2012; Brommer 2013). Doing so would require having repeated measures of many individuals, which may not be possible in field studies, due to logistical constraints, selective disappearance of individuals, and other factors preventing recapture. One possible solution is to increase sampling depth in terms of numbers of individuals, at the expense of doing more time-consuming behavioral assays. In our study, we assessed the among-individual association between measures of personality that

took ~60 s to collect from each individual (struggle time and exploration time), as well as those that took much longer (~30 min) to collect per individual (emergence and activity). If these two are correlated, the coarser but quicker measures of behavior (i.e., struggle time and exploration time) may enable researchers to increase the number of individuals measured while still accurately representing their behavior.

The final aim of this study was to assess the ecological relevance of our four measures of behavior. Docility, exploration, and activity are all commonly measured by placing animals into an artificial environment, which may or may not reflect their actual behavior in their natural environment. For example, some studies find that behavior measured in artificial conditions does not correspond to behavior measured in a familiar environment (Beckmann and Biro 2013), whereas other studies find that individuals behave similarly in captivity or while free-living (Herborn et al. 2010). Many researchers have called for better validation of measures of animal personality (Réale et al. 2007; Carter et al. 2013) or better selection of the behavioral traits that are measured (Dall and Griffith 2014), although this is often challenging to do in free-living animals. Consequently, at one of our study sites (at which only *P. leucopus* was present), we examined the ecological relevance of our four measures of behavior by assessing their among-individual association with a measure of home range size. We expected that those individuals who had higher struggle and exploration times, were more likely to emerge into the open field, and/or were more active in the open field would have larger home range sizes. We made this prediction based upon observations in other taxa, where individuals that were more active or exploratory in a novel environment also had higher natal dispersal distances (Fraser et al. 2001; Dingemanse et al. 2003; Cooper et al. 2017), were trapped in a greater number of different locations (Boon et al. 2008), or had larger home range sizes (Villegas-Ríos et al. 2018).

Methods

Study sites

We studied the behavior of two *Peromyscus* species (*P. leucopus* and *P. maniculatus)* from 2016 to 2019 in four different study areas in the Upper Peninsula of Michigan (located in Menominee, Delta, Schoolcraft, and Chippewa Counties) and four study areas in the Lower Peninsula of Michigan (two areas in Cheboygan and Washtenaw Counties, one area in both Livingston and Otsego Counties). Study areas were located at least 10 km apart and were estimated to be large enough to encompass the dispersal movements (< 175 m from birth site; Stickel 1968) of most juveniles born to female residents of that site, although dispersal may be highly variable across years.

Trapping and data collection procedures

Mice were live-trapped using Sherman traps (H.B. Sherman Co., Tallahassee, Florida) baited with oats. Traps were set at dusk (~2000–2200 h EST) and checked at dawn (~600–730 h EST). Sites in Cheboygan (but not at the University of Michigan Biological Station, see below), Delta, Otsego, and Schoolcraft Counties were each trapped for two consecutive nights in May, July, and September in 2016–2019, with traps spaced approximately 20 m apart in an 8 × 25 grid. Sites in Chippewa County were trapped in August (two consecutive nights) and October (two consecutive nights) in 2016 and in June (five consecutive nights) and July (three consecutive nights) in 2017. Sites in Menominee County were trapped once in October 2016 (two consecutive nights). Sites in Washtenaw County were trapped in May (one night in 2016, two consecutive nights in 2017), September (two consecutive nights in 2016, one night in 2017), and October (two nights in 2016, one night in 2017) in 2016 and in 2017, whereas one site in Livingston County was only trapped in October 2016 (one night). In Chippewa, Menominee, Washtenaw, and Livingston Counties, we set two to three traps at each spot on the study area for a total of 176–200 traps per night. The number of traps set per site was somewhat variable because of variation in personnel available to set traps, as well as the presence of broken traps.

At one of our field sites at the University of Michigan Biological Station (UMBS) in Cheboygan County, we conducted regular trapping of mice (only *P. leucopus* is present here) from June to August in 2016 and 2017 on a study area that covered ~250,000 m^2. At this site, we placed uniquely labeled grid stakes every 20 m so that we could trap at the same location each time we trapped on the grid and also so we could estimate home range size (see below). We trapped these areas every 1–2 days in 2016 and 2017 (median number of days elapsing between trapping = 2 days). The median number of traps set in 2016 ($n = 50$ traps) was much lower than the number in 2017 ($n = 194$ traps) because the abundance of mice in 2016 was so high that it outstripped the ability of personnel to handle all the mice. The number of traps set per night was also somewhat variable in 2016 (range = 44 to 98 traps) and 2017 (range = 54 to 390 traps). This was again largely due to differences in the availability of field personnel, where more traps were set when we had more people. We aimed to set two traps at each grid stake whenever we were trapping, but on occasion a trap at the stake was broken and was not set. Despite these differences in the number of traps set per night at UMBS, we do not think that this would impact our ability to estimate behavioral traits, and below we discuss the implications for home range size estimates.

At all trapping sites, mice were brought to a central location for processing but returned to the location where they were trapped after handling and processing were completed. At first

capture, each mouse was marked uniquely with two num- bered metal ear tags (National Band and Tag Co., Newport, KY, USA) so that recaptured individuals could be identified. Only two recaptured mice lost both ear tags between captures, indicating that any lack of recaptures was not due to tag loss, and these two mice were omitted from the study. Each mouse was removed from the trap and placed into a 1-gallon plastic bag to record struggle time and then removed from the bag to record exploration time (struggle and exploration time described below). Following these procedures, we determined the sex (based upon anogenital distance), reproductive condition, body mass (by weighing with a Pesola spring scale), length of the right ear (using a hand ruler), and approximate age. Reproductive condition was determined in males by whether the testes were abdominal or scrotal and in fe- males by whether nipples were small (probably not preg- nant or lactating) or enlarged (probably pregnant or lactat- ing). Males with scrotal testes and females with enlarged nipples were coded as reproductively active. Age was classified as either adult, subadult, or juvenile based on pelage characteristics. Adults have reddish-brown hair on their dorsal surface, juveniles are completely gray, and subadults have areas of both gray and brown hair. We note that although age classes based on pelage and body mass covaried, excluding subadults and juveniles from our analysis did not alter our results (shown below).

We had a total of 1060 captures of 716 individuals of *P. leucopus* and 531 captures of 512 individuals of *P. maniculatus* (Table S1). There are differences in the amount of suitable habitat surrounding the trapping sites, which affects the overall number of mice in an area and thus the recapture rate. Most of the recaptures were at the one LP site (UMBS) where *P. leucopus* was the only mouse species present and where we conducted a continuous study involving more regular trapping so that we could estimate home range size.

In some of our study areas, both *P. leucopus* and *P. maniculatus* were present, but there is no evidence for hy- bridization between these two species where they co-occur in Michigan (Baumgartner and Hoffman 2019). In the field, the most reliable way to distinguish these two species is using ear length (as measured from the base of the pinna to the outer edge), with *P. leucopus* having shorter ears than *P. maniculatus* (Stephens et al. 2014). We also collected ear tissue from each mouse for later genetic analysis and saliva samples from some individuals for an additional check on species identification (Baumgartner and Hoffman 2019). Of the 656 mice whose species identity was confirmed using salivary amylase (*n* = 339 mice) or genotyping (*n* = 317 mice), 90.8% were classified correctly in the field (i.e., species iden- tity in the field matched the species identity using salivary amylase or genotyping).

Behavioral assays

We recorded the behavior of mice using four different behav- ioral assays: (1) struggle time in a novel location (clean han- dling bag) after the mouse was first removed from the trap; (2) exploration time on a novel surface (the leg of the handler); (3) emergence from a dark box into an open-field trial box; and (4) overall activity in an open-field trial. The struggle time and novel surface activity assays were conducted every time a mouse was captured. The emergence and activity measures were collected during open-field trials, which were conducted immediately after the struggle and exploration time assays. Repeated open-field trials were conducted 2–4 weeks apart. Although it is possible that the amount of time spent in the traps was variable among individuals and that this could in- fluence their behavior, a recent study in *P. maniculatus* found that there was little impact of the duration of time in the trap on subsequent behavioral measures (Brehm et al. 2020). Moreover, while it is possible that associations between per- sonality traits and trappability biased our estimate of the true variation in the population (e.g., Boon et al. 2008; Carter et al. 2012), there is some evidence that trappability does not bias estimates of personality traits (e.g., Michelangeli et al. 2016; Jolly et al. 2019).

The first two assays (struggle time and exploration time) were conducted immediately after the individual was removed from its trap. Struggle time was recorded with two stop- watches as the total time out of 30 seconds that the mouse spent moving inside the handling bag. After completion of the struggle test, the mouse was removed from the bag by gently grasping its tail and allowing it to move freely on the knee/leg of the handler (or in a minority of instances, the arm). The time spent moving around the knee/leg out of a total of 30 seconds was recorded. We considered struggle time to reflect docility (*sensu* Réale et al. 2000; Martin and Réale 2008), whereas time spent exploring a novel surface reflected both exploratory and boldness behavior.

Following all the handling procedures described above, a subset of mice was placed into a dark chamber (solid black box) connected to an open-field trial box (61 × 61 × 61 cm with four "false holes" that were painted black). Each mouse was placed into the dark chamber for 3 min to allow habitua- tion to the box. Next, a door was opened so the mouse could voluntarily enter the open-field box or stay inside of the dark chamber. We recorded whether or not the mouse entered the open field over the next 3 min (recorded as a binary variable: entered or not entered). Some mice did not enter the open field voluntarily, but our dark chamber box allowed us to gently close the dark chamber and push the mouse into the open field at the end of 3 min. Next, we conducted the open-field trial by recording the behavior of the mice for the next 5 min with an overhead video camera mounted on a tripod. At the conclu- sion of the trial, the mouse was placed back into a live trap and

returned to the original site of capture. The number of fecal pellets in the open field was recorded at the conclusion of the trial, after which the whole testing chamber was cleaned with isopropyl alcohol. With mice we captured more than once, we aimed to perform open-field trials a second time only if two weeks had elapsed since their previous trial, in order to prevent habituation to the open-field trial box (Réale et al. 2007). In reality, a median of 19 days elapsed between two open-field trials on the same mice, except one mouse that mistakenly had two open-field trials performed with only 3 days separating them (range 3–41 days between open-field trials on the same mouse).

Behavioral data from the open-field trial (emergence and activity) were extracted from the videos using JWatcher Video 1.0 (Blumstein and Daniel 2007). An ethogram (Table S2) was used to classify behavior of the mice in the open field, focusing on their general activity patterns (moving, climbing, interacting with the blind holes, being still, etc.). Two different observers extracted the video data independently, and both were blind to the location where the trials were conducted or to any other attributes of the individuals (e.g., species, body mass, sex, reproductive condition).

Estimating home range size

At one of our sites (UMBS), we conducted regular trapping of *P. leucopus* on a study area that covered ~250,000 m^2 with grid stakes every 20 m, so that each trapping location could be spatially referenced to estimate home range sizes. We were only able to collect adequate data in one of the 2 years (2016, not 2017) when we studied mice at this site. In this year of data collection (2016), two traps were set at each grid stake and we set 44–98 traps per night on 24 different nights over a 46-day period (from June 24, 2016, to August 9, 2016), totaling 29,160 trap nights. We note that the median number of traps set per night was 50 traps but the first night we trapped we set 98 traps and a few other nights there were broken traps, causing the number of traps set to be less than 50 on occasion. Home range size was estimated using spatial coordinates from the trapping locations of collected individuals using minimum convex polygons in adehabitatHR v0.4.18 (Calenge 2006). We only estimated home range sizes for individuals that had at least 5 different trapping events/locations (median = 6 trapping events, range = 5–11). The requirement of at least five captures per individual meant we only had adequate data to calculate home range sizes for 26 *P. leucopus*. We note that home range sizes estimated using minimum convex polygons may better approximate maximum home range sizes and, like any method, has its limitations (Nilsen et al. 2008). However, we found the same qualitative results when data were analyzed using the number of unique trapping locations to estimate home range size, as other studies have done (Boon et al. 2008; Boyer et al. 2010).

Statistical analyses

A total of 1060 tests on 716 different individuals of *P. leucopus* and a total of 531 tests on 512 different individuals of *P. maniculatus* were conducted over a 4-year period (2016–2019) to measure struggle time and exploration time (descriptive data shown in Table S1). Of the total dataset for struggle time and exploration time in *P. leucopus*, 162 individuals were measured more than once (504 total tests conducted on 162 individuals). In addition, we collected data on the latency to enter an open field and activity inside an open field ($n = 195$ trials) from 151 adults of *P. leucopus* (112 F, 83 M) in 1 year (2016) from three different locations. Finally, using trapping data from one of our research sites in 1 year (2016) for only adults of *P. leucopus* (14 F, 12 M), we collected data on home range size.

We used Bayesian multivariate linear mixed-effects models (LMM) to estimate the repeatability of struggle time, exploration time, and body mass, as well as the among-individual correlation between struggle time and exploration time, struggle time and body mass, and exploration time and body mass. These models contained fixed effect terms for sex (female or male), age (adult, subadult, juvenile), date of sampling, reproductive condition (active or inactive), an interaction between sex and reproductive condition, and trial number (fit only at the level of struggle time and exploration time, not body mass), as well as a random intercept for mouse identity. We did not include a random intercept for year, site of collection, or observer because our sampling effort across years and sites was unequal, due to variable capture success. Also, preliminary univariate LMMs that we conducted using the same fixed and random effects for each response variable as for the multivariate LMMs showed that they explained relatively little of the variation in the response variables (year: 3.5–4.1%; site: 7.6–8.8%; observer 1.0–2.3%), and the multivariate LMMs showed evidence of poor mixing if they were included.

We conducted the multivariate LMMs for each species separately. One multivariate LMM for each species contained all the data we collected for individuals whose struggle and exploration time were recorded from one to twelve times. Below, we present adjusted repeatabilities, as variance due to the fixed effects was not included in the total phenotypic variance, so we note that the estimates may be upwardly biased (Wilson et al. 2010). Our multivariate LMMs were conducted using MCMCglmm (version 2.29, Hadfield 2010) in R (version 3.6.2, R Core Team 2019), assuming a Gaussian error structure using 4,000,000 iterations with a burnin of 200,000, and a sampling interval of 100. We used a prior that was only weakly uninformative for variances and weighted such that 80% of the variance was at the residual level and 20% at the among-individual level (as suggested by Brommer 2017). Our estimates for adjusted repeatability of struggle time, exploration time, and body mass were similar for results obtained

using univariate LMMs fit using restricted maximum likelihood (in lme4, version 1.1-23, Bates et al. 2015; 95% CI estimated using rptR: Stoffel et al. 2017) that contained the same fixed and random effects as our bivariate LMMs (Table 3), suggesting that our prior choice had little impact on our results. We also received similar qualitative results when we used parameter expanded priors (as suggested by Houslay and Wilson 2017), but trace plots from these models indicated that they did not mix/converge as well. Mixing of chains and convergence was confirmed visually using trace plots and all effective sample sizes were adequate (shown in Tables S4 and S5). There was no evidence of autocorrelation (all < 0.01), and we ran each model three times with this same prior structure and confirmed that the Gelman-Rubin statistic was ~1.

Unfortunately, we did not have adequate sample sizes to conduct a multivariate LMM to compare among-individual correlations for struggle time/exploration time/body mass with emergence or with their activity in the open field. Instead, we conducted a generalized linear mixed-effect model (GLMM) for whether or not individuals of *P. leucopus* emerged into the open field (modeled as a binary response variable) and one univariate LMM with activity in the open field as the response variable. We used a principal component analysis (using a correlation matrix) to reduce 11 variables (in ade4: version 1.7-13, Dray and Dufour 2007) to a single composite variable (principal component 1 or PC1) where high values corresponded to individuals that spent more time moving around within the open field (Table S3). To identify the within-individual and among-individual association between struggle time, exploration time, or body mass, as well as latency to enter the open field and activity in the open field (PC1), we performed a within-individual centering approach (van de Pol and Wright 2009). To do so, in each of these models, we included a fixed effect for the average value of struggle time, exploration time, or body mass to estimate the among-individual association and a fixed effect for the value of these variables, minus the average value for that specific individual to estimate the within-individual association. We also included fixed effects for trial number (some mice had > 1 open-field trial), date of the trial, sex, reproductive condition, and an interaction between sex and reproductive condition. A random intercept term for individual identity was also included, given that some individuals underwent more than one trial. We emphasize caution in the outcome of these models as this type of analysis makes assumptions that may be easily violated in studies such as ours with relatively small sample sizes, such as assuming that our fixed effects are estimated without error.

A GLMM was used for emergence with binomial errors because the data were better approximated with a binary distribution (entered the open field or did not enter) than a Gaussian distribution. As this is a binary response variable, a dispersion parameter was not estimated. Adjusted repeatabilities and their 95% CI for emergence and activity were estimated using REML in rptR (Stoffel et al. 2017) in models that contained the same fixed and random effect structure. Variance inflation factors (VIFs: Zuur et al. 2010) were all < 2.8 in these models, although these higher values were only for the interaction term between sex and reproductive condition, whereas VIFs for fixed effects not included in interactions were < 1.5, suggesting collinearity was not an issue in these models. We note that the model for estimating adjusted repeatability of emergence using rptR had convergence issues and caution should be taken when interpreting the adjusted repeatability and residual variance reported in Table 2.

We only had one estimate of home range size for adult *P. leucopus* from one site (UMBS) in 1 year (2016). We conducted one univariate general linear model to assess whether any of the behavioral variables (struggle time, exploration time, emergence, and activity) or body mass was associated with home range size. Individual mice who underwent more than one open-field trial had multiple observations in this dataset for the behavioral predictor variables but had the same home range size for each observation (i.e., there was variance within-individuals in the predictor variables but zero variance in the response variable). To identify the within-individual and among-individual association between home range size and struggle time, exploration time, emergence, activity in the open field, and body mass, we performed a within-individual centering approach (van de Pol and Wright 2009). To do so, we included a fixed effect for the average value of struggle time, exploration time, or body mass to estimate the among-individual association and a fixed effect for the value of these variables, minus the average value for that individual, to estimate the within-individual association. We also included fixed effects for sex and the total number of captures (mean-centered and scaled to 1 SD). The latter controlled for the fact that we had a different number of captures for these individual mice to estimate home range size. VIFs were all < 2, suggesting that collinearity among fixed effects was not an issue in this model. We did not include a random intercept term for individual identity because the models would not converge, likely because we only had repeated observations on a few individual mice.

We report all unstandardized variance components (Tables 3 and S5), as well as the means and SE of each trait (Tables S3, 1, and 3). We also estimated the mean standardized individual variation (I_I) for struggle time, exploration time, and body mass by dividing the among-individual variance by the mean value for the trait (Dochtermann and Royauté 2019). We did not do so for emergence as it was non-normally (binary) distributed (De Villemereuil et al. 2016), and we did not do so for PC1 (activity in the open field) as it did not have an objective value of 0, given that it was a composite variable.

All statistical analyses were conducted in R (version 3.6.2, R Core Team 2019). We verified the normality of residuals in all of the univariate LMMs described above. Prior to conducting the analyses, we mean-centered and scaled all continuous variables (body mass, Julian date of sampling) to 1 SD and we mean-centered categorical variables (sex, age, reproductive condition, trial number). Response variables in all models were mean-centered and scaled to 1 SD. Mean and 1 SE are shown below. Statistical significance for fixed effects in Bayesian multivariate LMMs was identified using 95% credible intervals (CRIs), whereas P values were used for the univariate LMMs or GLMM where density degrees of freedom were estimated using Satterthwaite approximation in lmerTest (version 3.1-0: Kuznetsova et al. 2017). Data for results presented in Tables 1, 3, S1, S4, and S5 (Dantzer 2020a) and Tables 2 and S3 (Dantzer 2020b) are located on FigShare.

Results

Causes of variation in struggle time, exploration time, body mass, emergence, and activity

On average, *P. leucopus* ($n = 1060$ tests on 716 individuals) spent 4.40 ± 0.23 (mean ± SE) seconds (s) struggling when first removed from a live-trap and 9.56 ± 0.31 s exploring a novel surface, whereas *P. maniculatus* ($n = 531$ tests on 512 individuals) spent 14.64 ± 0.48 s struggling and 18.90 ± 0.40 s exploring a novel surface. Individuals from both species exhibited progressively less struggle time as the number of tests that they were subjected to increased (Fig. 1a–c, Table S4). However, only in our analyses using all data collected from *P. leucopus* did we see a negative relationship between the amount of time individuals spent exploring a novel surface and the number of trials (Fig 1d–f, Table S4). Date of

collection, sex, reproductive activity, or the interaction between sex and reproductive activity were not significantly associated with struggle time or exploration time (Table S4). Subadults and adults were heavier than juveniles, and reproductively active individuals, especially females, were heavier than inactive individuals. In addition, females of *P. leucopus*, but not *P. maniculatus*, were slightly but significantly heavier than males on average (Table S4).

For *P. leucopus* adults ($n = 195$ trials on 151 individuals), there was no significant impact of collection date, sex, reproductive activity, or the interaction between sex and reproductive activity on emergence or overall activity (Table 2). There was no impact of trial number on the likelihood that individuals would emerge into the open field, but they were significantly less active in their second or third open-field trials (Table 2).

Repeatability of struggle time, exploration time, body mass, emergence, and activity

Using the data collected from all *P. leucopus*, whether they were measured only once or multiple times (median = 1 trial, range = 1–12 trials), struggle time (adjusted repeatability = 0.37 [95% CI: 0.31–0.44], Fig. 1a) and exploration time (adjusted repeatability = 0.38 [95% CI: 0.32–0.44], Fig. 1c) were both significantly repeatable (Table 1a). In our separate analyses for *P. maniculatus*, we also found significant repeatabilities for both struggle time (adjusted repeatability = 0.34 [95% CI: 0.28–0.40], Fig. 1c) and exploration time (adjusted repeatability = 0.34 [95% CI: 0.27–0.41], Fig. 1f, Table 1c). Body mass was also significantly repeatable in all our analyses (Fig. S2, Table 1).

For adult *P. leucopus* ($n = 195$ trials on 151 individuals, $n = 39$ individuals were sampled more than once), emergence into the open field (recorded as emerged or did not emerge) was not repeatable (adjusted repeatability = 0.078 [95% CI = 0–

Table 1 Adjusted repeatabilities (R) of struggle time, exploration time, and body mass in (a) *P. leucopus* ($n = 1060$ observations from 716 individuals) and (b) *P. maniculatus* ($n = 531$ observations from 512 individuals)

Species	Trait	Adjusted R and 95% CRI	Mean ± SE	Mean Std. individual variation	Adjusted R from REML
(a) P. leucopus	Struggle time	0.37 (0.31–0.44)	4.40 ± 0.23 s	2.32	0.36 (0.27–0.45)
	Exploration time	0.38 (0.32–0.44)	9.56 ± 0.31 s	0.56	0.37 (0.28–0.47)
	Body mass	0.59 (0.53–0.65)	18.75 ± 0.14 g	0.09	0.76 (0.72–0.80)
(b) P. maniculatus	Struggle time	0.34 (0.28–0.40)	14.64 ± 0.48 s	0.29	0.36 (0.14, 0.76)
	Exploration time	0.34 (0.27–0.41)	18.90 ± 0.40 s	0.15	0.52 (0.34–0.83)
	Body mass	0.36 (0.27–0.45)	17.64 ± 0.17 g	0.06	0.82 (0.77–0.94)

Estimates of adjusted R and their 95% credible intervals (CRI) are shown from Bayesian multivariate linear mixed-effects models (LMM) and we also present adjusted R estimated from univariate LMMs (fit using restricted maximum likelihood: REML) for each response variable only for comparison. Mean standardized individual variation was calculated by dividing the among-individual variance (shown in Table S5) over the mean^2 multiplied by 100

Table 2 Associations between behavioral traits (struggle time and exploration time) and body mass with (a) the likelihood that the individual emerged into an open field and (b) their activity in an open field (PC1) in adults of *P. leucopus* (*n* = 195 trials from 151 individuals)

Response variable	Fixed effects	Estimate	SE	z		P
(a) Emergence	Intercept	0.01	0.37	0.02		0.98
	Trial #	−0.07	0.19	−0.39		0.70
	Date	−0.26	0.46	−0.56		0.58
	Sex (F)	0.38	0.59	0.65		0.52
	Reproductive condition (active)	0.38	0.59	0.65		0.52
	Struggle time (within)	−0.01	0.07	−0.21		0.83
	Struggle time (between)	**0.06**	**0.03**	**2.08**		**0.04**
	Exploration time (within)	0.09	0.07	1.38		0.17
	Exploration time (between)	−0.007	0.02	−0.32		0.74
	Body mass (within)	−0.06	0.3	−0.21		0.83
	Body mass (between)	−0.02	0.05	−0.35		0.72
	Sex (F) × reprod. condition (active)	−0.06	0.8	−0.07		0.94
	Variance components					
	Among-individuals	0.72				
	Residual	4				
	Adjusted repeatability	0.15 (0−0.26)				

Response variable	Fixed effects	Estimate	*SE*	*t*	*df*	*P*
(b) Activity	Fixed effects	Estimate	*SE*	*t*	*df*	*P*
	Intercept	−0.08	0.15	−0.50	167.2	0.62
	Trial #	**−0.32**	**0.14**	**−2.17**	**106.1**	**0.03**
	Date	−0.021	0.08	−0.26	178.9	0.79
	Sex (F)	0.024	0.19	0.13	157.7	0.90
	Reproductive condition (active)	0.35	0.24	1.47	179.4	0.14
	Struggle time (within)	0.015	0.02	0.59	42.3	0.56
	Struggle time (between)	**0.021**	**0.01**	**2.05**	**141.3**	**0.04**
	Exploration time (within)	0.026	0.02	1.07	41.15	0.29
	Exploration time (between)	0.0001	0.01	0.01	135.6	0.99
	Body mass (within)	−0.06	0.11	−0.55	42.8	0.59
	Body mass (between)	−0.006	0.02	−0.28	150.6	0.78
	Sex (F) × reprod. condition (active)	−0.45	0.33	−1.38	181.9	0.17
	Variance components					
	Among-individuals	0.30				
	Residual	0.68				
	Adjusted repeatability					
	Among-individuals	0.31 (0.17–0.66)				

Response variable	Fixed effects	Estimate	*SE*	*t*	*df*	*P*
(c) Home range size	Fixed effects	Estimate	*SE*	*t*	*df*	*P*
	Intercept	0.11	0.12	0.89	30	0.38
	Total # of captures	**0.62**	**0.06**	**10.13**	**30**	**< 0.0001**
	Sex (F)	−0.19	0.17	−1.11	30	0.27
	Struggle time (within)	0.00	0.03	< 0.0001	30	1.00
	Struggle time (between)	−0.01	0.02	−0.46	30	0.65
	Exploration time (within)	0.00	0.02	< 0.0001	30	1.00
	Exploration time (between)	−0.01	0.01	−0.67	30	0.51
	Body mass (within)	0.00	0.12	< 0.0001	30	1.00
	Body mass (between)	0.002	0.02	0.09	30	0.93
	Emergence (within)	0.00	0.37	< 0.0001	30	1.00
	Emergence (between)	0.05	0.20	0.28	30	0.78
	Activity (within)	0.00	0.17	< 0.0001	30	1.00
	Activity (between)	−0.03	0.11	−0.26	30	0.80

Shows the association of home range size with struggle time, exploration time, body mass, emergence, and activity in adults of *P. leucopus* (*n* = 43 observations from 26 individuals). Both within-individual (value of trait minus their average) and between-individual (mean value of trait for that individual) are shown (*sensu* van de Pol and Wright 2009). Variance components and adjusted repeatabilities are also provided for emergence and activity as individuals were tested more than once whereas only one measure of home range size was available per individual. For emergence, the residual variance component was estimated as the distribution-specific variance plus the link-scale residual variance. Estimates for adjusted repeatability and variance should be viewed with caution given that this model had convergence issues. Reference values for sex and reproductive condition were male and inactive, respectively. Bolded lines/numbers correspond to statistically significant effects

Fig. 1 In both *P. leucopus* (a) and
P. maniculatus (b), the amount of
time individuals spent struggling
(a, b) when they were first re-
moved from a trap (maximum of
30 s) and the amount of time they
spent exploring a novel surface
(maximum of 30 s; c, d) was sig-
nificantly repeatable. Different
lines correspond to different indi-
vidual mice; some mice consis-
tently struggled or explored more
than others as the number of times
they were caught and handled in-
creased ("trial number").
Adjusted repeatabilities (R) with
95% credible intervals (CRI) from
Bayesian multivariate LMM are
shown. The amount of time mice
spent struggling or exploring also
declined with trial number, as
reflected by the dashed black line
(shading around line shows 95%
CI). Full results are shown in
Table 1
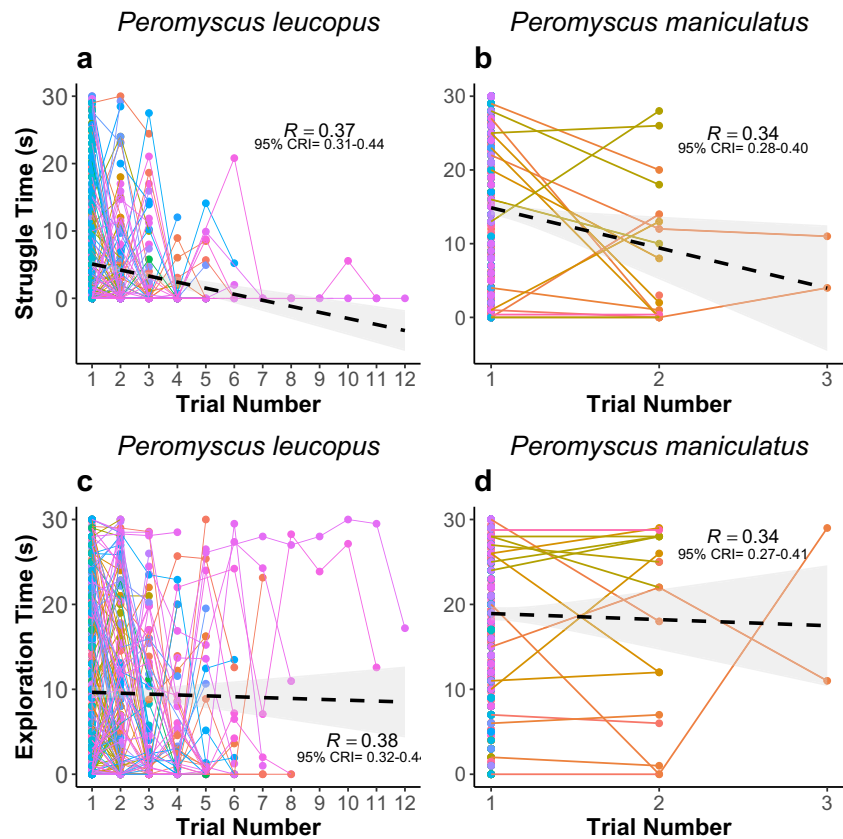
0.26], Table 3) but the overall activity level of mice in the
open field was significantly repeatable (adjusted repeatability
= 0.31 [95% CI = 0.17–0.66], Table 2).

Comparing the mean standardized individual variation
(I_I) indicated that there was greater among-individual
variation relative to the mean in struggle time compared
to exploration time in both species (Table 1) and greater
among-individual variation relative to the mean in both
struggle time and exploration time compared with body
mass in both species (Table 1). The amount of individ-
ual variation in these behaviors was higher in
P. leucopus than in *P. maniculatus*.

Among-individual correlations for struggle time, exploration time, and body mass

In both *P. leucopus* and *P. maniculatus*, raw phenotypic cor-
relations with unpartitioned variance indicated that the amount
of time individuals spent struggling when first removed from
the trap was significantly positively associated with the
amount of time they explored a novel surface (Pearson r for
P. leucopus = 0.30, $P < 0.0001$; $r = 0.42$, $P < 0.0001$ in
P. maniculatus, Fig. 2, Table 3). The multivariate LMMs also
revealed that there was significant positive among-individual
correlation between struggle and exploration time for

P. leucopus (mean = 0.29, 95% CRI = 0.16–0.42) and
P. maniculatus (mean = 0.24, 95% CRI = 0.10–0.39). There
was no evidence in any of our datasets that body mass exhib-
ited significant raw phenotypic association or significant
among-individual correlation with struggle time or explora-
tion time (Table 3).

Among-individual and within-individual correlation for struggle time, exploration time, and body mass with emergence and activity

There was a slight, but significant, positive effect of individual
mean struggle time (the among-individual component) on the
likelihood of emergence and overall activity (Table 2), indi-
cating that individuals who struggled more when they were
first removed from the trap were also more likely to emerge
into the open field and were more active inside the open field
(Fig. 3, note that the raw phenotypic correlation is shown).
There was no within-individual (individual deviation from
their mean) association between struggle time and emer-
gence or activity in the open field (Table 2). There were
also no among-individual or within-individual associa-
tions between exploration time and body mass with
emergence or activity (Table 2).

Table 3 Correlations between behavioral traits (struggle time and exploration time) and correlations between behavioral traits and body mass in (a) *P. leucopus* and (b) *P. maniculatus*

Species	Traits	Raw phenotypic correlation	Among-individual correlation	Residual correlation
(a) P. leucopus	Struggle and exploration time	0.30	0.29 (0.16–0.42)	0.20 (0.13–0.28)
	Struggle time and body mass	−0.024	−0.001 (−0.14–0.14)	0.00 (−0.09–0.09)
	Exploration time and body mass	0.033	0.01 (−0.12–0.14)	0.07 (−0.02–0.15)
(b) P. maniculatus	Struggle and exploration time	0.42	0.24 (0.10–0.39)	0.24 (0.14–0.34)
	Struggle time and body mass	0.02	0.03 (−0.14–0.20)	0.02 (−0.09–0.14)
	Exploration time and body mass	0.14	0.08 (−0.10–0.25)	0.07 (−0.05–0.19)

Raw phenotypic (Pearson) correlations where the variance was not partitioned (among-individual vs. residual) are shown in addition to the among-individual and residual correlations between the traits as estimated from multivariate LMMs. Sample sizes are the same as shown in Table 1

Association between home range size with struggle time, exploration time, body mass, emergence, or activity

Home range sizes of the *P. leucopus* we tested ranged from 0 to 0.28 ha (median = 0.02 ha), with some individuals (*n* = 9 of 26 total individuals) estimated to have a home range size of 0 because they were repeatedly captured at the same location. There was no evidence of a significant within-individual or among-individual association between home range size and any of the behavioral variables (struggle time, exploration time, emergence, and activity) or body mass (Table 2). Mice that were captured more frequently had larger home range sizes (Table 2).

Discussion

Struggle time and exploration time were significantly repeatable in both *Peromyscus* species, and both species showed significant among-individual correlation between struggle time and exploration time. In *P. leucopus*, we found that overall activity in an open field was repeatable, but the likelihood to emerge into an open field was not, and there was a significant among-individual association between struggle time and both emergence and activity. There was no significant among-individual correlation between body mass and any of the behaviors (struggle time, exploration time, emergence, activity), providing little evidence for an association between intrinsic state and these personality traits. Finally, there was no evidence that any of our estimates of personality were associated with home range size in *P. leucopus*.

Our results indicate that there are consistent individual differences in the four different behaviors we measured in *P. leucopus*, where some individual mice tend to struggle or explore a novel surface more than others, regardless of the number of trials an individual completes, or date of capture. Our estimates of adjusted repeatability of struggle time, exploration time, and activity in an open field (0.31–0.44) for both *Peromyscus* species are all near the average repeatabilities that have been previously reported for a diversity of behaviors (Bell et al. 2009). They are also similar to estimates of the repeatability of behaviors in an open-field trial in previous studies in *Peromyscus* species (Brehm and Mortelliti 2018;

Fig. 2 In both *P. leucopus* (a) and *P. maniculatus* (b), the amount of time individuals spent struggling when they were first removed from a trap (maximum of 30 s) was significantly positively associated with the amount of time they spent exploring a novel surface (maximum of 30 s). Raw phenotypic correlations (Pearson correlations: *r*) are shown. Solid blue line (shading around line shows 95% CI) reflects correlation between these two variables whereas full statistical results are shown in Table 3
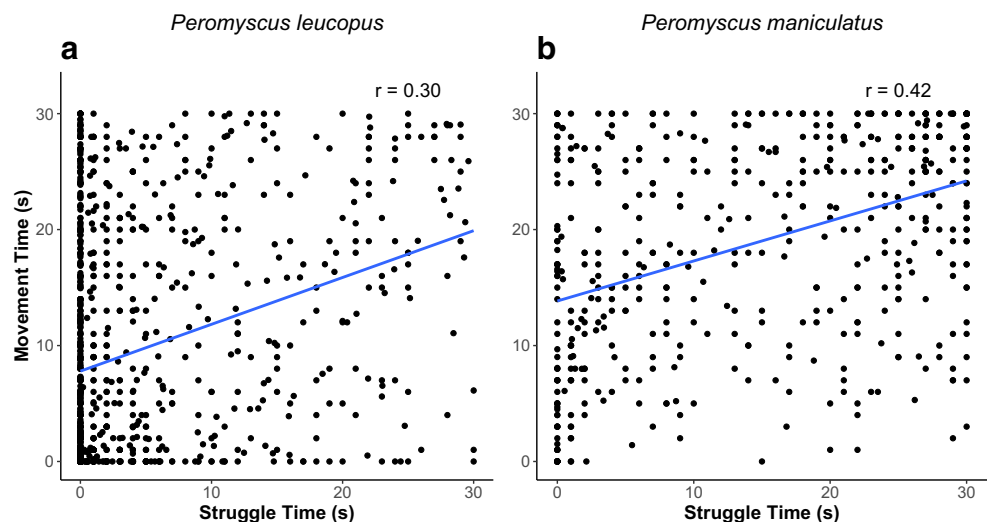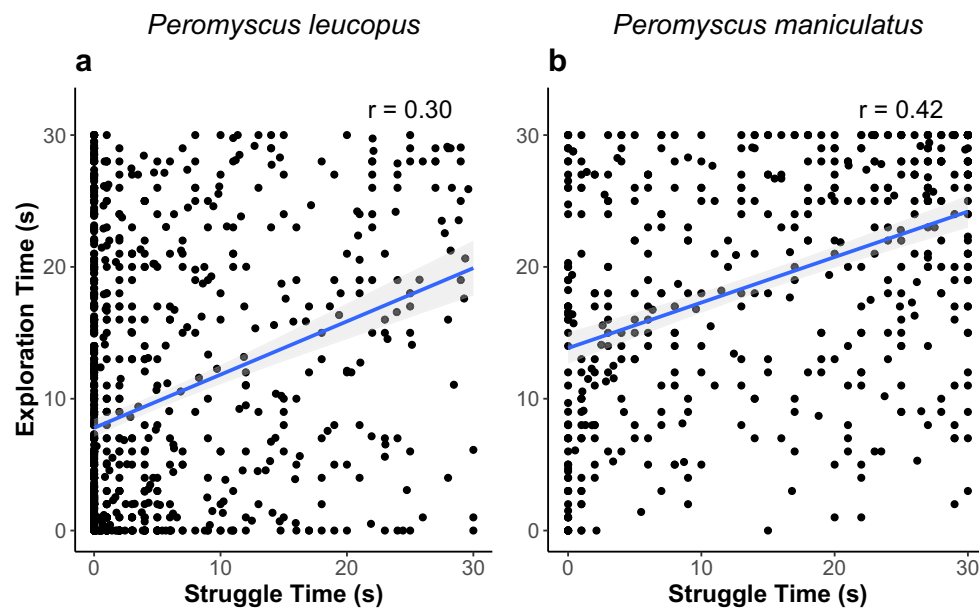
Fig. 3 The amount of time adults of *P. leucopus* spent struggling immediately after they were removed from a trap (maximum of 30 s) was significantly associated with the likelihood that they emerged from a dark box into an open field and (b) their subsequent overall activity level in the open-field trial (PC1). Results are partial residual plots from statistical models shown in Table 2. The among-individual (or between-individual) effect of struggle time (mean value of struggle time for each individual) is shown on x-axes. Solid line reflects correlation between these two variables. No confidence band is shown for these partial residual plots due to them being a generalized or linear mixed-effect model

Brehm et al. 2020). However, as discussed elsewhere (Dochtermann and Royauté 2019), repeatabilities are variance-standardized ratios, and therefore direct comparisons across different studies, behaviors, populations, or species are challenging. This is why we also reported mean standardized individual variation (I_I) for struggle time and exploration time, for which our data showed much greater individual variation in these behaviors in *P. leucopus* than in *P. maniculatus*. We also note that our estimates of repeatabilities in *P. maniculatus* were based on a small number of recaptures of the same individuals ($n = 531$ observations on 512 individuals).

There was some evidence to suggest a syndrome structure among the different behaviors we measured. Specifically, we found significant among-individual correlation between struggle time and exploration time in both species. In *P. leucopus*, we also found significant among-individual association between struggle time and both emergence and overall activity in the open-field trial. Individuals who struggled more also explored a novel surface more, were more likely to enter an open field, and had higher overall levels of activity in the open field. This suggests the presence of a behavioral syndrome connecting these different behavioral measures, although we note that the interpretation of each of these behaviors may be similar. Specifically, struggle time is often equated to "docility," emergence into an open field may approximate "boldness," and activity in an open field corresponds to the overall activity or "boldness" of an individual (Réale et al. 2007), although there are notable issues when it comes to

ascribing these terms to behaviors measured in standardized assays in artificial environments (Carter et al. 2013). In addition, there have been issues with multiple tests presumably targeting the same personality trait that may actually be measuring distinct behaviors (Huang et al. 2018). If we define our behavioral measures in a way consistent with other studies (Réale et al. 2007), our results indicate a behavioral syndrome where less docile mice exhibited greater exploration of a novel surface in both *Peromyscus* species and, in *P. leucopus* only, less docile mice were also more exploratory, bold, and active.

Adaptive explanations for the presence of these stable individual differences in behavior and the among-individual correlation among different behaviors often invoke an explicit association between intrinsic state and behavior (Luttbeg and Sih 2010; Réale et al. 2010; Sih et al. 2015). We found no evidence of among-individual correlation between our measure of intrinsic state (body mass) and any of the behavioral traits we measured (struggle time, exploration time, emergence, and activity). However, it is unclear if body mass is a good proxy of intrinsic state. Other studies using body size as a proxy for intrinsic state also have failed to find an association with behavior (Kluen et al. 2014). In a recent meta-analysis across animal taxa, heavier individuals also tended to be more aggressive, bold, and exploratory (Niemelä and Dingemanse 2018). However, similar to our results, differences in intrinsic state explained little of the variation in these personality traits (Niemelä and Dingemanse 2018). One possible explanation for the latter is that the ecology of the study species may

influence the among-individual correlation between intrinsic state and personality. Relevant factors for a species might include whether they are a capital or income breeder (Jönsson 1997) and where they store resources for maintenance and reproduction (on the body or cached). For example, in species that cache food, such as all *Peromyscus* species (Howard and Evans 1961; Vander Wall et al. 2001), the capital resources that are available for maintenance and reproduction may not be reflected in measures of body mass. In species that cache food, individuals with high energetic reserves may not weigh any more than those with low energetic reserves. This could obscure any general pattern between intrinsic state and animal personality, especially when it is measured using body mass, and suggests that future empirical studies should consider more integrative measures of body condition (such as quantitative magnetic resonance to estimate fat reserves or actual food hoard sizes) or the natural history of the species.

Although interest in measuring individual differences in behavior is high due to their possible ecological and evolutionary implications, empiricists working with free-living animals face several challenges when it comes to measuring behaviors. In-depth assessments of personality traits in free-living animals are often time-consuming, or they can introduce artificiality when they require moving the animals away from their home territory or site of capture for a significant length of time. There are also other statistical concerns, such as the ability of field studies to collect enough behavioral data on the same individuals to partition out the correlation between two behaviors into a within-individual (or residual) variation and among-individual covariation (Dingemanse et al. 2012; Garamszegi and Herczeg 2012; Brommer 2013). There is often an intrinsic trade-off between maximizing the number of individuals whose behavior is measured and maximizing the depth or thoroughness of the behavioral tests done on each individual. We estimated struggle time and time spent exploring a novel surface, which together took ~1 minute per mouse for collection and data entry. For some mice, we also measured the likelihood of emerging into an open field and their activity in an open field, which took ~15 min per individual mouse, plus another ~30–40 min of post-collection processing to accurately extract and archive the behavioral data for each individual. We found that mice who were more likely to enter the open field and who were more active in the open field also struggled more, suggesting that struggle time, but not exploration time, is a proxy for their behavior in an open field. This differs from previous studies that have not found an association between struggle times (or docility) and other more time-consuming behavioral assays (e.g., Martin and Réale 2008) but does suggest that our quick estimates of individual differences in behavior can be used by field biologists to maximize the number of individuals who are measured repeatedly.

In summary, our results indicate that measures of animal personality that can be quickly obtained in field settings, such as docility (struggle time) or exploration (exploration time),

may reliably predict the behavior of an individual in more time-consuming but more thorough assays, such as the open-field trial. One critique of the field of animal personality research is that it relies on highly artificial approaches (such as open-field trials) to quantify animal personality (Carter et al. 2013; Perals et al. 2017). It seems prudent to couple these measures of animal personality with investigations of the behavior of an individual when it is freely moving in its environment, such as is now being done by the use of remote tracking technology (Hertel et al. 2019).

We have found no evidence of an association between our measure of intrinsic state (body mass) and any of the behavioral traits we measured. Also, none of these measures correlate with the home range size of an individual, although sample sizes for this part of the study are small and our estimates of home range size were affected by how often mice were captured. Thus, our measures of personality obtained during capture and handling of the mice show no association with two factors that are presumably ecologically relevant. This lack of association between behavioral traits and ecologically relevant factors in mice mirrors a similar lack of association between activity or exploration of a novel environment and movement patterns in the wild for other vertebrate taxa (Minderman et al. 2010; Laskowski et al. 2015). Continuing challenges for the field of animal personality research will be to better determine the ecological relevance of measures of personality and to balance the trade-offs of conducting behavioral assays in a standardized environment.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethics approval All of our trapping and handling procedures were approved by Animal Care and Use Committees of the University of Michigan (#PRO00009067) and Miami University (#874_2021_Mar).

We acquired permission to carry out these procedures from areas owned or managed by the University of Michigan (Cheboygan and Livingston Counties), the United States National Forest Service (Chippewa and Delta Counties), the United States Fish and Wildlife Service (Schoolcraft County), the State of Michigan (Menominee and Otsego Counties), or private landowners (Washtenaw County). All applicable international, national, and/or institutional guidelines for the use of animals were followed.

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