

Environmental heterogeneity modifies the link between personality and survival in fluctuating small mammal populations

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Abstract

- Despite numerous studies examining the fitness consequences of animal personalities, predictions concerning the relationship between personality and survival are not consistent with empirical observations. Theory predicts that individuals who are risky (i.e. bold, active and aggressive) should have higher rates of mortality; however, empirical evidence shows high levels of variation in behaviour–survival relationships in wild populations.
- We suggest that this mismatch between predictions under theory and empirical observations results from environmental contingencies that drive heterogeneity in selection. This uncertainty may constrain any universal directional relationships between personality traits and survival. Specifically, we hypothesize that spatiotemporal fluctuations in perceived risk that arise from variability in refuge abundance and competitor density alter the relationship between personality traits and survival.
- In a large-scale manipulative experiment, we trapped four small mammal species in five subsequent years across six forest stands treated with different management practices in Maine, United States. Stands all occur within the same experimental forest but contain varying amounts of refuge and small mammal densities fluctuate over time and space. We quantified the effects of habitat structure and competitor density on the relationship between personality traits and survival to assess whether directional relationships differed depending on environmental contingencies.
- In the two most abundant species, deer mice and southern red-backed voles, risky behaviours (i.e. higher aggression and boldness) predicted apparent monthly survival probability. Mice that were more aggressive (less docile) had higher survival. Voles that were bolder (less timid) had higher survival, but in the risky forest stands only. Additionally, traits associated with stress coping and de-arousal increased survival probability in both species at high small mammal density but

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5. Our field experiment provides partial support for our hypothesis: that spatiotemporal fluctuations in refuge abundance and competitor density alter the relationship between personality traits and survival. Our findings also suggest that behaviours associated with stress coping and de-arousal may be subject to density-dependent selection and should be further assessed and incorporated into theory.

KEY WORDS

behavioural types, capture–mark–recapture, competition, forest management, life history

1 | INTRODUCTION

Across taxa, individuals of the same species behave consistently differently from one another. These behavioural differences are referred to as personalities (Dall et al., 2004; Sih et al., 2004) and directly affect how individuals perceive their surroundings, interact with others and respond to risk. Evolutionary hypotheses aimed at explaining how such variation in behavioural phenotypes is maintained in populations are often rooted in life-history theory. Life-history theory concerns the allocation of limited resources to survival, growth and current versus future reproduction to optimize fitness (Stearns, 1989). The allocation of resources to one fitness component typically requires an individual to make a trade-off elsewhere (but see van Noordwijk & de Jong, 1986). The 'pace-of-life syndrome' hypothesis (or POLS) posits that individuals operate under different strategies to resolve these trade-offs in allocation and that behaviours such as activity, aggression or boldness are subject to trade-offs at the individual level (Dammhahn et al., 2018; Réale et al., 2010). Under this hypothesis, more active, risk-prone or aggressive individuals are predicted to experience faster growth rates and higher reproductive output but incur trade-offs such as increased mortality and/or exposure to parasites (Barber & Dingemanse, 2010; Biro & Stamps, 2008; Réale et al., 2010).

Several studies have documented associations between animal personalities and fitness components such as survival and fecundity (reviewed by Moiron et al., 2020; Smith & Blumstein, 2008). However, observed correlations are often not in the direction predicted by theory. Two meta-analyses show equivocal associations between risky behaviours and fitness (Moiron et al., 2020; Smith & Blumstein, 2008). In the more recent paper, Moiron et al. (2020) reviewed empirical studies conducted in both the lab and on wild populations and found no universal directional relationship between risky behaviours and survival or longevity. Instead, in the wild, risky individuals (e.g. bolder, more aggressive or more active individuals) lived longer; in contradiction to predictions under the POLS hypothesis. Explanations for this disparity suggested by Moiron et al. (2020) include potentially imperfect measurements of truly risky behaviours (Carter et al., 2013; Niemelä & Dingemanse, 2014),

possibly biased estimates of survival, discrepancies between the level of variation at which theory has been laid out (the POLS hypothesis predicts covariation at the among-individual level) and at which it is typically being tested (the within-individual level), and differing selection pressures in the lab versus the wild (Dammhahn et al., 2018; Laskowski et al., 2022). Here, we aim to measure two key selective pressures over time and space and assess the potential for these to modify relationships between personality traits and survival in wild small mammal populations.

Heterogeneity in selection pressures is a second major proposed driver of individual behavioural variation (Laskowski et al., 2022) and individual variation more broadly (Endler, 1986). Individuals with different personality traits experience differential fitness under fluctuating selection pressures (reviewed by Dingemanse & Réale, 2013), such as heterogeneity in resource availability, predator density or competition for resources over space and/or time (le Cœur et al., 2015; Nicolaus et al., 2016; Wolf & Weissling, 2010). Since different personality types may be more or less advantageous depending on context, without examining the relationship between survival and personality traits across varying contexts, such as across environments with contrasting habitat structure, resource availability or competitor density, our ability to make predictions concerning the directional relationship between personality traits and fitness components is limited. Empirical studies are necessary to further understand the conditions under which covariation between behavioural traits and life-history traits may emerge.

The overarching goal of our study is to contribute to filling this knowledge gap regarding the factors affecting personality-driven survival in wild populations (Moiron et al., 2020). Specifically, we test the hypothesis that spatial and temporal variability cause misalignment between empirical results and theory. We suggest that spatial heterogeneity in habitat structure and fluctuations in population density are two selective pressures that mediate the relationship between personality traits and survival. Under this hypothesis, we predict that the relationship between personality traits and survival will differ among forests with varying habitat structure. Specifically, we focus on variation in ground cover and coarse woody debris, which may affect perceived predation risk, actual predation risk and the availability of resources

(Dueser & Shugart, 1978; Fauteux et al., 2012; Lima & Dill, 1990; Orrock et al., 2004). Since several mechanisms could generate disparity in selection on personality traits among forest stands with different structure (such as differences in antipredator behaviour, predation, habitat matching or foraging success), we do not make more specific predictions regarding directionality. Additionally, we hypothesize that variability in conspecific/competitor density will generate variation in the effect of personality traits on survival. It is possible that bolder, more aggressive individuals have a competitive advantage, which could increase survival during periods of high density (i.e. elevated competition for resources and refuge), but see Wright et al. (2019) for alternate predictions. In great tits (*Parus major*), intensity of competition has been shown to generate contrasting selection pressures for traits such as aggression, neophilia and exploration (Dingemanse et al., 2004), with aggressive, neophilic and more exploratory individuals having the advantage when competition is high. Additionally, bold, aggressive individuals are shown to take more risks while foraging and are likely more competitive at obtaining resources, utilizing novel resources or acquiring high-quality territories (Both et al., 2005; Dammhahn & Almeling, 2012). Boldness, therefore, may increase survival rates at high population densities through improved resource acquisition. We emphasize that this prediction assumes that the major driver of selection is starvation and not predation as higher risks taken by bold individuals would also imply a higher risk of predation. Last, we may expect that individuals who show better stress-coping capabilities (increased grooming in the open-field test) have higher survival at high small mammal densities (Fernández-Teruel & Estanislau, 2016) as it has been shown previously that less stress-sensitive individuals experience higher survival during periods of high intraspecific competition (Vanden Broecke et al., 2021).

To test our hypothesis, we conducted a large-scale manipulative experiment, wherein we trapped deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Myodes gapperi*), northern short-tailed shrews (*Blarina brevicauda*) and North American red squirrels (*Tamiasciurus hudsonicus*) in five subsequent years across six different forest stands treated with varying management practices (Figure 1a). We estimated apparently monthly survival using robust design capture–mark–recapture models (Kendall et al., 1997). The high degrees of variability in small mammal density over space and time in our study system (Figure 1b), paired with variation in habitat structure across forest stands (Figure 1c), give us a unique opportunity to examine the effects of environmental variability on the relationships between personality traits and survival.

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

This study was conducted at the Penobscot Experimental Forest (PEF, 44°51'N, 68°37'W) in central Maine, United States. The PEF is a 1578-hectare, mixed conifer–deciduous forest and is dominated by shade-tolerant conifer species including red spruce (*Picea rubens*),

balsam fir (*Abies balsamea*) and eastern hemlock (*Tsuga canadensis*; Brissette & Kenefic, 2014). The most abundant small mammal species on this landscape are deer mice, southern red-backed voles, northern short-tailed shrews and North American red squirrels. The primary experiment in this forest is a ‘compartment study’ wherein different silvicultural treatments were applied to randomly selected and replicated stand-level management units beginning in 1952 and continuing today (Brissette & Kenefic, 2014). Approximately 25 hectares of forest (unmanaged since the late 1800s) serve as reference.

In the current study, we worked in six separate forest stands. We selected two stands that have remained unmanaged since the late 1800s to serve as reference areas (REF; 2.9 and 1.1 hectares in area respectively). We selected four additional stands representing two different silvicultural treatments (two replicates each): a uniform shelterwood (USW; 10.6 and 10.9 hectares, respectively) cut using a two-stage overstory removal, and an irregular shelterwood (ISW; 19.6 and 8.6 hectares, respectively) cut using a two-stage overstory removal and retaining reserves, or trees from the older cohort. These two treatments have generated contrasting habitat types for small mammals (Figure 1a); the uniform shelterwood has produced dense stands of shade-tolerant trees that are all within the same age class and diameter and the irregular shelterwood has resulted in stands with enhanced vertical structure from the large, retained residual trees which provide shade, increased seed production, as well as snags and downed logs for refuge.

Microhabitat measurements were recorded in each study area (details in Appendix S1—Supplementary Methods). To assess whether the amount of refuge habitat (shrubby ground cover and coarse woody debris) varied among the stand types, we ran linear models with the microhabitat variable as the response variable, and stand type (REF, USW or ISW) as a predictor variable. As small mammals often respond to indirect cues of risk (such as refuge availability) more than direct cues (such as predator scents; Orrock et al., 2004), the amount of refuge habitat may be interpreted as a proxy for perceived risk. Specifically, we consider the REF stands to represent the lowest perceived risk, while the USW stands represent the highest perceived risk (Figure 1), but we acknowledge that actual predation risk could not be assessed in this study.

2.2 | Small mammal trapping

We positioned one trapping grid close to the centre of each forest stand. Grids were 0.81 ha in area and consisted of 100 trapping points spaced 10 m apart. The mean distance between trapping grids was approximately 1.42 km. At each trapping point, we placed one Longworth small mammal trap baited with a mixture of sunflower seeds, oats and freeze-dried mealworms. Cotton stuffing was provided for bedding. At every other trapping point, we placed one Tomahawk trap with a rain cover baited with a mixture of peanut butter and sunflower seeds. Longworth traps were checked just after sunrise and in the late afternoon and Tomahawk traps were activated just after sunrise, checked in the late morning and afternoon

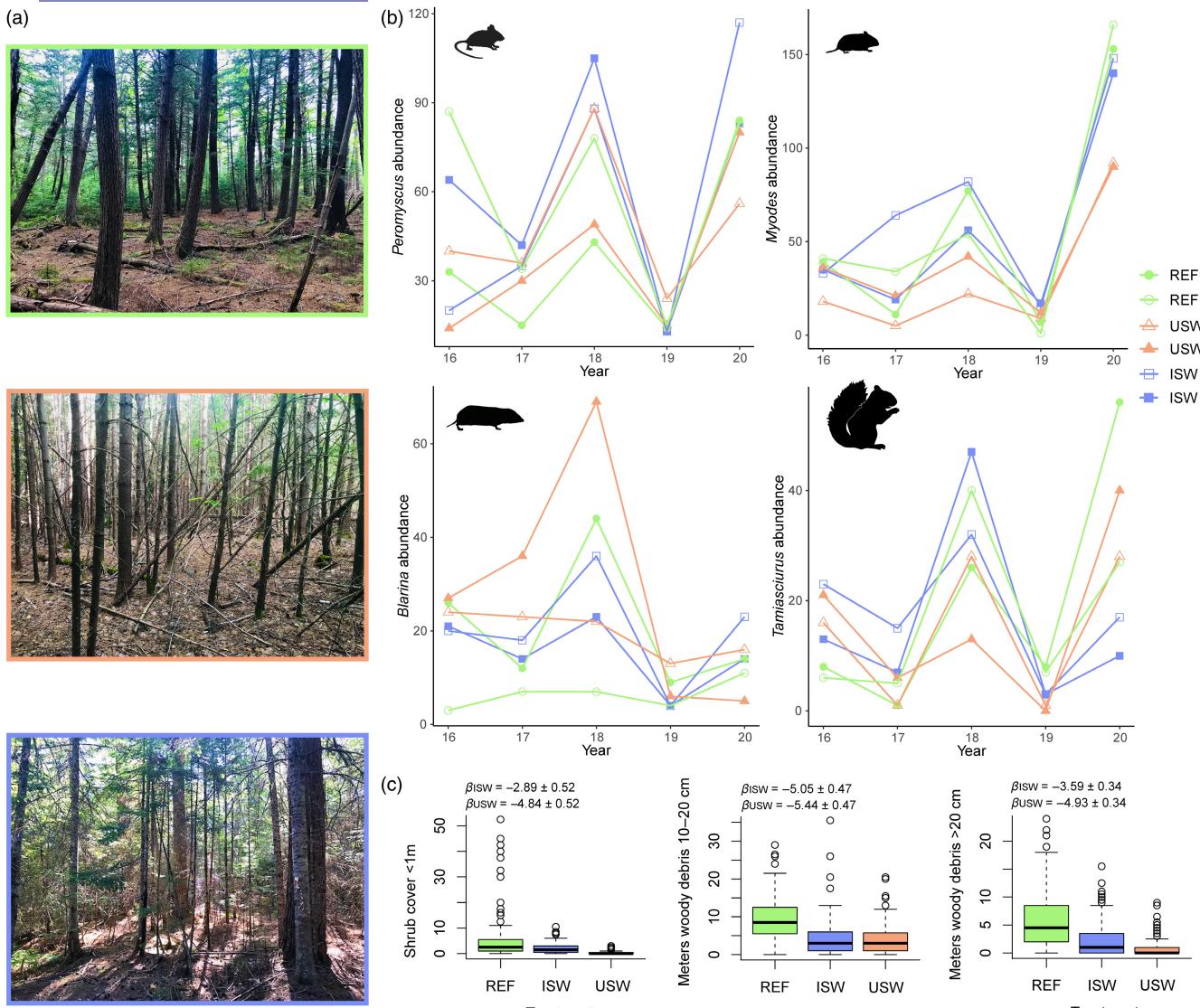


FIGURE 1 Overview of the experimental design. (a) Photos of study areas at the Penobscot Experimental Forest ($44^{\circ}51'N$, $68^{\circ}37'W$) in ME, United States. Shown (from top to bottom) are the reference/unmanaged (REF), uniform shelterwood (USW) and irregular shelterwood (ISW) stands. One $90m \times 90m$ trapping grid was positioned near the centre of each stand for a total of six grids. (b) Small mammal abundance varies over space (i.e. among grids) and time (over the 5 years) in this study system. (c) Major structural differences between the three stand types. The REF grids contained significantly more shrubs/herbaceous material (<1-m-tall) and total meters of coarse woody debris in two size classes (10–20 cm in diameter and 20+ cm in diameter) when compared to the USW and ISW grids (β and SE shown were estimated using linear models—see Section 2 for details).

and closed overnight. We trapped at each trapping grid for three consecutive days and nights each month for five consecutive months each year (June–October) from 2016 to 2020 totalling approximately 45,000 Longworth trap nights and over 22,000 Tomahawk trap days (trap night/day = number of active traps x number of nights/days).

2.3 | Animal processing and behavioural assays

All captures were taken to a location just outside the trapping grid for processing. Animals were transferred directly from the trap into three standard behavioural assays to measure behaviours that

would later be used to assess personality. An emergence test was used to assess boldness (Carter et al., 2013), an open-field test to measure activity and exploration in a novel environment (Perals et al., 2017) and a handling bag test to measure docility and the response to handling by an observer (Taylor et al., 2014). Although individuals were often recaptured within a single trapping session (3 day and night period), we performed behavioural assays on the first capture of the month only. This gave us repeated measures on marked individuals, but also ensured that animals would not become habituated, and each repeated measurement could be considered independent. Emergence and open-field tests were videotaped, and behaviours were quantified from videos in the laboratory. See

the [Supplementary Methods](#) for detailed field procedures, software and methods to quantify behaviour. See [Table S1](#) for a complete list of the behaviours measured, their description and interpretation, and supporting sources.

From the emergence test, we obtained measures of an animal's degree of boldness (the latency to emerge from a safe, enclosed space and the time spent at the entrance of the 'safe space' before emerging). From the open-field test, we obtained measures relating to activity rates (such as the mean speed of the individual), exploratory activity (such as the rate of exploratory rearing), anxiety and stress de-arousal (proportion of time spent grooming) and boldness during exploration (proportion of time spent in the centre portion of the arena; a deviation from thigmotaxis, or 'wall-seeking behaviour' as a form of safety-seeking; Choleris et al., [2001](#)). Finally, from the handling test, we obtained a measure of docility, or the reaction of an animal towards humans (the number of seconds spent immobile in a 1-minute test; this trait has been shown not to correlate with activity/exploration or stress reaction in other standardized behavioural assays; Martin & Réale, [2008](#)).

After the behavioural assays, we anaesthetised animals with isoflurane and inserted PIT tags (Biomark MiniHPT8 8, 134.2 kHz) subcutaneously at the midback. Except for shrews, animals were also marked with a small animal ear tag (Style 1005-1, National Band and Tag Co., USA). Squirrel ear tags were threaded with a combination of coloured wire (females) or pipe cleaner (males) for identification at a distance (Brehm & Mortelliti, [2018](#)). We recorded sex, body mass (measured using a 100 or 1000 g Pesola Lightline spring scale), body length and tail length (all species except squirrels), age class (juvenile, subadult or adult; based on body size and pelage coloration) and reproductive status (classified based on the presence of scrotal testes or signs of pregnancy/lactation). Animals were released at the site of capture post-processing. All research was approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC numbers A2015-11-02 and A2018-11-01).

2.4 | Statistical analyses

Detailed field procedures, software, methods to quantify behaviour and the defining characteristics of those behaviours ([Table S1](#)) are provided in the Supplementary Material. We note that we calculated the true repeatability, rather than an adjusted repeatability. We opted not to use a principal component analysis (PCA) because components retained from a PCA can become difficult to interpret biologically and lead to a loss of information (Lever et al., [2017](#)). We acknowledge that, as a result, our behavioural variables are not entirely independent, but we chose to use a number of non-correlated behavioural variables in our analyses. We calculated individual's mean BLUPs (best linear unbiased predictor) for each behavioural variable through 1000 simulations

(Dingemanse et al., [2020](#); Gharnit et al., [2020](#)) with package 'arm' (Gelman & Su, [2018](#)) to estimate each individual's average behaviour. The model used to estimate mean BLUPs included the following fixed effects as sources of variation in behaviour: sex, body mass, forest treatment and trapping session. Individual identity was set as a random effect. Subsequent mentions of personality refer to the mean BLUP value. We recognize that the use of BLUPs is criticized (Hadfield et al., [2010](#)), but alternative approaches including all repeated behavioural measurements in multivariate mixed models (Houslay & Wilson, [2017](#)) would not be appropriate in the current study as we do not have individual survival estimates to incorporate as trait values into a bivariate mixed model. Instead, a strength of capture-mark-recapture models (described below) is that an individual's whole capture history can be incorporated into the model to obtain more precise estimates of survival since imperfect detection and recapture probabilities can be implicitly accounted for. This study, therefore, trades the ability to account for within-individual behavioural variation for more precise estimates of apparent survival. Consequently, uncertainty in the effect sizes of personality on survival may be underestimated in this study since the uncertainty in the BLUPs was not accounted for in the Robust Design models, and the non-independence of observations across months from the same individuals could not be incorporated with a random effect of individual identity (however, the Huggin's estimator [see below] includes the ability to model individual heterogeneity as a function of recapture covariates).

To investigate whether personality traits affect survival in the target species, we estimated monthly apparent survival using robust design models for each target species separately with the Huggin's estimator (Kendall, [2011](#)). Briefly, robust design models allow the user to specify periods when the population is closed (i.e. between trap nights within a single trapping session, or *secondary sampling occasions*) as well as open periods (i.e. between trapping sessions, or *primary sampling occasions*). By incorporating statistical methodology from both closed and open population models, the model can derive an ad hoc estimate of emigration, as $\hat{\gamma} = 1 - (\hat{p}/\hat{p}^*)$ where $\hat{\gamma}$ = emigration probability, \hat{p} = estimated encounter probability from the open portion of the model and \hat{p}^* = estimated encounter probability from the closed portion of the model (Kendall, [2011](#)). These models allow considerable flexibility in estimating several demographic parameters of interest including: S (apparent survival probability), p (detection probability), c (recapture probability), γ' and γ'' (the probability of being temporarily absent from the study area, given that the individual was unavailable during the previous trapping session, and the probability of being temporarily absent from the study area, given that the individual was present during the previous trapping session respectively; Kendall, [2011](#)). We note that robust design models estimate apparent survival probability, rather than true survival, because mortality and permanent emigration cannot be distinguished. As such, the estimated apparent survival probability is the product of the probabilities of true survival and study area fidelity (Lebreton et al., [1992](#)). We used year, trapping

grid, forest treatment (reference/REF, uniform shelterwood/USW or irregular shelterwood/ISW) and sex as grouping variables. We assessed goodness of fit for each species using program RDSurviv (Kendall, 2001), and adjusted c-hat during model selection if overdispersion was detected in the data (Cooch & White, 2019).

We followed the information-theoretic approach to model selection (Burnham & Anderson, 2002) using the Akaike information criteria to rank competing models and considered models within 2.0Δ AICc to have equal support. We determined the top model for each parameter separately, modelling detection (p) and recapture (c) probabilities first, while holding emigration (γ' and γ'') and survival (S) constant and worked with S last as this was the parameter of most biological interest to our study. For parameters used to estimate the best structure for p , c , and γ , see the [Supplementary Methods](#).

Once working with the survival submodel, we used a two-step model selection procedure. In step one, we first built a series of candidate models to identify which variables might influence survival (and, thus, which variables to include in our 'full' model). These candidate models included: trapping session (tested as both a categorical and continuous variable), year, sex, forest treatment, trapping grid, body mass (as a proxy for age; i.e. adults will have greater mass than subadults, and juveniles with have the smallest mass [Creighton & Strauss, 1986]), body condition (estimated using the scaled-mass index for mice, voles and shrews [Peig & Green, 2009]), the density of conspecifics and personality traits. All variables were included in candidate models singly. We tested linear and quadratic effects of continuous predictor variables, but the quadratic form was never more supported than the linear. A count of the total number of tagged conspecifics in the trapping grid and year of interest was used as a proxy for density. As deer mice and red-backed voles fill similar niches, we also tested the combined mouse/vole density in addition to the density of conspecifics. For individuals with more than one body mass or body condition measurement, we used the individual's mean measurement.

In step two, we next specified a 'full' model, incorporating all variables from candidate models ranking within 2.0Δ AICc of the null model, and adding in interaction terms to test our hypothesis that the relationship between personality and survival differs between (1) forest treatments [personality*treatment] and (2) periods of high versus low small mammal density [personality*density]. In all models, continuous predictors were z-standardized and missing values were set to zero (the mean of a scaled variable). For short-tailed shrews, we omitted two individuals from the analysis due to extreme values (high leverage) in the behavioural variable 'Proportion of time in the centre' so that this trait would not inflate the strength of a regression in which it is included. We only included covariates where pairwise correlations did not exceed 0.7 (Dormann et al., 2013). See [Table S2](#) for pairwise correlations between all behavioural variables used in model selection. We performed robust design analyses using the package *RMark* in Program R (Laake, 2013) and the program *Mark* (White & Burnham, 1999).

3 | RESULTS

3.1 | Small mammal trapping

Small mammal trapping from June to October in 2016–2020 resulted in the capture of 827 individual *P. maniculatus*, 870 *M. gapperi*, 277 *B. brevicauda* and 249 *T. hudsonicus*. Capture histories included 25 primary sampling periods, each with three secondary sampling periods (except the primary period of October 2016, which had only two secondary sampling periods).

3.2 | Repeatability

We examined 819 behavioural observations from standardized behavioural assays of 301 individual deer mice and 880 observations from 344 individual voles with two or more observations and found all behavioural variables to be significantly repeatable ([Table S3](#)). Mean repeatability was 0.320 for deer mice (range: 0.193 to 0.419) and 0.222 for voles (range: 0.172–0.307) in line with similar field studies on deer mice (Underhill et al., 2021) and near the average previously reported for a variety of field and laboratory studies (Bell et al., 2009). We found four repeatable behavioural traits for northern short-tailed shrews after examining 204 observations from 79 individuals with two or more observations. Mean repeatability was 0.336 (range: 0.253–0.426). We found five repeatable behavioural traits for North American red squirrels after examining 303 observations from 109 individuals with two or more observations. Mean repeatability was 0.297 (range: 0.232–0.408). Repeatable traits for deer mice and voles included the following (described in detail in [Table S1](#)): mean speed (an indicator of activity), rear rate (activity and exploration), proportion time grooming (anxiety and stress de-arousal), proportion time centre (boldness), handling time (docility), latency to emerge (boldness) and time at end of tunnel (boldness). Repeatable traits for shrews included handling time, mean speed, rear rate and proportion time centre. Repeatable traits for squirrels included handling time, mean speed, proportion time grooming and rate of rearing.

3.3 | Full model structures for survival

The average apparent monthly survival probability, hereafter 'survival', (S) for deer mice across all groups was 0.62 ± 0.03 SE. Survival was greater with increasing body mass ($\beta = 0.29 \pm 0.07$ SE) but lower with increasing docility (handling time) ($\beta = -0.18 \pm 0.09$ SE; [Figure 2a](#)). Survival was lower in uniform shelterwood stands than in the reference and irregular shelterwood stands ($\beta_{USW} = -0.33 \pm 0.16$ SE), and lower in males than in females ($\beta_{males} = -0.27 \pm 0.13$ SE). Of the interaction terms specifying our hypothesis, only one had 95% confidence limits that did not contain zero. This was the interaction between stress de-arousal (the proportion of time spent grooming in the open-field test) and conspecific density ($\beta_{personality*density} = 0.36 \pm 0.08$ SE), where

FIGURE 2 Relationship between apparent survival and docility (seconds spent immobile in a handling test) as well as apparent survival and timidity (the latency to emerge in an emergence test) predicted from the full robust design models. Apparent survival is (a) lower in more docile deer mice (*Peromyscus maniculatus*) and (b) higher in bolder (less timid) southern red-backed voles (*Myodes gapperi*) in the uniform shelterwood stands (USW) only. Docility and timidity are z-standardized variables. Shaded areas represent 95% CI.

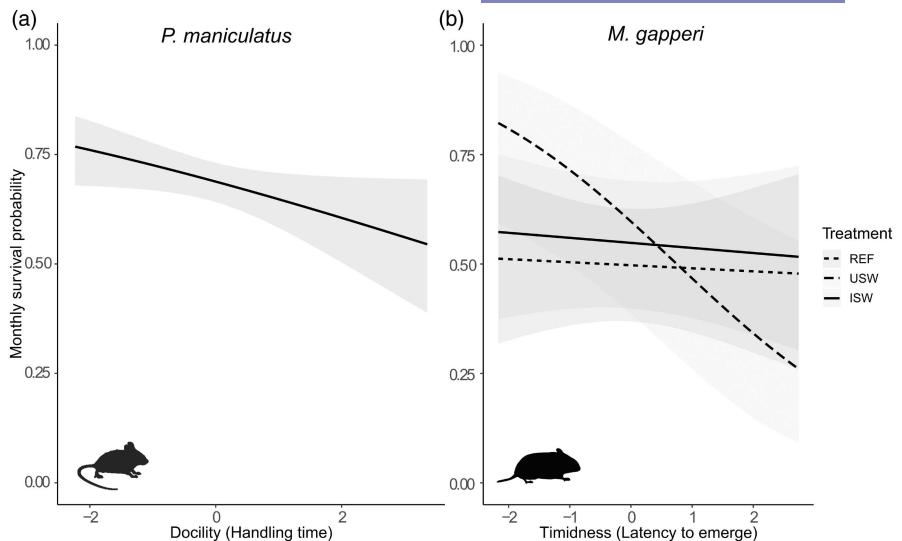
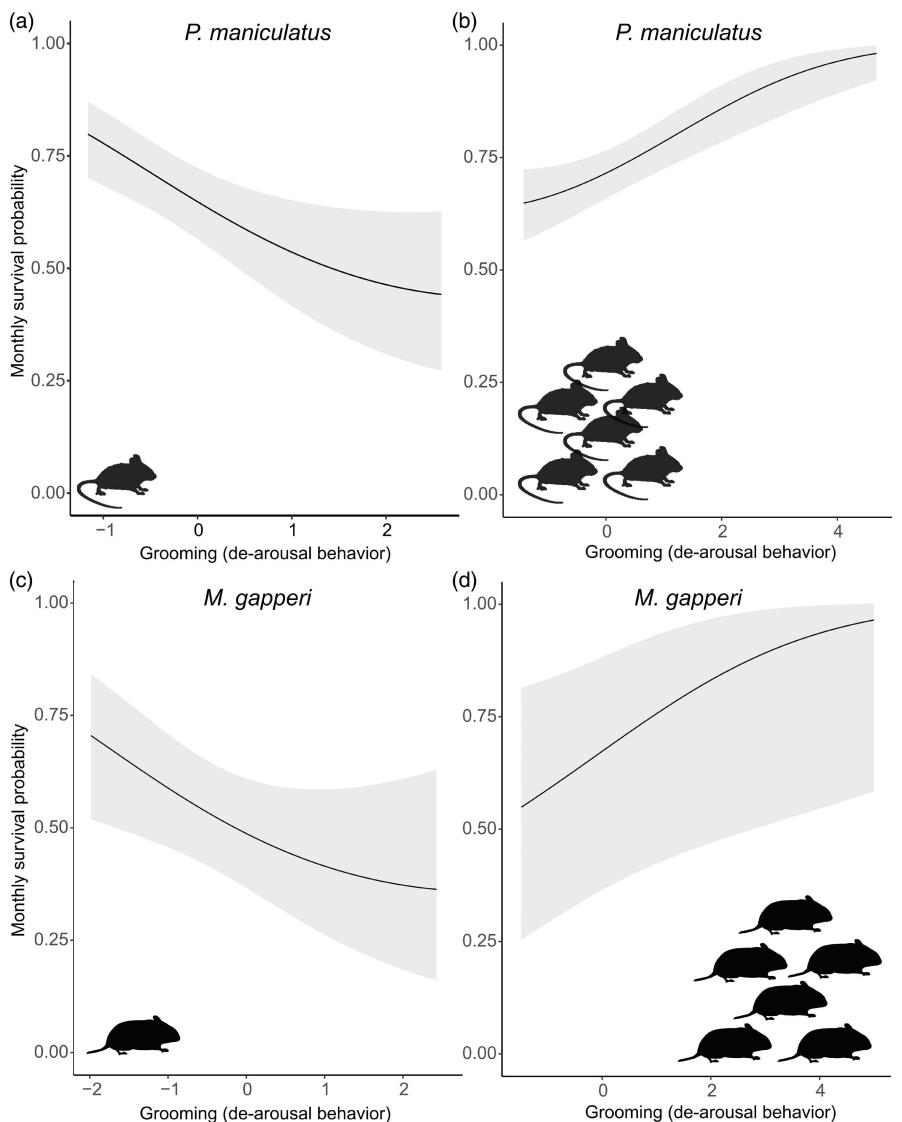


FIGURE 3 Relationship between apparent survival and stress de-arousal behaviour (the proportion of time spent grooming in the open-field test, z-standardized) at low versus high small mammal densities predicted from the full robust design model for (a, b) deer mice (*Peromyscus maniculatus*) and (c, d) southern red-backed voles (*Myodes gapperi*). Increased grooming predicts lower monthly survival probability at (a, c) low small mammal densities, but higher monthly survival probability at (b, d) high small mammal. For deer mouse models, a count of the total number of mice and voles in the trapping grid and year of interest was used as a proxy for density. For red-backed vole models, a count of voles only was used as a proxy for density (see Section 2 for more detail). Predicted relationships were made using a range of densities spanning (a, c) the first quartile and (b, d) the third to fourth quartile, and the grooming trait values present at those densities. Shaded areas represent 95% CI.



increased grooming predicted higher survival at high density only (Figure 3b). Deer mouse density and the combined density of deer mice and red-backed voles both had detectable interaction terms

with the grooming trait, but the model with the combined density was more than 8.0 Δ QAIc better, so we used the combined density instead.

Average survival (S) for red-backed voles across all groups was 0.59 ± 0.07 SE and was greater with increasing body mass ($\beta = 0.51 \pm 0.08$ SE). Survival was lower in males than in females ($\beta_{\text{Male}} = -0.37 \pm 0.14$ SE), and different among years (β_{16} [intercept] = 0.39 ± 0.44 SE; $\beta_{17} = 0.48 \pm 0.26$ SE; $\beta_{18} = 0.34 \pm 0.26$ SE; $\beta_{19} = 1.25 \pm 0.38$ SE; $\beta_{20} = 0.40 \pm 0.49$ SE). Of the interaction terms specifying our hypothesis, there were three meaningful interaction terms. The [personality*treatment] model showed that the relationship between timidity (latency to emerge from emergence test) and survival differed between treatments ($\beta_{\text{REF}} = 0.50 \pm 0.24$ SE; $\beta_{\text{ISW}} = 0.48 \pm 0.21$ SE) and increased timidity was associated with lower survival in the USW treatment only. Also, as was found for deer mice, the 'full' model included a significant interaction between stress de-arousal (the proportion of time spent grooming in the open-field test) and conspecific density ($\beta_{\text{personality*density}} = 0.30 \pm 0.08$ SE), where increased grooming predicted higher survival at high density only (Figure 3d). Red-backed vole density and the combined density of deer mice and red-backed voles both had significant interaction terms with the grooming trait, but the two models had nearly identical QAICc and QDeviance, so we used only vole density.

Average survival (S) for short-tailed shrews across all groups was 0.66 ± 0.06 SE, was greater with increasing body mass ($\beta = 0.50 \pm 0.12$ SE) and differed between years (β_{16} [intercept] = 0.56 ± 0.28 SE; $\beta_{17} = 0.71 \pm 0.30$ SE; $\beta_{18,19,20} = -0.33 \pm 0.32$ SE). The interactions of [personality*density] and [personality*treatment] were not significant.

Average survival (S) for red squirrels across all groups was 0.78 ± 0.08 SE, was greater with increasing body mass ($\beta = 0.74 \pm 0.22$ SE), was lower in males than in females ($\beta_{\text{Male}} = -0.69 \pm 0.26$ SE), different among years (β_{16} [intercept] = 1.21 ± 0.37 SE; $\beta_{17} = 1.04 \pm 0.51$ SE; $\beta_{18} = 0.16 \pm 0.40$ SE; $\beta_{19} = -0.25 \pm 0.75$ SE; $\beta_{20} = 0.45 \pm 0.56$ SE) and decreased as red squirrel density increased ($\beta = -0.53 \pm 0.23$ SE). The interactions of [personality*density] and [personality*treatment] were not significant.

For β estimates and real estimates from the 'full' robust design models with the Hugin's estimator, see Tables S4–S11.

4 | DISCUSSION

Using 5 years of mark–recapture data on four small mammal species, we found that in the two most abundant species only, personality traits influenced apparent monthly survival, but not in the direction predicted by life-history theory. Instead, increasing riskiness such as defensive aggression (i.e. movement during a handling bag test) and boldness (i.e. shorter latencies to emerge from a safe place during an emergence test) predicted increased survival rates in deer mice and southern red-backed voles respectively (Figure 2). Furthermore, we found that whether risky traits increase survival depends on environmental context (i.e. the availability of refuge and the density of competitors). In voles, bolder behavioural types only experienced higher survival in the USW forest type (which contains less refuge and may be interpreted as a riskier environment, Figure 1).

Additionally, in both mice and voles, the effects of personality on survival were density dependent and shifted direction depending on small mammal density (Figure 3). Previous meta-analyses have shown that the overall directional effects of personality traits on survival are weak (Moiron et al., 2020), but our findings indicate that this may be due to the temporal or spatial context (i.e. the density or microhabitat). Our findings also suggest that population density generates context dependence regarding the selective advantage of certain personality traits.

The pace-of-life-syndrome hypothesis (Réale et al., 2010) predicts that more active, aggressive and bolder individuals should experience elevated mortality rates, but empirical studies have found mixed support. Our study did not directly test the pace-of-life-syndrome hypothesis (i.e. we were unable to assess whether increased survival rates in our study system were associated with delayed or suppressed reproduction), but our results do not support key predictions made under this hypothesis. Instead, we saw that specific risky behaviours predicted higher survival rates in wild populations; in line with Moiron et al. (2020) (Figure 2). Defensive aggression and boldness predicted higher survival in deer mice and southern red-backed voles respectively. These findings may suggest that starvation is a stronger driver of demographic processes than predation in these study species, as if predation was a stronger driver, we would expect bolder individuals to have lower survival in areas with less refuge. Alternatively, previous work has shown bold, aggressive individuals to take more risks while foraging and suggests that risky behavioural types may be better at obtaining resources or acquiring high quality territories (Both et al., 2005; Dammhahn & Almelig, 2012). Consequently, these individuals may be able to maintain better body conditions and offset the costs of increased predation risk and/or be more efficient at winning access to refuge, lowering the risk of predation. Alternatively, it is possible that a positive feedback loop exists where individuals that acquire more resources can behave more boldly/take more risks, are better at evading predators and are better able to acquire resources in the future; effectively breaking the trade-off underpinning the expected relationship between risk-taking and survival (van Noordwijk & de Jong, 1986). Future work may focus on identifying whether there is evidence for this positive feedback loop (Sih et al., 2015).

In line with our predictions, bold voles had higher survival than timid voles only in the two uniform shelterwood (USW) stands where refuge is less abundant (Figure 1c). In the reference (REF) and irregular shelterwood (ISW) stands, there was no relationship between the degree of boldness and an individual's probability of survival (Figure 2b). The evidence that spatial heterogeneity in refuge generates context dependence in the fitness consequences of boldness in red-backed voles but not in deer mice may point to more specialist habitat requirements of southern red-backed voles when compared to deer mice (Wyrialowski, 1987). Aggressive deer mice may have a fitness advantage regardless of refuge abundance because they can offset the increased chance of predator-induced mortality through increased food acquisition and direct competition. Alternatively, red-backed voles are shown to preferentially select habitats with

more cover (Wylliawski, 1987) and are generally more abundant in moist habitats with an abundance of cover (Kirkland, 1990; Miller & Getz, 1977). Therefore, competition among voles for preferred microhabitats might be greater and result in the differential fitness that we observed between timid and bold individuals.

We also predicted that traits representing boldness, aggressiveness or exploratory activity would influence survival differently when density was high versus low due to better competitive abilities of risky individuals. Instead, in both deer mice and southern red-backed voles, we only observed a density-dependent relationship with the proportion of time spent grooming in the open field test (Figure 3). In many rodents, self-grooming is a form of stress coping and de-arousal (Fernández-Teruel & Estanislau, 2016) and individuals display this behaviour in response to stressful stimuli. Under mildly adverse stimuli, increased self-grooming seems to indicate increasing stress level, but under moderately to highly adverse stimuli, increased grooming is suggested to indicate lower stress levels, as self-grooming ceases under extremely adverse stimuli (Fernández-Teruel & Estanislau, 2016). Here, increased grooming predicted higher survival, but only at high small mammal density (perhaps reflecting that individuals better able to moderate stress have a fitness advantage when intraspecific competition is high). Otherwise, at low density, individuals who groomed more experienced lower survival rates (Figure 3a,c), possibly indicating that when social stresses are low, increased stress coping behaviours may be detrimental. These results suggest that fluctuations in competition may play a role in maintaining personality variation in populations with strong seasonal or yearly variation in density. One recent study on multimammate mice (*Mastomys natalensis*) observed a density-dependent relationship between a behavioural axis interpreted as 'stress sensitivity' (characterized by high grooming and low jumping) and survival, where increased grooming (lower stress sensitivity) predicted higher survival rates only during the population decrease phase in an intra-annual population cycle (Vanden Broecke et al., 2021). Consistency between our study and that of Vanden Broecke et al. suggests that the direction of selection on stress sensitivity is consistent when deconstructed into seasonal and yearly variation in intraspecific competition. The study by Vanden Broecke et al. was performed using a semi-wild experiment, monitoring individuals within enclosed fields; further work would be needed to assess this process in wild populations where immigration and emigration play a role. Future work may also combine seasonal increase/decrease phases as well as interannual fluctuations to expand more on these phenomena. Additionally, it is important to note that we did not observe direct effects of rodent density on survival in deer mice or red-backed voles. This may be because the relative effects of density on population regulation in these two species is weak or because over the 5 years of this study, these two rodent populations never hit density levels approaching carrying capacity.

These findings may inspire future work examining self-regulation of rodent populations. Population self-regulation occurs because high population density is a stressor which may control population

growth through morphological, physiological or behavioural changes that are stimulated by mutual interactions (Krebs, 2013). The 'polymorphic behaviour hypothesis' (Chitty, 1967) posits that at high densities, selection favours genotypes that have a worse effect on conspecifics (limiting population growth) whereas at low densities, selection favours genotypes that have a positive effect on conspecifics. Grooming behaviour may be involved in a form of population self-regulation (i.e. de-arousal behaviour may be connected to processes that limit population growth), but further research is needed to explore this hypothesis. Examining not only the quantity of grooming but also the quality (i.e. the analysis of grooming behavioural microstructure; Kalueff et al., 2016), or other behavioural changes that may associate with increased grooming (i.e. increased spacing behaviour; Krebs, 2013) will provide further insight into these findings. As density also varied spatially in this system, we may have been unable to disentangle the effects of habitat and density. Future studies with more than two spatial replicates per treatment would ensure that potential confounding between density at treatment is not at play (although in the present study this does not appear to be the case; Figure 1b).

Our findings for northern short-tailed shrews and red squirrels did not support risky personality traits predicting apparent survival. It is worth noting that the sample size for these species was limited compared to mice and voles, and a lack of evidence for personality-driven survival in these species could be a result of limited statistical power. Additionally, in our study system, population density fluctuates far less in these species compared to mice and voles (Figure S1) which may limit our ability to detect density-dependent relationships. Instead, apparent survival was higher in larger bodied individuals of both species (Tables S6 and S7), and lower when squirrel density (and, thus, intraspecific competition) was high (Table S7). Previous work on North American red squirrels has shown that more active females had lower overwinter survival (Boon et al., 2008), and work on Eurasian red squirrels (*Sciurus vulgaris*) identified changing fitness benefits of boldness in relation to habitat type (Santicchia et al., 2018), where bold squirrels had an advantage in forests with highly fluctuating food availability and shy squirrels had the advantage in forests with stable food supplies. A strength of our approach is that we directly accounted for detection probability. Specifically, we found that more docile red squirrels were more likely to be detected than aggressive squirrels (Table S7). These methodological differences may explain the differences between studies, but further research is needed to clarify this.

Most of the interactions we tested between personality traits and forest treatment were non-significant. For example, we expected that the fitness advantages of traits associated with increased riskiness (like boldness in an emergence test and higher defensive aggression in a handling bag test) would differ between forests with varying refuge availability, but the evidence for this was only true in one case for southern red-backed voles. One limitation in this study is that we did not have data regarding actual predation risk or food availability. Forest structure, including refuge availability provided by shrubs and downed woody debris,

will affect both the real and perceived risk of predation (as well as which predator species are most abundant), and the availability of food resources. In addition, behavioural traits like boldness, aggressiveness and high activity likely influence predation risk, foraging success and access to high-quality home ranges with more available refuge. Therefore, there were unknown variables in this study limiting our ability to understand the mechanisms behind the patterns we observed, and the potential for simultaneous but opposing effects of risky traits on mortality via foraging success, competitive ability and predation risk likely mask fitness advantages of many personality traits we tested. We also emphasize that, in this study, we use the BLUP value as a proxy for an individual's mean behavioural expression, but the repeatability estimated for the raw behavioural variables is only moderately repeatable. A repeatability value of 0.3, for example, suggests that 70% of the observed phenotypic variation in a behaviour is due to variance at the within-individual level. Our repeatability estimates fall around this value, so our BLUP values likely capture statistical noise and may be masking the true behavioural expression in some instances. This may also contribute to the large number of non-significant interactions observed in this study.

In the last two decades, flourishing research on animal personalities has identified links between animal personalities and individual responses to habitat modification, which can shift the diversity and composition of personality traits in populations through human-induced changes such as forest management (Mortelliti & Brehm, 2020), predator introduction (Lapiedra et al., 2018) and urbanization (Miranda et al., 2013). Understanding how selection on personality traits might act is critical, therefore, to predict future phenomena such as personality filtering in populations experiencing anthropogenic changes or anticipating personality-mediated disease spread into urban habitats (Wat et al., 2020). Using 5 years of mark-recapture data collected simultaneously on four species, we found that there were no observable survival costs of risky behaviours. Instead, we found evidence that risky behaviours increased apparent survival in the two most abundant species, and that variation in the environment generated context dependence in this relationship through heterogeneity in forest structure (including the availability of refuge habitat) and small mammal density. Our empirical findings suggest that spatiotemporal variation in selective pressures may mask our ability to obtain universal, directional relationships between intraspecific behavioural variation and fitness. These results emphasize the need to explore sources of context dependence using empirical studies and suggest that density may be important to consider when predicting personality-dependent selection in fluctuating systems.

AUTHOR CONTRIBUTIONS

Allison M. Brehm and Alessio Mortelliti conceived the ideas and designed methodology; Allison M. Brehm and Alessio Mortelliti collected the data; Allison M. Brehm analysed the data; Allison M. Brehm led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code available from the Figshare Digital Repository: <https://doi.org/10.6084/m9.figshare.24553582> (Brehm & Mortelliti, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supplementary methods.

Appendix S2. Supplementary results.

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