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Original Article

Exploration and docility in coexisting rodents

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ABSTRACT

There is increasing interest in understanding how behaviour influences trade-offs that facilitate species coexistence. In the absence of spatiotemporal habitat separation and resource partitioning, behavioural differences mediate competition among sympatric species. Here, we examine two behaviours, docility and exploration, using two standardized assays in three rodent species that coexist in Algonquin Provincial Park, Ontario, Canada, as part of an ongoing mark–recapture project. We used reproductive status as a proxy for energetic costs during a single breeding season, hypothesizing that differences in docility and exploration reflect species-specific reproductive life-history traits. We predicted that behavioural differences would be most notable between breeding and non-breeding individuals. We report mean differences in behavioural traits for deer mice (*Peromyscus maniculatus*), which are more explorative and less docile than red-backed voles (*Clethrionomys gapperi*) or woodland jumping mice (*Napaeozapus insignis*). We also report low among-individual variation in both behaviours across species. The populations observed in this study are known to be dependent on similar resources. Behaviour is an important, yet underexplored, mechanism of coexistence in the face of limiting resources. Here, we demonstrate that differences in exploration and docility are related to species reproductive life history. Thus, reproductive history traits and seasonal or annual changes in behaviours can be an important consideration for understanding the mechanisms that facilitate species coexistence.

Keywords: coexistence; competition; income breeding; niche partitioning; personality; reproduction

INTRODUCTION

Species coexistence is mediated through stabilizing and equalizing mechanisms that reduce interspecific competition and promote differences in fitness through trade-offs in resource acquisition and allocation (Chesson 2000, Chesson and Kuang 2008). Species reduce competition through trait differentiation, or niche partitioning, using behavioural or morphological advantages to exploit resources (Dewsbury *et al.* 1980, Klauschies *et al.* 2016). For example, differences in spatial and temporal foraging effort can allow species to maximize energy gain (Kneitel and Chase 2004). Across species, a suite of behavioural, physiological, and life-history traits promote divergence in resource use. Although classic niche theory predicts that co-occurring species are phylogenetically distant, niche partitioning can facilitate coexistence among closely related taxa (Webb *et al.* 2002). Recent studies have shown that repeatable among-individual behaviour related to resource partitioning reflects the suite of traits that enable cross-species coexistence (Morris and Palmer 2023). However, there are comparably few studies that link among-individual variation in behaviour as a mechanism promoting coexistence (Wauters *et al.* 2019, Morris and Palmer 2023).

Consistent differences in behaviour, referred to as 'animal personality' (Dall *et al.* 2004, Réale *et al.* 2007), affect foraging, fitness, parasite load, resource competition, and social dynamics (Smith and Blumstein 2008, Webster *et al.* 2009, Boyer *et al.* 2010, Montiglio *et al.* 2013, Gharnit *et al.* 2020). Variation in behaviour can also influence broader ecological processes, such as seed dispersal (Brehm and Mortelliti 2022). For example, social hierarchy influences seed zoochory, because more dominant individuals disperse a greater quantity of seeds (Zwolak 2018, Bartel and Orrock 2022). Behavioural variation often follows a 'fast' to 'slow' continuum alongside life-history and physiological traits (Promislow and Harvey 1990, Réale *et al.* 2010). Life history in faster species is characterized by a more rapid metabolism, growth, and reproductive maturation, with an elevated reproductive output at the expense of increased mortality, in comparison to slower species

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(Stearns 1998). Additionally, faster species are typically more bold, explorative, and less docile to accommodate a more rapid metabolism and reproductive output (Réale *et al.* 2010, Best *et al.* 2020).

Personality traits have been shown to play a role in facilitating species coexistence. For example, the habitat preferences of brown (*Lemmus trimucronatus*) and collared lemmings (*Dicrostonyx groenlandicus*) are associated with differences in exploration and activity (Morris *et al.* 2019). Among-individual personality differences can also promote coexistence because individuals capitalize on resources through different behavioural strategies. Boldness is strongly associated with space-use patterns facilitating the coexistence of bank voles (*Clethrionomys glareolus*) and striped field mice (*Apodemus agrarius*; Schirmer *et al.* 2020). Personality can influence dispersal, home range size, and foraging strategy because bolder, more explorative individuals are more likely to disperse further and be generalist foragers (Bolnick *et al.* 2003, Schirmer *et al.* 2020, Morris and Palmer 2023). For example, foraging site selection in red-backed voles (*Clethrionomys gapperi*) is influenced by docility and boldness, with less docile and more bold individuals having a greater propensity for foraging in novel sites (Merz *et al.* 2023).

Docility and exploration are two traits that reflect individual differences in spatial movement and engagement with novel stimuli (Morris 1984, Dingemanse *et al.* 2003, Réale *et al.* 2007, Careau *et al.* 2009, Petelle *et al.* 2013). Exploration is distinct from boldness, reflecting movement in novel, low-risk environments, whereas boldness is better suited to measure risk-taking in non-novel contexts (Réale *et al.* 2007). In contrast, docility is a response to a potential threat (namely, a predator) and is thus a proxy for risk-taking, because more docile individuals are generally more risk averse (Réale *et al.* 2000, Martin and Réale 2008a, Careau *et al.* 2010, Williams *et al.* 2023).

Given that exploration and docility influence the tendency of an individual to move around an environment and engage with novel stimuli, among-individual differences can reflect resource gain and expenditure. However, other energetically expensive processes, such as reproduction, can be influenced equally by differences in personality and are comparatively understudied (Gómez-Llano *et al.* 2021). For example, reproductive interference might promote spatial and temporal separation because cross-species mating can reduce reproductive success (Hochkirch *et al.* 2007). Likewise, reproduction might influence coexistence indirectly because behavioural changes related to mating strategy and energy intake during reproduction can vary across species (Eccard *et al.* 2011).

Reproduction is energetically expensive and requires a trade-off between future reproductive success and current self-maintenance (Promislow and Harvey 1990). Many rodents invest in seasonal breeding strategies to offset the energetic costs of reproduction (Bronson and Perrigo 1987, Bergeron *et al.* 2011). Although year-round breeding occurs in favourable conditions, seasonal reproduction is common where resources are scarce, such as breeding in the spring to offset winter food scarcity (Wolff and Sherman 2008, Eccard and Herde 2013). Personality traits related to the use of space can also influence interactions between sympatric species during breeding (Powell and Mitchell 2012, Dufour *et al.* 2015). Generally, breeding individuals require increased resources and are more aggressive owing to changes in their hormonal state, which alters the likelihood of interspecific interactions (Eccard *et al.* 2011). Therefore, if personality traits reflect the behavioural, physiological, and life-history traits that enable coexistence, understanding differences in personality across reproductive stages might be an important component to study.

Deer mice (*Peromyscus maniculatus*), red-backed voles, and woodland jumping mice (*Napaeozapus insignis*) are three rodent species that overlap in ecological niche (Fryxell *et al.* 1998). All three species are polyandrous and sire multiple litters from May to August. In wild environments, deer mice generally display fast behaviours (Careau *et al.* 2011), reproducing three to five times each breeding season, with each litter containing four to six pups (Maser *et al.* 1981). The gestation period for deer mice lasts ∼20 days, and juveniles become independent after 2 weeks (Kurta 2017). Deer mice have an average lifespan of 1–2 years and reach sexual maturation after 6–8 weeks (Dice 1936). Red-backed voles also live for 1–2 years and produce litter sizes that range from four to five pups, two to three times per reproductive season (Merrit 1981). Gestation in red-backed voles lasts for ∼2 weeks, and juvenile red-backed voles are independent after 17–20 days. Red-backed voles reach sexual maturity after 3 months (Merrit 1981, Linzey 1995). In contrast, woodland jumping mice live for 4–5 years (Wrigley 1972) and reproduce one or two times per season. Woodland jumping mice also produce fewer offspring per reproductive event than deer mice and red-backed voles, siring two to four pups per litter (Whitaker and Wrigley 1972). The gestation period for woodland jumping mice can take ∼30 days. Juvenile woodland jumping mice leave the den after 3 weeks and reach sexual maturity after 2 months (Wrigley 1972, Ovaska and Herman 1988).

Despite differences in life history, coexisting populations compete for the same resources. For example, co-occurring northern populations in Algonquin Provincial Park, Canada, are dependent on the same maple seed crop for food despite differences in micro-habitat (Schulte-Hostedde and Brooks 1997, Falls *et al.* 2007). Additionally, all three species are considered income-breeding rodents, which rely less on stored fat during reproduction and instead increase foraging intake to accommodate the increased energetic requirement associated with reproduction in females (Jönsson and Jonsson 1997, Bonnet *et al.* 1998, Broussard *et al.* 2005).

We aimed to evaluate behavioural variation among sympatric rodents during different stages of the reproductive season. Our study focused on three species: the deer mouse, red-backed vole, and woodland jumping mouse. Personality traits can reflect the behavioural mechanisms that enable coexistence, and reproduction can influence personality traits (Eccard *et al.* 2011, Morris and Palmer 2023). Therefore, we hypothesized that behavioural differences would emerge across species along a fast–slow continuum predicted by reproductive life-history traits. We predicted that across species, deer mice are more explorative and less docile than red-backed voles and woodland jumping mice, respectively. Given that exploration and docility contribute to resource and mate acquisition (Gharnit *et al.* 2022, Warrington *et al.* 2024), differences in these behaviours facilitate niche partitioning across co-occurring species (Montiglio *et al.* 2013). Furthermore, previous work has demonstrated significant interspecific differences in exploratory and docile behaviours among closely related rodents (Frynta 1994, Best *et al.* 2020, Morris and Palmer 2023). Species-specific reproductive strategy also reflects seasonal energy investment and can influence behaviour. Thus, differences in behaviours during breeding seasons could be one mechanism to reduce intraspecific competition and promote differential resource acquisition.

MATERIALS AND METHODS

Sampling

All animals were surveyed in accordance with proper animal care practices (animal care permit #6011106) approved by Laurentian University. Mice and voles were surveyed in Algonquin Provincial Park, Ontario, Canada (45°54′N, 78°26′W) from 17 pre-established (Fryxell *et al.* 1998) and three new traplines from May to August 2022. Each trapline consisted of 20 Sherman traps (H.B. Sherman Traps, Inc., Tallahassee, FL, USA), with two placed every 10 m. Traplines were set over three consecutive nights every 2 weeks on a staggered schedule. Each trap was filled with 10–20 water-soaked sunflower seeds and cotton bedding at dusk and was checked for animals at dawn. Traps were checked in the same order each morning to compare potential impacts of longer trap confinement on behaviour (Brehm *et al.* 2020). Trapped individuals were collected from Sherman traps and placed in a clear plastic handling bag. Individuals were tagged with a unique numeric ear tag as part of a long-term mark–recapture study, weighed using a Pesola scale (±0.1 g), sexed, and assigned an age class (juvenile, sub-adult, or adult) based on body mass and fur colour (Schmidt *et al.* 2019). Furthermore, current individual breeding status was assessed as scrotal or non-scrotal for males, based on the visibility of testes, and as pregnant, lactating, or non-reproductive (not actively expressing signs of ongoing gestation or lactation) for females, based on visible signs of pregnancy and lactation.

Behavioural assays

All testing took place directly in the field. Therefore, tests occurred in different locations with different surrounding environments, light levels, and canopies. Captured individuals were subjected to either a 1 min handling bag test or a 5 min open field test each trap day. Given that the collection of morphometric data would require handling the individual directly in the bag, all handling bag tests occurred before the collection of morphometric data, and the open field tests occurred after. Handling bag tests are used to quantify the response of an animal to presence of a human as a measure of docility (Martin and Réale 2008a). Thus, morphometrics were collected after the handling bag test to minimize confounding variables associated with handling time. During the handling bag test, individuals were released from the trap into a clear plastic bag and suspended at arm's length for 1 min (Fig. 1A). Given that individuals were transported directly from the trap to the bag, cotton or excess seeds could fall into the handling bag; therefore, interactions with these materials were included as separate behaviours. Docility was then measured as the total number of seconds an individual spent immobile or 'freezing' (Martin and Réale 2008a; Supporting Information, Table S1).

Open field tests are used to measure exploration in a novel, non-risky environment (Carter *et al.* 2013). During the open field test, individuals were retrieved from traps, underwent handling procedures, and were promptly introduced to the behavioural arena directly from the clear plastic bag, through a polyvinyl chloride (PVC) opening. Although the collection of morphometric data would influence exploration, recapturing the individual to collect morphometric data post-test would be more stressful for the animal. Total exploration behaviour was measured as the time an individual spent performing any locomotion except for grooming (forward motion, rearing, or scratching in place), whereas non-exploratory time was measured as time spent motionless either in the arena or in the entrance, marked as hiding behaviour (Supporting Information, Table S1). The 5 min began once the individual was placed successfully inside the PVC opening. Individuals commonly darted out of the bag, away from the handler; therefore, individuals entered the arena immediately without waiting inside the PVC entrance.

Once the test began, observers left the view of the animal inside the arena. The arena was cleaned between each trial using an 80% vinegar solution, then rinsed with water. Behavioural assays were recorded in the field using a video camera (Sony HDR-CX405) and were later analysed in the laboratory using the video recordings (Table 1).

Open field test arena design

The open field test was conducted inside a novel plastic arena (51 cm × 41 cm × 74 cm) fitted with an 8.89 cm PVC opening and a mesh barrier on top to prevent an individual from leaving the arena, while still allowing for recording. The plastic used was black, with a surrounding blue plastic lid that was not visible to the individual inside the arena (Fig. 1B).

Video processing

Videos were assessed by BH using COW LOG v.3.0 (Pastell 2016) to quantify behaviours using predefined ethograms (Supporting Information, Tables S1 and S2). For handling bag tests, codes included 'escape', 'move', 'groom', 'forage', and 'freeze', where escape and move behaviours were pooled together to measure docility (Supporting Information, Table S1). For open field tests, codes used were 'move', 'groom', 'freeze', and 'hide', where explorative behaviour was measured as the total time spent moving (Supporting Information, Table S2). Given that individuals were able to return to the PVC opening and remain mobile, we included this as a separate behaviour because the obscurity of a tunnel might encourage increased immobility. For both tests, non-visible time refers to the period during which an individual was not captured adequately by the camera, owing to a malfunction, improper camera positioning, or the presence of cotton during the handling bag test. Individuals with >30 s of non-visible time were excluded from data analysis. All recorded data can be found in Supporting Information, Data S1.

Statistical analyses

Statistical analyses were conducted using the statistical software R v.4.2.3 (R Core Team 2023). We ran a repeatability analysis on behavioural variables for each species to determine whether the behaviours observed in each video were repeatable across individuals and thus considered personality phenotypes (Wilson 2018). Because there were no repeated observations of woodland

Figure 1. A, a deer mouse (*Peromyscus maniculatus*) in a plastic bag, held <1 m off the ground, at arm's length from an observer for the handling bag test. B, a woodland jumping mouse (*Napaeozapus insignis*) inside the plastic open field testing arena, directly in the field. Individuals were subjected to this test in proximity to the location where they were trapped; thus, the associated canopy is presumed to be familiar. Each open field test lasted 5 min, after which observers opened the lid and released individuals in the same location. During the 5 min tests, observers were not visible to the animal and would proceed to the next set of traps until the end of the test.

jumping mice with the open field test, we were unable to test for repeatability in exploration in this species. For each model, the total times spent performing specific actions were pooled together and defined as the total expressed behaviour. For docility, this meant that any freezing, non-moving behaviour was considered docile. For the open field test, walking, running, jumping, rearing, and scratching in place were considered exploratory behaviour. Repeatability of each behaviour was estimated using the RPTR package in R (Stoffel *et al.* 2017), with a bootstrap interval of 5000 and 1000 permutations. Each model used individual identity (ID) as a random effect. We did not limit the repeatability test to individuals with more than one observation because this has been shown to miss variation in individual plasticity (Martin *et al.* 2011). We excluded any fixed effects from this analysis because the fixed effects used in this study (age, reproductive condition, date, and sex) had a negligible effect on the variation of exploration or docile behaviour.

For each species separately, docility was log-transformed for normality. Using the first instance of either behavioural test, only in individuals which had undergone both tests, we measured the correlation between docility and exploration in deer mice and red-backed voles using Spearman's correlation test. Given that all individuals were wild-caught, it was impossible to test the same number of individuals at each location, during each trap session. Thus, our dataset includes behavioural tests that might occur in relatively rapid succession, spaced apart by days, weeks, or months. Frequent testing and resulting habituation can influence behavioural analyses (Martin and Réale 2008a, Tranquillo *et al.* 2023). However, the most notable differences in personality occur between the first and second instances of the same behavioural test (Žampachová *et al.* 2017, Rudeck *et al.* 2020). Therefore, we grouped test occurrences by either the first occurrence for that individual or as a subsequent test. We then evaluated differences in behaviour between the first and subsequent test events using a Bayesian Markov Monte Carlo (MCMC) multivariate model in the package MCMCGLMM (Hadfield 2010), with individual ID as a random effect for each behavioural assay. We used the $\mathrm{MCMC}_{\mathrm{GLMM}}$ package to estimate the posterior probability (pMCMC) as an analoug to frequentist p-values to determine if there was a substantive effect in either behaviour. To select priors, the model was initially run with weak prior estimations (0, 10), then with different priors, and the resulting posterior distributions

Table 1. The total number of deer mice, red-backed voles, and woodland jumping mice recorded from the handling bag and open field test.

Category	**Handling bag tests (N)**	**Open field tests (N)**
Deer mice		
Total individuals (N)	137	93
Unique individuals	96	76
Male	80	55
Female	57	38
Adult	67	39
Sub-adult	44	32
Juvenile	26	22
Reproductive male	36	15
Non-reproductive male	44	40
Reproductive female	6	4
Non-reproductive female	51	34
Red-backed voles		
Total individuals (N)	65	44
Unique individuals	53	41
Male	41	26
Female	24	18
Adult	63	39
Sub-adult	0	5
Juvenile	2	0
Reproductive male	22	12
Non-reproductive male	19	14
Reproductive female	13	8
Non-reproductive female	11	10
Woodland jumping mice		
Total individuals (N)	19	18
Unique individuals	18	17
Male	7	8
Female	12	10
Adult	17	18
Sub-adult	1	0
Juvenile	1	0
Reproductive male	3	3
Non-reproductive male	4	5
Reproductive female	6	6
Non-reproductive female	6	5

Unique individuals represent the first instance of either test, whereas the total individuals includes subsequent samples. Also shown is the total number of individuals sampled from each age class (adult, sub-adult, or juvenile) or grouped reproductive condition. Reproductive females include individuals that were identified as either pregnant or lactating at the time of the test.

were checked (Hadfield 2010). Models were run using inverse Wishart priors and a Gaussian distribution with 8500000 iterations, with a thinning interval of 10000, and a burn-in of 150000, which yielded an effective sample size of 566. To ensure model convergence, we visually inspected autocorrelation plots developed using the package CODA (Plummer *et al.* 2006).

We then ran separate MCMC models with either docility or exploration as the response variable for all individuals grouped as reproductive (scrotal for males; pregnant or lactating for females) or non-reproductive (non-scrotal for males; non-reproductive for females). Each model then used age, species, date, and sex as fixed effects, with individual ID as a random effect. Date was used as a categorical fixed effect (May, June, July, August, or September) because samples are non-independent; however, date provided poor model convergence as a random effect. Although among-individual correlations (R_{ind}) are most often estimated alongside residual correlations (within individual) when traits are measured simultaneously in a set of individuals (Dingemanse and Dochtermann 2013), it is still possible to estimate correlations among individuals when traits are observed separately (Careau *et al.* 2015). However, it is not possible to measure the residual correlations when traits are assayed individually. To calculate R_{ind}, we used the proportion of variance attributed to individual ID divided by the total variance (random ID + residual variance). For docility, we back-transformed the log difference between each category and the reference level to show the approximate difference in seconds. All models were run using the same iteration, thinning interval, and burn-in used for the model measuring differences between subsequent tests, yielding an effective sample size of 835. We visually inspected the trace and autocorrelation plots to ensure that the models converged properly (Supporting Information, Data S2).

RESULTS

Repeatability estimates

We used behavioural observations from 202 handling bag tests, including observations of 83 deer mice (137 total tests), 48 red-backed voles (65 total tests), and 15 woodland jumping mice (19 total tests). We also analysed 157 open field tests, including observations of 84 deer mice (93 total tests), 37 red-backed voles (42 total tests), and 15 woodland jumping mice (19 total tests). Only docility behaviour in deer mice expressed significant repeatability, with 38% of variation in docility attributable to differences between individuals [95% confidence interval (CI) = (.082, .62), d.f. = 1, likelihood-ratio test = 4.46]. Regarding exploration behaviour, 23% of variation was related to differences between individuals [95% CI = (0, .66), d.f. = 1, likelihood-ratio test = 1.15]; however, this result was not statistically significant ($P = .14$). Exploration in deer mice and both docility and exploration in red-backed voles were not considered statistically significant (Supporting Information, Table S3).

Relationships between behaviour and repeated sampling

Spearman's rank correlation test did not reveal any significant correlation between exploratory and docile behaviour using the first instance of both tests for all species (deer mice, $\rho = -0.29$, $P = .1$; red-backed voles, $\rho = -0.41$, $P = .06$; woodland jumping mice, $\rho = 0.8$, $P = .13$). There was no support for a strong difference in docility between the first and subsequent instances of the handling bag test for either deer mice [posterior mean = .0041, 95% credible interval (CrI) = (−0.46, .59), effective sample size = 766, pMCMC = .86] or red-backed voles [posterior mean = 0.046, 95% CrI = (−0.44, .45), effective sample size = 566, pMCMC = .87]. Likewise, there was no support for differences between the first and subsequent instances of the open field test for deer mice [posterior mean = −7.05, 95% CrI = (−41.74, 25.24), effective sample size = 566, pMCMC = .71] or red-backed voles [posterior mean = −27, 95% CrI = (−123.9, 57.85), effective sample

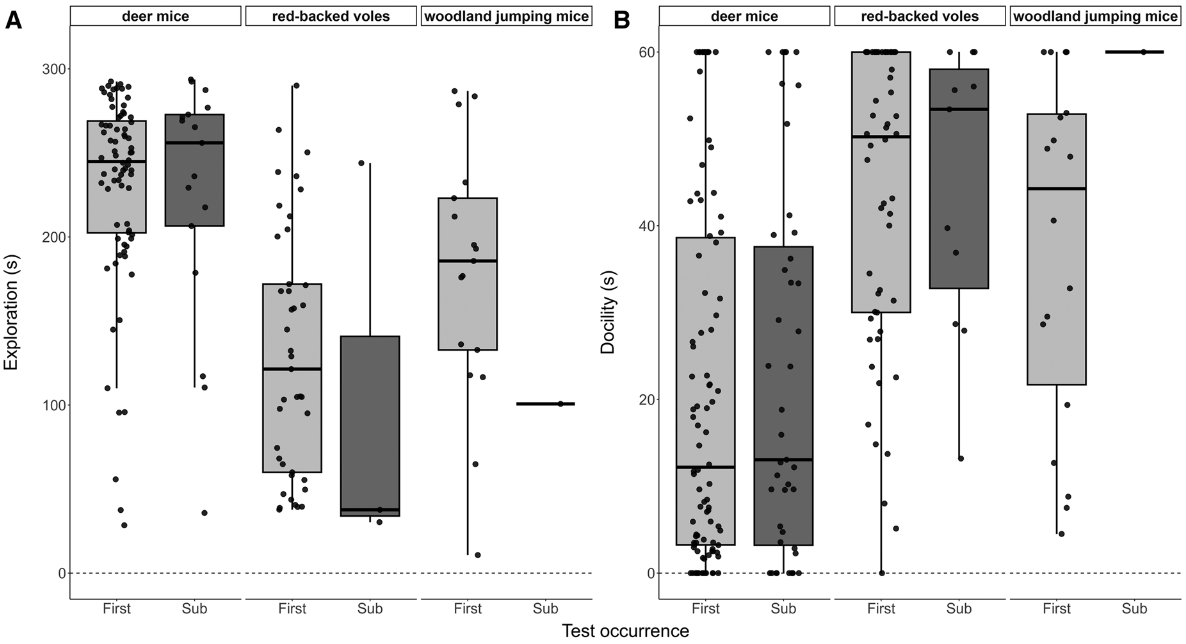

Figure 2. A boxplot depicting time spent performing each behaviour in the open field test (A) or handling bag test (B), showing the mean exploration and docility times for deer mice, red-backed voles, and woodland jumping mice. For each species, shown is the mean time for the first vs. all subsequent tests grouped together (denoted as Sub). Jitters represent each unique handling bag or open field test. Boxes represent the interquartile range, and whiskers represent 1.5SD from the interquartile range.

size = 566, pMCMC = .53]. Thus, species behaviour did not seem to be affected systematically by repeated sampling in any of our surveyed species (Fig. 2).

Cross-species comparison of docility and exploration

The model for docility revealed among-individual variation in docility for reproductive individuals to be 11% [*N* = 86, R_{ind} = .11, 95% CrI = (.0006, .46), effective sample = 835]. The mean docility time for reproductive red-backed voles was ~38 s [*N* = 35, posterior mean = 1.19, 95% CrI = (.61, 1.77), effective sample = 835, pMCMC ≤ .001]. Meanwhile, the mean docility time in reproductive woodland jumping mice was ~45 s [*N* = 9, posterior mean = 1.35, 95% CrI = (.52, 2.21), effective sample = 835, pMCMC = .007]. In comparison to reproductive deer mice, reproductive red-backed voles were more docile for ~27 s, and woodland jumping mice for ~33 s (Table 2).

In contrast, among-individual variation in non-reproductive individuals accounted for 22% of variance [*N* = 139, R_{ind} = .22, 95% CrI = (.0016, .52), effective sample size = 835]. The mean docility time for non-reproductive red-backed voles was ~44 s [*N* = 30, posterior mean = 1.17, 95% CrI = (.62, 1.74), effective sample size = 835, pMCMC ≤ .001]. Thus, non-reproductive red-backed voles were ~31 s more docile than non-reproductive deer mice. For woodland jumping mice, the predicted mean docility time was ~24 s [*N* = 10, posterior mean = 0.58, 95% CrI = (−0.15, 1.23), effective sample size = 835, pMCMC = .12]. Non-reproductive woodland jumping mice were ~11 s more docile than non-reproductive deer mice (Table 2).

There was no support for strong associations between any of the fixed effects used (age, sex, or date) along with docility time for either reproductive category (Table 2). Meanwhile, there were negligible differences in the log-transformed docility scores between red-backed voles and woodland jumping mice (Fig. 3).

Among-individual variation accounted for 3.8% of variance in exploratory behaviour in reproductive males and females [*N* = 48, R_{ind} = .036, 95% CrI = (0.00, .33), effective sample size = 835]. Male and female woodland jumping mice in the reproductive category were ~64 s less explorative than reproductive deer mice [*N* = 9, posterior mean = −63.8, 95% CrI = (−137.7, 11.3), effective sample size = 835, pMCMC = .093], although the credible interval crossed zero, hence there was no support for a strong difference in exploration. In contrast, male and female red-backed voles were ~75 s less explorative than deer mice [*N* = 20, posterior mean = −74.7, 95% CrI = (−123.3, −10.6), effective sample size = 836, pMCMC = 0.0024].

For non-reproductive males and females, among-individual variation accounted for 9.8% of variance in exploratory behaviour [*N* = 108, R_{ind} = .096, 95% CrI = (0.00, .56), effective sample size = 835]. Non-reproductive woodland jumping mice were ~45 s less explorative than deer mice [*N* = 10, posterior mean = −44.8, 95% CrI = (−92.7, .047), effective sample size = 1010, pMCMC = .06], with a credible interval that crossed zero. Likewise, non-reproductive red-backed voles were ~101 s less explorative than deer mice [*N* = 24, posterior mean = −100.6, 95% CrI = (−134.9, −69.3), effective sample size = 641, pMCMC ≤ .001]. Non-reproductive males and females that were surveyed in May were also less explorative than non-reproductive males and females surveyed in August [*N* = 3, posterior mean = −104.2, 95% CrI = (−184.9, −31.1), effective sample size = 835, pMCMC = .007]. Thus, there were some mean differences in exploratory behaviour across species (Fig. 4).

Table 2. Summary of fixed effects for Bayesian Markov Monte Carlo multivariate model for docile and explorative behaviour revealed from all handling bag and open field tests.

Fixed effects	Posterior mean	95% Credible interval	Effective sample	pMCMC
Docility				
Reproductive individuals				
Intercept	2.45	[1.76; 3.15]	835	<.001*
Age$_{\text{SA}}$	−0.02	[−0.75; .71]	835	.95
Species$_{\text{RBV}}$	1.19	[.61; 1.77]	835	<.001*
Species$_{\text{WJM}}$	1.35	[.52; 2.21]	835	.007*
Date$_{\text{May}}$	−0.02	[−0.95; .96]	835	.96
Date$_{\text{June}}$	.02	[−0.63; .78]	835	.95
Date$_{\text{July}}$	−0.10	[−0.65; .44]	953	.68
Sex$_{\text{M}}$	.06	[−0.50; .70]	835	.84
Non-reproductive individuals				
Intercept	2.63	[2.19; 3.06]	923	<.001*
Age$_{\text{J}}$	.21	[−0.26; .68]	835	.41
Age$_{\text{SA}}$	−0.17	[−0.72; .29]	891	.52
Species$_{\text{RBV}}$	1.17	[.62; 1.74]	835	<.001
Species$_{\text{WJM}}$	.58	[−0.15; 1.23]	835	.12
Date$_{\text{May}}$	−0.39	[−1.07; .26]	835	.25
Date$_{\text{June}}$	.23	[−0.47; .99]	813	.51
Date$_{\text{July}}$	−0.29	[−0.77; .12]	835	.17
Sex$_{\text{M}}$	.26	[−0.15; .63]	958	.21
Exploration				
Reproductive individuals				
Intercept	245.5	[170.5; 334.3]	835	<.001*
Age$_{\text{SA}}$	19.03	[−73.02; 106.6]	835	.66
Species$_{\text{RBV}}$	−74.7	[−123.3; −10.6]	836	.0024*
Species$_{\text{WJM}}$	−63.8	[−137.7; 11.3]	835	.093
Sex$_{\text{M}}$	−27.4	[−79.1; 27.7]	970	.31
Date$_{\text{May}}$	−16.9	[−87.3; 51.2]	835	.66
Date$_{\text{June}}$	−4.502	[−75.3; 67.5]	835	.91
Date$_{\text{July}}$	−51.9	[−158.5; 46.01	835	.33
Non-reproductive individuals				
Intercept	222.9	[195.2; 254.9]	935	<.001*
Age$_{\text{J}}$	3.14	[−31.7; 36.7]	835	.83
Age$_{\text{SA}}$	10.15	[−22.9; 37.9]	835	.49
Species$_{\text{RBV}}$	−100.6	[−134.9; −69.3]	641	<.001*
Species$_{\text{WJM}}$	−44.8	[−92.7; .047]	1010	.06
Date$_{\text{May}}$	−104.2	[−184.9; −31.1]	835	.007*
Date$_{\text{June}}$	−2.03	[−43.1; 45.7]	835	.93
Date$_{\text{July}}$	8.30	[−24.58; 39.9]	835	.63
Date$_{\text{Septemeber}}$	15.6	[−22.8; −49.1]	672	.41
Sex$_{\text{M}}$	2.88	[−21.7; 24.5]	834	.83

For each model, species (RBV, red-backed vole; WJM, woodland jumping mouse), age (J, juvenile; SA, sub-adult), and date of test are included as fixed effects, and individual identity was used as a random effect. Reproductive individuals include scrotal males and pregnant or lactating females. Non-reproductive individuals include non-scrotal males and females with no visible signs of pregnancy or lactation. All models used Gaussian distributions with inverse Wishart priors.

*Significance if credible interval failed to overlap zero and pMCMC > 0.05.

DISCUSSION

We hypothesized that reproductive life history would reflect exploration and docile behaviour across sympatric species and that these differences would be more prominent between seasonal breeding stages. Based on species life-history traits, we predicted that deer mice would be more explorative and less docile than red-backed voles and that red-backed voles and deer mice would both be more explorative and less docile than woodland jumping mice. However, we found only that deer mice were consistently more explorative and less docile than red-backed voles and woodland jumping mice. Meanwhile, differences in docility between red-backed voles and woodland jumping mice were negligible, and woodland jumping mice were more explorative than red-backed voles. Given that only docility in deer mice was repeatable in this study, the behaviours observed here can be used only as a proxy of mean trait expression and do not fully reflect animal personality (Niemelä and Dingemanse 2018). Likewise, we conducted our behavioural assays independently, adapting the 'individual gambit' (Brommer 2013), assuming that individual traits reflect phenotypic variation even when measured in isolation.

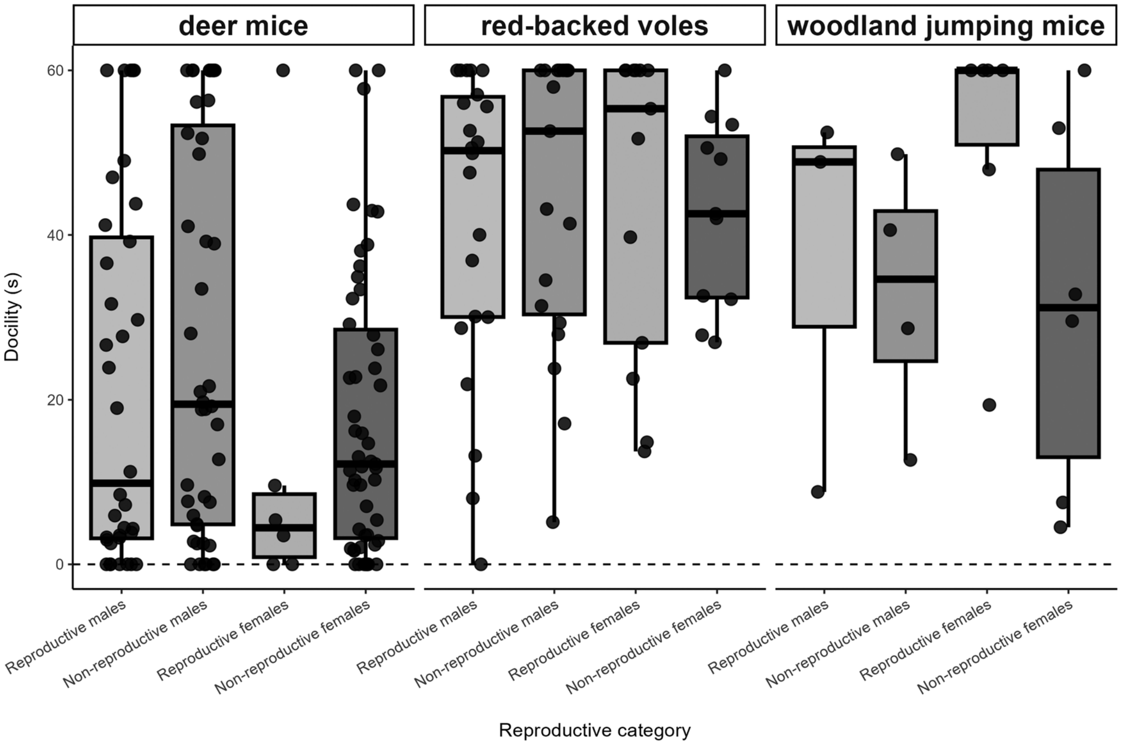

Figure 3. A box plot representing the mean docility times from all handling bag tests performed on deer mice ($N = 137$), red-backed voles ($N = 65$), and woodland jumping mice ($N = 19$). All species are grouped into either reproductive (scrotal for males; pregnant or lactating for females) or non-reproductive (non-scrotal for males; not visibly showing signs of pregnancy or lactation for females) categories. Jitters represent each observation of a handling bag test; boxes represent the interquartile range, and whiskers represent 1.5SD from the interquartile range.

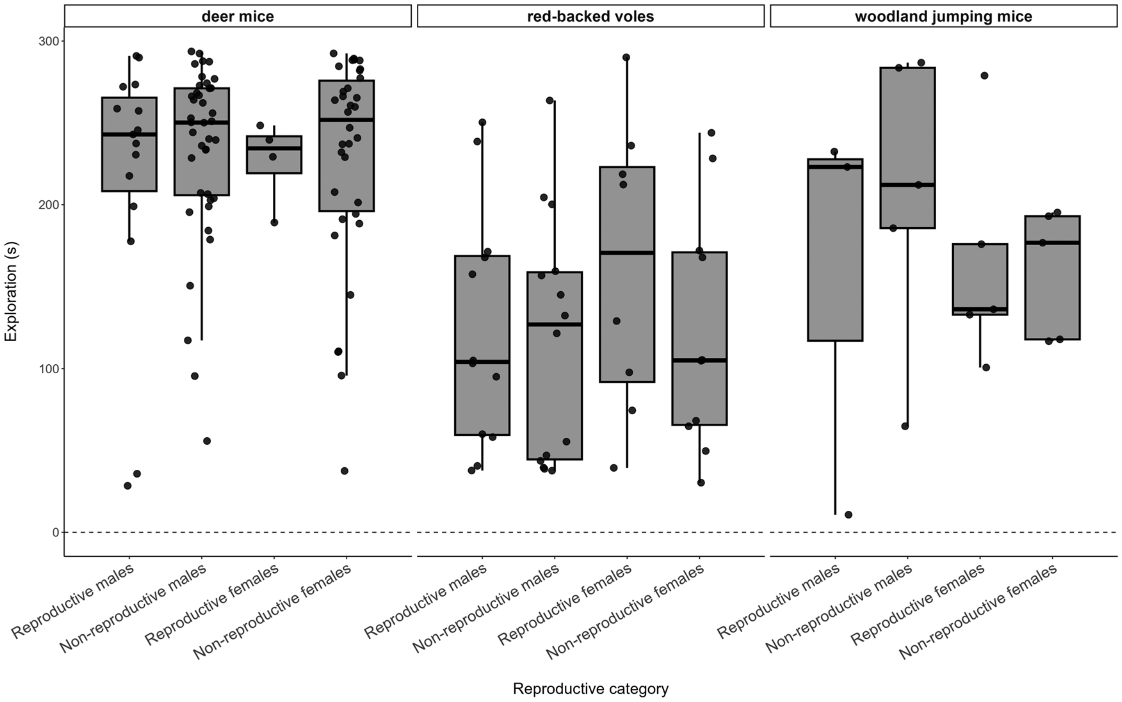

Figure 4. A box plot showing mean differences in exploratory behaviour from the open field test, including deer mice ($N = 93$), red-backed voles ($N = 44$), and woodland jumping mice ($N = 18$). All species are grouped into either reproductive (scrotal for males; pregnant or lactating for females) or non-reproductive (non-scrotal for males; not visibly showing signs of pregnancy or lactation for females) categories. Jitters represent each observation of a handling bag test; boxes represent the interquartile range, and whiskers represent 1.5SD from the interquartile range.

Although this limits the interpretation of behavioural syndromes, it remains a valid framework for examining phenotypic variation underlying the coexistence of sympatric species examined in this study.

Although we did not observe a significant relationship between docility and exploration in this population, this result is not uncommon (see Martin and Réale 2008b) and might be explained by our reliance on examining phenotypic correlations (Dingemanse *et al.* 2012). Furthermore, the handling bag and open field tests are commonly used to measure docility and exploration in wild animals; repeated exposure to tests can increase acclimation and influence behaviour (Wilson *et al.* 1976, Webster *et al.* 1979, Martin and Réale 2008a, Mazzamuto *et al.* 2019, Brehm *et al.* 2020, Brehm and Mortelliti 2021, Humphreys and Mortelliti 2024). However, subsequent testing within this study did not show any significant impact on either behaviour.

We observed repeatable inter-individual variation in docility only of deer mice. However, such variation is not necessarily absent for each species. For example, studies observing other *Peromyscus* mice using open field tests have found a significant and repeatable among-individual correlation between struggle time and exploratory behaviours, but not body mass (Underhill *et al.* 2021). Likewise, studies on common voles (*Microtus arvalis*) have shown that behaviours related to exploration are repeatable, and in some circumstances, these behaviours are related to social group dynamics (Lantová *et al.* 2011). Thus, the lack of repeatability observed in the present study might be linked to the number of repeated samples across individuals. Therefore, increased sampling across seasons might better reflect exploratory and docile behaviours in this population. Given that the behavioural traits observed in this study are known to be repeatable in closely related systems from other populations, the behavioural observations of this study can contribute to ongoing research on how behaviour drives cross-species interactions.

Additionally, within this study, we focused on measuring between-individual variation in behaviour to measure relationships in reproductive life-history traits across species. Within-individual variation, using synchronous behavioural tests of the same individuals, can be another potential avenue to explore the mechanisms driving coexistence. Indeed, we show that reproductive history and mean trait expression of exploratory and docile behaviour are related in deer mice. However, measuring within-individual variation across a breeding season, or across multiple breeding seasons, can help us to understand better how individual reproductive traits and associated changes in hormonal state affect behaviour.

Coexistence is dependent, in part, on trade-offs in resource acquisition and allocation. Thus, individuals experience a trade-off between resource gain (i.e. foraging) and risk from competition or predation (Halliday and Morris 2013). Foraging propensity is influenced by behavioural and morphological characteristics that facilitate risk avoidance. For example, larger and thus less conspicuous individuals are more sensitive to light and decrease foraging effort in response to increased luminescence (Vasquez 1996). Of course, niche partitioning and spatial separation are strong mechanisms that enable coexistence. The species surveyed in this study are primarily dependent on the maple seed crop (Falls *et al.* 2007). Some rodent species that overlap in habitat and resource use, which were not surveyed in this study, also compete for the same resources. For example, eastern chipmunks (*Tamias striatus*) and North American red squirrels (*Tamiasciurus hudsonicus*) are diurnal and, although they can overlap in habitat and resource dependence, rarely engage in direct competition (Brunner *et al.* 2013). In contrast, northern and southern flying squirrels (*Glaucomys sabrinus* and *Glaucomys volans*) are nocturnal but have vastly different morphological characteristics and foraging strategies and might express larger niche partitioning efforts because some flying squirrels are more dependent on various fungi (Currah *et al.* 2000).

In contrast, deer mice, red-backed voles, and woodland jumping mice often engage in more direct competition avoidance despite variation in microhabitat preferences (Schulte-Hostedde and Brooks 1997, Hughes 2023). Although we do observe differences across species, we did not observe a strong difference between breeding and non-breeding individuals as expected. All species examined in this study are income breeders, and females increase foraging effort to accommodate reproductive costs, rather than relying on fat reserves (Jönsson and Jonsson 1997, Bonnet *et al.* 1998). The increased foraging effort during the breeding season can also influence exploration and docility, but this effect is not sex dependent (Hughes *et al.* 2025). Indeed, several studies have observed an association between behaviour and reproductive status, including pheromone-induced aggression (Martín-Sánchez *et al.* 2015), increased vigilance to protect against infanticide (Breedveld *et al.* 2019), and, perhaps most significantly, hypo-responsiveness in lactating females (Fleming and Luebke 1981, Lonstein 2005, Windle *et al.* 1997, Chauke *et al.* 2011). Behavioural traits, including exploration and docility, are linked to food intake, productivity, and population density (Biro and Stamps 2008, Korpela *et al.* 2011). Thus, the lack of differences in exploration and docile behaviour observed between breeding and non-breeding individuals in this study might be driven by resource availability, which was not examined in this study.

CONCLUSION

Traits explored here highlight some behavioural strategies between species and help to posit some plausible differences in closely related sympatric species. Deer mice were consistently more explorative and less docile than red-backed voles and woodland jumping mice. However, woodland jumping mice were more explorative than red-backed voles; meanwhile, differences in docility were negligible between these two species. Likewise, there was little support for strong differences in either behaviour between breeding or non-breeding individuals of the same species. Evidently, co-occurring species commonly compete for the same spatial area and resources. Likewise, repeatable within-individual variation in behaviours related to exploration has been observed in other rodent species. Thus, examining the relationships between behaviour and various components of species-specific life histories is important for understanding the mechanisms that facilitate coexistence. Further investigation into mechanisms related to niche differentiation and behavioural adaptations might help in partitioning evolutionary relationships that promote coexistence. We encourage future research to focus on potential relationships between reproduction, energetics, and behaviour as a starting point for exploring sympatric species coexistence.

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AUTHOR CONTRIBUTIONS

Bryan Hughes (Conceptualization, Methodology, Formal analysis, Investigation, Writing—original draft, Writing—review and editing, Visualization), Jeff Bowman (Conceptualization, Resources, Writing—review and editing, Supervision, Funding acquisition), and Albrecht Schulte-Hostedde (Conceptualization, Resources, Writing—review and editing, Supervision, Funding acquisition)

CONFLICT OF INTEREST

None declared.

SUPPORTING INFORMATION

Supporting Information is available at *Biological Journal of the Linnean Society* online.

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DATA AVAILABILITY STATEMENT

The data underlying this article are available in the article and its online supporting material.

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