



# Movement behaviour of woodland salamanders is repeatable and varies with forest age in a fragmented landscape



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Landscape modification (loss, fragmentation and degradation of habitat) is a universal form of human-induced rapid environmental change that creates strong spatial variation in environmental conditions. Behaviourally mediated responses to landscape modification may generate behavioural divergence among populations along environmental gradients. We tested whether movement behaviour of red-backed salamanders, *Plethodon cinereus*, is repeatable and whether it varies within and between forest stands of different ages in a fragmented landscape in New York, U.S.A. Water loss is a major constraint on *P. cinereus* mobility, and forest fragmentation creates spatial variation in desiccation risk. We quantified multiple components of individual movement behaviour in an unfamiliar environment in the laboratory and used ordination to identify behavioural variation among individuals in multivariate space. We tested for repeatability of individual behaviour and then examined behavioural differences between individuals captured from populations at two spatial scales where desiccation risk was expected to vary: (1) between edge and interior locations within forest stands and (2) between forest stands varying in time since agricultural abandonment. Variation in movement behaviour among individuals was characterized by three components: total movement activity (e.g. surface activity, distance moved, boundary crossings), substrate use (time on moist soil versus dry sand) and latency to initial movement. Each behavioural component was significantly repeatable. At the population level, individuals from old forest stands ( $\geq 77$  years) showed greater movement activity than individuals from young stands. Movement behaviour did not differ between individuals from edge and interior locations within forest stands. Our results demonstrate that *P. cinereus* individuals show consistent differences in movement behaviour in an unfamiliar environment. Moreover, we show that movement behaviour can be spatially structured within fragmented landscapes, but that behavioural divergence among populations depends on spatial scale. © 2016 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Because of its labile expression, behaviour is often the first response of animals to human-induced rapid environmental change (Sih, Stamps, Yang, McElreath, & Ramenofsky, 2010; Tuomainen & Candolin, 2011). Thus, a clear understanding of the impacts of environmental change on species requires knowledge of behavioural plasticity (Sih, 2013; Sih, Ferrari, & Harris, 2011). Behavioural plasticity is generally thought of as the ability of individuals to express different behavioural phenotypes in different environment contexts (Snell-Rood, 2013). However, individuals within populations often express consistent differences in behaviour (i.e. 'behavioural types' or 'personalities'; Bell, Hankison, & Laskowski, 2009; Réale, Reader, Sol, McDougall, & Dingemanse,

2007; Sih, Bell, & Johnson, 2004), and persistence of populations may be promoted by standing genetic variation for personality differences. For example, differential fitness among individuals with different personalities can facilitate evolutionary response to environmental change. In spatially variable environments, behavioural variation may be structured geographically due to historical responses to environmental change, including divergent selection (Bell & Sih, 2007; Dingemanse et al., 2007), nonrandom gene flow (i.e. spatial sorting of behavioural types; Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Edelaar & Bolnick, 2012; Jacob, Bestion, Legrand, Clobert, & Cote, 2015), or plastic responses of individuals (Sol, Lapiedra, & González-Lagos, 2013).

Landscape modification (i.e. loss, fragmentation and degradation of habitat) is a pervasive form of environmental change that generates environmental gradients and heterogeneity in land cover types (Fischer & Lindenmayer, 2007). Behaviourally mediated responses to landscape modification may result in behavioural

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divergence among populations in habitats with varying environmental conditions. For example, urbanization creates a sharp gradient in impervious surface (e.g. roads, buildings) and natural vegetation between urban and rural areas, and individuals in urban environments differ behaviourally from individuals in rural environments for many animal species (Sol et al., 2013). Landscape modification also generates environmental gradients within rural landscapes due to edge effects within habitat patches and variation in habitat structure among patches (Fischer & Lindenmayer, 2007). Whereas animal behaviour has been found to vary among landscapes with varying levels of fragmentation (e.g. Bonte, Boore, Lens, & Maelfait, 2006; Brodin, Lind, Wiberg, & Johansson, 2013; Maes, Van Damme, & Matthysen, 2013; Schtickzelle, Mennechez, & Baguette, 2006), little is known about geographical variation in behaviour within fragmented landscapes.

We examined variation in movement behaviour of individuals within and among populations of red-backed salamanders, *Plethodon cinereus*, in a forest ecosystem with a recent history of landscape change (i.e. forest fragmentation and regeneration). We focused on movement behaviour because animal movement plays a critical role in determining individual fitness and population persistence in fragmented landscapes (Clobert, Baguette, Benton, & Bullock, 2012). *Plethodon cinereus* is a terrestrial lungless salamander that occurs in forests in the eastern United States and southeastern Canada. Individuals actively forage for invertebrates in leaf litter and low-lying plants, but mobility is strongly constrained by desiccation due to the reliance of individuals on cutaneous respiration (Spotila, 1972). During warm and dry conditions, individuals seek refuge under logs and rocks (Fraser, 1976; Jaeger, 1972, 1978), and most individuals are on a negative energy budget due to reduced foraging success (Jaeger, 1980). Individuals deploy chemical signalling and aggressive behaviour to defend territories that contain cover objects and high-quality food resources (e.g. Jaeger, 1981; Jaeger & Gergits, 1979; Mathis, 1991), although the degree of territoriality can vary spatially (Maerz & Madison, 2000; Rollinson & Hackett, 2015). Adult home ranges are small (<25 m<sup>2</sup>; Kleeberger & Werner, 1982), and dispersal is male biased and typically <10 m (Liebgold, Brodie, & Cabe, 2011), although movements up to 143 m (Sterrett, Brand, Fields, Katz, & Grant, 2015) and across open fields (Marsh, Thakur, Bulka, & Clarke, 2004) have been observed. At a landscape scale, abundance of terrestrial salamanders has been shown to be greatest in cool, moist areas, presumably due to low desiccation risk and high foraging and reproductive success in those areas (Peterman & Semlitsch, 2013).

Given the significance of water balance for terrestrial salamanders, spatial variation in movement behaviour for *P. cinereus* may be shaped by gradients in desiccation risk at multiple spatial scales in fragmented landscapes. Within forest stands, microclimatic conditions at the forest floor can become increasingly cool and moist along a gradient from edge to interior locations due to variation in light and wind penetration (i.e. edge effects; Gehlhausen, Schwartz, & Augspurger, 2000; Matlack, 1993). At a large spatial scale, microclimatic conditions and availability of cover (e.g. coarse woody debris, leaf litter) may differ among forest stands that vary in successional state due to differences in time since agricultural abandonment or timber harvest (Welsh & Droege, 2001).

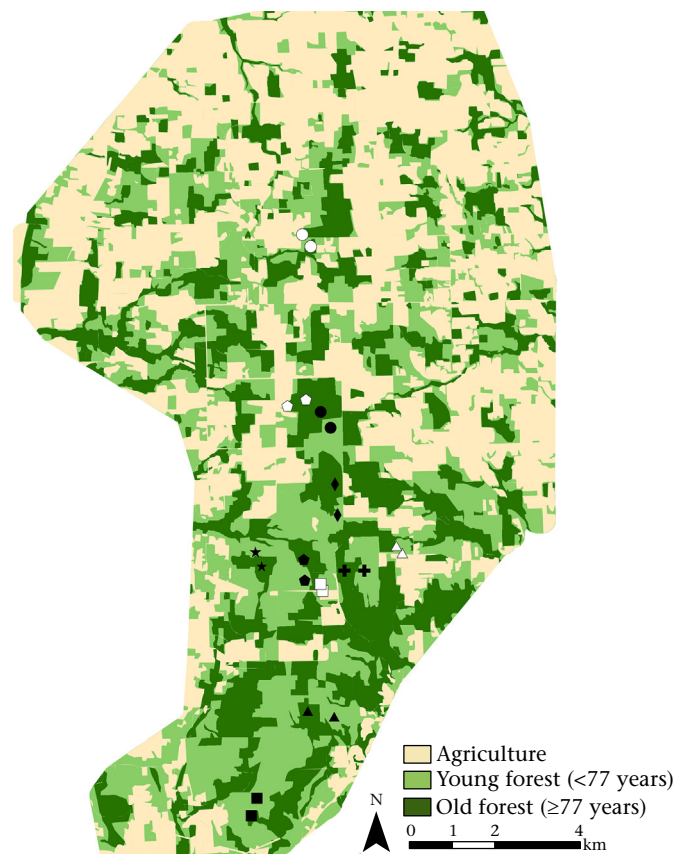
We examined whether *P. cinereus* individuals would vary in movement behaviour when placed in an unfamiliar environment in the laboratory. Because movement behaviour is complex and unlikely to be described by one variable, we recorded several aspects of movement and described individual behaviour with a multivariate metric. We then tested whether behavioural differences among individuals were repeatable in order to identify movement personalities that are stable over time. Given that repeatability

typically sets an upper limit on heritability (Falconer & Mackay, 1996; but see Dohm, 2002), testing for repeatability might also provide insight into the potential for natural selection to result in diversification of behavioural traits within this fragmented landscape. Next, we examined whether movement behaviour differed between individuals collected from populations at two spatial scales: (1) between edge and interior locations within forest stands and (2) between forest stands that varied in time since agricultural abandonment. Treatment comparisons were paired spatially to help isolate the roles of edge effects and stand age in driving behavioural divergence. To assess whether desiccation risk was an important cost of movement, we tested whether individual water loss was associated with movement behaviour. We also examined the relationships between movement behaviour of individuals and sex, body condition and morphology to ascertain whether these traits are components of a general behavioural syndrome related to movement (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009).

## METHODS

### Study Area and Sampling Design

We collected salamanders ( $N = 132$ ) from forest stands at the 6561 ha Finger Lakes National Forest (FLNF) in Hector, New York, U.S.A. (Fig. 1; 76°47'29"W, 42°30'55"N). Oak forests dominated the study area until the late 18th century when most forests were cleared for agriculture (Marks & Gardescu, 1992). Agricultural production declined in the 19th century, and FLNF now consists of



**Figure 1.** Map of land cover at the Finger Lakes National Forest in New York, U.S.A. Symbol shape indicates paired sampling locations for the edge–interior (unfilled) and forest age (filled) comparisons. Aerial imagery from 1938 was used to classify forests as young (farmed in 1938) or old (forested in 1938).

farms purchased piecemeal by willing sellers beginning in 1938. Agricultural fields on purchased farms were either unmanaged or planted with conifers and, at the time of the present study, were in various stages of succession. The FLNF also includes 809 ha of deciduous forest that was also present in 1938 (DeGloria, 1998). Current dominant land cover types at FLNF include forest (54%) and grassland maintained for grassland-dependent wildlife and cattle grazing (35%). Common tree species include *Acer rubrum*, *Acer saccharum*, *Carya ovata*, *Fraxinus americana*, *Quercus rubra* and *Pinus strobus*. Terrestrial salamanders at FLNF include *P. cinereus* and the northern slimy salamander, *Plethodon glutinosus*, but *P. glutinosus* is rare and was not found during our study.

Two separate groups of salamanders were collected to compare movement behaviour between edge and interior forest locations and young and old forests. For the edge–interior comparison, we collected a total of 66 salamanders across four sites between 5 and 18 June 2015 (Fig. 1). At each site, we established paired sampling plots that were  $\leq 20$  m from a forest edge ('edge') and  $> 100$  m from a forest edge ('interior'). Edge effects for *P. cinereus* have been estimated to persist up to 20–35 m from forest edges (e.g. Hocking, Babbitt, & Yamasaki, 2013; Marsh & Beckman, 2004; deMaynadier & Hunter, 1998). All edge plots were west-facing or south-facing edges, which can have stronger edge effects on salamanders than north-facing and east-facing edges due to hotter and drier conditions (Moseley, Ford, & Edwards, 2009). Two edge plots were bordered by paved roads, and two edge plots were bordered by grasslands. Paired edge and interior plots were within 150–450 m and were selected to minimize variation in soil type, stand age and broad-scale forest composition and configuration. We collected seven to nine salamanders (mean = 8.25) from each plot by turning natural cover objects (logs and rocks).

For the forest age comparison, we collected a total of 66 salamanders across seven sites between 25 and 29 June 2015 (Fig. 1). At each site, we established paired sampling plots that were classified as either young or old forests. Paired sampling plots were within 350–700 m and were selected to minimize variation in soil type and broad-scale forest composition and configuration. We used aerial imagery to determine whether each plot was farmed ('young') or forested ('old') in 1938, which corresponded to when farms making up FLNF were first purchased. We collected three to five salamanders (mean = 4.7) from each plot.

After capture, we transferred salamanders to the laboratory and measured each individual's snout–vent length (SVL), mass and sex. SVL ranged from 2.5 to 4.6 cm (mean = 3.78), and mean SVL was similar between levels of treatments being compared: edge = 3.72 cm (SE = 0.06), interior = 3.75 cm (SE = 0.05); young = 3.77 cm (SE = 0.05), old = 3.87 cm (SE = 0.05). Sex was determined by shining a light to check for the presence of testes (Gillette & Peterson, 2001). We collected about twice as many males as females for each experiment, but sex ratio was consistent across treatment levels in our samples (Supplementary Table S1). Salamanders were housed individually in plastic containers (13 × 13 × 5 cm) lined with moist paper towels at 18–22 °C and a 12:12 h light:dark (LD) cycle. Individuals were fed wingless *Drosophila melanogaster* ad libitum. For logistical reasons, we reversed the LD cycle so that the first hour of complete darkness corresponded to 0800 hours in the laboratory. Individuals were acclimated to the reversed LD cycle for 1 week before behavioural observations.

### Behavioural Observations

Our objective was to quantify multiple aspects of an individual's movement behaviour immediately after being placed in an unfamiliar environment. Although individuals were naïve to the

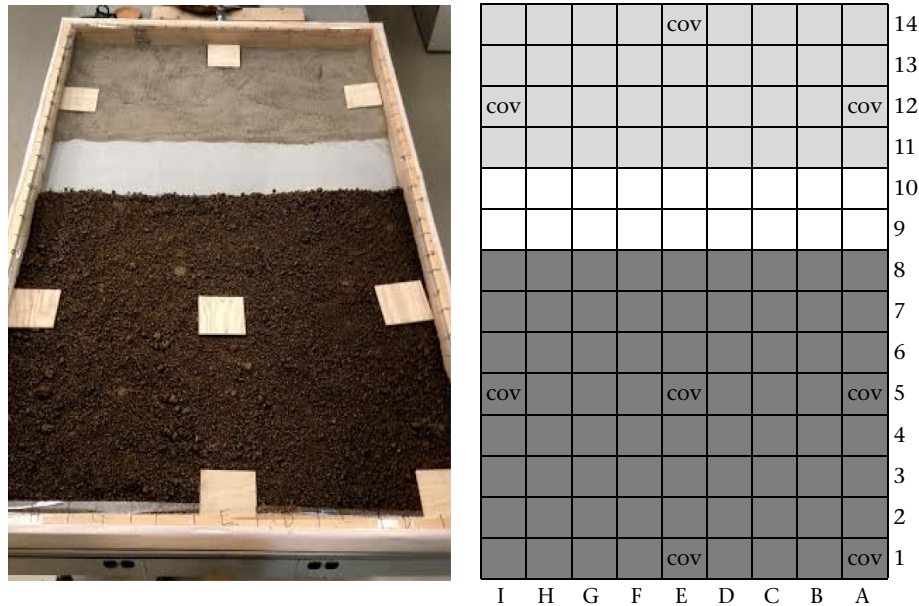
laboratory enclosures, the arenas contained cues typical of natural habitat for *P. cinereus* (e.g. moist and dry substrates, wood cover objects, 'open' surfaces; see below) that should elicit behaviours similar to individuals in nature (Butler, Toomey, McGraw, & Rowe, 2011; Niemelä & Dingemanse, 2014).

Observation arenas were constructed by attaching 0.51 mm plastic to a wood frame (inside dimensions (L × W × H): 1.78 × 1.14 × 0.087 m). The sides of the frame were marked off at 12.7 cm increments to form a grid used to record the location of individuals within the arena (Fig. 2). We placed clear tape overhanging the top of the wood frame to prevent individuals from escaping the arena. Each arena had three substrate types (Fig. 2): (1) topsoil moistened with aged tap water (1.02 × 1.14 m), (2) bare plastic (0.25 × 1.14 m) and (3) dry sand (0.51 × 1.14 m). Soil and sand substrates were 2 cm deep. We placed eight oak plywood cover boards (12.7 × 12.7 × 0.63 cm) in the arena; five were placed in the soil, and three were placed in the sand (Fig. 2). Areas under all cover boards were moistened with aged tap water. The arena design forced individuals to make decisions about surface activity and whether to move through areas that might be perceived differently in terms of desiccation or other risks.

We performed behavioural trials during 1–24 July 2015 in a laboratory maintained at 18–22 °C. We observed six individuals during each trial between 0800 and 1415 hours in six replicate arenas (i.e. one individual per arena) in a completely darkened room. Observations were made by two observers with red lights, and each observer was assigned to observe three individuals at a time. Salamanders were randomly assigned to trials and arenas, with the exception that half of the individuals observed during trials were from each level of the treatments being compared (i.e. three individuals each from young and old forests). Each individual was tested twice in order to calculate repeatability of behavioural traits, and there were 4–9 days between repeated trials (mean = 7). All 'edge–interior' trials were completed before conducting forest age trials. We avoided biases associated with observer effects by ensuring that each observer tested each salamander once (i.e. any observer error was randomized across trials) and was unaware of the origin of salamanders. We stopped feeding individuals 2 days before observations to standardize hunger levels among individuals being tested. *Plethodon cinereus* is known to mark territories with pheromones (Jaeger & Gergits, 1979); we mixed soil and sand among arenas between trials to avoid biases associated with effects of chemical signalling on behaviour.

Trials were initiated by placing one individual on top of the cover object in a corner of the soil substrate (grid cell A1; Fig. 2). The individual was immediately covered with a 10.5 cm terra-cotta saucer and given 5 min to acclimate. After the 5 min acclimation period, the saucer was lifted and observations were made for 60 min using point-time sampling (Dingemanse et al., 2007). Observers circulated among arenas every 15–30 s. For each individual, observers recorded time since trial began, location within the enclosure (i.e. grid cell position) and one of four behavioural states: (1) stationary at the point of release, (2) active on soil, sand or open substrate, (3) climbing vertically on the arena frame, or (4) stationary under a cover object. Changes in position were defined as all four limbs of the animal changing grid cells. The median number of observations of each salamander was 58 (range 38–77). The average number of observations did not vary significantly between levels of treatments: edge = 58.2 (SE = 0.89), interior = 58.6 (SE = 0.87); young = 53.9 (SE = 0.70), old = 54.2 (SE = 0.69). We measured the mass of each salamander to the nearest 0.01 g immediately before and after trials using an electronic balance (Ohaus Scout Pro Balance, Pine Grove, NJ, U.S.A.) in order to quantify weight loss during the trial.





**Figure 2.** Arena and grid system used to conduct behavioural trials with red-backed salamanders, *Plethodon cinereus*. The arena included soil (bottom; dark grey), open (middle; white) and sand (top; light grey) substrates as well as wood cover boards for refuge (squares; 'cov'). Image of grid system is not to scale. See main text for dimensions.

We quantified eight traits: (1) latency: time to movement away from the release point; (2) activity: time active on soil, sand or open substrates; (3) cover: time under cover objects; (4) climbing: time climbing vertically on the arena frame; (5) crossing: number of substrate boundaries crossed; (6) distance: total distance moved; (7) soil: time on the soil substrate; and (8) sand: time on the sand substrate. We used the observation records of time, position and state to quantify the eight traits.

#### Morphological Traits

After completion of behavioural trials, photographs were taken of all salamanders to facilitate morphological measurements. Individuals were placed on a level, lighted surface with a ruler that functioned as a size standard. We used a camera held 27 cm directly above the animal on a tripod to photograph the dorsal surface of the animal. A single observer used the photographs to quantify six common morphological measurements for salamanders (e.g. Adams & Beachy, 2001; Lowe & McPeck, 2012) with the program ImageJ (Schneider, Rasband, & Eliceiri, 2012): (1) head length: maximum length from the snout to the gular fold; (2) head width: maximum width posterior to the orbit; (3) trunk length: distance between the posterior insertion of the forelimbs and the anterior insertion of the hindlimbs; (4) trunk width: maximum width between the posterior insertion of the forelimbs and the anterior insertion of the hindlimbs; (5) humerus length: distance between the posterior insertion of the forelimb and the first joint; and (6) femur length: distance between posterior insertion of the hindlimb and the first joint. Three independent measurements of each trait were made for each individual, and we used the average of the three measurements for statistical analyses.

#### Statistical Analyses

We used principal component analysis (PCA) with varimax rotation to identify suites of correlated traits measured during behavioural trials (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013), and all subsequent analyses of behaviour were performed on component scores (e.g. Dingemanse et al., 2007;

Maes et al., 2013). We retained principal components with eigenvalues  $\geq 1$ . Behaviour of all individuals from both population-level comparisons (edge versus interior and young versus old) was described with a single PCA to enable statistical comparisons of principal component scores with identical interpretations. Components from PCAs conducted separately for each trial and population comparison were virtually identical to the PCA with all individuals and repeated measures combined (Supplementary Tables S2 and S3). We used the package 'psych' (Revelle, 2015) in R 3.1.2 (R Core Team, 2015) to conduct the PCAs.

We determined whether there were consistent differences in behaviour among individuals (i.e. repeatability) by quantifying intraclass correlation coefficients (ICC; Wolak, Fairbairn, & Paulsen, 2012) for each principal component extracted from the PCA. Because this was an individual-level analysis, ICCs were quantified using all individuals in our study. We log-transformed each principal component because the component distributions were positively skewed. We considered a trait to be repeatable if the ICC estimate was positive and the 95% confidence interval did not include 0 (Wolak et al., 2012). ICC estimates and 95% confidence intervals were quantified with the package 'ICC' (Wolak et al., 2012) in R 3.1.2.

We used linear mixed models to examine whether there were behavioural differences between salamanders collected from edge and interior plots and between young and old forests (hereafter referred to as 'populations'). The response variables were principal components extracted from the PCA. We specified a Gaussian error distribution for each principal component, and the principal components were log-transformed to improve normality of the residuals and reduce heteroscedasticity. We included four random effects in the models: (1) individual to account for repeated measures on each individual, (2) plot (i.e. location from which an individual was collected) nested within site (i.e. paired sampling plots) to account for correlated behaviours among individuals collected from the same area, (3) date of trial to account for behavioural variation associated with differences in conditions (e.g. temperature) among days and (4) arena to account for behavioural variation associated with the location of each arena in the laboratory. We tested for differences in behaviour between the

populations of interest by comparing the fit of a model with a fixed effect of population to a model with an intercept only using Akaike's Information Criterion (AIC; Burnham & Anderson, 2002).

Because desiccation can negatively affect fitness of *P. cinereus* (Jaeger, 1980), we examined whether desiccation rate was associated with individual behaviour by quantifying the change in mass of each individual between the beginning and end of the behavioural trial. The permeable skin of amphibians makes them highly susceptible to water loss (Spight, 1968), and we assumed mass loss during the behavioural trials was primarily due to water loss (e.g. Cosentino, Schooley, & Phillips, 2011; Peterman, Locke, & Semlitsch, 2013; Rothermel & Luhring, 2005). We used linear mixed models with a Gaussian error distribution to examine associations between water loss and each behavioural principal component. We used proportion of mass lost during the trial as the response variable (Cosentino et al., 2011; Rothermel & Luhring, 2005), and we applied a logit transformation to reduce heteroscedasticity (Warton & Hui, 2011). Random effects included individual, plot nested within site, date of trial and arena. AIC was used to compare the relative support of models with a single behavioural principal component to a model with an intercept only.

We used linear mixed models to evaluate the association of individual movement behaviour with sex, body condition and morphology. Body condition was quantified as the residuals from a regression of log-transformed mass on SVL (Green, 2001). Morphological measurements included head, trunk and limb morphology. *Plethodon cinereus* has two colour morphs (striped, unstriped) that have previously been shown to vary behaviourally (Moreno, 1989; Venesky & Anthony, 2007), so we included colour morph as a morphological covariate. We used a PCA with varimax rotation to summarize morphological variation in the head, trunk and limb. We retained two principal components that explained 81% of the variance: general body size and leg length (Supplementary Table S4). We examined associations between each of the behavioural principal components and sex, body condition, colour morph, body size and leg length. All individuals were used in a single analysis. Behavioural principal components were log-transformed, and we used a Gaussian error distribution with random effects of individual, plot nested within site, date of trial and arena. AIC was used to compare the relative support of models with a single explanatory variable to a model with an intercept only.

In all cases of model comparisons with AIC, we considered models to have competitive support when  $\Delta AIC \leq 2$  (Burnham & Anderson, 2002). All linear mixed models in this study were fitted with package 'lme4' (Bates, Maechler, Bolker, & Walker, 2015) in R 3.1.2.

#### Ethical Note

Animals were collected under license 1881 issued by the New York State Department of Environmental Conservation. Animal care and experimental protocols were approved by the Institutional Animal Care and Use Committee at Hobart and William Smith Colleges (protocol 2014-01). All housing and experimental protocols followed guidelines on ethical treatment of animals of the Association for the Study of Animal Behaviour and Animal Behavior Society. Individuals were tested only twice in experimental arenas and returned to the point of capture following the experiments.

## RESULTS

PCA revealed three principal components with eigenvalues  $\geq 1$ , which collectively accounted for 87% of the variance (Table 1, Supplementary Fig. S1). The first axis (B1) explained most of the

variance, with highly positive loadings for activity on the surface, number of boundaries crossed, distance moved, time spent climbing the arena walls, and a negative loading for time under cover. We interpreted B1 as an index of total movement activity in the arena. The second axis (B2) reflected the difference between the time an individual was on moist soil versus dry sand (hereafter 'substrate use'). Most of the variation in substrate use was accounted for by individuals remaining stationary under cover objects on soil or sand (Supplementary Fig. S1). We interpreted the third axis (B3) as immediate response to a stressful stimulus because B3 was dominated by a positive loading for latency to movement after cover was removed. All three multivariate behavioural components were repeatable (Table 2).

No aspect of movement behaviour differed between individuals collected from edge and interior locations within forest stands (Table 3). However, movement activity was associated with forest age. Individuals collected from old forests had significantly greater movement activity (i.e. greater B1 values) than individuals collected from young forests (Table 3, Fig. 3). Substrate use and latency were not associated with forest age (Table 3). Our conclusions about relationships between movement behaviour and forest age were reinforced when we classified forest age for sites used in the edge–interior comparison and included them in the forest age analysis (Supplementary Table S5). A post hoc analysis also showed that the effect of forest age on movement activity was significant when including sex, body condition, body size, leg length and colour morph in the model (likelihood ratio test:  $\chi^2 = 8.96$ ,  $P = 0.003$ ).

Individuals lost an average of 5% of their body mass during behavioural trials (range 0–18%). Mass loss was positively related to movement activity and latency, although the relationship was much stronger for movement activity (Table 4, Fig. 4). Mass loss was not related to substrate use (Table 4). Movement activity and substrate use did not strongly depend on sex, body condition or morphology, but females had marginally greater latency than males (Supplementary Table S6, Fig. S2).

## DISCUSSION

Describing the nature of behavioural responses to unfamiliar environments is critical for understanding how species respond to novel ecological conditions resulting from human-induced environmental change. We found that movement behaviour of *P. cinereus* in laboratory arenas was highly variable in general, but perhaps more importantly, varied significantly between populations in a fragmented landscape. Movement activity, substrate use and latency to move varied among individuals within populations, and individuals were temporally consistent in each trait,

**Table 1**

Principal component analysis (PCA) of behavioural traits for red-backed salamanders, *Plethodon cinereus*, in central New York

Behavioural trait	Factor loadings		
	B1	B2	B3
Latency to move	−0.06	0.08	0.96
Time active on surface	0.91	−0.14	0.12
Time under cover	−0.88	0.11	−0.37
Time climbing	0.73	0.12	−0.11
Number of boundaries crossed	0.86	0.14	−0.17
Distance moved	0.94	0.02	−0.12
Time on soil	−0.08	−0.97	−0.22
Time on sand	−0.04	0.98	−0.12
Eigen value	3.78	1.97	1.19
Proportion of variance explained	0.47	0.25	0.15

**Table 2**

Intraclass correlation coefficients (ICC) and 95% confidence intervals for principal component axes summarizing movement behaviour of red-backed salamanders, *Plethodon cinereus*, in central New York ( $N = 132$  individuals)

Variable	ICC	95% CI
Movement activity (B1)	0.23	0.06–0.39
Substrate use (B2)	0.31	0.14–0.45
Latency (B3)	0.23	0.06–0.39

indicating the existence of movement personalities within populations. The three behaviours were generally not related to sex, body condition or morphology, except that females had longer latencies to move than males. At the population level, we found that salamanders collected from old forest stands had greater movement activity than salamanders from young stands. There was no behavioural differentiation between edge and interior locations within forest stands. These results suggest landscape change may

play an important role in structuring behavioural variation at the population level, but that behavioural divergence depends on spatial scale.

### Individual Behaviour

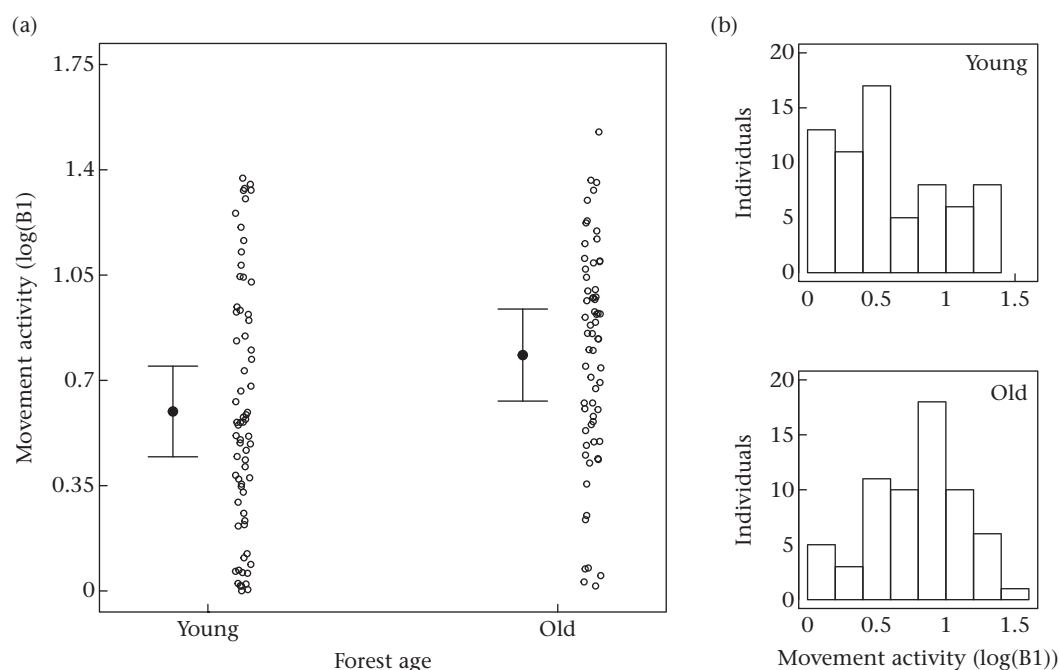
The behavioural response of *P. cinereus* individuals to an unfamiliar environment was variable and described by a multivariate suite of traits. The PCA revealed that the behavioural responses of individuals were mainly differentiated by how active individuals were in moving around the arena (component B1). At the extremes, some individuals moved over the arena for the entirety of the observation period (i.e. high values for time on surface, distance moved, boundaries crossed and time climbing), whereas others moved little or not at all. Known fitness costs of movement for *P. cinereus* include increased predation risk (Maerz, Panebianco, & Madison, 2001) and desiccation (e.g. Jaeger, 1978, 1980). In fact, we found that highly active individuals lost more mass than less

**Table 3**

Model selection statistics and beta coefficients ( $b$ ) for effects of forest location (edge vs interior) and forest age on movement behaviour of red-backed salamanders, *Plethodon cinereus*, in central New York

Comparison	Response variable	Model	$\Delta AIC$	$\omega_i$	$L$	$K$	$b$ (SE)
Forest edge vs interior	Movement activity (B1)	Intercept	0.00	0.68	−81.13	7	—
		Edge-Interior	1.51	0.32	−80.89	8	0.06 (0.08)
	Substrate use (B2)	Intercept	0.00	0.60	−68.24	7	—
		Edge-Interior	0.82	0.40	−67.65	8	−0.10 (0.09)
	Latency (B3)	Intercept	0.00	0.72	−32.57	7	—
		Edge-Interior	1.86	0.28	−32.50	8	0.03 (0.09)
Forest age	Movement activity (B1)	Forest age	0.00	0.83	−52.91	8	0.19 (0.07)
		Intercept	3.24	0.17	−55.53	7	—
	Substrate use (B2)	Intercept	0.00	0.72	−22.81	7	—
		Forest age	1.84	0.28	−22.73	8	−0.02 (0.05)
	Latency (B3)	Forest age	0.00	0.58	−19.73	8	0.08 (0.05)
		Intercept	0.66	0.42	−21.06	7	—

$\Delta AIC_C$  is the difference between  $AIC_C$  of each model and the most-supported model,  $\omega_i$  is the Akaike weight of model  $i$ ,  $L$  is the log likelihood, and  $K$  is the number of parameters.



**Figure 3.** (a) Movement activity (filled circles = means; open circles = individual data points) and (b) frequency distributions of movement activity for red-backed salamanders, *Plethodon cinereus*, from young and old forests in central New York. Movement activity was measured as B1 scores from a principal component analysis describing *P. cinereus* behaviour (Table 1). Error bars represent 95% confidence intervals calculated from the 'effects' package in R (Fox, 2003). Standard deviations were 0.41 for young forests and 0.36 for old forests.

**Table 4**

Model selection statistics and beta coefficients ( $b$ ) for effects of behaviour on water loss for red-backed salamanders, *Plethodon cinereus*, in central New York

Model	$\Delta AIC_c$	$\omega_i$	$L$	$K$	$b$ (SE)
Movement activity (B1)	0.00	1.00	−182.87	8	0.16 (0.03)
Latency (B3)	17.81	0.00	−191.78	8	0.08 (0.03)
Intercept	22.76	0.00	−195.26	7	—
Substrate use (B2)	24.52	0.00	−195.13	8	0.02 (0.03)

$\Delta AIC_c$  is the difference between  $AIC_c$  of each model and the most-supported model,  $\omega_i$  is the Akaike weight of model  $i$ ,  $L$  is the log likelihood, and  $K$  is the number of parameters. Main effects include principal component axes describing behaviour (B1, B2, B3; Table 1).

active individuals. Thus, variation in movement activity may represent different strategies for navigating the trade-off between information acquisition about resources and risks (i.e. exploration; von Merten & Siemers, 2012; Rodríguez-Prieto, Martín, & Fernández-Juricic, 2011; Verbeek, Drent, & Wiepkema, 1994) and costs of physiological stress or predation.

The PCA revealed two secondary components of movement behaviour, each of which explained less behavioural variation than movement activity. First, there was variation in where an individual was likely to be located in the arena (i.e. soil versus sand; component B2). Because soil and sand varied in moisture content and were separated by two boundaries and a bare surface, it is tempting to interpret substrate use as a measure of risk taking. A small group of individuals spent virtually the entire trial on sand, although these individuals had low movement activity, suggesting they mitigated desiccation risk by remaining motionless under a cover object (Supplementary Fig. S1). Alternatively, some individuals may have reclusive personalities and respond to stress (i.e. being released in the arena) by moving far away from the stressor. Second, individuals varied in their initial response to the unfamiliar environment after the cover object was lifted at the start of the trial (component B3). Some individuals moved immediately to another part of the arena after release, whereas others remained motionless for extended periods. Extremes in latency to movement may represent different behavioural tactics of response to sudden stress.

Collectively, the three behavioural components indicate substantial variation in how *P. cinereus* individuals respond to novel environments. Moreover, each behavioural component was significantly repeatable within individuals, suggesting that populations are heterogeneous assemblages of individuals with

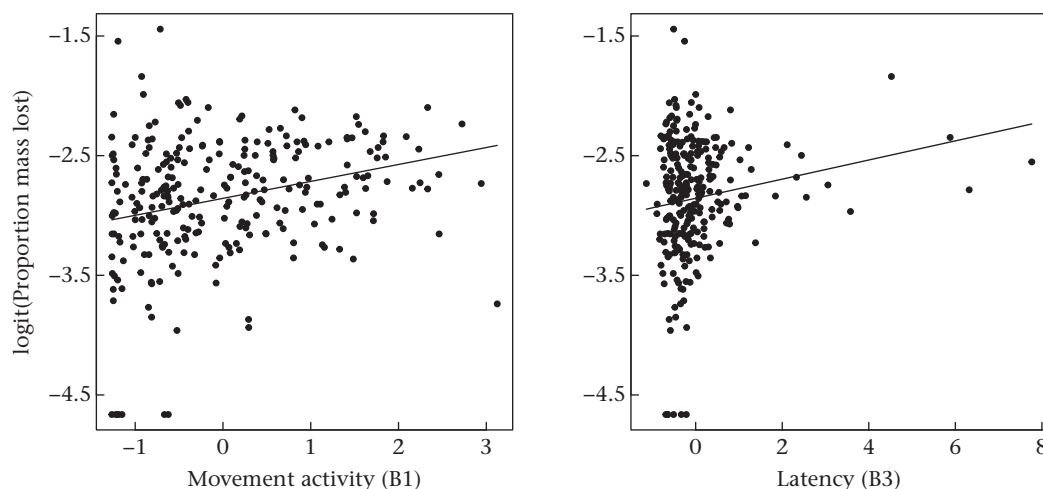
varying behavioural types. Significant repeatability suggests that the behavioural variation documented in this study may have a heritable genetic component, although repeatability may also be due in part to maternal effects or imprinting during early development (Dohm, 2002). Overall, our study adds to the growing body of literature showing that animals show consistent individual differences in behaviour (Bell et al., 2009).

### Geographical Variation in Behaviour

Intraspecific trait variation can be important for understanding species' responses to environmental change, particularly when trait variation is heritable and spatially structured (Moran, Hartig, & Bell, 2016). Our results show that the distribution of movement activity in *P. cinereus* depended on land use history in a fragmented landscape. Mean movement activity of salamanders originating from old forest stands was greater than that of salamanders from young forest stands, despite close proximity of old and young stands throughout the landscape (Fig. 1). Additionally, we found evidence of behavioural divergence between young and old forest stands despite considerable variation in movement activity within stands (Fig. 3). High behavioural variation within stands may be due in part to the use of coarse categories of forest age, spatial variation among site pairs, within-individual variation and variation in experimental conditions (e.g. date of trial, arena).

Our finding suggests that landscape change in the form of forest fragmentation and regeneration can be important for driving behavioural variation among populations. Studies on the effects of landscape change on among-population differences in personality traits have primarily involved comparisons between urban and rural populations (Miranda, Schielzeth, Sonntag, & Partecke, 2013; Sol et al., 2013). Outside of urban areas, behavioural traits have also been associated with the degree of isolation among populations (Baguette & Van Dyck, 2007). Because we used a paired sampling design with young and old forest stands paired by location (Fig. 1), the difference in movement activity between young and old stands is unlikely to be explained by differences in physical isolation.

There are several possible explanations for why movement activity of salamanders from old forest stands was greater than that of salamanders from young forest stands. First, *P. cinereus* may be locally adapted to environmental conditions that vary between old and young forests. Natural selection could cause divergence in



**Figure 4.** Relationship of water loss of red-backed salamanders, *Plethodon cinereus*, to movement activity and latency to movement. Water loss was measured as the proportion of mass lost during behavioural trials. Movement activity and latency were measured as scores from a principal component analysis describing *P. cinereus* behaviour (Table 1). Best-fit lines are based on parameter estimates from models in Table 4.



movement activity between stands if the cost-to-benefit ratio of movement varies with stand age. Mass loss was positively related to movement activity, suggesting that desiccation might be an important cost of activity for *P. cinereus*. At FLNF, canopy cover is lower in young than old forests (Cosentino & Brubaker, 2016), and reduced canopy cover may increase desiccation risk during movement by causing high solar radiation and temperature at the soil surface (Peterman & Semlitsch, 2013). However, density of *P. cinereus* is greater in old stands than in young stands (Cosentino & Brubaker, 2016), so differences in movement activity may be associated with density-dependent processes, including social interactions (e.g. Cote & Clobert, 2007). A clear next step is to examine the fitness consequences of movement personalities when manipulating environmental (e.g. canopy cover, predator density, food availability) and social factors (e.g. density) that differ between old and young forests.

Second, variation in movement activity between salamanders from young and old forests could be due to nonrandom gene flow associated with timber harvest and forest regeneration (Edelaar & Bolnick, 2012; Jacob et al., 2015). Young forest stands at FLNF were cleared in the late 18th century and used for hay and grain production until at least 1938 (DeGloria, 1998), likely resulting in extirpations of *P. cinereus*. Individuals with low movement activity may be more represented in young stands than in old stands if colonists of young stands tend to have low movement activity. *Plethodon cinereus* individuals with high movement activity may acquire more information about spatial variation in habitat quality than individuals with low movement activity, leading movers to actively select older stands of higher quality (e.g. van Overveld & Matthysen, 2010). Alternatively, individuals with low movement activity may be forced to disperse from high-quality stands to low-quality stands if movement activity is positively associated with competitive ability for territories. For example, migratory behaviour in elk is more common among individuals with shy personality traits such as submissiveness and low exploration activity (Found & St Clair, 2016). We need additional experiments to test whether colonists of regenerating forest stands represent a nonrandom subset of movement personalities, and determine whether movement activity, dispersal and competitive ability (e.g. aggression, sociability) are part of a behavioural syndrome.

We found no differences in movement behaviour between individuals collected from edge and interior locations within forest stands, suggesting that behavioural differentiation depends on spatial scale. It is possible that environmental conditions affecting the costs and benefits of movement behaviour did not vary significantly between edge and interior locations, which would be required for natural selection or habitat selection to cause behavioural differentiation. However, canopy cover is known to be positively related to distance from forest edges at FLNF (Cosentino & Brubaker, 2016). If selection pressures do differ between edge and interior locations, behavioural divergence could be prevented by strong gene flow within forest stands, particularly if within-stand gene flow is random with respect to genotypes underlying movement behaviour (Richardson, Urban, Bolnick, & Skelly, 2014).

## Conclusions

There is keen interest in using models of animal movement and population connectivity to predict how environmental change will affect species distributions and to identify corridors for protection (e.g. Rudnick et al., 2012). However, these models often rely on GIS or remotely sensed data (e.g. distance, land cover), and they typically assume that individuals are identical with respect to

movement behaviour, or that variance in movement behaviour is stochastic (Baguette & Van Dyck, 2007; Lowe & McPeck, 2014; Morales & Ellner, 2002). Our study emphasizes that individuals within populations can show consistent differences in movement behaviour, and that individual variation in movement can be spatially structured in fragmented landscapes. Given that intra-specific trait variation can have a strong impact on species' responses to environmental change (Bestion, Clobert, & Cote, 2015; Moran et al., 2016; Valladares et al., 2014), further research is needed to characterize individual variation and to understand the ecological and evolutionary forces generating variation across spatial scales.

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## Supplementary Material

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