Effects of trap confinement on personality measurements in two terrestrial rodents

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Short title: Effects of trap confinement on personality measurements

Abstract

In recent years individual differences in the behavior of animals, or personalities, have been shown to influence the response of individuals to changing environments and have important ecological implications. As researchers strive to understand and predict the responses of individuals and populations to anthropogenic changes, personality studies in wild populations will likely continue to increase. Studies of personality in wild populations often require that animals are live-trapped before behavioral observation can occur; however, it is unknown what impact live trapping may have on the behavior of trapped individuals. Specifically, if the duration of trap confinement directly influences behavior, then by obtaining wild animals through live-trapping are we confounding the very measurements we are most interested in? To investigate this question, we performed a study using two small mammal species. We positioned high-definition trail cameras on Longworth small mammal traps in the field to observe capture events and record the time of capture. We then measured personality in captured deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*) using three standardized tests. With a repeatability analysis, we confirmed which behaviors could be considered personality traits, and through linear and generalized linear models, we found that the time an animal had spent confined to a trap before testing did not affect the majority of behaviors exhibited. Our results showed two weak behavioral effects of confinement duration on boldness and docility depending on whether an individual had been trapped previously. Our results suggest that personality measurements of wild, trapped small mammals are not determined by trapping procedures, but that researchers should control for whether an animal is naïve to trapping during analysis.

Introduction

Over the past few decades, the acknowledgement that many species of animals display consistent individual differences in behavior, or *personalities,* has become widespread (1–4). Personalities are heritable (5), have consequences for fitness (6–9), and can limit the ability of individuals to exhibit behavioral plasticity (10) resulting in trade-offs where certain personality types perform well in some ecological contexts but not in others (11). Because individual personalities can determine the response of individuals to changing environments (12,13) and have important ecological implications (14–16), personality studies in wild populations will likely continue to increase as researchers strive to understand and predict the responses of individuals and populations to anthropogenic changes (17–20).

Studies of personality in wild populations usually require that wild animals are live-trapped so that one or more standardized behavioral tests can be undertaken (21–24) but see (25) for a method of personality observation in non-captured animals. Because being trapped may induce stress (26–31), the process of capturing animals and subsequently measuring their personality offers additional challenges. Specifically, the stress of being trapped might influence the behaviors exhibited by wild animals, confounding the very phenomena we are investigating.

Several studies have explored the relationship between live trapping and the stress response of animals (29–31), and it is generally accepted that the stress of being captured releases glucocorticoids into the bloodstream (32). Glucocorticoids act to elevate breathing rate, heart rate, and blood pressure (29) which, following exposure to the threat of a predator attack, stimulates the mobilization of energy to facilitate an escape. When an animal is confined to a trap, however, this prolonged stressor may result in higher concentrations of glucocorticoids after longer durations spent in a trap (30), perhaps impacting behaviors exhibited during routine behavioral tests such as grooming, time spent moving, etc. (33–35). Thus far, studies looking to assess this phenomenon have focused on the hormonal/physiological response to trap-induced stress and results have been mixed (29,31,36). For example, live trapping does induce an initial stress response in southern red-backed voles (*Myodes gapperi*) and meadow voles (*Microtus pennsylvanicus*), but longer times spent in traps do not correlate with increased stress levels (29,36). In contrast, studies found that in deer mice (*Peromyscus maniculatus*) and North American red squirrels (*Tamiasciurus hudsonicus*) prolonged time spent in traps was positively correlated with stress hormone levels (31,36). In either scenario, it is unknown whether the time spent in traps may produce a behavioral response, since a change in stress hormones doesn't necessarily precede a change in behavior. If confinement duration affected the behavior exhibited during routine testing, this would require studies using personality data from trapped animals to control for confinement duration. This could be done by: checking traps more frequently, recording the time of capture (obtained using videos from camera traps placed on live traps) then controlling for the duration using imposed covariates in analysis, or using devices that signal when a capture has been made so that animals can be removed promptly (37,38). Empirical evidence is needed to explore the relationship between the time spent in a trap and behavioral response.

The objective of this study was to assess whether personality measurements obtained from live-trapped individuals are being confounded by the amount of time spent inside of a trap. Specifically, we sought to determine whether confinement duration affects the behaviors exhibited in routine behavioral tests. To meet this objective, we conducted a field experiment focused on the deer mouse (*Peromyscus maniculatus*) and the southern red-backed vole (*Myodes gapperi*), which have been the subject of previous personality studies (16,39). Using high-definition trail cameras positioned on Longworth small mammal traps in the field, we quantified the duration of time that individuals had spent inside a trap before behavior was observed in standardized behavioral tests the following morning. We explored these data to see whether behaviors exhibited in behavioral tests varied with the time spent inside the trap.

Results from this study will have implications for researchers who measure personality following the live-capture of an animal. These results will highlight whether we should take additional steps to ensure that our behavioral measurements are accurate and not unduly influenced by the trapping.

Materials and methods

Study site and small mammal trapping

This study was conducted in the Penobscot Experimental Forest (PEF, 44 51’ N, 68 37’ W) at the southern edge of the Acadian forest in east-central Maine, USA. This experimental forest consists of forest units chosen at random and logged separately with varying silvicultural treatments (minimum of two replicates per treatment). Management units average 8.5 ha in area (range 8.1–16.2 ha) and nearly 25 ha of forest (retained in two separate units) serves as reference and has remained unmanaged since the late 1800s (39,40).

We implemented a large-scale mark-recapture study on six trapping grids (Figure 1): two control (located in reference forest) and four experimental (two replicates in even-aged forest units and two in units treated with a two-stage shelterwood with retention). Trapping grids were 0.81 ha in area and consisted of 100 flagged points spaced 10 m apart. One Longworth trap was positioned at each flagged point. Traps were bedded with cotton and baited with a mixture of sunflower seeds, oats, and freeze-dried mealworms. We positioned trapping grids close to the center of the management unit to minimize edge-effects (mean distance between grids was 1.44 km; greater than the movements of our study species). We trapped at each trapping grid for three consecutive days and nights and checked traps each morning and evening. Trapping occurred once per month for five consecutive months each year (June–October 2016, 2017, 2018).

Figure 1. Map of our study area at the Penobscot Experimental Forest, Maine U.S.A.

Behavioral tests

We used three standard behavioral tests to measure personality of trapped individuals (Figure 2): an *emergence* test to assess boldness (33,41), an *open-field* test to measure activity and exploration in a novel environment (42,43), and a *handling bag* test to measure docility and the response to handling by an observer (23,44–46). Behavioral tests were performed in the order above prior to handling or marking. All tests and processing occurred at a base area in the home grid of the focal individual.

Figure 2. Three behavioral tests used to assess personality of deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*).

(A) An individual emerges from a Longworth trap in an emergence test. (B) An individual in motion during an open-field test. (C) An observer suspends an individual over a controlled arena during the handling bag test.

Behavioral tests were performed as follows: first, the animal was transferred directly from the trap of capture into a clean, empty Longworth trap. This trap was then placed on the floor of a box sized 46 x 46 x 60 cm (placed underneath a tarp to control for light levels and perceived canopy cover). To create a more natural environment, the inside of the box had been painted a light brown with a small amount of debris (dead leaves and pine needles) placed on the floor. A digital camera (Nikon CoolPix S3700) was mounted facing the opening of the Longworth trap, and the observer locked the trap door open before leaving the test area. After three minutes, the observer returned and ended the test. Individuals were caught in a plastic bag and then released into the center of the open-field arena. A five minute open-field test was performed in an arena (46 x 46 x 50 cm), placed on a level platform with perceived canopy cover controlled (39), and a mounted digital camera (Nikon CoolPix S3700) recorded the test. After five minutes, an observer ended the recording, caught the animal in a plastic bag, and performed a handling bag test by suspending the bag into the open-field arena to control the visual surroundings. The observer measured the proportion of time that the individual spent immobile during one minute (referred to as handling time hereafter). Traps used for emergence tests and the open-field test box were cleaned thoroughly with 70% isopropyl alcohol and wiped with a dry cloth in-between all tests. Behavioral tests were performed once monthly to ensure that animals would not habituate to the tests.

After the completion of the behavioral tests, we anesthetized animals with isoflurane and inserted PIT tags (Biomark MiniHPT8) subcutaneously at the midback. Animals were also marked with a small animal ear tag (National Band, Style 1005-1) and a distinctive haircut. We recorded sex, body mass (measured using a 100 g Pesola Lightline spring scale), body length, tail length, reproductive status, and age class (juvenile, subadult, or adult). Animals were released at the exact site of capture post-processing.

To quantify behavior from videotaped emergence and open-field tests, recordings were played back in the laboratory. For emergence tests, an observer recorded the following: whether or not the animal emerged (defined as all four feet having left the trap), the latency to emerge, and the total time spent at the end of the tunnel before emerging. Open-field tests were analyzed using the behavioral tracking software ANY-maze © (version 5.1; Stoelting CO, USA). For the remainder of analyses, we focused on a reduced number of non-redundant behavioral variables (16). See Table 1 for a complete list of the behaviors used.

Table 1. Personality variables measured in the deer mouse (*Peromyscus maniculatus*) and the southern red-backed vole (*Myodes gapperi*). Provided are: the behavior, description, behavioral test it was measured using, notes on interpretation, and a non-exhaustive list of references.

Behavior	**Personality trait**	**Description**	**Behavioral Test**	**Notes about interpretation**	**Sources**
Handling time	Docility	Total number of seconds of inactivity during a 1-minute handling bag test	Handling bag	An individual's handling score is typically interpreted as a measure of the docility of an individual or as a response to confinement in a stressful area.	(23,44–46)
Latency to emerge	Boldness	Latency (in seconds) to emerge from trap in the emergence test. An animal was considered to have emerged when all four feet left the trap	Emergence	The latency to emerge from a shelter and into a novel or open environment is typically quantified on a bold/ timid continuum where decreased latency signals increased boldness.	(33,34,41)
Time at end of tunnel	Boldness	Total number of seconds spent at the end of the tunnel before emerging	Emergence	See note for Latency to emerge. Since mice who spent more time in the tunnel were less prone to emerge overall (cor = -0.42; p <0.05), this suggests that these individuals had a more fearful/timid behavior and required more time to survey the arena before emergence. Consequently, we interpreted less time at the end of the tunnel to signal increased boldness.	
Mean speed	Activity	Mean speed in the open-field test in (m/s). Calculated by dividing the total distance traveled in	Open-field	This is a direct measurement of activity and locomotion in the open-field test arena.	(33,34)

		the test by the test duration			
Prop. time grooming	Anxiety	Proportion of test duration spent grooming	Open-field	Grooming in small mammals is typically considered an indicator of anxiety and stress. Previous studies have shown that in highly aversive environments, self-grooming is a form of de-arousal and the highest levels of grooming may indicate a lower anxiety level and better coping than lower levels of grooming. The open-field test exposes small mammals to several naturally aversive stimuli (i.e. bright light and novel, open areas). Thus, it is likely that to the deer mouse, a nocturnal species, the open-field test represents an environment of high aversiveness and increased grooming suggests less anxiety. In contrast, for the vole (a relatively diurnal species) low to moderate grooming seems to signal coping, whereas high levels of grooming indicate high anxiety.	(35,47,48)
Rear rate	Activity	Rate of rearing (rears/s). Rearing is defined as forelegs leaving the arena floor	Open-field	Rearing is typically assessed as correlating positively with activity.	(23,48,49)
Prop. time center	Boldness	Proportion of test duration spent in the center portion of the arena	Open-field	Thigmotaxis, or the avoidance of open spaces, is a common fear/anxiety reaction in small mammals (*35*) wherein individuals will maintain contact with perimeters. Consequently, the act of entering into open, “unsafe” areas is interpreted as boldness and avoidance of these areas indicates timidness.	(34,48,50–53)

Monitoring capture events

To observe the event of an individual’s capture and calculate the time spent inside the trap before behavioral testing, we positioned camera traps (Bushnell NatureView HD 119740) facing the door of the Longworth trap and its surroundings. Cameras were positioned ~50–100 cm from the trap at a height of ~50 cm. 13 camera traps were used in total and were positioned on a subset of the 100 available trap locations (Figure 3). We chose camera locations to optimize the chance of observing capture events (hence, we chose trap locations that had successful captures during the previous month's trapping session). Cameras were positioned simultaneously with Longworth traps and were kept active for the same duration as the traps (three consecutive days and nights at each study grid). We monitored Longworth capture events using camera traps from July–October 2018 (936 total camera trap nights). Cameras were programmed to record a one-minute video whenever movement was perceived (with a one second delay between videos). Because camera traps occasionally fail to detect movement, we also programmed them to take a one-minute video once per hour (the "field scan" setting). This allowed us to approximate the hour of capture in an instance where the camera failed to trigger at the capture event.

Figure 3. A camera trap (Bushnell NatureView HD) monitors a Longworth trap in the field.

Videos of capture events were played back in the laboratory, and an observer identified the individual by pairing the information of the date and trap with available capture data. The observer then recorded the time that the individual entered the trap and calculated the total time (in minutes) spent inside the trap before behavioral testing (taken from the time stamp of the open-field video for consistency). This variable will be referred to hereafter as "time in trap". See S1 Video and S2 Video in the supporting information for examples of observed capture events.

S1 Video. Observed capture event of a southern red-backed vole (*Myodes gapperi*).

S2 Video. Observed capture event of a deermouse (*Peromyscus maniculatus*).

Data analysis

To determine which behaviors could be considered personality, we first performed a repeatability analysis on the behavioral variables obtained from the emergence, open-field, and handling bag tests (54,55). For this analysis, we used data from our study population collected during the 2016, 2017, and 2018 field seasons. We used R version 3.4.1 (56) and package *lme4* (57) to run mixed-effects models and included potential confounding factors as covariates in the models. Specifically, we included sex, body condition (calculated using the scaled mass index (58)), silvicultural treatment, trapping session (June–October), and trapping year (2016, 2017, or 2018). Individual identity was included as a random intercept in the models to account for the proportion of the variance that can be attributed to differences among individuals (59). As response variables, we used the behavior of interest and ran separate mixed-effects models for each behavior of interest. We assessed normality by visually inspecting Q–Q plots and histograms of the residuals, and by plotting the fitted values against the residual values (60). We logit-transformed the response variable when it was a proportion (59,61) to meet the assumption of normality. We then calculated the adjusted repeatabilities and associated confidence intervals (55,62–64) using methods described in detail by (16,39).

Once it was determined which behaviors were repeatable and could, therefore, be considered personality, we tested the hypothesis that these behaviors would be influenced by the time spent inside the Longworth trap before behavioral testing. We used a nested hypothesis testing approach (65) using linear models and generalized linear models with the repeatable behaviors as response variables. In the instances where we had repeated measures from the same individual (because we caught their capture on a camera trap in subsequent trapping sessions), we used only the first event (18 out of 92 individuals). Again, proportional response variables were logit-transformed to meet the assumptions of normality, and count variables were examined using generalized linear models with a poisson or negative binomial family (depending on dispersion).

We introduced predictor variables one by one to build a base model to control for most of the variability in the data. Predictor variables included sex, body condition, silvicultural treatment, trapping session, body mass, and a variable termed "naïve" which controlled for whether the animal had been captured previously or was naïve to trapping. Models containing each of these variables alone were compared to the null model using the Akaike information criterion corrected for small sample size (AICc) (65,66) and models within 2.0 ΔAICc of the top model were considered to have equal support. If more than one variable was better than the null, a model including multiple additive effects was explored. Once this base model was built, we compared this model to the same model with the addition of the variable "time in trap" to see whether this addition improved the model by AICc. Previous research has shown that males and females may respond differently to trap-induced stress (31), so we subsequently tested for an interaction between the time spent in the trap and sex. Last, to test the hypothesis that individuals who are naïve to trapping may be impacted by the time spent inside the trap differently than individuals who have been captured previously, we tested for an interaction between time spent in the trap and the variable "naïve".

Ethical note

Animal trapping, handling, and marking procedures were approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC number A2015_11_02). Animals were anaesthetized with isoflurane prior to tagging, and tagging equipment was sanitized with 70% isopropyl alcohol in between animals. All small mammal handling was performed by trained researchers, and all efforts were made to minimize suffering by small mammals.

Results

We examined behavioral data from standardized tests for 1791 observations from 603 individual deer mice and 1558 observations from 529 individual red-backed voles, and we found all behavioral variables to be significantly repeatable, with a mean repeatability value of 0.81 for deer mice and 0.78 for voles (Table 2). This indicates that these behaviors can be considered personality (55,67). The mean 95% confidence intervals for these values were (0.79, 0.84) and (0.74, 0.81), respectively (Table 2). The number of observations and individuals shown in Table 2 differ for behavioral variables obtained from the emergence and handling bag tests since these tests were not performed in 2016. The mean number of repeated observations per individual was approximately three for both deer mice and red-backed voles.

Table 2. Repeatability estimates for target behaviors measured in three behavioral tests (handling bag, emergence, and open-field) in deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*).

Behavioral Variable	Mean	Range	Repeatability (95% CI)	Observations	Individuals
P. maniculatus					
Handling time	15.41	(0, 60)	**0.836 (0.807, 0.862)**	1122	376
Latency to emerge	27.17	(0, 180)	**0.812 (0.780, 0.842)**	1122	376
Time at end of tunnel	7.15	(0, 180)	**0.863 (0.841, 0.884)**	1122	376
Mean speed (m/sec)	0.10	(0, 0.25)	**0.832 (0.809, 0.853)**	1791	603
Prop. time grooming	0.11	(0, 0.96)	**0.762 (0.735, 0.792)**	1791	603
Rear rate	0.19	(0, 0.68)	**0.809 (0.785, 0.831)**	1791	603
Prop. time center	0.03	(0, 0.73)	**0.775 (0.747, 0.804)**	1791	603
M. gapperi					
Handling time	47.77	(0, 60)	**0.675 (0.62, 0.726)**	940	305
Latency to emerge	34.94	(0, 180)	**0.831 (0.799, 0.859)**	940	305
Time at end of tunnel	12.05	(0, 180)	**0.823 (0.791, 0.851)**	940	305
Mean speed (m/sec)	0.05	(0, 0.20)	**0.792 (0.765, 0.818)**	1558	529

Prop. time grooming	0.06	(0, 0.81)	**0.729 (0.694, 0.764)**	1558	529
Rear rate	0.09	(0, 0.56)	**0.770 (0.739, 0.801)**	1558	529
Prop. time center	0.04	(0, 0.99)	**0.827 (0.805, 0.850)**	1558	529

Repeatability was calculated from univariate mixed-effect models with identity included as a random effect. Parametric bootstrapping was used to calculate 95% confidence intervals. See Methods for more information. Significant repeatability estimates are shown in bold.

In the majority of models (~86%) predicting behaviors exhibited in standardized tests, the top model did not include “time in trap”. Instead, out of the predictor variables considered (sex, body condition, silvicultural treatment, trapping session, body mass, and a variable termed “naïve” which controlled for whether the animal had been captured previously or was naïve to trapping) behaviors in deer mice were predicted by trapping session and body mass (Table 3, Figure 4a-b). Deer mice with greater body mass showed longer latencies to emerge from the emergence test and the proportion of time spent grooming in the open-field test correlated positively with trapping session (β = 0.26, SE = 0.08, rsq = 0.20 and β = 0.58, SE = 0.16, rsq = 0.23, respectively). In two cases, (once for deer mice and once for voles) the top model included an interaction between “time in trap” and whether or not the individual was naïve to trapping (Figure 4c-d). Model fit was relatively low for top models (excluding those where the top model included only an intercept), with an average multiple R-squared value of 0.23 (Table 3).

Table 3. Model output of top-ranked linear models* predicting behaviors performed during standardized tests in deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*).

P. maniculatus							
Latency to emerge	β	St.Error	P-value	**Prop. time grooming**	β	St.Error	P-value
(Intercept)	1.21	0.08	<0.001	(Intercept)	-3.88	0.51	<0.001
Body mass	0.26	0.08	0.003	Session	0.58	0.16	<0.001
R-squared	0.20			R-squared	0.23		
Observations	41			Observations	46		
Prop. time center	β	St.Error	P-value				

(Intercept)	-3.52	0.123	<0.001
Time in trap	0.17	0.12	0.18
Naïve	0.04	0.17	0.82
Time in trap*Naïve	-0.53	0.17	0.005
R-squared	0.19		
Observations	46		
M. gapperi			
Handling time	β	St.Error	P-value
(Intercept)	45.37	3.68	<0.001
Time in trap	-12.4	3.71	0.002
Naïve	6.04	4.53	0.19
Time in trap*Naïve	11.3	4.71	0.02
R-squared	0.28		
Observations	43		

* Only results from the top model (based on AICc scores) are shown. We have omitted occasions where the null model was the top model. See materials and methods for more information.

Fig 4. Factors predicting repeatable behaviors performed in the open-field test in deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*). (a) Deer mice with greater body mass took longer to emerge from the emergence test. **(b)** Trapping session influenced the proportion of time deer mice spent grooming in the open-field test (2 refers to July and 5 is October). **(c)** Deer mice who were naïve to trapping showed a negative relationship between time in the trap and the proportion of time spent in the center portion of the open-field test. Non-naïve mice showed the reverse relationship. **(d)** Voles who were not naïve to trapping showed a negative relationship between time in the trap and handling time. Results were obtained from linear models, and 95% CI from the models are shown. Variables "time in trap" and "body mass" have been z-standardized, and the variables "latency to emerge", "prop. time grooming", and "prop. time center" are on a log10 scale.

Discussion

We studied the effects of live trapping on behaviors performed during three standard behavioral tests in deer mice and southern red-backed voles. Our major findings were that for these species, 12 out of 14 behaviors exhibited during routine behavioral tests were not affected by the amount of time that individuals had spent confined in traps. In the two instances where the time spent confined in traps did predict behavior, effect sizes were relatively small, and the direction of the relationship was different for individuals who were naïve to trapping than those who had been trapped previously, indicating that an individual's previous experience with a trap interacts with this process. Overall, these results suggest that personality data collected from wild, trapped small mammals is not confounded by the trapping process and, where an effect might be present, the predictive power of the time spent confined to traps is relatively weak and possibly not affecting the overall interpretation of results.

Previous research has not explored the effects of live trapping on personality measurements, however, studies investigating the impacts of live trapping on hormonal stress responses have had mixed findings. Specifically, it has been shown in southern red-backed voles and meadow voles that live trapping induces an initial stress response, but that this response is not heightened following prolonged confinement inside traps (29,36). In our study, the observed behavior of red-backed voles in behavioral tests was consistent with these findings and 6 out of 7 behaviors showed no correlation with the time that the animal had spent previously confined inside of a trap. Previous studies investigating the correlation between stress response and duration of trap confinement in deer mice saw that after prolonged time spent in traps, stress hormone levels were significantly higher than after a short duration of trap confinement (36). By contrast, our results show no correlation between 6 out of 7 behavioral measurements and trap duration in the deer mouse. Although a hormonal change does not necessarily precede a change in behavior, we would expect to see an observable behavioral change in individual deer mice experiencing elevated glucocorticoid levels (for example, by affecting behaviors that indicate activity level such as speed of locomotion and rearing). Instead, the one behavior in deer mice for which “time in trap” occurred in the top model was the proportion of time spent in the center of the open-field test, a behavior which is most commonly interpreted as indicating the degree of boldness (Table 1). Interestingly, our results show that individuals who had never been trapped previously behaved more boldly in the open-field test (spending more time in the center portion) when their confinement duration was short rather than long. Individuals who had been trapped at least once previously showed the opposite effect; bolder behavior was seen in animals who had spent longer durations in the trap than those who had spent shorter durations (Figure 4c.). In voles, the one behavior that was affected by the “time in trap” was handling time, or the amount of time spent immobile during a one-minute handling bag test. This behavior is commonly used to assess docility (Table 1). Our results showed that for non-naïve individuals only (i.e., only those who had been trapped at least once previously), shorter durations in the trap correlated with increased docility (Figure 4d.).

Since 86% of observed behaviors by deer mice and voles showed no correlation with the variable “time in trap”, and all four variables indicating activity showed no correlations, we suspect that the duration of trap confinement is not providing a prolonged stressor for small mammals. It may be noteworthy that the previous trap response studies of deer mice and voles used Sherman traps instead of the Longworth traps used in this study. Longworth traps differ from Sherman traps in that they have a separate nest chamber (providing additional warmth and protection). Additionally, we took steps to limit stress by ensure that bedding remained dry (i.e., limiting trapping in adverse weather and replacing damp bedding immediately), and providing ample bait inside the traps. Further, we checked traps twice a day to limit confinement durations. We can't speculate on whether these precautions were adequate in our study to stop a subsequent release of glucocorticoids after the initial stressor of the trapping event, but regardless, prolonged confinement in a Longworth trap does not seem to result in an observable change for the majority of behaviors in either study species. Future research examining this relationship in other species and other study populations will help to assess and confirm the generalizability of these findings. In the two cases where "time in trap" showed relatively weak predictive power, both arose as an interaction with the variable "naïve". We suggest that other studies investigating personality in small mammals control in analyses for whether or not animals have been captured previously.

An animal's personality depicts its unique way of experiencing the world and coping with life's challenges (3). Using standardized behavioral tests, it is possible to capture different components of an individual's complex personality, for example by observing activity levels and interactions with novel objects and environments (33). Our results show some evidence that an individual's behavior in standard tests can be predicted in part by body mass and seasonality (Figure 4). Specifically, we found that heavier deer mice were slightly more timid than lighter mice (seen in their longer latencies to emerge from the emergence test), and that mice groomed more (indicating coping) in the autumn than they did in the early and mid-summer. These models showed low fit to the data; suggesting that the complexity of an individual's personality is a difficult thing to predict.

Personality studies on wild populations will likely continue to become more common as further research demonstrates the cascade-effects that individual behavioral traits can have on populations and communities (14,16,18,19,68). Hence, it is critical to ensure that the very process we seek to illuminate is not being confounded by our methods of obtaining data. Our findings provide evidence that time spent inside of Longworth traps does not determine behaviors performed during standardized tests in two different small mammal species. Therefore, our results suggest that personality measurements on wild, trapped small mammals are not regulated by trapping procedures.

Acknowledgments

This work was supported by the USDA-National Institute of Food and Agriculture McIntire-Stennis projects (ME041620 and ME041913) through the Maine Agricultural and Forest Experiment Station. We also thank a number of dedicated field and lab technicians for helping with data collection and video analysis, Bryn Evans for help with map preparation, Malcolm Hunter for comments on a previous version of this manuscript, Laura Kenefic (U.S. Forest Service), and Keith Kanoti for maintaining and facilitating research at the Penobscot Experimental Forest. A special thanks goes to Sara Boone for support in the field.

Author contributions

AM, ST, and AMB conceived and designed the experiment. ST and AMB performed the experiment. AMB analyzed the data and wrote the first draft of the manuscript. All authors contributed to the final version of the manuscript.

References

1. Pennisi E. The power of personality. Science. 2016;352(6286):644–7.
2. Sih A, Bell AM, Johnson JC, Ziemba RE. Behavioral syndromes, an integrative overview.

Q Rev Biol. 2004;79(3):241–77.

3. Carere C, Maestripieri D. Animal personalities: behavior, physiology and evolution. Chicago, Illinois: University of Chicago Press; 2013.

4. Gosling SD. From mice to men: what can we learn about personality from animal research? Psychol Bull. 2001;127(1):45–86.

5. van Oers K, de Jong G, van Noordwijk AJ, Kempenaers B, Drent PJ. Contribution of genetics to the study of animal personalities: a review of case studies. Behaviour. 2005;142(9–10):1185–206.

6. Smith BR, Blumstein DT. Fitness consequences of personality: a meta-analysis. Behav Ecol. 2008;19(2):448–55.

7. Biro PA, Stamps JA. Are animal personality traits linked to life-history productivity? Trends Ecol Evol. 2008;23(7):361–8.

8. Dingemanse NJ, Réale D. Natural selection and animal personality. Behaviour. 2005;142(9):1159–84. Available from: http://booksandjournals.brillonline.com/content/10.1163/156853905774539445

9. Haage M, Maran T, Bergvall UA, Elmhagen B, Angerbjörn A. The influence of spatiotemporal conditions and personality on survival in reintroductions–evolutionary implications. Oecologia. 2017;183(1):45–56.

10. Dingemanse NJ, Kazem AJN, Re D, Wright J. Behavioural reaction norms: animal personality meets individual plasticity. Trends Ecol Evol. 2009;25(2):81–9.

11. Sih A, Kats LB, Maurer EF. Behavioural correlations across situations and the evolution

of antipredator behaviour in a sunfish-salamander system. Anim Behav. 2003;65(1):29–44.

12. Wong BBM, Candolin U. Behavioral responses to changing environments. Behav Ecol. 2015;26(3):665–73.

13. Tuomainen U, Candolin U. Behavioural responses to human-induced environmental change. Biol Rev. 2011;86(3):640–57.

14. Sih A, Cote J, Evans M, Fogarty S, Pruitt J. Ecological implications of behavioural syndromes. Ecol Lett. 2012;15(3):278–89.

15. Wolf M, Weissing FJ. Animal personalities: consequences for ecology and evolution. Trends Ecol Evol. 2012;27(8):452–61. Available from: http://dx.doi.org/10.1016/j.tree.2012.05.001

16. Brehm AM, Zydlewski J, Maynard GA, Mortelliti A. Land use change and the ecological consequences of personality in small mammals. Ecol Lett. 2019; doi: 10.1111/ele.13324.

17. Miranda AC, Schielzeth H, Sonntag T, Partecke J. Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? Glob Chang Biol. 2013;19(9):2634–44.

18. Merrick MJ, Koprowski JL. Should we consider individual behavior differences in applied wildlife conservation studies? Biol Conserv. 2017;209:34–44. Available from: http://dx.doi.org/10.1016/j.biocon.2017.01.021

19. Lapiedra O, Schoener TW, Leal M, Losos JB, Kolbe JJ. Predator-driven natural selection on risk-taking behavior in anole lizards. Science. 2018;360(6392):1017–20.

20. Berger-Tal O, Blumstein DT, Carroll S, Fisher RN, Mesnick SL, Owen MA, et al. A systematic survey of the integration of animal behavior into conservation. Conserv Biol. 2016;30(4):744–53.

21. Carter AJ, Heinsohn R, Goldizen AW, Biro PA. Boldness, trappability and sampling bias in wild lizards. YANBE [Internet]. 2012;83(4):1051–8. Available from: http://dx.doi.org/10.1016/j.anbehav.2012.01.033

22. Boon AK, Réale D, Boutin S. Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. Oikos. 2008;117(April):1321–8.

23. Martin JGA, Réale D. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. Anim Behav. 2008;75(1):309–18.

24. Carere C, Drent PJ, Privitera L, Koolhaas JM, Groothuis TGG. Personalities in great tits, *Parus major*: stability and consistency. Anim Behav. 2005;70(4):795–805.

25. Dammhahn M, Almeling L. Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness. Anim Behav [Internet]. 2012;84(5):1131–9. Available from: http://dx.doi.org/10.1016/j.anbehav.2012.08.014

26. Ortiz RM, Worthy GAJ. Effects of capture on adrenal steroid and vasopressin concentrations in free-ranging bottlenose dolphins (*Tursiops truncatus*). Comp Biochem Physiol - A Mol Integr Physiol. 2000;125(3):317–24.

27. Boonstra R, Mccoll CJ, Karels TJ. Reproduction at all costs : The adaptive stress response of male arctic ground squirrels. America (NY). 2009;82(7):1930–46.

28. Reeder DAM, Kosteczko NS, Kunz TH, Widmaier EP. Changes in baseline and stress-induced glucocorticoid levels during the active period in free-ranging male and female little brown myotis, *Myotis lucifugus* (Chiroptera: Vespertilionidae). Gen Comp Endocrinol. 2004;136(2):260–9.

29. Fletcher QE, Boonstra R. Impact of live trapping on the stress response of the meadow vole (*Microtus pennsylvanicus*). J Zool. 2006;270(3):473–8.

30. Kenagy NJPGJ. Seasonal changes in plasma testosterone and glucocorticosteroids in free-living male yellow-pine chipmunks and the response to capture and handling. 2000;245–51.

31. Bosson CO, Islam Z, Boonstra R, Bosson CO, Prés R. The impact of live trapping and trap model on the stress profiles of North American red squirrels. J Zool. 2012;288:159–69.

32. Sapolsky RM, Romero ML, Munck AU. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocr Rev. 2000;21(1):55–89.

33. Carter AJ, Feeney WE, Marshall HH, Cowlishaw G, Heinsohn R. Animal personality: what are behavioural ecologists measuring? Biol Rev. 2013;88(2):465–75.

34. Gracceva G, Herde A, Groothuis TGG, Koolhaas JM, Palme R, Eccard JA. Turning shy on a winter's day: effects of season on personality and stress response in *Microtus arvalis*. Ethology. 2014;120(8):753–67.

35. Kalueff A V., Stewart AM, Song C, Berridge KC, Graybiel AM, Fentress JC.

Neurobiology of rodent self-grooming and its value for translational neuroscience. Nat Rev Neurosci. 2016;17(1):45–59.

36. Harper JM, Austad SN. Effect of capture and season on fecal glucocorticoid levels in deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*). Gen Comp Endocrinol. 2001;123(3):337–44.

37. Benevides AFL, Hansen H, Hess SC. Design and evaluation of a simple signaling device for live traps. J Wildl Manage. 2008;72(6):1434–6.

38. Larkin RP, Vandeelen TR, Sabick RM, Gosselink TE, Warner RE. Electronic signaling for prompt removal of an animal from a trap. Wildl Soc Bull. 2003;31(2):392–8. Available from: http://www.jstor.org/stable/3784318

39. Brehm AM, Mortelliti A. Mind the trap: large-scale field experiment shows that trappability is not a proxy for personality. Anim Behav. 2018;142:101–12. Available from: https://doi.org/10.1016/j.anbehav.2018.06.009

40. Brissette JC, Kenefic LS. History of the penobscot experimental forest, 1950-2010. In: Penobscot experimental forest: 60 years of research and demonstration in Maine, 1950-2010 GTR-NRS-P-123. USDA Forest Service; 2014. p. 1–20.

41. Brown C, Braithwaite VA. Effects of predation pressure on the cognitive ability of the poeciliid *Brachyraphis episcopi*. Behav Ecol. 2004;16(2):482–7.

42. Perals D, Griffin AS, Bartomeus I, Sol D. Revisiting the open-field test: what does it really tell us about animal personality? Anim Behav. 2017;123:69–79.

43. Walsh RN, Cummins R a. The open-field test: a critical review. Psychol Bull.

1976;83(3):482–504.

44. Boon AK, Réale D, Boutin S. The interaction between personality, offspring fitness and food abundance in North American red squirrels. Ecol Lett. 2007;10(11):1094–104.

45. Montiglio PO, Garant D, Pelletier F, Réale D. Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. Anim Behav. 2012;84(4):1071–9. Available from: http://dx.doi.org/10.1016/j.anbehav.2012.08.010

46. Taylor RW, Boutin S, Humphries MM, Mcadam AG. Selection on female behaviour fluctuates with offspring environment. J Evol Biol. 2014;27(11):2308–21.

47. Fernández-Teruel A, Estanislau C. Meanings of self-grooming depend on an inverted U-shaped function with aversiveness. Nat Rev Neurosci. 2016;17(9):591. Available from: http://dx.doi.org/10.1038/nrn.2016.102

48. Choleris E, Thomas A, Kavaliers M, Prato F. A detailed ethological analysis of the mouse open field test: effects of diazepam, chlordiazepoxide and an extremely low frequency pulsed magnetic field. Neurosci Biobehav Rev. 2001;25(2001):235–60. Available from: http://www.sciencedirect.com/science/article/pii/S0149763401000112

49. Prut L, Belzung C. The open field as a paradigm to measure the effects of drugs on anxiety-like behaviors: a review. Eur J Pharmacol. 2003;463(1–3):3–33.

50. Eccard JA, Herde A. Consistency in boldness, activity and exploration at different stages of life. BMC Ecol. 2013;103(1):61–8.

51. Ramos A, Berton O, Mormède P, Chaouloff F. A multiple-test study of anxiety-related

behaviours in six inbred rat strains. Behav Brain Res. 1997;85(1):57–69.

52. Treit D, Fundytus M. Thigmotaxis as a test for anxiolytic activity in rats. Pharmacol Biochem Behav. 1989;31:959–62. Available from: papers2://publication/uuid/5F4FD48A-712B-4CFC-AC12-0C54750B2FF9

53. Barnett S. The Rat - A Study in Behavior. ANU Press; 1976.

54. Cleasby IR, Nakagawa S, Schielzeth H. Quantifying the predictability of behaviour: statistical approaches for the study of between-individual variation in the within-individual variance. Methods Ecol Evol. 2015;6(1):27–37.

55. Dingemanse NJ, Dochtermann NA. Quantifying individual variation in behaviour: mixed-effect modelling approaches. J Anim Ecol. 2013;82(1):39–54.

56. R Core Team. R: A language and environment for statistical computing. R Found Stat Comput. 2017; Available from: http://www.r-project.org/

57. Bates DM, Maechler M, Bolker BM, Walker S. lme4: Linear mixed-effects models using Eigen and S4. 2015.

58. Peig J, Green AJ. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos. 2009;118(12):1883–91.

59. Zuur AF, Leno EN, Walker N, Saveliev AA, Smith GM. Mixed effects models and extensions in ecology with R. New York: Springer-Verlag New York; 2009.

60. Sokal VL, Rohlf FJ. Biometry: the principles and practice of statistics in biological research. 3rd ed. New York: Freeman; 1995.

61. Warton DI, Hui FKC. The arcsine is asinine: the analysis of proportions in ecology.

Ecology. 2011;92(1):3–10.

62. Nakagawa S, Schielzeth H. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev. 2010;85(4):935–56.

63. Stoffel MA, Nakagawa S, Schielzeth H. rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol Evol. 2017;8(11):1639–44. Available from: http://onlinelibrary.wiley.com/doi/10.1111/2041-210X.12797/full

64. Houslay TM, Wilson AJ. Avoiding the misuse of BLUP in behavioural ecology. Behav Ecol. 2017;28(4):948–52.

65. Burnham KP, Anderson DR. Model selection and multimodel inference: a practical information - theoretic approach. 2nd ed. New York: Springer-Verlag New York; 2002.

66. Buckland ST, Burnham KP, Augustin NH. Model selection: an integral part of inference. Biometrics. 1997;53(2):603–18.

67. Bell AM, Hankison SJ, Laskowski KL. The repeatability of behaviour: a meta-analysis. Anim Behav. 2009;77(4):771–83. Available from: http://dx.doi.org/10.1016/j.anbehav.2008.12.022

68. Lapiedra O, Chejanovski Z, Kolbe JJ. Urbanization and biological invasion shape animal personalities. Glob Chang Biol. 2017;23(2):592–603.

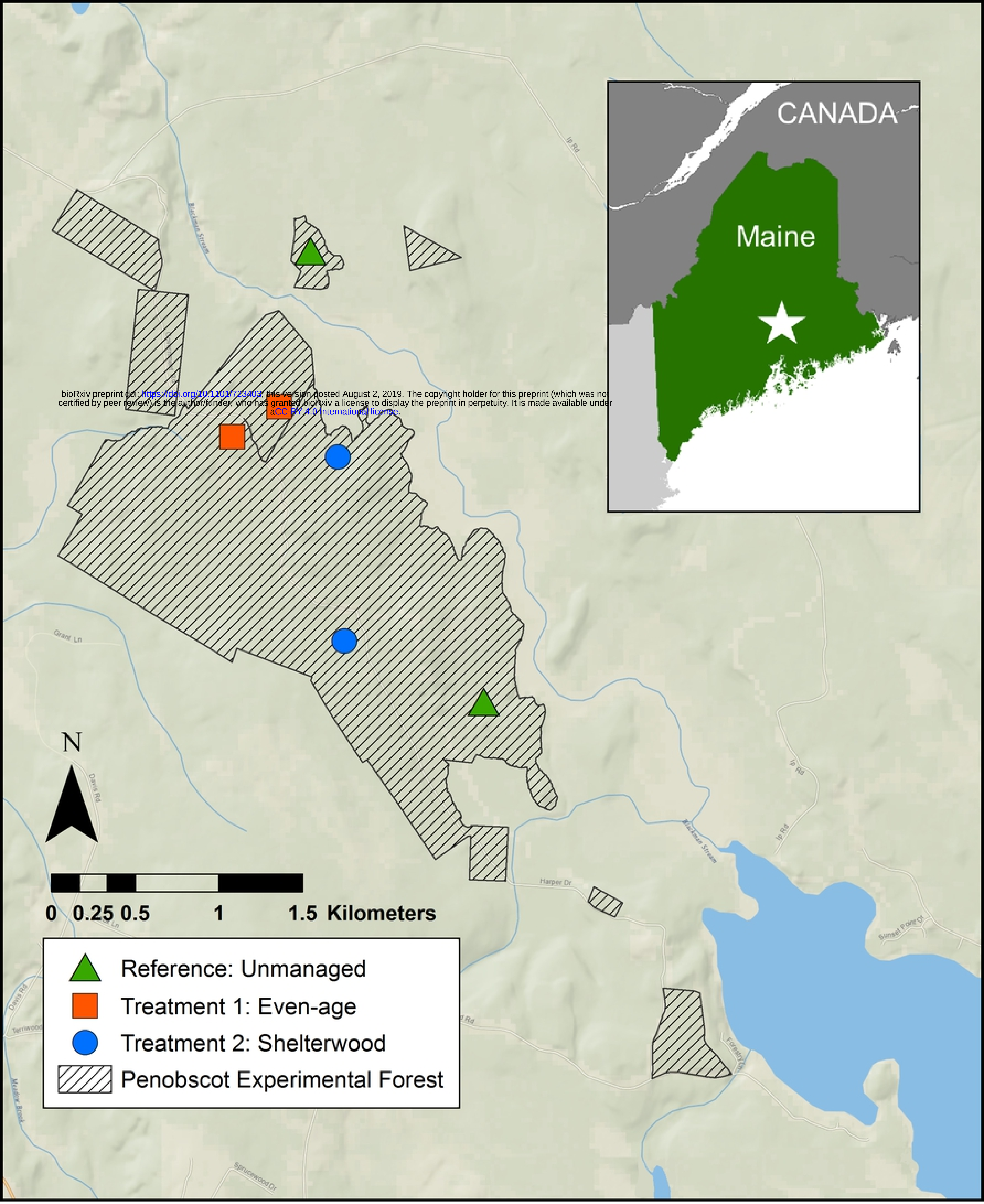
CANADA
Maine
N
0
0.25
0.5
1
1.5 Kilometers
Reference: Unmanaged
Treatment 1: Even-age
Treatment 2: Shelterwood
Penobscot Experimental Forest
Ip Rd
Blackman Stream
Grant Ln
Davis Rd
Harper Dr
Sunset Point Dr
Sprucewood Dr
Meadow Brook

Figure1

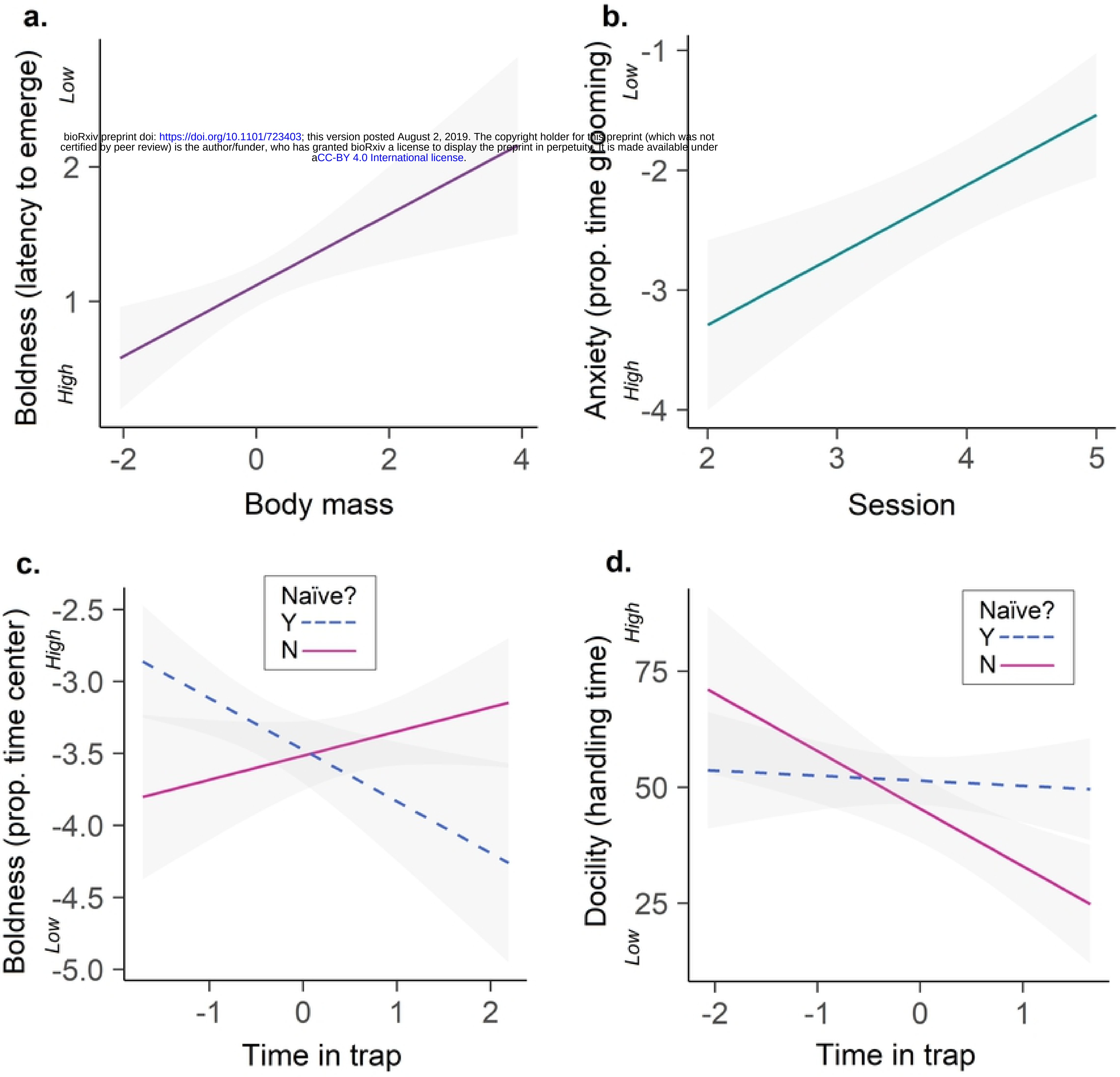
a.
Boldness (latency to emerge)
Low
High
2
1
-2
0
2
4
Body mass
b.
Anxiety (prop. time grooming)
Low
High
-1
-2
-3
-4
2
3
4
5
Session
c.
Boldness (prop. time center)
High
Low
-2.5
-3.0
-3.5
-4.0
-4.5
-5.0
Naïve?
Y
N
-1
0
1
2
Time in trap
d.
Docility (handling time)
High
Low
75
50
25
Naïve?
Y
N
-2
-1
0
1
Time in trap

Figure4

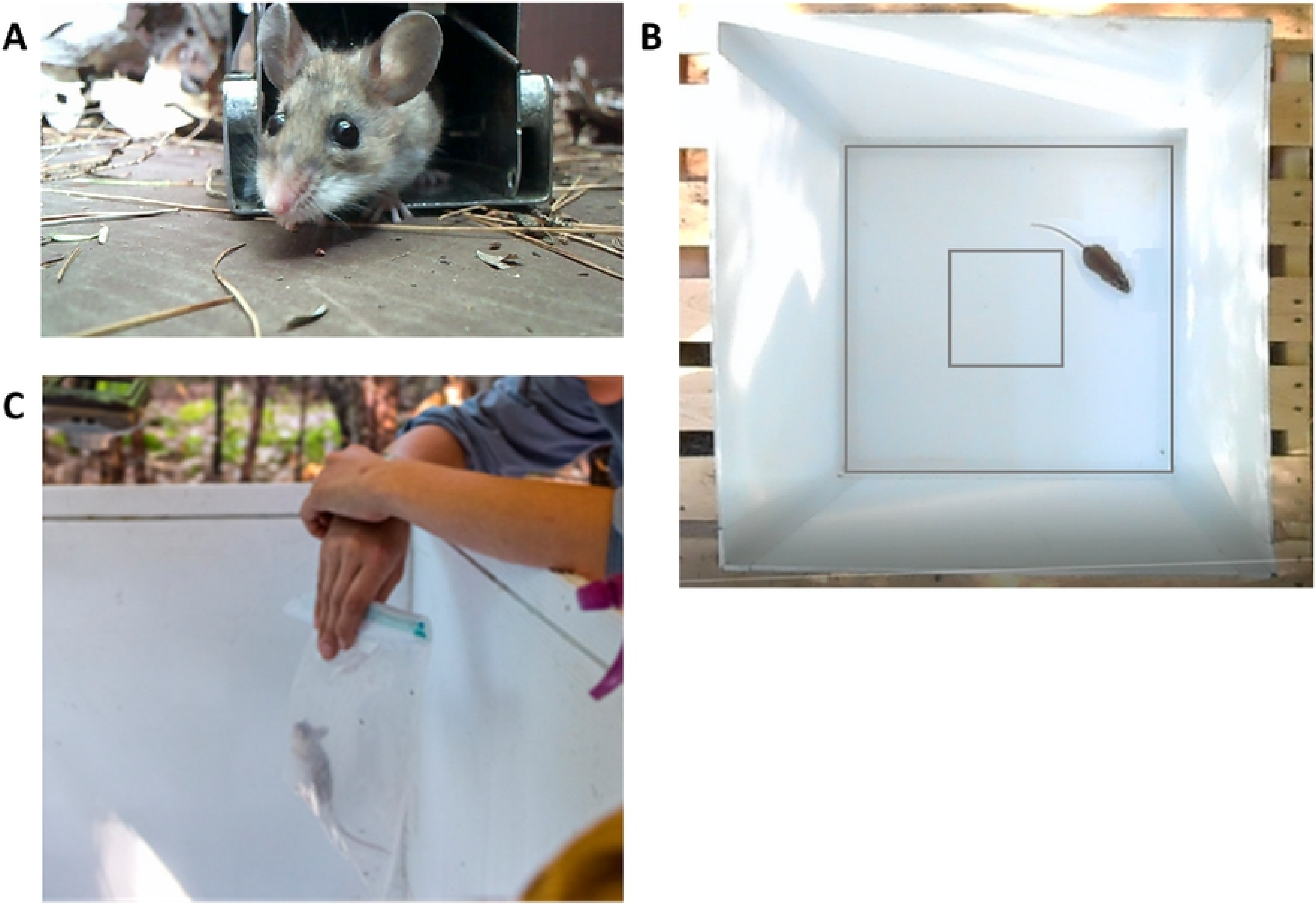

Figure2

Figure3