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Original Article

Selective disappearance does not underlie age-related changes in trait repeatability in red squirrels

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Understanding the causes and consequences of repeatable among-individual differences in behavior (i.e., animal personality) is a major area of research in behavioral and evolutionary ecology. Recently, attention has turned to understanding the processes behind changes in repeatability through ontogeny because of their implications for populations. We evaluated the relative importance of selective disappearance (i.e., differential mortality), an among-individual mechanism, in generating age-related changes in the repeatability of aggression and activity in juvenile North American red squirrels (*Tamiasciurus hudsonicus*). We observed age-related decreases in the repeatability of aggression across ages, arising from lower among-individual variance. Although we found evidence for directional selection on aggressiveness, it was insufficient to erode among-individual variance. Thus, ontogenetic decreases in the repeatability of aggression do not appear to be due to selective disappearance. In contrast, the repeatability of activity was higher across ages due to higher among-individual variance in activity, but there was no support for selective disappearance based on activity. Taken together, our results suggest that age-related changes in trait repeatability in red squirrels are not the result of selective disappearance and instead may be the result of within-individual developmental processes, such as individual differences in developmental trajectories.

Key words: **among-individual variation, animal personality, coefficient of variation, plasticity, selective disappearance, within-individual variation**

INTRODUCTION

Repeatable among-individual variation in behavioral traits, referred to as animal personality (Bell et al. 2009), are widespread and can have important ecological and evolutionary consequences (reviewed in Wolf and Weissing 2012). For example, the timing of life-history events, including dispersal, primiparity, and mortality, may be a consequence of variation in animal personality (Réale et al. 2000; Biro and Stamps 2008). On a larger scale, animal personality can affect population establishment and stability, particularly because dispersers are likely to represent a nonrandom (e.g., by state, morphology, physiology, or behavior) subset of a population (Matthysen 2012). Consequently, understanding the mechanisms that lead to consistent among-individual variation is a major research theme in contemporary behavioral and evolutionary ecology (Sih et al. 2015).

Animal personality is typically quantified by repeatability—the proportion of total phenotypic variation that is attributable to individuals (Lessells and Boag 1987). Recent studies have documented age-related changes in the repeatability of behavior (Stamps and Groothuis 2010; Castanheira et al. 2013; Petelle et al. 2013; Kok et al. 2019). Although the most common pattern is an increase in repeatability with age, other studies have documented both decreases and no change in repeatability with age (reviewed in Kok et al. 2019). Multiple developmental processes could generate age-related changes in trait repeatability, including among-individual

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differences in developmental plasticity (Stamps and Krishnan 2014a, 2014b), state-behavior feedbacks (Dall et al. 2004; Luttbeg and Sih 2010; Sih et al. 2015), or age-related changes in intraindividual variability (Stamps et al. 2012; Japyassu and Malange 2014), for example, due to within-individual trait canalization (Kok et al. 2019). Longitudinal studies in captive populations have provided evidence that each of these processes can contribute to age-related changes in repeatability (reviewed in Kok et al. 2019).

In wild animals, age-related changes in repeatable among-individual variation can also arise through selective disappearance (Adriaenssens and Johnsson 2013; Petelle et al. 2013). Selective disappearance is a form of viability selection, whereby certain phenotypes are selected for, creating a change in population composition over time (Nussey et al. 2006, 2008). For example, if extreme behavioral phenotypes experience higher mortality (i.e., stabilizing selection), all else being equal, this will reduce the extent of among-individual variation as a function of age, resulting in age-related decreases in repeatability (Grant and Mettler 1969). This could come about if individuals with more extreme phenotypes exhibit niche specialization and thus exhibit less within-individual variability than intermediate phenotypes (Wilson 1998; Schmidt et al. 2001; Stamps and Groothuis 2010; Bastille-Rousseau et al. 2011). Alternatively, if intermediate behavioral types suffer higher mortality (i.e., disruptive selection), this will increase the relative degree of among-individual variation, resulting in age-related increases in repeatability (Adriaenssens and Johnsson 2013; Bergeron et al. 2013; Petelle et al. 2013).

Selective disappearance can also act on within-individual variances. If selection favors individuals that are behaviorally predictable (Wilson 1998; Biro and Stamps 2008; Chang et al. 2017), the loss of individuals from a population that is relatively unpredictable in its behavior (i.e., have higher residual variance or intraindividual variability) would result in increased estimated repeatability across ages. For example, individuals that are predictable in their level of aggression (be it high or low) may have greater survival if unpredictability affects territory retention independent of absolute aggressiveness, especially during intraspecific encounters (Wolf et al. 2008; Wolf and McNamara 2013). Alternatively, if predictability is disadvantageous (e.g., Maye et al. 2007: Brembs 2011; Chang et al. 2017), the loss of predictable individuals from a population could result in decreased repeatability with age through an increase in residual variance or intraindividual variability.

Here, we investigated if selective disappearance leads to age-related changes in behavioral repeatability during the juvenile life stage in a population of North American red squirrels (*Tamiasciurus hudsonicus*, hereafter red squirrels) in Yukon, Canada. In this population, significant repeatability (*r*), has been documented after weaning (>70 days old) for both activity and aggression (Boon et al. 2007; Taylor et al. 2012; Kelley et al. 2015). These behaviors are heritable (Taylor et al. 2012) and related to fitness, with more aggressive females having offspring with increased survival to adulthood (Boon et al. 2007), particularly in years with high intraspecific competition for territories (Taylor et al. 2014). Within-individual plasticity, while not appropriate to evaluate here quantitatively due to our sampling methods (see Methods below), has previously been reported as contributing to age-related changes in behavior in this population (Kelley et al. 2015). In a sample of 16 red squirrels assayed after weaning and again as yearlings, individuals that were relatively active or aggressive as juveniles decreased in mean activity or aggression as yearlings, while individuals that were relatively inactive or nonaggressive as juveniles increased in mean activity or aggression as yearlings (Kelley et al. 2015). This regression to the mean reflected a within-individual change, resulting in lower among-individual variance with increasing age and, presumably, age-related decreases in repeatability.

In this study, we assessed whether selective disappearance also contributed to age-related changes in the repeatability of activity and aggression. To test this, we first qualitatively compared the trait repeatabilities obtained in this study (in juveniles between emergence and weaning and for a subset of individuals that survived summer and winter) with repeatabilities from earlier studies of yearlings (Kelley et al. 2015) and adults (Boon et al. 2007; Taylor et al. 2012) from the same population. Next, we evaluated the level of support for four mechanisms consistent with the observed age-related patterns: 1) under the "intermediate advantage" hypothesis, intermediate phenotypes are expected to survive better (i.e., stabilizing selection), leading to age-related decreases in repeatability across ages; 2) under the "extreme advantage" hypothesis, extreme phenotypes are expected to survive better (i.e., disruptive selection), leading to age-related increases in repeatability across ages; 3) under the "unpredictable advantage" hypothesis, unpredictable individuals are expected to survive better, leading to lower estimated repeatability across ages; and 4) under the "predictable advantage" hypothesis, predictable individuals are expected to survive better, leading to higher estimated repeatability across ages.

METHODS

Study area

Our study area comprises two 40-ha plots located near Kluane Lake in the traditional territory of the Champagne and Aishihik First Nations in southwest Yukon, Canada (61°N, 138°W). The vegetation in this region is predominantly mature white spruce (*Picea glauca*), willow (*Salix* spp.), trembling aspen (*Populus tremuloides*), and bog birch (*Betula glandulosa*; Douglas 1974).

Animal ethics approval

This project was approved by the University of Alberta (Animal Care Permit: AUP000000028) and the Yukon Government's Department of Tourism and Culture (Yukon Science and Explorers Permit: 17-13S&E and 18-08S&E) and Department of Environment (Wildlife Research Permit: WRP 205 and 218).

Study species

Red squirrels are diurnal rodents found in the boreal forest throughout North America (Steele 1998). Their primary food source is white spruce seeds that are cached as unopened cones in a central larder (Smith 1968). They defend exclusive territories year round, making them highly trappable because of their site fidelity (Smith 1968; Boon et al. 2008). Females have, on average, three juveniles per litter (McAdam et al. 2007). Juveniles must establish their own territory after they are weaned from their mothers. Juveniles emerge from their natal nest at 48 days old ± 0.7 standard error (SE; Martinig AR, Boutin S, unpublished data) and are weaned at around 70 days old (Boutin and Larsen 1993). Weaning occurs when a juvenile is no longer reliant on its mother's milk and is used here to differentiate selective episodes (preweaning and postweaning), particularly because survival through the first year of life is low and is a predictor of lifetime fitness (McAdam et al. 2007). Male immigration is favored (Martinig et al. 2020b) and females acquire territories closer to their natal territory than males in the autumn (female average: 606 m ± 49 SE, median: 88 m vs. male average: 817 m ± 194 SE, median: 144 m; Martinig AR, Lane JE, Dantzer B, McAdam AG, Boutin S, unpublished results), but both sexes have similar recruitment distances the following spring (within 100 m of the natal site; Larsen and Boutin 1994; Berteaux and Boutin 2000).

Conducting behavioral assays

We conducted behavioral assays on 102 juvenile red squirrels (58 females and 44 males) from 55 litters across 2 years: May to August 2017 and 2018 (n = 72 and 30 individuals, respectively). We trapped red squirrels using live traps (Tomahawk Live Trap, Hazelhurst, GA) baited with peanut butter. We checked traps every 20 min. We verified individual identity using alphanumeric metal ear tags (0.25 g per tag; Monel # 1; 5 digits; National Band and Tag, Newport, KY). As part of a long-term study, locally born juveniles receive lifelong ear tags at 25 days old using an ear punch. Ear tag color does not affect predation (Stuart-Smith and Boutin 1995). We monitored juvenile movement through a combination of telemetry (model PD-2C, 4 g, Holohil Systems Limited, Carp, Canada) and observation. We confirmed death by retrieving the carcass.

Once trapped, we immediately transferred red squirrels to the testing arena at the site of capture for the standardized behavioral assays. The testing arena was a plastic box (60 × 50 × 80 cm) with a clear acrylic lid through which we recorded the behavioral assays with a camcorder (Sony Handycam, Sony of Canada Ltd., Toronto, Canada). The floor of the arena included four blind holes, 3.7 cm in diameter. We used open field trials to quantify activity (activity assay), defined as movement in a novel environment (Walsh and Cummins 1976), and mirror-image stimulation trials to measure aggression (aggression assay), defined as antagonistic behavior directed toward a simulated conspecific (i.e., their mirror image; Svendsen and Armitage 1973).

The activity assay lasted for 7.5 min. After 7.5 min, we exposed a mirror (28.7 × 40 cm) on the right side of the box and the aggression assay lasted for an additional 5 min. We released individuals at the site of capture afterward. We performed the first assay after emergence (mean age 55.95 days ± 6.88 standard deviation [SD], n = 102 individuals), the second assay after weaning (mean age 78.71 days ± 5.96 SD, n = 62 individuals), and the third assay the following spring when juveniles were yearlings (404.45 days ± 34.62 SD, n = 11 individuals). Earlier work demonstrated that red squirrels do no habituate to these assays with repeated exposure over the short term (i.e., within years; Taylor et al. 2012). We scored behaviors using an ethogram adapted from Boon (2007; and references therein; see Supplementary Table S1 for behavior definitions) using the Behavioral Observation Research Interactive Software (Friard and Gamba 2016). Videos were scored by three different observers (all Spearman rank correlation coefficients were 1.0).

We recorded body mass (grams) at birth and at 25 days old using a Taylor precision digital scale (Model 1250-49, IL), and during trapping using a 600-g spring scale (Pesola AG, Baar, Switzerland). We measured growth rate (grams per day) as the linear increase in mass between ~25 and ~56 days old and between ~50 and ~79 days old. The growth rate during that time is approximately linear (Supplementary Figure S1).

Principal component analyses

We performed two separate principal component analyses (PCAs) for our behavioral assays using the *prcomp* function in the baseline "stats" package in the statistical environment R, version 3.5.2 (R Development Core Team 2018). We used the first principal component (PC1) from each of the activity and aggression assays to generate a single score for each behavior (Boon et al. 2007; Taylor et al. 2012; Kelley et al. 2015). Activity PC1 explained 41.59% of the variance and the behaviors loading most heavily on this component were walk, jump, and still (the latter of which loaded negatively; Table 1). Aggression PC1 explained 49.97% of the total variance and the behaviors loading most heavily on this component were time spent in the front (which loaded positively) and back of the arena, attack latency, and approach latency (the latter three behaviors loaded negatively; defined in Supplementary Table S1; Table 1). We considered behaviors to be heavily loaded if their loadings were >0.40 (Budaev 2010).

In the aggression assays, some individuals (14.72% of assays) never approached the mirror, right censoring their approach and attack latencies (Supplementary Table S1). Once the mirror was exposed, these individuals made no eye contact with their reflection, nor did they attack their reflection. Whether we assigned these individuals with the maximum latency value (5 min) or treated them as missing data yielded quantitatively similar results (results not shown), suggesting that these nonresponding individuals were accurately characterized as representing extreme latency values in the aggression assay. We present the results for when these individuals were assigned the maximum latencies to retain the largest sample size.

Estimation of repeatabilities

We estimated adjusted repeatabilities, derived from univariate models with assay number, natal location (one of two study areas), and sex as fixed effects and individual identity as a random effect, for activity and aggression separately (Nakagawa and Schielzeth 2013), after visually inspecting the residuals for normality and homoscedasticity (including Fligner–Killeen's tests for homogeneity of variances (Fligner and Killeen 1976)). We calculated repeatability (r; benchmarks for repeatability outlined in Bell et al. 2009) as the among-individual variance/(among-individual variance + within-individual variance; Lessells and Boag 1987) for all juveniles between emergence and weaning (juvenile repeatability) and between weaning and the following year (repeatability from juvenile to yearling age). We estimated repeatability between emergence and weaning for 1) all individuals and only the subset that survived summer and the repeatability between weaning and the following year for 2) all individuals that survived summer and only the subset that survived winter. By comparing repeatability and variance components between all individuals and only the survivors for each selection period, we were able to assess the role of selective disappearance based on individual phenotype across two age-classes (juvenile and yearling) within the same individuals. Repeatabilities were considered to be significantly different based on the amount of overlap of their 95% credible intervals (CrIs). When testing for differences between two groups, we use the term "significant" when the 95% CrIs did not show any overlap or when the overlap between groups is up to 15%. We elaborate on the use of this approach in the next section.

Summer and winter survival analyses

We assessed the predictors of summer (i.e., survival between emergence and weaning; 2017: n = 72 individuals, 42 survived summer; 2018: n = 30 individuals, 20 survived summer) and winter (i.e., survival between weaning and yearling age; 2017: n = 42 individuals, 17 survived winter; 2018: n = 20 individuals, 0 survived winter) survival (binary response variable; 0 = dead, 1 = alive) using univariate generalized linear mixed-effects models (binomial with logit link). We checked for both directional (activity and aggression) or quadratic effects (activity^2 and aggression^2) of behavior on survival to test for selective disappearance based on phenotype or disruptive (i.e., extreme phenotypes survive better) and stabilizing (i.e., intermediate phenotypes survive better) selection, respectively.

We additionally assessed if selection was based on predictability independent of an individual's mean trait value. We did this by testing for differences in the coefficient of variation (CV) for activity and aggression with significance set to α = 0.05 using an analysis of variance test with R (R Development Core Team 2018). The CV mean standardizes individual variance (Taylor 1961; Houle 1992). Because individuals needed a minimum of two assays to calculate their CV, this meant we could only calculate CV for individuals that survived summer (n = 62 individuals) and thus assess winter selection (i.e., from weaning to yearling age) for predictability between emergence and weaning.

Given that activity and aggression were relatively repeatable in this study (r = 0.29 [95% CrI: 0.23–0.33] and r = 0.30 [95% CrI: 0.24–0.34], respectively; see Results) and in previous studies (Boon et al. 2007; Taylor et al. 2012; Kelley et al. 2015), we used each individual's first assay in the contrast (i.e., at emergence for summer and at weaning for winter). We did this because using the average of the first two assays would give higher precision to juveniles with more than one assay. Results were qualitatively similar for winter survival when using the assay at emergence or the average of the first two assays for winter survival (Table 3 and Supplementary Table S2).

Although growth rate, parturition date, and sex have previously been shown to be key predictors of juvenile survival in this population using larger sample sizes (Hendrix et al. 2020 and references therein), we did not find any effect of these variables on survival in this dataset (see Supplementary Tables S3 and S4). We did not include any environmental variables as fixed effects because our study was conducted over 2 years with similar conditions (e.g., low food years: 5–60 white spruce cones per tree; Krebs et al. 2017). We had insufficient power to include year as a fixed effect because no individuals survived winter from the 2018 cohort. Therefore, we present the results both with years pooled and with separate analyses for each year.

As death only occurs once (i.e., each individual is only in the models once), we did not include individual identity as a random effect and instead used litter identity as a random effect in all models to account for nonindependence between siblings. We tested for collinearity between predictor variables and found none (all Pearson's $r < 0.43$; i.e., below the threshold of 0.6, above which estimates could be biased; Freckleton 2011). We also checked for overdispersion (and found none) by verifying that the ratio of model deviance to the number of observations was approximately 1:1.

We were unable to explicitly test whether individual differences in behavioral plasticity (Supplementary Figure S2), a within-individual mechanism, contributed to age-related changes in behavior by modeling I × E. Such analyses require minimum sample sizes of 20 individuals with 10 replicates per individual to achieve modest power (Martin et al. 2011). We had 62 individuals with two or three replicates.

We fitted our univariate models using the "blme" package, version 1.0–4 (Chung et al. 2013), to deal with model singularity in two of our models. We used the *sim* function of the "arm" package, version 1.10-1 (Gelman and Su 2018), to simulate values of the posterior distributions of the model parameters. For all univariate models, we extracted the mode (β) of the estimated effect and its 95% CrIs based on 10 000 simulations using the *posterior.mode* function of the "MCMCglmm" package, version 2.29 (Hadfield 2010), and the *HPDinterval* function of the "coda" package, version 0.19–3 (Plummer et al. 2006), respectively.

We then evaluated support for an effect using the estimated effect sizes (β) and their 95% CrIs (Cumming and Finch 2005; Wasserstein and Lazar 2016) and reported Bayesian P values where relevant (i.e., the proportion of estimates that are >0 if the estimate is negative or <0 if the estimate is positive). This approach acknowledges that support (or lack of support) for an effect varies continuously and provides the most likely effect size and its likelihood (Cohen 1994). We interpreted estimates and 95% CrIs that did not overlap zero as providing strong support for an effect. If the 95% CrI was centered on zero (i.e., effect size zero or near zero, with equal distribution of CrI on either side of zero), we interpreted this as strong support for a lack of an effect. If the 95% CrI overlapped zero but the point estimate was not centered on zero (≤15% overlap; Cumming 2009), we interpreted this as moderate support for an effect. For reference, a Bayesian P value of <0.15 provides at least five times greater support for an interpretation of an effect than it does for the interpretation of a lack of an effect. To facilitate comparisons of effect sizes across variables, we mean-centered and standardized all numerical variables to 1 SD within cohort and study area (Schielzeth 2010). We calculated activity^2 and aggression^2 and individual-specific CVs from raw scores before standardization.

RESULTS

Age-related shifts in behavioral repeatability

We observed age-related changes in repeatability for both activity and aggression, where the repeatability of activity was higher across ages, whereas the repeatability of aggression was lower across ages (Table 1; Figure 1). The repeatability of activity between emergence and weaning was 0.29 (95% CrI: 0.23–0.33; n = 102 individuals) and between weaning and yearling ages was 0.59

Table 1

PCA loadings for activity (from open field trial) and aggression (mirror image stimulation) in North American red squirrels (*Tamiasciurus hudsonicus*) in Yukon, Canada, for 2017 (n = 72 individuals) and 2018 (n = 30 individuals) juvenile cohorts. Bolded numbers indicate behaviors that were heavily loaded (>0.40) on the PC

Activity assay	Activity PC1	Aggression assay	Aggression PC1
Walk	**0.50**	Front	**0.51**
Jump	**0.44**	Back	**−0.51**
Hole	0.33	Attack	0.33
Hang	−0.17	Attack latency	**−0.40**
Chew	0.37	Approach latency	**−0.46**
Groom	−0.11		
Still	**−0.52**		
Standard deviation	1.71		1.58
Percent variation	41.59 %		49.97 %
Cumulative proportion	0.42		0.50

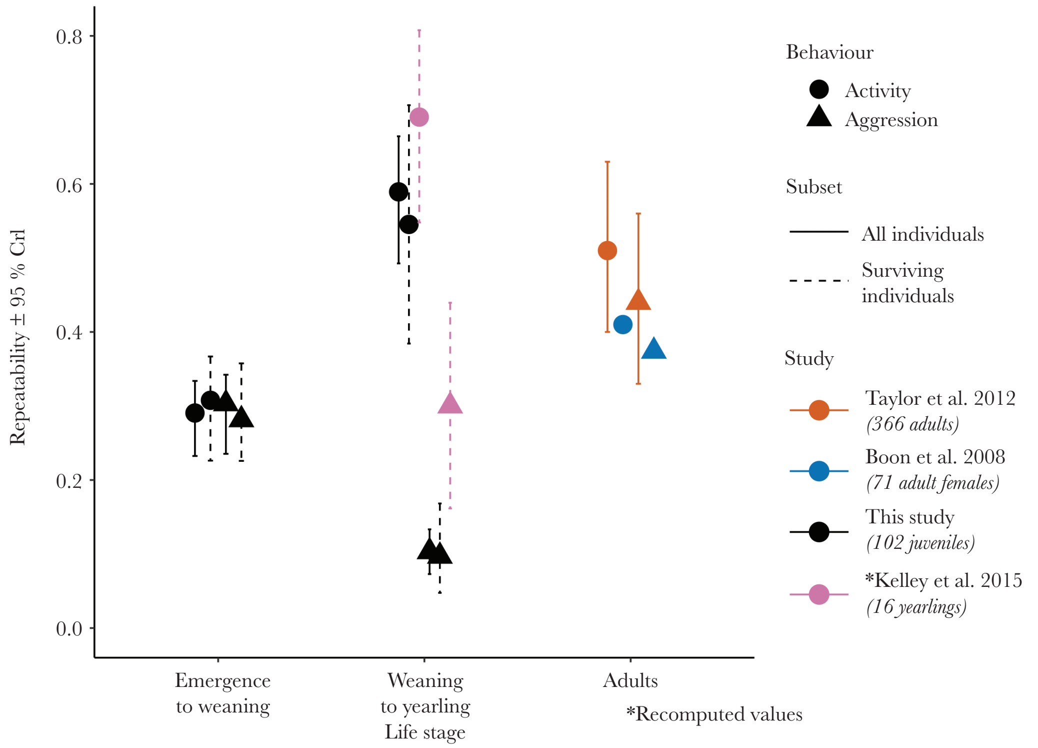

Figure 1

Repeatability (r) estimates with 95% CrIs for activity and aggression across ontogeny in this population of North American red squirrels in Yukon, Canada. We present data for the emergence to weaning (n = 102 individuals, n = 62 survived) and weaning to yearling (n = 62 individuals, n = 17 survived) life stages ("This study"; 2017 and 2018 grouped). We present estimates from Kelley et al. 2015 (1 year study, only survivors; recalculated using methodology here); Taylor et al. 2012 (4 year study, 95% confidence intervals provided); and Boon et al. 2007 (4 year study; no confidence/credible intervals provided).

(95% CrI: 0.49–0.66; n = 62 individuals; Supplementary Table S5). The repeatability of aggression between emergence and weaning was 0.30 (95% CrI: 0.24–0.34; n = 102 individuals) and declined to 0.10 (95% CrI: 0.07–0.13; n = 62 individuals) between weaning and yearling ages (Supplementary Table S5).

Among-individual processes generating age-related shifts in repeatability

We evaluated the relative importance of among-individual processes, such as selection on individual means or individual predictability, on the observed age-related shifts in the repeatability of activity and aggression by comparing repeatabilities between 1) datasets including all individuals to 2) datasets restricted to only surviving individuals (Table 2 and Supplementary Table S5), and by estimating the strength of directional and quadratic selection on trait means and within-individual trait variances for each cohort (Table 3).

The repeatability of activity from emergence to weaning was similar between 2017 (r = 0.29, 95% CrI = 0.23–0.36; n = 72 individuals) and 2018 (r = 0.31, 95% CrI = 0.21–0.41; n = 30 individuals), as were the relative contributions of among- and within-individual variance (Table 2). In contrast, we did observe year differences in the repeatability of aggression. The repeatability of aggression from emergence to weaning was qualitatively and quantitatively higher in 2017 (r = 0.44, 95% CrI = 0.34–0.50; n = 72 individuals) compared with the 2018 cohort (r = 0.21, 95% CrI = 0.14–0.31; n = 30 individuals) due to a combination of lower among-individual and higher within-individual variances in 2018 (Table 2).

Importantly, however, in both selective periods (summer and winter), comparisons of repeatability between datasets (all red squirrels vs. surviving red squirrels only) were qualitatively and quantitatively similar for both activity and aggression for both the 2017 and 2018 cohorts (Table 2 and Supplementary Table S5). The repeatability of activity for all individuals from emergence to weaning was qualitatively and quantitatively similar across years (2017 r = 0.29, 95% CrI = 0.23–0.36; n = 72 individuals; 2018 r = 0.31, 95% CrI = 0.21–0.41; n = 30 individuals) compared with only the survivors for each year (2017 r = 0.33, 95% CrI = 0.23–0.40; n = 42 individuals; 2018 r = 0.30, 95% CrI = 0.19–0.44; n = 20 individuals; Table 2). The repeatability of aggression for all individuals from weaning to yearling ages was qualitatively and quantitatively similar across years (2017 r = 0.44, 95% CrI = 0.34–0.50; n = 72 individuals; 2018 r = 0.21, 95% CrI = 0.14–0.31; n = 30 individuals) compared with only the survivors for each year (2017 r = 0.41, 95% CrI = 0.31–0.51; n = 42 individuals; 2018 r = 0.22, 95% CrI = 0.13–0.34; n = 20 individuals; Table 2). This was also true for within- and among-individual variance components (Table 2 and Supplementary Table S5). These results suggest that selective disappearance is not an important contributor to the age-related shifts observed.

Selection analyses largely corroborated this interpretation. There was no evidence for directional or quadratic selection on activity (Table 3 and Supplementary Table S2). Similarly, there was no evidence of quadratic selection on aggression, though there was moderate support for directional selection on aggression during the summer for the 2018 cohort (β = −1.43, 95 % CrI: −3.40–0.14, Bayesian P value = 0.03; n = 30 individuals; Figure 2a). This directional selection on aggression was sufficiently weak that it did not erode among-individual variance (Table 2). No squirrels survived winter in 2018, precluding the analysis of predictors of survival.

Table 2

Among-individual and residual variance components for activity and aggression repeatability estimates (*r*) and variances with 95% CrIs for juvenile North American red squirrels. Contrasts were considered to be significantly different if there was a 0–15% overlap in the 95% CrIs

Activity	Data subset	*r* (95% CrI)	Among-individual variance (95 % CrI)	Within-individual variance (95 % CrI)
Emergence to weaning				
2017 cohort	All (n = 72)	0.29 (0.23, 0.36)	0.74 (0.50, 1.05)	1.71 (1.38, 2.33)
	Survivors (n = 42)	0.33 (0.23, 0.40)	0.79 (0.56, 1.31)	1.84 (1.42, 2.54)
2018 cohort	All (n = 30)	0.31 (0.21, 0.41)	1.06 (0.58, 1.76)	2.14 (1.63, 3.62)
	Survivors (n = 20)	0.30 (0.19, 0.44)	1.04 (0.48, 1.88)	2.01 (1.49, 3.58)
Weaning to yearling[a]				
	All (n = 42)	0.57 (0.46, 0.66)	1.90 (1.26, 2.70)	1.35 (0.99, 2.15)
	Survivors (n = 17)	0.56 (0.40, 0.70)	1.90 (0.95, 3.53)	1.43 (0.89, 2.80)
Aggression	Data subset	*r* (95 % CrI)	Among-individual variance (95 % CrI)	Within-individual variance (95 % CrI)
Emergence to weaning				
2017 cohort	All (n = 72)	0.44 (0.34, 0.50)	0.93 (0.69, 1.31)	1.33 (1.04, 1.80)
	Survivors (n = 42)	0.41 (0.31, 0.51)	0.99 (0.62, 1.39)	1.25 (1.00, 1.84)
2018 cohort	All (n = 30)	0.21 (0.14, 0.31)	0.70 (0.37, 1.23)	2.80 (1.69, 3.87)
	Survivors (n = 20)	0.22 (0.13, 0.34)	0.71 (0.31, 1.41)	2.35 (1.79, 4.27)
Weaning to yearling[a]				
	All (n = 42)	0.09 (0.06, 0.13)	0.22 (0.10, 0.35)	1.97 (1.38, 3.13)
	Survivors (n = 17)	0.09 (0.04, 0.17)	0.26 (0.07 0.57)	1.84 (1.21, 4.01)

[a] Only includes 2017 cohort. Excluded 2018 cohort because no individuals from that cohort survived winter. Results for both cohorts grouped can be found in Supplementary Table S5.

Table 3

Sources of variation in summer (emergence to weaning) and winter (weaning to yearling) survival for juvenile North American red squirrels. We use the first assay for summer and winter. We provide point estimates from univariate generalized linear mixed-effects models for fixed effects (posterior mode β) with 95% CrI and random effects with a binomial error distribution. Bold values indicate moderate support for an effect based on the 95% CrIs having <15% overlap with zero

	Summer (emergence to weaning)		Winter (weaning to yearling)[a]
	2017 cohort (n = 72 individuals, 42 survived)	2018 cohort (n = 30 individuals, 20 survived)	2017 cohort (n = 42 individuals, 17 survived)
Fixed effects[b]	β (95 % CrI)	β (95 % CrI)	β (95 % CrI)
Activity	−0.07 (−0.63, 0.47)	0.79 (−0.62, 2.18)	0.17 (−0.84, 1.09)
Aggression	−0.08 (−0.71, 0.62)	**−1.43 (−3.40, 0.14)**	0.72 (−0.68, 1.64)
Activity[b]	0.19 (−0.49, 0.60)	−0.29 (−1.59, 0.81)	0.34 (−0.63, 1.21)
Aggression[b]	0.06 (−0.69, 0.64)	0.11 (−0.91, 1.50)	0.58 (−0.58, 1.67)
Random effect			
Among-litter variance	0.74 (0.39, 1.11)	0.45 (0.22, 0.74)	2.38 (1.51, 4.30)
Residual variance	1	1	1

[a] Excluded 2018 cohort because no individuals from that cohort survived winter. Results for both cohorts grouped can be found in Supplementary Table S2.
[b] Mean standardized numerical variables within cohort and study area.

However, in 2017, there was no support for selection on behavior over the winter (Table 3 and Supplementary Table S2).

We could not evaluate support for selection on trait variance during the period from emergence to weaning because we only had repeated measures of survivors and, therefore, could not estimate variance in behavioral expression for nonsurvivors. However, for the weaning to yearling period, we evaluated whether the CV of the two repeated assays (emergence and weaning) predicted winter survival. As expected from the results in Table 2, there was no support for selection for or against predictability for either activity (*t*-test, $F_{1,59} = 1.05$, $P = 0.31$) or aggression (*t*-test, $F_{1,59} = 0.63$, $P = 0.43$; Figure 2b). Results were qualitatively similar when excluding the 2018 cohort (activity: *t*-test, $F_{1,39} = 1.26$, $P = 0.27$; aggression: *t*-test, $F_{1,39} = 0.76$, $P = 0.39$).

DISCUSSION

We observed age-related shifts in the repeatability of aggression and activity in red squirrels. Although there are multiple mechanisms that can generate such patterns, a key episode of selection is survival through the juvenile life stage (Ferguson and Fox 1984; Gaillard et al. 1998; Both et al. 1999; Hoey and McCormick 2004). Thus, selection during this period is expected to be strong, and we predicted that selection might be important in contributing to the age-related shifts in observed repeatability. Contrary to our expectation, we did not detect selective disappearance based on juveniles' activity or aggression despite age-related shifts in the repeatability of activity and aggression (increasing and decreasing, respectively). Instead, we found that selection fluctuated across years and suggest

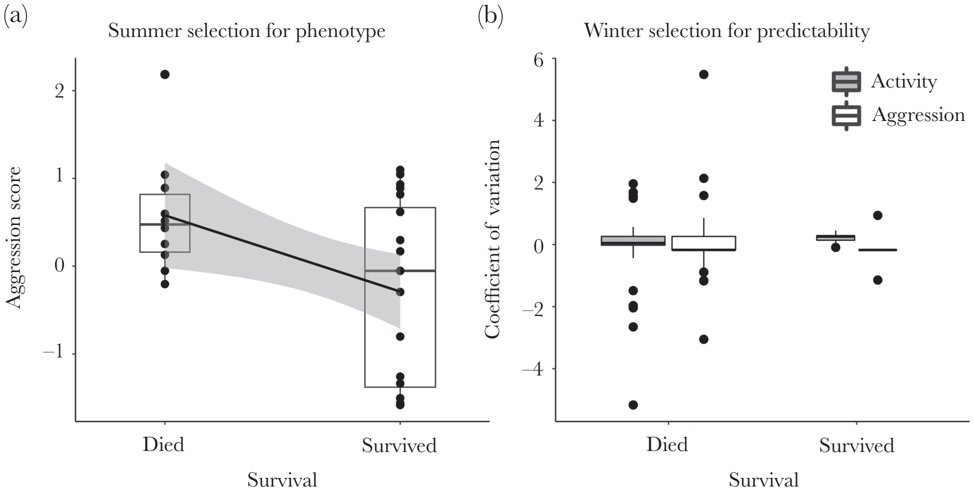

Figure 2
(a) Summer survival to weaning was lower for aggressive juvenile red squirrels in 2018 (*n* = 30 individuals, *n* = 20 survived; using emergence assay). (b) CVs (using emergence and weaning assays) for activity and aggression for juveniles between weaning and yearling life stages in 2017 and 2018 (*n* = 62 individuals, *n* = 17 survived). Lines of best fit (a) or box plots (b) are plotted with SE shading (a) or bars (b).

that mechanisms other than selective disappearance may be responsible for the age-related shifts in repeatability we observed.

If selective disappearance contributed to the observed changes in repeatability for activity, we expected to find differences in survival based on activity because active behavior is frequently associated with higher mortality risk through predation (Cote et al. 2010, 2013) and is often a function of familiarity (e.g., location of refuges, escape routes, predator nests, or dens; Bonte et al. 2012). However, we found no support for the selective disappearance of more active juvenile red squirrels. Juvenile red squirrels, regardless of activity level, may be buffered from this type of mortality as juveniles tend to live on their natal midden until they acquire a territory of their own, thereby spending minimal time in unfamiliar environments except during prospecting forays, which are not always done alone (Martinig AR, personal observations). Alternatively, predation risk may be too low or our understanding of the relationship between risky behavior (i.e., active, bold, and exploratory) could need updating (Moiron et al. 2020). In Barbary ground squirrels (*Atlantoxerus getulus*), boldness, a trait also assumed to incur a survival cost through predation, was associated with increased survival through bolder individuals experiencing predation release (Piquet et al. 2018)—a result further supported for exploratory behavior (another trait similarly associated with predation risk) in *Anolis sagrei* lizards (Lapiedra et al. 2018). Similarly, boldness in bighorn sheep (*Ovis canadensis*) was associated with higher survival and only had a survival cost for the oldest ewes (Réale and Festa-Bianchet 2003). While studies on behavioral trait selection during the juvenile period are relatively scarce (Quinn et al. 2009; Bergeron et al. 2013), there is strong evidence that risky behavior does not always lead to higher mortality across a diversity of taxa (reviewed in Moiron et al. 2020).

Likewise, the relationship between aggression and survival (moderate effect of directional selection against aggression) may depend on whether aggressive signaling is honest. For example, in song sparrows (*Melospiza melodia*), individuals that under-signal have been found to have a survival advantage (Akçay et al. 2015) because predation risk increases during aggressive encounters (Jakobsson et al. 1995). If aggression in red squirrels is a reliable signal of an individual's actual aggression, individuals that respond to intruders with high aggression could incur increased mortality. When aggression is expressed relative to major life-history events, such as territory acquisition, would also explain why aggressive individuals had lower survival. During our study, some of the juveniles with a territory (9 out of 33 cases) shared their natal territory with their mother or sibling their first winter. If nonaggressive red squirrels are tolerated as secondary settlers on a territory but aggressive red squirrels are not, this could result in higher survival for less aggressive red squirrels when vacancies are scarce. The need to have a territory, even a shared one, may explain why less aggressive juveniles had higher survival. Sharing territories in cold winters could also offer thermal benefits from proximity to conspecifics, explaining why an earlier study found that single juvenile territory holders had lower survival in colder winters (see Hendrix et al. 2020).

Although we did not detect selective disappearance based on juveniles' activity or aggression, we did detect weak evidence of fluctuating selection across years for aggression but not activity. There has been evidence of fluctuating selection acting on adults in this population (Boon et al. 2007) and fluctuating selection would also explain why repeatability estimates vary across studies in our system. To test this using an earlier study that measured 16 red squirrels assayed after weaning and again as yearlings (Kelley et al. 2015), we recomputed activity and aggression estimates (Supplementary Table S6) using the methodology employed here. The slightly higher activity repeatability estimate in the earlier study was the result of higher among-individual variance and lower within-individual variance, while the significantly higher aggression repeatability estimate for the same period was the result of both higher among- and within-individual variances. Therefore, these patterns are likely driven by differences in among- and within-individual variance fluctuating across years and support the idea that multiple behavioral phenotypes are maintained by fluctuating selection (Bergeron et al. 2013).

Our results suggest that age-related changes in the repeatability of activity and aggression in red squirrels are driven by mechanisms other than selective disappearance. We observed a narrowing of within-individual variation in activity, a process that can generate increased repeatability through two mechanisms: selection for predictability or canalization. We did not find support for selection on trait variance for either trait. While selection for predictability does not appear to be operating, canalization with age—less variable trait expression within individuals—remains a possibility (Schuster et al. 2017; Kaiser et al. 2018). More repeated measures per individual in each life stage are required to directly address the role of within-individual canalization in mediating age-related shifts in repeatability.

Individual differences in plasticity or development trajectories, while not assessed, may also underlie the behavioral development of activity and aggression we observed. Small, early differences in behavioral plasticity due to genetic, physiological, or life-history variation that result in individual differences in behavioral plasticity would result in a "fanning out" of behavior over ontogeny (Sih et al. 2015; Stamps and Biro 2016). For example, red squirrels that were more active early in life would—through reinforcement—become even more active with age, while red squirrels that were less active early in life would further decrease their activity. In contrast, red squirrels who had different aggression levels at birth may converge over development if slight differences in individual estimates of their environment (e.g., perception) are eroded over time based on shared environmental cues (Stamps and Krishnan 2014a; Polverino et al. 2016; Stamps and Biro 2016).

CONCLUSION

We report age-related changes in repeatability for two behavioral traits, activity and aggression, in juvenile North American red squirrels from a population in Yukon, Canada. Contrary to our expectation that selective disappearance would be an important mechanism underlying the age-related shifts in trait repeatability, our results suggest some degree of fluctuating selection across years. This lends further support to the notion that consistent behavioral differences among individuals may be maintained through fluctuating selection. Our results are consistent with individual differences in developmental trajectories or canalization, though we were unable to evaluate either of these mechanisms with the available data. Further empirical studies are needed to shed light on what role these alternative mechanisms have in shaping age-related changes in trait repeatability.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Conflict of interest: We have no conflict of interest to declare.

Data availability: To allow for future publications, all data are archived on figshare and will be available from https://doi.org/10.6084/m9.figshare.13281269.v1 after December 28, 2021 (Martinig et al. 2020a). During this embargo period, we will respect any reasonable request regarding data accessibility.

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