Animal Behaviour 234 (2026) 123514

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Special Issue: Conservation Behaviour and the Anthropocene

# Managing personalities: effects of forestry on North American red squirrel personality distributions and activity

Brigit R. Humphreys [a], Allison M. Brehm [b, 1], Alessio Mortelliti [a, c, *]

[a] Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, Orono, ME, U.S.A.
[b] Department of Integrative Biology, University of Wisconsin-Madison, Madison, WI, U.S.A.
[c] Department of Life Science, University of Trieste, Trieste, Italy

ARTICLE INFO

*Article history:*
Received 4 September 2024
Initial acceptance 3 June 2025
Final acceptance 28 January 2026
Available online 27 February 2026
MS. number: SI-24-00546

*Keywords:*
aggression
animal personality
behavioural shift
exploration
forest management
land use change
light-level geolocator
open-field test
repeatability

Managed forests make up over half of forests globally, with the majority used for timber harvest. To ensure efficient forest regeneration, it is vital that we understand how different management regimes affect the behaviours of seed-dispersing and seed-predating animals. Personalities, or consistent among-individual differences in behaviour, are a key factor driving all stages of the seed selection and dispersal process, including consumption versus caching decisions, and it is therefore critical to understand how differing anthropogenic forest manipulations may shift the personality distributions of a population. Within the context of a long-term capture–mark–recapture study in Maine, U.S.A., we used standardized tests to measure personality traits of 325 individual North American red squirrels, *Tamiasciurus hudsonicus*, over 8 years across two contrasting silvicultural treatments and reference plots (totalling six sites). During 2 years of the study, we deployed collar-mounted light-level geolocators on 14 unique individuals to measure daily activity patterns at a 5 min resolution and distinguish between when an individual was in its nest versus out of its nest. Our analysis revealed that personality distributions measured in standardized tests differ between unmanaged and managed forests, and that certain personality traits appeared to influence free-ranging activity patterns. Specifically, both uniform and irregular shelterwood forests had lower proportions of aggressive individuals than unmanaged forests, and more exploratory individuals spent less time active per day on average. Our study adds to the growing body of research showing that anthropogenic alterations to landscapes are associated with distinct behavioural compositions. The ecological consequences of these changes must be considered, especially for rodent populations that control seed dispersal.

© 2026 The Author(s). Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

Anthropogenic changes to the land have drastically increased over the past few decades (Elmqvist et al., 2013; FAO, 2020). Forest management is a critical type of land use to consider, as over 50% of the world's forests are managed, with the majority used for timber harvest (FAO, 2020). Efficient forest regeneration is a necessary component of successful and sustainable forest management, and therefore it is vital to understand how different management regimes affect seed-dispersing and seed-predating animals in forests. Interindividual differences in behaviour that remain consistent across time and context are referred to as 'animal personality' and have been observed throughout the animal kingdom (Gosling, 2001; Sih et al., 2004, 2015). Personality has been found to be a key factor driving animal decision making at all stages of the seed selection and seed dispersal process (Boone et al., 2021; Humphreys & Mortelliti, 2024; Merz et al., 2023), including consumption versus caching decisions, so if differing anthropogenic forest manipulations shift the personality distribution of a population, this could change seed dispersal outcomes (Brehm et al., 2019; Brehm & Mortelliti, 2022).

The effects of an individual's personality are far-reaching, impacting its habitat use (Brehm & Mortelliti, 2021), antipredator strategies, territorial dominance (Dingemanse & de Goede, 2004), reproductive success and survival in some instances (Martinig et al., 2021; Moiron et al., 2020; Smith & Blumstein, 2008). However, personalities may also influence individual contributions to ecological and evolutionary processes and thus have important consequences at the ecosystem level (Hunter, Boone,

* Corresponding author.
*E-mail address:* alessio.mortelliti@maine.edu (A. Mortelliti).
[1] A. M. Brehm is now at the New Hampshire Fish and Game Department, Concord, NH, U.S.A.

https://doi.org/10.1016/j.anbehav.2026.123514
0003-3472/© 2026 The Author(s). Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

Brehm, & Mortelliti, 2022; Wolf & Weissing, 2012). Therefore, the unique personality composition of a population is important to consider due to the potential for scaled-up outcomes. For example, the functioning of an ecosystem with mostly bold or exploratory individuals will differ from that of an ecosystem with mostly shy individuals because of personality-dependent seed dispersal outcomes, including seed selection, dispersal distance and cache site (Brehm et al., 2019; Brehm & Mortelliti, 2022; Humphreys & Mortelliti, 2024). For example, even-aged (also known as uniform shelterwood) silvicultural practices increase the proportion of highly active deer mice, *Peromyscus maniculatus*, and because active mice are more likely to consume seeds instead of leaving them intact, this land use change may lead to reduced germination and tree recruitment (Brehm et al., 2019).

Different types of land use can affect personality distributions in a population. For example, urbanization has been associated with personality trait shifts across taxa (Dammhahn et al., 2020; Miranda et al., 2013; Schuett et al., 2018). Fragmented forests are a second type of anthropogenic landscape that have been associated with behavioural shifts, leading to increased human–wildlife conflicts (Dhawale et al., 2020). Furthermore, forest management activities can alter the distributions of personalities in a population of scatter hoarders, which are animals that store food in numerous dispersed caches, increasing the proportion of bold, active and anxious individuals, which affects seed dispersal outcomes (Brehm et al., 2019). However, we have a limited understanding and little empirical evidence for how land use change influences personality distributions of larder hoarders, which are animals that store food in one or a few protected central caches and often heavily contribute to seed predation rather than successful seed dispersal. Therefore, better understanding land use impacts to larder hoarders will allow for a more accurate estimate of seed predation rates in modified landscapes. Furthermore, insufficient research has looked at the consequences of personality distribution shifts resulting from land use change for the ecology and activity of larder hoarders.

For food-hoarding, nonhibernating small mammals, a balance between activity and rest is critical for obtaining enough stored resources for overwinter survival in temperate regions (Larivee et al., 2010; Morrison et al., 2009; Roth et al., 2010). Essential tasks are accomplished during an animal's active state out of their nest, including foraging, mating, defending a home range and exploring novel resources, yet the rest state within the nest is also essential for sleeping, eating, grooming and nursing (Ashby, 1972; Halle & Stenseth, 2000; McGuire & Bemis, 2007; Siegel, 2008; Studd et al., 2019). Foraging is a fundamental activity for animals, yet individual variation exists within a species, with some individuals more efficiently acquiring food than others, allowing them to spend less time foraging and more time resting (Eccard et al., 2020; Norberg, 1977). Daily time allocations to these different activities result in fitness consequences, including growth rate and mortality risk trade-offs (Werner & Anholt, 1993), and therefore it is of great interest to better understand the ecological consequences of individual variation in activity.

A host of factors drive the daily activity patterns of animals, including photoperiodic cycles (Rusak & Zucker, 1975), predation avoidance (Suselbeek et al., 2014), resource availability (Doherty et al., 2019), social factors (Favreau et al., 2009), competition (Kronfeld-Schor & Dayan, 2003) and sex (Lodberg-Holm et al., 2021), and clear fitness costs and benefits exist with individual differences in activity-related personality traits. For example, more active female North American red squirrels, *Tamiasciurus hudsonicus*, have offspring with higher growth rates (Boon et al., 2007), yet more active and exploratory Siberian chipmunks, *Eutamias sibiricus*, have higher parasite loads (Boyer et al., 2010), and bolder, more exploratory eastern grey squirrels, *Sciurus carolinensis*, are more likely to be infected by parasites (Santicchia et al., 2019). Intraspecific activity differences may shed light on human-induced changes to behaviours, species interactions and niche partitioning (Frey et al., 2017), with potential advantages for some individuals under changing climatic and land use conditions.

In a large-scale field experiment, we trapped and tested the personality traits of 325 North American red squirrels using standardized tests across two different silvicultural treatments and unmanaged reference forests to evaluate how forest management impacts personality distributions in a population. We then fastened light-level geolocator collars on individuals ($N = 14$ individuals) to monitor daily activity patterns to determine how the affected personality traits influence daily activity patterns in the wild (Fig. 1). The North American red squirrel is a major seed predator in North American coniferous forests and plays an ecologically important role in forest regeneration rates and movement of plant species across the landscape (Goheen & Swihart, 2003). In our study system, red squirrels are largely larder hoarders, storing all or most of their food, especially cones, in one or a few middens centrally located in their territories. The behaviours of this species are largely driven by conspecific coexistence and competition for resources (Dantzer et al., 2020), and with aggressive territorial behaviour, including loud and frequent rattle vocalizations and physical disputes, this tree squirrel is a strong model species for investigating animal behaviour and activity.

We predicted that anthropogenic forest modification would be associated with distinct means and distributions of personalities (Brehm et al., 2019). Specifically, for our first objective, we hypothesized that (1) unmanaged reference forests, on average, would have individuals that were less active (lower mean speed in the open-field test), as these forests have open understories with higher perceived predation risk for small mammals, and past research has found less active rodents in these types of forests (Brehm et al., 2019). In addition, we predicted that (2) personality traits measured in the standardized tests would have the most variation in distribution in irregular shelterwood forests due to the larger diversity of tree sizes and microhabitats, which have been found to promote behavioural diversity and niche specialization (Bolnick et al., 2003; Mortelliti & Brehm, 2020; Schirmer et al., 2019). For our second objective, we predicted that activity patterns would vary with personality (Boon et al., 2008; Brehm et al., 2019). Specifically, we expected that (3) individuals with more active, exploratory and aggressive personalities (i.e. higher rear rate and higher proportion of time spent aggressive towards the mirror) would spend more time out of their nests, have more active bouts and have longer active bouts (Gharnit et al., 2020; Haigh et al., 2017; Schirmer et al., 2019). Past research has found that personality is consistent across contexts, including in captivity and in the wild (Boon et al., 2008; Herborn et al., 2010; Yuen et al., 2016), leading us to predict that individuals that were more active in our personality tests would also be more active in the wild. For example, more active North American red squirrels (measured in an open-field test) were trapped significantly more often and at more locations (Boon et al., 2008), and therefore likely moved around more and travelled farther. In a different species of squirrel, researchers found that more aggressive individuals (measured in a mirror test) spent more time active in the wild (Haigh et al., 2017).

## METHODS

### *Study Site*

We conducted our study in the Penobscot Experimental Forest (44°51′N, 68°37′W, ME, U.S.A.), consisting of a mixture of conifer

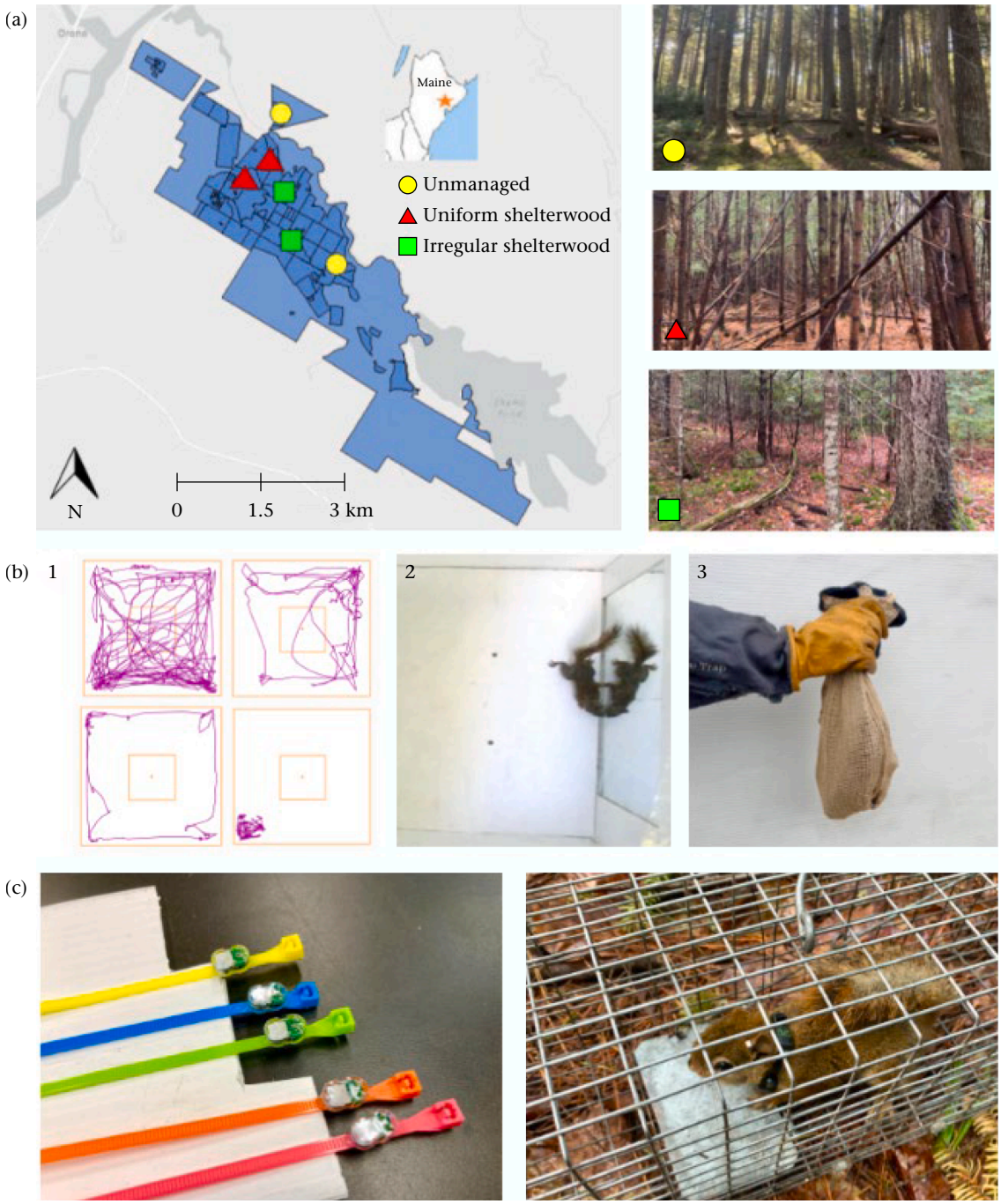


**Figure 1.** Overview of our study design. (a) We conducted our experiment in the Penobscot Experimental Forest in Maine, U.S.A. where we investigated the effects of three contrasting forest management techniques on the personality distributions of populations of North American red squirrels. The blue area on the map indicates the experimental forest boundaries and the black outlines show distinct management units. (b) Each captured individual was subject to three behavioural tests: (1) open-field test; (2) mirror test; (3) handling bag test. The purple lines represent examples of movement tracks from four different individuals. (c) Following testing, we gave individuals coloured collars mounted with light-level geolocators and released the animals. These devices recorded ambient light values every 5 min, allowing us to determine when an individual was active out of its nest versus inactive within its nest.

and deciduous trees with distinct management units created through contrasting logging regimes (Kenefic & Brissette, 2014). In this study, we compared three different silvicultural treatments that create unique microhabitats for small mammals, each with two replicates, totalling six trapping grids: (1) uniform shelterwood forest (most intensively managed), characterized by small tightly packed trees and sparse understory light, (2) irregular shelterwood forest, characterized by large and small trees, a mossy understory and abundant woody material, and (3) unmanaged forest (since the late 1800s), characterized by large spaced trees, abundant coarse woody debris and large open areas (Fig. 1a).

### *Red Squirrel Trapping*

As part of an extensive 8-year (2016–2023) capture–mark–recapture study, we baited 50 Tomahawk traps (Tomahawk Live-Trap Company, Hazelhurst, WI, U.S.A.) with peanut butter in each of our six trapping grids measuring 90 × 90 m (0.81 ha). Traps

were set at the base of large trees facing the trunks or along fallen logs and were spaced 20 m apart in a grid pattern. Traps were placed in each grid for three consecutive days in the beginning of each month from June to October each year and targeted North American red squirrels. We checked and closed them in the evenings and opened them in the mornings. Personality data for our experiment came from all 8 years, totalling over 35 000 Tomahawk trap days.

*Behavioural Testing and Processing*

Each captured squirrel was subject to three behavioural tests (Fig. 1b) a maximum of once per month to avoid habituation: (1) open-field test, measuring activity and exploration in a novel context (Perals et al., 2017; Walsh & Cummins, 1976); (2) mirror test, measuring sociality and aggression (Svendsen & Armitage, 1973); (3) handling bag test, measuring docility and response to being handled by a human (Martin & Réale, 2008). All tests were performed in the field at a processing area beside each trapping grid. For the open-field test, individuals were transferred from the trap in which they were captured into a 79 × 79 × 79 cm white open-field box with a clear lid. Squirrel behaviour in the arena was filmed for 5 min using a camera pointing straight down from above. For the mirror test, one side of the open-field box was slid open, revealing a mirror, and the camera recorded the squirrel's behaviour for 2.5 min after the mirror was exposed. For the handling bag test, individuals were transferred to a cloth bag and held while an observer recorded the time (s) the animal spent immobile for 1 min. All tests were performed on palettes beneath tarps to ensure a level surface and consistent light conditions. During tests, observers left the area and remained quiet. Open-field boxes were cleaned with 70% isopropyl alcohol between individuals.

Following behavioural testing, we collected the following information on each individual: weight, sex, age class and reproductive status. In each individual, we inserted a passive integrated transponder (Biomark PIT tags, Biomark, Inc., Boise, ID, U.S.A.; MiniHPT8, 134.2 kHz) subcutaneously on the middle back and fitted them with two alphanumeric eartags with wire of a unique colour combination for visual identification.

*Collaring Squirrels*

We deployed collars on 14 squirrels (11 males, 3 females; 4 in unmanaged reference forests, 4 in uniform shelterwood forests, 6 in irregular shelterwood forests) for our activity experiment between June and October during 2018 and 2023. We anaesthetized each individual in a large plastic bag using vaporized isoflurane, and once unconscious, we fastened collars onto individuals (Fig. 1c). We only collared adult squirrels, and we did not collar pregnant or lactating females. We made collars from a coloured zip tie for visual identification covered with flexible heat shrink tubing to minimize irritation (Siracusa et al., 2019) with a light-level geolocator (Migrate Technologies, Dallas, TX, U.S.A.; C65-SUPER, mode 1) mounted securely with nontoxic glue and tape. The average weight of the geolocator collars was 2.67 g, which is 1.77% of the average captured red squirrel body weight. This is below the recommended maximum of 4–7% of the individual's body weight to avoid impacting the normal behaviour of the animal (Stevenson et al., 2013). These devices sampled light every minute, recording the highest value within 5 min, and sampled temperature every 5 min, recording the minimum and maximum within 4 h. We subsequently released each individual in the exact location at which they were captured. After at least 1 month, upon recapture, we removed collars with medical scissors and offloaded geolocator data. We conducted targeted trapping in observed home ranges after our 3 days of grid trapping each month to maximize the likelihood of successful recapture of collared individuals.

*Geolocator Verification*

To verify the geolocators were operating correctly, we mounted radiotransmitters (Advanced Telemetry Solutions Inc., Isanti, MN, U.S.A.; M1540) on four collars to track squirrels through VHF radiotelemetry to locate nests for targeted trapping and visual surveys. The average weight of the collars with both a geolocator and radiotransmitter was 6.95 g, which is 4.61% of the average captured red squirrel body weight, which is below the recommended maximum of 4–7% (Stevenson et al., 2013). We also conducted visual surveys by walking through our grid locations after trapping was completed each month and searching for collared red squirrels, which we could identify based on collar and eartag colours. We placed trail cameras near known squirrel locations to obtain points of verification at which we knew an individual was out of its nest. When we had a visual sighting (including from trapping) or photo of a collared squirrel, we recorded the date and time to verify that the geolocator also recorded out-of-nest levels of light at that time. For further verification, we used control geolocator collars placed in each of the three silvicultural treatments in 2023. We placed each collar on a tree branch at eye level for at least a full sunny and cloudy day, choosing locations not in the open, to be able to account for darkness that may result from vegetation cover. In the uniform shelterwood treatment, which had the least light penetration, we also placed the control collar for a full rainy day. In addition to placing the collar on a tree branch, in the uniform shelterwood treatment, we also placed the collar approximately 30 cm into two different burrows. In 2018, in the unmanaged reference treatment, we also placed a control collar on the ground in the centre of the trapping grid.

*Personality Analysis*

We analysed each behavioural test video to quantify personality traits of captured squirrels. We define personality, in line with the commonly used definition, as 'the repeatable part of an individual's behaviour' (Dingemanse & Wright, 2020, p. 865). We analysed the open-field and mirror tests using ANY-maze behavioural tracking software (version 5.1; Stoelting, CO, U.S.A.), which allowed us to measure mean speed (activity), rear rate (exploration; a rear is when an individual raises itself upright on its hindlegs) and the proportion of the individual's time spent grooming (ability to cope with stress or anxiety), spent in the centre of the box (boldness), spent being aggressive towards the mirror (aggressiveness; i.e. lunging, tail flicking, vocalizations and an antagonistic stance), spent being social towards the mirror (sociality; i.e. sniffing, walking beside, rearing and relaxed stance) and spent close to the mirror (curiosity or interaction with others; see Supplementary Video S1). Time spent inactive during the handling bag test (docility) was already quantified in the field (see Supplementary Table S1 for complete descriptions and interpretations of each behavioural variable).

We estimated repeatability, defined as the amount of variation attributed to differences among individuals, rather than differences within individuals (Dingemanse & Dochtermann, 2013). Therefore, a highly repeatable trait where individuals are behaving consistently between instances represents a small proportion of total trait variation within an individual and the majority of variation among individuals. For all eight measured behavioural variables across all 8 years of our long-term field study, we calculated

the adjusted and nonadjusted repeatability for each variable using the 'lme4' package (version 1.1–35.2; Bates et al., 2015) to determine which traits could be considered personality. For both repeatability values, we used individual identity as a random effect, and for adjusted repeatability, we used sex, body weight, silvicultural treatment, trapping session (month) and trial number as fixed effects. We included body weight as a proxy for both age and reproductive status, which we expected would influence trait expression. We included silvicultural treatment to account for ambient light and noise differences, and trapping session to account for behavioural changes associated with the autumn season in which squirrels have distinct activity patterns due to increased foraging. We included trial number to potentially account for any test habituation that may have occurred. We used the 'rptR' package (version 0.9.22; Stoffel et al., 2017) to calculate repeatability estimates using 95% confidence intervals (CI) and 1000-permutation bootstrapping. We also calculated the among-individual and within-individual (residual) variance components of adjusted repeatability. We conducted Box–Cox transformations (Box & Cox, 1964) on all behavioural variables to approach normality. We considered any trait that had an adjusted repeatability estimate over 0.2 with a 95% CI removed from zero a personality trait (Nakagawa & Schielzeth, 2010).

For each personality variable, we fitted a linear mixed model with individual identity as a random effect, and sex and trapping grid as fixed effects. For each individual, we extracted best linear unbiased prediction (BLUP) values for each personality variable across 1000 simulations and calculated the mean value for obtaining a mean simulated BLUP value using the 'arm' package (version 1.10–1; Gelman & Su, 2018). This method is used for obtaining a single-point estimate of a random effect (Dingemanse et al., 2020), in this case, of individual identity. The use of BLUP calculations without simulations has been criticized for overlooking uncertainty in estimates (Houslay & Wilson, 2017), so we used simulated BLUP values as a less precise yet unbiased approach for obtaining a single mean BLUP estimate for each personality trait measured in the standardized tests for each individual (Dingemanse et al., 2020; Villegas-Ríos et al., 2018). Subsequent references to personality refer to this mean BLUP value.

We chose to not use a principal component analysis (PCA) due to several disadvantages, including the inability to use multiple repeated measurements within the PCA and the fact that two individuals may have the same PCA score but for different reasons (i.e. a high value for different traits with medium loadings on the same axis), which ultimately may homogenize data rather than emphasize individual variation (Savazza et al., 2025). In addition, PCA is most useful when traits are highly correlated, which was not the case here. To avoid collinearity, we tested for correlations between each combination of personality traits measured in the standardized tests using all individuals captured within the 8-year period. All combinations of behavioural variables used in our subsequent analyses (rear rate, time spent inactive during the handling bag test and proportion of time spent aggressive) had correlation coefficients less than 0.4, which is below the commonly accepted threshold of 0.7 (Dormann et al., 2013) and below the threshold of 0.6 for when the independent effects on the response variable are uncertain (Morrissey & Ruxton, 2018). The highest correlation was between handling and rear rate at -0.35. We performed these analyses using R software (version 4.4.1; R Core Team, 2022).

*Personality Distributions*

To determine whether the mean ranks of personality traits measured in the standardized tests were significantly different between silvicultural treatments (testing hypothesis 1), we evaluated the probability density function of each trait for individuals living in each of the distinct forest types using nonparametric Kruskal–Wallis tests. In addition, we compared personality distributions (testing hypothesis 2) by calculating the phenotypic distance for each personality trait between populations using the nonparametric $\Delta p$ method, which calculates this measure based on a joint cumulative distribution function across multiple traits among populations (Safran et al., 2012). We conducted $\Delta p$ tests in MATLAB software (version 9.13.0; MathWorks, Natick, MA, U.S.A., https://www.mathworks.com). We also conducted a Kruskal–Wallis test followed by Dunn's post hoc test to determine whether mean ranks of squirrel body weight differed between silvicultural treatments, as this could be a potential proximate factor underlying certain personality central tendencies and distribution differences. For all tests, we applied the Benjamini–Hochberg correction, which controls false discovery rate and reduces type I errors, to get an adjusted set of $P$ values corrected for multiple testing (Benjamini & Hochberg, 1995).

*Activity Analysis*

Using the raw light measurement data from the geolocators, we were able to distinguish nest occupancy at a 5 min resolution on days of varying weather conditions. We used a threshold of 25 lx (Anders et al., 2017; Williams et al., 2014); for any light value below this threshold during the daytime, we inferred that the squirrel was in its nest, either in an underground burrow or chamber nest in a tree. Approximately 30 min after sunrise, light values consistently reached above 25 lx, and approximately 30 min before sunset, light values consistently dropped below 25 lx, so we did not include these twilight periods in which nest occupancy was difficult to determine in our analysis. We used sunrise and sunset time data for Bradley, Maine, U.S.A. (U.S. Naval Observatory Astronomical Applications Department, 2018; 2023). We also excluded the day of collaring for each individual, as isoflurane impacts activity for a few hours, and the day of decollaring, as trap confinement upon recapture impacts normal activity. From the raw light data, we calculated three metrics of activity: (1) average total time active per day; (2) average number of active bouts per day; (3) daily average length of active bout. We define an active bout as a continuous period when an individual is out of its nest.

However, our three activity variables were highly correlated. The amount of time spent active per day had relatively high correlation coefficients with the number of active bouts per day (−0.50) and with the average length of active bouts (0.56). The correlation coefficient between the number of active bouts per day and the average time length of active bouts was -0.86. Due to these high correlations between activity variables, the only dependent variable we investigated was the amount of time spent active per day, as this was what we considered the most biologically relevant aspect of red squirrel activity patterns under natural conditions.

We verified activity assignments using three control collars in 2023 in each of the three silvicultural treatments and one control collar in 2018 in a reference forest plot placed on the ground in the centre of our trapping grid, totalling 6129 control light measurements across 26 days (Supplementary Table S3). Light values recorded inside burrows ranged from 1.136 to 9.084 lx (mean ± SD = 2.726 ± 2.057 lx). Light values recorded by control collars on the ground or on tree branches during August rarely dropped below 25 lx during the daytime period (between 30 min after sunrise and 30 min before sunset), regardless of weather conditions. Overall, 0.07% and 1.04% of light values in uniform shelterwood and unmanaged forests, respectively, were below 25 lx during the daytime for control collars set during August. In contrast, 23.6% and

27.7% of light values in irregular shelterwood and unmanaged forests, respectively, were below 25 lx for control collars set during late September, with these dark values occurring within 2 h after sunrise and 2 h before sunset, potentially indicating an effect of sun angle change over the season. However, light measurements from squirrels in September and October in these treatments consistently revealed light values >25 lx starting 30–90 min after sunrise, indicating first emergence from the nest, and light values <25 lx at 30–90 min before sunset, indicating final entrance to the nest that day. Overall, squirrel activity was typically clear based on the recorded light measurements (see Supplementary Fig. S1 for an example of a squirrel from an irregular shelterwood forest in October, Supplementary Fig. S2 for an example control collar from an unmanaged forest in September and Supplementary Fig. S3 for a comparison between light changes recorded by geolocators on a control collar and collared squirrel on the same day in August in the same unmanaged forest trapping grid). This is potentially due to the squirrels commonly being active high in trees where sunlight intensity differs from near the forest floor where control collars were placed.

We conducted general linear modelling in R (version 4.4.1; R Core Team, 2022) with the average total time active per day as our dependent variable, with one value per individual. We used a forward model selection technique (Blanchet et al., 2008), beginning with a null model with no predictors. First, models with single individual variables (i.e. sex, number of days monitored) were compared to the null. If a model ranked more than 2 ΔAIC above the null, then the individual variable was carried forward to all subsequent steps. Next, time-varying variables (i.e. year, average trapping session monitored) were added and tested in the same way, followed by environmental characteristics (i.e. forest treatment). No variables were moved on to subsequent models unless they were included in the previous top model above the null model. If multiple models ranked above the null, we combined the variables from each model to test for additive effects. If the additive model was more than 2 ΔAIC above the previous single variable top model, then the additive model moved on. The resulting top model from this set became the null model for the next set, including all of its covariates in all subsequent models. Finally, we tested the effects of three repeatable behavioural variables (i.e. rear rate, proportion of time aggressive and time spent inactive during the handling bag test; testing hypothesis 3), which were all *z*-transformed to make the coefficients comparable. We selected the top model from this final set for inference.

### *Ethical Note*

This research followed procedures designed to ensure the health and safety of all animals and researchers. All trapping and handling procedures were approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC A2021-12-01, A2018-11-02 and A2015-11-02). We checked squirrel traps each afternoon and closed them overnight to limit the amount of time animals spent inside the traps and prevent exposure to weather. In the case of inclement weather, we checked traps earlier in the day. Bait consisted of peanut butter, which sustained animals during the day. We sanitized PIT tag applicators using 70% isopropyl alcohol between individuals. We only collared adult squirrels and did not collar pregnant or lactating females. We anaesthetized squirrels receiving collars using isoflurane, allowing individuals to be unconscious for the duration of the collaring process (approximately 20 s) to limit distress to the animals during handling and increase safety for researchers. After placing squirrels back into the trap in which they were caught, we waited a minimum of 10 min, closely monitoring their behaviour for any irregularities, prior to releasing them back in the exact location in which they were trapped. We ensured collar weights were below or within the recommended maximum of 4–7% of the individual's body weight to avoid impacting the normal behaviour of the animal (Stevenson et al., 2013).

## RESULTS

### *Personality*

We tested and analysed the personality of 325 North American red squirrels (179 males, 144 females) across 872 observations from 2016 to 2023 and found significant adjusted repeatability estimates (mean = 0.260, range 0.165–0.400) and nonadjusted repeatability estimates (mean = 0.256, range 0.172–0.376) for all eight behavioural variables tested (Table 1). Of the 325 unique squirrels, 181 were tested once, 65 were tested twice, 36 were tested three times, 24 were tested four times, 16 were tested five times, 1 was tested six times and 2 were tested eight times (44.3% of squirrels were tested more than once and 13.2% were tested four or more times). We used three personality traits with adjusted repeatability >0.2 (mean = 0.295, range 0.202–0.400) and correlation coefficients <0.7 in our analysis.

Mean rank values of aggression (proportion of time spent aggressive during the mirror test) differed between red squirrel populations living in different forest types, with unmanaged forests having significantly higher aggression than both managed forest types (Kruskal–Wallis test: $\chi^2_2 = 24.587$, $P < 0.001$; Table 2). Distributions of aggression also differed between populations, with a significantly larger proportion of aggressive individuals living in unmanaged reference forest compared with populations living in uniform shelterwood ($\Delta p = 23.388$, $P = 0.005$) and irregular shelterwood ($\Delta p = 34.056$, $P < 0.001$) treatments

**Table 1**
Adjusted and nonadjusted repeatability estimates (RPT) for behavioural variables of North American red squirrels calculated from behavioural tests from 2016 to 2023

| Behavioural variable | Mean | Range | Adjusted RPT [95% CI] | Nonadjusted RPT [95% CI] | No. of observations | No. of individuals |
|---|---|---|---|---|---|---|
| Rear rate | 0.025 | 0–0.253 | 0.233 [0.119, 0.338] | 0.257 [0.149, 0.363] | 563 | 304 (168 M, 136 F) |
| Handling | 31.208 | 0–60 | 0.394 [0.279, 0.491] | 0.376 [0.255, 0.490] | 504 | 283 (153 M, 130 F) |
| Proportion of time spent aggressive | 0.007 | 0–0.469 | 0.200 [0.059, 0.308] | 0.223 [0.108, 0.334] | 552 | 300 (165 M, 135 F) |
| Proportion of time spent grooming | 0.029 | 0–0.801 | 0.200 [0.083, 0.314] | 0.195 [0.085, 0.309] | 547 | 296 (162 M, 134 F) |
| Mean speed[1] | 0.031 | 0–0.409 | 0.253 [0.140, 0.360] | 0.289 [0.178, 0.401] | 564 | 305 (167 M, 138 F) |
| Proportion of time spent in the centre[1] | 0.035 | 0–1 | 0.340 [0.225, 0.456] | 0.351 [0.231, 0.461] | 532 | 295 (160 M, 135 F) |
| Proportion of time spent social | 0.020 | 0–0.475 | 0.181 [0.075, 0.294] | 0.193 [0.086, 0.296] | 552 | 300 (165 M, 135 F) |
| Proportion of time spent close to the mirror | 0.244 | 0–1 | 0.170 [0.059, 0.286] | 0.172 [0.066, 0.281] | 554 | 300 (164 M, 136 F) |

M: males; F: females. See Supplementary Table S1 for descriptions of each personality trait and Supplementary Table S2 for among-individual and within-individual variance components of adjusted repeatability. Number of individuals varies between behavioural variables due to videos being too low quality to accurately determine timing of certain behaviours, tracking software errors and escapes partway through testing.

[1] Behavioural variables with correlation coefficients >0.7 with rear rate and each other.

**Table 2**
Results of analysis comparing North American red squirrel personality traits across three silvicultural treatments

| Behavioural variable | Personality trait | No. of individuals | Kruskal–Wallis $\chi^2_2$ ($P$) | $\Delta p$ ($P$) | | |
|---|---|---|---|---|---|---|
| | | | | REF/SW2 | REF/ISW | SW2/ISW |
| Rear rate | Exploration | 304 | 0.074 (0.937) | -2.509 (0.831) | -8.805 (0.482) | -6.296 (0.682) |
| Handling | Docility | 283 | 0.491 (0.937) | 1.221 (0.870) | 4.248 (0.831) | 3.027 (0.831) |
| Proportion of time spent aggressive | Aggression | 300 | **24.587 (<0.001)** | **23.388 (0.005)** | **34.056 (<0.001)** | 10.667 (0.390) |

REF: unmanaged reference forests; SW2: uniform shelterwood forests; ISW: irregular shelterwood forests. Kruskal–Wallis tests compared mean trait ranks and $\Delta p$ tests compared trait distributions. We applied the Benjamini–Hochberg correction to generate an adjusted set of $P$ values reported in the table. Bold values indicate statistically significant results ($P < 0.05$).

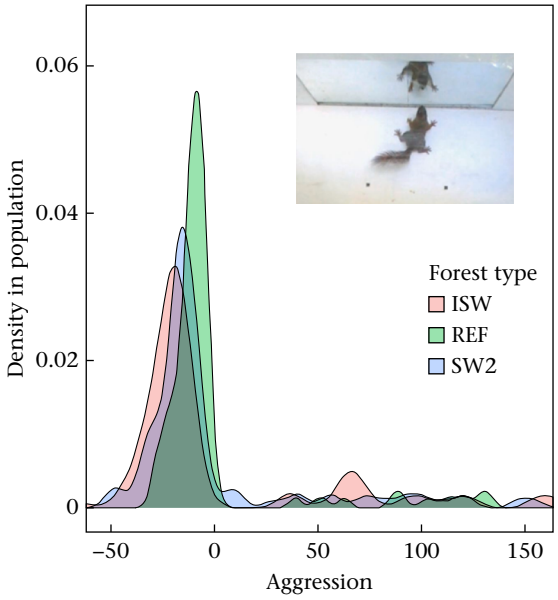


**Figure 2.** Distributions of aggression scores (proportion of time spent aggressive during the mirror test) of North American red squirrel populations living in unmanaged reference forests (REF), uniform shelterwood forests (SW2) and irregular shelterwood forests (ISW) ($N = 300$ individuals; 164 males, 136 females).

(Table 2, Fig. 2). There were no significant differences between mean ranks or distributions for rear rate (exploration) or handling (docility) across silvicultural treatments (Table 2).

Mean squirrel body weights among the three different forest types (mean ± SD: unmanaged reference forest: 152.8 ± 23.1 g; uniform shelterwood forest: 147.0 ± 20.8 g; irregular shelterwood forest: 152.6 ± 22.4 g) significantly differed (Kruskal–Wallis test: $\chi^2_2 = 6.274$, $P = 0.043$), with reference forests having red squirrels that were significantly heavier than those in the uniform shelterwood forests (Dunn test: unmanaged reference forest/uniform shelterwood forest: $Z = 2.472$, $P = 0.040$).

### *Activity*

Our geolocator light analysis included 183 000 light measurements from 617 days of activity from 14 individual North American red squirrels (3 males, 11 females; 4 unmanaged reference forest, 4 uniform shelterwood forest, 6 irregular shelterwood forest; number of days monitored per individual: mean = 44.1, range 26–123). The mean (± SD) amount of time spent active (out of the nest) per day was 575 ± 81 min (range 407–679), the mean number of active bouts per day was 8.2 ± 5.7 bouts (range 2.2–19.8), and the mean average time length of active bouts was 169 ± 118 min (range 21–393). Again, due to high correlation, we only investigated the average amount of time spent active per day.

The top model predicting the average amount of time spent active per day included an additive effect of rear rate ($\beta \pm SE = -0.523 \pm 0.203$) and year ($\beta \pm SE = -0.228 \pm 0.082$), with $R^2 = 0.506$ (Table 3). Individuals that had higher rear rates in the open-field test (more exploratory) spent less time active per day (Fig. 3).

## DISCUSSION

Through our long-term field experiment conducted on North American red squirrels in Maine (U.S.A.) we found that forest

**Table 3**
Full model set (all models ranked above the null model) from our linear model selection analysis

| Response variable | Top models | $K$ | $\Delta AIC_c$ | $AIC_cWT$ |
|---|---|---|---|---|
| Average total time active per day | Rear rate + year | 4 | 0 | 0.62 |
| | Year | 3 | 2.54 | 0.17 |
| | Rear rate | 3 | 3.44 | 0.11 |
| | ~1 | 2 | 3.75 | 0.09 |

The response variable is the average total time active per day for each individual red squirrel ($N = 14$ individuals; 3 males, 11 females). For each model, the number of parameters ($K$), corrected Akaike information criterion ($\Delta AIC_c$) and AIC weight ($AIC_cWT$) are given.

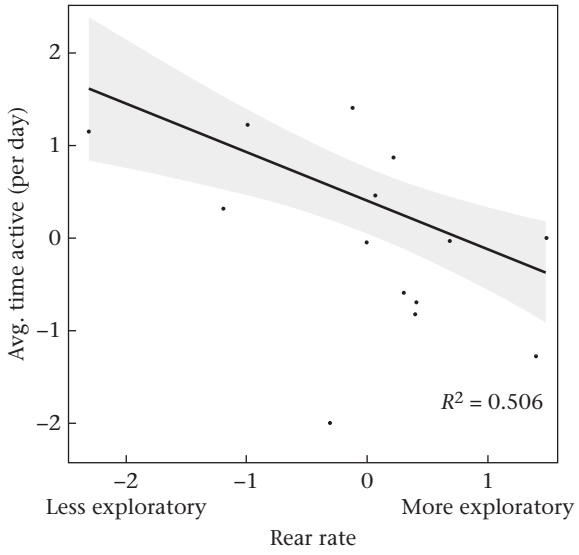


**Figure 3.** Relationship between exploratory behaviour (i.e. rear rate in the open-field test) of North American red squirrels and time spent active per day ($N = 14$ individuals; 3 males, 11 females). Predictions were obtained from the top model and the 85% confidence interval is shown. The predicted relationship is shown for 2018. Data points depict raw data and axes variables are scaled.

management is associated with distinct personality distributions in a population and that personality, as measured using standardized tests, influences free-ranging activity patterns in the wild. Specifically, our results indicate that silvicultural management practices (i.e. uniform shelterwood and irregular shelterwood) are associated with a decrease in the proportion of aggressive individuals, displaying the importance of considering anthropogenic disturbance as a potential driver of behavioural compositions within a population. In addition, our results show that individuals with more exploratory personalities spend less time active per day. Differing activity levels in seed-hoarding animals can potentially impact seed dispersal processes and forest regeneration rates, which are vital for productive forest management.

*Effects of Land Use on Personality Distributions*

Aggression (measured in the mirror test) was significantly higher among individuals living in unmanaged forests compared to both uniform and irregular shelterwood managed forest types, suggesting that there is a lower proportion of aggressive individuals living in managed forests. Past research has found that land use change, notably urbanization, is associated with shifts in behavioural compositions (Dammhahn et al., 2020; Dhawale et al., 2020; Miranda et al., 2013; Sol et al., 2013; Tranquillo et al., 2024), yet few studies have investigated forest management techniques in this context (Brehm et al., 2019). Our finding that silvicultural treatment is a potential cause of shifting personality compositions is in line with past research, yet the specific personality traits affected differed for other species of small mammals, including boldness, activity and anxiety (Brehm et al., 2019) rather than aggression (not previously measured). In another study, researchers compared personality of Eurasian red squirrels, *Sciurus vulgaris*, between different qualities of conifer forests and found significant personality differences, including that squirrels living in the marginal edge habitat were more active and social than in the other higher-quality forests (Tranquillo et al., 2022). Although the study was focused on habitat quality rather than anthropogenic disturbance, it is in line with our findings that different forest structures are associated with distinct tree squirrel personalities.

Past research investigating behaviours in lion-tailed macaques, *Macaca silenus*, across four forest types of varying anthropogenic modification found that aggressive interactions between conspecifics were significantly less common in undisturbed forest interiors compared to forest edges, open forest patches and human settlements (Dhawale et al., 2020), contrasting our finding. However, this disparity could be because we investigated different species, or because of differences in forest structure between our open unmanaged forests and the study's dense undisturbed rainforest (Dhawale et al., 2020). Additionally, it is important to note that the macaque study was focused on aggressive interactions rather than consistent among-individual differences in aggression measured in a standardized behavioural assay.

There is evidence that aggression may be one of the more flexible personality traits (Bell & Sih, 2007; Kelley et al., 2015; Wauters et al., 2019). Past research has found that more aggressive individuals are more likely to elicit aggressiveness in others (McGlothlin et al., 2010), which could be a mechanism for how the squirrels inhabiting reference forests became more aggressive. The large open areas between widely spaced large trees that characterize unmanaged forests could facilitate a higher frequency of individuals visually perceiving one another, leading to increased aggressive displays, vocalizations and interactions. For North American red squirrels in particular, there is evidence that aggression may change as an individual matures, with more aggressive juveniles becoming less aggressive over time, and less aggressive juveniles becoming more aggressive over time, resulting in no mean change in aggression with maturation at the population level (Kelley et al., 2015). Part of the maturation process for red squirrels is territory acquisition, which may be a key factor in aggressive tendencies (Kelley et al., 2015). Therefore, our finding that a greater proportion of aggressive individuals were living in the unmanaged forests could be a result of having a higher proportion of younger, more aggressive individuals. However, upon investigation of squirrel body weight as a proxy for age, we found that unmanaged forests had heavier squirrels, suggesting that mean age differences may not explain higher aggression in unmanaged forests. However, squirrel body weights varied substantially, so weight may not be the best proxy for age in our system. Adult body weight may fluctuate more strongly with seasonal food resources or an individual's ability to acquire such resources, rather than with age, so caution must be taken in drawing conclusions regarding the relationship between age and body weight. Other studies on North American red squirrels have found that aggression is highly repeatable across ontogeny (Martinig et al., 2021, 2022).

Alternatively, perhaps forests that lack human disturbance are of the highest quality and therefore highly desired habitats, allowing only the most aggressive individuals to establish and maintain their territories (Riechert, 1998; Scales et al., 2013). Because quality of territory varies with the competitive ability of the individual, following an ideal despotic distribution (Calsbeek & Sinervo, 2002), the more aggressive individuals inhabiting undisturbed forests may have superior competitive abilities. For example, higher aggression in females was associated with more offspring across their life span (Haines et al., 2020), as well as increased offspring survival in most years (Boon et al., 2007; Taylor et al., 2014), meaning that overall, the squirrel populations in the unmanaged forests, which are overall more aggressive, may have higher fitness compared to squirrel populations in managed forests. In addition, because the successful acquisition or maintenance of territory ownership in North American red squirrels is related to having a larger body size (Stuart-Smith & Boutin, 1994), our finding that unmanaged forests had heavier squirrels than the uniform shelterwood forests may support the idea that the squirrels living in the unmanaged forest had slightly superior competitive abilities. However, squirrel body weight varied substantially, so although statistically significant, it is difficult to know whether the weight difference of 5.8 g between squirrels in unmanaged and uniform shelterwood forests is biologically relevant.

In Eurasian red squirrels, areas of high population density had the least aggressive individuals (Haigh et al., 2017), potentially indicating habituation and familiarization with neighbours, leading to higher tolerance (Siracusa et al., 2019; Temeles, 1994). In North American red squirrels, frequency of aggressive physical interactions between individuals was found to be higher at lower densities (Dantzer et al., 2020). Across our 8-year study, the unmanaged forests commonly had the least captures, so low population density and neighbour unfamiliarity could be potential reasons for increased aggression in unmanaged forests.

*Effects of Personality on Activity*

More exploratory individuals (i.e. higher rear rate in the open-field test) spent less time active per day on average. This finding is counter to our hypotheses that more active, exploratory and aggressive individuals would spend more time active in the wild (Boon et al., 2008; Gharnit et al., 2020; Haigh et al., 2017). We expected individuals exhibiting more active behaviours in our standardized tests would also exhibit more active behaviours in the wild

due to personality being consistent across time and contexts (Sih et al., 2004, 2015), including in captivity and in the wild (Boon et al., 2008; Herborn et al., 2010; Yuen et al., 2016). However, our result is not necessarily in opposition with past research finding personality consistency across contexts. Although these more exploratory individuals spent less time active per day, perhaps they were more active during the time they spent out of their nests. For example, they could have moved farther distances, travelled quicker, acquired food more efficiently and used up energy at a higher rate, allowing them, or even requiring them, to take longer rests. Different foraging strategies are favoured depending on individual personality (Jeffries et al., 2021), and past studies have found that more exploratory individuals locate food more frequently due to their higher motivation to feed (David et al., 2012), reduced consideration of risk (Sih & Del Giudice, 2012) and increased movement (Budaev, 1997). This allows more exploratory individuals to have higher competitive abilities in locating (B. Humphreys & Mortelliti, 2024) and acquiring (Cole & Quinn, 2012) food resources. In addition, exploratory behaviours have higher energy requirements, which can be facilitated by digestive efficiency, increasing available energy for individuals with these personality types (Careau & Garland, 2012). Perhaps by being more efficient in finding resources, dominating patches and digesting food, more exploratory individuals are able to complete survival tasks in less time, resulting in more time spent inactive in their nests, yet future work would be required to test this hypothesis.

Activity may also be influenced by the degree of sociality with neighbours or personality-dependent resource acquisition strategies. North American red squirrels have been found to increase nest occupancy as a response to increasing familiarity with neighbours, potentially because they do not have to be as vigilant (Siracusa et al., 2019). In our study, perhaps the individuals that spent the least amount of time in their nests (more exploratory) were more tolerant to new, unknown neighbours, or their exploratory tendencies allowed them to become more familiar with any new neighbours more quickly than less exploratory individuals. Also, it has been suggested that different personality types, including exploratory tendency, utilize different space use strategies to increase available food and mates (Wauters et al., 2021), which could be a reason for the personality–activity relationship we observed.

### *Aggression and Activity*

While the personality variable that we found to be affected by land use (aggression during mirror test) was not the trait that led to ecological consequences relating to activity patterns (rear rate during open-field test), aggression and activity may be linked. There is evidence of positive correlations between aggression and activity as a result of both genetic and maternal effects (Taylor et al., 2012), and research on behavioural syndromes commonly finds correlations between these two traits across taxa (Chapman et al., 2011; Dingemanse et al., 2007). In addition, both activity and aggression are often positively correlated with food intake rate and productivity, indicating fast behavioural types (Biro & Stamps, 2008). In summary, our result that aggression is a key trait impacted by land use change may still potentially indicate subsequent ecological consequences related to activity patterns and foraging dynamics, despite us finding no significant effect of aggression on time spent active.

### *Limitations of Our Study*

We acknowledge that limitations exist in our study. First, we had a relatively small sample size of individual squirrels for the activity analysis ($N = 14$). While more individuals would have reinforced our results, the geolocators were deployed during two different years (2018 and 2023), collecting fine resolution light data every 5 min, generating many discrete data points for analysis. In addition, our 8 years of personality data on 325 individual red squirrels allowed for robustness in our personality analyses, with similar or larger proportions of retested individuals compared to other squirrel personality studies (Kelley et al., 2015; Mazzamuto et al., 2019; Santicchia et al., 2019).

In assigning in nest and out of nest status, some uncertainty existed, especially during the low light morning and evening twilight periods, and dark values could have arisen from thick vegetation shadows and weather variability. However, our four control collars spread across silvicultural treatments and years allowed us to collect typical light data inside burrows, on the ground and on tree branches across 26 total days during sunny, cloudy and rainy weather. Careful observation of control light patterns provided useful comparisons for our squirrel light data. Finally, it is possible that individuals may have been inactive, but not in their nests, as past studies observed tree squirrels resting on branches in full sunlight (Anders et al., 2017; Bosch & Lurz, 2013), and resting could make up approximately 3–4% of their time out of the nest (Wauters et al., 1992). However, in nest and out of nest status still provides a biologically relevant measurement, despite some instances of inactivity out of the nest.

### *Behavioural Conservation*

Our study adds to the growing body of research showing that anthropogenic alterations to landscapes are associated with distinct behavioural compositions (Brehm et al., 2019; Miranda et al., 2013), and the ecological consequences of these changes must be considered. For example, environmental degradation can result in decreased personality diversity over time (Jeffries et al., 2021), which may reduce the functionality of the impacted ecosystem if individuals with key personality traits are lost. Although forest management often retains some habitat for wildlife (Hunter, 1990; Lindenmayer et al., 2006), the removal of trees inevitably modifies the surrounding natural environment, impacting animal species diversity, with different species responding in unique ways (Fredericksen & Fredericksen, 2002). Beyond the species level, it is critical that we are aware of how forest harvesting regimes impact different personalities in different ways because of their unique roles in the community (Brehm et al., 2019).

Understanding the effects of forest management on seed-hoarding animals is of particular importance, due to their key role in seed movement and forest regeneration rates, which is of critical interest to forest managers. Optimizing the efficiency and success of forest growth may rely on the local seed-dispersing animal guild to contain a balanced composition of personalities. Because some individuals disproportionately contribute to seed predation as opposed to successful seed dispersal, behavioural shifts from anthropogenic forest alterations may decrease the functioning of this vital ecosystem service. With increasing human impacts to the land, maintaining behavioural diversity should be a priority for conservation managers.

## Author Contributions

**Brigit R. Humphreys:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Allison M. Brehm:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration,

Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Alessio Mortelliti:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

## Data Availability

Data and code used for this analysis are available from the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.26928658 (Humphreys et al., 2026).

## Declaration of Interest

The authors declare no conflict of interest.

## Acknowledgments

This work was funded by a U.S. National Science Foundation Career Award (IOS number 1940525), Penobscot Experimental Forest Research Funds and the United States Department of Agriculture McIntire-Stennis Project (ME041620 and ME041913). In addition, we thank Margaret Merz, Ivy Yen, Margaux Duparcq and Sara Boone for data collection and project management, our many field and lab technicians for data collection and video analysis, Laura Kenefic (U.S. Forest Service) and Keith Kanoti (University of Maine) for facilitating and coordinating research in the Penobscot Experimental Forest, and Sydne Record, Danielle Levesque and Gabriela Franzoi Dri for manuscript edits.

## Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2026.123514.

## References

Anders, J. L., Uchida, K., Watanabe, M., Tanio, I., Shimamoto, T., Hamada, M., Yanagawa, H., & Koizumi, I. (2017). Usefulness and limitation of a tiny light-temperature logger to monitor daily activity levels of arboreal squirrels in temperate areas. *Mammal Research, 62*, 397–404.

Ashby, K. R. (1972). Patterns of daily activity in mammals. *Mammal Review, 1*(7-8), 171–185.

Bates, D. M., Maechler, M., Bolker, B. M., & Walker, S. (2015). *Lme4: Linear mixed-effects models using eigen and S4* (R package Version 1.1-35.2). https://cran.r-project.org/web/packages/lme4/lme4.pdf.

Bell, A. M., & Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters, 10*(9), 828–834.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B, 57*(1), 289–300.

Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution, 23*(7), 361–368.

Blanchet, F. G., Legendre, P., & Borcard, D. (2008). Forward selection of explanatory variables. *Ecology, 89*(9), 2623–2632.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist, 161*(1), 1–28.

Boon, A. K., Réale, D., & Boutin, S. (2007). The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters, 10*(11), 1094–1104.

Boon, A. K., Réale, D., & Boutin, S. (2008). Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos, 117*(9), 1321–1328.

Boone, S. R., Brehm, A. M., & Mortelliti, A. (2021). Seed predation and dispersal by small mammals in a landscape of fear: Effects of personality, predation risk and land-use change. *Oikos, 22*(2), Article e08232.

Bosch, S., & Lurz, P. W. W. (2013). The process of drey construction in red squirrels–nestbox observations based on a hidden camera. *Italian Journal of Mammalogy, 24*(2), 199–202.

Box, G. E., & Cox, D. R. (1964). An analysis of transformations. *Journal of the Royal Statistical Society, Series B: Statistical Methodology, 26*(2), 211–243.

Boyer, N., Réale, D., Marmet, J., Pisanu, B., & Chapuis, J. L. (2010). Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *Journal of Animal Ecology, 79*(3), 538–547.

Brehm, A. M., & Mortelliti, A. (2021). Land-use change alters associations between personality and microhabitat selection. *Ecological Applications, 31*(8), Article e02443.

Brehm, A. M., & Mortelliti, A. (2022). Small mammal personalities generate context dependence in the seed dispersal mutualism. *Proceedings of the National Academy of Sciences of the United States of America, 119*(15), Article e2113870119.

Brehm, A. M., Mortelliti, A., Maynard, G. A., & Zydlewski, J. (2019). Land-use change and the ecological consequences of personality in small mammals. *Ecology Letters, 22*(9), 1387–1395.

Budaev, S. V. (1997). Alternative styles in the European wrasse, *Symphodus ocellatus*: Boldness-related schooling tendency. *Environmental Biology of Fishes, 49*, 71–78.

Calsbeek, R., & Sinervo, B. (2002). An experimental test of the ideal despotic distribution. *Journal of Animal Ecology, 71*(3), 513–523.

Careau, V., & Garland, T., Jr. (2012). Performance, personality, and energetics: Correlation, causation, and mechanism. *Physiological and Biochemical Zoology, 85*(6), 543–571.

Chapman, B. B., Thain, H., Coughlin, J., & Hughes, W. O. (2011). Behavioural syndromes at multiple scales in *Myrmica* ants. *Animal Behaviour, 82*(2), 391–397.

Cole, E. F., & Quinn, J. L. (2012). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences, 279*(1731), 1168–1175.

Dammhahn, M., Mazza, V., Schirmer, A., Göttsche, C., & Eccard, J. A. (2020). Of city and village mice: Behavioural adjustments of striped field mice to urban environments. *Scientific Reports, 10*(1), Article 13056.

Dantzer, B., McAdam, A. G., Humphries, M. M., Lane, J. E., & Boutin, S. (2020). Decoupling the effects of food and density on life-history plasticity of wild animals using field experiments: Insights from the steward who sits in the shadow of its tail, the North American red squirrel. *Journal of Animal Ecology, 89*(11), 2397–2414.

David, M., Auclair, Y., Giraldeau, L.-A., & Cézilly, F. (2012). Personality and body condition have additive effects on motivation to feed in zebra finches *Taeniopygia guttata*. *Ibis, 154*(2), 372–378.

Dhawale, A. K., Kumar, M. A., & Sinha, A. (2020). Changing ecologies, shifting behaviours: Behavioural responses of a rainforest primate, the lion-tailed macaque *Macaca silenus*, to a matrix of anthropogenic habitats in southern India. *PLoS One, 15*(9), Article e0238695.

Dingemanse, N. J., & de Goede, P. (2004). The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology, 15*(6), 1023–1030.

Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology, 82*(1), 39–54.

Dingemanse, N. J., Moiron, M., Araya-Ajoy, Y. G., Mouchet, A., & Abbey-Lee, R. N. (2020). Individual variation in age-dependent reproduction: Fast explorers live fast but senesce young? *Journal of Animal Ecology, 89*(2), 601–613.

Dingemanse, N. J., & Wright, J. (2020). Criteria for acceptable studies of animal personality and behavioural syndromes. *Ethology, 126*(9), 865–869.

Dingemanse, N. J., Wright, J., Kazem, A. J., Thomas, D. K., Hickling, R., & Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology, 76*(6), 1128–1138.

Doherty, T. S., Fist, C. N., & Driscoll, D. A. (2019). Animal movement varies with resource availability, landscape configuration and body size: A conceptual model and empirical example. *Landscape Ecology, 34*(3), 603–614.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R., Gruber, B., Lafourcade, B., Leitão, P. J., & Münkemüller, T. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography, 36*(1), 27–46.

Eccard, J. A., Liesenjohann, T., & Dammhahn, M. (2020). Among-individual differences in foraging modulate resource exploitation under perceived predation risk. *Oecologia, 194*(4), 621–634.

Elmqvist, T., Fragkias, M., Goodness, J., Güneralp, B., Marcotullio, P. J., McDonald, R. I., Parnell, S., Schewenius, M., Sendstad, M., Seto, K. C., & Wilkinson, C. (2013). *Urbanization, biodiversity and ecosystem services: Challenges and opportunities: A global assessment*. Springer Nature.

FAO. (2020). Main report. In Global forest resources assessment 2020. *Food and Agriculture Organization of the United Nations*. https://www.fao.org/interactive/forest-resources-assessment/2020/en/.

Favreau, A., Richard-Yris, M. A., Bertin, A., Houdelier, C., & Lumineau, S. (2009). Social influences on circadian behavioural rhythms in vertebrates. *Animal Behaviour, 77*(5), 983–989.

Fredericksen, N. J., & Fredericksen, T. S. (2002). Terrestrial wildlife responses to logging and fire in a Bolivian tropical humid forest. *Biodiversity & Conservation, 11*(1), 27–38.

Frey, S., Fisher, J. T., Burton, A. C., & Volpe, J. P. (2017). Investigating animal activity patterns and temporal niche partitioning using camera-trap data: Challenges and opportunities. *Remote Sensing in Ecology and Conservation, 3*(3), 123–132.

Gelman, A., & Su, Y. S. (2018). *arm: Data analysis using regression and multilevel/hierarchical models*. R package Version 1.10-1) https://cran.r-project.org/web/packages/arm/arm.pdf.

Gharnit, E., Bergeron, P., Garant, D., & Réale, D. (2020). Exploration profiles drive activity patterns and temporal niche specialization in a wild rodent. *Behavioral Ecology, 31*(3), 772–783.

Goheen, J. R., & Swihart, R. K. (2003). Food-hoarding behavior of gray squirrels and North American red squirrels in the central hardwoods region: Implications for forest regeneration. *Canadian Journal of Zoology, 81*(9), 1636–1639.

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin, 127*(1), 45–86.

Haigh, A., O'Riordan, R., & Butler, F. (2017). Variations in aggression and activity levels amongst squirrels inhabiting low and high density areas. *Ecological Research, 32*(6), 931–941.

Haines, J. A., Nason, S. E., Skurdal, A. M., Bourchier, T., Boutin, S., Taylor, R. W., McAdam, A. G., Lane, J. E., Kelley, A. D., Humphries, M. M., & Gorrell, J. C. (2020). Sex- and context-specific associations between personality and a measure of fitness but no link with life history traits. *Animal Behaviour, 167*, 23–39.

Halle, S., & Stenseth, N. C. (Eds.). (2000). *Activity patterns in small mammals: An ecological approach*. Springer Science & Business Media.

Herborn, K. A., Macleod, R., Miles, W. T., Schofield, A. N., Alexander, L., & Arnold, K. E. (2010). Personality in captivity reflects personality in the wild. *Animal Behaviour, 79*(4), 835–843.

Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural ecology. *Behavioral Ecology, 28*(4), 948–952.

Humphreys, B. R., Brehm, A. M., & Mortelliti, A. (2026). Data: Managing personalities: Effects of forestry on North American red squirrel personality distributions and activity. *Figshare Digital Repository*. https://doi.org/10.6084/m9.figshare.26928658.

Humphreys, B. R., & Mortelliti, A. (2024). Pilfering personalities: Effects of small mammal personality on cache pilferage. *Journal of Animal Ecology, 94*(3), 291–302.

Hunter, M. L. (1990). *Wildlife, forests, and forestry. Principles of managing forests for biological diversity*. Prentice Hall.

Hunter, M. L., Boone, S. R., Brehm, A. M., & Mortelliti, A. (2022). Modulation of ecosystem services by animal personalities. *Frontiers in Ecology and the Environment, 20*(1), 58–63.

Jeffries, P. M., Patrick, S. C., & Potts, J. R. (2021). Be different to be better: The effect of personality on optimal foraging with incomplete knowledge. *heoretical Ecology, 14*(4), 575–587.

Kelley, A. D., Humphries, M. M., McAdam, A. G., & Boutin, S. (2015). Changes in wild red squirrel personality across ontogeny: Activity and aggression regress towards the mean. *Behaviour, 152*(10), 1291–1306.

Kenefic, L. S., & Brissette, J. C. (2014). History of the Penobscot Experimental Forest, 1950–2010. In *Penobscot Experimental Forest: 60 years of research and demonstration in Maine, 1950–2010* (pp. 1–20). United States Department of Agriculture Forest Service [General Technical Report, Northern Research Station Proceedings, GTR-NRS-P-123] https://www.govinfo.gov/content/pkg/GOVPUB-A13-PURL-gpo46945/pdf/GOVPUB-A13-PURL-gpo46945.pdf.

Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual review of Ecology, Evolution, and Systematics, 34*(1), 153–181.

Larivee, M. L., Boutin, S., Speakman, J. R., McAdam, A. G., & Humphries, M. M. (2010). Associations between over-winter survival and resting metabolic rate in juvenile North American red squirrels. *Functional Ecology, 24*(3), 597–607.

Lindenmayer, D. B., Franklin, J. F., & Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation, 131*(3), 433–445.

Lodberg-Holm, H. K., Steyaert, S. M., Reinhardt, S., & Rosell, F. (2021). Size is not everything: Differing activity and foraging patterns between the sexes in a monomorphic mammal. *Behavioral Ecology and Sociobiology, 75*(76), 76.

Martin, J. G., & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Animal Behaviour, 75*(1), 309–318.

Martinig, A. R., Karst, H. J., Siracusa, E. R., Studd, E. K., McAdam, A. G., Dantzer, B., Delaney, D. M., Lane, J. E., Pokharel, P., & Boutin, S. (2022). Animal personality: A comparison of standardized assays and focal observations in North American red squirrels. *Animal Behaviour, 190*, 221–232.

Martinig, A. R., Mathot, K. J., Lane, J. E., Dantzer, B., & Boutin, S. (2021). Selective disappearance does not underlie age-related changes in trait repeatability in red squirrels. *Behavioral Ecology, 32*(2), 306–315.

Mazzamuto, M. V., Cremonesi, G., Santicchia, F., Preatoni, D., Martinoli, A., & Wauters, L. A. (2019). Rodents in the arena: A critical evaluation of methods measuring personality traits. *Ethology Ecology & Evolution, 31*(1), 38–58.

McGlothlin, J. W., Moore, A. J., Wolf, J. B., & Brodie, E. D., III. (2010). Interacting phenotypes and the evolutionary process. III. Social evolution. *Evolution, 64*(9), 2558–2574.

McGuire, B., & Bemis, W. E. (2007). Parental care. In J. O. Wolff, & P. W. Sherman (Eds.), *Rodent societies: An ecological and evolutionary perspective* (pp. 231–242). University of Chicago Press.

Merz, M. R., Boone, S. R., & Mortelliti, A. (2023). Predation risk and personality influence seed predation and dispersal by a scatter-hoarding small mammal. *Ecosphere, 14*(1), e4377.

Miranda, A. C., Schielzeth, H., Sonntag, T., & Partecke, J. (2013). Urbanization and its effects on personality traits: A result of microevolution or phenotypic plasticity? *Global Change Biology, 19*(9), 2634–2644.

Moiron, M., Laskowski, K. L., & Niemelä, P. T. (2020). Individual differences in behaviour explain variation in survival: A meta-analysis. *Ecology Letters, 23*(2), 399–408.

Morrison, S. F., Pelchat, G., Donahue, A., & Hik, D. S. (2009). Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. *Oecologia, 159*, 107–116.

Morrissey, M. B., & Ruxton, G. D. (2018). Multiple regression is not multiple regressions: The meaning of multiple regression and the non-problem of collinearity. *Philosophy, Theory, and Practice in Biology, 10*, 3. https://doi.org/10.3998/ptpbio.16039257.0010.003

Mortelliti, A., & Brehm, A. M. (2020). Environmental heterogeneity and population density affect the functional diversity of personality traits in small mammal populations. *Proceedings of the Royal Society B: Biological Sciences, 287*(1940). Article 20201713.

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews, 85*(4), 935–956.

Norberg, R. A. (1977). An ecological theory on foraging time and energetics and choice of optimal food-searching method. *Journal of Animal Ecology, 46*(2), 511–529.

Perals, D., Griffin, A. S., Bartomeus, I., & Sol, D. (2017). Revisiting the open-field test: What does it really tell us about animal personality? *Animal Behaviour, 123*, 69–79.

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing Version 4.4.1. https://www.R-project.org/.

Riechert, S. E. (1998). Game theory and animal contests. In L. A. Dugatkin, & H. K. Reeve (Eds.), *Game theory & animal behavior* (pp. 64–93). Oxford University Press.

Roth, T. C., Rattenborg, N. C., & Pravosudov, V. V. (2010). The ecological relevance of sleep: The trade-off between sleep, memory and energy conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1542), 945–959.

Rusak, B., & Zucker, I. (1975). Biological rhythms and animal behavior. *Annual Review of Psychology, 26*(1), 137–171.

Safran, R., Flaxman, S., Kopp, M., Irwin, D. E., Briggs, D., Evans, M. R., Funk, W. C., Gray, D. A., Hebets, E. A., Seddon, N., & Scordato, E. (2012). A robust new metric of phenotypic distance to estimate and compare multiple trait differences among populations. *Current Zoology, 58*(3), 426–439.

Santicchia, F., Romeo, C., Ferrari, N., Matthysen, E., Vanlauwe, L., Wauters, L. A., & Martinoli, A. (2019). The price of being bold? Relationship between personality and endoparasitic infection in a tree squirrel. *Mammalian Biology, 97*, 1–8.

Savazza, S., Merz, M. R., & Mortelliti, A. (2025). Measuring personality in wild small mammals: A review of methods and proposal for a standardised approach. *Mammal Review, 56*(1). Article e70010.

Scales, J., Hyman, J., & Hughes, M. (2013). Fortune favours the aggressive: Territory quality and behavioural syndromes in song sparrows, *Melospiza melodia*. *Animal Behaviour, 85*(2), 441–451.

Schirmer, A., Herde, A., Eccard, J. A., & Dammhahn, M. (2019). Individuals in space: Personality-dependent space use, movement and microhabitat use facilitate individual spatial niche specialization. *Oecologia, 189*(3), 647–660.

Schuett, W., Delfs, B., Haller, R., Kruber, S., Roolfs, S., Timm, D., Willmann, M., & Drees, C. (2018). Ground beetles in city forests: Does urbanization predict a personality trait? *PeerJ, 6*. Article e4360.

Siegel, J. M. (2008). Do all animals sleep? *Trends in Neurosciences, 31*(4), 208–213.

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution, 19*(7), 372–378.

Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1603), 2762–2772.

Sih, A., Mathot, K. J., Moiron, M., Montiglio, P. O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state–behaviour feedbacks: A review and guide for empiricists. *Trends in Ecology & Evolution, 30*(1), 50–60.

Siracusa, E. R., Wilson, D. R., Studd, E. K., Boutin, S., Humphries, M. M., Dantzer, B., Lane, J. E., & McAdam, A. G. (2019). North American red squirrels mitigate costs of territory defence through social plasticity. *Animal Behaviour, 151*, 29–42.

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology, 19*(2), 448–455.

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour, 85*(5), 1101–1112.

Stevenson, C. D., Ferryman, M., Nevin, O. T., Ramsey, A. D., Bailey, S., & Watts, K. (2013). Using GPS telemetry to validate least-cost modeling of gray squirrel (*Sciurus carolinensis*) movement within a fragmented landscape. *Ecology and Evolution, 3*(7), 2350–2361.

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution, 8*(11), 1639–1644.

Stuart-Smith, A. K., & Boutin, S. (1994). Costs of escalated territorial defence in red squirrels. *Canadian Journal of Zoology, 72*(6), 1162–1167.

Studd, E. K., Landry-Cuerrier, M., Menzies, A. K., Boutin, S., McAdam, A. G., Lane, J. E., & Humphries, M. M. (2019). Behavioral classification of low-frequency acceleration and temperature data from a free-ranging small mammal. *Ecology and Evolution, 9*(1), 619–630.

Suselbeek, L., Emsens, W. J., Hirsch, B. T., Kays, R., Rowcliffe, J. M., Zamora-Gutierrez, V., & Jansen, P. A. (2014). Food acquisition and predator avoidance in a Neotropical rodent. *Animal Behaviour, 88*, 41–48.

Svendsen, G. E., & Armitage, K. B. (1973). Mirror-image stimulation applied to field behavioral studies. *Ecology, 54*(3), 623–627.

Taylor, R. W., Boon, A. K., Dantzer, B., Réale, D., Humphries, M. M., Boutin, S., Gorrell, J. C., Coltman, D. W., & McAdam, A. G. (2012). Low heritabilities, but genetic and maternal correlations between red squirrel behaviours. *Journal of Evolutionary Biology, 25*(4), 614–624.

Taylor, R. W., Boutin, S., Humphries, M. M., & McAdam, A. G. (2014). Selection on female behaviour fluctuates with offspring environment. *Journal of Evolutionary Biology, 27*(11), 2308–2321.

Temeles, E. J. (1994). The role of neighbours in territorial systems: When are they 'dear enemies'? *Animal Behaviour, 47*(2), 339–350.

Tranquillo, C., Santicchia, F., Romeo, C., Bisi, F., Panzeri, M., Preatoni, D., Martinoli, A., Alberdi, A., & Wauters, L. A. (2024). Going urban: Variation in personality traits of an invasive species along an urbanization gradient. *Journal of Mammalogy, 105*(6), 1300–1308.

Tranquillo, C., Wauters, L. A., Santicchia, F., Preatoni, D., & Martinoli, A. (2022). Living on the edge: Morphological and behavioral adaptations to a marginal high-elevation habitat in an arboreal mammal. *Integrative Zoology, 18*(4), 746–761.

U.S. Naval Observatory Astronomical Applications Department. (2018). *Table of sunrise/sunset*. Bradley, Maine https://aa.usno.navy.mil/data/RS_OneYear.

U.S. Naval Observatory Astronomical Applications Department. (2023). *Table of sunrise/sunset*. Bradley, Maine https://aa.usno.navy.mil/data/RS_OneYear.

Villegas-Ríos, D., Réale, D., Freitas, C., Moland, E., & Olsen, E. M. (2018). Personalities influence spatial responses to environmental fluctuations in wild fish. *Journal of Animal Ecology, 87*(5), 1309–1319.

Walsh, R. N., & Cummins, R. A. (1976). The open-field test: A critical review. *Psychological Bulletin, 83*(3), 482–504.

Wauters, L. A., Mazzamuto, M. V., Santicchia, F., Martinoli, A., Preatoni, D. G., Lurz, P. W., Bertolino, S., & Romeo, C. (2021). Personality traits, sex and food abundance shape space use in an arboreal mammal. *Oecologia, 196*, 65–76.

Wauters, L. A., Mazzamuto, M. V., Santicchia, F., Van Dongen, S., Preatoni, D. G., & Martinoli, A. (2019). Interspecific competition affects the expression of personality-traits in natural populations. *Scientific Reports, 9*(1), Article 11189.

Wauters, L., Swinnen, C., & Dhondt, A. A. (1992). Activity budget and foraging behaviour of red squirrels (*Sciurus vulgaris*) in coniferous and deciduous habitats. *Journal of Zoology, 227*(1), 71–86.

Werner, E. E., & Anholt, B. R. (1993). Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist, 142*(2), 242–272.

Williams, C. T., Wilsterman, K., Kelley, A. D., Breton, A. R., Stark, H., Humphries, M. M., McAdam, A. G., Barnes, B. M., Boutin, S., & Buck, C. L. (2014). Light loggers reveal weather-driven changes in the daily activity patterns of arboreal and semifossorial rodents. *Journal of Mammalogy, 95*(6), 1230–1239.

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution, 27*(8), 452–461.

Yuen, C. H., Pillay, N., Heinrichs, M., Schoepf, I., & Schradin, C. (2016). Personality traits are consistent when measured in the field and in the laboratory in African striped mice (*Rhabdomys pumilio*). *Behavioral Ecology and Sociobiology, 70*, 1235–1246.