# Behavioural and ecological predictors of dispersal outcomes in red squirrels

by

April Robin Martinig

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## ABSTRACT

Dispersal is one of the most important life-history events facing an individual, but how and why individuals arrive at the decision to leave home is largely unknown. This decision has immediate and lifelong fitness consequences. Therefore, understanding how individuals make dispersal decisions is key to dispersal theory and fundamental to species management and recovery. Using North American red squirrels (Tamiasciurus hudsonicus), I examine the drivers and consequences of dispersal at the individual and population level. During prospection (the time between leaving the natal site and settlement), movement was greater when there were more local competitors (juveniles of the same age within 130 meters of the focal individual), while the location of territory acquisition was closer when local adult density was higher (adult territory holders within 130 meters of the focal individual). These effects were phenotype-dependent, with aggressive juveniles, whose behaviour develops over ontogeny, settling closer to their natal site. I further found that red squirrels exhibited sex-biased dispersal and that the benefits and costs to dispersal after settlement were sex-dependent and extended across generations. Collectively, this thesis demonstrates that the drivers of juvenile dispersal are phenotype- and environment-dependent, and suggest that lifetime fitness and intergenerational effects must be considered to better understand what factors drive dispersal.

## PREFACE

This dissertation is an original work by April Robin Martinig. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Animal Care and Use Committee for Biosciences, “Effects of resource variability on behavioural and life history characteristics of red squirrels.”

The research conducted for this thesis forms part of an international research collaboration with the Kluane Red Squirrel Project; the lead collaborator at the University of Alberta is Dr. Stan Boutin. The chapters in this thesis were designed and written by April Robin Martinig. The field data was collected as part of this collaboration and collaborators also contributed to refining of the chapters. Full author contributions are indicated at the end of each chapter.

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# DEDICATION

I dedicate this thesis to my dad, Lucio, who took his own life three years ago. His struggle is a reminder that there is more to life than work.

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I would like to also acknowledge that the numbered Treaties did not honour the oral and ceremonial agreements between First Nation signatories and the Crown. While there are multiple First Nations with their own oral tradition of what these treaties represented, the written document is not the entirety of any of the numbered Treaties. The numbered Treaties imposed the concept of land ownership on Indigenous people, but the Spirit and Intent of Treaty 6 from a Nêhiyawak oral historical perspective was an adoption ceremony promising to take care of each other as relatives, maintain their right of livelihood as Indigenous people, and that there would be peace. The Indian Act violated the spirit and intent of these agreements, making it possible for the Canadian government to force a new economy, language, religion, educational system, and legal system on multiple generations with devastating consequences that are still felt today. While the Shadhäla and Äshèyi Kwädän did not have numbered Treaties, they were subject to similar injustices through the Indian Act before negotiating their own land claims agreement and self-government starting in 1972 and becoming effective in 1995.

Without the generosity of these communities today, none of our research would be possible. We must all acknowledge the genocide that forms the foundation of contemporary Canada and the ongoing colonialism through our occupation of land that was deceitfully taken.

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# CHAPTER 1: General introduction

## Context

The diversity of behaviour found in nature is extensive, with individuals varying in the behaviours they express. Historically, behaviour was thought to either be centred on a single adaptive optimum, or on two or more co-existing evolutionarily stable strategies, with variation viewed as noise. My dissertation considers this "noise" informative, particularly because optimization theory assumes that each individual expresses the behaviour that is optimal for them. This leads us to the larger question being addressed by my thesis: why are multiple phenotypes maintained in a population?

One such mechanism is fluctuating selection – whereby environmental variation over time and space causes selection pressures to change and prevents fixation. If there is no single optimal phenotype from the point of view of fitness, multiple phenotypes can coexist. Behaviour during developmental periods or crucial life-history events, such as dispersal, are prime examples of how individuals can respond behaviourally to changing environmental conditions (Bonte and Dahirel 2017; Crowley et al. 2019). Indeed, the predominant explanations for the evolution of dispersal (i.e., inbreeding avoidance, kin competition, and nepotism (Dobson 1982; Dobson and Jones 1985; Fraser et al. 2001; Greenwood 1980; Johnson and Gaines 1990)) predict individuals will behave in a way that maximizes the differences between the costs and benefits of a given behaviour – that is, to behave optimally. This not only assumes some degree of variation among-individuals, but suggests phenotypic variation at the individual level could explain differences in pay-offs.

The causes and consequences of among-individual differences in behaviour are not limited to individual fitness. For example, dispersers are often morphologically, physiologically, and behaviourally different from non-dispersers (Ashenden et al. 2017; Bekoff 1977; Belgrad and Griffen 2018; Dingemanse et al. 2003). Because of this, differences can compound; what were once minor differences in the subset of individuals that dispersed can become larger, population-level differences (Duckworth 2008; Duckworth and Badyaev 2007) and, eventually, even lead to speciation (Garant et al. 2005; Horta-Lacueva et al. 2021; Ingley and Johnson 2014; Mullon et al.

2016). Dispersers, therefore, have tangible effects on the ability of populations to recover after climate change, and on invasive species dynamics and species reintroductions (Garant et al. 2005; Merrick and Koprowski 2017).

As such, dispersal poses a unique problem in conservation (Pintor et al. 2008; Schtickzelle et al. 2006). As translocations and reintroductions, even managed eradications, become increasingly used management tools in altered or fragmented landscapes (Berger-Tal et al. 2019; Fischer and Lindenmayer 2000) a more nuanced understanding of which individuals are more likely to disperse and why as well as how individuals make dispersal decisions is especially relevant. Population reintroduction programs contend with low survival and high rates of dispersal outside of the target areas (Le Gouar et al. 2012; Stamps and Swaisgood 2007), preventing successful population reestablishment (Fischer and Lindenmayer 2000). Invasive species eradication efforts face the opposite problem – high rates of population establishment by non-native species (Merrick and Koprowski 2017; Phillips et al. 2006), often at the detriment of local fauna or flora (Ellner et al. 2011). Given the economic cost of such conservation efforts (Epanchin-Niell and Hastings 2010; Pimentel et al. 2000), there is an urgent need to understand how dispersal, a key demographic parameter, interacts with phenotype, and, ultimately, the environment.

## Goal of this dissertation

Northern ecosystems are undergoing unprecedented changes. What these ecosystems will look like in the future largely depends on how species respond in the present. Dispersal, a key demographic parameter, can be a crucial component of species persistence in light of climate change and aggressive land-use by humans. This is because individuals can change the local conditions they experience through dispersal.

My dissertation focuses on understanding how fine-scale decisions made by individuals have lifelong impacts. Taking a mechanistic approach, I use phenotype and fitness metrics to understand the ecological and evolutionary consequences of individual differences in dispersal and behaviour in response to biotic drivers.

Focusing on North American red squirrels (Tamiasciurus hudsonicus, hereafter red squirrels), 30 years of monitoring has yielded an extensive database that includes the fates of all locally born individuals from birth to death. Because we completely enumerate the populations, we are able to quantify the lifetime fitness of adults and their offspring. Our extensive censusing, behavioural observations, mark-recapture, tissue sampling, and telemetry also make it possible to track emigration and to detect the presence of any new individuals that immigrate into our study areas. From this, we can classify individuals based on where they are born (i.e., residents versus immigrants).

Using this model system, my dissertation builds on the fundamental work of Hamilton and May (1977), who first described the short-term consequences of dispersal. A few years later, this observation was formalized in theory by Greenwood (1980). Greenwood (1980) hypothesized that individuals left home to avoid inbreeding, or to reduce competition for mates or resources. In Chapter 2, I address these three hypotheses in combination, while also incorporating a more recent hypothesis – local resource enhancement – put forward by Lawson Handley and Perrin (2007). Using the natural history of red squirrels, I then generated sex-dependent predictions. Because each of the four hypotheses (inbreeding avoidance, local resource competition, local mate competition, and local resource enhancement) had a different set of predictions, I was able to test each hypothesis independently for females and males.

Focusing on two major fitness metrics, lifetime breeding success and longevity, I found that dispersal incurred a sex-dependent, and intergenerational cost. Female philopatry was motivated by local resource enhancement, while male immigration was driven by local mate competition. Unexpectedly, I documented an intergenerational cost to dispersal, whereby offspring born to immigrants experienced a fitness cost themselves. The latter result suggests that the consequences of dispersal can extend beyond the first generation, and that dispersal may not represent an evolutionary stable strategy.

While dispersal is recognized as a crucial evolutionary mechanism, it can also be phenotype-dependent. For example, individuals that are bolder and more willing to take risks might travel longer distances (reviewed in Cote et al. 2010). In earlier work (Cooper et al. 2017), we showed how behavioural phenotype and recruitment interact. Expanding on this study in my dissertation, I found no differences in movement or settlement between active and inactive red squirrels, but aggressive red squirrels did end up settling closer to their natal site than less aggressive individuals (Chapter 3). I additionally found that faster growing juveniles settled farther from their natal site (referred to as the "colonizer syndrome"; Baker and Stebbins 1965; Bonte et al. 2012 and references therein; Duckworth 2008). They also settled earlier when adult densities were lower, despite staying closer to their natal site when they were in areas with more juvenile competitors during prospection.

This body of work led me to question how multiple behavioural types are maintained over time in this species (Chapter 4). Fluctuating selection, in combination with life-history trade-offs, particularly during dispersal, may play a role in the maintenance of behavioural variation. In Chapter 4, I explore how selective disappearance may explain the age-related changes in the repeatability of activity and aggression. While I found that fluctuating selection was a likely mechanism responsible for shaping age-related changes in trait repeatability in this system, there is still the need to test alternative mechanisms, such as individual differences in developmental trajectories or canalization.

If individuals are indeed behaving in a way that can maximize their realized costs and benefits, this dissertation suggests that phenotypic variation and the prevailing environmental conditions an individual finds themselves in could explain individual fitness differences in both the short- and long-term. Moving forward, a better understanding of the costs and benefits of dispersal will be vital to make accurate predictions about how and, in particular, who, will respond to environmental change.

## CHAPTER 2

## The new kid on the block: Immigrant males win big whereas females pay fitness cost after dispersal

Published in Ecology Letters

### Abstract

Dispersal is nearly universal; yet, which sex tends to disperse more and their success thereafter depends on the fitness consequences of dispersal. We asked if lifetime fitness differed between residents and immigrants (successful dispersers) and their offspring using 29 years of monitoring from North American red squirrels (Tamiasciurus hudsonicus) in Canada. Compared to residents, immigrant females had 23% lower lifetime breeding success (LBS), while immigrant males had 29% higher LBS. Male immigration and female residency were favoured. Offspring born to immigrants had 15 – 43% lower LBS than offspring born to residents. We conclude that immigration benefitted males, but not females, which appeared to be making the best of a bad lot. Our results are in line with male-biased dispersal being driven by local mate competition and local resource enhancement, while the intergenerational cost to immigration is a new complication in explaining the drivers of sex-biased dispersal.

### Introduction

All offspring that survive to independence must find a place to settle if they are to have any potential for future reproductive success. In cases where the natal site is occupied, some proportion of offspring must undergo natal dispersal, i.e., movement between the birth site and first breeding site (Howard 1960). Despite dispersal being an event of limited duration early in life, it is assumed to have fitness costs that reach beyond the event itself (reviewed by Bonte et al. 2012; Green and Hatchwell 2018). The short-term costs of the act of dispersal (incurred during the prospection/transience phase) are well documented (Johnson et al. 2009), but the potential for costs to extend beyond successful recruitment to a new population (immigration) has received less attention (reviewed in Bowler and Benton 2005). The empirical data needed to test this are logistically challenging to collect as it requires: 1) following individuals across their lifetimes after they leave a study area or 2) the ability to identify true immigrants in study populations across generations.

Dispersal is nearly ubiquitous in populations and often sex-biased (Greenwood 1980). This differential dispersal propensity between the sexes is thought to occur when one sex experiences increased benefits or decreased costs relative to the other sex. Inbreeding avoidance (Bengtsson 1978; Clutton-Brock 1989; Packer 1979; Perrin and Mazalov 2000), and kin selection, including local resource (Clarke 1978) and mate competition (Hamilton 1967; Moore and Ali 1984), and, most recently, cooperation (i.e., local resource enhancement; Green and Hatchwell 2018; Lawson Handley and Perrin 2007; Le Galliard et al. 2006; Perrin and Lehmann 2001) are the prevailing hypotheses for what drives the observed sex-bias in dispersal (Dobson 1982; Dobson and Jones 1985; Greenwood 1980; Lawson Handley and Perrin 2007; Perrin and Mazalov 2000). If inbreeding avoidance reduces local mating opportunities relatively more for one sex, the sex experiencing the greater reduction should show a greater propensity to disperse. Likewise, they should experience greater reproductive success once they have recruited to an area where inbreeding is reduced. While the inbreeding avoidance hypothesis does not predict which sex should disperse, the kin selection hypotheses predicts that the sex that invests more in offspring and cooperation is expected to gain the most from being philopatric, while the sex that shows the highest level of intrasexual competition for mates would disperse (reviewed in Johnson and Gaines 1990; Lawson Handley and Perrin 2007; Perrin and Mazalov 2000; Trochet et al. 2016). In all cases, dispersers must leave not only their natal site, but settle outside their local neighbourhoods where these mechanisms prevail.

In our present study on North American red squirrels (Tamiasciurus hudsonicus, hereafter red squirrels), we asked if residents and immigrants or their offspring differ in fitness after recruitment using lifetime breeding success (LBS) as a metric for individual fitness over a 29-year period. Red squirrels are diurnal, solitary, and semi-arboreal rodents (Smith 1968; Steele 1998) that defend exclusive territories (average diameter of 60 m; Anderson and Boutin 2002) centered on a food cache referred to as a ‘midden’ (Smith 1968; Steele 1998). They venture off their territory infrequently (Smith 1968), and are highly trappable (Boon et al. 2008), making it easy to locate and recapture individuals throughout their lifetimes. Females and males do not exhibit size dimorphism (Boutin and Larsen 1993; Stuart-Smith and Boutin 1994), or show significant differences in territory size (Larsen 1993) or territory acquisition (Hendrix, J.G., personal communication). Red squirrels exhibit a scramble competition mating system, with females mating with an average of seven males during oestrus (Lane et al. 2009; 2008). Mean litter size is three (McAdam et al. 2007) with multiple paternity in each litter being the norm (Lane et al. 2008). Breeding starts in mid- to late-winter, with females giving birth in the spring after a ~ 35-day gestation period (Lane et al. 2009). Juveniles experience high mortality (40 – 60%) between birth and weaning (Boutin and Larsen 1993). Most red squirrels exhibit a degree of philopatry (Haughland and Larsen 2004; Larsen and Boutin 1994), recruiting an average of two territory widths from their natal site (Berteaux and Boutin 2000; Cooper et al. 2017). Breeding dispersal (i.e., when an adult female acquires a new territory and gives part or all of her territory to offspring during territorial bequeathal; Price 1992; Price and Boutin 1993) is rare (average across years is 19%; Lane et al. 2015), with most individuals remaining on the territory they inhabit as yearlings for the rest of their lives (Berteaux and Boutin 2000). As assessed by successful local recruitment (i.e., only includes individuals that survive their first winter and acquire and defend a territory with a midden in our populations), females and males have similar dispersal distances (Berteaux and Boutin 2000; Cooper et al. 2017), although females tend to recruit slightly closer to their natal site than do males (Berteaux and Boutin 2000) and are more likely to have a natal site bequeathed to them (Berteaux and Boutin 2000; Lane et al. 2015). Juveniles that recruit on their natal site have higher winter survival than juveniles that recruited elsewhere in their first winter (75% versus 58%, respectively; Berteaux and Boutin 2000).

Given red squirrels are a territorial polygamous species, we would expect the costs during transience to not differ between the sexes. The inbreeding avoidance hypothesis predicts that one sex should be more likely to disperse, but which sex this should be varies with each kin selection hypothesis. We predict that both sexes will have an equal propensity to appear as immigrants and to experience the same fitness costs or benefits after recruitment, in line with what would be expected if dispersal were driven by local resource competition (Waser et al. 2013). If dispersal is instead driven by local mate competition, we would expect males to have a higher propensity to immigrate. Likewise, if dispersal is driven by local resource enhancement, we expect female philopatry to be favoured (as is supported by female red squirrels being more likely to have a territory bequeathed to them by their mother). Consequently, resident females should have higher fitness than immigrant females with the opposite prediction for males. Because dispersal theory does not hypothesize dispersal costs and benefits to be intergenerational, we do not expect there to be intergenerational effects. Earlier studies (Germain et al. 2017; Waser et al. 2013) reported results consistent with immigrants making the best of a bad lot, but found no sex differences.

## Methods

### Study area

We monitored red squirrel territory locations, reproduction, and survival over 29 years (1989 – 2017) in southwestern Yukon, Canada (61 ° N, 138 ° W) on two study areas (KL and SU; ~ 40 ha each) adjacent to the Alaska Highway on the traditional lands of the Champagne and Aishihik First Nations. The vegetation in the study areas includes large patches of mature white spruce (Picea glauca) interspersed with smaller pockets of aspen (Populus tremuloides), wetlands, and meadows containing willow (Salix spp.) and birch (Betula glandulosa) (Douglas 1974). Conditions are highly temporally variable, with a seasonal climate, and extreme annual fluctuations in resource availability due to the masting of white spruce (LaMontagne and Boutin 2007). Masting events are characterized by episodic, synchronized seed production by trees with an average inter-mast interval of approximately four years (Nienstaedt and Zasada 1990). Our study spanned five masts with three to six years between each. These masting events are positively correlated with red squirrel population density (Dantzer et al. 2013), and the number of masts encountered in a lifetime increases an individual's fitness (Hämäläinen et al. 2017).

### Data collection

We intensively (six days a week) monitored the survival and reproduction of all individually marked red squirrels in our populations from March through September each year using a combination of live-trapping, behavioural observations, and telemetry monitoring. We divided each study area into 30 meter squares with markers, which allowed us to provide spatial coordinates for all records. We trapped individuals every 3 to 14 days using live traps (Tomahawk Live Trap, Hazelhurst, USA) baited with peanut butter and placed on or near each individual's midden. To facilitate future identification without trapping, we gave each red squirrel a unique coloured wire combination placed on numbered ear tags (Monel # 1; 5 digits) when they were approximately 25 days old or at first capture for individuals not born in our populations. Because red squirrels defend exclusive territories year-round (Smith 1968; Steele 1998) we could record territory ownership of each midden through observations of territorial behaviour (rattles; Lair 1990) and trapping. The high trappability of red squirrels (recapture rates > 0.95; see Descamps 2006), their diurnal activity patterns, and territorial behaviour allows us be confident that all individuals in our populations were enumerated and allowed us to distinguish between residents and immigrants with strong certainty (detailed below).

To quantify female reproductive performance and monitor offspring born in our populations, we located nests via behavioural observations or with telemetry using radio-collars (model PD-2C, 4 g, Holohil Systems Limited, Carp, Canada). We assigned maternity based on a female's attendance at the nest, and we sampled tissue from offspring shortly after birth to assign paternity (paternity assignment began in 2002). Details of the molecular methods used to reliably assign paternity can be found elsewhere (Gunn et al. 2005; Lane et al. 2007, 2008).

Each May and August we conducted population censuses whereby all red squirrels in our populations were recorded along with the location of their territory. We classified every red squirrel that reached breeding age (yearling) in our populations as residents or immigrants. To be considered a resident, an individual had to be born in the population (we knew their birth location) and recorded as having successfully recruited (i.e., acquired and defended a territory with a midden) in their natal population in at least one census in the year following their birth. These individuals were further classified as either showing philopatry (i.e., location of territory when they were scored as having recruited was the same as the location of their natal site) or as being a within-population disperser (recruited off their natal site, but in their natal population). Immigrants were untagged at first capture (i.e., we took a tissue sample for possible parental assignment and all immigrants were not born in our populations) and recorded as having successfully recruited (i.e., acquired and defended a territory with a midden) in a population in at least one census in the year following their birth. We also classified between-population dispersers (only 12 of 1275 records) as immigrants because they did not recruit in their natal population. Philopatric individuals made up 191 of 1275 records in our final sample, and excluding them from the analysis or grouping them with within-population dispersers did not change our main conclusions (results not shown). We present the results grouping both philopatric individuals and within-population dispersers as residents.

Our delineation of residents and immigrants could be confounded due to edge effects. Our populations were surrounded by poor quality habitat for red squirrels (white spruce density <100 trees per hectare; Yukon Vegetation Inventory 2012). Pockets of suitable habitat (white spruce density >1000 trees per hectare) were, on average, 465 m ± 241 SE away (Yukon Vegetation Inventory 2012). These distances are greater than the dispersal distances of local recruits that move an average of only two territory widths from their natal site (96 m ± 94 SD, Berteaux and Boutin 2000; 102 m ± 107 SD, Cooper et al. 2017). We also tested for edge effects by designating a "core" area in the centre of each population and comparing individuals living in the core with those living outside this area (but still in the population), thereby restricting our analysis to only individuals born in our populations. We found no fitness differences between core and edge individuals (Supplementary Table S1).

We acknowledge that the technical constraints of demographic techniques (e.g., mark-recapture, telemetry, censusing, etc.) can be biased against individuals that travel long distances and underestimate dispersal distances (Koenig et al. 1996), making it particularly difficult to obtain lifetime fitness measures for all individuals. However, our methodology allowed us to classify immigrants as true dispersers because of our ability to enumerate and track all individuals defending territories in our populations.

We calculated lifespan for residents as being the number of days between birth and the last recorded sighting of an individual alive. We assumed immigrants were the same age as residents at recruitment (i.e., yearling), assigning immigrants a starting age of one year at the first capture (n = 478 individuals; following Lane et al. 2009), and were differentiated from immigrant juveniles (i.e., young of the year; n = 27 individuals) based on mass (juveniles ≤220 g) and the absence of developed mammae for females or scrotum for males. We expected both sexes to be more likely to recruit in the population as yearlings instead of later because territory moves by adults are rare (Larsen and Boutin 1995; Stuart-Smith and Boutin 1994), breeding dispersal, which only involves adult females, is relatively infrequent (Price 1992; Price and Boutin 1993), and territory ownership significantly increases juvenile winter survival (Hendrix et al. 2020; Kemp and Keith 1970).

## Data analysis

We used lifetime breeding success (LBS), defined as the total number of offspring produced by a female or sired by a male during its lifetime, as a metric for individual fitness. We also measured longevity and for females we further measured breeding attempts and litter size. We excluded any red squirrels that were killed by unnatural causes or had a year or more of their reproductive information missing. We also censored individuals that were still alive. For similar methodology, see Descamps et al. (2008a).

We quantified LBS and longevity of 843 females (born between 1989 and 2015) and 432 males (born between 2002 and 2015) in two populations (750 on KL and 525 on SU) over the study period (Table S2). The sex ratio in our populations is balanced (Wishart et al. 2018), so the difference in sample sizes between the sexes is because we started to assess paternity in 2002. Censoring female data to the same timeframe as males did not change our main conclusions (results not shown). We separated the maternity and paternity data to maximize sample size for offspring with only one known parent. For offspring with known maternity there were 771 complete records (582 females and 189 males), and for offspring with known paternity there were 313 complete records (174 females and 139 males). Both parents were known for 161 females and 124 males (results for subset with both known parents were consistent with results for offspring with only one known parent; Table S3). By virtue of staying in the populations, individuals with known parents were all residents themselves.

We fit all LBS, breeding attempts, and litter size models using Poisson regressions with the “lme4” package, version 1.1-19 (Bates et al. 2015). We fit all longevity models using negative binomial regressions with the “glmmTMB” package, version 0.2.2.0 (Brooks et al. 2017), to deal with overdispersion. We estimated 95% confidence intervals (CI) using the “confint” function. We used R, version 3.5.1 (R Development Core Team 2019), for all analyses. We included an individual’s recruitment population (KL or SU) and dispersal type (resident or immigrant) only for parents (not offspring) as fixed effects in all analyses. We included a random effect for birth year to account for any cohort-specific variation and a fixed effect for whether an individual encountered a mast year or not during its lifetime. We tested for any sex differences in the proportion of resident and immigrant recruitment, and also for differences in the probability of producing offspring that recruited for females who mated with resident or immigrant males post-hoc using G-tests with the "DescTools" package, version 0.99.28 (Signorell 2019). Data are reported as means ± one standard error, unless stated otherwise. Significance was set to $\alpha = 0.05$.

## Results

We recorded 1155 residents and 686 immigrants over 29 years. The sex ratio for residents was female-biased (59%; $G = 33.77$, $df = 1$, $p < 0.001$), while immigrants were male-biased (64%; $G = 57.97$, $df = 1$, $p < 0.001$). In the case of residents, both philopatric and within-population dispersers were female-biased (59% and 56%, respectively).

### Do residents outperform immigrants?

We obtained complete lifetime fitness measures on 805 residents and 470 immigrants. Resident females had longer lifespans than immigrant females (2.81 ± 0.04 versus 2.43 ± 0.06 years, respectively), more breeding attempts (2.63 ± 0.03 versus 2.32 ± 0.07 litters, respectively), and larger litter sizes (3.17 ± 0.01 versus 3.02 ± 0.01 pups per litter, respectively), but none of these differences were statistically significant (Table 2.1; Table S4; Table S5; Figure 2.1B). These combined differences led to resident females having 23% more offspring over their lifetime relative to immigrant females (5.94 ± 0.15 versus 3.95 ± 0.18 offspring, respectively; $\beta$: -0.26, 95% CI: -0.34 to -0.19; Table 2.2; Figure 2.1A).

In contrast, resident males sired 29% less offspring over their lifetime relative to immigrant males (1.82 ± 0.10 versus 2.70 ± 0.13 offspring, respectively; $\beta$: 0.25, 95% CI: 0.12 to 0.39; Table 2.2; Figure 2.1A). Resident males' lifespan was also 16% shorter than immigrant males (1.94 ± 0.04 versus 2.26 ± 0.05 years, respectively; $\beta$: 0.15, 95% CI: 0.04 to 0.26; Table 2.1; Figure 2.1B). While of no direct interest to this study, there were significant differences between populations and if individuals encountered a mast year or not (Table 2.1; Table 2.2).

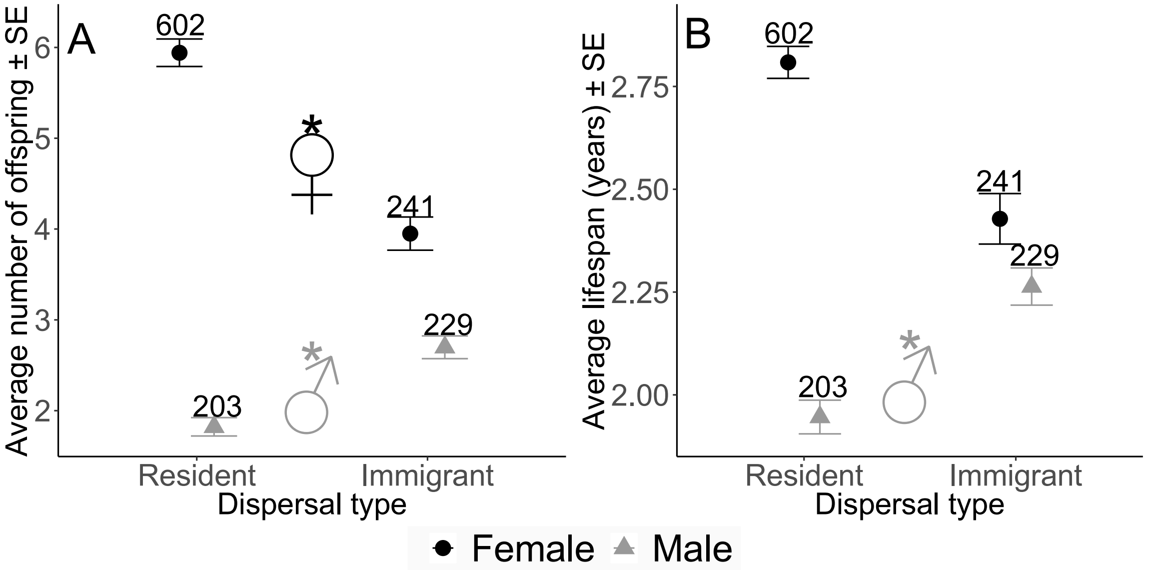

Figure 2.1. Residents and immigrants had differential fitness after recruitment from 1989 (females) and 2002 (males) to 2017. (A) Immigrant females had lower and immigrant males had higher lifetime breeding success (average number of offspring) than residents; and was brought about by (B) immigrant females having lower and immigrant males having higher longevity than residents. Values on y-axis are (A) average number of offspring born/sired or (B) average lifespan (years). Asterisks and pictograms denote statistical significance (Table 2.1 and 2.2). Error bars indicate ± SE. Sample sizes above bars.

Table 2.1. Parameter estimates from the generalized linear mixed effects model output with longevity (days alive) as a response variable for resident and immigrant red squirrels (n = 1275) from 1989 (females) and 2002 (males) to 2017.

| Fixed and random effects * | Estimate | SE | Z | 2.5% CI | 97.5% CI |
|---|---|---|---|---|---|
| Model: adult female, n = 843 | | | | | |
| Immigrants | -0.06 | 0.04 | -1.41 | -0.14 | 0.02 |
| Population (SU) | 0.06 | 0.04 | 1.62 | -0.01 | 0.13 |
| Encountered mast year | 1.04 | 0.06 | 17.49 | 0.92 | 1.16 |
| Birth year [a] | 0.10 | 0.32 | NA | NA | NA |
| Model: adult male, n = 432 | | | | | |
| Immigrants | 0.15 | 0.06 | 2.62 | 0.04 | 0.26 |
| Population (SU) | 0.03 | 0.05 | 0.61 | -0.07 | 0.14 |
| Encountered mast year | 0.83 | 0.09 | 9.55 | 0.66 | 1.00 |
| Birth year [a] | 0.06 | 0.24 | NA | NA | NA |

* Reference categories for fixed effects were set to ‘residents’ (for ‘immigrants’), ‘KL’ (for ‘population (SU)’), ‘did not encounter mast year’ (for ‘encountered mast year’), ‘resident mothers’ (for ‘immigrant mothers’), and ‘resident fathers’ (for ‘immigrant fathers’).

[a] Random effect; estimate column is variance ($\sigma^2$) and SE column is standard deviation.

Table 2.2. Parameter estimates from the generalized linear mixed effects model output with lifetime breeding success (number of offspring produced) as a response variable for residents and immigrants (n = 1275) and their offspring [a] from 1989 (females) and 2002 (males) to 2017.

| Fixed and random effects * | Estimate | SE | Z | 2.5% CI | 97.5% CI |
|---|---|---|---|---|---|
| Model: adult female, n = 843 | | | | | |
| Immigrants | -0.26 | 0.04 | -6.42 | -0.32 | -0.17 |
| Population (SU) | -0.01 | 0.03 | -0.36 | -0.07 | 0.05 |
| Encountered mast year | 2.00 | 0.06 | 31.04 | 1.88 | 2.14 |
| Birth year [b] | 0.66 | 0.81 | NA | NA | NA |
| Model: adult male, n = 432 | | | | | |
| Immigrants | 0.25 | 0.07 | 3.69 | 0.12 | 0.39 |
| Population (SU) | -0.16 | 0.07 | -2.38 | -0.29 | -0.03 |
| Encountered mast year | 1.90 | 0.14 | 13.21 | 1.61 | 2.18 |
| Birth year [b] | 1.29 | 1.14 | NA | NA | NA |
| Model: daughter - known maternity, n = 582 | | | | | |
| Immigrant mother | -0.16 | 0.04 | -3.67 | -0.25 | -0.08 |
| Population (SU) | -0.06 | 0.04 | -1.62 | -0.13 | 0.01 |
| Encountered mast year | 1.91 | 0.08 | 24.12 | 1.75 | 2.06 |
| Birth year [b] | 0.67 | 0.82 | NA | NA | NA |
| Model: son - known maternity, n = 189 | | | | | |
| Immigrant mother | -0.16 | 0.17 | -0.94 | -0.48 | 0.17 |
| Population (SU) | -0.13 | 0.12 | -1.06 | -0.37 | 0.11 |
| Encountered mast year | 2.12 | 0.26 | 8.30 | 1.62 | 2.62 |
| Birth year [b] | 1.11 | 1.06 | NA | NA | NA |
| Model: daughter - known paternity, n = 174 | | | | | |
| Immigrant father | -0.17 | 0.07 | -2.46 | -0.30 | -0.03 |

| | | | | | |
|---|---|---|---|---|---|
| Population (SU) | -0.04 | 0.07 | -0.55 | -0.18 | 0.10 |
| Encountered mast year | 1.60 | 0.13 | 12.28 | 1.34 | 1.85 |
| Birth year [b] | 1.95 | 1.40 | NA | NA | NA |
| Model: son - known paternity, n = 139 | | | | | |
| Immigrant father | -0.55 | 0.13 | -4.29 | -0.81 | -0.30 |
| Population (SU) | -0.45 | 0.14 | -3.18 | -0.72 | -0.17 |
| Encountered mast year | 2.27 | 0.32 | 7.05 | 1.64 | 2.91 |
| Birth year [b] | 1.19 | 1.09 | NA | NA | NA |

* Reference categories for fixed effects were set to ‘residents’ (for ‘immigrants’), ‘KL’ (for ‘population (SU)’), ‘did not encounter mast year’ (for ‘encountered mast year’), ’resident mothers’ (for ‘immigrant mothers’), and ‘resident fathers’ (for ‘immigrant fathers’).

[a] Offspring with known maternity (n = 771) or known paternity (n = 313).

[b] Random effect; estimate column is variance ($\sigma^2$) and SE column is standard deviation.

### Intergenerational effects of immigration

Daughters born to resident females had no differences in longevity relative to daughters of immigrant females (2.85 ± 0.05 versus 2.85 ± 0.08 years, respectively), but they did have more breeding attempts (2.69 ± 0.04 versus 2.57 ± 0.07 litters, respectively), and larger litter sizes (3.19 ± 0.01 versus 2.99 ± 0.01 pups per litter, respectively), but none of these differences were statistically significant (Table S4; Table S5; Table S6; Figure 2.2B). These combined differences led to daughters born to resident females having 15% more offspring over their lifetime relative to daughters of immigrant females (6.13 ± 0.19 versus 5.56 ± 0.27 offspring, respectively; β: -0.16, 95% CI: -0.25 to -0.08; Table 2.2; Figure 2.2A).

Daughters sired by resident males had shorter lifespans compared to daughters sired by immigrant males (2.45 ± 0.13 versus 2.64 ± 0.09 years, respectively), but more breeding attempts (3.03 ± 0.11 versus 2.54 ± 0.06 litters, respectively), and smaller litter sizes (3.07 ± 0.02 versus 3.39 ± 0.01 pups per litter, respectively), but none of these differences were statistically significant (Table 2.1; Table S4; Table S5; Table S6; Figure 2.2). These combined differences still led to daughters sired by resident males having 15% more offspring over their lifetime relative to daughters of immigrant males (5.97 ± 0.57 versus 5.59 ± 0.36 offspring, respectively; β: -0.17, 95% CI: -0.30 to -0.03; Table 2.2; Figure 2.2A).

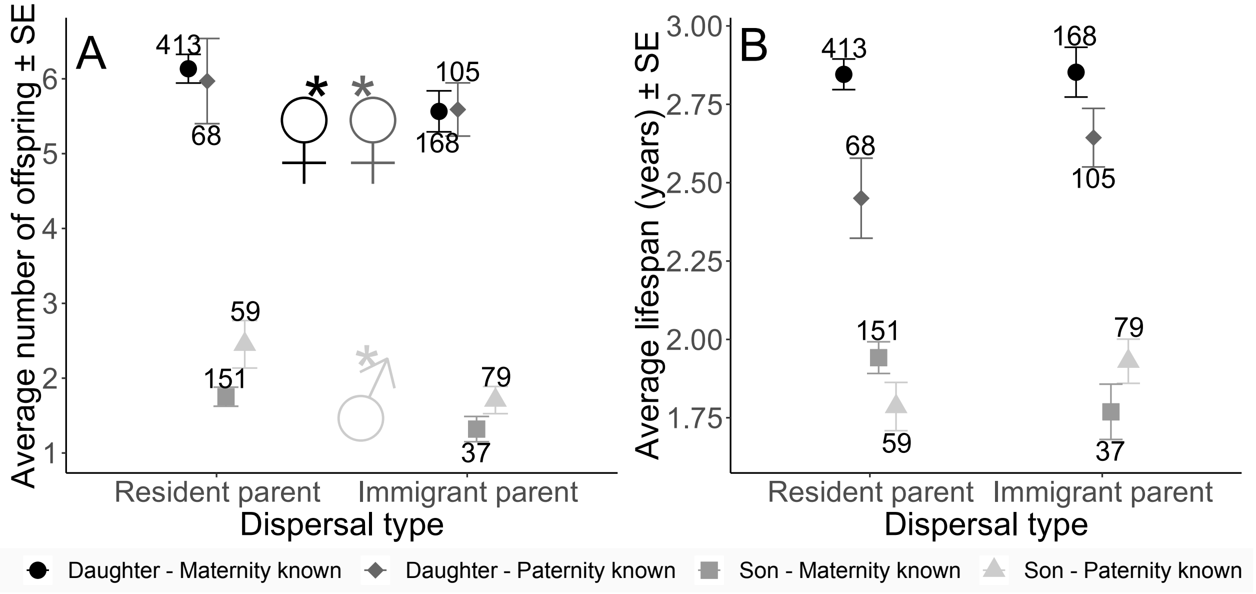

Figure 2.2. Offspring born to residents and immigrants had differential fitness after recruitment from 1989 (females) and 2002 (males) to 2017. (A) Daughters born to immigrant females and males and sons born to immigrant males had lower lifetime reproductive success than offspring born to residents. (B) Offspring born to immigrants had no longevity differences compared to offspring born to residents. Values on y-axis are (A) average number of offspring born/sired or (B) average lifespan (years). Asterisks and pictograms denote statistical significance (Table 2.1 and 2.2). Error bars indicate ± SE. Sample sizes by bars.

Sons born to resident females sired more offspring over their lifetime than sons born to immigrant females (1.75 ± 0.13 versus 1.32 ± 0.17 offspring) and lived longer (1.94 ± 0.05 versus 1.77 ± 0.09 years, respectively), but these differences were not statistically significant (Table 2.2; Table S6; Figure 2.2). In contrast, sons born to resident males sired 43% more offspring over their lifetime relative to sons of immigrant males (2.45 ± 0.32 versus 1.71 ± 0.18 offspring, respectively; β: -0.55, 95% CI: -0.81 to -0.30), but had no significant difference in lifespan (1.79 ± 0.07 versus 1.93 ± 0.07 years, respectively; Table 2.2; Table S6; Figure 2.2). While of no direct interest to this study, there were significant differences between populations and if individuals encountered a mast year or not (Table 2.2; Table S6).

Daughters born to resident females were more likely to recruit in the population than their sons (G = 3.89, df = 1, p = 0.049), while there was no sex difference in recruitment for offspring produced by immigrant females (G = 0.927, df = 1, p = 0.34) or for offspring sired by resident males (G = 2.34, p = 0.13) or immigrant males (G = 2.53, df = 1, p = 0.11) (Table S7). Resident females (G = 8.40, df = 1, p = 0.004) and immigrant females (G = 8.55, df = 1, p = 0.01) were most likely to produce offspring that recruited into the population from matings with immigrant males (Table S8).

## Discussion

We have shown that the lifetime fitness consequences of dispersal after successful recruitment to a new population are not only sex-dependent, but also intergenerational. Immigrant males showed a clear fitness benefit relative to residents by having a longer lifespan, resulting in more offspring, while immigrant females underperformed relative to resident females by having fewer offspring over their lifetime through a combination of reduced longevity, fewer breeding attempts, and smaller litter sizes. The fitness effects of dispersal were also intergenerational; we detected fitness costs for offspring born to immigrants that further added to the long-term costs of dispersal.

While male-biased dispersal is documented in many mammalian species (Dobson 1982; Greenwood 1980), in red squirrels, both sexes recruit similar distances (Berteaux and Boutin 2000; Cooper et al. 2017). Despite these previous studies documenting a lack of sex-difference in recruitment distances when looking at successful within-population movement, we documented a clear sex-bias towards female residency and male immigration, and sex-dependent fitness differences after recruitment when accounting for immigration.

Our results are not consistent with earlier studies (Germain et al. 2017; Gienapp and Merilä 2011; Waser et al. 2013) where dispersers did not incur fitness costs after recruitment. In the one earlier mammalian study (Waser et al. 2013), they did not detect long-term fitness benefits for either sex likely because kangaroo rats (Dipodomys spectabilis) do not show sex-biased dispersal. Waser et al. (2013) concluded that kangaroo rats dispersed because they were unable to occupy their natal site and were thus making the best of a bad lot. This may also be the case with immigrant female red squirrels.

For male red squirrels coming from afar has some advantages. Immigrant males showed compensatory benefits after recruitment. This advantage to immigration is in line with what would be expected if the benefits to remaining close to home were sex-dependent, and in favour of male-biased dispersal (as documented here). If males do not experience the same benefits to settling locally as females, the decision to immigrate elsewhere should be favoured, as it would still release them from kin competition (Hamilton and May 1977; Waser 1985) and inbreeding depression (Bengtsson 1978; Lehmann and Perrin 2003).

Female choice may play a part too. Females in other species show a preference for mating with unfamiliar males (e.g., olive baboons (Papio anubis) (Packer 1979; Smuts 1983), house mice (Mus musculus) (Winn and Vestal 1986), and naked mole-rats (Heterocephalus glaber) (Clarke and Faulkes 1999)). Beyond being an inbreeding avoidance mechanism (Bengtsson 1978), this behaviour can conceal paternity to forestall infanticide (Hrdy 1977) and may be evidence of intersexual selection by females for traits that display male quality (Kurland 1977; Richard 1974), such as the ability to survive dispersal. It is unlikely that female red squirrels favour mating with unfamiliar males (Hughes et al. 1999; Winn and Vestal 1986) as an inbreeding avoidance mechanism (Bengtsson 1978; Lehmann and Perrin 2003) because available evidence suggests that female red squirrels do not bias paternity based on relatedness (Lane et al. 2007). Infanticide does occur in red squirrels (Haines et al. 2018), albeit this is not likely to be the only driving force. If immigrant males are competitively superior dispersers (termed “colonizer syndromes”; Baker and Stebbins 1965; Bonte et al. 2012 and references therein; Duckworth 2008), they would be expected to show a positive correlation between condition and dispersal. In red squirrels, this would be expected to result in superior individuals settling on high-quality territories (Rémy et al. 2011; Stuart-Smith and Boutin 1995b); the so-called silver-spoon effect (Bonte et al. 2012; Descamps et al. 2008b; Stamps 2006). The fact that we do not see any benefits to immigrant females, who, by this logic, should also be competitively superior dispersers, suggests that either this is not occurring for either sex or the benefits to immigration are sex-dependent and in favour of female residency as we have documented here. Of note, it is puzzling that immigrant male red squirrels appear to be favoured when they produce “unsexy” sons. This may instead be evidence of maladaptive mate choice on the part of females. Regardless of the mechanism, the observed benefits of immigration for males are in line with multiple theoretical predictions for why male-biased dispersal is predominant in mammals (Dobson 1982; Greenwood 1980).

Immigrant females may be making the best of a bad lot (see also Waser et al. 2013). This is in agreement with various theoretical models that assume an advantage to remaining close to the natal site (Green and Hatchwell 2018; Hamilton and May 1977; Shields 1982, 1983; Waser 1987, 1988). While the mechanism of selection is unknown, resident females may benefit from local resource enhancement (Lawson Handley and Perrin 2007; Le Galliard et al. 2006; Perrin and Lehmann 2001) through kin-selected cooperation (Green and Hatchwell 2018) in the form of bequeathals (Berteaux and Boutin 2000; Williams et al. 2013). Immigrant females have less familiarity with the environment and their neighbours (Beletsky and Orians 1989; Temeles 1994), thereby possibly increasing energy needed for territorial defense (McGregor 1993; Siracusa et al. 2019). When faced with the problem of not being able to occupy their natal site, immigrant females may move only to maximize their own chance for reproduction (Hamilton and May 1977; Johnson and Gaines 1990; Murray 1967).

However, being the offspring of an immigrant parent was not good. The presence of a home field advantage is seen in the next generation where offspring of residents that recruit in the population perform equally well or better after recruitment themselves. This suggests there is an intergenerational cost to immigration. The offspring of immigrants that recruit locally may remain at a disadvantage if they are unable to realize the same advantages that residents may transfer to their offspring (e.g., maternal investment through bequeathals; Berteaux and Boutin 2000; Williams et al. 2013). Phenotype matching of offspring to the local environment through directed gene flow (Davis and Stamps 2004; Edelaar et al. 2008) would also explain these results, as this would impact competitive ability and fitness in the next generation (Burton et al. 2010; Doligez and Pärt 2008; Hidalgo et al. 2016).

While comparing individuals that leave an area permanently to those that move within a population overlooks viability selection (e.g., ‘the invisible fraction’; Grafen 1988; Hadfield 2008) and possible intrinsic behavioural differences between residents and immigrants that may also explain the fitness differences observed here (Jensen 1995), we detected sex-dependent immigration costs and benefits for residents and immigrants after recruitment that carryover to the next generation. Because individuals were only compared after dispersal, any selection pressures experienced before successful recruitment cannot be assessed here (Jensen 1995);

however, by focusing exclusively on the environment after settlement we were able to test whether or not individuals paid any long-term costs to dispersal after recruitment.

## Conclusion

We found evidence of long-term fitness effects to immigration that carried over to the next generation. Males were most likely to immigrate and experienced a fitness benefit to immigration, while females paid a cost in line with what would be expected if male-biased dispersal in mammals was driven by both local mate competition and local recourse enhancement. Further, there was an intergenerational cost to immigration; the offspring of immigrant parents had lower fitness compared to residents' offspring. Subsequent lifetime fitness costs to offspring have not been previously quantified; and theoretical models have not assumed dispersal costs extend beyond the settlement phase, let alone are intergenerational. These findings raise unanswered questions about the drivers of dispersal given we have shown that any costs experienced by immigrants after settlement are not compensated for in the next generation.

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## Author contributions

ARM and SB developed the rationale of the manuscript, all the authors assisted in data collection and maintenance of the longterm database, and ARM analyzed the data and led writing of the manuscript with input from coauthors.

Supporting information and data availability

Supporting information available at https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fele.13436&file=ele13436-sup-0001-Supinfo.pdf.

All data are archived on figshare: https://doi.org/10.6084/m9.figshare.10055366.v1.

# CHAPTER 3

# Going the distance: local competition for space drives prospection and settlement

## Abstract

Virtually all species make a dispersal movement at some stage in their life cycle. Dispersal is assumed to be risky and is unavoidable when philopatry is rarely an option. We explored how phenotype and environmental conditions impacted dispersal propensity, daily movements, timing of settlement, and final settlement distance using telemetry data from a population of North American red squirrels (Tamiasciurus hudsonicus) in Yukon, Canada. Juveniles with more local competitors (juveniles living within 130 m of focal juvenile) travelled shorter distances from their natal site, while juveniles settled earlier when the density of established territory holders was low. Final settlement distance was phenotype-dependent, with more aggressive, slower growing juveniles settling closer to their natal site. Individual phenotype and competition for space appear to be two of the primary factors operating across all stages of dispersal, particularly during prospection and settlement.

## Introduction

The process of dispersal involves the movement of an organism from its natal site to a new site (Howard 1960) and is comprised of successive stages (Figure 3.1). This crucial life-history event can affect individual fitness (Bélichon et al. 1996; Doligez and Pärt 2008; Germain et al. 2017; Martinig et al. 2020; Waser et al. 2013) and future reproduction (Martinig et al. 2020) with far-reaching demographic effects (e.g., gene flow, population persistence, species distributions, etc.) (Bowler and Benton 2005). Indeed, moving to a new site is one of the most immediate ways individuals can respond to changing environmental conditions (Bonte et al. 2012; Crowley et al. 2019). In light of this, there is a pressing need to understand the causes and consequences of dispersal, particularly from an adaptive perspective.

Growing evidence indicates that how profitable dispersal is as a life-history strategy can vary spatiotemporally and among individuals (Bowler and Benton 2005; Cote et al. 2010; Quinn et al. 2011). As a result, different strategies are expected under varying individual internal and external conditions. In the first phase of dispersal (i.e., departure phase) an individual may or may not initiate dispersal and individuals can differ in their tendency to do so. An individual's internal state and kin competition should, almost exclusively, impact initiation. When an individual does initiate dispersal, it then enters the prospection (or transience) phase (Delgado et al. 2014; Ponchon et al. 2013) where it can begin gathering information about environmental conditions (Jacob et al. 2015), including the location of vacancies. During prospection, different search strategies, both the product of internal state and response to external conditions (Wey et al. 2015), may change the likelihood of finding a vacancy and mortality risk (Belgrad and Griffen 2018). For survivors that do find a place to settle, internal and external conditions, including those governing density and behaviour, should influence settlement location and success therein. While not the focus here, individuals have to then live through to breeding age to achieve any fitness benefits (i.e., recruitment (Martinig et al. 2020) or establishment (Spiegel and Nathan 2012)).

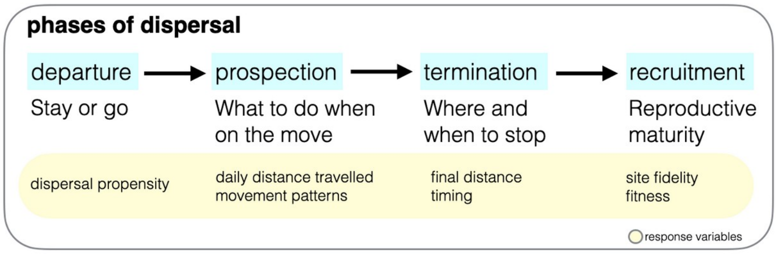

Figure 3.1. A general schematic overview illustrating the phases of dispersal (blue highlights) and the proposed explanatory variables, indicated under each phase.

Consistent individual differences in behaviour have also recently been recognized as an important component of dispersal (Cote et al. 2010; 2013). If contrasting behavioural types differentially acquire resources, evade predators, and experience their social landscape, then dispersal should be phenotype-dependent. Despite fundamental reviews outlining the importance of investigating the link between behavioural type and dispersal (Cote et al. 2010; Réale et al. 2007; Sih et al. 2004), existing studies are limited (e.g., Cote et al. 2011; 2013; Nicolaus et al. 2016).

Our ability to empirically study the drivers and consequences of among-individual variation along the different phases of dispersal is rare due to the practical and logistical problems associated with following both dispersers and non-dispersers. Such empirical datasets require longterm monitoring of free-ranging individuals, including the whereabouts of conspecifics in the relevant subpopulations (Cote and Clobert 2007), from birth to death and preferably across years with variable environmental conditions. This is not generally feasible, but is possible using territorial and spatially limited dispersers like North American red squirrels (Tamiasciurus hudsonicus, hereafter red squirrels) in Yukon, Canada. Given the spatial structure and social organization of red squirrels, we explored what factors influence: 1) when an individual first leaves their natal site, 2) variation in distance moved during prospection, and 3) timing of settlement and final settlement distance.

## Methods

### Study area

We monitored natal dispersal in juvenile red squirrels over two years (2017 and 2018) from two study areas (~ 40 hectares each) in southwestern Yukon, Canada (61° N, 138° W, 900 m a.s.l) separated by the Alaska Highway on the traditional lands of the Champagne and Aishihik First Nations. Our study areas are situated in a broad glacial valley, the Shakwak Trench, bordered to the southwest and northeast by alpine boreal forest (Matthews 1986). The valley region has a highly seasonal climate that is cold and continental (Laxton et al. 1996). The region is dominated by white spruce (Picea glauca), interspersed with willow (Salix spp.), birch (Betula glandulosa), and aspen (Populus tremuloides) (Douglas 1974). The area experiences interannual fluctuations in seed production due to masting events (LaMontagne and Boutin 2007), which occur when large seed crops are produced in synchrony by white spruce trees approximately every four years (LaMontagne and Boutin 2007; Nienstaedt and Zasada 1990). Red squirrel densities ranged from 1 to 21 adults and 0 to 17 juveniles within 130 meters for each focal juvenile.

Our study was conducted over two years with similar biotic conditions. Relative to mast years, cone production was close to zero (i.e., 5 to 60 compared to 300 to 600 white spruce cones per tree, respectively; Dantzer et al. 2020). Red squirrels are also alternative prey for the main predators in this system (e.g., Canada lynx (Lynx canadensis), coyotes (Canis latrans), and Northern goshawks (Accipiter gentilis)). But because of the cyclic dynamics in this region, predators only switch to red squirrels when snowshoe hare (Lepus americanus) abundances are low relative to predator abundances (O'Donoghue et al. 2001). In the summer of 2017 and 2018, snowshoe hares were at peak densities (available at http://www.zoology.ubc.ca/~krebs/kluane.html) and predator numbers were consistent across both years (Dantzer et al. 2020).

### Study species

Red squirrels are solitary rodents (Smith 1968; Steele 1998) that defend exclusive territories (60 m average diameter; Anderson and Boutin 2002) encompassing a central food cache called a “midden” (Smith 1968; Steele 1998). Red squirrels in our populations primarily subsist on white spruce seeds they obtain by husking cones (Dantzer et al. 2012; Descamps et al. 2008b). Spruce trees produce superabundant cones (i.e., masting) followed by years of cone failure. The spatial structure of this system in combination with the high trappability and strong site-fidelity of red squirrels make it possible to locate and recapture individuals across their lifetimes.

Red squirrels are a polygamous species (Lane et al. 2008), exhibiting a scramble competition mating system (Lane et al. 2007). Females have a mean litter size of three pups (McAdam et al. 2007) and multiple paternity is common as females mate with an average of seven males during oestrus (Lane et al. 2008). Breeding can occur as early as March and as late as August and females give birth after a ~ 35 day gestation period (Lane et al. 2009). During their first year of life, juvenile mortality between birth and the following year is highly variable (e.g., 20-97%; Boutin and Larsen 1993; Larsen and Boutin 1994; McAdam and Boutin 2003; Steele 1998; Stuart-Smith and Boutin 1995a) and juveniles with faster postnatal growth and an earlier birth date exhibit higher survival to recruitment (Boon et al. 2007; Dantzer et al. 2013; Fisher et al. 2017; Hendrix et al. 2020; McAdam and Boutin 2003; Williams et al. 2014). However, this survival effect appears mediated by acquisition of a territory; once territory ownership is accounted for survival is unrelated to growth or birth date (Hendrix et al. 2020).

Nearly all juvenile red squirrels initiate natal dispersal (this study); however, the cause of initiation remains unknown. Juveniles begin entering the prospection phase after they have emerged from their natal nest at ~ 48 days old (this study). Prospection is marked by daily forays off their natal territory (>30 m from the natal nest), with juveniles returning to their natal site each night if they have not yet found a place to settle (this study). Settlement occurs in the late summer and early autumn (this study). While the drivers of settlement remain poorly understood in red squirrels, successful local recruitment (i.e., individuals that survive their first winter and acquire a territory with a midden in our populations) is well studied (Berteaux and Boutin 2000; Lane et al. 2015). Females and males recruit, on average, two territory widths from their natal site

(Berteaux and Boutin 2000; Cooper et al. 2017). However, red squirrels exhibit sex-biased dispersal and females do recruit closer to their natal site than males (Berteaux and Boutin 2000; Martinig et al. 2020). When comparing individuals that survived until recruitment, staying closer to the natal site yields higher fitness for female red squirrels than leaving (Martinig et al. 2020), while immigrating to a new population results in higher fitness for males relative to those that recruit locally (Martinig et al. 2020). In some cases (yearly average 19 %; Lane et al. 2015), mothers exhibit breeding dispersal (Price 1992; Price and Boutin 1993) and bequeath all or part of their territory to one offspring, typically female (Berteaux and Boutin 2000), after acquiring a new territory herself. Even more rarely (this study), mothers may share their territory with one offspring during winter. Juveniles that recruit on their natal site experience higher winter survival compared to juveniles that recruit elsewhere (75 versus 58 %, respectively; Berteaux and Boutin 2000). Despite these differences, the sexes do not exhibit size dimorphism (Boutin and Larsen 1993; Stuart-Smith and Boutin 1994), nor differences in territory acquisition (Hendrix, J. G., personal communication) or territory size (Larsen 1993).

Red squirrels also exhibit consistent individual differences in activity and aggression (Boon et al. 2008; Kelley et al. 2015; Martinig et al. 2021; Taylor et al. 2014). While these behaviours develop over ontogeny (Kelley et al. 2015; Martinig et al. 2021), they are heritable (Taylor et al. 2012) and have fitness consequences (Boon et al. 2007). These traits are also predictive of final recruitment distance, with activity resulting in variable recruitment depending on overall population density (Cooper et al. 2017), more daily movements (Boon et al. 2008), and longer trips (Boon et al. 2008), while aggression is consistently not related to recruitment distance (Cooper et al. 2017) or movement patterns (Boon et al. 2008).

### Population monitoring

Each year we monitored individual territory ownership and reproduction using a combination of behavioural observations, trapping, handling, and telemetry. Each May and August we conducted a population census, noting any changes in territory ownership from the previous census. We determined territory ownership through observations of territorial behaviours (rattle calls; Lair 1990) and caching behaviours in middens, in addition to recapture. Red squirrels use rattles to defend their territory once acquired (Dantzer et al. 2012; Siracusa et al. 2019). We are confident that we are able to completely enumerate our populations because of the high territorial fidelity after recruitment (Berteaux and Boutin 2000), high trappability (recapture rates > 0.95; see Descamps 2006), and diurnal activity and vocal territorial defence patterns of red squirrels. Because territorial vocalizations (Smith 1978), social neighbourhoods (Siracusa et al. 2017), selection (Fisher et al. 2017), and density-dependence responses (Dantzer et al. 2012) are limited to 130 m in red squirrels, we used our population censuses, trapping records, and behavioural observations to calculate daily local density (squirrels/hectare within 130 meters of natal site). We also monitored food abundance by counting white spruce cones according to the protocol outlined and calibrated in LaMontagne et al. (2005). We did this once cones became fully formed and visible but before red squirrels started harvesting them (typically in late July).

We monitored females for pregnancy using manual palpation of their abdomen during the breeding season. Immediately following parturition, we located nests through a combination of behavioural observations and radio telemetry (radio-collar model PD-2C, 4 g, Holohil Systems Limited, Carp, Canada) and we temporarily removed pups from their nest to obtain a tissue sample and recorded sex and weight using a digital Taylor precision scale in 2017 and 2018 (Model 1250-49, Illinois, USA). Around 25 days of age, we temporarily removed the pups a second time, employing the same protocol with the addition of giving each juvenile one unique alphanumeric metal ear-tag in each ear (Monel # 1; 5 digits; National Band and Tag, Newport, KY, U.S.A.), and attached coloured plastic discs for visual identification. We calculated growth rate (g/day) between successive measurements. Before returning juveniles to the nest, we fit a subset of pups from each litter with radio collars (model PD-2C, 4 g, Holohil Systems Limited, Carp, Canada). In 2017 and 2018, we systematically selected pups: first, we ordered litters by birth date, then ordered pups by weight (lowest to highest), and then selected every other juvenile.

Using these birth records, we calculated daily local juvenile competitor density (juvenile squirrels/hectare within 130 meters of focal juvenile's natal site) for each collared juvenile. Any living juveniles within 130 meters of the focal juvenile's natal site were considered competitors.

### Juvenile telemetry monitoring

We monitored a total of 93 juveniles from 64 litters over two years (Table 3.1). We checked nests twice daily to see when juveniles emerged from their natal nest beginning when juveniles were 35 days old (as per Humphries and Boutin 1996). Juveniles emerged, on average, at 48.2 days old ± 0.07 SE. Once emerged, we used telemetry to track individuals, locating each collared juvenile an average of 2.59 times per day ± 0.03 SE (median: 3.00, range: 1-9) until death or territory acquisition. We recorded each juvenile's location using a handheld GPS (Garmin, Olathe, USA). This allowed us to record distance from the natal nest (m). We excluded juveniles that were still transient when radio-collars were removed (2017: 5 females and 2 males; 2018: 1 female), as we do not know their fate.

### Standardized behavioural assays

To measure behavioural traits, we caught juveniles (n = 40 individuals in 2017 and n = 30 individuals in 2018) twice: once after emergence (mean age 56.8 days ± 0.08 SE, n = 70 individuals), and once after weaning (mean age 78.7 days ± 0.08 SE, n = 47 individuals). There were 47 juveniles that were tested twice (emergence and weaning), and 23 juveniles that were tested once (emergence) because they did not survive until weaning.

We set live-traps (Tomahawk Live Trap, Hazelhurst, USA) near the last known location and baited the traps with peanut butter. We checked traps every 30 minutes during each trapping period (0900 to 1300 and 1500 to 1800). When a juvenile was captured, we transferred them to a handling bag, confirmed their identity by checking their ear-tags, and recorded their mass using a 600-g Pesola spring scale. We then transferred them to the testing arena for the standardized behavioural assays. We made the testing arena (60 x 50 x 80 cm) out of corrugated plastic secured with aluminum rivets, including four blind holes 3.7 cm in diameter on the floor, and a clear acrylic lid. We recorded the behavioural assays with a camcorder (Sony Handycam, Sony of Canada Ltd., Toronto, Canada) positioned to give an aerial view of the testing arena. The first 7.5 minutes a juvenile was in the testing area were used to quantify activity (i.e., movement in a novel environment; Walsh and Cummins 1976). After 7.5 minutes, we revealed a mirror (28.7 x

40 cm) on the right side of the box for an additional five minutes to measure aggression (i.e., antagonistic behaviour directed towards conspecifics; Svendsen and Armitage 1973).

We used the Behavioural Observation Research Interactive Software (Friard and Gamba 2016) to classify behaviours according to an ethogram (see Martinig et al. 2021 for more details). Because activity and aggression are repeatable between emergence and weaning (Martinig et al. 2021), we used the first behavioural assay for all juveniles. We used principal component analyses (PCAs) to extract activity and aggression scores for each individual. Full details of the principal component analyses are in Martinig et al. (2021). In brief, we used principle component analyses to determine activity and aggression scores. We used the first principal component (PC1) to generate a single score for each behaviour. PC1 explained 40.7% and 51.0% of the total variance for activity and aggression, respectively.

### Data analysis

We used the statistical environment R, version 3.6.2 (R Development Core Team 2019), for all analyses. We tested for multicollinearity. In all cases, local competitor density and local adult density were highly correlated (Pearson's $r^2 = 0.69\text{-}0.72$). Following Morrissey and Ruxton (2018), we kept both variables in our models and note that when two explanatory variables are correlated, then their independent effects on the response variable are uncertain as they cannot be separated. To improve interpretability of effect sizes across variables (Gelman 2008), we mean centered and standardized all numerical explanatory variables to one standard deviation (Schielzeth 2010) within cohort and study area, with the exception of growth rate, which was standardized within litters, providing the deviation of individuals from their litter-mates.

We used linear regressions throughout, unless otherwise stated. Whenever the response variable was binary, we used a generalized linear mixed effects regression (binomial family, logit link) with the "lme4" package, version 1.1-21 (Bates et al. 2015). When the response variable was continuous we used a negative binomial generalized linear mixed effects regression with the "glmmTMB" package, version 1.0.1 (Brooks et al. 2017) because of overdispersion and/or zero-inflation unless indicated otherwise. We included a random effect for litter identity in all models to account for any litter-specific variation. We present all model estimates with their estimated

95% confidence intervals (CI) using the “confint” function. If the 95% CI did not overlap zero, we concluded there was support for an effect. If the 95% CI overlapped with zero, we concluded there was support for no effect.

### Departure phase

All but three individuals left their natal site (travelled >30 m from the natal nest) at least once before finding a place to settle. In light of this, we made a model with age first off the natal site as a continuous response variable using a linear mixed effects model (Gaussian family, identity link) with the “lme4” package, version 1.1-21 (Bates et al. 2015). The model included sex, birth date, litter size, growth rate (a surrogate for quality), and activity and aggression scores as predictors. No explanatory variables were highly correlated (all Pearson’s $r^2 < 0.38$).

### Prospection phase

We investigated prospection behaviour, as measured by distance from the natal nest (meters; continuous variable), with one model, which included sex, birth date, litter size, growth rate, emergence age, age, activity and aggression scores, local competitor density, local adult density, and average number of locations per day (to correct for search effort) as predictors. None of our explanatory variables were highly correlated (all Pearson’s $r^2 < 0.39$). Because of repeated measures on both individuals and within-litters, we included a random effect for both squirrel and litter identity to account for any individual- or litter-specific variation.

### Settlement phase

We investigated final settlement distance (meters; continuous variable) and timing of settlement (days old; continuous variable) in separate models. Sample size limitations meant that each response variable had two corresponding models. Our first model included sex, birth date, litter size, growth rate, and emergence age as predictors. Our second model included activity and aggression scores, local competitor density, and local adult density as predictors. None of our explanatory variables were highly correlated (all Pearson’s $r^2 < 0.39$). To test for behavioural type differences between individuals that settled on or off their natal site, we used a t-test.

## Results

### Departure phase

Individuals that left the natal site did so for the first time at, on average, 51.0 days old ± 0.77 SE (median: 50.5 days old, range: 41-73 days old; n = 67 individuals). None of the explanatory variables predicted the age an individual was first seen off their natal site (Table 3.1).

### Prospection phase

Juvenile movements during prospection exhibited a leptokurtic distribution (Figure 3.2a), moving up to 948 m away from their natal site, with a median of 33 m (average of 65 m ± 1.5 SE) (n = 4542 locations for 70 individuals). Within 130 m of the focal juvenile's natal nest, the number of adults ranged from 1-21 (mean: 12 adults ± 0.08 SE, median: 13 adults), while the number of juvenile competitors ranged from 0-17 (mean: 6 juveniles ± 0.06 SE, median: 6 juveniles). Older juveniles were found further from their natal site (β: 0.41, 95% CI: 0.37 to 0.44; Figure 3.2b), and juveniles with lower competitor densities went farther distances daily (β: -0.58, 95% CI: -0.65 to -0.51; Figure 3.2c) (Table 3.1). None of the other explanatory variables predicted movement during prospection (Table 3.1).

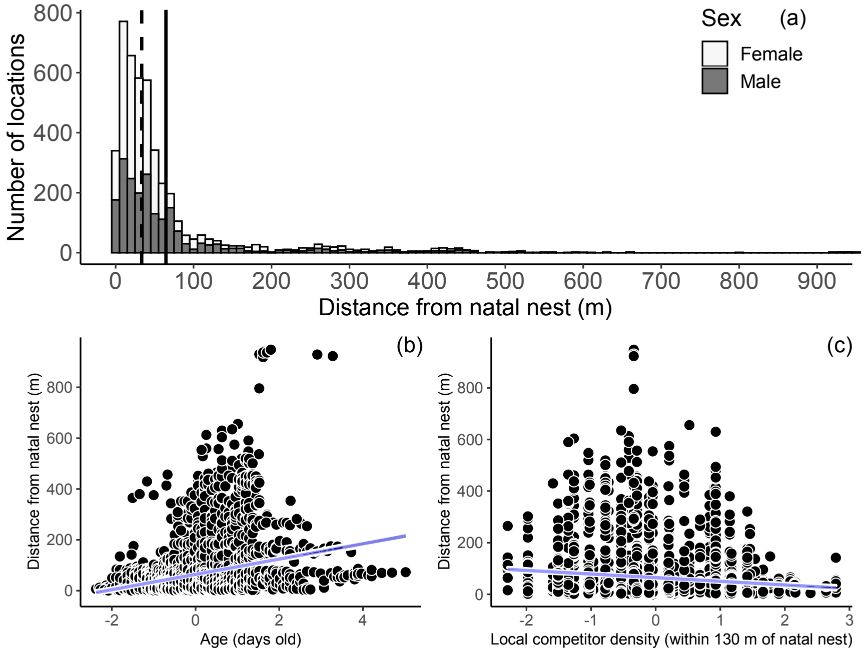

Figure 3.2. During prospection, (a) juveniles travelled, on average (solid line), 65 m ± 1.5 SE away (median 33 m; dashed line) and up to 948 m away (n = 4542 locations for 70 individuals). Older individuals (days old) travelled farther from their natal nest (m) (b) and juveniles with

more local competitors (local competitor density: number of juveniles within 130 m of natal nest) stayed closer to the natal nest (m) (c).

### Settlement phase

Median settlement location for juveniles (n = 18 females and 17 males) was 38 m (average 104 m ± 29 SE) from their natal site, but one juvenile settled up to 923 m away (Table 2; Figure 3a). Individuals settled at, on average, 69 days old ± 2.21 SE (median: 70 days old, range: 48-90 days old). Overall, 40.0% of juveniles were philopatric, 37.1% settled in the same neighbourhood, 20.0% settled in the same population but outside of their natal neighbourhood, and 2.86% emigrated to a new population (Table 3.2). Of the 22 individuals that were philopatric, nine individuals shared their natal site with their mother, while the remaining 13 were bequeathals.

Individuals with higher within-litter growth rates settled further away from their natal site (β: 0.20, 95% CI: 0.25 to 0.89; Table 3.1; Figure 3b). Individuals settled at an older age when local adult density was higher (β: 0.08, 95% CI: 0.003 to 0.15; Table 3.1; Figure 3.3d). While individuals that had higher aggression scores settled closer to their natal site (β: -0.43, 95% CI: -0.65 to -0.22; Table 3.1; Figure 3.3c), there were no behavioural type differences when comparing philopatric individuals and those that dispersed (activity: t-value = -1.14, df = 28, 95% CIs: -1.09 to 0.31; aggression: t-value = -0.08, df = 28, 95% CIs: -0.73 to 0.68). None of the other explanatory variables predicted settlement distance or timing of settlement (Table 3.1).

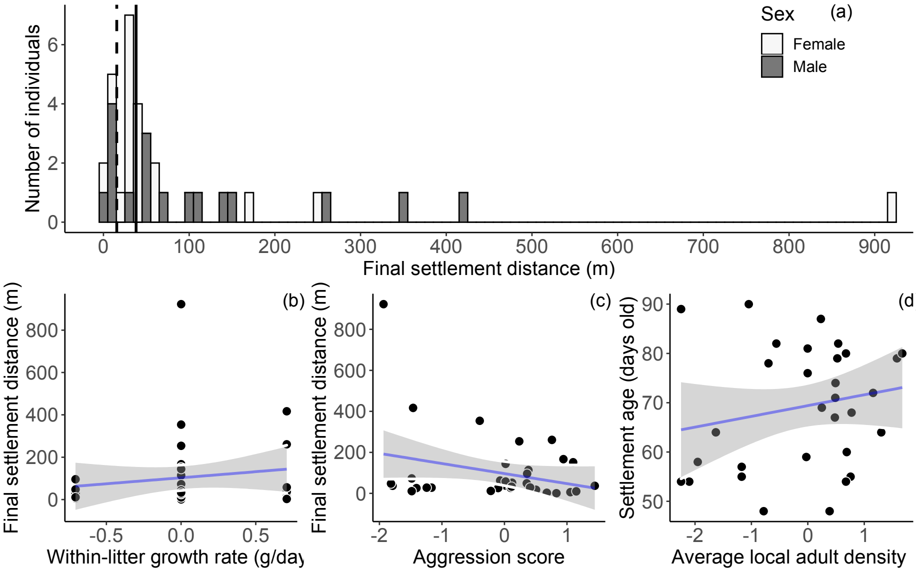

Figure 3.3. (a) Juveniles settled, on average (solid line), 104 m ± 29 SE away (median 38 m; dashed line) and up to 948 m away (n = 35 individuals). Individuals settled further away (m)

when they had (b) a higher within-litter growth rate (g/day), (c) were less aggressive, or (d) came from an area with a higher average local adult density (adult squirrels within 130 m of natal site).

Table 3.1. Parameter estimates from generalized linear mixed effects models for the departure, prospection, and termination phases for juvenile red squirrels. A linear mixed model was used for age first off the natal site (days; continuous response variable; n = 67 individuals), and a negative binomial generalized linear mixed effects model was used for distance from the natal nest (continuous response variable; n = 4542 locations), final distance (continuous response variable; n = 35 individuals), and settlement age (continuous response variable; n = 35 individuals). Bold values indicate significance.

| | Departure phase | | Prospection phase | Termination phase | |
|---|---|---|---|---|---|
| | Movement type (0: stayers, 1: goers) | Age first off natal site (days old) | Distance from the natal nest (m) | Final distance (m) | Settlement age (days old) |
| Fixed effects [1] | β (95% CI) | β (95% CI) | β (95% CI) | β (95% CI) | β (95% CI) |
| Sex (Male) | 0.26 (-0.80, 1.09) | 1.98 (-0.94, 4.90) | -0.04 (-0.19, 0.28) | -0.07 (-0.66, 0.53) | 0.07 (-0.03, 0.18) |
| Birth date | -0.88 (-1.90, 0.14) | -0.04 (-1.96, 1.87) | -0.06 (-0.22, 0.10) | -0.23 (-0.58, 0.11) | -0.03 (-0.08, 0.02) |
| Litter size | -1.28 (-2.65, 0.09) | 0.93 (-0.86, 2.72) | -0.06 (-0.22, 0.09) | -0.01 (-0.36, 0.34) | -0.01 (-0.06, 0.05) |
| Growth rate | -0.34 (-1.70, 1.02) | -0.17 (-2.20, 1.87) | 0.06 (-0.05, 0.16) | 0.20 (0.25, 0.89) | -0.01 (-0.10, 0.08) |
| Activity score | -0.18 (-0.95, 0.59) | -0.55 (-2.21, 1.12) | 0.04 (-0.10, 0.18) | 0.17 (-0.15, 0.49) | 0.01 (-0.04, 0.07) |
| Aggression score | 0.74 (-0.30, 1.77) | -0.39 (-1.89, 1.11) | 0.03 (-0.08, 0.13) | -0.43 (-0.65, -0.22) | -0.01 (-0.06, 0.05) |
| Emergence age | - | - | 0.07 (-0.07, 0.21) | 0.10 (-0.20, 0.41) | -0.02 (-0.07, 0.03) |
| Local competitor density | - | - | -0.15 (-0.23, -0.07) | -0.13 (-0.61, 0.35) | -0.06 (-0.13, 0.02) |
| Local adult density | - | - | 0.01 (-0.08, 0.09) | 0.07 (-0.41, 0.55) | 0.08 (0.003, 0.15) |
| Age | - | - | 0.41 (0.37, 0.44) | - | - |
| Average number of locations/day | - | - | -0.01 (-0.04, 0.03) | - | - |
| Random effect | $\sigma^2$ ± SD | $\sigma^2$ ± SD | $\sigma^2$ ± SD | $\sigma^2$ ± SD | $\sigma^2$ ± SD |
| Individual identity | - | - | 0.06 ± 0.24 | - | - |

| | | | | | |
|---|---|---|---|---|---|
| Litter identity | 1.59 ± 1.26 | 24.85 ± 4.98 | 0.23 ± 0.48 | 0.75 ± 0.87 | 0.01 ± 0.11 |
| Residual error | 1 | 14.61 ± 3.82 | 1 | 1 | 1 |

[1] Reference categories for fixed effects were set to ‘female’ (for ‘sex’). We mean standardized growth rate within litters and mean standardized all other numerical explanatory variables within cohort and study area.

Table 3.2. Descriptive statistics for juvenile red squirrels in our study populations from June 7 to August 10, 2017 and May 15 to August 12, 2018.

| | Birth year | | | |
|---|---|---|---|---|
| | 2017 | | 2018 | |
| | Females | Males | Females | Males |
| Number collared | 30 | 22 | 20 | 21 |
| Number survived past emergence | 22 | 18 | 16 | 14 |
| Settlement | | | | |
| Number settled | 9 | 8 | 8 | 7 |
| Mean ± SE (m from natal site) | 135 ± 99 | 114 ± 44 | 69 ± 32 | 118 ± 55 |
| Median (m from natal site) | 37 | 51 | 28 | 73 |
| Range (m from natal site) | 1 – 923 | 6 – 354 | 3 – 254 | 11 – 417 |
| Number of individuals | | | | |
| Philopatric | 8 | 6 | 5 | 3 |
| Same neighbourhood | 7 | 6 | 1 | 1 |
| Same population | 2 | 5 | 2 | 3 |
| Different population (emigrant) | 1 | 0 | 0 | 0 |

## Discussion

At the most fundamental level, dispersal is comprised of successive stages. For individuals that initiated the dispersal process, individuals stayed closer to their natal site when there was a high level of intraspecific competition for space and settled earlier when local adult density was lower, but this did not translate to closer settlement, which was phenotype-dependent. Given breeding dispersal is relatively rare in red squirrels, the majority of juveniles appear to have to initiate dispersal, which would explain why individuals did not differ in their tendency to do so.

Surprisingly, we did not detect sex-biased dispersal, as would be expected from previous work (Martinig et al. 2020). This result makes sense in light of resource levels. When food abundances are high, territory viability is high and red squirrels are able to make new territories in the interstitial space between existing and established neighbours (Price and Boutin 1993; Wheatley et al. 2002). But when food abundances are low, like in 2017 and 2018, new territories cannot be made and already existing territories become less viable. Given the habitat surrounding our study areas are relatively low quality to begin with (see Martinig et al. 2020), the ability for individuals to successfully settle longer distances would be diminished. This is exemplified by only one individual settling in a new population and numerous instances of a mother sharing her territory with one of her juveniles during winter. While previous work suggested that females should settle closer to and males farther from their natal sites, in line with females benefiting from kin selected cooperation (Green and Hatchwell 2018) in the form of bequeathals (Berteaux and Boutin 2000; Williams et al. 2013) and males benefitting from female mate choice being biased towards unfamiliar males, as expected from the local mate competition (Hamilton 1967; Moore and Ali 1984) and inbreeding avoidance hypotheses (Bengtsson 1978; Clutton-Brock 1989; Packer 1979; Perrin and Mazalov 2000), local resource competition could erode these relationships when territory viability is too low (sensu Getz and McGuire 2008). Competition for space would also explain why we detected earlier settlement when local adult densities were low and movements were concentrated closer to the natal site when local juvenile densities were high (assuming intraspecific encounters with other juveniles carry a cost).

Competition for space may also explain why individuals with higher growth rates settled farther from their natal site. Growth rates can not only reflect developmental differences and variation in individual quality, but can potentially affect competitive ability (reviewed in Mangel and Stamps 2001). If growth rate is a reliable proxy for individual quality relative to littermates, survival at greater distances from the natal site may be biased towards better quality individuals and could explain why faster growing juveniles settled farther from their natal site, especially in low resource conditions. The ability to survive and then successfully acquire a territory off your natal site may even act as a signal of quality to future mates, as is seen in primates (Kurland 1977; reviewed in Moore and Ali 1984; Richard 1974).

Territory acquisition was also behaviour-dependent. The general notion that dispersal is related to consistent individual differences in activity and aggression has been corroborated in this population of red squirrels when looking at recruitment only (Cooper et al. 2017). However, we found that activity was not linked to dispersal initiation, movement during prospection, or settlement. This was surprising given that activity is often linked to locating resources and detection by predators, whereby active individuals have been found to have higher encounter rates with predators (Gerritsen & Strickler 1977) and resources (Anholt et al. 2000) compared to inactive individuals. Given the relatively similar (and poor) conditions across years any differences in predation risk (Gendron & Staddon 1984) and resource acquisition (Lima 1998) between active and inactive individuals may not have been large enough to result in differences across any of the dispersal phases. Aggressive individuals, on the other hand, settled closer to their natal site. This is in line with the aggression-dispersal hypothesis (Christian 1970), where aggressive individuals push out less aggressive individuals (O'Riain et al. 1996). However, this does not mean aggressive individuals are necessarily better competitors.

## Conclusion

Competition for space appears to be one of the major drivers of dispersal in red squirrels when resource abundances are low, but it was not the only factor. Individual quality and competitive ability, as captured by growth rate and aggression, affected how close an individual settled to their natal site. Together, this suggests that in a system with exclusive territoriality and where the majority of individuals have to initiate dispersal, competition from conspecifics, both in the form of adult territory holders and juveniles without territories, and individual phenotype are strong predictors of dispersal trajectories.

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## CHAPTER 4

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

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## Abstract

Understanding the causes and consequences of repeatable among-individual differences in behaviour (i.e., animal personality) is a major area of research in behavioural 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. 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.

## Introduction

Repeatable among-individual variation in behavioural traits, referred to as animal personality (Bell et al. 2009), are widespread, and can have important ecology 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 (Biro and Stamps 2008; Réale et al. 2000). At a larger scale, animal personality can affect population establishment and stability, particularly because dispersers are likely to represent a non-random subset of a population (e.g., by state, morphology, physiology, or behavior; Matthysen 2012). Consequently, understanding the mechanisms that lead to consistent among-individual variation is a major research theme in contemporary behavioural 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 behaviour (Castanheira et al. 2013; Kok et al. 2019; Petelle et al. 2013; Stamps and Groothuis 2010). 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 differences in developmental plasticity (Stamps and Krishnan 2014a, b), state-behaviour feedbacks (Dall et al. 2004; Luttbeg and Sih 2010; Sih et al. 2015), or age-related changes in intra-individual variability (Japyassu and Malange 2014; Stamps et al. 2012), 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. 2008; 2006). For example, if extreme behavioural 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 1968). This could come about if individuals with more extreme phenotypes exhibit niche specialization and thus less within-individual variability than intermediate phenotypes (Bastille-Rousseau et al. 2011; Schmidt et al. 2001; Stamps and Groothuis 2010; Wilson 1998). Alternatively, if intermediate behavioural 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 favours individuals that are behaviourally predictable (Biro and Stamps 2008; Chang et al. 2017; Wilson 1998), the loss of individuals that are relatively unpredictable in their behaviour (i.e., have higher residual variance or intra-individual 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 and McNamara 2013; Wolf et al. 2008). Alternatively, if predictability is disadvantageous (e.g., Brembs 2011; Chang et al. 2017; Maye et al. 2007) the loss of predictable individuals could result in decreased repeatability with age through an increase in residual variance or intra-individual variability.

Here we investigated if selective disappearance lead to age-related changes in behavioural 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; Kelley et al. 2015; Taylor et al. 2012). These behaviours 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 due to our sampling methods (see Methods below), has previously been reported as contributing to age-related changes in behaviour 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 non-aggressive 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 comprised two 40-hectare plots located near Kluane Lake on the traditional territory of the Champagne and Aishihik First Nations in 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).

### Study species

Red squirrels are diurnal rodents found in the boreal forest throughout North America (Steele 1998). Their primary food source are 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 (Boon et al. 2008; Smith 1968). 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 SE (Chapter 3) 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 (pre-weaning and post-weaning), 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 favoured (Martinig et al. 2020), but both sexes have similar recruitment distances the following spring (within ~100 m of natal site; Berteaux and Boutin 2000; Cooper et al. 2017).

### Conducting behavioural assays

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

Once trapped, we immediately transferred red squirrels to the testing arena at the site of capture for the standardized behavioural assays. The testing arena was a plastic box (60 x 50 x 80 cm) with a clear acrylic lid through which we recorded the behavioural 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 behaviour directed towards a simulated conspecific (i.e., their mirror image; Svendsen and Armitage 1973).

The activity assay lasted for 7.5 minutes. After 7.5 minutes, we exposed a mirror (28.7 x 40 cm) on the right side of the box and the aggression assay lasted for an additional five minutes. We released individuals at the site of capture afterwards. We performed the first assay after emergence (mean age 55.95 days ± 6.88 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 not habituate to these assays with repeated exposure over the short-term (i.e., within-years; Taylor et al. 2012). We scored behaviours using an ethogram (Table S1) adapted from Boon (2007 and references therein) 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, Illinois, USA), and during trapping using a 600-g spring scale (Pesola AG, Baar, Switzerland). We measured growth rate (g/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 (Figure S1).

### Principal component analyses

We performed two separate principal component analyses (PCAs) for our behavioural assays using the prcomp function in the baseline ‘stats’ package in the statistical environment R, version 3.5.2 (R Development Core Team 2019). We used the first principal component (PC1) from each of the activity and aggression assays to generate a single score for each behaviour (Boon et al. 2007; Taylor et al. 2012). Activity PC1 explained 41.59% of the variance and the behaviours loading most heavily on this component were walk, jump, and still (the latter of which loaded negatively; Table 4.1). Aggression PC1 explained 49.97% of the total variance and the behaviours 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 behaviours loaded negatively; Table 4.1). We considered behaviours to be heavily loaded if their loadings were >0.40 (Budaev 2010).

Table 4.1. Principal component analysis loadings for activity (from open field trial) and aggression (mirror image stimulation) for 2017 (n = 72 individuals) and 2018 (n = 30 individuals) juvenile cohorts. Bolded numbers indicate behaviours that were heavily loaded (>0.40) on the principal component (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 |

In the aggression assays, some individuals (14.72% of assays) never approached the mirror, right censoring their approach and attack latencies. 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 (five minutes) or treated them as missing data yielded quantitatively similar results (results not shown), suggesting that these non-responding 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 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 (CrI). 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 survival (i.e., survival between emergence and weaning; 2017: n = 72 individuals, 42 survived summer; 2018: n = 30 individuals, 20 survived summer) and winter survival (i.e., survival between weaning and yearling age; 2017: n = 42 individuals, 17 survived winter; 2018: n = 20 individuals, 0 survived winter) using univariate generalized linear mixed effects models (binomial with logit link; binary response variable; 0 = dead, 1 = alive). We checked for both directional (activity and aggression) or quadratic effects (activity$^2$ and aggression$^2$) of behaviour 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 $\alpha = 0.05$ using an analysis of variance test in R (R Development Core Team 2019). The CV mean standardizes individual variance (Houle 1992; Taylor 1961). 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 activity and aggression were relatively repeatable in this study (r = 0.29 (95% CrI: 0.23 to 0.33) and r = 0.30 (95% CrI: 0.24 to 0.34), respectively; see results) and in previous studies (Boon et al. 2007; Kelley et al. 2015; Taylor et al. 2012), 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 (Tables 4.3 and 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 (Tables S3 and S4). We did not include any environmental variables as fixed effects because our study was conducted over two years with similar conditions (e.g., low food years: 5 to 60 white spruce cones per tree; Dantzer et al. 2020). 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 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 used litter identity as a random effect instead of individual identity in all models to account for non-independence between siblings. We tested for collinearity between explanatory 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 number of observations was approximately 1:1.

We were unable to explicitly test whether individual differences in behavioural plasticity (Figure S2), a within-individual mechanism, contributed to age-related changes in behaviour by modelling IxE. 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 2-3 replicates each.

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% credible intervals based on 10000 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 report 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% CrI 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 one standard deviation within cohort and study area (Schielzeth 2010). We calculated activity$^2$ and aggression$^2$ and individual-specific coefficient of variations from raw scores before standardization.

## Results

### Age-related shifts in behavioural repeatability

We observed age-related changes in repeatability for activity and aggression. The repeatability of activity was higher across ages whereas the repeatability of aggression was lower across ages (Table 4.1; Figure 4.1). Repeatability of activity between emergence and weaning was 0.29 (95% CrI: 0.23 to 0.33; n = 102 individuals), and between weaning and yearling ages was 0.59 (95% CrI: 0.49 to 0.66; n = 62 individuals; Table S5). Repeatability of aggression between emergence and weaning was 0.30 (95% CrI: 0.24 to 0.34; n = 102 individuals) and between weaning and yearling ages was 0.10 (95% CrI: 0.07 to 0.13; n = 62 individuals; Table S5).

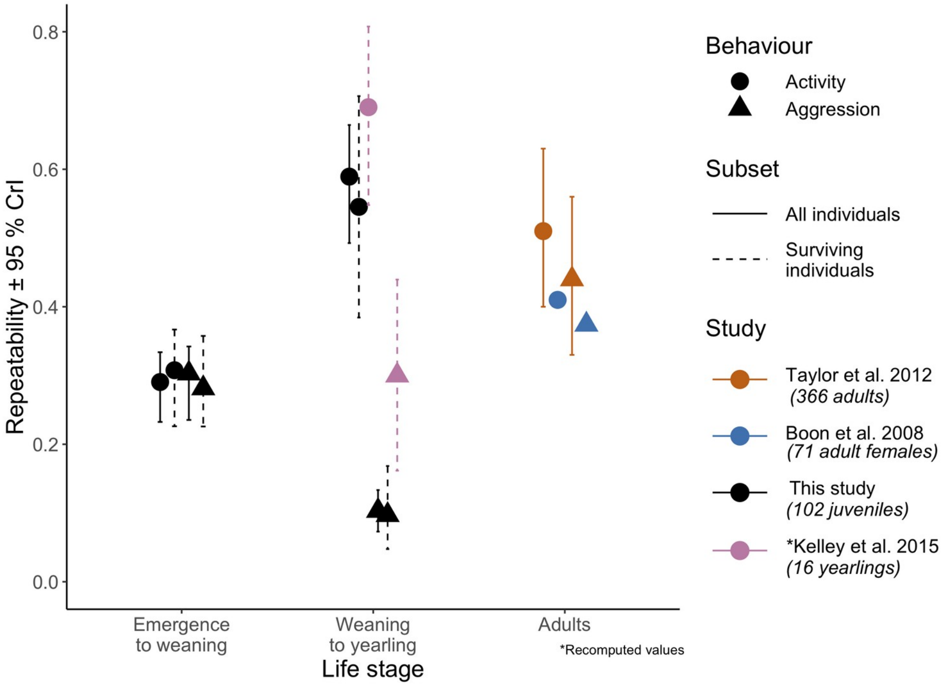

Figure 4.1. Repeatability (r) estimates with 95% credible intervals (CrI) for activity and aggression across ontogeny in this population. We present data for the emergence to weaning (n = 102 individuals, n = 62 survived) and weaning to yearling (n = 62 individuals, n = 17 survived) life stages ("This 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); and Boon et al. 2007 (4 year study; no confidence/credible intervals reported).

## 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 repeatability of activity and aggression by comparing repeatabilities between 1) datasets including all individuals to 2) datasets restricted to only surviving individuals (Tables 4.2 and S5) and by estimating the strength of directional and quadratic selection on trait means, and within-individual trait variances for each cohort (Table 4.3).

Table 4.2. Among-individual and residual variance components for activity and aggression repeatability estimates (r) and variances with 95% credible intervals (CrI) for juveniles. Contrasts were considered to be significantly different if there was <15% overlap in 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 [1] | | | | |
| | 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 [1] | | | | |
| | 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) |

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

The repeatability of activity from emergence to weaning was similar between 2017 (r: 0.29, 95% CrI: 0.23 to 0.36; n = 72 individuals) and 2018 (r: 0.31, 95% CrI: 0.21 to 0.41; n = 30 individuals), as were the relative contributions of among- and within-individual variance (Table 4.2). In contrast, we did observe year differences in the repeatability of aggression. Repeatability of aggression from emergence to weaning was qualitatively and quantitatively higher in 2017 (r: 0.44, 95% CrI: 0.34 to 0.50; n = 72 individuals) compared with the 2018 cohort (r: 0.21, 95% CrI: 0.14 to 0.31; n = 30 individuals), due to a combination of lower among-individual and higher within-individual variances in 2018 (Table 4.2).

Importantly however, in both selective periods (summer and winter), comparisons of repeatability between datasets (all red squirrels versus surviving red squirrels only) were qualitatively and quantitatively similar for both activity and aggression for both the 2017 and

2018 cohorts (Tables 4.2 and S5). 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 to 0.36; n = 72 individuals; 2018 r: 0.31, 95% CrI: 0.21 to 0.41; n = 30 individuals) compared with only the survivors for each year (2017 r: 0.33, 95% CrI: 0.23 to 0.40; n = 42 individuals; 2018 r: 0.30, 95% CrI: 0.19 to 0.44; n = 20 individuals; Table 4.2). 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 to 0.50; n = 72 individuals; 2018 r: 0.21, 95% CrI: 0.14 to 0.31; n = 30 individuals) compared with only the survivors for each year (2017 r: 0.41, 95% CrI: 0.31 to 0.51; n = 42 individuals; 2018 r: 0.22, 95% CrI: 0.13 to 0.34; n = 20 individuals; Table 4.2). This was also true for within- and among-individual variance components (Tables 4.2 and S5). These results suggest that selective disappearance is not an important contributor to the age-related shifts observed.

Table 4.3. Sources of variation in summer (emergence to weaning) and winter (weaning to yearling) survival for juveniles. We use the first assay for summer and winter. We provide point estimates from univariate generalized linear models for fixed effects (posterior mode β) with 95% credible intervals (CrI) and random effects with a binomial error distribution. Bold values indicate moderate support for an effect if 95% CrIs have a <15% overlap with zero.

| | Summer (emergence to weaning) | | Winter (weaning to yearling) [1] |
|---|---|---|---|
| | 2017 cohort (n = 72 individuals, 42 survived) | 2018 cohort (n = 30 individuals, 20 survived) | 2017 cohort (n = 42 individuals, 17 survived) |
| Fixed effects [2] | 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$^2$ | 0.19 (-0.49, 0.60) | -0.29 (-1.59, 0.81) | 0.34 (-0.63, 1.21) |
| Aggression$^2$ | 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 |

[1] Excluded 2018 cohort because no individuals from that cohort survived winter. Results for both cohorts grouped can be found in Table S2.

[2] Mean standardized numerical explanatory variables within cohort and study area.

Selection analyses largely corroborated this interpretation. There was no evidence for directional or quadratic selection on activity (Tables 4.3 and 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 ($\beta = -1.43$, 95% CrI: -3.40 to 0.14, Bayesian p-value = 0.03; n = 30 individuals; Figure 4.2a). This directional selection on aggression was sufficiently weak that it did not erode among-individual variance (Table 4.2). No squirrels survived winter in 2018, precluding analysis of predictors of survival. However, in 2017, there was no support for selection on behaviour over the winter (Tables 4.3 and 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 behavioural expression for non-survivors. 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 4.2, 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).

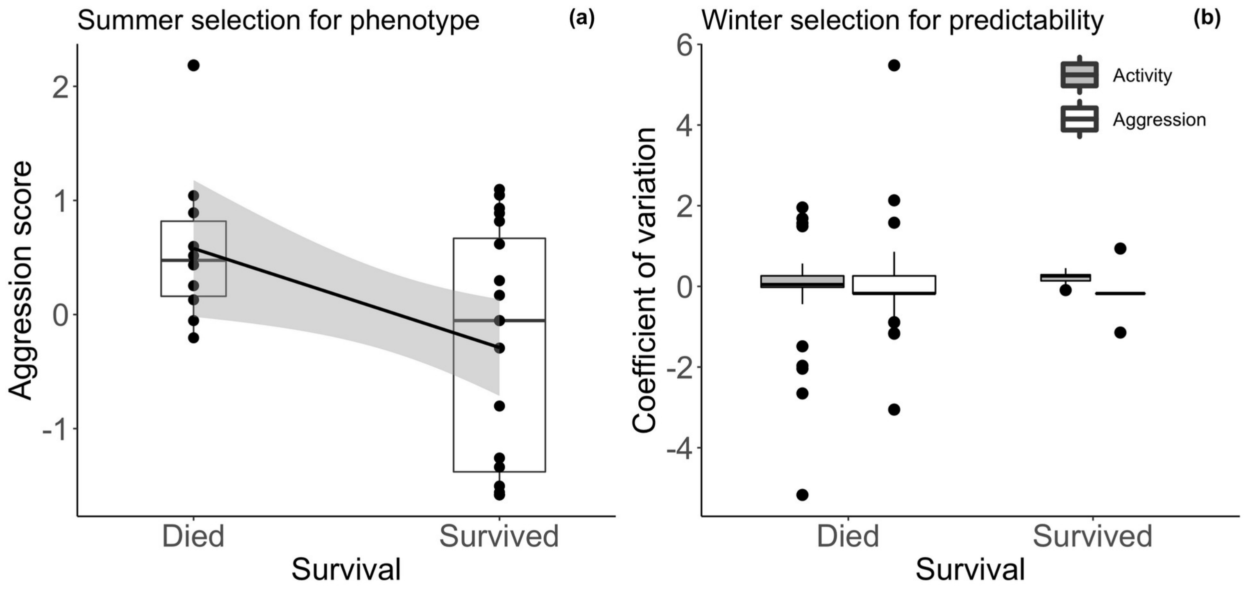

Figure 4.2. (a) Summer survival to weaning was lower for aggressive juveniles in 2018 (n = 30

individuals, n = 20 survived; using emergence assay). (b) Coefficient of variations (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).

## 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 (Both et al. 1999; Ferguson and Fox 1984; Gaillard et al. 1998; 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 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 behaviour 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, etc.; Bonte et al. 2012). However, we found no support for 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, A. R., personal observations). Alternatively, predation risk may be too low or our understanding of the relationship between risky behaviour (i.e., active, bold, and exploratory) could need updating (Moiron et al. 2020). In Barbary ground squirrels (Atlantoxerus getulus), boldness, a trait 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 behaviour (another trait 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 behavioural trait selection during the juvenile period are relatively scarce (Bergeron et al. 2013; Quinn et al. 2009), there is strong evidence that risky behaviour 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 signalling 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 (nine out of 33 cases) shared their natal territory with their mother or sibling their first winter. If non-aggressive 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 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 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 using the methodology employed here (Table S6). 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 behavioural phenotypes are maintained by fluctuating selection (Bergeron et al. 2013).

Our results suggest that age-related changes in 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 (Kaiser et al. 2018; Schuster et al. 2017). 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 may also underlie the behavioural development of activity and aggression we observed. Small, early differences in behavioural plasticity due to genetic, physiological, or life history variation that result in individual differences in behavioural plasticity would result in a "fanning out" of behaviour 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 with 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 (Polverino et al. 2016; Stamps and Biro 2016; Stamps and Krishnan 2014a).

## Conclusion

We report age-related changes in repeatability for two behavioural 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 behavioural 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.

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### Author contributions

ARM and KJM conceived of the study, ARM collected the data and analyzed the data with input from KJM. ARM and KJM wrote the manuscript, and all authors contributed substantially to revisions.

### Supporting information and data availability

Supporting information is available from https://oup.silverchair-cdn.com/oup/Journal/beheco/PAP/10.1093_beheco_araa136/2/araa136_suppl_supplemental_material.pdf.

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.

# CHAPTER 5: General Conclusion

Organisms require a diversity of strategies to cope with environmental change. Within a population, individuals can meet the challenges imposed by external variability by either tolerating, adapting, dispersing, or declining locally in light of the new conditions (Hidalgo et al. 2016; Stevens et al. 2013). Dispersal, the movement from a natal site to new site, is a crucial life-history response by which individuals can react to the environment (Bonte and Dahirel 2017). But the seeming contradiction between the low survival probability facing individual dispersers and the importance of dispersal movements for gene flow and colonization of unoccupied, suitable habitat (Grinnell 1922) and species persistence makes dispersal a contemporary issue (Hughes et al. 2003).

A phenotypic polymorphism also exists during dispersal. While some individuals remain on their natal site, others relocate. It is assumed that the costs facing dispersers are high (Bonte et al. 2012; Hamilton and May 1977; Johnson et al. 2009; Waser et al. 2013), but benefits can be incurred (Cote et al. 2010; Greenwood 1980; Martinig et al. 2020). Under such conditions, mixed dispersal strategies are expected and the trade-off between fitness components should change as an animal leaves their natal territory, moves between patches, and establishes a new territory (Cote et al. 2010). Dispersers should also differ from non-dispersers in predictable ways (Cote et al. 2010; 2013; Hidalgo et al. 2016). Phenotypic differences can include morphological or behavioural adaptations, with consistent among-individual differences in behaviour only recently being recognized as an important component of dispersal (Cote et al. 2010; 2013). Taken together, this dissertation highlights how phenotypic differences during dispersal can incur lifelong and intergenerational fitness consequences while testing the drivers of dispersal and possible mechanisms facilitating the maintenance of consistent among-individual differences in behaviour.

Leveraging close to 30 years of fitness data, this dissertation provides strong evidence in support of the hypothesis that sex-biased dispersal should be expected under conditions where the costs and benefits are also sex-dependent (Greenwood 1980). Males were not only more likely to immigrate to a new population compared to females, they also experienced the largest fitness benefits after immigration compared to resident males (Martinig et al. 2020). Females, on the other hand, were more likely to stay closer to their natal site than males, and resident females experienced higher fitness than females that immigrated elsewhere (Martinig et al. 2020). These results suggest that male-biased dispersal is driven by local mate competition, while female-biased philopatry is driven by local resource enhancement. I also documented an intergenerational cost to immigration, where resident offspring with at least one immigrant parent experienced lifelong fitness costs compared to resident offspring with resident parents. This latter result was especially surprising given that theoretical models had historically limited fitness effects to the prospection and settlement phases of dispersal, not beyond or across generations.

Because dispersers are not a random subset of the population (Cote et al. 2011; Massot et al. 2002; Scandolara et al. 2014), phenotypic variation at the individual level in other traits besides sex may explain this diversity in pay-offs. To address this required following dispersers and non-dispersers between birth and recruitment. Using two years of telemetry data, Chapter 3 offers a preliminary investigation into how phenotype (particularly behavioural traits) and dispersal interact. While I did not detect a sex-bias to dispersal, unlike in Martinig et al. (2020), this may be because the two years of telemetry data are from relatively poor quality years. These results, although preliminary, suggest that local resource competition, a hypothesis that is not expected to play out differently between the sexes, is especially important in this system when food availability is at an all-time low. In support of this, I found that movement during prospection and timing of settlement were driven by competition for space. Settlement location, on the other hand, was phenotype-dependent. While there were no differences between active and inactive individuals, aggressive, slower growing individuals settled closer to their natal site. This idea – that more aggressive individuals can "push" out less aggressive individuals (O'Riain et al. 1996) – is called the aggression-dispersal hypothesis (Christian 1970). While evidence is mixed, and many studies document the opposite effect (reviewed in Bekoff 1977; Duckworth and Badyaev 2007; Myers and Krebs 1971) – where aggressive individuals initiate dispersal as a mechanism to avoid contact with conspecifics – the ability to acquire and defend a territory as a red squirrel (assuming aggression is a reliable proxy of these qualities) is important to survival as a juvenile.

Indeed, our ability to understand how selection operates during dispersal also requires identifying agents of selection early in life. To explore this, I tested if the age-related changes in repeatable among-individual variation in behaviour exhibited by red squirrels was the result of selective disappearance. While selective disappearance did not appear to result in the age-related changes in behavioural repeatability documented in this population, I did find evidence to suggest that selection fluctuated across years (Martinig et al. 2021) – similar to what has been documented in adults (Boon et al. 2007). This suggests that different behavioural types, particularly during the formative life stages when dispersal occurs, experience differing selective pressures depending on the prevailing environmental conditions. In addition to this mechanism, it is possible that the behavioural development of activity and aggression were the result of trait canalization or individual differences in plasticity or developmental trajectories. While I did not have the power to test these mechanisms with the available data, these different mechanisms offer promising future directions.

Taken together, this dissertation highlights that in order to make accurate predictions about the profitability of different life-history strategies we need a better understanding of what drives individual variation in fitness consequences. Phenotypic variation could explain differences in pay-offs, as might fluctuating selection, but there are still unanswered questions about the drivers of dispersal in light of the intergenerational cost facing immigrants.

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